

The Evolution of Men and Women

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Abstract

The ‘selfish gene’ is an excellent metaphor. Evolution seeks to maximise gene replication within the local reproducing group in the context of the environment. It does so by distributing genes among vehicles (organisms) which are each motivated to maximize their inclusive fitness, making the most of the genes that they have been allocated. We show how this gives rise to asexual and sexual reproduction, males and females, and four distinct mating systems, polygyny, monogamy, polyandry and eusociality. Humans are monogamous, which gives rise to a male dominance hierarchy and pairbonding, with men being assessed by their rank and reliability, and women by their fertility. the ultimate trajectory of evolution is towards making reproduction increasingly efficient, which manifests itself in societies evolving such that their primary goal is to police the male dominance hierarchy.

1 Introduction

The modern theory of evolution was essentially spawned in 1858 when Charles Darwin and Alfred Russel Wallace independently conceived of natural selection, the details of which Darwin published in *On the Origin of Species* (Darwin 1859). Whilst the gene-centred view of evolution was first described by George Williams (Williams 1966) and popularised by Richard Dawkins when he wrote the first edition of *The Selfish Gene* 40 years ago (Dawkins 1976). Once we accept that, contrary to Dawkins, we cannot ‘transcend’ our genes (Moxon 2010), the importance of the gene-centred view of evolution is difficult to underestimate. This paper derives evolution from the bottom up, starting with the origins of life, summarising Dawkins’ concept of replicators and the selfish gene and deducing natural selection. Next, the emergence of vehicles for genes and the all-important inclusive fitness are explained. Then reproduction, asexual then sexual, is deduced, giving rise to males and females, and four mating systems, polygyny, monogamy, polyandry and eusociality are deduced. Finally, the focus is on humans, and Steve Moxon’s recent work on the male dominance hierarchy and pairbonding is summarised. Men are assessed by their rank in the male dominance hierarchy and reliability, whilst women are assessed by their fertility. It turns out that the ultimate trajectory of evolution is towards maximising gene replication within the local reproducing group by making reproduction increasingly efficient. This manifests itself in societies by making their primary goal that of policing the male dominance hierarchy. The implications, both

scientific and societal, are enormous, and there is plenty of interesting work that remains to be done in the field.

2 Life

The present is a product of the past, and the future a product of the present. But what, in general, (if anything) can we say about the future with any certainty? Physicists, via the second law of thermodynamics, inform us that all we can say is that through the passage of time the entropy of an isolated system can remain the same or increase, but not decrease. However, truly isolated systems cannot exist in practice, other than possibly the universe itself, and entropy can decrease locally at the expense of increased entropy elsewhere. For example, entropy increases as pebbles on the beach, through the action of other pebbles and the sea, turn to sand. In the meantime, the pebbles become increasingly smooth and rounded. The shape of pebbles is not random, but biased towards persisting in their current state, whilst the ultimate trajectory of the pebbles is sand. All of this takes place over a long period of time. So we have entities that appear to be ‘designed’ to ‘survive’, plus a long-term direction. All of this in the absence of any designer, director, god, intelligence or even life.

Thus far, over enough time, the universe appears to be populated by entities that appear to be ‘designed’ to ‘survive’. Could such entities lead to a *process* that appeared to be ‘designed’ to ‘survive’? That is, a process that persists because it is self-perpetuating and robust. For example, if an entity was somehow able to replicate itself, accurately but robustly, such entities would become increasingly prevalent. The entities themselves need not survive for very long, so long as coded instructions for building further entities survived through the generations. Conceptually, it would just be the information that survived. But how could such a process possibly start? Consider the concept of a very long time, billions of years. An event considered possible but highly unlikely in our lifetime, such as winning the lottery, becomes an almost certainty. The present, after billions of years, can be significantly affected by events that merely happened once, if such an event initiated a process that is ‘designed’ to ‘survive’, but relatively unaffected by much more frequent events that fail to persist. Such an event did happen on earth, perhaps between two molecules in the primeval soup. It seems surprising, but it only had to happen once in a billion years or so. The event may be described as a *biological process*, and therefore arguably marked the beginning of *life* on earth. The process of life arising from non-living matter is known as *abiogenesis* and is thought to have occurred on Earth between 3.8 and 4 billion years ago. What follows is a description of *evolution*—the change in the heritable traits of biological populations over successive generations.

The replication described above takes place within the context of the environment, the environment consisting of both the physical (non-replicating) world, and other populations of replicators. Whilst the robustness we speak of means the ability to survive despite a change in the environment. We have seen how physical entities appear to be ‘designed’ to ‘survive’ via a ‘memory’ of the past. But this was in the context of a stable environment. Time only moves forwards, the present is a product of the past, and knows nothing of the future. A ‘memory’ of the past helps only insofar as the future resembles the past. Both the physical and replicating environments are constantly subject to

change. The climate changes, and the replicating world is inherently dynamic. It is with the backdrop of a changing environment that *mutation* evolved, which is a random change in a replicator. Mutations are essentially mis-copyings, and these mistakes were cumulative, but they introduced novelty and diversity into a population of replicators. Mutations are random, not intelligent, and cannot predict the future, so may be beneficial, neutral or deleterious. In practice, the majority of mutations will turn out to be neutral or deleterious (because over time the existing replicators have already evolved to be better than random) with only rarely mutations being advantageous. However, replicators that had no mutations (or developed perfect error correction) would be vulnerable to extinction. An optimal mutation rate would be positively correlated with the rate of environmental change, and negatively correlated with the size of the replicator (this is known as *Drake's rule*) so that the probability of a replicator having a mutation is not dependent on its size. So evolution evolved to employ an optimal compromise between evolutionary memory (via survivorship bias) and evolutionary novelty (via mutation).

Thanks to the evolution of mutation, as mis-copyings were made and propagated, the primeval soup became filled, not by a population of identical molecules, but by several different varieties of replicating molecules. Some molecules may have a tendency to break up, and some may cease replicating. Whilst some molecules likely evolved a mechanism for protecting themselves, either chemically, or by surrounding themselves in a coat of protein. Over time any population of self-replicating entities will be biased in favour of those that survive (longevity), those that replicate more rapidly (fecundity) and those that replicate accurately (copying fidelity), but not too accurately (those with an optimal mutation rate for their environment). This differential survival and replication of entities is the basis of a key mechanism of evolution, *natural selection*. Conceptually, we have two aspects to the process. We have the coded instructions for building entities, and their instantiations. The coded instructions may be thought of as information, data, a blueprint or a template; whilst the instantiations are the physical manifestations of the code, which would include the body of the replicator and any other effects caused by the code. The information is known as the *gene*, and its physical manifestation the *phenotype*. Genes reside within DNA molecules, so DNA molecules would be the minimal physical entity that contains the genetic code. However, if natural selection tried to act on DNA molecules directly it would struggle to find any criterion by which to do so, because all DNA molecules look alike, just as all DVDs look alike. Natural selection operates on genes through their phenotypic effects. Genes that exist have, in the past, succeeded in surviving, most likely over many thousands of generations (mutations are rare), and the more numerous they are, the more successful they have been at replicating over the generations. This creates a huge bias in genes towards striving to maximise their survival and replication through their phenotypic effects. It is as though genes have been designed to survive and propagate, and this is the sense in which genes may be considered 'selfish' (Dawkins 1976). Of course Dawkins was not imputing conscious action to genes, and technically it's the *allele*, one of a number of alternative forms of the same gene, rather than the gene, that should be considered 'selfish'. Nevertheless, the 'selfish gene' is an excellent metaphor, as it succinctly summarises the mechanism by which evolution works. Dawkins got this right 40 years ago. And that is it, evolution explained, without recourse to individual organisms,

groups or species. Life can be viewed as consisting of replicators with recourse to their phenotypic effects. We saw earlier that inanimate objects could appear to be ‘designed’ to ‘survive’, and had an ultimate trajectory. Life enables us to go further, from mere survival, to survive and multiply. Here the ‘blueprint’ of the entity survives and replicates. Originally natural selection consisted of the differential survival of replicators floating free in the primeval soup, but it now acts on conscious intelligent beings such as ourselves. So why do we exist? The answer lies, not in selfishness, but in cooperation. The ultimate trajectory of the pebbles was sand, whilst the long-term trajectory for genes would be for them to increase their efficiency at leaving behind the maximum number of copies of themselves in the population.

Before we start thinking about ourselves, a brief detour is in order to explain why individual organisms, or groups, are the last things that we should be thinking about, at least in terms of understanding evolution. To properly understand what is going on we need to address the various levels of abstraction in the correct order. First and foremost is the gene, which has evolved to maximize its own replication. The genes are distributed throughout the population of a species that have the proximity to potentially reproduce with one another which in turn has evolved to maximise overall gene replication (in the context of the environment). So, secondly, we must consider the entire *local reproducing group*. Only then are we in a position to consider questions about individual organisms, but always in the context of maximising overall gene replication, in the context of the environment, in the local reproducing group. For example, what different types are likely to have evolved (e.g. male and female), what are the major differences between them and how are the genes distributed within each group? So in order to understand ourselves we should avoid the self-centred urge to think in terms of the individual, and the natural urge to think in terms of groups (we are indisputably adapted to group living) below the entire local reproducing group.

Each gene is biased towards survival, but is otherwise neutral towards the survival of other genes, which in practice means that genes (technically, alleles) will compete or cooperate as and when necessary. For example, if the size of a population is stable, perhaps resources and predators have created an equilibrium, competition among alleles would be zero-sum, so alleles can only increase their frequency at the expense of other alleles. In contrast, our own genes cooperate with one another because they share the same outlet—sperm or egg—into the future. Genes may compete or cooperate, but they are always selfish.

3 Vehicles

Cooperation among genes was so strongly favoured that units coherent enough to be called ‘vehicles’ containing colonies of genes emerged (Dawkins 1976). Such vehicles are better known as individual organisms, such as you or I. An organism is a temporary vehicle for a cooperative of genes and a coherent bundle of phenotypic effects, but with one end goal, gene replication. As mentioned above, the trajectory of evolution is to make gene replication, in the context of the environment, more efficient. Through replicators necessarily started off as simple, perhaps as molecules floating in the sea, their trajectory was one of an increasingly large and complex phenotype.

Now let's consider any local reproducing group, it could be the primeval soup, single-celled organisms, humans or a population of ants. A particular gene exists in many physical copies throughout the world, each of which has evolved to leave behind the maximum number of copies of itself in the population. A particular gene would thus promote phenotypic effects that helped any other instances of an identical gene replicate regardless of their proximity. This is an important concept in evolution and is known as *inclusive fitness*. Individual organisms have evolved such that they are each motivated to maximize their inclusive fitness.

The state of an entity is influenced by its environment over time, and the environment is subject to change. For example, if rocks fell from a cliff, jagged stones would litter the beach, and few would survive in their current state as they became eroded over time. If the environment is subject to change, an entity would be better able to survive if it had the ability to adapt. The biological world, prevalent on the surface of the earth, utilizes information that exists in short-lived vehicles, but is able to 'self-replicate'. Although mass is conserved, the vehicles come alive then die, and can only pass on the information to the next vehicles within that period. The short-lived vehicles are the local population of *organisms*, the information passed on from parents to offspring being contained in the units of inheritance, the *genes*, genes are organised in bundles called *chromosomes*, an organism's entire set of genes are known as its *genome*, and the process by which the local population enables the genes to self-replicate is known as *reproduction*. An organism's hereditary information is known as its *genotype*, whilst its actual observed properties are known as its *phenotype*, which is a product of the genotype plus the environment. The entire process is known as *evolution*.

Reproduction is a fundamental feature of all species; the entire local reproducing group exists as the result of reproduction. Every organism is the product of its parents, which in turn are the products of their parents, and so on. Therefore every single member of the entire lineage of every species (excepting the most recent generation) reproduced. This creates a massive bias in the genes towards motivating the individual carrying the genes into reaching the age of sexual maturity and successful reproduction. In other words, genes are hugely biased towards survival, whilst for the individuals, survival is irrelevant except insofar as it affects reproduction (Ghiselin 1997, p. 292). In summary, the *genes* are biased towards *survival* (Dawkins 1976), whilst the *local reproducing group* is biased towards *reproduction*, see Reeve and Keller (1999), and the ultimate trajectory of evolution is towards maximising gene replication within the local reproducing group by making reproduction increasingly efficient.

Asexual reproduction is a mode of reproduction by which offspring arise from a single parent, and inherit their genes from that parent only. Asexual reproduction utilises *mitosis*, a form of cell division that produces two daughter cells with the same genetic component as the parent cell. Each cell is *haploid*, so contains a single set of chromosomes. So the daughter cells are clones of the parent cell, except for any mutations, which will be spread to all subsequent offspring. The first living organisms were asexually-reproducing single-celled organisms, known as *prokaryotes* which include bacteria and archaea. Around 2.5 billion years ago prokaryotes evolved into *eukaryotes* and gained a nucleus containing their DNA. Then around 1.5 billion years ago single-celled eukaryotes split into three separate lineages: plants, animals and fungi (Wang, Kumar and

Hedges 1999).

Recall that the long-term trajectory of evolution is towards making reproduction increasingly efficient. For species with a small number of genes (a small genome) asexual reproduction works well, as it is fast and cheap, and unfit lineages simply die out. The trajectory towards increasing reproductive efficiency led to the evolution of species with increasingly large genomes. For species with large genomes, a smaller proportion of genes will suffer a mutation (Drake's rule), and the effect of each gene on the individual is diminished, so in the short term organisms with deleterious genes will likely still live and reproduce, but over time the accumulation of mutations (*genetic load*) will increase at a steady rate, eventually leading to a fall in population size. This is known as *Muller's ratchet*, so called because the population accumulates deleterious mutations in an irreversible manner. The problem is how to eliminate deleterious mutations from the gene pool as soon as possible, whilst retaining any advantageous mutations. Naturally, evolution found a solution, *sexual reproduction*, a form of reproduction that involves the fusion of male and female reproductive cells. The great majority of eukaryotes (animals, plants and fungi) reproduce sexually.

Let's consider how sexual reproduction may have evolved. If two haploid cells touched, the cell walls could join, and the two cells would become a single cell with two sets of chromosomes, known as a *diploid* cell. These diploid cells would continue reproducing asexually via mitosis. There is always the chance that these cells could split, and on occasion the cell would divide so that each half contained one set of chromosomes. So we have a diploid cell splitting into two haploids, this is known as *meiosis*. If two of the new haploids were to meet, as with the original type, they could fuse to create a new type of diploid. The diploid to haploid via meiosis to diploid again cycle is sexual reproduction, the cells that fuse are known as *gametes* and the resulting cell a *zygote*. The *diploontic life cycle* evolved so that the cells would have spent more and more of their time as diploids, with haploid cells only being used briefly, during reproduction, because during the diploid state there are two copies of every gene in each cell, so genetic damage can be repaired. The zygotes grow via mitosis to form multicellular diploid organisms. Initially these would have consisted of clusters of identical cells, but over time it became more efficient for the cells to be organised so that certain functions would be performed by only some of the cells. For example, those specialised in producing haploid cells. The gametes are all of a similar size and shape, and this form of sexual reproduction is known as *isogamy*. Whilst the organisms have reproductive organs normally associated with both male and female sexes, they are *hermaphrodites*.

Imagine a population of gametes. Through time, due to mutations, the gametes would differ in size. Some will be large, and thus potentially fitter. Others will be genetically biased towards putting more time and effort into seeking out the larger, potentially fitter, gametes to fuse with. Those individuals who lie in the middle, and specialise in neither activity, will die out. The first type leads to a small active gamete, the second to a larger static gamete. Intra-genomic competition ensures that this dichotomy persists. See Parker, Baker and Smith (1972). This form of sexual reproduction involving the union or fusion of two dissimilar gametes is known as *anisogamy*. The smaller gametes are known as *sperm cells*, whilst the larger gametes are known as *egg cells*. An asymmetry in quantity also evolved, in terms of energy the most efficient solution was to make the smaller, cheaper, sperm plentiful, and the more expensive eggs

sparser.

Genes, and, in turn, species, have evolved to maximise overall gene replication via reproduction within the context of the environment. But in order to achieve this there are still various trade-offs to be made. For example, maximum life span, period of fertility, number of offspring and parental investment. The trade-off an organism makes between quantity of offspring produced and quality of parental investment per offspring is known as *r/K selection theory*. *r*-strategists typically evolve within a sparse ecological niche with room for population growth and prioritise quantity produced leading to a high growth rate. Whilst *K*-strategists typically evolve in a crowded ecological niche with greater competition and prioritise quality of parental investment.

Imagine a population of hermaphrodites. Some will be genetically biased towards putting more time and effort into producing sperm cells and their genes will thrive as they inseminate many others. Others will be biased towards expending energy by producing egg cells and bearing offspring, they will also be genetically successful as can do their best to ensure their offspring survive. Those individuals who lie in the middle, and specialise in neither activity, will die out. Intrasexual competition, and the law of comparative advantage, ensures that this dichotomy persists. The former group evolved into *males*, and the latter group *females*. And thus was born Adam and Eve. For males nearly all effort is concentrated pre-fertilization, whilst females concentrate most of their effort on post-fertilization. If there were fewer males than females, then males would have a higher chance of mating, and would thus be genetically fitter than females. In turn, females who were biased towards producing more sons than daughters would become fitter, leading to a greater number of males. So the population would tend back towards the only *evolutionarily stable strategy* of a 1:1 sex ratio. This is known as *Fisher's principle*.

To recap, evolution seeks to maximise gene replication within the local reproducing group in the context of the environment (the physical environment plus other species) which is subject to change. We have shown that, in order to attain this goal, mutations, sexual reproduction and males and females have evolved in a 1:1 sex ratio. Evolution needs mutations to keep up with a changing environment, but most mutations will turn out to be neutral or deleterious, and only a few advantageous. Evolution therefore needs an efficient method of introducing mutations and eliminating those that are deleterious as soon as possible, whilst keeping the advantageous. We mentioned above that sexual reproduction solves a problem with asexual reproduction, Muller's ratchet, the steady accumulation of deleterious mutations (genetic load). Because reproduction is a multiplicative process, by default we may assume that the fitness of a genome follows a lognormal distribution, and that \ln fitness is additive. An idealised method of reducing genetic load would be to have all the deleterious mutations accumulate in the same genomes, and have them eliminated for the lineage. This would give us a small number of genomes with extreme negative values, so the distribution of \ln fitness would have negative skew. Such a distribution is achieved via *epistasis*, the interaction between genes. Specifically, *negative epistasis*, whereby the combination of beneficial mutations causes less-than-additive fitness improvements, whilst, more importantly, the combination of deleterious mutations causes a greater-than-additive decrease in fitness.

The effects of negative epistasis may be accelerated further via sexual, rather than asexual, reproduction, as this allows for *positive assortative mating*, a mat-

ing pattern in which individuals with similar genotypes and/or phenotypes mate with one another more frequently than would be expected under a random mating pattern. Given that deleterious mutations are more frequent than beneficial mutations, positive assortative mating will lower the skewness of the distribution further. Note that negative epistasis and positive assortative mating will also increase the variance of the distribution of genome fitness, making selection more efficient.

When considering evolution we should not lose track of time. Relative to our own short lifetimes evolution would appear to be a slow process, but it is also very old, and has been in progress for billions of years. We have shown that evolutionary success ultimately depends on maximising gene replication within the local reproducing group. So, *ceteris paribus*, faster should be better. However, evolution needs to be robust to changes in the environment. If an evolutionary strategy is fast, but is more susceptible to extinction than a slower strategy, then the slower strategy will dominate. In this sense, evolution is playing the ultimate long game. In the short-term a mutation, on average, will reduce the fitness of the local reproducing group. However, because below-average genes are often purged from the lineage, over time the fitness of the local reproducing group benefits from mutations (that have evolved at an optimal rate). In the short-term asexual reproduction would be faster than sexual reproduction, but we have shown that for species with large genomes sexual reproduction is better able to maximise gene replication. In the short-term negative epistasis decreases the fitness of the local reproducing group. But, again, in the long term negative epistasis helps increase the fitness of the local reproducing group. Evolution has been in progress for around 3.6 billion years, and favours the long term over the short term, a concept that has been termed *lineage selection* (Nunney 1999). Evolution has evolved such that genes have an implied discount rate that must be close to zero.

Not all mutations are inherited. The *germline* consists of the population of cells that may pass on their genetic material to any offspring, and includes the gametes (sperm or egg), plus the cells that divide to produce the gametes, all the way back to the zygote. Eggs are energetically expensive, large and limited in number, whilst sperm are cheap, mobile and plentiful. Whilst females produce egg cells and bear offspring, males merely produce sperm. Therefore evolution should utilise as many as possible, and take fewer risks with, eggs and females, whilst expending effort selecting the best sperm and males, the remainder (a majority) being relatively expendable. It makes sense, therefore, to have a higher mutation rate in the male germline than the female. And in animals this is indeed the case, because a larger number of cell divisions are involved in the production of sperm. So we have greater selection in the male germline via a greater variance in fitness and a larger number of evolutionary dead ends. The skewness of the distribution of fitness will be constantly eroded as the genomes in the left tail die out, resulting in a lognormal distribution.

We have discussed above how, in order to maximise gene replication, a species must evolve trade-offs, for example between number of offspring and parental investment per offspring. With two sexes, different trade-offs between mating effort and parental investment will likely evolve for each sex. *Mating effort* is the time and energy devoted to finding and seducing a partner, whilst *parental investment* (Trivers 1972) is the time, energy and resources devoted to an individual offspring. As the female, by definition, always produces the

larger gametes (ova), we should not, *a priori*, expect symmetry in parental investment. We have already shown, when explaining how the two sexes evolved, that for males nearly all effort is concentrated pre-fertilization, whilst females concentrate most of their effort on post-fertilization. Furthermore, in mammals the female alone must take time out for gestation and lactation. In all sexually reproducing species, the relative investment that is made by the male and the female in their offspring determines the degree of discrimination exercised by the individual when selecting a mate. This is known as *Bateman's principle* (Bateman 1948).

If, as is typical, the female makes the greater investment in offspring, she will be in a position to be relatively choosy. So the males must compete. One potential solution would be a free-for-all scramble, with all males competing aggressively with other males for access to females. But this would be costly, males would spend all their time fighting each other instead of mating, and even the males with good genes would risk serious injury and even death from adversaries who may have little to lose. Males evolved to remember the outcomes of any past encounters and apply transitive reasoning (if A beat B and B beat C then A would beat C) so would only resort to contesting another man if the outcome was in doubt. Such dyadic interactions give rise to an asymmetric 'power' relationship between individuals, known as *dominance*. The net result is that males self-organize into a *dominance hierarchy*, this is emergent behaviour. A dominance hierarchy is an ordinal series (first, second, third, fourth, etc.) so can serve to amplify differences between males that may be very small in absolute fitness terms. Females seek 'good genes' in males and the dominance hierarchy better enables females to assess mate value as they can map a male's rank onto the quality of his genes. Such a method of differential reproductive suppression serves the purpose of retaining genetic material that enhances the lineage, whilst deleterious genetic material is eliminated as lower ranked males have few, if any, offspring (Moxon 2008). Note that there is no dominance relationship among females or between males and females.

There are now two criteria by which a female can select a mate. First and foremost, the quality of the male's genes which may be judged by his rank in the dominance hierarchy, and secondly, to a varying degree, the reliability of the male in terms of parental investment. The importance, or otherwise, of parental investment (and the relevance of the male) evolved in tandem with different mating systems. We briefly consider polygyny, monogamy, polyandry and eusociality in turn.

In species that require relatively low parental investment, the males have little use once they have inseminated a female. We have shown that the most efficient way of maximising gene replication would be by utilising all or most of the females, but only the highest ranked males. The highest status men will likely have a relationship with more than one female, whilst the females remain predominantly bonded to a single male. This is known as *polygyny*. In practice the majority of males will maintain monogamous relationships or remain single.

In species that require relatively high parental investment, the males are needed to help take care of offspring, so *monogamy* and *pair-bonding* evolved. However, sexual monogamy is evolutionarily unstable, because the most efficient way of maximising gene replication would be by utilising all or most of the females, but only the highest ranked males. So what evolved is pairbonding plus clandestine polygyny for the highest ranked males.

In a species that requires extremely high parental investment, including significantly long periods of gestation and lactation, it makes sense to skew resources towards helping the most fertile female(s). One solution, known as *polyandry*, is for the female to mate and receive resources from several males. The problem with polyandry is that the various males in partnership with the same female would be antagonistic towards each other, each wishing to mate with her at the expense of the others, and may be reluctant to support the female in cases of paternity uncertainty. Furthermore, the female may appreciate the paternal support that the various males provide, but she will often be better off mating with just the highest fitness male. Unsurprisingly, polyandry is relatively rare in practice.

In a species that requires extremely high parental investment in general, but has relatively short periods of gestation and lactation, it makes sense for the population to consist of both male and female reproductive and non-reproductive castes, and the sterile individuals work to further the reproductive success of those individuals capable of reproducing. This is known as *eusociality*. We end up with extreme reproductive skew, especially on the female side, as most of the individuals cooperatively care for the brood of a single reproductive female (the queen). Genes across the local reproducing group cooperate with each other by evolving both reproductive and non-reproductive phenotypes that will share many genes. Consistent with maximising their inclusive fitness the non-reproductive castes' genes motivate them to help the reproductive castes successfully pass on their genes to the future.

So at one extreme we have polygyny, a mating system that leads the females to select a mate according to his rank in the dominance hierarchy. At the other extreme we have eusociality, requiring such high male parental investment that males will evolve to compete on the basis of reliability, lifetime monogamy will be the norm and the male dominance hierarchy will collapse. Monogamy lies between these two extremes.

4 Humans

Humans are monogamous, as described above. What does Bateman's principle tell us about humans? In humans, females give birth to their offspring, whilst men do not, so females can be expected to be the more discriminating sex. The distribution of men's mate value has a greater variance than the corresponding distribution for women. Females limit the reproductive success of males, and men compete with other men for access to women.

As humans are monogamous, the males are needed to help take care of offspring. This means that the reliability of a male is a consideration. *Reliability* is the perceived propensity of a male to help in the care of offspring.

In economics, when a choice needs to be made between several mutually exclusive alternatives the *opportunity cost* of a choice is the value of the best alternative forgone. For men, there is virtually no opportunity cost when mating. A man can reproduce with multiple partners within a short time-frame. For women, the opportunity cost could be reproducing with a higher fitness male because she would be pregnant for nine months. For obvious reasons, men are attracted to faithful non-pregnant women, so for a woman to be seen merely associating with other men would put off a higher mate value man. It makes

sense, therefore, for a woman to recruit a man of as high mate value as possible, to *mate guard*, and deter unwanted attention from lower mate value males. In practice the woman would secure a long-term mate in accordance with positive assortive mating. The woman would still be free to engage in extra-pair sex with men of higher mate value than her long-term partner, because the long-term partner would lose any agonistic contest to a more dominant male (Moxon 2013). This was the likely origin of the human *pair-bond*. The tendency of humans to form pair-bonds is universal, with an average duration of five to six years. This is enough time to produce two children. This benefits the woman further. For without such a pair-bond, she would need to seek a second man to father her second born. By which time she will be five years older, and her mate value will have decreased (fertility peaks at around 18 years old), so the father of her next child would likely be of lower mate value too. Furthermore, her husband's mate value may well have increased, as he gains resources and seniority within the social group. We have explained why pair-bonding is in the interests of women, but what about men? A man will pair-bond with a woman if and only if the woman is of a higher mate value than the women who would be prepared to have extra-pair sex with him. He would then be guaranteed sex for the duration of the pairbond with such a woman. Indeed, *marriage* (in any culture) is when the husband makes an explicit contract enforceable by the whole social group to provision a woman and any resulting children in exchange for exclusive sexual access to her.

Humans are monogamous which, as described above, means pairbonding plus clandestine polygyny for the highest ranked males. In common with other male animals that practice polygyny or monogamy, men self-organize into a dominance hierarchy. This is emergent behaviour and an epiphenomenon of the social psychology of the individuals. A dominance hierarchy is an ordinal series and is a zero-sum game among males so it makes no difference how egalitarian a society is (dominance hierarchy concerns reproduction, not resources (Moxon 2008)). Furthermore, the dominance hierarchy is a self-reinforcing system of social organisation, so is conspicuous throughout society.

Given the enormous reproductive benefits afforded to a low-ranked male who can circumvent the dominance hierarchy, we have an obvious *free rider problem* that, naturally, evolution addressed. A cognitive mechanism known as *cheater detection* (Cosmides 1989) evolved to police tactical subversion of the dominance hierarchy. The 'policing' is largely internalised, so that most low-ranked men avoid the costs of transgression ever arising. For example, the ultimate act of cheating would be rape, which is severely punished by society, whilst the vast majority of males police themselves and do not engage in unsolicited sex, or even expect to date women out of their league. The primary goal of societies is to police the male dominance hierarchy.

Women seek 'good genes' in men. We have seen that women seek, first and foremost, a long-term partner to pairbond with, and, secondly, short-term relationships with men of higher ranked than her own husband. For long-term relationships, women seek high-ranked men as a primary consideration, and reliability as a secondary consideration. For short-term relationships, women seek only high-ranked men. Men must compete with other men for their rank in the male dominance hierarchy and this translates directly into men contesting each other for positions within organisations. A man's rank in the dominance hierarchy is correlated with height, muscularity, broad shoulders, confidence,

symmetry, attractiveness, intelligence, wealth, income and willingness to take risks.

Men seek fertility in women, that is, they seek to complement their own good genes. So a female's mate value is simply her degree of fertility, which is a product of her age and beauty. A woman can do nothing about her age, and beauty is mainly heritable, furthermore both can be assessed by males in a split second. As men seek to complement their own good genes, different men may prefer different women. Men desire fertile, non-pregnant and faithful women. Women have a limited period of fertility, so men are attracted to youth, slenderness, beauty, chastity and fidelity (Buss, *et al.* 1990). So the best that a woman can do is to maintain or effect a slender figure, and place herself in the path of high ranking men.

5 Conclusion

To conclude, we have shown that the 'selfish gene' is an excellent metaphor. Evolution seeks to maximise gene replication within the local reproducing group in the context of the environment. It does so by distributing genes among vehicles (organisms) which are each motivated to maximize their inclusive fitness, making the most of the genes that they have been allocated. This gives rise to asexual and sexual reproduction, males and females, and four distinct mating systems, polygyny, monogamy, polyandry and eusociality. Humans are monogamous, which gives rise to a male dominance hierarchy and pairbonding, with men being assessed by their rank and reliability, and women by their fertility. The ultimate trajectory of evolution is towards maximising gene replication within the local reproducing group by making reproduction increasingly efficient, and this manifests itself in societies by making their primary goal that of policing the male dominance hierarchy.

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