Darwin and human reproduction: a long way to gynaecology

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The following 9 chapters summarize the most essential steps that through evolution led to the reproductive behaviour of humans. Hence, the text is not necessarily confined to our species. It is a brief personal view, written as background information for reproductive specialists and gynaecologists. The objective is to give a rough sketch of the evolutionary framework in which some current reproductive phenomena may fit.

1. The long way from isogamous reproduction to gender differences

Most sexual eukaryotic species are anisogamous, which means that male and female genotypes are contained in gametes of different size and characteristics. Anisogamy has evolved by disruptive selection from ancestors with isogamous reproduction (Bulmer *et al*., 2002), and is believed to be the origin of all further sexual dimorphism, based on two assumptions. First, the amount of resources that an individual allocates to reproduction is constant, necessitating a trade off between gamete size and the number of gametes produced. The second assumption is that the survival of a zygote depends on its size, which is determined by the size of the two gametes that fuse to form the zygote. Selection favoured offspring of gametes provided with reserve substances (yolk), leading to the production of macrogametes (egg cells). Other gametes of the same species didn't invest in the ballast of yolk, allowing them to move faster to the macrogametes for fertilization than the competing gametes. They became the mobile microgametes (sperm).

Two opposing forces therefore impinge on the evolution of gamete size: production of a large number of small gametes increases the number of fusions, whereas a smaller number of larger gametes increases the survival of the resulting zygotes. Moreover, the relative importance of these forces is frequency-dependent: the more large gametes are present, the more advantageous it is to produce many small gametes. Parker *et al*. (1972) showed that this frequency-dependence can lead to disruptive selection on gamete size. Alleles encoding for large and small gametes are favoured over alleles encoding for gametes of intermediate size if the range of gamete size is large enough. For the same amount of energy and raw materials many more sperm than eggs are produced, resulting in a permanent excess of sperm available for a relative shortage of eggs. By extension, the competition between sperm for fertilization of ova is the basis of male competition and behaviour in search for fertile females, rather than vice versa.

2. Parental care

Many germ cells need to be produced in order to compensate for the huge loss of gametes after spawning. An alternative is to invest in parental care, so that fewer eggs are needed. At least one individual takes responsibility for parental care, usually the last of the reproductive partners which is in contact with the offspring at the moment of spawning or birth (delivery). For most of the species, eggs are fertilized after oviposition in an aquatic environment (external fertilization), and the male provides the breeding care. In other cases, as in mammals, fertilization precedes delivery, resulting in female parental care. Because both partners have a proportionate share in the genetic make-up of their offspring, parenthood of the two sexes is an adaptation to limiting environmental conditions.

Depending on the environment, adaptations for parental care evolve, ranging from genetic monogamy (this behaviour is genetically fixed) to polygamy. In between all kinds of transitions exist among species, including social monogamy with extra pair copulations. The partners seem to be monogamous, but females go for sperm shopping to advertising males (Immler *et al*., 2009). This is known as sexual selection (chapter 3). By choosing

more suitable partners for fertilization, females spread the genetic risk in favor of the survival of their genes in the offspring. Males, for their part may in this way get extra offspring without additional investment in parental care. In popular speech we know this phenomenon as committing adultery.

3. Sexual selection and sperm competition

Sexual selection, the screening for the best partner, is followed by sperm competition between semen of different ejaculates in the female genital tract. Sperm competition, a form of sexual selection, describes the postcopulatory rivalry, which occurs between the ejaculates of different males for the fertilization of a given set of ova. Depending on the species, there is a large variability in competition strategies to benefit the own ejaculate and to block the strangers. The vast majority of sperm performs rather a defense function in the female genital apparatus and is not involved in fertilization. So, a smaller number of vital spermatozoa do not necessarily mean therefore that a male is less fertile, although cultural factors may have an important influence. Many lifestyle variables influence semen quality, including the storage of mobile phones close to the testes (Kilgallon et al., 2005).

Sperm competition plays an important role in populations where females have multiple partners during the same fertile period. High sperm competition in a species correlates with high spermatogenesis and larger testes. This phenomenon is widespread in nature. In primates, relative testis size is a prime example of a morphological trait that is affected by sexual selection acting via sperm competition (Anderson et al., 2007). Relative testes weights are greatest in those species where females mate with multiple partners during a single peri-ovulatory period. The increase in testis size is due, primarily, to the greater mass of gamete-producing tissues (seminiferous tubules). The testes of humans surpass in volume those of a gorilla, even in absolute value.

Selection pressures emanating from sperm competition also affect sperm morphology (Lincoln, 2007). Males of multiple partner species produce spermatozoa with higher motility and larger volumes of ejaculate than those in which females typically mate with a single male. The sperm midpiece houses energy producing mitochondria, which are spirally arranged around the first portion of the tail. Primates with multiple partner mating systems possess sperms with larger midpiece volume, whilst all other measures (sperm head and tail, both linear and volumetric) lack such differences (Anderson et al., 2002).

Males have a remarkable ability for adjusting their ejaculate expenditure according to the risk of sperm competition. They ejaculate more sperm, or sperm of better quality, when the risk of competition is high (DelBarco-Trillo et al., 2004), but reduce the number of sperm ejaculated when the intensity of sperm competition increases beyond two rivals (Pizzari et al., 2003). Human males viewing images depicting sperm competition had a higher percentage of motile sperm in their ejaculates (Kilgallon et al., 2005). For competing males, it is important to have large quantities of vital young sperm. If needed old semen is discarded through masturbation, an evolutionary adaptation for males in social mammals where sperm competition is strong (Waterman, 2007).

Sperm competition is only one facet, which can differ between mating systems, and it is not occurring in a passive arena within the female reproductive tract. Differences in cryptic female choice could create differing demands on sperm function and sperm motility as well. These include: differences in composition of secretions such as cervical mucins and tubular fluid, differences in affinity between oviduct epithelium and sperm, composition and viscosity of oviduct secretions, and vestments through which sperm have to swim. The functional anatomy of the vagina and the penis in erection in humans is designed as an old-fashioned water pump. The vagina is the cylindrical wall of the pump and the glans penis corresponds to the piston. As water is pumped upwards and outwards by pressure variation, here the sperm of a predecessor is eliminated to the outside during the rhythmic movements preceding the ejaculation. In the context of sperm competition it mechanically prevents the conflict with sperm of predecessors. The more intense the physical activity of intercourse, the greater the efficiency of sperm removal will be.

Partner monitoring and jealousy fit in this context. Males avoid being involved in the upbringing of unrelated offspring. Females have no benefit from a man who divides his efforts among the offspring of two or more rivals, as his help is urgently needed by his partner. As a consequence, both partners try to prevent extra pair copulations of the other spouse. If the help of a partner is less necessary, the way opens for polygamy and jealousy tapers off. We discuss here partnership in relation to reproduction. Topics as friendship and love are beyond the issue of this paper.

4. Cyclic reproduction in female mammals

The vast majority of species is iteroparous, which means that not all offspring is produced in a single clutch at the end of life, such as in semelparous organisms (e.g. salmon). Iteroparity means spreading of risks. An adult female goes through several

successive reproduction cycles. A cycle begins roughly with the maturation of one or more egg cells, which are mostly fertilized during the ovulation period, followed by an embryonic development in the uterus. A human neonate is suckling till the age of weaning ranging from 1 to 4.5 years (median 2.5), which is considerably younger than the 4 to 8 years for chimpanzees and bonobos (Marlowe, 2005). Weaning induces the next reproductive cycle. Not only the genital apparatus completes this cycle, but also all the tissues related to reproduction, such as the mammary glands. Male contribution to diet in foraging societies predicts a younger age at weaning, a higher total fertility rate, and greater female reproductive success, but not a lower offspring mortality rate (Marlowe, 2001). This implies that women may use food from men mainly to speed up their rate of reproduction.

If we assume that the reproduction cycle of women in natural conditions lasts 4 years (pregnancy and lactation), one arrives at 10 cycles from menarche to menopause. In modern times, however, by the use of contraceptive methods, many more cycles occur in a year, than otherwise in a whole lifetime. This means that all the tissues, including the glandular tissues of the breasts, are much more exposed to replication, increasing the risks of mutagenic deficiencies. In other words, modern women have not become intrinsically more prone to breast cancer, but the risk increases through a cycle frequency that is not adapted to natural conditions. From this viewpoint, there is an imperative to develop other types of contraceptives (Wyatt, 2009).

Menopause marks the end of the female reproductive capacity and occurs at approximately 50 years in all populations. The preceding 10-15 years are characterized by declining fertility, so most of a woman's reproductive potential is compressed into only 20 years of a longer biological lifespan (Shanley *et al.*, 2007). This difference between the life-history of human and non-human primates needs an explanation (chapter 9).

5. Families, kin selection, fitness and preventing inbreeding (incest)

The environment can be very heterogeneous. Sometimes the habitat is less suitable for survival and reproduction. In acute shortage of good patches, remaining at home is the best adaptation, even if one is grown into adulthood. This is how families originate. By definition, a family exists as soon as adult (sexual mature) offspring cohabit with their parent(s). Descendants then inherit the territory when the parents die. In the meantime, they increase their reproductive fitness (success) indirectly, as

helpers in the raising of younger kin (brothers, sisters) or other relatives. Direct fitness is obtained by growing own children. Indirect fitness increases by promoting the mutual genetic material that is available to relatives, in other words by helping relatives. Direct and indirect fitness together constitute the integral fitness of an individual. Individuals who do not have children, such as homosexuals, can get a significant fitness by assisting relatives (kin selection).

Solitary organisms spread before maturity, so the risk of inbreeding is extremely small. For families and social species, the likelihood of inbreeding (incest) is real. In natural circumstances, however, there is a strong selection against inbreeding (preventing harmful combinations of homozygous alleles). This results in exogamy or dispersion of one sex, while the opposite sex remains. In social mammals, as a rule,females stay behind and males disperse to other groups. This implies that the residing sex consists of genetic related individuals and kin selection (e.g. helping) becomes more obvious than in the dispersing sex. The resident females will care for the offspring of their kin, and even suckle, as males simply can not, so increasing their indirect fitness. Among nonhuman primates, females often form strong bonds with kin and other group members. The inclination of mothers to socializing is positively associated with infant survival, an important component of variation in female fitness. The effects of socializing on infants are independent of dominance rank, group membership, and environmental conditions. In this context, the social life of baboons is fairly well documented (Silk *et al.*, 2003).

6. Copulation devaluation and infanticide

Males can take care of their offspring very well, but they have no interest in doing so for unrelated youngsters. In most species, the receptive period of a female, being the period she is prepared to copulate, coincides with her fertile period, the ovulation time. If a female copulates with multiple males of the group, she creates uncertainty about paternity. The best option for a male in social species, such as lions, is to care for all offspring in the pride, as if it were his descendants. This results in selection for copulation devaluation (frequent copulations precede a conception) during estrus, being uncommon in monogamous species. It is a socially stabilizing factor preventing infanticide by males in the pride. While females lactate, they don't ovulate and they are not prepared for copulation. This poses no problem as long as the males of the pride are the potential fathers of the offspring. But when the resident males are chased by an invasion of foreign bachelors,

which are not related to the infants, infanticide interrupts the lactation period of the females, changing their hormonal balance. This initiates a new ovulation cycle, estrus and a receptive period, resulting in the paternity of the new males. There is selection for infanticide whenever a new group of males takes over from the resident males.

7. From female to male filopatric systems with an extensive receptive period in females

In some species, however, the risk of infanticide is avoided by accepting new males not as a bachelor group, but individually and spread over the clan. Aggressive behaviour of a newcomer is not tolerated,and he cannot afford it without risk of severe penalties. Female dispersal is a general rule for our closest primate relatives, chimpanzees (*Pan troglodytes*), and bonobos (*Pan paniscus*). The majority of our cultures too practice patrilocal marital residence (females move from the natal group to live with their husband's family). The genetic evidence that spatial variability in Y chromosomes appears to be less than in mtDNA or X chromosomes, shows we are essentially patrilocal. So women are more likely to migrate (Seielstad *et al*., 1998). Therefore, all men of the clan are relatives to a greater or lesser degree, promoting altruistic behaviour by kin selection. Because of this kinship among males infanticide has no fitness advantage. It opens the way to companionship, promotes cooperation and altruism and reduces rivalry within the group. Conversely, altruistic interactions between non-related women are based on win-win operations. Furthermore, females of the three mentioned species (*Pan* and *Homo*) developed a much larger receptive period than the fertile period (copulation willingness extended over time). This tempers the rivalry among males for sexual access and increases the uncertainty of paternity too. In our species, this adaptation has is most extreme effect.

8. Synchronization of the cycle when women live together

Pheromones (chemical communication between species) are common in mammals. The only pheromone known in humans synchronizes ovulation and the menstrual cycle through skin contact of upper arms and armpits (Stern *et al*., 1998). Synchronous ovulating women are thus fertilized simultaneously and get their babies around the same period. The advantage is that women could care for their infants in a cooperative altruistic context, including lactation as a win-win operation. When some women go out foraging, companions care for the children at home. The next time the roles reverse. Note that this is natural cooperation between individuals who are not genetically related (Nowak, 2006).

9. Menopause and grandmother hypothesis

Whereas other long-lived mammals can continue to breed until the end of life (elephants into their 60s, baleen whales into their 90s), the mean ages at last birth in natural human populations cluster around 38 (Kennedy, 2003). After this age, the female reproductive system undergoes a phase of rapid senescence, culminating in the menopause ± 10 years later (Shanley *et al*., 2007). Why do women cease fertility rather abruptly at an age well before generalized senescence renders child rearing biologically impossible? Yet, even in hunter-gatherer societies women who reach menopausal age can expect to live well into their 60s (Marlowe 2005). This disparity between reproductive and total life span is puzzling because generally there is no selection for non reproductive survival. Since the age of menopause is at least partly genetically determined, selection may have optimized the length of the fertile portion of the life cycle (Pettay *et al*., 2005).

The two main evolutionary hypotheses are that menopause serves either (1) for grandmothers to enhance their integral eproductive fitness by helping to care for their grandchildren (grandmother hypothesis), or (2) to protect mothers from rising age-specific maternal mortality risks, thereby preventing their highly dependent younger children from death if the mother dies. Both factors together can be responsible for the evolution of menopause (Shanley *et al*., 2007).

– Grandmother hypothesis.

According to the 'grandmother hypothesis' a grandmother has a direct beneficial effect on the reproductive success of her children and the survival of her grandchildren (Lahdenperä *et al*., 2004). The question of human longevity has deeper evolutionary importance than many think. It is often assumed that the steady increase in life expectancy over the past century and a half has resulted in a larger proportion of older people than ever before. But, until the past few decades, increases in life expectancy reflected reductions in infant and juvenile mortality, and made little difference to the fraction of women past child-bearing age. It is levels of fertility, not life expectancy (mortality), that shift the proportion of elders in a population. In both historical and hunter-gatherer populations, a third or more of women are usually beyond the age of 45 (Hawkes, 2004). This large proportion of older people has fundamental implications for all human social organizations.

We might assume that the large fraction of elders reflects a characteristically human social safety net. Developments in evolutionary life-history theory suggest that, instead of help for older members of the population, it is help from postmenopausal grandmothers that accounts for the age structures of human societies. Unlike other primates, human children are unable to feed themselves when they reach weaning age. The foods we rely on are too difficult for children to handle. This gives women whose fertility is ending an opportunity to influence the reproductive success of their children and survival of their grandchildren through assistance in food provision and education. In an ancestral population that was shifting from chimpanzee-like feeding to hard-to-handle foods, the more vigorous elder females could help more, thereby increasing the representation of their vigor in descendant generations, shifting rates of ageing, and lengthening average adult lifespan. Family assistance provided by grandmothers is a central determinant of our longevity (Lahdenperä *et al*., 2004).

– Mother dies.

In primates, a female who is already lactating may nurse a needful infant either briefly, while the mother is feeding or ill, or totally, involving full adoption (Kennedy, 2003). In our species, all lactating women in the group are not related to the infant. Kin selection cannot be invoked as a reason for food aid. Remember that milk production is a major metabolic effort. Without any return, women prefer their own child to suckle. They are not prepared to put their offspring at a disadvantage for the benefit of a child who is not related. Consequently, an orphaned infant risks starvation. In consequence, evolution has arrested the fertile period when the statistical probability that a woman will die is significantly increased.. It then becomes an option no longer to invest in direct fitness, but to move to indirect, by caring for children and grandchildren. But the sexual activity of postmenopausal women remains high under the 'sex for food' hypothesis. This is the price our species pays for the highly developed social cohesion without male infanticide. So it may make sense to cease having more children when the risks outweigh the benefits. This argument alone can account for a post-reproductive life equivalent to the time it takes to raise the last born successfully to independence (Shanley, 2007).

– A complementary hypothesis

Among primates, humans exhibit an extraordinarily low degree of reproductive overlap between generations. The rapid ending of the female reproduction coincides with the age at which, in natural popula-

tions, women are expected to encounter reproductive competition from breeding females of the next generation. As mentioned above (chapter 7) several lines of evidence suggest that in ancestral hominids, this younger generation typically comprised immigrant females, giving younger females an advantage in reproductive conflict with older women. The fertility trajectory has been shaped to minimize reproductive competition between generations within the same social unit (Kennedy, 2003).

In many cooperative vertebrates it is almost always the older generation that retains breeding status and the younger generation is reproductively suppressed. What might account for a reversal of this pattern in humans? Females leave their natal groups at maturity, and join a new social group. Consequently, when a female first arrives in the group, she has no other genetic relatives present. She can choose to breed herself and produce offspring to whom she is related by 1/2 or to refrain from breeding and assist the breeding attempts of the older female (i.e., the mother of her mate), who produces offspring to whom the younger female is unrelated. As a result, a female will have an advantage in reproductive competition with older females because she is insensitive to the costs she inflicts on older females by breeding and because elders have more to gain by helping. Game-theoretical treatment of the model yields an evolutionarily stable solution in which the older female commits irreversibly to zero reproduction when the younger starts to reproduce. This result holds even in the absence of any kin-selected fitness benefits that older females might gain as post reproductive helpers. Thus, the result does not require us to assume any grandmother benefits, although any such benefits will only strengthen the selection to cease reproduction. Moreover, an initial shift in the female life history to redistribute reproductive investment from later to earlier ages is likely to augment the advantage of young females in reproductive conflict with older females, reinforcing selection for early reproductive cessation and a separation of reproductive generations. The hypothesis should be seen as complementary, rather than as an alternative, to the grandmother hypothesis as an explanation for the divergence of rates of somatic and reproductive senescence (Kennedy, 2003).

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