



The Inescapable Game of Life



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"All's fair in love and war" leads us to a point of no return. To all intents and purposes, love is the uniting force of empathy and requital, and war is the ultimate Armageddon, conflict run amok on a collective scale. How can the two ends of the spectrum be so indistinguishably entwined? What does this spell out about our striving for unity in the face of disunion? What hope do we have of reaching a resolution, if love and war are so equatable - indeed equitable - as if dark and light were simply faces of one another? And what does it mean to say that ALL is fair, as if every position we could take, from integrity to deceit, from faithfulness to betrayal, are all legitimate players of a summer game? And how do we successfully negotiate these paradoxically entwined paths, one of which leads to a wasteland of attrition, wounding and death and the other to paradoxical reunion, completion, abundance and life? This is the answer to the Prisoners' Dilemma in sexual paradox.

Of course, life is a game we can never escape except in death. The evolutionary struggle is no better, doomed to a purgatory of survival amid conflict and cooperation, so long as our genes mutate and survive. The only culmination of this game is extinction. The outright wins all animals have, in the predatory process of feeding, are merely another step on the road of survival, staving of the hour of final reckoning.

The Prisoners' Dilemma as a classical game matrix. Payoffs for each player are such that each is 'tempted' into defection, resulting in mutual nemesis. Attempts to resolve the devastating simplicity of the matrix may involve conditional strategies (e.g. 'I'll do what you do) or mixed strategies playing both strategies with probabilities. Real tournaments also involve repeated and sequential exchanges, which encourage cooperation, at least until the last round or two.

	C	D
C	1 - 2 = -1	2 - 1 = 1
D	3 - 1 = 2	

The Prisoners' Dilemma

The Prisoners' Dilemma is a universal paradox in game theory in which mutual defection leads to the 'double jeopardy' of collective downfall. In the classic case, two criminals are to be tried for a joint offence. If one betrays the other and becomes an informant, they will get protection, but the other will go down as the ringleader with no parole. If they both stay silent, they will only get done for a minor offence, but if both defect and spill the beans they will get a jail term for conspiracy. If the game is played only once, any rational player will defect. If they cooperate in silence they will at best get a minor felony and worst no parole, but if they defect, they might get sprung with a middle term, or they might get off with a non-custodial sentence. However an astute player facing repeat encounters will be much more canny and cooperate, at least until the last round's high noon.

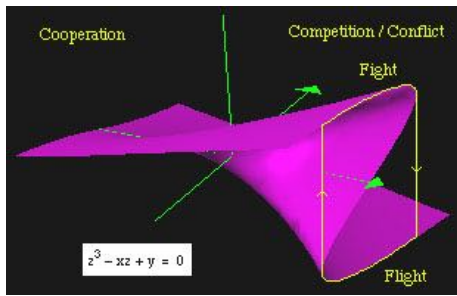
Intriguingly female prison inmates appear to play prisoners' dilemma games more cooperatively than female students (Khadjavi & Lange 2013 Prisoners and their dilemma *J. of Economic Behavior & Organization* 92 163-175), possibly because they need to stick together for their own survival under incarceration.

Joseph Heller's "Catch 22" ([R306](#)), describes a classic form of the Prisoners' Dilemma as a logically paradoxical double bind. With a growing hatred of flying, Yossarian pleads to be grounded on the basis of insanity. His appeal is however useless because, according to army regulation Catch-22, insane men who ask to be grounded prove themselves sane through a concern for personal safety. The only truly crazy people are those who readily agree to fly more missions. The only way to be grounded is to ask for it, yet this act demonstrates sanity and thus demands further flying. Crazy or not, Yossarian is stuck.

The Prisoners' Dilemma is a root paradox permeating all areas of knowledge, from the stability of rational assumptions of best interest in economics ([R102](#)) to the fractal complexity of climax forests ([p.506](#)). It's status has been acknowledged by economists and utopian thinkers, from Hobbes to Rousseau. All its diverse forms involve the splitting of a process, under increasing polarization into competing domains leading to nemesis - any situation in which the participating entities are 'tempted' into a course of action which would bring disaster if everyone did the same thing. The game applies in a chilling manner to the risks of nuclear war and the knife-edge advantage of first strike.

Ironically one of the first people to introduce the concept of cooperation into a view of nature as a pitiless "war of each against all" as Thomas Huxley described it in Hobbes' words, was the Russian anarchist Prince Petr Kropotkin (Ridley [R578](#)), who had himself escaped prison in a daring ingenious feat of cooperative insurrection. In 'Mutual Aid' ([R395](#)) he rejected the notion that selfishness is an animal legacy and morality a civilized one, claiming that supportive species were fitter than those endlessly at war, challenging a long tradition, going back through Malthus and Machiavelli to Augustine, shared today in the stress on competition as a motivating force for the free market. We can see in Kropotkin's twist of fate just how conducive to 'inscrutable cooperation' in a Machiavellian context, the

Prisoners' Dilemma can be. Kropotkin's work emphasizing the role of cooperation and his intuitive opposition to an exclusive focus on competition has recently received recognition from authors as diverse as Ridley ([R577](#)) and de Waal ([R162](#)).



The cusp, the first of Rene Thom's classical catastrophes ([R686](#)) enters criticality, causing the process to bifurcate between competing regimes. As x passes through 0 the surface folds, causing cooperation to move into competition, and behavior to flip between fight and flight. Prisoners' dilemma games attempt to resolve the disparity between these two conditions and their varying payoffs.

The Prisoners' Dilemma became transformed into the battleground of the genetic arms race by the work of evolutionary biologists George Williams and William Hamilton in the 1960s epitomized by Richard Dawkins ([R151](#)) infectious phrase "the selfish gene". This shifted the pendulum from collective concepts, of 'survival of the species' and 'group selection' to a detailed analysis of how genes act as agents of their own selection in a way which leaves the organism little more than a doomed collection of apparently selfish genes, barely held in check in a common, yet shifting genome. While group selection and the capacity for social selection has not been entirely extinguished, George Williams in 1966 demonstrated that it is unstable to individual defection. The primacy of genetic selection shone a new spotlight on the exact processes providing stable strategies in evolution, which are robust to defection.

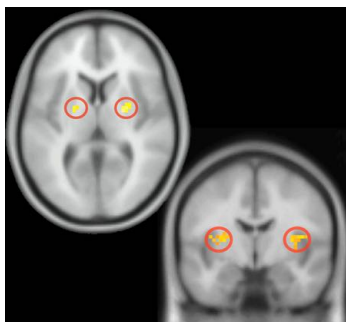
The Red Queen hypothesis of sexuality ([p 26](#)) with its paradoxes between parasite and host and between female and male genetically and more particularly sexual evolution, both of which we shall examine next, are outstanding examples of the Prisoners' Dilemma. In the sexual context the Prisoners' Dilemma genetic race between female and male is also bifurcated between the differing strategies of female out-front long-term investment and the male strategies of sneaky short term fertilization and direct male-male reproductive conflict. Thus not only do we have male and female locked in a genetic race from which neither can escape, but the male strategy is prone to natural flight and fight of its own accord. This male tendency to conflict is liable to a break down of the game into a male dominance over the female, profoundly exaggerating the tendency to violence and war. Thus while the male and female are both strategic players of the game, they also represent relative extremes of the energy landscape in terms of cooperation or conflict. The emergence of patriarchal dominance in human society has been explained as a response to ecological stress (Sanday [R609](#) 181) in terms entirely consistent with a symmetry-breaking of the Prisoners' Dilemma between male and female into a protracted impasse involving crisis and instability.

The arms races that result from the Red Queen process extend via the Prisoners' Dilemma to all forms of competitive arms race, such as the mutually assured destruction from nuclear holocaust we have all continued to face since the beginning of the Cold War despite symbolic efforts at nuclear arms reduction, the knife-edge cooperator-defector zero-infinity dilemmas of launching a first strike and all runaway militarization races between competing powers, who could also cooperate to their mutual but less successfully exploitative benefit. It also applies to mediation between inter-group competition, protection from aggression and the consequent need for cooperation within groups in evolving the kinds of systems we come to associate with morality, ethics and the rule of law.

Richard Alexander ([R6](#)) in "The Biology of Moral Systems" has given an in-depth analysis of the relationship between these two phenomena which has been widely applied by many researchers ([p 44](#)). Key here is the interaction between inevitable competition between groups which are large in the case of humanity and the complementary ensuing need to evoke systems of social selection which ensure the group is internally cooperative enough to remain competitive or even dominant. The theory thus explains the emergence of moral systems and ethics based on principles of natural selection, rather than cultural constructs alone. The breakdown of such moral conventions often involves the breaking of a common pact for individual gain, as when a ring of hunters joining to encircle a deer is broken by one person or another diving off after a rabbit he is sure to catch, as noted originally by Rousseau. A similar analysis by Turchin ([R706](#)) examines cycles of cooperative foundation, empire, growth of inequality, disaffection on the turbulent perimeter, and rebellion.

In the experiment (right) people could either divert a tram from a line killing five people to one killing only one. Almost everyone will do this, but if they are asked to push one person into the path of the tram to stop it to save five most people demur, indicating killing has a moral inhibition where diverting the tram, even though it results in a death doesn't. Now the telling part comes. While 85 percent of people said it was morally wrong, 28 per cent said they would still push a stranger off to save five, but a full 47 per cent said they would push a brother off to save five brothers indicating saving kin becomes paramount over the inhibition against murder (Evolution and Human Behavior, DOI: 10.1016/j.evolhumbehav.2011.11.002).

Recent research, as of 2011, suggests we have more than one moral system, one related to protecting kin and the other a more general one, for example inhibiting us killing others. This implies that societies have a capacity to develop moral rules unrelated to kin and that these rules are socially adaptable, meaning we can in principle fix flawed moral systems. Moral choices also appear to involve complementary and opposing brain processes.



When people try to equitably distribute charitable donations, activity in the putamen (left) may reflect what's best for the greater good, whereas the insula (right) tracks inequities between individuals. (M. Hsu, C. Anen, and S. R. Quartz, Science Express, 8 May 2008, Science 320/5877 734 - 737 DOI: 10.1126/science.320.5877.734).

The Prisoners' Dilemma also comes in more complex ecosystemic forms than the one-on-one arms races of host-parasite and sexual relations. The complexity of a climax forest is the result of a prisoners dilemma relationship between many plant species competing for light. It also permeates animal species in the natural competition between the members of a population for reproductive, and food resources and for personal power and fortune. Nowak and Sigmund ([R510](#)) point out that evolutionary game theory places the usually presumed constant fitness landscape of natural selection in a feedback process, in which payoffs can be reversed by population changes, leading to rare strategies being reinforced ([p 60](#)), amid stable coexistence or unstable oscillation, or punctuated equilibrium.

A graphic illustration of the diversity of life as a Prisoners' Dilemma game caught mid-way between cooperation and defection is given by the diversification into plants and animals, ([p 327](#)). Plants are broadly cooperative although there is always competition for limiting resources since they fix their energy from sunlight rather than depending on consuming one another. Animals defect by directly consuming plants, subsequently bifurcating into second order defections in the form of predatory carnivores who also eat other animals. The earliest life forms were either phototrophs, or converted free mineral energy such as that in hydrothermal vents, so the evolution of life into diversity is a movement from initial cooperative exploitation of an external energy source, subsequently filling sufficient defection niches to provide ever-increasing diversity to climax and the pyramidal populations of food webs.



The evolutionary tree of life is our richest example of the Prisoners' Dilemma. The survival of every gene of every species is a Prisoners' Dilemma. Each gene, organism and species lives as long as its Prisoners' Dilemma of coexistence as parasite and host, predator and prey, symbiotic, saprophytic and reciprocal interactions with others of its kind. As long as we survive, we remain locked in the Prisoners' Dilemma mediation of cooperative and competitive forces that we call life. Death is a loss. The only hope is to remain in the game. This however condemns each species to evolutionary adaption through mutation. This brings in the issue of genetic algorithms and the entire concept of gene as a fundamental response to the Prisoners' Dilemma in molecular terms.

A paradigm-defining example of Prisoners' Dilemma is the 'tragedy of the commons', which Gareth Hardin ([R289](#)) used as the title of his renowned paper on the exploitation of the commons in economics ([p 439](#)). In this form of the paradox, it always pays off exploiters of the commons better to claim the competitive certainty of exploitation than the 'altruists' who cooperate to preserve the common wealth. The end result is multiple jeopardy, the commons is destroyed and every one loses out. Various forms of the tragedy of the commons underlie all of the major forms of human exploitation on the planet, from depletion of non-renewable resources to causing the mass extinction of biodiversity. Tragedies of the Commons have been cited as a potentially inevitable [source of increasing violence](#) due to diminishing world resources (The Rand Journal of Economics, vol 45, p 521).

Puccini's opera Tosca well illustrates how deeply related the Prisoners' Dilemma is to sex and sexual betrayal. Tosca's lover Cavaradosi has been condemned to death by the police chief Scarpia. He offers her to tell the firing squad to use blanks if she will sleep with him. She resolves to pretend to agree to lie with him only to stab him to death as soon he has given the order. He gives a coded order to use live bullets and she stabs him, instead of submitting to his advances, only to find he has also betrayed her and executed her lover regardless. She commits suicide in despair. Double betrayal. Triple jeopardy.

The sexual relationship is from beginning to end a permanent state of Prisoners' Dilemma paradox. The two sexes are reproductively entwined, so neither can escape the other. Even parthenogenesis is only a temporary fix, until evolving circumstances, such as disease, require sexual adaption for survival. For this reason sex has remained an essential feature of higher organisms. Although the interests of the female and male coincide in reproductive fertilization, their overall reproductive strategies and genetic 'drives' are competing in significant ways, both reproductively and genetically.

In describing the dilemma of female chimps mating promiscuously with every male to avert the threat of infanticide from the males, Sarah Hrdy ([R331](#)) notes the cutting truth of William Rice's term "sexually antagonistic coevolution" ([R575](#)), emphasizing the Prisoners' Dilemma of the interaction for each sex. Increasing female choosiness in relation to the lengthening peacocks tail is an example of sexually-antagonistic coevolution, as is the race between an increasingly turgid penis and an increasingly discriminating clitoris.

Mutually antagonistic coevolution: (a) Mallard duck vagina and penis display an evolutionary arms race, with an increasingly convoluted penis which can jolt to erection in 1/3 sec and an increasingly coiled vagina to inhibit forced fertilization from the male (Coghlan A 2009 Female ducks fight back against 'raping' males New Scientist 18 Jun, Brennan P 2009 doi: 10.1098/rspb.2009.2139). (b) Chicken and rooster evolution appears to have been driven by female choosiness, with the roosters penis reduced to a vestigial stump, requiring a 'cloacal kiss' between partners to pass sperm from one to the other. Many of the genes which drive penis growth in ducks appear to be still expressed in chickens except that *bmp4* which causes local cell death is expressed in higher quantities near the tip of the tubercle

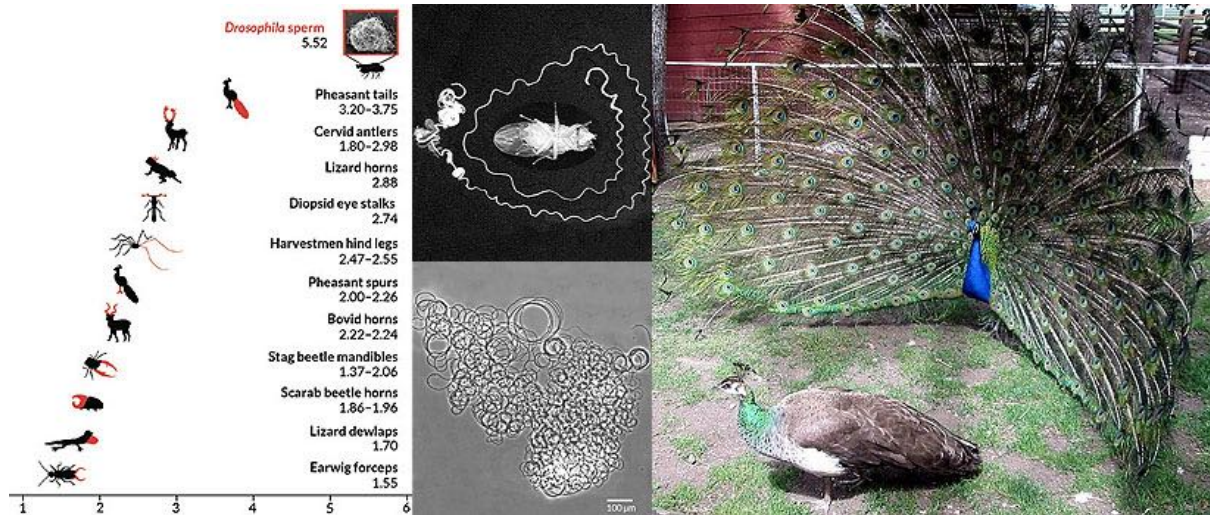
(doi:10.1038/nature.2013.13152). (c) Hermaphroditic barnacle penis is up to eight times the length of the body to reach closer to nearby 'suitors', since they are rooted to the rocks (Evolution doi: 10.1111/j.1558-5646.2009.00668.x). (d) Erect squid penis longer than the entire body (Walker M 2010 Super squid sex organ discovered BBC 7 July). (e) In Bookworm-like Netroglia insects the female has evolved a spiky 'penis' so she can literally latch onto the male and suck the sperm out of him via his vagina-like docking cavity (Marshall M. Gender-bending cave insects found in Brazil New Scientist 17 April 2014). (f) Male pipe fish get 'pregnant' by gathering the eggs from the female in his pouch. Since the male is making the principal parenting investment he has become very choosy and prefers the largest females which have the best chance of surviving offspring vacillating at length over smaller females. It is also the female that initiates courtship: she erects her dorsal fin, darkens the skin around the silvery stripes, and holds her body in an S-shape. Just to make the point, she sticks out her ovipositor, the organ with which she lays eggs. Then both the male and the female swim with their long thin bodies held vertically. If the fussy male is willing, they intertwine their bodies and the female "ejaculates" her eggs into a pouch on his chest (Marshall M. Pregnant males are pro-choice for abortion New Scientist 17 March 2010). (g) Bat bugs and their relatives bed bugs indulge traumatic insemination the males literally stabbing the females in the abdomen with the sperm swimming through the blood system to the ovaries. Female bat bugs have evolved paragenitals - a false vagina on their abdomen with spongy immune tissue as self protection. Males have in turn developed similar structures to protect against homosexual attack. 84% of females in turn have evolved versions of the male false genitals (Hooper R. Bat bugs turn transsexual to avoid stabbing penises New Scientist 19 September 2007).



Darwin noted somewhat chauvinistically: "man has ultimately become superior to woman. It is indeed fortunate that the law of equal transmission of characters to both sexes prevails with mammals. Otherwise it is probable that man would have become as superior in mental endowment to woman as the peacock is in ornamental plumage to the peahen". The fallacy of this position is itself an irony - the attribution of reproductive choice principally to females and runaway sexual selection principally to males. The realities of human sexual evolution, while they do support sperm competition and moderate polygyny speak strongly of a more complex pattern of mutual mate

selection, something Darwin also recognized was possible as Geoffrey Miller has noted. It is this very complexity that we shall claim is at the centre of our cultural emergence.

William Rice's cogent commentary comes from his experiments into the mating habits of flies, where male semen reduces the subsequent fertility of the female at the expense of rearing the current male's progeny, either by plugging her, inserting digestive enzymes, or affecting her hormonally. For this reason a female house fly mates only once, because her partner's poisons are so potent she can never mate again (Jones [R349](#)). In other species of fly, where multiple mating occurs, an arms race sets in between male toxins and female resistance. Consequently these genes are the most rapidly evolving in insects. This process is accentuated when mating is frequent but diminishes when mating occurs only rarely or once in a lifetime. During fruit-fly sex, the proteins in the semen enter the bloodstream of the female and migrate to, among other places, her brain. There they have the effect of reducing the female's sexual appetite and increasing her ovulation rate. The male's seminal fluid redirects her behaviour to that end. After breeding generations of increasingly 'super-macho' male flies while allowing the females' resistance to diminish, Rice found the semen had become toxic to the point of being lethal (Friedman [R227](#) 235, Ridley [R579](#)). Hrdy ([R330](#) 41) comments that this demonstrates the way in which not only female reproductive choice but its curtailment can have profound consequences.



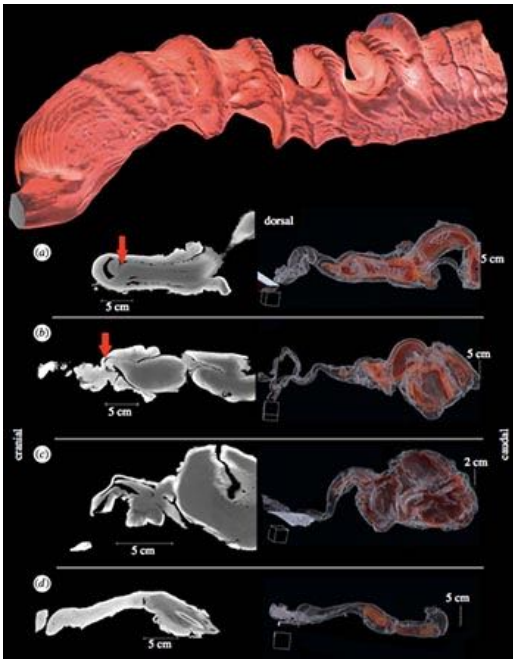
Centre: In the fruit fly *Drosophila bifurca*, males measuring just a few millimeters produce sperm with a tail as long as 5.8-centimeters (doi:10.1038/nature04683). Males with longer sperm deliver fewer sperm, bucking a more-is-better trend, yet, they still manage to transfer a few dozen to a few hundred per mating. And as newly arrived sperm compete to displace those already waiting in a female's storage organ, longer is better. Fewer sperm per mating means females tend to mate more often, intensifying the sperm-vs.-sperm competition. Females that have the longest storage organs, which favor the longest sperm, benefit too: Males producing megasperm, the researchers found, tend to be the ones with good genes likely to produce robust offspring. This extreme of anisogamy is also an extreme of male sexual characteristics (left) which exceeds even that of the peacock (right).

There is an intriguing difference between ZW and XY [sexual chromosome inheritance](#) that explains why male birds are often more flashy than the females (Albert A & Otto S 2005 Sexual Selection Can Resolve Sex-Linked Sexual Antagonism Science 310 119). A sexually antagonistic trait on the X chromosome (males XY, females XX), females evolve to prefer mates carrying alleles beneficial to daughters. In contrast, with a Z-linked trait (males ZZ, females ZW), females more often evolve mating preferences for mates carrying alleles beneficial to sons (that is, flashy displays). With sexual antagonism, chromosomal location should strongly affect the evolution of female preferences. Simply put, an X-linked male trait is never passed on from an attractive father to his sons, whereas his daughters suffer the cost of carrying the display trait. Offspring in XY species therefore do not gain a fitness benefit from females preferring males with a more extreme X-linked display trait. In contrast, both males and females contribute a Z chromosome to sons in ZW species. Thus, females preferring a Z-linked display trait receive the fitness benefit of sexy sons, even though their daughters suffer a fitness cost. This cost is lessened by the fact that daughters inherit only one of their father's Z chromosomes.

A fundamental characteristic of modern mammals - the birth of live young - is another extreme example of this phenomenon. The placenta is controlled by rapidly evolving paternal genes. As noted a double Y induces a placental pregnancy called a hydatidiform mole. David Haig (Ridley [R579](#)) considers the placenta to be a parasitic takeover of the mother's body by paternal genes in the fetus. The placenta tries, against maternal resistance, to control her blood-sugar levels and blood pressure to the benefit of the fetus. By contrast X-inactivation in female embryos is skewed from a random process in cells inside the embryo towards inactivating the paternally-imprinted X in the placenta ([p 346](#)). Boys also impose a greater strain on the mother, causing her to have a longer lapse until her next child, possibly increasing the chances of abnormalities in subsequent pregnancies and reducing the mother's life expectancy by about 6 months. By contrast a girl child slightly increases it. The male determining gene SRY and the female pathway driven by DAX are similarly in a state of sex-determining conflict. One SRY defeats DAX giving our usual male profile but an accidental two DAX in the genome overwhelm SRY resulting in a female ([p 359](#)). Intriguingly, endogenous retroviruses or ERVs, transmitted down the germ line of every mammal, may have also played a starring role in the evolution of mammalian life and its crowning achievement-live birth. ERVs which bloom on the placental tissue, appear to be critical to the emergence of the placental membrane and the mechanisms that protect the fetus from pathogens and the mother's immune system. Without ERVs, humans might still be laying eggs ([p 333](#)).

Coitus in marine mammals requires a degree of congruent co-evolution to provide a good fit between penis and vagina to ensure fertilization while swimming, but, as with ducks, some species have evolved vaginal folds (above) which researchers hypothesize aids the female's capacity to accept or reject a male suitor's sperm, depending on how she feels, in another case of mutually antagonistic co-evolution. (a, b) harbour porpoises and bottlenose dolphins have vaginal folds which can restrict fertilization but short beaked dolphins and harbour seal do not (Orbach D et al. 2017 Genital interactions during simulated copulation among marine mammals. Proc. Royal Soc. B doi:10.1098/rspb.2017.1265).

Ridley ([R579](#)) notes that communication itself becomes an informational pawn in the game: "Rice and Holland come to the disturbing conclusion that the more social and communicative a species is, the more likely it is to suffer from sexually antagonistic genes, because communication between the sexes provides the medium in which sexually antagonistic genes thrive. The most social and communicative species on the planet is humankind. Suddenly it begins to make sense why relations between the human sexes are such a mine field, and why men have such vastly different interpretations of what constitutes sexual harassment from women. Rice now believes that sexual antagonism is at work in all sorts of environments. It leaves its signature as rapidly evolving genes." Consistent with this, Dawkins has pointed out that 'information' serves the 'giver' only if it includes a component of self-serving deceit. This is not however true of genuine indicators of fitness, such as the peacock's tail, which have to be costly to be effective in the sexual race.



We may have genetic conflict to thank for the fact that we have feelings toward other people at all. One might at first think that evolution would endow a species in which the genetic interests of two mates were identical, with a blissful perfection of sexual, romantic, and companionate love, but, Donald Symons argues the relation between the mates would then evolve to be like the relation among the cells of a single body, whose genetic interests are also identical. There would be no falling in love, because there would be no alternative mates to choose among, and falling in love would be a huge waste. You would literally love your mate as yourself, but - you don't really love yourself, you are yourself. The same is true for our emotions toward family and friends: the richness and intensity of the feelings in our minds are proof of the preciousness and fragility of those bonds in real life. In short, without the possibility of suffering, what we would have is not harmonious bliss, but little or no emotional consciousness (Pinker [R544](#) 268).

The phenomenon extends to conflicts of reproductive interest between sisters and between mothers and daughters, each of which share half their genes termed the 'Julie' effect for the illustration of the familial conflict in Shakespeare's play. Mothers and sisters have an interest in a female selecting a partner who will form a reliable long-term bond and help bring up any children, but the femme fatale in the piece may prefer to seek a 'hunk' she feels has the best genes possible for her children (Biegler R, Kennair L 2016 Sisterly love: Within-generation differences in ideal partner for sister and self *Evolutionary Behavioral Sciences* 10/1 29 doi:10.1037/ebs000060).

This kind of conflict between complexes of genes does not just apply to sex but to all forms of deceit and detection of cheating the Prisoners' Dilemma game implies. A gene that increases the telling of lies might thrive by making its possessors successful con-artists. But then any set of genes that improves the detecting of lies would thrive to the extent that it enabled its possessors to avoid being taken in. The two would evolve antagonistically, each gene encouraging the other, even though it would be quite possible for the same person to possess both. Rice and Holland call this 'interlocus contest evolution' ([R576](#)). If the conflicting genes are on different chromosomes or not closely linked they can both evolve. The signature of such genes is rapid evolution and in comparing human and mouse genomes, such genes are notably found in immunity and sex determination.

Ridley notes: "Exactly such a competitive process probably did indeed drive the growth of human intelligence over the past three million years. Most evolutionists believe in the Machiavellian theory that bigger brains were needed in an arms race between manipulation and resistance to manipulation. In Rice and Holland's words: "The phenomena we refer to as intelligence may be a by-product of intergenomic conflict between genes mediating offense and defense in the context of language".

However in spite of competition, sexual destinies are inextricably entangled. Two male imprinted genes in mice, *Mest* and *Peg-3* are both involved in good mothering in daughters ([p 346](#)). *Peg-3* affects neurons that react to oxytocin, inducing lactation and mediating maternal behavior. Mice with defective *Peg* were slower to build a nest and gather stray pups, losing 9/10ths rather than the normal 2/10ths of their first litters. It is difficult to interpret good mothering in daughters as selectively benefiting male genes.

Sexual selection by the opposite sex, particularly the female is pivotal in evolutionary viability. We need sex to survive, while sacrificing half our genetic endowment to another and suffering the ultimate penalty - mortality - in seeking the variety sex produces. We can ultimately succeed at playing this Prisoners' Dilemma game only through producing viable offspring and in this the investments and strategies of men and women are clearly as different as our haploid manifestation as sperm and ovum. A man's investment can be as small as a few drops of semen, but a woman's is as overwhelming as pregnancy, as needful as lactation and as enduring as childhood. Men marry and sow wild oats, while women seek a resourceful monogamous partner and have secretive affairs. Neither is strictly faithful overall, nor could they be and fully protect their own genetic heritage. There is thus no escape from the paradox of sexual betrayal either, just temporary respite in fidelity and love's sweet embrace. The downfall of the Prisoners' Dilemma game in marital discord, jealousy, divorce, violence and desertion is a frequent cause of murder and suicide.

The sexually paradoxical nature of the mind-body relationship brings with it the implicit risk of 'double jeopardy'. The root of the existential dilemma is to experience consciousness through a physical body suffering inevitable decay and mortality. Yet the physical world and with it our body and sensory organs are our gateway to conscious experience ([p 364](#)). In the breakdown of this paradox into conflict comes the notion of light and dark forces and the mortal combat of god and satan. This has led religious thinkers, from the first gnostics, through Augustine, all the way to modern Western culture to perceive conscious existence as a spiritual, godlike self or soul trapped in lustful, fallible, flesh ([p 242](#)). A flesh that both condemns us to mortality through its frailty and robs us of our freedom through sexual desire. The penis, which is the source of future life for mankind, then becomes an agent of the devil's work. In turn, lubricious sexual intercourse with demons became a central fantasy in the witch hunts. This degenerate view of sex as evil exploitative lust still pervades Western society's views. It continues to surface in diverse forms of perversion, pornography and prostitution.

Given the universal nature of the Prisoners' Dilemma, it is of little surprise to discover that humans are innately attuned to distinguishing cheating, deceit and betrayal. In many experiments Leda Cosmides and John Tooby have shown that we can far more easily solve a logical puzzle if it is presented as a question of detecting betrayal. To detect proof of unmitigated altruism is far more counter-intuitive. Matt Ridley ([R578](#)) illustrates this in the following story. Chief Kiku, who demands his followers are tattooed, tells four hungry villagers "If you get a tattoo on your face you will get a cassava root in the morning". A visiting economist wonders "Will he keep his word?", while an anthropologist, thinking he is bluffing says "Surely he would not refuse food to a man just because he didn't get a tattoo!" Kiku's reply is "Tell me this or I will tattoo your faces myself. The first got a tattoo, the second had nothing to eat, the third did not get a tattoo and the fourth I gave a large cassava root. Now tell me which of them you must ask of to answer your question." This is an example of the "Wason test", which is counter-intuitive as a logical puzzle unless it is presented as a test of breaking a social contract. Three quarters of Stanford students get the answer to economist's puzzle right, but most flunk the anthropologist's test.

The paradox underlying the Prisoners' Dilemma has a kind of physical realization in the form of a 'spin glass' - a material in which a set of embedded spins, acting in the same way as molecular domains in a magnet, are coupled by a random, normally distributed linkage. Unlike a ferromagnet, where all the spins line up in one dominant, polarized minimum energy state, a spin glass has a large number of potential energy minima in which cooperation between some spins results in frustration between others. The medium partitions into zones of cooperation punctuated by interfaces of defection. This displays a deep relationship between symmetry-breaking, complexity, instability, and the Prisoners' Dilemma.

The intractable nature of the Prisoners' Dilemma in the 1960s made it a cause celebre in the burgeoning area of game theory in economics. At first theorists believed there was no escape from the implications that the game equilibrium favoured selfishness because the relative payoffs of the strategies of each meant that defection remained a strategic equilibrium for both players. Human generosity thus seemed an aberrant and foolish deviation. But then a new generation of game tournaments set a stage for a more realistic appreciation for a way out. In the first of these, it was noted that real humans playing repeated Prisoners' Dilemma games are much nicer to one another than the single game payoffs would suggest. Knowing the rules of the game they generally cooperated till the end of the tournament when they would stage final defections to secure a terminal advantage.

In the 1970s there came a convergence with evolutionary biology in the form of John Maynard-Smith's concept of an 'evolutionarily stable strategy' - a product of natural selection which would arrive at a game theoretic strategic equilibrium and hence be sustainable in evolutionary terms because no strategy of an opponent could lead to break down of the selected trait. Towards the end of the decade the rise of computers made strategic tournaments possible and the political scientist Robert Axelrod, exploring the logic of cooperation, catalyzed the first strategic answer to the Prisoners' Dilemma. He invited all comers to submit computer programs to a repeated tournament of 200 games. The astounding result was that a simple strategy in the form of 'tit-for-tat', submitted by Anatol Rapoport, another political scientist, with an interest in problems of nuclear confrontation, proved the decisive winner. We all know tit-for-tat in the form of the Biblical invocation of 'an eye for an eye and a tooth for a tooth'. We also know tit-for-tat is forgiving in cooperation, doesn't seek to defect, but punishes defectors by retaliation. However it does have one serious flaw - intractable bouts of revenge retaliation. Following on from this discovery emerged a whole series of challenges in a development of the game in which strategies could compete and proliferate according to their success in the manner of an artificial life experiment. While 'tit-for-tat' was singularly effective at driving out the hawks of defection, even 'nicer' strategies which broke the impasse of retaliation surfaced. Upon his discovery, Axelrod contacted William Hamilton and a further expansion of understanding occurred. Evolutionary genetics was at this time in full retreat from the notion of group and species selection, with the realization that selection was predominantly on an individual, not a species basis, and that it was genes and certain genetic traits which were being selected for, not the welfare of the organism or the species as a whole. Richard Dawkins' notion of 'the selfish gene' ([R151](#)), although a clichéd oversimplification, carries a root truth - that it is genes which are being selected, even if the vast majority do so under the constraints of co-residing in a given organism, which must itself survive under social, and environmental, conditions, including running the gauntlets of sexual enticement, and good parenting, shared by a species.

This pendulum has now swung back from the brink of extreme genetic selfishness, in a recognition that group social selection can also play an important role in shaping individual traits. If battery hens are selected for individual laying capacity they tend to compete, become stressed, and not to lay well in cages. However selecting for good laying cages results in socially more compatible chickens which lay better over all. Likewise lionesses cooperate to protect a territory in a manner in which the leaders incur a cost which freeloaders can exploit. The natural explanation is that between group selection is operating in an evolutionarily stable manner. More generally, forms of social selection, from ostracism to violence, do have selective evolutionary effect and human social morality has been cited as a key manifestation of group selection reinforced by traits of altruistic punishment.

Nevertheless genetic selection is the key to the whole mechanism of mutation and selective advantage, so biologists have ever since sought with ingenuity to elucidate ways in which genetic selection could give rise to the altruism we find in human interactions.

A key step was Hamilton's discovery of 'kin selection' - the idea that organisms will evolve not just to preserve and reproduce their own genes but will also invest in the protection of the common genes they share with their relatives and offspring. This relation is neatly expressed in the inequality $C < Br$, where C is the cost, B the fitness benefits and r the relatedness of the benefited relative. We thus expect raw genetic considerations to favour strategies where an organism will invest around half as much effort in protecting immediate offspring and siblings as in one's own livelihood. A host of examples confirm these principles in nature, from the honey bee to chimpanzees. As Hamilton ([R285](#)) put it: "a gene causing altruistic behavior towards brothers or sisters will be selected only if the behavior and the circumstances are generally such that the gain is more than twice the loss ... to put the matter more vividly, an animal acting on principle would sacrifice its life if it could thereby save more than two brothers, but not for less" (Hrady [R330](#) 64).

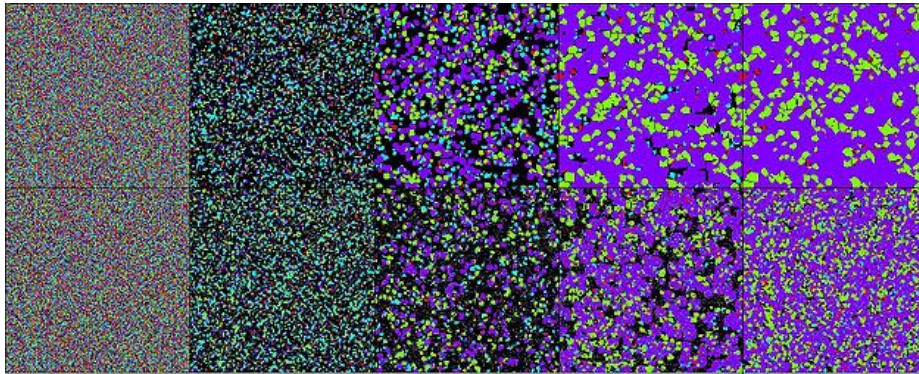
Robert Trivers ([R702](#)) then introduced the wider arena of reciprocal altruism. De Waal ([R163](#) 24), in exploring friendship and mutual aid, notes the outstanding characteristics of reciprocation: "Rather than simplifying the relations between genes and behavior, [Trivers' article] pays full attention to the intermediate levels such as emotions and psychological processes. It also distinguishes different types of cooperation based on what each participant puts into and gets out of it. For example cooperation for immediate reward does not qualify as reciprocal altruism. ... Because of the instant payoff, this kind of cooperation is widespread [and could be viewed as mutual self-interest]. Reciprocal altruism on the other hand costs something before it delivers benefits. It has the following three characteristics: (a) the exchanged acts, while beneficial to the recipient are costly to the performer, (b) there is a time lag between giving and receiving, (c) giving is contingent on receiving."

Hamilton was struck by the correspondence of Axelrod's results with Trivers' idea of reciprocal selection. This would require each to punish cheating by reciprocating only with individuals who had fulfilled their part of the reciprocation bargain, and would thus require careful social discrimination and recognition. During the 1980s, field evidence of such reciprocation began to emerge. Vampire bats, who roost together in hollow trees, can generally get more than a meal for themselves if they do score a hapless victim in the night. They can only survive a day or two without blood and roost together so they have evolved an elaborate system of reciprocation to feed their neighbours, who are not necessarily genetically related. They have evolved to vomit excess blood to their co-residents on a reciprocal basis. These 'neighbours' have relatively stable roosting places although they are not necessarily related individuals. Reciprocation requires careful score keeping, rewarding cooperators and punishing defectors. To do this it needs stable long-term relationships without frequent mixing of individuals or the tally cannot be kept. Notably Vampire bats have the largest brains of bats, consistent with the relative complexity of such social discrimination. They also groom one another closely in the stomach region, which could be a giveaway for cheating. African vervet monkeys are similarly reciprocal in getting aid in fights. Cleaner fish on reefs are in a mutually reciprocal relationship with those they clean of parasites, who never seem to take advantage and eat the cleaners. Although this doesn't involve strict reciprocation, it clearly has reciprocal advantages.

However reciprocation is actually quite rare in the natural world, apart from a handful of additional examples from dolphins, monkeys and apes. Miller (2000 *The Mating Mind* Random House 301) notes "Evolution appears to avoid reciprocity whenever possible". For example lionesses investigating a potential threat do not enforce reciprocal favours. Some lead the counter-threat and though they may look balefully at their laggardly sisters who slink behind, do not punish them for their cowardice even when it is repeated, or fails when most needed. In many situations, the payoffs may be too indifferent, the populations too mobile and the score keeping too cumbersome to maintain reciprocity. In addition the tit-for-tat nature of reciprocity, as we have noted, leads to intractable cycles of revenge punishment. De Waal notes "this process is evidently a lot more complicated than simultaneous cooperation. There is for example the problem of the first helpful act - a gamble since every partner does not follow the rules. ... Reciprocal altruism does not work for individuals who rarely meet or who have trouble keeping track of who has done what for whom: It requires good memories and stable relationships, such as are found in primates. De Waal then explores the evolution of what we might call 'morality' in "Good Natured" in

the variety of mutual 'friendship' behavior in apes based on the similarity principle - contemporary individuals (particularly females) sharing mutual interests in a similar life situation and social ranking.

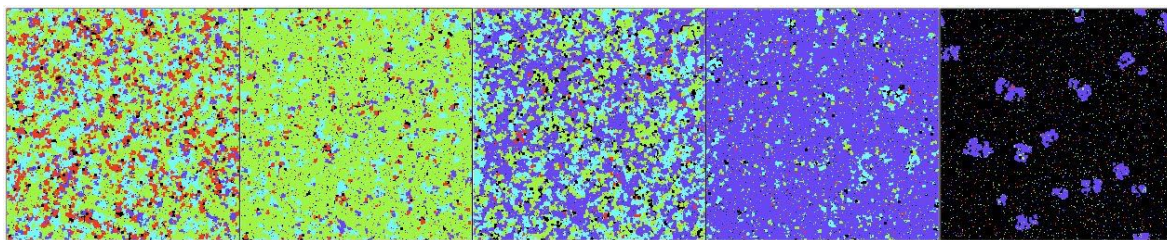
Game theorists such as Martin Nowak were quick to pick up on tit-for-tat's weaknesses and an artificial life contest ensued between different strategies under a variety of conditions. Probabilistic strategies now came into play which could vary their response a proportion of the time. In addition, learning from mistakes and successes were now allowed to take place. Out of this milieu came new strategic variants which could engulf 'tit-for-tat', such as 'generous', which forgives single defections about a third of the time but rejects them sufficiently to repel 'always defect'. Thus 'turning the other cheek' becomes part of astute Machiavellian behaviour. Among 'generous' players, 'always cooperate' can now thrive, but this again becomes susceptible to 'always defect', resulting in a complex system with no fully effective strategy, leaving a solution to the Prisoners' Dilemma again beyond reach. This cyclic ambiguity caused consternation until 'simpleton', a game originally invented by Rapoport, with a 'win-stay; lose-shift' strategy, called 'simpleton' or 'Pavlov', once discarded because it was a 'sucker' to 'always defect' now proved to be able to trounce 'tit-for-tat' once 'always defect' was eliminated. Essentially tit-for-tat is an extrovert, who does what the opponent did last, and simpleton is an introvert who switches if they get punished. There is evidence for such behaviour in nature. In the alternate leading and following of stickleback scouting parties testing the reaction of predatory pike, which superficially looks like tit-for-tat reciprocation, the scout fish will alternate between defection and cooperation, when faced with persistent defection.



Various forms of the Prisoners' Dilemma game can be played as cellular automata, (p 510), which display complex punctuated equilibria between defectors (black), cooperators (red), tit-for-tatters (purple), 'simpletons' using win-stay lose-shift (green) and random strategies (cyan) (ex. Flake R213). Players on the grid play in pairs for several rounds and then each cell adopts the most successful strategy in its neighbourhood. The top row shows the 1st, 2nd, 5th, 10th and 50th tournaments. An initial wave of defection is taken over by reactive strategies. The system stratifies in a state dominated by tit-for-tat and 'simpleton' with a few islands of cooperators and the odd defector. The bottom row includes 10% mutation and noise and is in dynamic flux. Such interactions can help explain how reciprocal altruism can emerge without complex memory, if nearest neighbours remain stable, for example because of fixed territories in a given habitat (Nowak et. al. R506, R510).

Download [CA2D for Mac](#) produced by the author to see the prisoners' dilemma in action!

By introducing alternating moves, as in reciprocation, Marcus Frean (R786) established 'firm-but-fair' as a winning strategy. Like 'simpleton', this cooperates with cooperators, returns to cooperating after a mutual defection and punishes a sucker by further defection, but it also continues to cooperate after being the sucker in the previous round. This accords with the common sense of giving a good impression if you want others to act in your example. Even lowly guppies have complex scouting strategies, preferring reliable colleagues in scouting parties, ostracizing laggards, and being more tolerant of defections in consistent cooperators. Grim (R270) has noted that the sequence of such strategies results in the ultimate winner of the Prisoners' Dilemma becoming an undecidable proposition (p 491).



A prisoners' dilemma game set generated to illustrate one can afford to be kind and turn the other cheek out of tit-for-tat a quarter of the time and survive under a spread of payoffs (centre standard game) Red is always cooperate, green 'simpleton' or Pavlov i.e. stay unless the other guy punished you last time in which case swap, purple 'tit-for-tat' i.e. do what the other guy did last, cyan 'firm-but-fair' (tit-for-tat with 25% turning the other cheek to encourage cooperation), and black outright defection. Depending on the payoffs for CC (wine and roses), CD (beaten to submission) DC (ultimate victory) and DD (double jeopardy), under a regime of noise and some mutation, we get different populations. The images go 3 0 4 0, 3 0 4 1, 3 0 5 1 (the standard payoffs), 3 0 6 1 and 3 0 6 2 each at the 25th 5-game tournament round. Firm-but-fair is usually defined in an alternating, rather than simultaneous play-off, game. Tit-for-tat will eventually dominate in the right hand-game with defection coming number 2.

- [Bacterial cheaters do not prosper](#) Mar 12

Prisoners' dilemma games can readily be played as cellular automata (p 510), leading to complex and punctuated equilibria. Nowak et. al. (R506) have run such competitions with genetic algorithms for mutation and natural selection of strategies for millions of generations. Outcomes even for fixed automata may become formally undecidable (p 491) because they can only be modeled by a computational simulation.

Recently new classes of probabilistic strategy have been found with completely new features, in particular setting the payoff of opponents to their strategic disadvantage, however, intriguingly, these are evolutionarily unstable. In 2012 Press & Dyson (PNAS 109 10409–13) discovered zero-determinant (ZD) strategies, a new class of probabilistic and conditional strategies that are able to unilaterally set the expected payoff of an opponent in iterated plays of the Prisoner's Dilemma irrespective of the opponent's strategy (coercive strategies), or else to set the ratio between the player's and their opponent's expected payoff (extortionate strategies). Like tit-

for-tat they are 'Memory-one' strategies that make their move depending on theirs as well as their opponent's last move as in 'tit-for-tat', but they are stochastic, defined by probabilities to engage in one move or the other depending on the four previous states CC, DC, CD and DD. However a 2013 study in Nature Communications (Adami & Hintze DOI:10.1038/ncomms3193) has shown that ZD strategies are at most weakly dominant, are not evolutionarily stable, and will instead evolve into less coercive strategies. ZD strategies with an informational advantage over other players that allows them to recognize each other can be evolutionarily stable (and able to exploit other players), however, such an advantage is again bound to be short-lived as opposing strategies evolve to counteract the recognition.

Of course, in a real world, defection is the 'criminal' element that can never be fully eliminated once and for all. Mutation and selection are always throwing up such strategies in evolution in a manner which can never be eliminated. Parasites and disease are an inextricable part of the tooth and claw of the evolutionary endowment. Furthermore the realities of population movement allowing cheaters to drift to new victims and the varying payoffs each life situation provoke make it difficult or impossible for any single strategy to prevail. The ineradicability of defecting strategies is as signal of human society as it is of the evolutionary paradigm. Most people will learn to take advantage of flagrant opportunities foolishly presented. While criminality can be contained through a mix of penalties and good social policy, only in a naive world would it be expected to disappear entirely. Moreover in real situations, rare strategies often invoke equally high payoffs which guarantee no escape. In a promiscuous society of deceiving whores, a single faithful wife can command a king's ransom and will become at an inestimable advantage reproductively. By the same token in a monotonously monogamous society, a single scarlet woman can command the affections of every man to the highest station. Evolutionary geneticists comment that for this reason, pure genetic monogamy is not an evolutionarily stable strategy, always liable to invasion by 'fast' females and 'philandering' males. Thus the real games of life often tend to an equilibrium between cooperating and defecting strategies, making the Prisoners' Dilemma a permanent feature of natural and social survival. The [Red Queen](#) evolutionary arms race between parasites and prey is likewise a perpetuating prisoners dilemma, giving high enough payoffs to maintain sexuality, despite the halving of each parent's genetic endowment.

In mammalian evolution we also have the emergence of emotions and the effects of emotional reactions on the whole question of genetic determinism, selfishness and altruism. Rather than following instinctual or imprinted genetic strategies, mammalian brains have evolved a meta-strategy providing an emotional spectrum of reactions, from flight to fight, from love and close intimate bonding to hate, and the violence of hunting play, within which the direct simplicity of kin and reciprocal altruism become a complex emotional dynamic only partly genetically based. Instances abound, not just of seemingly irrational human generosity, which cannot be interpreted to benefit the individual directly or indirectly, but irrationally altruistic emotional reactions of mammals. A hippopotamus may repeatedly rescue a wounded gazelle from an alligator, or a lioness raise a young ungulate. We need to explain how evolution could have arrived at such an indirect emotional process as a universal win-win, given the raw constraints of natural genetic selection.

Even in human society, where we have large brains, and abundant capacity to detect cheating and punish defection, neither kin, nor reciprocal altruism, fully explain our behaviour. In differing circumstances, we may retaliate like the vampire, or endure laggards like the lioness. We also have an innate capacity to respond to the plight of others, who may be unrelated, or not even of the same species, with acts of compassion, for which no reward can be gained, or expected. Although human societies have imposed Draconian punishments for criminal defection and sexual betrayal, our life relationships are motivated by the unbounded quest for love and belonging as by astute judgement of character.

A good indication of the degree to which human societies respond to the general issue of egalitarian cooperation comes from the ultimatum bargaining game, where a player is offered a financial reward which they can keep only if they give sufficient to a second player for them to accept the bargain. The second player thus receives either the offered portion, or nothing if they refuse and one might expect them to accept only a small portion. However they also know the first player will receive nothing either if they do so they can quickly punish for perceived 'cheating' on a fair bargain. Even when players play anonymously, so do not suffer a retaliatory round, the experienced players in many cultures from Los Angeles (48%) to Yogyakarta and Tokyo (45%) end up offering only a little less than half - with the most frequent amount being a half share, reflecting the keen eye humans in many cultures have for not accepting a second-class treatment. The people of Jerusalem were a little more stingy at 36% and the Machiguenga of the upper Amazon were a notable exception, offering only a meagre 24% of the booty (Henrich [R307](#)). Chimps have been found to also play the ultimatum game in a fair play manner suggesting this is evolutionarily ancient.

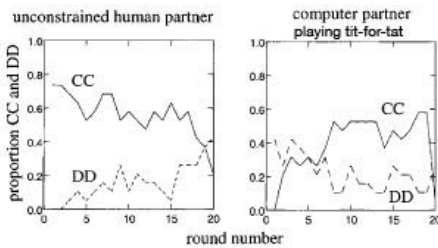
In the Dictator game, the proposer simply divides the sum between the two players and there is nothing the respondent can do about it. With no fear of reprisal, the proposer makes a far stingier offer. The offer still tends to be more generous than it has to be, because the proposer worries about getting a reputation for stinginess that could come back to bite him in the long run. We know this because of the outcome of the Double-Blind Dictator game, where proposals from many players are sealed and neither the respondent nor the experimenter knows who offered how much. In this variant, generosity plummets; a majority of the proposers keep everything for themselves (Pinker [R544](#) 256).

Another game which aptly demonstrates tendency to a winning defection by a dominant group and has major implications for first past the post election, majority democracy and the consequent 'tyranny of the majority' is illustrated as follows. Seven people are given anonymous numbers and connected by computer network. If they are asked to reach consensual agreement to gain a reward, they will negotiate to do so. However, if they are told simply to find a majority to get the reward, they will quickly engage the minimum number of four at random or by pattern, e.g. 1,2,3 and 4 or 1,3,5, and 7, and go straight for the booty, cutting the other three out of the bargain. Majority 'defection' against the whole becomes the rule.

In the 'public good' game, everyone makes a voluntary contribution to a common pot of money, the experimenter doubles it, and the pot is divided evenly among the participants regardless of what they contributed. The optimal strategy for each player acting individually is to be a free rider and contribute nothing, hoping others will contribute something and he can get a share of their contribution. Of course, if every player thinks that way, the pot stays empty and no one earns a dime. The optimum for the group is for all the players to contribute everything they have so they can all double their money. When the game is played repeatedly, however, everyone tries to become a free rider, and the pot dwindles to a self-defeating zero. On the other hand, if people are allowed both to contribute to the pot and to levy fines on those who don't contribute, conscience doth make cowards of them all, and almost everyone contributes to the common and profitable good ([R544](#) 257).

Left: Real play in the prisoners dilemma game between pairs of women involves high levels of mutual cooperation until the last few rounds. Right: Play against a computer engaging tit-for-tat results in reciprocal defection ([R583](#)).

People do more for their fellows than return favors and punish cheaters. They often perform generous acts without the slightest hope for pay back, ranging from leaving a tip in a restaurant they will never visit again to throwing themselves on a live grenade to save their brothers in arms. Trivers, and economists Robert Frank and Jack Hirshleifer, have pointed out that pure magnanimity can evolve in an environment of people seeking to discriminate fair-weather friends from loyal allies. Signs of heartfelt loyalty and generosity serve as



guarantors of one's promises, reducing a partner's worry that you will default on them. The best way to convince others that you are trustworthy and generous is to be trustworthy and generous. Indeed many players of the prisoners dilemma game choose to cooperate consistently until the last few rounds and altruistic punishing of defectors even at high cost to the perpetrator is another paradoxical sign of 'moral' defection for the common good.

Simple virtue cannot be the dominant mode of human interaction or we could dispense with the deliberate financial and legal processes designed to keep exchanges fair and base our economy on the honor system. At the other extreme, people also commit acts of outright treachery and deceitful or criminal exploitation. Machiavellian traits are a central part of

human nature, with most people displaying mixtures of, pure generosity, reciprocity and expedience ([R544](#) 259). Brain experiments ([p 377](#)) have verified that the common emotional basis of both cooperation and altruistic punishment stems from anticipation of social satisfaction associated with pleasure - hence the term 'revenge is sweet'.

We thus need to look more deeply for sources for the natural goodness we associate with social altruism, emotional bonding and human agreeableness and love. It is here that Geoffrey Miller's ideas of sexual selection ([p 53](#)) come into their own. Miller notes that all forms of social selection are weak and indirect by comparison with the inescapable powerful positive feedback provided by sexual selection. Every organism has to both survive and reproduce to run the evolutionary gauntlet. To reproduce, we must pass the test of mating selection by the opposite sex, a positive feedback process with capacity for runaway and complexity. Furthermore it is in sexual selection that detecting cheating comes to the knife edge of betrayal, requiring genuine indicators of fitness such as the peacock's tail, the male guppy's orange stripes, and with it, human generosity in love. In Miller's terms the complexity of human society is a product of such fitness indicators, elaborated in response to runaway discerning partner choice, and along with it our innate capacity to detect cheating, while retaining a generosity of heart necessary to entice the other sex into choosing us as worthy mates. In conceiving the complexity of human society and its teeming Prisoners' Dilemmas of social coexistence and competition, sexual paradox thus remains central as the gateway through which all our intellectual and cultural pretensions go down the plug hole to the next generation. It is also our heart centre, our *raison d'être* motivating our passion and our jealousy in a way which all the other panoply of social interactions from hard nosed business to internecine strife serve as a resourceful backdrop. We thus need to strike a creative balance between the dictates of reciprocity and its manifestations in social game theory and sexual selection as a generator of cultural complexity.

The Prisoners' Dilemma does not have to lead to dissonance and a war of attrition. In its fully contradictory form, the paradox it contains leads to sexual interdependence and climax diversity. The fulfillment of sexual paradox is constructive engagement with the opposite sex in choices which abet successful child rearing, trading off the nemesis of deceit and betrayal with the sexual freedom of choice each gender must needs retain to fulfill their own reproductive design. The solution to the existential Prisoners' Dilemma of conscious existence is likewise constructive engagement with the living universe, through realizing love in the passage of the generations, assuming personal responsibility for ones willed actions and their cumulative affect on the future world around us. This is essentially the sustainable reproductive solution - evolutionary sustainability. But it is also the psychic resolution in mature interdependence, rather succumbing to mutual defection in the face of the win-lose strategies of submission and dominion, with their consequent tragedy of planetary destruction and the loss of future quality of life for the generations to come.

The success of reality TV shows such as "Survivor" depend on human interest in Machiavellian strategies in a Prisoners' Dilemma trial in which one person from a group wins a million dollars in a succession of eliminations in contests and tribal councils in which coalitions and betrayals are climaxed by a final vote of the eliminated members for the victor.

Many of the crises and tragedies of human 'civilization' arise from the loss of sexual paradox through prisoners dilemma betrayal by one party or another, leading to a degenerate process of domination, exploitation and atrophy. Rather than coming to the conclusion that humanity is a sick or dangerous species, which through its implicit violence poses a threat to the future of the living planet, our answer here to these maladies will be to restore the state of sexual paradox and with it our evolutionary and cultural sustainability as a species.

'Don't get even, get mad': Why Emotions Matter

Studies of brain function attest to emotional responses being central to how humans respond to issues of fidelity, and deceit, trust, cooperation altruistic punishment ([p 378](#)) and revenge ([p 391](#)).

Attempts to make game theory applicable to real life date back to the 1950s, when mathematicians used it to advise the US Air Force on Cold War strategy. Even then, it was obvious that most real-life problems aren't remotely like zero sum games where what is good for one is bad for the other and in which game theory recommends choosing the highest scoring tactic in the worst situation. What is bad for one 'player' can often be equally bad for the other, as the Prisoners' Dilemma shows. A classic is the game of Chicken, immortalized in James Dean's 'Rebel Without a Cause'.

As with zero-sum games, there's a rule for finding optimal strategies for these more complex games, which won RAND mathematician John Nash a share of the 1994 Nobel Prize for Economics. Nash's theorem says that it is possible for a player to choose a strategy that is best for him or her when all the other players are also following their best strategies. In this 'equilibrium', no player can improve his or her prospects by choosing an alternative strategy. But there is no single state of equilibrium for a game like Chicken. There are two: you can decide to swerve, while the other person plans to keep driving, or vice versa. In either case, neither you nor your opponent can improve your score by unilaterally changing your mind, reflecting the cusp catastrophe's two states ([p 14](#)).

Enter the role of emotions. Only truly irrational players can credibly threaten to drive on no matter what - and so a rational strategy is to be completely irrational. Such 'paradoxes of rationality' dogged game theorists through the 1970s and 1980s. A huge effort was made to find rules for selecting the most 'rational' strategy in every game; none really worked. Nigel Howard, a veteran game theorist who had advised the US government in the Strategic Arms Limitation Talks during the 1960s was well used to applying game theory in real-life situations - and well aware of its limitations and called a meeting of game theorists at Sheffield University in 1991 in which 'drama theory' or 'soft game theory' was born ([R450](#)). He points out that the effects of rationality can be dire, recounting the following story. Two economists are taking a taxi to their hotel in Jerusalem. Worried that they are going to be overcharged, they decide not to haggle about the price until they reach the hotel. But the driver is so outraged at their conduct that he locks the taxi doors, drives them back to where they started, and dumps them on the street. "What we were really dealing with here weren't just games," recalls Howard. "They're dramas, where the beliefs and values of the characters evolve as the plot unfolds." At its heart is the idea that games are not static, one-shot deals decided by rationality, but dynamic situations that can be utterly transformed by the emotions of the players.

During the 1960s, Howard himself had developed 'metagame theory', which focused on the role of paradoxes in determining the outcomes of games. In the game of Chicken, for example, it seems pretty rational for Jimbo to want to win. Yet to do this, he must

convince Buzz that he will not swerve, no matter how much Buzz insists he won't either. But coming from a rational person, Jimbo's threat is hardly credible: no sane person would declare a determination to follow hell-bent Buzz clear off the edge of the cliff. There's a way out of this 'credibility paradox', however: Jimbo should stop acting rationally, and instead behave as if he is crazy before he goes anywhere near his car. Suddenly, his threat to keep on driving becomes all too credible. Irrational behaviour thus sometimes pays, although it seems to be more to impress male mates and become a popular hero than to directly impress the girls ([p 55](#)). Howard has showed that the idea of credibility paradoxes gives a firm mathematical basis for drama theory ([R328](#)). "The basic idea is that paradoxes have an emotional effect on the characters and the reason these emotions emerge - like anger and fear, or affection and goodwill - is that they have a drama-theoretic role. They shake the characters out of old ways of thinking, allowing them to see a new way forward."

Chicken involves an 'inducement paradox', in which Jimbo must use an irrational threat to induce Buzz to swerve. Others, including the Prisoner's Dilemma, involve a 'cooperation paradox'. For each prisoner as an individual, Nash's theorem gives a unique, rational solution: accept the police offer, and start talking. But for the pair as a team, both spending a month in prison is preferable to one being locked away for years. But the only way of achieving this is for both prisoners to put their trust in each other and stay silent. This creates a cooperation paradox: each must convince the other that they will act as a team despite the fact that each could do better for themselves by defecting. For long-standing partners in crime emotional bonds will come to the fore when they face the cooperation paradox. But if one of the prisoners has always been an unwilling accomplice, the cooperation paradox will trigger anger and distrust and he'll act to save his own skin.



The Red Queen on the Origin of Sex

In "The Red Queen" (Ridley [R577](#)) explains the origin of sex ([p 334](#)) in a way which makes it effective, even in a single generation, despite losing half the genes transferred to the next, an acid test for the process having evolutionary stability at the outset:

"Sex is not about reproduction, gender is not about males and females, courtship is not about persuasion, fashion is not about beauty and love is not about affection. It is about getting your genes into the next generation, and trumping the Terrible Three: predators, parasites, and the neighbors. Of that trio, parasites rank as the greatest foe."

The idea is that sexuality evolved from an immediate potent advantage in the first generation that results from confounding parasites and predators because of genomic diversity that results from sexual recombination ([p 329](#)). Parasites and hosts are locked in a genetic arms race in which sexuality provides a potent advantage in generating variety, making it difficult for a parasite to adapt to varying individual hosts. It gives the clearest and most powerful explanation for the widespread occurrence of sex in higher organisms. There has to be at least a twofold advantage to make up for transmitting only fifty percent of our genes per generation sexually rather than the hundred percent transmission in parthenogenesis. It answers the bootstrap question in a way which doesn't make sense otherwise. Although we now know that sexual recombination is a powerful source of variety, enabling complex organisms to evolve, this goes no way to explaining how the process could get going in the first place. It's really no use trying to explain this in terms of an evolutionary advantage of greater adaptability if this only emerges very gradually in the long-term over a large number of generations. We need a powerful immediate effect in the first generation, otherwise sexual game theory will say we still have a better chance of survival to invest all our genes in parthenogenesis than only half in a sexual exploit that would take up to a hundred thousand years to come to fruition. We would all die waiting, swamped by our parthenogenetic predecessors.

The answer to this is that sex provides an immediate answer to the epidemic cataclysm awaiting a parthenogenetic organism when parasites or diseases adapt to a single genotype. The Red Queen is thus the 'scarlet woman' in sexual evolution. A similar one-generation advantage will accrue if an organism is subjected to any form of stress which compromises survival of daughter offspring of the current clone ([p 336](#)).

A beautiful experimental confirmation of this process has been achieved in 2011 by genetically engineering two strains of the generic roundworm *Caenorhabditis elegans*, one of which is obligately parthenogenic and the other obligately sexual, and then exposing them for 20 generations to the invasive bacterium *Serratia marcescens*. While the sexual strain well-survived the red-queen race of mutual sexual adaption between host and prey, evolutionary adaption of the bacteria to overwhelm the fixed genomic resistance of the parthenogenetic worms became eventually fatal, even though the original strain of bacteria was not lethal to the parthenogenetic worms ([Worms' sex life yields advantage over parasites](#) BBC July 2011).

Small mouthed salamanders (*Ambystoma texanum*) will risk death and dehydration to travel almost 9 km on average and as far as 14 to find a mate, but all-female populations of a closely related group of salamanders that reproduce by cloning can't go nearly as far. Unisexual salamanders could only go a quarter of the treadmill distance that the small-mouthed salamanders could. And in the wild, they only dispersed about half as far from the pools where they were born. By making the treacherous trek to a different pool to mate, *A. texanum* salamanders can mix up their genes and keep healthy variation in each population. Unisexual salamanders may have less stamina because they don't mate in the usual way. Instead of searching for the perfect partner, they steal sperm from nearby male salamanders of different species. The sperm kick-start egg production but rarely actually fertilize eggs. Only occasionally does a male's DNA sneak into a female's offspring, apparently providing too little variation to maintain vitality.

[The Trouble with Sex](#) 2003 Chris Wills (password="model")

The "Red Queen" hypothesis has itself evolved historically through a sequence of based on coevolution. The original idea is that in tightly coevolved interactions, evolutionary change by one species (e.g., a prey or host) could lead to extinction of other species (e.g. a predator or parasite). Van Valen ([R715](#)) named the idea "the Red Queen hypothesis," because, under this view, species had to "run" (evolve) in order to stay in the same place. The next idea is that coevolution, particularly between hosts and parasites, could lead to sustained oscillations in genotype frequencies (Bell [R54](#)). In species where asexual reproduction is possible, coevolutionary interactions with parasites may select for sexual reproduction in hosts as a way to reduce the risk of infection in offspring. The idea of the Red Queen hypothesis as a founding strategy leading to sexuality has been given a compelling case by Ridley ([R577](#)).

In Alice's dream (Carroll [R109](#)) about the looking glass house, she first finds that things appear left-to-right, as if shown in a mirror. She then finds that chess pieces are alive. Alice decides that it would be easier to see the garden if she first climbs the hill, to which there appears to be a very straight path. However, as she follows the path, she finds that it leads her back to the house. When she tries to speed up, she not only returns to the house, she crashes into it. Hence, forward movement takes Alice back to her starting point (Red Queen dynamics), and rapid movement causes abrupt stops (extinction). The flowers tell Alice that someone like her often passes through, and Alice decides to seek the Red Queen. She begins moving toward her, but, the Red Queen quickly disappears from sight. Alice decides to follow the advice of the rose: "walk the other way". Immediately she comes face-to-face with the Red Queen (Lythgoe

and Read R429). Already, in this world, straight can become curvy, and progress can be made only by going the opposite direction; now, according to the Red Queen, hills can become valleys and valleys can become hills (a peak in a sexually reproducing host population leads to a coevolutionary peak in parasites and a subsequent valley in the hosts). At the top of the hill, the Red Queen begins to run, faster and faster. Alice runs after the Red Queen, but is further perplexed to find that neither one seems to be moving. When they stop running, they are in exactly the same place. Alice remarks on this, to which the Red Queen responds: "Now, here, you see, it takes all the running you can do to keep in the same place". And so it may be with coevolution. Lewis Carroll's Red Queen is running while standing still, just as we end up as sexual species running while standing just about still with respect to our parasites and diseases in a paradoxical arms race with no final resolution. Evolutionary change may be required to stay in the same place. Cessation of change may result in extinction. We may find it hard to accept that we are evolving and evolved sexuality just to evade our parasites, but we nevertheless acknowledge that parasitism and infectious disease is a principal cause of death, even in the age of modern technology.

A basic feature of both immune system genes and the histocompatibility genes that make each individual's tissue unique is the existence of a large library of variant genes in individually unique combinations. A single mammalian species contains over a hundred different histocompatibility genes. The immune system is even more complex combining the effects from several light and heavy chain gene libraries and further induced mutations at the variable binding site, to generate millions of different antibodies. Sex acts as an agent to promote the diversity required to evolve such libraries. It also recombines them genetically each generation in a way which makes it difficult for pathogens to adapt to more than one generation of host. Sex gives a doubly powerful first-generation advantage because the descendants of each individual have both different immunity and different idiosyncrasy.

An outstanding example, which illustrates the dynamic nature of intermittent sex occurs in freshwater snails in Africa which are hermaphroditic in a self-contained way. Whenever the nematode parasite *Bulinus truncatus* strikes with the rains, the snail responds by growing penises and sexually recombining (Blum [R66](#) 8). In many species, evolution of sexual genes is very rapid as a result of a Red Queen arms race between male and female. This is true of the abalone, where the sperm secretes lysins which dissolve the egg membrane admitting parasites, so there is a genetic immunity arms race between the egg and the sperm (Jones [R349](#) 133). It is also true of the human Y chromosome where maleness genes are evolving rapidly. Ursula Goodenough also sees in such rapidly evolving sex genes the capacity to induce speciation, and believes this is happening between the Cuban and American ocean populations of the single-celled alga *Chlamydomonas* ([R66](#) 11). Likewise social patterns of promiscuity in higher apes are reflected in increased rates of evolution of the SEMG2 gene which makes semen thicken after ejaculation ([R771](#)).

Sex also has a manifest advantage in situations where an organism needs to adapt to a sequence of changing circumstances. In a test of the viability of sexual reproduction in the face of greater capacity of asexual strains to diversify in the absence of homogenizing sexual recombination, sexual and non-sexual yeasts were submitted to two successive stressful environments with and without gene flow, the sexual yeasts outdid the non-sexual because sexual recombination enabled a species to become more advantageously optimized at dealing with both forms of stress (Gray J & Goddard M (2012) Gene-flow between niches facilitates local adaptation in sexual populations *Ecology Letters*, doi: 10.1111/j.1461-0248.2012.01814.x).

There are intriguing indications of an arms race in humans between sperm production and cancer resistance. The genes most rapidly evolving between humans and chimps are immune defense genes - a classic Red Queen race between parasites and hosts, and cell apoptosis genes programming cell death. Protection against cancer resulting from apoptosis may compete with the need for sperm to evade apoptosis in competitive reproduction (Nielsen [R502](#)). There is a similar evolutionary arms race in the SEMG2 gene coding the thickness of semen correlating with promiscuity in differing ape species (Wyckoff [R771](#)).

The result of sex is profound. Once established, sexual recombination makes possible the most powerful means of creating genetic diversity known. Genetic crossing-over in meiosis and the careful sorting of the DNA this entails ([p.329](#)), enables a precise and complete genetic combination of the genes of each parent, crossing the sister alleles so perfectly that virtually every sexual offspring contains a fully viable genome when the sex cells merge again in fertilization. It is this almost endless variety and the powerful selection it provides that has made the evolution of higher organisms possible. Hence all higher organisms have evolved from sexual species and the vast majority are obligately sexual.

Species which have both sexual and asexual reproduction tell us a lot about what causes the equilibrium to shift between the two. Asexual reproduction is good at rapidly multiplying to invade a habitat, as with aphids and vegetative reproduction of the Nile lotus. In the freshwater minnow *Pocillopsis* asexual individuals are good at populating extreme environments, where sexual recombination would dilute adaptive characteristics. But sexual individuals are better at populating varied, fluctuating and evolving environments.

Sexual recombination has the capacity for eliminating undesirable mutations which are continually accruing, by concentrating them in only some offspring, where natural selection can effectively eliminate them - a process cryptically called 'Muller's ratchet'. If we reproduced clonally, all our offspring and their offspring would inevitably suffer the random mutations of entropy. Selection cannot necessarily keep all these in line and prevent gradual degradation of a complex genome, despite selection unless there are some forms of recombination as insurance of error protection. We already have sophisticated error-correcting enzymes which read off one strand of DNA to correct the non-complementary or damaged bases on the complementary strand. But even these processes cannot distinguish which strand is a mutation and which is the original, so error correction also involves keeping and comparing variants and allowing these a chance of survival. If we are sexual beings, our children each contain half our genes in a unique combination. If each of us have only one or a few mutations at the tolerable load per generation, some of our children may have two mutations but others will be free of any. This ensures some individuals are carrying unmutated genomes. Lynn Margulis has suggested that a similar error-correction process may have driven bacterial pan-sexuality. Notably asexual rotifer species have a much smaller load of transposable genetic elements ([p.331](#)) consistent with a basis for sexual recombination in avoiding the cumulative effects of coordinated mutations from reproducing transposable elements. For eucaryotes existing before life generated the oxygen atmosphere and the protective ozone layer, a solid reason for sexual recombination, again consistent with the Red Queen, would have been to protect the genomic information of small exposed single-celled organisms from the ravages of ultraviolet mutagenesis.

However it has recently become apparent that it is the internal load of variant genes under endo-symbiosis that has most likely become the central theme for the actual origin of recombinant sexuality in eucaryotes. After the Red Queen hypothesis was first proposed, it became clear that the persistent level of parasites would have to be prohibitively higher than actual loads to make the entire process work. When we look back at eucaryote evolution, we find that sexuality, at least in terms of genetic evidence for sexual recombination, goes back to the earliest eucaryote cells, including *Giardia*. Moreover *Giardia*, although it is anaerobic and lacks normal mitochondria, shows evidence of mitochondrial remnants, as do all similar organisms such as *Trimastix*, demonstrating that both sexuality and mitochondria run back to the founding eucaryote lineage (['Has the mystery of sex been explained at last?'](#) Nick Lane, *New Scientist* 15 June 2009).

Although mitochondria have now only a few essential genes, most of their original genome has migrated to the eucaryote cell nucleus, where the majority of metabolic genes (up to 75% of nuclear genes whose ancestry has been elucidated) appear to originate from the delta-proteobacterial genome of the founding mitochondrion, with the informational genes in the nucleus, coming from the founding amoeboid ancestor which engulfed the mitochondrion, along with its heightened RNA-processing activities, including RNA-splicing and the non-coding introns, which now intersperse eucaryote nuclear genes, which themselves appear to have evolutionary relationships with transposable elements infecting delta-proteobacteria (See: [The Tree of Life: Tangled Roots and Sexy Shoots. Tracing the genetic pathway from the first Eukaryotes to Homo sapiens](#) Chris King Jan 2009).

The overall picture thus supports a variant of the red queen hypothesis, in which the founding eucaryote, faced with a high mutational load and competition between the mobile genes of its amoeboid and mitochondrial endo-symbionts, created conditions where a gene, or genes leading to sexual recombination had a pronounced red-queen selective advantage over genes facilitating parthenogenesis. The critical advantage here is a form of Muller's ratchet, namely that without sexual recombination, a parthenogenic clone with an advantageous allele in one gene is doomed to have this locked in with average, or inferior alleles, of the other genes, while the presence of a gene facilitating sexual recombination will permit the formation of a recombinant genomes containing the best alleles of several genes simultaneously. Under the conditions of high variation and high mutational load, pertaining in the founding endo-symbionts, this would cause a gene facilitating sexual recombination of its own alleles along with those of other genes, to thrive and to drive the eucaryote gene pool towards fully-fledged sexual recombination (Nick Lane, [ibid](#)).

There are two distinct genetic forms of parthenogenesis. In half-clone parthenogenesis, for example in boa constrictors, the usual doubling of chromosomes occurs, resulting in a diploid first polar body and a haploid second polar body, which then fuses with the egg. Because of the way meiosis occurs in this situation, this results in an offspring with two essentially identical sets of chromosomes, no heterozygous alleles and significant problems of inbreeding weakness, leading to high mortality rates. In full-clone parthenogenesis, there is an extra doubling of chromosomes, resulting in a tetraploid precursor cell and a diploid egg containing the same diploid set as the mother. Species that utilize full-clone tend to require sperms of a sister species to induce cell division (gynogenesis) although the sperms DNA is usually discarded, but in the process can sometimes steal snippets or even whole chromosomes of the sperm DNA (kleptogenesis). (Pilcher, H 2013 Clone alone: Who needs sex? New Scientist 5 Mar).

This provides a route to offset the mutational degradation of parthenogenic genes lacking a Muller's ratchet on their own. Some parthenogenic species, such as turkeys, where female birds have ZW sex chromosomes and so could give parthenogenic birth to male or female offspring only male offspring result which can provide a mechanism to repopulate from an isolated female by sexual breeding with her own parthenogenic male offspring. Several parthenogenic species such as whiptail lizards appear to have originated from an instantaneous fortuitous cross between closely related species setting off a parthenogenetic clone with initial high hybrid vigor. Other apparently parthenogenic species solve the Muller's ratchet problem by having intermittent cryptic sex sometimes with another closely-related species.

Ironically the genes promoting sexual recombination may themselves have been transposable. [LINES](#) for example are closely linked to the recombination cycle, replicating in the germ line of both sexes during meiosis. A transposable element inducing sexual recombination would have a win-win trade-off, by necessity, transmitting 100% of its genome while each sex transmits only 50% of their's. Ironically this would prevent other transposable elements taking advantage of Muller's ratchet and overloading the genome.

The Red Queen hypothesis also naturally leads naturally to a partially competitive genetic and evolutionary race with the opposite sex, an amatory arms race, genetically interdependent, yet with conflicting reproductive strategies and modes of genetic selection. These arms races are evident in the natural world. A male fly may introduce toxins into the female which cause her to invest more energy in the current offspring than her natural investment spread evenly among all her offspring, thereby maximizing her investment in his offspring ([p 16](#)). These have other effects, reducing the females capacity to eject sperm and her capacity to mate successfully with other males. She responds by developing immunity. Repeated fertilization can become poisonous to the female. The Red Queen can thus be extended directly to the genetic arena in the form of 'interlocus contest evolution' between competing genetic influences, for example antagonistic genetic selection between opposing sexual characteristics in males and females, characteristic of sexually antagonistic co-evolution.

A stunning extreme of this conflict between the sexes occurs in the little fire ant, where the haplo-diploid sexuality where workers are produced by normal sexual reproduction, but daughter queens are clonally reproduced. Although clonal reproduction increases the queen's relatedness to reproductive daughters, it can potentially reduce the male reproductive success to zero. To compensate the males have also evolved to reproduce clonally from father to son in a sexual standoff, probably by expelling the maternal chromosomes, which leaves their gene pools entirely separate and selected only through the workers although it remains possible that males may occasionally mate with a top queen ([R219](#)).

The Red Queen is an instance of the Prisoners' Dilemma. Both parasite and host and male and female are running a treadmill in evolutionary terms while standing still in an arms race from which in the case of the sexual arms race neither party can escape.

Sexual Selection, Reproductive Fitness and Sexual Paradox

"The idea that females are discriminating and can actively choose with whom to mate was controversial from its inception - perhaps because male-male battles can be quite spectacular. ... In comparison female choice is much more subtle. Over the past 25 years, a considerable body of evidence for female choice has accumulated. Females actively choose their mates in a large variety of species." (Dugatkin and Godin [R177](#)).

Even 'lowly' guppy fish display a complementation of genetic 'nature' and social 'culture' in female reproductive choice. Although female guppies prefer larger, brighter orange, daring males who closely explore predators, a test of both their metabolic (carotenoid pigments are costly to make) and physical fitness and alertness, they will also follow a previous female's choice in 'social copying', and favour a less-orange mate, provided the differences in orange colouration between two males are less than 25%. However if a female is living under genuinely threatening conditions, she may prefer to mate with a less showy male who provokes less direct risk and genes which carry this lower risk. Her sexual choices are thus a subtle mix of genetic and social and involve both natural and sexual selection. Although people are more complex than guppies and lekking sage grouse, the same mate-choice rules apply to human mating. According to popular wisdom, it is human females who are the choosier sex when it comes to selecting a mate. As a species, humans meet the criteria for female choice: men for the most part, will avoid fighting to the death for the hand of a maiden. And females distinguish between various males on the basis of their characteristics.

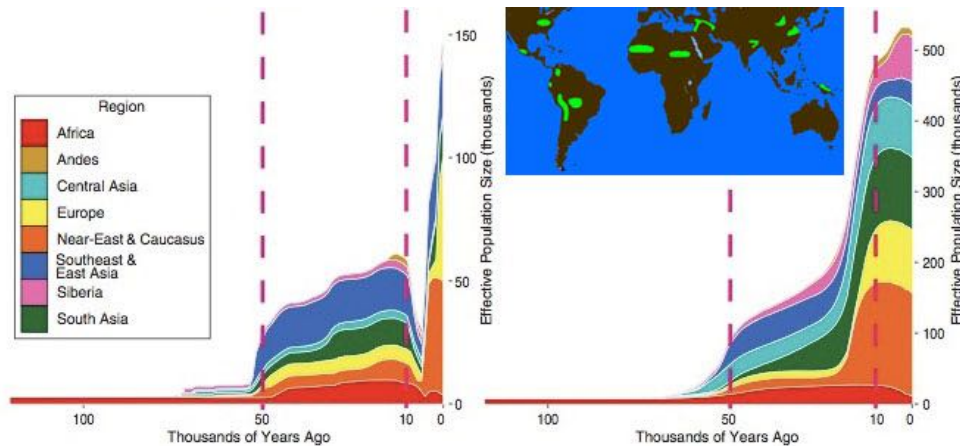
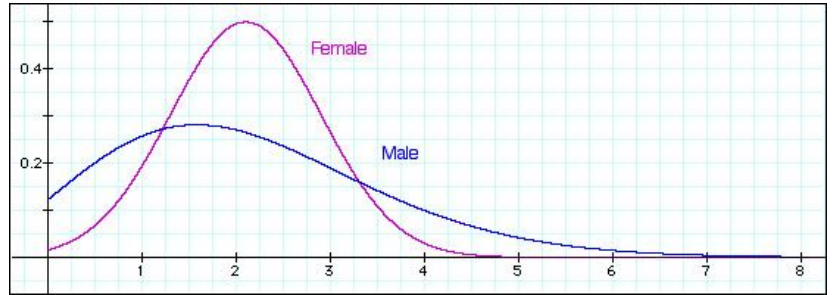
Sexual choice can lead to runaway sexual selection, particularly in birds, which have flashy males partly due to the ZW sex chromosome system ([p 342](#)). The peacock's tail is a genuine indicator of fitness because, although mesmerizing to females, it makes

the peacock vulnerable to predators. There is a runaway selection happening here between the peacock's tail and the choosy genes of pattern discrimination in the female brain. Song birds have partially evaded this penalty by choosing ultra-violet markings. Birds have four-colour vision, but song birds push one colour receptor up into the ultra-violet where mates see it stands out but out of the visual range of predatory birds which use a lower wavelength receptor (R14). Sperm are a scarce resource which invites sophisticated social strategies. Male fowl devote considerably more sperm to their first encounter with a new mate than with a familiar one. They will also increase sperm if rival males are around. An attractive hen with a large comb will receive more sperm. Cockrels will even seduce regular partners with sperm-free mountings which trick the female into fidelity even though they would expel the sperm of an inferior mate within seconds of copulation (R547, R548).

Humans are no exception to the rule that variance in reproductive fitness is greater in males than in females. While a significant number of males have no children at all, a few sire hundreds or even thousands of children. In biological terms, humanity is moderately polygynous, regardless of cultural mating systems. It holds as true in serially-monogamous America as it does in polygamous Africa.

The sexes are intrinsically polarized in their reproductive investments (p 334), with females contributing cytoplasmic eggs and the males only contributing DNA, becoming the 'sneaky' sex (p 335). Females can bear offspring by any fertile male, but males must compete to fertilize females, or their larger less abundant eggs, to reproduce. This greater female investment tends to make the female more choosy about her mate and gives female sexual selection a primary role in sexual evolution. This polarization is extreme in mammals, where internal fertilization, gestation, live birth and lactation cause the female investment to be maximally different to the male. It is particularly true of the human female with her vulnerable enormity of pregnancy (p 84).

Trivers (R703) first laid out the impacts of the differing investments made by males and females in reproduction and their consequences for sexual selection (Hrdy R330 37). Mating investment has a large fixed cost to succeed at all, so males tend to invest primarily in mating, tending towards competitive polygyny (Low R427 42), while females invest primarily in parenting. Males thus look for reproductive value in females, while females look more to resourcing value.



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). Inset shows 11 independent areas of primal agriculture discovered. Evidence of animal husbandry has also been found in Turkey 10500 years ago. (The real first farmers: How agriculture was a global invention New Sci 28 Oct 2015).

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, R735 99). Several other great founders of Y-chromosome lineages have been discovered (Callaway E 2015 Nature doi:10.1038/nature.2015.16767, Balaresque, P et al. 2014 Eur. J. Hum. Genet. doi:10.1038/ejhg.2014.285).

However Ian Morris notes that farming introduced a change from egalitarian foraging morality where small bands depended on one another as equals to survive to an intensely hierarchical farming morality:

Farming was invented around 9500 BC in what we now call the Middle East, and by AD 1500 it had taken over every usable niche in the world. For more than 5000 years, almost everyone on Earth belonged to a farming society. Virtually all these groups operated on the principle that a fair society was not one where all were treated more or less the same; rather, it was one where different individuals were treated differently. Some were wiser and more virtuous than others, and deserved to be rich and powerful. It was right to own slaves, for women to defer to men and everyone to defer to rulers who had been chosen by the gods - or actually were gods - because people who were male, free and royal were better than people who were not. Hierarchy was fair (Morris I 2015 Morality is rooted in the way societies get their energy New Scientist 20 April).

This comes as an ironic 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.

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.

An explanation for this extreme genetic skewing has been proposed in terms of cultural hitch-hiking amid extreme competition between patrilineal kin groups (Zeng, Aw & Feldman 2018 *Nature Comms.* 9:2077 doi:10.1038/s41467-018-04375-6). The effect emerges around 10,000 years ago and continues for 5,000 years, largely predating the agrarian urban empires.

Even given excessive centralization of reproductive power from overlords, leading to the Genghis Khan effect, where due to three generations of Khan rulers establishing huge reproductive harems, 0.5% of the Y-chromosomes on the planet come from Genghis Khan and no less than 8% in areas of central Asia representing 16 million men in all (Zerjal T et al. 2003 *The Genetic Legacy of the Mongols Am J Hum Genet.* 72/3 717-721 doi:10.1086/367774). Nevertheless, reproductive inequality in agricultural societies is unlikely to become skewed to as high a sex ratio as 1:17.

A key proposal reinforced by dynamical systems simulations and historical analysis is that patrilineal kin groups fighting competitive battles between clans of related individuals, act to eradicate entire patriarchal genealogies from the record through lethal conflicts which annihilate an entire genetic clade of males at a single sitting. The winners can then enjoy the enhanced reproductive success of the opposing clan's women folk who in a patrilineal system have joined the group exogenously the victorious clan reaping enhanced reproductive success, while the defeated clan disappears from the record entirely. The combine effects of deletion of whole Y lineages combined with cultural hitch-hiking by taking advantage of the enlarged pool of fertile females gives a two-process explanation of how the Y-diversity can plummet while the mitochondrial diversity does not. A similar process can be found among warrior societies such as the [Yanomamo](#).

On longer time scales, the age of the Y-chromosome Adam appears to be consistently about half the age of the mitochondrial Eve, both when taken across the entire human population and when individual peoples are investigated indicating that about twice as many females have been involved as males in the reproductive chain. 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).

A sex bias in rates of migration among human populations can also affect the respective ages. It has been observed that various human populations have differential rates of migration between men and women. Patrilineal patterns of culture promote female migration to the paternal family's locale. These patterns also occur between cultures. For example Bantu farmers often seek out Pygmy women as wives for their fertility. While the overall mitochondrial Eve locates to San Bushmen the overall Adam locates to the horn of Africa showing sexual differences in migration are ancient.

In a 2004 study in which 389 individuals in 4 populations from Africa and 2 each from Europe, Asia and Oceania) the proportion of between-group variation was 0.334 for the Y and 0.382 for mtDNA suggesting that on a global scale migration is not higher among women (Wilder J et al. 2004 *Global patterns of human mitochondrial DNA and Y-chromosome structure are not influenced by higher migration rates of females versus males Nature Genetics*, 36, 1122-1125)

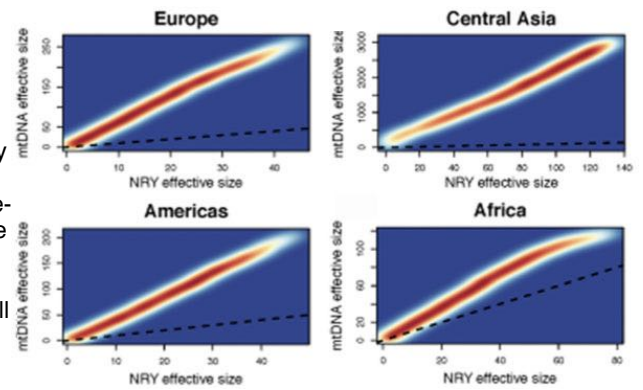
However in 2014 more detailed research comparing the divergences in Y-chromosomal and mtDNA in 623 males in 51 different populations throws up evidence of differential migration, which varies between cultures. In the entire worldwide dataset, the between-population differences are bigger for the NRY (~36% of the variance) than for mtDNA (~25% of the variance) however there are significant regional differences, with Europe, Near East and East Asia showing strong evidence of differential female migration but Africa, Oceania and the Americas having the reverse pattern (Lippold S et al. 2014 *Human paternal and maternal demographic histories: insights from high-resolution Y chromosome and mtDNA sequences Investigative Genetics* 2014, 5:13). This research also confirms consistently higher differential values for the female and male reproductive populations varying between 1.5:1 in Africa and 21.4:1 in Central Asia implying a Genghis Khan effect there.

Larger female effective populations than male occur consistently across diverse cultures with extreme variations Europe 6:1 Central Asia 21.4:1 Americas 4.3:1 Africa 1.5:1 (Lippold et al). The 1:1 line is dashed.

This pattern continues today in diverse modern cultures where male reproductive success is strongly a function of income and resources, while female reproductive success is either unrelated to income or inversely related to it. For example in Brazil 33% of men in the bottom quartile of income were childless at 40 while only 17% in the other three were. By contrast the figures for women were 10% for the lowest quartile and 20% for the highest (Fieder M, Huber S, Bookstein F 2011 *Socioeconomic Status, Marital Status And Childlessness In Men And Women: An Analysis Of Census Data From Six Countries J. Biosoc. Sci.*, 43 619-635 doi:10.1017/S002193201100023X).

Measures of polygyny are biologically related to the differential variance in reproductive efficacy which is generally higher in males. The means of the two are always the same since it takes a male and a female to reproduce sexually. Thus by biological measures human societies are moderately polygynous, even though we are predominantly socially monogamous. This manifests in a variety of ways. 85% of human societies permit polygyny and in these about as many males as can resource two partners at once do so.

Some males engage despotic sexuality. Moulay Ismail the Bloodthirsty of Morocco had 888 offspring and 40 sons in a single month (Hrdy [R330](#) 84). Ghengis Khan's Y-chromosome occurs in about one in 200 people as a result of several generations of polygynous descendents and 1 in 12 Irish men are descended from Niall of the Nine Hostages. Wandering males seducing women also contribute, through the standard mammalian strategy of simple sexual courtship. Although we call many human societies 'monogamous' this is clearly a biological misnomer. Most societies with one-spouse-at-a-time rules are called polygynous in a biological definition: more men than women fail to marry, and more men than women remarry after death or divorce, producing more offspring in these later unions. The most reproductive men have many more children than the most fertile women. All of these phenomena increase the variability of men's reproductive success compared to women's, making us polygynous by a biologist's definition (Low [R427](#) 54).



The larger divergence in male reproductive opportunity in humans at first caused sociobiologists to concentrate on male evolutionary selection by females, assuming females all reproduced close to the maximum feasible rate. Sarah Hrdy ([R329](#)) in "The Woman that Never Evolved" set out to correct this anomaly, noting that real reproductive differences and competition exist in females, particularly in the central issue of successful parenting.



New Zealand Tui are socially monogamous, which is more common in birds than mammals, as two parents are often needed to feed the young, but a whopping 56% of tui chicks are sired by another male than the female's nesting partner. Despite socially monogamous pairings, males engage in singing contests, often watched over by the females. Males are 50% larger than females and the largest and most healthy with the most prominent white bobs have fewest interlopers in their nest. Tuis also check out neighbouring nests and some males checking a nest do so to check out their own outsired offspring, as true fathers of the chicks.

On the other hand, female choice also implies that females will not necessarily remain faithful to a socially monogamous pair bond. A female in socially monogamous species which seek paternal support will seek a resourceful partner but also engage other sexual liaisons in up to 20% of her siring. Females in

polygynous species with dominant males also covertly seek non-alpha partners. This pattern of female 'infidelity' is as true for colonial birds as it is for humans. The principal reason is as insurance so her large parental investment in eggs and in mammals pregnancy and lactation are not entirely bound up in an inferior set of genes. However there are more complex reasons. Females need not just to find a male with the best genes but the most compatible complementarity to hers. Smells of [MHC](#) histocompatibility proteins give mammals sensitive indications of sexually attractive mates with good immuno-complementarity. Females also mate with many males to confuse paternity and invite more paternal support and less infanticide. Finally they may mate with non-alpha males to avoid being forced into a undesirable decision by the forces of male competition.

At an extreme of choosiness, female Californian fiddler crabs, *Uca cernulata*, will investigate up to 100 male burrows, beckoned inside by the males' large waving claws, to find a burrow of just the right size which will hatch their progeny just in time for them to be spread by the peak outward night time flow of the bi-weekly tidal cycle.

Trivers and Willard ([R704](#)) went on to establish the relation between such variation and sex ratios: "wherever variation is greater in reproductive success for one sex than the other, and where the reproductive success of individuals of that sex depends on maternal effects, then mothers in good condition should favour the sex with the greatest variance in reproductive success". It has been confirmed in species as diverse as deer, baboons and rodents. Broadly speaking, we expect mothers in poor condition to have more girls and those in good condition to have more boys, possibly mediated by hormonal mechanisms such as testosterone (Grant [R254](#)). Women who expect a long life (and are thus likely to be in good condition) have more boys (Johns [R341](#)) and Gibson and Macey ([R238](#)) showed that rural Ethiopian women with low levels of nutrition are more likely to give birth to girls ([p 97](#)). It applies also to human dowry and bride price, where low ranking families save for a dowry to 'marry up' daughters and high ranking families favour only sons and may kill their infant daughters ([p 286](#)). Such 'hypergamic' marriage patterns become pronounced under conditions of environmental stress, where upper class families are better protected against famine and can afford males, while lower class families may starve (Low [R427](#) 70, Hrdy [R330](#) 338) and whose best reproductive prospects over time involve 'marrying up' daughters, in what is called hypergamy.

The rule applies when sexual selection, (access to females) is the dominating factor, but may be reversed when other factors, such as female dominance limit resources. When daughters remain within the group and resources are scant, as in savannah baboons, high ranking mothers produce daughters, but low ranking ones sons who can at least migrate (Hrdy [R330](#) 333-5). When daughters can be harnessed for allo-parenting, this advantage can determine the sex ratio, as in Seychelles warblers. Such sex imbalances tend to return to Fisher equilibrium of equality ([R212](#)) when the driving factors are mitigated, because the rarer sex gains a strategic advantage. Each sex thus has its own distinct and often conflicting strategy of reproduction. To fulfil a given sex's reproductive imperative requires also fulfilling the reproductive strategy and choice of the opposite sex. Male competition is subject to the paradox of female reproductive choice because it is the most powerful agent of sexual selection in most species. Even in species with pronounced male conflict, female choice remains a prominent selector of male fitness.

Sexual selection is prone to runaway feedback, as for example the outgrowth of the peacock's tail as a genuine indicator of fitness which can't be faked and imposes a significant cost on the bearer in terms of predation. This in turn is driven by the ever-more-choosy retinas and visual areas of the peahen. The balance of these forces and the actual state of strategic advantage one or other sex enjoys varies from species to species. For example in non-monogamous birds where the male contributes only his genes, the prominent display of the peacock's tail and the bower bird are driven by precocious female sexual selection. To be a genuine indicator of reproductive fitness these ornaments are often chosen to be costly, as the peacock's tale is, as well as being a sensitive indicator of highly tuned developmental symmetry indicative of good genes. Experiments have shown that females in displaying avian species will continue to prefer artificially enhanced ornaments and mate with males possessing them confirming runaway selection. The male has little choice here but to make the best job of capitalizing on its runaway evolutionary burdens, which may give it a good chance of siring offspring, but bring costs in vulnerability to predators as a bulky and garish genuine indicator of fitness. This is partly a reflection of the minimal investment made by such males and the incapacity of the males to monopolize female reproduction except through enticement.

Human beauty is has been found to be linked with more perfect symmetry, and mor recently in an experiment reducing dancing performances to identical computer mannequins, it has been found that, the best dancers are also those who are the most symmetrical

and beautiful (Brown [R91](#)). The effect was stronger for women watching male dances than for men watching women and the dances performed by men scored more highly overall than those by women, consistent with male display of fitness and female choice.

Even alpha males, who would prefer to engage male competition to win a harem, rather than submit to female choice, find themselves subject to genuine indicators of fitness. An alpha male gelada baboon has a highly visible red chest mark, which indicates his condition. This is probably a sign that also tells others that females are sexually bonded in a way which will be harder to break into. Coalitions of bachelor males will confront a leader of a harem and try to take it over only if his genuine indicators of fitness are lacklustre.

In monogamous species which have mutual mate choice, pronounced sexual differences of display are reduced or non-evident, however as Darwin noted mutual mate choice can still drive selection and consequent evolution, albeit without such strong or polarized sexually selective forces operating. Humans are mildly sexually dimorphic, with testicle size and sperm competition suggesting pair-bonding in a climate of moderate polygyny with mutual mate choice skewed somewhat towards female reproductive choice. Male reproductive variance is greater than that of females. Sexual strategies are complex and mixed with a considerable number of medium to long-term pair bonds, a minority of polygynous associations, serially 'monogamous' partnerships which tend to favour male reproductive polygyny, overlaying a shifting pattern of covert female affairs and sometimes blatant male philandering, all contributing to varying reproductive strategies and outcomes.

At an opposite extreme, the bull elephant seal appears to have caught the female in a not too tender trap as a result of male resource guarding. Because seals often breed in low temperature climates, the females have evolved to have a counter-cyclical pregnancy and lactating season and gather on sheltered warmer beaches where they can nurse the pups often without feeding, using their blubber alone to keep both mother and offspring alive, at the same time becoming pregnant for the next season. A dominant male secures these spots before the females arrive and thus can guard a large harem (Low [R427](#) 44). The much greater size of the male is a reflection of the harem size and male competition. How efficient this counter-cyclical nursing has evolved to become is shown by the hooded seal who gives birth on ice flows and whose creamy milk with 60% fat can cause a pup to gain fifty pounds in a matter of days (Hrdy [R330](#) 129).



Sexual dimorphism: Elephant seals (see Maier [R431](#)). The picture of dominant males may be a deception as females elect to mate in the ocean where they have more choice (Animal Behaviour, DOI: 10.1016/j.anbehav.2011.06.006).

We should note that this form of male domination only exists because of the relative success of the female strategy of counter-cyclical pregnancy and breast-feeding. Females do secure superior genes for their pups, but at the cost of having some trampled by the bull and having to endure being raped and bitten by sub-dominant males should they leave the colony to fish (Low [R427](#) 45). A dominant male elephant seal can sire up to 90 pups and a female 10. Complementing the male strategy, it has been proposed that elephant seal females signal their receptivity to a broad array of males specifically to incite competition among the bulls to apply female choice

genetically (Cox and LeBoeuf [R135](#)). Females apparently take advantage of this situation to actively pursue smaller subdominant males on the side, partly because they run a small risk (1/1000) of being suffocated by a large dominant male. Female choice between herding and time on the side is acting to keep the hugely larger male size in equilibrium (Sparks [R654](#) 13). In some seal species such as Weddell seal, dominant males may die from exhaustion at the end of a season. In others they are simply overtaken exhausted by younger fitter males. On the other hand when a female seal leaves the colony she is liable to assault and rape by sub-dominant males who bite her if she doesn't submit. In some senses these patterns are not too different from human male dominant warrior societies trading their women as reproductive tokens where a [Yanomamo](#) village head such as 'Shinbone' sired 43 children by 11 wives (Chagnon [R111](#) 150). Much larger sirings have been made by human potentates who have clearly established the largest harems of any species. One in 200 people today carry the Y-chromosome of Ghengis Khan. One can only speculate where this would take human dimorphism, continued over evolutionary time scales.

An Antarctic fur seal trying to have sex with a king penguin. The brazenness of the seal's behaviour left those who saw it in no doubt as to what was happening (BBC 2 May 2008 <http://news.bbc.co.uk/2/hi/science/nature/7379554.stm>).



Sexual coercion among animals is extremely common: males of many species often harass, coerce or force females of their own kind to mate, while animals are also known occasionally to harass sexually a member of a closely related species. Harassment is common among pinnipeds, the group of animals that includes seals, fur seals, and sea lions; and occasionally it happens between related species. Male grey seals have been known to harass and mate with female harbour seals, for example, producing hybrids. Sexual harassment is often more commonplace in non-monogamous mating systems, and in species where males are physically much larger than the other sex and thus physically capable of coercion or harassment. But this is thought to be the first recorded example of a mammal trying to have sex with a member of another class of vertebrate, such as a bird, fish, reptile, or amphibian. Chinstrap penguins occasionally indulge in homosexual behaviour, and adielie penguins sometimes "prostitute" themselves to get stones for nest-building; while one in seven emperor penguins will change partners from one year to the next.

Night-singing songbirds have a two-fold sexual strategy monogamy by day and promiscuity by night. The American field sparrow, *Spizella pusilla* is territorial and socially monogamous, though they engage in opportunistic infidelity. The males sing courtship songs in the daytime, as well as more complex songs to ward off competitors. But at night, partnered males also sing more subtle brief songs. Instead of loudly calling for females, they sing, very discreetly, 'Hey, I'm here... Do you want to mate with me?' to any interested female just around the corner and these females are all too willing to wake up for a night-time rendezvous. Males sing more during periods when females are reproductively receptive, and the females respond to such song more often when they are fertile. The female's mate doesn't appear to kick up a fuss and counter-sing - which would be expected if nocturnal songs served to repel rivals. If the male isn't already out singing at some other female, it appears to remain asleep, while the female responds earnestly (Animal Behaviour, doi: 10.1016/j.anbehav.2016.04.023).

Orangutans have pronounced dimorphic male phenotypes. Degrees of phenotypic dimorphism may be very important in maintaining diverse mating strategies which enable a species to adapt rapidly to changing circumstances with now socialization patterns by altering the frequencies of the corresponding alleles in the population. Female coho salmon display a similar form of two phase female choice, in which there are two dimorphic forms of male, hooknoses which are fighting fit but took two seasons to mature and younger leaner jacks which came up river the first year. Contrary to expectations, females prefer the jacks, possibly because they are showing early fitness. Jacks just wiggle to signal an invitation and the females comply. By contrast they face a conflict of interest with the aggressive hooknoses who will bite them if they don't have sex (Mason [R448](#)). Roughgarden ([R593](#)) suggests that in polyphenic fish species there is reproductive cooperation between dominant male 'controllers', and the sub-dominant male phenotype which he calls 'cooperators', however the viability of this idea remains to be established. It is also doubtful that 'sneaker' male crickets, which sit silently behind a singing alpha male, assist the alpha, rather than exploit his efforts. Male cuttlefish are even known to become transvestites, assuming the form and colouring of a female to trick a dominant male and the female he is guarding into allowing his sperm to intervene in about a third of fertilizations ([R288](#)).

Male orangutans are called 'polyphenic' because there are two distinct male phenotypes, one a gangling 'peter pan' who tries to insidiously sidle up to and rape females, even when they are out of estrus, and the other an alpha male who beats his chest and roars through the forest enticing estrus females to his call (Hrdy [R330](#) 74).



The difference in reproductive investment strategies between the sexes, with males investing less causes the vast majority of animals to be polygynous. This applies consistently to invertebrates, fish and mammals. Only birds which uniquely are both egg-laying and warm-blooded are commonly monogamous because hatching the egg requires the cooperation of both

partners. But even then, monogamy is social, rather than genetic and there are frequent clandestine affairs. Monogamy in the biological sense is social mating and does not imply sexual fidelity. Only 10% of 180 socially monogamous bird species are sexually faithful. Both monogamous birds and mammals clandestinely 'outsire' up to 20% of the offspring due to individual reproductive choice by either or both sexes to spread or extend their genetic investment. Recent research has unearthed an intriguing inversion of the '[fertile mother effect](#)' linked to 14% of human male homosexuality. In socially-monogamous zebra finches we have the 'fertile father effect' about female infidelity. Philandering males sire more offspring and their daughters who carry their father's philandering genes are also more liable to female promiscuity, although their chicks are of lower weight and they lay no more eggs than the faithful females. The reproductive success of the fathers thus drives the promiscuity of the daughters ([Why female zebra finches cheat on their partners](#) Ferris Jabr New Scientist June 2011).

Only about 3% of mammals and 3-8% of primates are socially monogamous and possibly only two monkeys, the marmoset and the tamarin, are truly monogamous. In mammals, where females both gestate live young and lactate, mating patterns are primarily determined by the way females distribute themselves, e.g. in relation to the food resource. Males will responsively distribute themselves in such a way as to guard either scarce resources (e.g. special territory) to monopolize females using them, or groups of females themselves (mate guarding) if they are wandering freely, foraging in wide areas in groups. At an extreme, if there are no means to monopolize female fertility, a few mammal species also resort to the lekking well known in birds, where males competitively display to the females for sex on an arbitrarily chosen stomping ground. Variations in how spread apart the females are in relation to plant food distributions in apes are believed to determine the spread from monogamy in gibbons through fission-fusion promiscuity in chimps to harem building in gorillas. Although the advantages of paternal help with child-rearing as well as widely spread females have been cited as factors predisposing to mammalian monogamy, the key factor appears to be simply how females use space (Komers and Brotherton [R386](#)). In many of the monogamous mammal species monogamy results not from male parental investment, but from males being forced to guard a lone female with a small exclusive range. In monogamous marmosets and tamarins, for example, females compete to pair with quality males and drive off competing females (Miller 2000 *The Mating Mind* Random House 185).

Two principal explanations for social monogamy are sparsely distributed females, for which it is reproductively advantageous for any male to commit to. This appears to be the principle driver across mammals as a whole and is clearly the case in [gibbons](#). The alternative - infanticide by rival males appeared in a second study to be the consistent precursor of social monogamy in primate evolution but this has not been replicated in the previous study (Howgego J. 2013 *Conflicting studies rekindle monogamy debate* Nature News 29 July).

Prairie voles have become renowned for their pair-bonding based on the neuropeptides oxytocin and vasopressin ([p.353](#)). But their monogamy is unusual in that the founding pair are the sole breeders in a wider family group whose other females remain sexually immature and help to rear the young until they eventually mate with and form a pair bond with another outside male, causing the onset of ovulation and a new dynasty. Monogamous hibernating marmot mothers similarly engage aggressive displays towards their daughters as winter sets in causing them to fail to ovulate and remain with the nest, adding enough warmth to tide the next round of her infants through the cold spell. Noting its correspondence to human history Hrdy ([R329](#) 173) calls one female forestalling reproduction in another "the Hagar phenomenon". The coincidence of social monogamy and allo-parenting 'day care' is a common feature of mammal species in which the mother is adapted to produce a greater load in offspring than she can care for on her own. Cotton-top tamarins likewise depend on cooperative child rearing and give multiple birth to enable rapid population increase when the conditions are right. Mothers routinely give birth to twins and rely on the father or other group members to help rear them, or the babies may be abandoned within 72 hours of birth (Hrdy [R330](#) 180). In humans even one slow growing relatively helpless infant is more than a mother can easily care for and gather food for at the same time, so both pair-bonding and allo-parenting are readily evoked in a manner exceptional for other apes. The titi monkey is also monogamous. A couple regularly sit together on a branch, tails entwined. The mother is so engrossed with the father that she appears to pay marginal attention to her offspring, who drink from the mother, but cling to the father when she pushes them off. Nevertheless extra-pair couplings were observed in titis before female philandering in monogamous birds caused a sensation. Her attention to her partner makes perfect sense, because if he strays his resourcing commitment may be lost. As with tamarins and marmosets the female drives away females who enter her territory to avoid dividing her partner's attentions ([R330](#) 213). Infidelity in monogamy applies even to prairie voles: "What we say about prairie voles is that they'll sleep with anyone but they'll only sit by their partners" (Blum [R66](#) 95). It's no surprise that as soon as a prairie vole mates, he becomes more suspicious and aggressive of other males ([R66](#) 241).

Evolution towards extremely rapid increase in complexity, as exemplified by human cultural emergence, is consistent with a state of paradox in which neither sex is fully dominant over the sexual choices of the other, rather than any state of sexual dominion where the strategy of only one sex is brought fully into play. The emergence of culture is an abrupt process consistent with powerful sexual

selection. The state of sexual paradox entices each sex to strive to gain the choice of the other through genuine indicators of fitness, involving both prowess and social astuteness as well as kindness and generosity to one's partners. These are all features characteristic of human emergence.

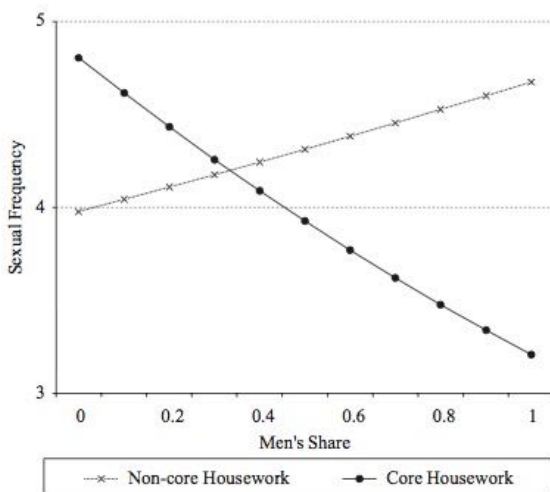
Moreover infidelity in modern society is something that is electively handled in relation to the stages of life's commitment, for example to raising children, and is not in any form a simple question of betrayal. In 2006 a study by of the British Sexual Fantasy Research Project led by Brett Kahr, found that the proportion of those having an affair increases with age group. 14% of under 30s in a long-term relationship admit to having an affair, 23% of 30s to 40s and 30% of over 50s. The average number of women a man has had sexual contact with is 15.64 and the average number of men a woman has had contact with is nearly as high at 14.56, scarcely consistent with our naive ideas of moral monogamy.

Key and Aiello ([R359](#)) have applied the prisoners dilemma game in detail to sexual relations in human emergence and concluded that "when male reproductive costs are less than female reproductive costs, males cooperate with females even when females do not reciprocate" entitling this 'non-reciprocal altruism' - an investment in a female and her offspring. The game showed that as costs increase, females will begin to help one another. Key notes: "That's because females have the same interests, such as food and child care". While it was to females' advantage to put all their effort into raising a small number of offspring, the best strategy for males was to attempt to father as many offspring as possible and not stick around to watch them grow up. However the model showed that males and females will cooperate when two conditions are met: first, when female reproductive costs are much higher than those of males, and second, if females can somehow punish uncooperative males. This associates with human emergence and the increasing head size of a larger and more complicated brain, motifs in which human females may have cooperated and applied forms of sexual enticement or even cooperative coercion to ensure male cooperation, possibly phased with the lunar and menstrual cycle ([p.77](#)). Noting that females are frequently more sexually active in socially monogamous species Enquist and Rodriguez-Girones ([R195](#)) developed a game-theoretic model to establish the idea that male 'fidelity' is driven by female 'deceit' in the form of concealed ovulation and opportunistic extra-pair couplings because the advantages to male philandering are reduced.

Mating Minds and Flowering Cultures

Geoffrey Miller's "The Mating Mind" ([R475](#)) provides a potent, and prophetically in his own words, "Dionysian" and "chaotic" release unveiling the origins of virtue, and human complexity in culture, specifically through sexual selection. This is an antidote to both the Judeo-Christian foundations of Western conservatism and capitalist greed. It has immense implications for all creative aspects of humanity, from art and music to science, and for the future of our institutions, human society and culture. The core of this idea is that our social structures and our emotional and intellectual life originate from irresolvable paradoxes of reproductive interdependence, through sexual selection. Sexual 'intercourse', the source of our immortality, is now discovered to be also the source of our generosity. All other pretensions of society and intellect are ephemeral, except in so far as they serve this reproductive end for ourselves, or spread to other reproducing beings through literature and culture.

Darwin, in pondering the peacock's tail, recognized that sexual selection is a key complement to natural selection - a chaotic runaway phenomenon, while natural selection is largely conservative. Human evolution has occurred in a context where our principal competitors are other members of our own species and sexual selection is likely to have been the principal force in the evolution of a universal species with an absence of clear predators or specific species on which we depend, being omnivorous gatherers and hunters.



The importance of gender display - complementary rather than identical roles - for sexual frequency in US heterosexual marriage: Couples where men participate more in core tasks - work typically done by women - report lower sexual frequency. Similarly, couples where men participate more in non-core, traditionally masculine tasks report higher sexual frequency, suggesting the importance of gender-typed participation in household labor. Regressions using the share of total housework also show a negative and significant coefficient for men's share of housework (Kornrich, S, Brines, J Leupp K 2012 Egalitarianism, Housework, and Sexual Frequency in Marriage American Sociological Review 78/1 26-50).

If we are thinking of social institutions, or future utopian world orders, we need to consider that all ape societies are delicate dynamical systems based on a complementation of two disparate social groupings. Firstly the females, distributed across the environment in relation to the occurrence of rich plant foods. In turn the males, either individually or in troops, distribute themselves in different patterns to induce the females into reproductive liaisons. Any attempts we make to design utopian world orders have to take into account evolutionary equilibrium if they are going to be sustainable and not merely imposed structures giving rise to unstable societies which destroy themselves or one another through coercive structures and institutions which fail to recognize evolutionary realities. Our own society is just emerging from several thousand years

of frank sexual dominion of man over woman which has resulted in highly artificial institutions and a perception that law can be imposed in contradiction to our own best evolutionary interests. That boom and bust exploitation is a viable strategy, although it is destroying our planet's future fecundity.

Darwin also noted that mutual mate choice could give rise to effective evolutionary selection if mates were able to combine through mutual mate choice to form couplings according to fitness, noting species which had symmetrical characteristics in the light of this, so our dominant motif of overt serial monogamy is an evolutionarily stable strategy. However as we have seen, monogamy always occurs in a fertile covert ground-swell of clandestine affairs which contribute an additional fifth of our offspring, chosen principally through male genetic fitness rather than resources, which ensure a wider mixing of the gene pool than strict monogamy would allow, so strict monogamy is not. Polygyny, and the wandering male as well as female affairs add to our genetic diversity through sexual selection.

Human mate choice is not entirely mutual, but strongly skewed by the natural tendency of males to try to reproduce with many females and to compete and show off to achieve that end. Males in most species display indicators of genetic fitness since they bear no offspring themselves are dependent on females to reproduce, offering only their genes in their sperm. By contrast the human female can get pregnant by any male and will always give birth to her own offspring. Females are thus choosy and males showy. This can give rise to rapid runaway selection, as exemplified by the peacock's tail. To be a genuine indicator of fitness, a display must be costly and hard to fake. Sexual selection also requires the females to be able to be as choosy as the males can manage to display. In the context of

intellectual displays, this requires females to be as discerning judges as the males can be performers, requiring both to keep ahead in the red queen race for increasing intellect.

Miller attributes all the creative developments of culture, art, the humanities, intellect and the virtues of compassion and agreeableness to mate choice, partly mutual, but skewed towards female reproductive choice. Darwin who also perceived this possibility, made a serious error in his estimation of this situation: "man [could] have become as superior in mental endowment to woman, as the peacock is in ornamental plumage to the peahen" (Jolly [R346](#) 361). Miller correctly points out here that this evolution of woman in the coat tails of man theory does not stack up. It is the demanding nature of the peahen's visual apparatus and her ever-escalating choosiness about display which has driven the poor peacock to a Prisoners' Dilemma of frank, through resplendent disability. If we are considering cultural evolution, the choosiness of the female is always a step ahead of the male and discerning appreciation of eloquent fable and fine art requires as refined an intellect as the performer or the performance can be a faked and shallow affair.

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."

Since the advent of the selfish gene, and the eclipse of group and species selection, evolutionary theorists have pondered how altruism can come to exist. As accounted in Matt Ridley's "Origins of Virtue" ([R578](#)), Hamilton firstly introduced the concept of kin altruism - caring for the survival of your relatives because they share some of our own genes, and Trivers complemented this with reciprocal altruism between possibly unrelated individuals. However reciprocation requires a keen episodic memory and is rare in nature. Neither do either of these explain the obvious capacity of humans to be altruistic beyond these horizons in situations where no reciprocation is possible. Compassionate love knows no bounds and asks no specific favours in return.

Miller's answer to this dilemma is that social selection (which is catalytic on sexual opportunity, but in its controlling aspects against defection, is often negative - thou shalt not commit adultery even though 70% of us do it) is too indirect an effect in relation to the immense power of direct reproductive selection, to be the prime mover. The 'true' picture is probably an overlapping mixture with sex the driving force. Miller presents convincing reasons why generosity and compassionate love are the necessarily costly tokens of genuine fitness, that it is sex which has produced not only lust and passionate love, but compassion, agreeableness and generosity to boot. "Sympathy, agreeableness, leadership, fidelity, good parenting, charitable generosity" in Miller's words all derive from sex. It is thus sex which makes us good ethical beings, not social or moral control alone or even principally. This is reflected strongly in the key priorities people have in choosing a partner recorded by David Buss: "love or mutual attraction, dependable character, emotional stability, maturity, pleasing disposition, kind, healthy, smart, educated, sociable, interested in home and family." It is clear these attributes would select for good, amicable, relatively faithful, home builders, particularly among the males, who through astute female reproductive choice, would become innovatively good artists and musicians, entertaining story tellers, affectionate lovers, and humorous companions, while remaining, stealthy hunters, good protectors and astute diplomats. In Matt Ridley's words "domestic bliss". This kind of selection is possible only while females have the conditions and power to apply female reproductive choice. Patriarchal dominion leads rather to women who will produce many sons who can achieve power through status or the force of arms.

Furthermore risk-taking male bravado, which makes little Darwinian sense, doesn't impress females, who prefer cautious men (Farthing [R201](#)) although they also prefer dominant males (Pelligrini and Long [R534](#)). Bravado may rather function to raise male status by impressing other males, only indirectly enhancing mate choice. In speed-dating experiments, although people cite similar social status and background - as the basis of their choices, they act largely on biological indicators - female nubility and male physical attractiveness (Douglas [R172](#)), leaving the ideal soul mate for posterity, in the artificially accelerated rush to courtship.

Although there is some evidence that personality traits such as low agreeableness and contentiousness, high extroversion, narcissism, manipulateness and psychopathy may be linked to increased sexual success, particularly with respect to short-term mating, contrasting this notion is the study of altruism as a positive sexual signal. Converging evidence has suggested that altruism may play an important role in mate selection (Barclay, P, Van Vugt M 2015 *The Evolutionary Psychology of Human Prosociality: Adaptations, Byproducts, and Mistakes*, in D. Schroeder and B. Graziano, *Handbook of Prosocial Behavior*. Oxford Univ. Pr. 37-60), highlighting a potentially important avenue along which good deeds done toward unrelated individuals may have evolved, suggesting that altruism may serve, in part, to convey one's value as a mating partner. Research has shown that we prefer altruistic partners, especially for long-term mating (Farrelly D et al. 2007 *Altruists Attract Evolutionary Psychology* 5/2 313-329). Some research has shown that men will actively compete with one another (competitive altruism) by making charitable donations to women (McAndrew F, Perilloux C 2012 *Is self-sacrificial competitive altruism primarily a male activity?* *Evol Psychol* 10/1 50-65). Interestingly, these increase when the target of one's altruism is physically attractive (Raihani N & Smith S 2015 *Competitive Helping in Online Giving* *Current Biology* 25, 1183-1186).

Previous findings from hunter-gatherer populations have shown that men who hunt and share meat often enjoy greater reproductive access to women (Jaeggi A, Gurven M 2013 *Natural cooperators: food sharing in humans and other primates* *Evol Anthropol*. 22/4 186-95. doi:10.1002/evan.21364). But do these links hold up in contemporary? To find out, researchers conducted a set of two studies (Arnocky S 2016 *Altruism predicts mating success in humans* *British Journal of Psychology* doi:10.1111/bjop.12208). In the first, undergraduate men and women completed an altruism questionnaire, along with a sexual history survey. Participants also completed a personality inventory. We found that people who scored higher on altruism also reported they were more desirable to the opposite sex, had more sex partners, more casual sex partners, and had sex more often within relationships (although this latter finding was not statistically-significant after controlling for personality variables). The statistical models (including covariates) explained between 13 and 26% of the variance in sexual behavior. Moreover, altruism mattered more for men's number of lifetime and casual sex partners than for women's.

Some research has shown men to over-report, and women to under-report their lifetime number of sex partners. To address this, in a second study the researchers used a more subtle behavioral measure of altruism. At the end of the survey, each participant was entered onto a draw for \$100, and was given the choice to keep their winnings or to donate it to a charity. Participants again reported on their sexual histories, completed a personality measure, as well as a scale to capture socially-desirable responding and a measure of narcissism. Results showed that, even when controlling for these variables, those who donated reported having more lifetime sex partners, more casual sex partners, and more sex partners over the past year, with the models explaining between 7 and 28% of

variance in sexual behavior. Men who were willing to donate also reported having more lifetime dating partners. Conversely, personality traits (including competitive and aggressive tendencies) did not relate meaningfully to sexual histories.

Altruistic sharing of housework is also important in avoiding infidelity. A major French study has found that Women are more likely to cheat on men who fail to do enough housework. In a poll of 10,000 female subscribers to Gleedon, an online site for married and unfaithful people, 73% claimed this was the reason they were driven to infidelity. 86% of respondents said they were deeply frustrated by their mail partner's tendency to avoid housework. A 2014 Ifop poll found 55 per cent of French men and 32 per cent of French women are unfaithful and that infidelity is on the rise, but it also revealed the French are champions of forgiveness (Samuel H 2016 Men's failure to do housework drives women to infidelity Daily Telegraph Nov 16).

Of course, we are generous because we experience the full spectrum of the mammalian emotional repertoire from hate to love, a huge step of evolution towards a paradigm that goes far beyond individual genetic instincts. However these emotions survive not just because they are 'good', but because they abet survival and pivotally the reproduction of those possessing genes giving rise to such 'empathic' emotions. Rather than strict reciprocation, we have evolved two independent and yet keenly opposed emotional senses, both molded by sexual selection, firstly the capacity for compassionate and generous love and the second to be acutely sensitive to cheating and prepared to punish defection.

In human society, despite mild polygynous tendencies, reproductive fitness is measured principally through heterosexual partnering and parenting, particularly mothering. Outside artificial insemination and politically proactive forms of IVF, same-sex bonding is non-reproductive. Nor is it integral to the parenting aspect of reproduction, since the social support required for reproductive success is largely dependent on familial and coalitional relationships of mutual trust in one's community which are manifestly asexual. It is far from clear that same-sex socio-sexual encounters, or the concept of social 'gender' rainbow (Roughgarden [R593](#)), mediate human reproductive success in any significant way.

Women show great acuity in selecting men for both their mating potential and can rank men according to their testosterone levels for a fling, and independently make accurate assessments of a male's parenting potential watching them with children as a potential long-term relationship (Proceedings of the Royal Society B DOI:10.1098/rspb.2006.3569).

Miller goes on to describe human intellectual, and artistic evolution as a fitness indicator to demonstrate abundant, entertaining, exciting creations, myths, stories and themes which, although not necessarily essential for survival, do indicate a genuine resourceful capacity to fend for a family and to bring skills into play which will, in their application, dramatically improve the survival chances of offspring, partly through the reproductive benefits they will also endow. Mutual mate selection is significantly slewed by the obvious degree to which males display sexually in displays of creativity and power, so in complementary measure by female reproductive choice. This explains why men spend a disproportionate amount of time insinuating themselves into positions of power and striving to become virtuoso geniuses and why consequently more innovation seems to be made by men. This is again consistent with moderate polygyny, rather than strict monogamy.

The adage that men like to be good jokers and that women are discerning appreciators of humour is supported by brain studies ([p 390](#)). This lends support to the notion that humour exists socially as an indicator of male mating fitness. Miller notes: "It's a very powerful and reliable way to show creativity and intelligence". A woman choosing a funny man as a partner would be more likely to have genetically healthy children who will survive and reproduce themselves. Such sexual selection may favour women who like humorous men, and men who like women with an appreciation for humour, as has been evidenced in extensive studies by Bressler and co-workers ([R75](#)) with a follow-up in the same journal).

Confirmation of the central thesis in Miller's work - that art, poetry, story-telling and musical and other forms of creativity are indicators of reproductive fitness, giving strategic advantage to the bearer in terms of sexual favours - has received confirmation in the form of research by David Nettle of the University of Newcastle upon Tyne (Get creative for a varied sex life Steve Connor NZ Herald 3 Dec 2005). The researchers interviewed 425 men and women about their sexual partners, and found the average number of partners for professional artists and poets (regardless of their fame or otherwise) to be between 4 and 10 compared with just 3 for non-creative people.

Modern humans do display significant sexual differences in cognitive and intellectual adaption ([p 388](#)), which are consistent with reproductive realities and the sexual complementation of gatherer-hunter life-styles. Men are better at map readers, good at mechanical cognitive tasks and relaxed in situations of working in parallel, as well as tight knit planning, all consistent with good hunting. Women are more proficient at language and at familiarizing themselves a large number of varied objects in the environment, and at networking, consistent with gathering. Consistent with gender complementarities in reproductive needs, men tend to hunger for young fertile looking women, while women seek older men with good status and resources. Men are naturally attuned to competing to form hierarchical coalitions while women are broadly better at egalitarian emotional networking. Both sexes however display competition and cooperation, hierarchies and coalitions, depending on the circumstances, and individual human variation is anyway greater than that between the sexes as a whole. The central nature of the sexual relationship in generating loving good-nature, raises a root question of whether external social control imposed by law and punishment, or the positive filtering of socio-sexual bonding is how society redeems itself, or whether the lubricious slime of reproductive sex is our royal route to the consummation of love. This requires a reevaluation of society as a product of human personal interaction, rather than a collective structure imposed upon us.

Bonobo affection (de Waal and Lanting [R163](#)). As of 2003 projections, all Chimp and Gorilla species may become extinct in the wild within 20 years as a result of the bush-meat industry, habitat damage and ebola.

Part of the evolutionary endowment of human nature is to be sensitively astute at detecting cheating and betrayal and to show personal judgement in balancing real or implied retribution for perceived wrongs, sufficient to avoid exploitation, but tempered with forgiveness and bonding. Defection is as natural a complement to cooperation as chaos is to order, essential to complexity itself. Defection can be creative in a healthy society, where it is outright dangerous in an alienated one subject to inequity and violent repression. Art and music in one society can be perceived as subversion in another.

The source nature of sexual selection in goodness raises serious questions about the concept of original sin. Our society has been dominated for the last 4000 years by themes of male dominion expressed towards woman and nature, in the Eden myth, and in laws and social and religious institutions, from the code of Hammurabi, which prescribes death by drowning for adultery, on down. Our social institutions reflect most closely the hierarchies of dominant male troops. The fight between God and the devil is a male combat myth. Wars and genocide are committed predominantly by men. The competitive nature of capitalism and its boom and bust winner-take-all exploitation are precisely the male reproductive strategy without the balance of female long-term investment which is spread among



offspring and over time in a more sustainable way. The rule of law and the imposition of social control are also central characteristics of the alpha male hierarchy.

Roughgarden ([R593](#)), citing the examples of animal 'homosexuality' (Bagemihl [R33](#)), and the biology of sex-changing species ([p 340](#)), has proposed that social selection, including same-sex bonding ([p 384](#)), acts as a major filter to reproductive opportunity. Roughgarden takes issue with the primacy of sexual selection and even goes as far as saying 'sexual selection should be tossed out completely' on the basis of sex changes and the occasional incidence of same sex 'relations' in the natural world:

There are two glaring flaws in Darwin's thinking. In 1871 he wrote, 'Females choose mates' who are 'more attractive ... vigorous and well-armed' just as 'man can give beauty ...to his male poultry' by selective breeding. Hence the peacock's tail, Darwin's frequent example, is supposed to reflect peahen taste in male fashion, and antlers a preference for strong warrior stags. 'Males of almost all animals have stronger passions than females,' he wrote, and, 'The female ... with the rarest of exceptions is less eager than the male... she is coy.' In Darwin's view, males and females almost universally conform to their preordained roles of horny handsome warriors and discreetly discerning

damsels. But the real world is far more diverse than that. In many species, including ours, females are not necessarily less eager than males, nor do females all yearn for Arnold Schwarzenegger. Females often solicit males, and males often decline. Moreover, in many species the supposed sex roles reverse. Even Darwin acknowledged species of birds, like the jacana, in which the females are highly ornamented and the males dull and drab, reversing the peafowl story.

In highly social animals with pronounced sexual activity, such as bonobos ([p 66](#)), female reproductive opportunity is influenced by social selection. Participating in same-sex favours which strengthen female coalitions is a key step in social integration for a young exogamous female joining a new troop. Bonobo female-female sexual bonding is strongly linked to the conflict of reproductive interests between female and male in a unique society in which female exogamy combines with female 'dominance' through female coalitions, tipping the sexual dominance from males as in chimps ([p 63](#)) to females.

Female Spotted Hyena female with pseudo-penis
(Scientific American Jan 94 102)



However many species have only a short estrus mating season, and engage in social grooming and amatory behaviors which are not explicitly sexual. This applies to the spotted hyena *Crocuta crocuta*, another species noted for its gender bending, whose dominant aggressive females are 10-20% larger than the males. The hyena is at an extreme of a pattern of female dominance and masculinization common to several mammalian species. One-quarter of mammalian families contain species in which females are larger than males, and there are other female mammals with genitals that are masculinized to some degree, including the spider monkey and European mole. Spotted hyenas have an elongated penis-like vagina, complete with a false scrotum which makes them almost indistinguishable from a male (Gould [R251](#)). Consequently their angular birth canal, makes birth a perilous process, with infant mortality up to 40% in first births (Hrdy [R330](#) 51). The pseudopenis is unable to accommodate the first birth and the end is inevitably torn open during the first delivery. It is erectile and functions as a 'tool' of social appeasement and familiarization. Subdominant males and females expose their genitals in a paradoxical sign in which erection signals submission, rather than desire, risking serious reproductive injury if the dominant female fails to acknowledge the submission.

However estrus is brief and these encounters are not sexual, but social processes to appease aggression in a mammal so uniquely violent that newborn twins tear at one another, leaving bleeding puncture wounds that frequently result in one or other starving from fear (Meadows [R465](#)). Up to a quarter of all young die in this way. The masculinization of the female begins in utero with the conversion of the androstenedione steroid synthesis pathway in the placenta from estrogen to testosterone. However treatments that reduce penis size in other species - prenatal exposure to compounds that inhibit androgens, and castration before puberty - have little effect on genital size in either sex in spotted hyenas, suggesting other genetic mechanisms are involved. The explanation that hyenas are aggressive group feeders whose high-ranking females enforce strict dominance is also common to several mammal species which do not display these traits. Although a successfully aggressive species, moving from scavenging to predation of animals as large as wildebeast, many of the spotted hyena's characteristics are a direct consequence of adapting to the genetic and hormonal sequelae of female masculinization, whose high costs in many respects are offset by their predatory niche.

The intriguing examples of sex change in reef fish ([p 340](#)), while allowing social factors to influence non-chromosomal sex determination, still hold true to the principles of the Prisoners' Dilemma of sexual selection. Hermaphroditism and socially-driven sex change are adaptations to ensure heterosexual reproductive sex is facilitated under situations of social stratification, which limit opportunities for mating, and are antipodally opposite to same-sex socio-sexual bonding. Neither the natural incidence of hermaphroditism, widespread in plants, as well as animal species such as snails and worms, nor socially driven sex change undermines the power and directness of sexual selection. Nor does it establish that the peacock's tail is to impress other male peacocks, rather than the untamably choosy retinas of peahens seeking sensitive indicators of fitness. Nor does an incidence of frequent socio-sexual bonding, including same-sex couplings, in a few social species such as bonobo, mean that social selection takes primacy, to the exclusion of sexual selection, nor that sexuality is primarily for social bonding rather than reproductive fitness and the survival of successive generations. Only in so far as these two come together, with sexual selection in full play, does the whole process make evolutionary sense.

Original Virtue and the Evolution of Love

In "The Origins of Virtue", Matt Ridley ([R578](#)) explores what causes moral sentiment and social altruism, given an organism which, at the genetic level, might appear to be a bundle of selfish genes. Pivotal to this idea is the common role of emotion. Ridley casts moral sentiments in the practical light of reciprocal exchange and cites the work of Cosmides and Tooby as portraying the deep role detecting cheating has in maintaining commitment and transactional 'trust' in social groups. The great sensitivity of humans to tests defined in terms of deceit and fidelity such as the Wason test tends to emphasize how sophisticated our social sense of long-term commitment is in the shifting interplay of human liaisons.

The pendulum having swung to some extent away from notions of group selection and survival of the species towards survival of genes, we have to investigate all forms of social altruism in a genetic context. We have already discussed Hamilton's concept of kin altruism (p 19). Because we share our genes sexually, most species display forms of kin altruism in which for example crocodiles will carefully protect their offspring in their mouths. Obviously if each of our offspring contains half our genes, our genes' survival is furthered by making a 50% investment in each of our offspring of that we make in our own survival. The same argument applies to our siblings. The extension of this by Trivers to reciprocal altruism (p 19) still falls within strict guidelines of reciprocal exchange, which is initially detrimental to the initiator, eliminating simultaneous mutual cooperation as potentially self-serving.

This leaves a heritage, which at face value falls short of the universal love expressed in the notion of divine union. It abets a society where unrelated competing individuals may take the expedient route and try to do away with their competitors, or take advantage of them in hard-nosed competition. It does not immediately lead to humanitarian compassion for the unrelated 'other' in plight. Defection always emerges as a competitor to cooperation in any game theoretic situation. However humanity has also evolved in ways which promote a resolution of this social dilemma. Much of human social evolution has been to do with learning when people in our immediate personal lives are trustworthy and distinguishing deceit from sincerity. We are also endowed with a strong urge for meaning and a place in life and for partnership. We are emotional and yearn for sexual and filial love.

Emotions are a common currency of declaring commitment and revealing about our personal situations and intentions sufficiently enough to facilitate cooperation socially, which is conducive to a common interest which compensates for the supposed selfishness at the level of the gene and to a certain extent also in the genetic competition between individuals. Emotions themselves thus form a central arena where moral sentiments gain credible biological meaning and explain why, despite a twenty times higher level of violence in males than females, humans are nevertheless far less violent to one another on an individual footing than many animal societies. The discovery of 'mirror neurons' (p 379) puts this universality of emotions, and along with it the capacity to make strategic choices about the way other individuals are behaving on to a sound physiological footing.

The idea that we have original virtue is central to this perspective. Although organisms act to conserve and replicate their genetic identities, the evolution of the mammalian emotional 'limbic' system has set the stage for the evolution of love. Although we further our own personal and family interests, we have evolved to be emotionally responsive in a way which gives us all an evolutionary advantage through constructive social cooperation. It is from the development of universal algorithms in the mammalian emotional system that our emotional view of the world and society derives and our paradoxical mix of freedom of choice, guilt, compassion, empathy and expedience. This system is also closely coupled with one which links peak emotional experiences with spiritual feelings of great significance in the links between the limbic system and temporal lobes, suggesting the religious imperative may be a social expression of a genetic trait towards coherent societies with a sense of common meaning and destiny, illustrated by seemingly paradoxical acts such as altruistic punishment of defectors at cost to the individual (p 377).

As we have noted, evolutionary game theorists have drawn attention to the need to realistically picture the evolutionary stability of any strategy to test questions of altruism and survival in an environment of cooperators and defectors (p 13). Many of these games bear very directly on the central moral teachings of Judaism and Jesus. A very effective game strategy is tit-for-tat. This manifests in cooperative and retributive forms "an eye for an eye and a tooth for a tooth". For a significant initial period, tit-for-tat was extolled as an evolutionarily stable strategy, but it is prone to wasteful internecine strife and costly vendettas. So there are strategies which are more compassionate but don't go so far as saying if you slap me I will always turn my cheek. For example firm-but-fair makes sorties out of tit-for-tat loops to see if cooperation might be insightful to the 'opponent'. This is taking us to territory right in the grey area between Jesus frank "love your enemies even to the point of martyrdom" and Leviticus' "love your neighbour as yourself", or Jesus' "do unto others as you would they should do unto you", or as Hillel said more protectively before him "Do not do unto others as you would they should not do unto you".

The idea of fair punishment has been found to help maintain altruism in human groups (Fehr and Rockenbach R206). Costly punishment has been deduced to be a driver of altruism across diverse cultures (Henrich et. al. R308, Pain R527). An egalitarian sense of fair play is shared by chimps and capuchins as well as humans, with a similar sense of justification for gains and protestation at discrimination (R82). Strategic bluffing is also characteristic of such large brained primates. People playing an investing game with real money rapidly abandoned their altruistic behaviour if they felt the punishment given for selfish acts was unwarranted, suggesting that groups of our ancestors who found the best strategies to promote altruism prospered, and bequeathed their behaviours to us. In an anonymous investing game, the 'investor' can invest up to 10 'dollars' with a 'trustee', requesting a specific rate of return. The trustee receives triple the investment put in by the investor and then can choose how much, if any, to return. Even though anonymous trustees could have just kept the investment without being identified, 19 out of 24 of them returned some money. And the more money invested - implying faith in the trustee by the investor - the more they returned. Next, the researchers gave the investors the option of setting a punishment for the trustee in advance, if they did not return the amount asked for - a fine of four 'dollars'. Choosing not to impose any punishment went down well with the trustees - they gave back 50 per cent more money on average. They feel an obligation to pay back, because they have been treated nicely by the investor. But, crucially, trustees make a distinction between fair and unfair punishments. When the requested return is low, meaning the trustee will make more than the investor, imposing a fine did not significantly change the payoff. However, if the investor is more greedy and asks for a large return that leaves the trustee worse off, then an additional threat of punishment makes trustees slash their payouts by nearly two thirds. If people feel the punishment is fair, they cooperate, but defect against an unfair punishment.

Intriguingly hormones can alter the whole strategic basis of the game. In a variant of the trustee game (Kosfeld et. al. R390, R145), 45% of those sniffing oxytocin (p 352) entrusted all their funds to the trustee while only 12% of those on a placebo did so, probably because it helps overcome avoidance behavior and helps cement emotional bonding. Paradoxically oxytocin is also liable to promote group-serving dishonesty. Participants receiving oxytocin lied more to benefit their groups, did so quicker, and did so without expectation of reciprocal dishonesty from their group members. A control setting ruled out that oxytocin drives self-serving dishonesty (Shalvi, S de Dreu C 2014 Oxytocin promotes group-serving dishonesty PNAS 111/15 5503-5507, doi: 10.1073/pnas.1400724111). However it has been claimed that some of these studies have failed to be replicated and that the claims persist due to publishing bias (Oxenham S 2016 Everything you've heard about sniffing oxytocin might be wrong New Scientist 16 May).

Geoffrey Miller (R475) proposes an antidote to the dilemma of selfishness, ingenious in its explanation at a single stroke of the ultimate origins of compassionate generosity beyond any form of kin or reciprocal altruism. This is the positive filter of sexual selection for generosity as a genuinely costly indicator of genetic fitness which is also conducive to social harmony and affectionate loving nature. If our potential sexual partners choose tokens of fitness which result in uncheatable expressions of generosity, not only will we choose a fit resourceful partner but we will have a fulfilling partnership whose offspring have an excellent chance of survival. From this source original virtue flows like an eternal spring.

In this context, mammals have evolved a new type of evolutionary response to the question of genetic altruism through the limbic emotional brain. By endowing us with emotions it has become possible for us to respond with an emotional kinship which is far more subtle than instinctual genetic responses. We can respond fully to one another as devoted friends, not just because we further direct reciprocal altruism but because the emotional landscape of friendship is a type of resource made possible by emotional bonding, which is a win-win situation for survival and for coexistence. Although mammals do display shocking behaviour such as a cat playing with a mouse, or killer whale batting a baby seal to death for sport, these generally have a survival explanation in maintaining good hunting prowess and motivation, so that they do not constitute the evil of tooth and claw, but life attuned to the hunt. The limbic system is capable of experiencing all the states of emotion from the heaven of divine ecstasy, to the hell of fear at impending doom. Within this magnificent and terrifying spectrum lie all the colours of emotion from true love, through to heated infatuation, jealousy, and guilt to anger, hate and mortal dread. We have thus been fully-equipped to experience the entire ecosystemic condition as sentient beings.

We have evolved to be capable of universal love through wisdom, through the coevolution of the limbic system and neocortex. This love is not locked in endless battle with hate, it is the win-win healing of the mortal dread of hate in peaceful coexistence. Through our wisdom we can heal the human condition to make the human passage of incarnation a loving and sacred experience of minimal pain and maximal fulfillment. This does not require moral conditioning and the rule of law and punishment alone to achieve, but an appreciation for the integrating power of love as a consensual integrative process by which we can come to be able to experience the universe in a way which promotes constructive harmony and compassionate responsibility for our actions.

The transition to love is however an act of choice for each of us. We are all capable of selfishness and calculated unfeeling expedience, particularly when we can exercise winner-take-all advantage by stealth and greed. This is the 'evil' within that we need stand firmly but fairly against in ourselves and in our dealings with others, so that we can fulfill the collective unfolding of cooperative emotional love. In this sense we can say that god is really love. The 'evil' within is not an active satanic force, but a form of defection which we have the free choice not to exercise - our powers of selfish or unfeeling exploitation or pleasure at the expense of others. The universe has evolved so that we have the free will to love and are genetically-endowed to be capable of love as the fabric of the continuity of life.

The universe has thus evolved to make us capable of love, destined even. One can argue that powerful evolutionary selection for both sensual and compassionate love, and with it what William Blake called 'incarnational jouissance' - the whole panoply of sexual and emotional pleasure - has occurred because, given our increasingly self-conscious freedom of choice, it is only beings endowed with such richly motivating emotional experiences who have the innate capacity to evoke a comprehensive and coherent tenacity for survival amid the vagaries of an existence caught in the mortal coil.

Being of good character, agreeable, consistent, fair and trustworthy, especially when the chips are down, is to be trusted, loved and sought after as an adviser, comrade and social leader. Mediating conflict in others is a key asset in the quest for a secure social position. There is even honour among thieves, as the saying goes - the key to the Prisoners' Dilemma.. Thus even if we accept a Machiavellian Intelligence hypothesis (Whiten and Byrne [R742](#)) including tactical deception, as lying at the root of human complexity, and with it, all of Alexander's arguments about inter-group morality being driven by intra-group competition ([p.14](#)), such astute responses as Machiavellian intelligence inspires are likely to embrace genuine indicators of cooperative trust to espouse a win-win, as well as opportunistic covert defection for strategic gain. The filtering by natural selection proposed by Sarah Hrdy, in which maternal ambivalence is attuned to the long term survival of a mother and her descendents applies to all social contracts and to both sexes. We all make a trade off between good character and expedience and we do so trading immediate opportunities for long-term advantages in social standing and the survival of our offspring.

Variance in altruism has been found in a study of 322 twins to have a 42% genetic basis for socially responsible behaviour, with 23% coming from the shared family environment and a further 35% coming from peer group and other non-shared factors Rushton ([R601](#)) . Rushton notes: "goodness is somewhat inherent in people. We all join groups and we all want to do the right thing by our group ... there's even honour among thieves." Overall women had higher social responsibility and parents seems to invest more in the social responsibility of their daughters, claiming "boys will be boys". The effect of the family environment is contradicted in some other studies. We thus see both our evolutionary heritage and our culture have strong influences on our human 'goodness'.

Human love is multidimensional. We start by falling in love and continue from sexual infatuation to a close emotional partnership and for many of us, the fulfillment of sexual love in reproduction, leading to a long-term or lifetime adventure of coexistence:

Stay me with apples, for I am sick with love.

These sentiments elaborate down and across the generations in love between parent and child, filial familial love and propensity for good character. Sexual love is more than just reproduction. It is the most powerful force of social bonding in humans, not just a programmed instinct in the reproductive cycle. Sexuality and socialization intermingle psychosexually. Society revolves around the power of sexual love, in song and human drama, from comedy through passion to tragedy. It is also the object of patriarchal religious edict, and violent oppression, because of the very untameable nature of the force it is.

The sexual act itself is a physical and not necessarily loving act, as rape and prostitution confirm, but in sexual love the sexual act becomes the complete expression of the complementation of two beings in the immortal continuity of life. However filial love is a virtue also contained in the natural mammalian endowment of the limbic system. Although not all people are moved to tears, many are, when faced with emotional situations of life, death separation and reconciliation which betray a deep will to love dwelling in the human psyche. Joseph wept in secret when his brothers came even as he sorely tested them. Jesus wept. People literally weep for love! People are also moved to compassion witnessing the plight of others and some live to serve the greater good as their fulfillment in life. Although the psyche can show great egotism, when the barriers of love come down, we finally become one. Through an unswerving faith to one another, borne of ice and fire, out of free choice in the transaction of love, we all gain our place in the completion of existence. This is filial love at its highest - love for all humanity and for life in all its forms.

Love drives even deeper to a deep soul love for all beings simply for the mortal tragedy of ours and their existence as birds of fire on the all-too-brief journey of incarnation. This is also the love of the mystic. The heights of epiphany or samadhi are incomplete without the exaltation of divine love pouring as a cataract of light, as a flame of joy, through our very being, convulsed by the power, gentility, grace and peace of the divine condition and the utter compassion showed by the universe to all incarnate beings. This is also a journey of infinite sadness for all mortal beings, but is also a reconciliation and reunion in atonement for all of us - the homecoming. The mystery of mysteries is that we have evolved into this condition. Key to this is a cosmic change of perspective. The only living strategy with any real future is to participate in the flowering of evolutionary culture. We are then fully part of the fabric, coming to terms with our cosmic responsibility for our actions, as co-creators of the living planet's genetic evolutionary and intentional conscious future.

Human Sexual Strategies, the Breakdown of Sexual Paradox and Patriarchal Dominion

Power is the ultimate aphrodisiac
Henry Kissinger - NY Times Jan 19 1971

In 1967 Johnson astounded several top aides and Interior Secretary Stewart Udall by launching into a tirade about his war. Who the hell was Ho Chi Min to think 'He could push America around'? Then he showed in the most unmistakable manner imaginable just what the war meant to him - and it was literally what Carlin insists the war was all about: 'the bigger dick foreign policy theory'. ... The president unzipped his pants, pulled out the member he had named 'ol' Jumbo' and proclaimed 'Has Ho Chi Min got anything like that?' (McElvaine [R457](#) 311).

Running throughout this whole account is the unspoken green-eyed monster of jealousy and betrayal, which has always been a universal aspect of the prisoners dilemma of cooperation and defection, despite all attempts to banish or destroy defection by force of violent punishment. In a society of faithful wives, one scarlet woman can command a king's fortune. In a society of faithless harlots one faithful wife can expect the Earth. Neither can be eliminated because the very attempt to do so makes the rarer the more precious.

One can however taboo certain actions by threat or exercise of violent retribution. While not eliminating them entirely, this will at least serve to drive them into the covert undergrowth. This is certainly the case with patriarchal dominion. Once large urban societies developed, the rule of law and the patriarchal imperative passed the ascendancy to the male through social and military instruments of power. Male jealousy resulted in adoption of mores which ensured powerful men could secure their own descendents from doubts about paternity which plague the male but are incontestable for the female:

"Momma's baby, Poppa's maybe."

Variation in paternity certainty - the probability that a man is his 'child's' father - can evoke differing forms of society, based either on uncles rearing offspring of their sisters, as with Laban in Genesis, or men rearing the children of their partners, as Jacob chose to do in the patriarchal paradigm. At the critical value of 1/3 the following are equal:

You are related to your 'own' children (by your sexual partner) by $(1/2)(1/3) = (1/6)$.

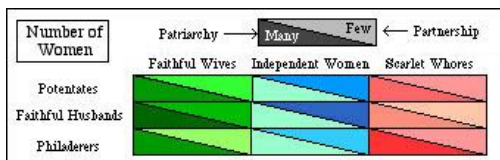
Your relatedness to your "full" sister is at least 1/4 (representing your common mother) plus 1/4 (your putative common father) times the paternity certainty of 1/3, totaling $1/4 + (1/4)(1/3) = 1/3$. Since you thus share 1/3 of your genes with your sister and she provides 1/2 the genes of her children, you are related to her children by $(1/2)(1/3) = 1/6$.

In this situation, sociobiology predicts you will invest equally in both your sister's children and your own, all things being equal, since you are related to both sets of children by 1/6. In societies in which paternity certainty falls under 1/3, you should invest more heavily in your sister's children than your own; if paternity certainty is more than 1/3, you should favor your wife's children (Thompson [R688](#) 57). It is here also that the balance between allo-parenting by kin and partnership has its basic divide. One also has to take into account that all apes are female exogamous, so the matrilineal human model is exceptional and may constitute only a phase of human cultural development associated with early agricultural cultures such as Catal Huyuk ([p 176](#)), though ancient 'venus figurines' ([p 92](#)) may suggest an earlier origin.

Genetic testing (Baker and Bellis [R38](#)) suggests that 10 - 20% of offspring of an ostensible father are sired by another man - a fundamental expression of covert female reproductive choice so central to evolution and to the greater female reproductive investment. This figure has been questioned however by a 2009 study of surnames and Y-chromosome patterns by Mark Jobling and Turi King at the University of Leicester, UK, published in the journal Molecular Biology & Evolution, which suggests only 1 - 4% of children are covertly sired by another male.

If we turn for a moment to the chimpanzee, we will discover that up to half the offspring are sired in secret trysts outside the immediate male group. This happens despite a consistent presence of a dominant alpha male hierarchy seeking to secure reproductive certainty by a variety of strategies from mate guarding to infanticide. The human statistic represents a moderate swing in favour of human male paternity certainty, well above the level that would equally favour men acting as uncles for their sisters children, however it is still enough to cause extreme violence on the part of males who find out they have been cheated and quite sufficient to provoke a sexist backlash against female reproductive choice.

The principal aim of the patriarchy has been to split the female strategy into clearly-separated faithful wives and whores, thus providing procreation and pleasure. The darker the shade, the more women participating. Upper right triangles are for a 'partnership society', lower left show the female strategy largely bifurcated (divided) by moral edict.



The [Rock-Paper-Scissors](#) like three-way game matrix (left) illustrates three strategies each for woman and men. In a population of faithful wives a rare scarlet woman can have all she asks for. Conversely, a faithful wife is a prized asset in a society of loose women. This rareness factor prevents the annihilation of either strategy and is a common feature of the Prisoners' Dilemma, exemplified in polyphenic species ([p 33](#)). This phenomenon in evolution is called "negative frequency-dependent sexual selection". A high ranking male may gather a harem, or he may attract an additional concubine, or 'kept woman'. A lower ranking male may choose to be 'dad' declaring as a faithful husband to retain the fidelity of his wife. Others will adopt the 'cad' strategy of loving 'em and leaving 'em. Evolutionary mechanisms for such polymorphic traits in humans and other organisms have been elucidated (PLOS Computational Biology doi:10.1371/journal.pcbi.1005006).

The principal thrust of patriarchy is to repress female reproductive choice, which is both pivotal to XY-based sex chromosome evolution and which is essential for women because of the huge parenting investment and danger of human pregnancy lactation and child-rearing and the much smaller number of offspring a woman can nurture by comparison with a powerful or popular male. Invocations against adultery are primarily targeted at women as the 'devils gateway' along with dire punishments such as stoning. Men are happy to exploit both the defecting scarlet women and the faithful wives, but the idea of a female who looks like a faithful wife doing it on the sly with the brawny bloke down at the pub is an anathema to male paternity certainty.

The strategy of deception arises naturally as a function of the strategic bluffing which is the hallmark of the Machiavellian intelligence that enables the complex social niches of larger brained species from capuchins to humans. Virtually all social concourse and the tests of good character revolve around detecting subtle social signals indicating whether a person can be trusted in a climate of charisma and spin. Machiavellian intelligence complements the genuine indicators of fitness involved in the sexual complementation of courtship - the "mating mind" - of good husbanding and astute reproductive choice based on sexual love. Strategic bluffing is a form of strategic

deception designed to increase the existing payoffs from a broadly cooperative milieu by taking advantage of easily deceived participants of low cast. The end result is that deceit plays a central role as a third option in all human societies despite being demonized as the purveyor of betrayal.

It is easy to see how in both men and women for differing reasons, temptation to form an external liaison can enter into a committed relationship partly because it is perceived as an additional bonus. In men it is a natural part of the core investment in reproduction at the expense of parenting because a man can get many women pregnant. As existing relationships become a burden it is also easy to see how deception can also give way to outright defection, when a man finds his wild oats investment is more suited to his power and sexual charisma.

For women not putting all one's eggs in one possibly inferior genetic basket can lead to a form of deceit in which a resource-bearing male complements an outsired child in perhaps ten to twenty percent of pregnancies, leading to continuing paternity uncertainty on the part of jealous men. Likewise a scarlet woman, although good fare for sex play is defecting both against the reproductive paternity of the opposite sex and the institution of faithful 'marriage' which defines sexual fidelity by custom.

We thus effectively end up with a complex sexual dynamic of prisoners' dilemma strategies between the conflicting reproductive investments of the two sexes amid a rock-paper-scissors cyclic dominance in each sex's strategic milieu.

An explanation for the scarlet woman - faithful wife equilibrium, in which each becomes more valuable as a function of their rarity, comes from recent research into handedness. As of 2010 a slew of research has emerged, which shows that handedness is not just confined to humans, but extends widely throughout the 'bilaterally-symmetric' animal kingdom spanning arthropods and vertebrates. Vertebrates from fish through birds to mammals are liable to hunt or forage with their right eyes and look for predators with their left, which allows brain areas in each cortex to become better adapted at serving each of these challenges. Prisoner's dilemma game theory simulations show that the safety in numbers when many members of a species adopt the same asymmetric strategy is offset to the best advantage of all players when there is a smaller subpopulation adopting the contralateral strategy thus confusing the predator without becoming a primary target ([Southpaws: The evolution of Handedness 2010 Nora Schultz New Scientist](#)).

As we have seen, males specializing in both declared enticement and sneak mate capture occur in many species, from crickets to salmon. In some species these strategies can become entrenched in polyphenism where individuals of a given mating type sport distinct physiologies ([p 33](#)). Male orangs have two physiologies, a macho dominant male and a sub-dominant sneak rapist (Hrdy [R330 76](#)). Women likewise can adopt several strategies between being 'fast and loose' attracting a temporary mate for immediate gain or a longer term strategy of ostensible monogamy seeking a longer-term resource-bearing partner. Somewhere in between, particularly in matrilineal societies, a woman may decide to retain her own independent status of reproductive choice. As a result of sexual privacy, covert affairs may occur in any of these situations. Such a game theoretic model is supported at a deeper genetic level. It has been found in a study of 3200 women - all identical or non-identical twins, by Tim Spector (Twin Research 2004, [R655](#)) that there is a genetic basis for female infidelity, contributing 40% of the variance discovered. There is not a single infidelity gene, but 50 to 100 genes are important, although the researchers managed to pinpoint some of the traits to 3 of the 23 pairs of human chromosomes. The study suggests that a genetic predisposition towards female infidelity may have evolved because it was important in allowing women married to 'low-status' men surreptitiously to become pregnant by 'high-status' men. Spector notes: "Work in the UK has shown that human females generally have affairs with men of higher status than their husbands, perhaps illustrating an effort to mate with a genetically superior partner," consistent with hypergamy (p 30). Slightly more than 20 per cent admitted to being unfaithful in a stable relationship. Some reported no extra-marital affairs or no sexual partners but others said they had had more than 100 sex partners, the average number being between 4 and 5.

If female infidelity and number of sexual partners are under considerable genetic influence, as this study demonstrates, the logical conclusion is that these behaviours persist because they have been evolutionary advantageous for women.

In an intriguing reflection of the 'dads' and 'cads' male strategy it has been reported that daughters growing up without fathers present reach menarche earlier, suggesting that they may be primed by their early experiences to adopt a more opportunistic 'loose' reproductive strategy based on short term gains in mates, becoming sexually active earlier and with more different partners. This is the opposite of most primates where 'low-ranking' females under stress delay puberty, presumably because of their more perilous reproductive prospects. This has caused some to question whether the effect is simply a maternally-inherited short term investment strategy ([R330 189](#)). Noting that precocious sexual maturity can make a girl popular with boys and rejected by other girls in discussing female competition, Anne Campbell ([R103 193](#)) comments "early maturing girls have a distinct advantage in terms of mate selection. They garner a disproportionate amount of male interest and by entering the mate market earlier, have a wider choice of prospective men."

"The dizzying diversity of human sexual strategies" has been highlighted by a number of studies ([New Sci 29 Nov 2008 32-35](#)). Some people level in a reputation as a Casanova and others proudly proclaim their chastity. But most of us probably prefer not to advertise our sexual proclivities. Still, if you think your attitudes to sex are a private affair consider this. Earlier this year, Lynda Boothroyd of the University of Durham, UK, and colleagues published a study showing that the majority of men and women were able to accurately judge whether a person would be a good bet for a committed relationship or were more interested in a fling, just by looking at a photograph of their face.

Men tend to score high on the sociosexuality scale more often than women. Although men often invest considerably in their offspring, all they actually have to do to father a child is have sex, so there has been strong evolutionary pressure for men to be open to short-term relationships. Women, on the other hand, bear the heavy costs of pregnancy and breastfeeding, and in every culture they tend to do the bulk of childcare. So they are best off being choosy about sexual partners.

Several studies have shown that women are more likely to fancy a fling around the time they are ovulating - although there is no suggestion that this is a conscious decision. Women also show a shift in preference to men who look more masculine and symmetrical - both indicators of good genes. Women may have a dual strategy going, suggests David Schmitt of Bradley University, Illinois. "Humans infants need a lot of help, so we have pair-bonding where males and females help raise a child, but the woman can obtain good genes - perhaps better genes than from the husband - through short-term mating right before ovulation."

Boothroyd found men with more masculine-looking faces scored higher on sociosexuality, and it seems to be the same story for women. Sarah Mikach and Michael Bailey of Northwestern University in Evanston, Illinois, examined how women's sociosexuality related to the degree to which they looked, felt or behaved in a masculine way. They found that heterosexual women who had high numbers of sexual partners were more likely to show higher levels of masculinity.

Peter Gray of the University of Nevada in Las Vegas and his colleagues found that saliva samples taken from married men and fathers contained lower levels of testosterone than in other men. Since testosterone is associated with competitive and mating behaviour in a wide range of mammals, the researchers proposed that lower testosterone in fathers allows them to channel more of their energy into their children (Evolution and Human Behavior, 23, 193).

Fhionna Moore at the University of St Andrews, UK, has also shown that a woman's status affects her choice of sexual partner. She found that women with a high level of control over their own finances tend to place higher importance on physical attractiveness in a man than on his financial prospects.

In a survey of 48 countries, David Schmitt found the higher the number of men relative to women in a particular society, the less promiscuous the culture was. So for instance, in east Asian countries such as China, Japan and South Korea, where the population is heavily male biased there is a relatively low level of interest in uncommitted, casual sex. Meanwhile, urban areas of the US with low ratios of men to women, had a correspondingly high level of short-term relationships and divorce.

In an attempt to study innate sexual preferences in a gatherer-hunter group still isolated from TV and other cultural influences, oren Apicella took voice recordings of [Hadza](#) women and men saying 'Hujambo', which means 'hello' and also documented their reproductive history - how many children the men had fathered. She found that males who hit lower notes as they talked had about two more children on average than squeaky speakers. Deep tones are suggestive of increased testosterone levels, which could lead females to perceive such men as better hunters and therefore better providers, "Or it could be that men with deeper voices simply start reproducing earlier. ... Puts thinks that deeper voices might be more important for asserting dominance than wooing females. Experimental alterations in male voice pitch affect male perceptions far more than those of females, he has found. It makes a guy look like he could win fights, and it makes him a little bit more attractive to women." There were no corresponding differences in female voices. Subsequently she found women nursing a child prefer higher-pitched male voices than fertile women who had not recently given birth, possibly because these men are better child care providers. (Proc. Royal Soc. B DOI: 10.1098/rspb.2008.1542)

The key issue in human culture historically is the imposition of stark divisions on the female sex in the rise of patriarchal dominance. With the emergence of the early urban cultures, male power became enforced by militarization and a simultaneous application of religious and legal edicts under pain of violence and death. The patriarchal imperative seeks to reinforce paternity certainty by rejecting the cultural predicates of matriarchal succession, driving a wedge into the female population to clearly separate women between two exclusive archetypes of the faithful wife for reproduction and the scarlet whore for sexual pleasure, with no ambiguities in between; removing male vulnerability, by threat of death against loss of the tokens of virginity and adultery, in which the female is particularly vulnerable, given stipulations, such as not having cried out. The 'whoring' mixed fertility rites of the goddess and her consort by their many and various names are outlawed by degrees. Imposition of patriarchal dominance would appear to remove the mortal dread men have that their children are not really theirs, but it abets forms of male power which gives some men a disproportionate share of the reproductive resources, as well. The patriarchal imperative does not stop simply with the issue of resolving paternity uncertainty. As power passes to the dominant males, themes of male competition lead to religious and social ideas based on exclusive male domination, the combat between light and dark, jealousy and violence, arms races, expansionist wars, exploitation of resources, and the establishment of hierarchical means of control by the threat and use of force. Mutual grooming and friendship gives way to aggression, abuse and enslavement.

Coupled with the patriarchal imperative are a nexus of effects, all associated with the breakdown of mutual sexual paradox into paradigms of domination - dominion over woman and nature alike. These have been expressed in social power structures, religion, and the rule of law. Patriarchal societies no longer invest cooperatively in abundance, but seek to conquer in unrestrained growth, through militarization, exhortations to population growth, attitudes towards girl children which give males who can be used in combat higher status. They abet attitudes of winner-take-all exploitation, boom and bust, rape of the planet and ultimately that cosmic high noon of male combat myth the apocalypse of armageddon and the final day of judgement, the 'rapture' and discarding of the entire natural realm as a husk of the germ of God's will. The result is a frankly unsustainable paradigm of the rule of order in which complexity and diversity atrophy in a war of attrition whose results are scarcity, inequity and further competition or perhaps the final darkness of extinction. The myth of man the hunter thus has its final nemesis, in man the grim reaper of his own misfortune. The Prisoners' Dilemma teaches us that the only sustainable respite from such mutual nemesis is to restore sexual paradox to its condition of climax diversity.

The example of the bonobo ([p 66](#)) shows us that social sexuality can act powerfully enough on reproductive choice (and hence reproductive sexuality) to shape it sufficiently to cause a runaway inverse peacock's tail in the form of their enlarged clitorises and ecstatic female-female sexual hoka-hoka. However here social sexuality is integrated with the reproductive sexuality of the bonobo matriarchs and is thus not acting against it. Rather the two sexes, caught in a Prisoners' Dilemma game by virtue of their reproductive interdependence, each try to shape social sexuality to their own advantage. In the bonobo's case, the females have gained a relative advantage of female social sexual bonding aiding strategic support in dealing with the opposite sex. In some ways the classical Greek male sexual infatuation with the intrinsic superiority of the male sex ([p 202](#)) is a cultural equivalent of the bonobo female strategy, however the human clitoris, far from being a spandrel as some suggest ([p 86](#)), has also had a heady influence on human social sexuality and romantic and family bonding that is key to sexual paradox in our cultural emergence.

The fabric of sexual relations and all the phenomena and styles of relationship, from monogamous devotion, through polygamy, serial monogamy (leading to polygyny in another form), promiscuity (newly packaged in the swingers' lifestyle) and bisexuality (as an extension of sexual openness) are ultimately manifestations of the ongoing reproductive prisoners' dilemma game between the sexes, extended into its social themes of trust and betrayal in relationship, love and security, as well as adventure, conquest and ultimately Tantric fusion. Polyamory intriguingly tries to invert the game and its contradictions by redefining betrayal as cooperation in an atmosphere of heightened trust, adding profoundly to the fluidity and instability of an already chaotic untameable force of life.

In humans, social sexuality has become a Machivellian and often violent field of contest and conflict over its influence on the reproductive life of the sexes through the bon ding and allegiances it invokes. The Old Testament patriarchal invections by God against Laban's matrilocal traditions ([p 189](#)), the whoring ways of the fertility Goddess ([p 214](#)) and the associated homosexuality around the temple, are all part of a central Prisoners' Dilemma game, in which the world's major religions, and cultures and empires have risen and fallen by their reactions to social sexuality in their attempts to control the reproductive choice of women and male access to their reproductive capacity. This contest leads to the very precipice of apocalypse, in an inevitable Rape of the Planet, and the mortal male combat of Mutually-assured Destruction and the War on Terror.

Parental Investment and Mother-Child Conflicts of Interest

Sarah Hrdy ([R330](#) 42) points out that selection of mothering traits is central to the equation of sexual evolution, particularly in mammals. "Over the course of her life, a female bound for fitness is required to make a series of physiological and developmental 'decisions' about

how big to grow, when to mature, how soon to reproduce, and how much time to allow between offspring. One of the biggest challenges for understanding selection pressures on mother that confronted sociobiologists in the early years was getting the balance right between considering traits that are sexually-selected (for example through female choice or male choice) and equally important, if not more important, female traits that are naturally selected because they increased survival of the mother and her offspring." Females are thus applying a variety of skills in raising and caring for their offspring, all of which are critical and subject to natural selection for successful mothers in addition to sexual selection. In considering the question of reproductive sexual paradox we have to understand it not just in terms of sexual selection, but in terms of the overall reproductive strategies of each sex and their combined mating and parental investments. Sexual paradox is not thus a paradox of sexual selection but complete reproductive investment.

Although the female, particularly in gestating, lactating mammals invests more directly in parenting, the male's overall reproductive success is measured in offspring survival as well. Although a male elephant seal is primarily making a mating investment, his actions are part of a successful reproductive strategy in which his efforts are also indirectly parental. By providing a large harem with a warm relatively safe nursing space and driving off potentially infanticidal male competitors, and even ironically by killing off other males' competing offspring, he is furthering survival of his own progeny and hence his genes.

In "Mother Nature" Sarah Hrdy ([R330](#)) sets out a monumental account of why maternal ambivalence is a central evolutionary feature of the human condition with a long set of parallels shared in various forms by diverse primates and mammals. Many of these relate closely to the predominantly parental reproductive investment a female mammal makes and the trade-offs involved in dealing with limited resources, insufficient reserves, infanticidal males and the lack of condition and experience of a first time mother. In addition to the conditional mothering we have seen in the monogamous species such as tamarins and titi monkeys, she documents a variety of cases of maternal discretion, from absorption of a pregnancy in many rodents when an alien male makes an incursion which signals the threat of infanticide ([R330](#) 89), to maternal infanticide. In the monogamous California mouse a mother who loses her partner may kill the pups rather than try to rear them alone. This species is reputedly also monogamously faithful reflecting the fact that a bonded pair can raise four times as many offspring as a lone mother. Likewise to abandonment or even participatory cannibalism occurs in about one in ten prairie dogs when a pregnancy results in a newborn for whom the mother has insufficient resources ([R330](#) 93). Weddell seals likewise often abandon their first set of pups because they have not accumulated enough fat to support them through the nursing season, where they have little opportunity to feed.

Hrdy exposes a litany of forms of frequently resource-based maternal ambivalence in human practices of exposure, infanticide, and very large scale abandonment in European societies during the Christian era, which run completely counter to our idealistic notions of maternal devotion to the ultimate blessing of helpless dependent lovable yet demanding infants. Hrdy ([R330](#) 345) suggests that fixed strategies in other mammals such as reabsorbing a litter in mice and the biasing of sex ratios, for example in wasps are transferred to a discriminating maternal ambivalence in humans which leaves a decision whether to keep an offspring of a given sex to the last feasible moment, allowing for greater responsiveness to ecological and social contingencies. The consistent theme of this work is that, despite two conflicting views one of 'essentialist maternal instinct' and the other a cultural 'blank slate', human mothering responses are contingent, varied and a natural consequence of Hamilton's rule. "The cost function of Hamilton's rule calls [mother-infant harmony] into question. Instead of viewing it as an abnormality, a pathology to be treated, sociobiologists accept some degree of maternal ambivalence as inevitable. ... For as designed by Mother Nature, the delectability of infants seduces to quite different ends [from consuming them] ... to be consumed by them, to give up bodily resources, and time ... so that we could all (more or less) take our place at posterity's table" ([R330](#) 539).

In 1972 Robert Trivers ([R703](#)) extended Hamilton's rule of kin altruism to child-parent conflict. A child naturally shares all their own genes but only a quarter to a half those of their maternal siblings, depending on whether they have a common father. A child will thus settle for shared resources or attention only if it benefits a full sibling twice as much as the cost to themselves. Hence the apparent selfish greed of the squalling toddler vying for the attention of the mother makes genetic sense (Hrdy [R330](#) 427). It also applies to discriminating maternal responses to keep or abandon an infant based on its condition and potential impact on the viability of older offspring ([R330](#) 365), something Western society, still under the influence of patriarchal religions and social mind set, has great difficulty coming to terms with. In mammals, Haig's work shows the demands of the child in everything from placental invasion to relative size are partly a function of paternal influences.

Humans with massive pregnancies, difficult births and long periods of lactation and immediate infant care take an excessive toll on the mother. Hrdy ([R330](#) 175) expresses this succinctly as "a tooth for a child." Thus the prisoner's dilemma between mother and child is a direct extension of the sexual tug of war between sexually antagonistic paternal and maternal influences. One can cast this dilemma more generally in terms of parent-child conflict, but in most mammals the male reproductive investment is primarily in mating, rather than parenting and even in strongly pair-bonding humans the mother's child-care investment is primary. In the case of the male we, move from ambivalence to discriminating infanticide. In a large number of mammal species, males will immediately kill any offspring of a female they gain access to as a potential mate. Langurs are cautious and kill only infants which couldn't be theirs, both removing genetic competition and triggering early ovulation and pregnancy of their own offspring ([R330](#) 34). Chimps are less conservative and kill infants who might not be sired by the troop. Male mice have a biological clock which is primed to inhibit infanticide just long enough for a female they have impregnated to come to full term ([R330](#) 89).

It is the mother-child relationship and its implications for female autonomy that became the deepest evolutionary affront to feminist sensibilities. On the one hand we have a traditional patriarchal view, exacerbated by 19th century social Darwinism, of woman as merely a 'reproductive human' destined to be a mother rather than an innovator and expected to possess an unqualified maternal 'instinct' in response to the profound needs for love and security in the human infant, the absence of which is assumed to be a pathological condition. On the other we have a cultural view shared by many feminists, and a generation of anthropologists and sociologists that maternal reactions are culturally determined and that infants have no specific attachment needs but only desires.

Simone de Beauvoir pivotally expressed the concern that biological stereotypes would lead to the "enslavement of the female to the species and the limitations of her various powers". Reacting to attachment theory - the idea that human infants have an innate need for a primary attachment figure in the first years of life - a role that mothers are uniquely qualified to fill caused feminists to define female biological roles as 'essentialist' and to deny that biology is relevant to human affairs or that infants have innate needs for any personalized care on the basis that the human brain and our capacity for culture make us so different from other animals that humans can learn to be anything they choose.

Hrdy ([R330](#) 24) however notes that, although humans can learn a lot, this does not apply without biological restraint to such ancient emotional domains as those involved with 'love'. Nevertheless, the idea took on that maternal love was a socially-constructed sentiment without any biological basis." ([R330](#) 308):

"Decades before the sudden-infant-death-syndrome scandals surfaced in the 1990s, or before data on foundling homes started to be quantified in the 1970s, psychiatrists, historians, and social scientists all noted the poor match between real-life mothers and nineteenth and early twentieth century stereotypes of instinctively nurturing mothers. Feminists in particular had long ago lost patience with Darwinian perspectives that struck them as essentialist and which patently disregarded women's felt experience. They were eager to discount biological explanations, and had little incentive to keep up with what was going on in reproductive ecology or sociobiology. They continued to project on to those fields their own worst assessments about essentialist and determinist assessments of 'female nature' even after biologists had themselves abandoned these types of explanations. The result was that feminist theorists were producing models to explain what was essentially a biological phenomenon (namely the failure of an infant to elicit nurturing responses from its mother) but without any reference to biology. They used the evidence of the high numbers of non-nurturing mothers as a tool to jettison altogether the confining stereotype of the instinctively nurturing mother that had long been used to prescribe social roles for women ... Instead of taking a closer, critical look at the original biologically-based explanations to see if perhaps something had been left out, feminists (along with other social scientists who were trying to explain the widespread practice of abandonment by mothers) patently rejected evolutionary explanations. The biological basis of motherhood was replaced by a new environmentalism. The way a mother feels toward her infant must be solely determined by her cultural milieu. - epitomized by Elizabeth Badinter's comment 'I am not questioning maternal love - I am questioning maternal instinct!'"

This is echoed archetypally in Gerda Lerner's (R407 52) reaction to Freud's statement that for women "anatomy is destiny". "What Freud should have said is that anatomy once was destiny. This statement is accurate and historical. What once was, no longer is so, nor should it be so." Yet this biological destiny remains true for both men and women, so long as we reproduce naturally on the planet. Hrdy continues:

"Growing numbers of women were coming to regard attachment theory, [the idea that a growing infant had strong needs for a close mother] as an anathema. Rarely mentioned in feminist circles, [John] Bowlby's name, when it did come up, was uttered with derision. Why might women have a stake in discrediting research ostensibly focussed on infant well-being? Having panicked often enough myself over whether I could live up to the stiff responsibilities of motherhood I understand why" (R330 489).

Just how sensitive this issue became is etched out by Hrdy (R330 406):

"Compared with Darwin's 'dangerous idea' the evolutionary philosophy that Daniel Dennett has termed 'universal acid' because it cuts so deeply into human conceits about our place in the universe, Bowlby's intellectual acid was less corrosive. Yet for psychoanalysts, for feminists and for any woman with ambitions, it burns very deeply indeed. ... By situating the mother (or primary care taker) at the center of each developing infant's universe, Bowlby's theory of attachment stings most smartly where it pricks the conscience of every mother who is aware of her infant's needs but who aspires to a life beyond bondage to them".

Hrdy notes that the debate over whether or not women have 'maternal instincts' has taken decades to unravel to the point where the patriarchal assumptions of earlier generations of moralists have been corrected and 'Darwin's evolutionary paradigm widened to both sexes. But by this time, feminists, social historians and philosophers were convinced that what evolutionists had to offer was essentially flawed, determinist and unsightful. Natural selection, and with it the most powerful and comprehensive theory available for understanding the basic natures of mothers and infants was rejected, as feminists and social scientists took a path, rejecting biology and science, constructing their own version of wishful thinking about socially constructed men and women, and infants born with merely a 'desire' for mothers rather than a 'need'. Maternal love could then safely be interpreted as a 'gift' consciously bestowed, or a by-product of changing fashions and sentiments. The more multifaceted view of mothers, being developed by biologists, featuring flexible actors whose responses were contingent on circumstances went largely unheeded. "Lost in the shuffle over what it was natural for mother to do and dust ups over bonding and mother love was the infant's often noisy two cents worth "No matter who gives it, I need it. And need it now."

Hrdy (R330 535) notes that Bowlby provided scientific legitimacy to the anxiety, distress terror and finally desolation that infants experience when they fail to detect 'the meeting eyes of love' and that although many of the dangers turn out to be different from those he initially envisioned, his central explanation of how and why infants become attached to their caretakers was on target. He was correct that primate infants, including humans, are born immobile and vulnerable. He rightly pointed out that they respond very poorly to being left alone, or otherwise being made to feel insecure. Human infants have a nearly insatiable desire to be held and to bask in the sense that they are loved. To this extent the needs of human infants are enormous and largely non-negotiable. The question that remains is, what are the implications of this for their mothers? Part of the problem is that there is little agreement about whose interests are to be maximized in a world where conflicting self-interests, are endemic between parents and offspring, between mothers and fathers, within families, between families. Hrdy comments:

"Understandably, perhaps, those most threatened by acknowledging infant needs - mothers with aspirations to do things other than mother - were the ones who felt most compelled to down play infant needs" (R330 493).

We see in this a succinct expression of Hamilton's rule and the extension of sexually antagonistic coevolution striking home directly to the feminist reaction to the mother-child issue in a strategic attempt by mothers, if not to entirely gain control over the infants their reproductive investment depends on, by a culturally relativistic finesse, at least to regain from moralizing males the freedom of choice for that very maternal ambivalence that lies at the root of the Prisoners' Dilemma of long-term survival between mother and offspring.

This discussion of the mother-child relationship raises a further question about the role of the father. Hrdy has proposed that much of the child-rearing effort in early humans was done by allo-mothers or allo-parents - other helpers, such as older daughters, sisters, relatives such as aunts and uncles and reciprocal female friends in addition to or in spite of the father's role, which in most societies does not come anywhere to a near match to the mother's at least in the early years. This follows a mammalian pattern in which mothers who need extra help do so from several sources even in many socially monogamous species. It is notable that in Sandays' (R609) survey of human societies that in most societies fathers were involved only rarely or occasionally with child care.

This leads to another interesting hypothesis. Judith Rich Harris (R292, R293) has all but demolished the socialization theory of parental molding as a process of reward and punishment, however the genetic links between the personalities and many aspects of the mental life of parents and children do have a manifest genetic basis. Her alternative hypothesis - that the peer group forms the major influence on the socialization of the growing child also has a basis in evolutionary sociobiology. As Ridley (R580 259) points out the peer group provides a context for niche diversification and specialization of a growing individual to find skills and specialities a growing person discovers are appreciated and sought after by the group they will spend their early adult life with. The formative influences on children during human emergence are likely to have been a fluid mix of influences from their mother, father, allo-parents, extended family and peer/play group in a small band of gatherer-hunters, rather than a rigid nuclear family structure. We are thus likely to see young humans genetically kin with their parents sharing a vertical affinity across the generations while engaged in a struggle of partial conflict of

interest. At the same time they have an adaptive horizontal social orientation towards the peer groups which will also be essential in their social survival.

The major theme of Ridley's (R580) "Nature via Nurture" is that the biological role is not one of genetic determinism, but of genes adaptively influencing and not rigidly determining a complex conscious neurodynamic response to circumstances. However nature via nurture also implies the nurture needs only to be sufficiently responsive and diverse to allow the natural genetic potentials to emerge. Hrady (R330 378) concurs "Every human mother's response to her infant is influenced by a composite of biological responses of mammalian, primate and human origin. These include endocrinal priming during pregnancy, physical changes (including changes in the brain) during and after birth, the complex feedback loops of lactation, and the cognitive mechanisms that enhance the likelihood of recognizing and learning to prefer kin. But almost none of these responses are automatic. To survive in evolutionary time all of these systems had to pass through the evolutionary crucible so well summarized by Hamilton's rule ... probable costs or benefits are factored in. In humans whose infants are so costly and for whom conscious planning (thanks to the neocortex) is a factor, maternal investment in offspring is complicated by a range of new considerations: cultural expectations, gender roles, sentiments like honour or shame, sex preferences, and the mother's awareness of the future. ... We are still far from understanding how genetically influenced receptors in the brain, thresholds for responding to different chemical signals hormone levels, and feelings of anxiety and contentment interact to produce the myriad 'decisions' that continuously affect maternal development."

But what about species in which the fathers take a disproportionate role in parenting? This would seem to be an evolutionary paradox since sperm are much smaller than eggs in all species, so the male investment is lower.

Darwin was perplexed by species in which males cared for the offspring. In *The Descent of Man, and Selection in Relation to Sex* (1871) he notes that the male emu, "not only performs the whole duty of incubation, but has to defend the young from their mother". He proposed two explanations for such behaviour. Males may have "lost their ardour, so that they no longer search eagerly for their females", putting their efforts into raising their offspring instead. Alternatively, "females have become much more numerous than the males...[so that] it is not improbable that the females would have been led to court the males, instead of being courted by them". However in shore birds such as jacanas, it seems rather to have a close relationship with there being an excess of adult males. Females are polygamous and compete with one another for mates, while males, once mated, care for the offspring rather than take their chances on finding another mate.

Robert Trivers originated the idea that the energetic costs of producing large eggs versus tiny sperm means that from the outset females have invested more in offspring, and caring for young helps them protect that investment. However modern biologists realise that when it comes to parental investment, it is the future that matters, not the past. The idea that parental care can be explained by past investment has come to be known as the "Concorde fallacy" after the failure to realize the Concorde aircraft did not have future profitability. Trivers had a separate explanation for doting fathers - that single fatherhood is common in species where egg fertilisation occurs outside the body. His "cruel bind" hypothesis is based on the idea that whichever sex deposits its gametes last gets stuck looking after the young.

However in some species with paternal care, the delay can only be milliseconds so neither sex is really last. Newer mathematical models offer some alternative explanations (Evolution, 67, p 2207). One reason a male fish might guard the eggs after releasing sperm is to prevent rivals from getting close and fertilising them. In such models, provided males mate with several females and offspring have a high survival rate, paternity doesn't need to be high for male care to evolve. What's important is not the percentage of eggs a male has fertilised, but the total number that are his.

In many birds, parents stuff food into the mouths of each offspring separately, a job that in 90 per cent of species is shared by two parents, sometimes with helpers. Single parents are rare, and exclusive male care occurs in only about 1 per cent of birds. Among teleost fish, although parental care is rare, where it does exist, males do it by themselves 9 times as often as females. Such care usually involves nest-building and defence, with fin-fanning movements used for security patrols also aerating the eggs. Such multitasking, together with the fact that they do not have to feed the young, means energy expenditure is relatively low. Adding to the incentive, females often prefer to mate with a male that is already looking after eggs.

The Naturalistic Fallacy, Human Nature, and Evolutionary Ethics

Alexander (R6 167) and others (Hrady R330 23) highlight the importance of the 'naturalistic fallacy' - that what sometimes 'is' in evolution tells us what 'ought' to be in ethics and morality - in understanding pitfalls in applying evolutionary ideas to culture and morality. This has been used to claim a variety of positions later critiqued as fallible. A classic example which has reverberated down the decades was Herbert Spencer's division of labour by sex - 'men produce but women reproduce' - the founding tenet of 'social Darwinism' - on the basis that there was too little variation among females for proper selection to occur, precluding the evolution in women of higher 'intellectual and emotional' faculties which are the 'latest products of evolution'. Darwin noted "whether requiring deep thought, reason or imagination, or merely the use of the sense and the hands, [man will attain] a higher eminence ... than can woman" (Hrady R330 15-19) basing his notions squarely on sexual selection "man [could] have become as superior in mental endowment to women, as the peacock is in ornamental plumage to the peahen" (Jolly R346 361).

Gerda Lerner (R407 19) brands the entire sociobiological position as traditionalist.

"E.O. Wilson's sociobiology has offered the traditionalist view on gender in an argument which applies Darwinian ideas of natural selection to human behavior. Wilson and his followers reason that human behaviors which are 'adaptive' for group survival become encoded in the genes, and that they include in these behaviors such complex traits as altruism, loyalty and maternalism. ... Mothering is not only a socially assigned role but one fitting women's physical and psychological needs. Here once again biological determinism becomes prescriptive, in fact a political defence of the status quo in scientific language. Feminist critics have revealed the circular reasoning absence of evidence and unscientific assumptions of Wilsonian sociobiology. From the point of view of the non-scientist, the most obvious fallacy of sociobiologists is their ahistoricity in disregarding the fact that modern men and women do not live in a state of nature".

When some sociobiologists argued that rape among humans, though undesirable, is really quite understandable because, after all, the males perpetuating it are merely trying (however unconsciously) to spread their genes (Symons R678; Thornhill and Thornhill R689), Anne Fausto-Sterling (R202 5), noted what a short step it would be from this line of thinking to the legal defense of a male rapist on the grounds that 'his genes made him do it'.

Linda Stone (R667) notes: "Other sociobiologists have contrasted human male and female 'reproductive strategies' ... moreover, they say, because women want to improve their children's fitness by increasing the parental investment of their mate, they devise ways of

keeping a man around as provider and protector; and in trying to hold on to the man, they become 'coy' and 'clinging' females. Understandably, this line of argument drove many women to distraction. Criticism of this form of sociobiology has come from within the field as well as from outside it. Sarah Hrdy ([R330](#)), complained that previous sociobiologists had either ignored or misinterpreted females and female sexuality in their study of primate behavior and evolution ... that female primates, far from being sexually passive, could be active, competitive, and aggressive and that their roles in human evolution were important". Hrdy ([R330](#) 24) quips that David Buss's "Evolution of Desire" throws similar sops to Spencer's idea of beauty as a signal of fertility and genetic quality: "all women today are unique, distinctive winners of a five million year Pleistocene beauty contest of natural selection. Every female ancestor of the readers of these words was attractive enough to obtain enough male investment to raise at least one child to reproductive age".

Into the centerpiece of this debate we find Edward O. Wilson ([R751](#)) the founder of sociobiology ([R752](#)) takes an ambiguous position. Although he claims "the naturalistic fallacy has not been erased by improved biological knowledge, which still describes the 'is' of life but cannot prescribe the 'ought' of moral action", he then demurs "An understanding of the roots of human nature now seems essential to ethical philosophy. Any judgement concerning whether an act is natural or abnormal depends on such information, through behavioral categories as diverse as cousin marriage, homosexuality, territorial prerogatives and cannibalism. All attempts to define 'natural law' by unaided intuition are dangerously incompetent. This is equally true whether applied to such personal matters as the wisdom of contraception or to the supposedly inevitable trajectory of economic history."

Wilson's point here is valid. Our future viability is not just a function of cultural or economic expectations which are notoriously unstable and in the absence of an understanding of sociobiology prone to self-deceptive pitfalls which could be lethal. The evolutionary evidence both from our past and from other species, all who have had to pass the evolutionary test over cumulative lifetimes is the best indication we can hope to avail ourselves of in assessing our own directions and course of action in future. Neither does this determine any social course of action based on biological grounds, but rather gives a wider deeper context in which to understand culture and our own evolutionary decisions.

In his essay "The Biological Basis of Morality" (Atlantic Monthly [Apr 1998](#)) Wilson specifically makes the point that the belief in ethical and moral principles as absolutes independent of biological origins, especially as enshrined in religion, is in fundamental conflict with the empirical approach to the accumulation of verifiable knowledge in the natural sciences including an increasing body of knowledge about morality as a social manifestation of biological processes:

"Either ethical principles, such as justice and human rights, are independent of human experience, or they are human inventions. The distinction is more than an exercise for academic philosophers. The choice between these two understandings makes all the difference in the way we view ourselves as a species. It measures the authority of religion, and it determines the conduct of moral reasoning. The two assumptions in competition are like islands in a sea of chaos, as different as life and death, matter and the void. One cannot learn which is correct by pure logic; the answer will eventually be reached through an accumulation of objective evidence. Moral reasoning, I believe, is at every level intrinsically consilient with -- compatible with, intertwined with - the natural sciences. (I use a form of the word "consilience" - literally a "jumping together" of knowledge as a result of the linking of facts and fact-based theory across disciplines to create a common groundwork of explanation - because its rarity has preserved its precision.)"

In closing, he looks to the future:

"Which world view prevails, religious transcendentalism or scientific empiricism, will make a great difference in the way humanity claims the future. ... Ethics and religion are still too complex for present-day science to explain in depth. They are, however, far more a product of autonomous evolution than has hitherto been conceded by most theologians. Science faces in ethics and religion its most interesting and possibly most humbling challenge, while religion must somehow find the way to incorporate the discoveries of science in order to retain credibility. Religion will possess strength to the extent that it codifies and puts into enduring, poetic form the highest values of humanity consistent with empirical knowledge. That is the only way to provide compelling moral leadership. Blind faith, no matter how passionately expressed, will not suffice. Science, for its part, will test relentlessly every assumption about the human condition and in time uncover the bedrock of moral and religious sentiments."

Central here is the vexed question of whether there is in fact such a thing as human nature. This argument has woven back and forth throughout the last few centuries and theories of evolution have only served to up the ante between the conflicting proponents of nature versus nurture, evolution versus morality, and genetic determinism versus cultural relativity.

Steven Pinker ([R544](#) 169) mounts a systematic case against the sociological notion that human nature is essentially a tabula rasa or 'blank slate' on which we can superimpose cultural, social or religious imperatives without regard to our evolutionary heritage. His concerns are highly justified. Social paradigms that assume the right to dictate and reshape human nature rapidly veer into totalitarian agendas. "Skinner was a staunch blank-slater and a passionate utopian. His uncommonly pure vision allows us to examine the implications of the 'optimistic' denial of human nature. Given his premise that undesirable behavior is not in the genes but a product of the environment, it follows that we should control that environment-for all we would be doing is replacing haphazard schedules of reinforcement by planned ones. Why are most people repelled by this vision? Critics of Skinner's Beyond Freedom and Dignity pointed out that no one doubts that behavior can be controlled; putting a gun to someone's head or threatening him with torture are time-honored techniques. Even Skinner's preferred method of operant conditioning required starving the organism to 80 percent of its free-feeding weight and confining it to a box where schedules of reinforcement were carefully controlled. The issue is not whether we can change human behavior, but at what cost".

Like Hrdy, Pinker ([R544](#) 171) applies this criticism specifically to the culturally relativistic positions of 'glass body' feminism:

"Nothing in the concept of human nature is inconsistent with the ideals of feminism ... But some feminist theoreticians have embraced the Blank Slate and with it an authoritarian political philosophy that would give the government sweeping powers to implement their vision of gender-free minds. In a 1975 dialogue, Simone de Beauvoir said: 'No woman should be authorized to stay at home to raise her children. Society should be totally different. Women should not have that choice, precisely because if there is such a choice, too many women will make that one.' Gloria Steinem was a bit more liberal; in a 1970 Time article she wrote: 'The [feminist] revolution would not take away the option of being a housewife. A woman who prefers to be her husband's housekeeper and/or hostess would receive a percentage of his pay determined by the domestic-relations courts.' Betty Friedan has spoken out in favor of 'compulsory preschool' for two-year-olds. Catharine MacKinnon (who with Andrea Dworkin has pushed for laws against erotica) has said, 'What you need is people who see through literature like Andrea Dworkin, who see through law like me, to see through art and create the uncompromised women's visual vocabulary' -oblivious to the danger inherent in a few intellectuals' arrogating the role of deciding which art and literature the rest of society will enjoy. In an interview in the New York Times Magazine, Carol Gilligan explained the implications of her (preposterous) theory that behavior problems in boys, such as stuttering and hyperactivity, are caused by cultural norms that pressure them to separate from their mothers: Q ' You would argue that men's biology is not so powerful that we can't change the culture of men?'

A: 'Right. We have to build a culture that doesn't reward that separation from the person who raised them'.... Q: 'Everything you've said suggests that unless men change in fundamental ways, we're not going to have a sea change in the culture'. A: 'That seems right to me'. An incredulous reader, hearing an echo of the attempt to engineer a 'new socialist man,' asked, 'Does anyone, even in academia, still believe that this sort of thing turns out well?' He was right to be concerned. In many schools, teachers have been told, falsely, that there is an 'opportunity zone' in which a child's gender identification is malleable. They have used this zone to try to stamp out boyhood: banning same-sex play groups and birthday parties, forcing children to do gender-atypical activities, suspending boys who run during recess or play cops and robbers. In her book *The War Against Boys*, the philosopher Christina Hoff Sommers rightly calls this agenda 'meddlesome, abusive, and quite beyond what educators in a free society are mandated to do.'

Pinker ([R544](#) 172) sees an urgent need for biological feminism:

"Feminism, far from needing a blank slate, needs the opposite, a clear conception of human nature. One of the most pressing feminist causes today is the condition of women in the developing world. In many places female fetuses are selectively aborted, newborn girls are killed, daughters are malnourished and kept from school, adolescent girls have their genitals cut out, young women are cloaked from head to toe, adulteresses are stoned to death, and widows are expected to fall onto their husbands' funeral pyres. The relativist climate in many academic circles does not allow these horrors to be criticized because they are practices of other cultures, and cultures are superorganisms that, like people, have inalienable rights. To escape this trap, the feminist philosopher Martha Nussbaum has invoked 'central functional capabilities' that all humans have a right to exercise, such as physical integrity, liberty of conscience, and political participation. She has been criticized in turn for taking on a colonial 'civilizing mission or (white woman's burden,' in which arrogant Europeans would instruct the poor people of the world in what they want. But Nussbaum's moral argument is defensible if her 'capabilities' are grounded, directly or indirectly, in a universal human nature."

Anne Campbell ([R103](#)) defends human nature in similar terms:

"The denial of human universals is central to the liberal agenda because of critics' erroneous acceptance of the naturalistic fallacy and their mistaken belief that biology is destiny. If something is universal it may reflect a fundamental human nature and if such a thing exists at a biological level then attempts to ameliorate the status quo are doomed". However she notes: "Critics often seem confused about just what is meant by human nature. Consider the following quote from Sandra Bem ([R57](#) 21) 'As a biological species, human beings do not have wings, which once meant that it was part of universal human nature to be unable to fly. But now human beings have invented airplanes, which means that it is no longer part of human nature to be unable to fly'. Now the idea that sitting in a seat a few thousand miles above the ground [Anne is a very high flyer] constitutes an alteration of 'human nature' is an odd distortion of the concept. ... Do we seriously suppose that aeroplane passengers have a [fundamentally] different psychology or physiology from those who have not flown? ... It is equally hard to know what to make of Fausto-Sterling's ([R202](#) 199) claim that 'there is no singly undisputed claim about universal human behavior (sexual or otherwise).' Presumably even the most ardent cultural relativist would accept that everywhere people live in societies, that they eat, sleep and make love, and that women give birth and men do not. The problems seem to arise when we move from basic biological functions to behavior. Though everywhere women are the principal caretakers of children, the fact that there may be variation in how that task is fulfilled leads some anthropologists to conclude that mothering is not universal".

At issue is not just the question of whether humans have an evolutionary heritage, including sexual differences, or whether human culture can be modeled on natural and particularly evolutionary principles, but whether there can be considered to be any universals characterizing humanity. This is itself a paradoxical situation, because humanity has clearly evolved in a way which places itself in a universal position. We have become a meta-species creating and discovering as many niches within the burgeoning complexity of human culture and its many vocations as a diverse ecosystem in a tangled bank. We have achieved this through an adaptive trend in the brain towards universality of perception, emotion and conception, which has made it possible for philosophers to contend we are a tabula rasa - a blank slate upon which the diversity of the cultural record can be imposed freely. It is thus a deep contradiction for cultural relativists to deny human universality, even if of an evolutionary ilk.

Donald Brown ([R84](#)) in 'Human Universals' has documented ethnographically the extent of such universals, including gossip, lying, verbal humour, story telling, metaphor, distinction between mother and father, kinship categories, logical relations (not, same, equivalent, opposite), interpreting intention from behavior and recognition of six basic emotions. In regard to gender we find binary distinctions between men and women, more aggression and violence by men, acknowledgment of the differences between male and female natures and domination by men in the public political sphere. In 1973 Stephen Goldberg ([R246](#)) wrote documenting the universality of patriarchy, with upper positions in hierarchies occupied by males across even ostensibly matrilineal societies. Despite a showering of claimed exceptions his second work ([R247](#)) in 1993 continues to insist the thesis stands.

The Western tradition proceeds from a cultural background in which nature has been regarded as a lower realm subject to animal lust and the violence of tooth and claw in opposition to the purity of God's commands, despite the pristine beauty of Genesis 1's creation. The basic notion that we have been given the power to choose good and evil over natural instincts leads inevitably to a potential conflict between evolution and higher motives in which morality plays an enigmatic role.

The naturalistic fallacy is neatly expressed in David Hume's 'A Treatise of Human Nature' ([R332](#)): "In every system of morality, which I have hitherto met with, I have always remarked that the author proceeds for some time in the ordinary way of reasoning, and establishes the being of God, or makes observations concerning human affairs; when of a sudden I am surprised to find, that instead of the usual copulation of propositions, is and is not, I meet with no proposition that is not connected with an ought, or an ought not. This change is imperceptible; but is however, of the last consequence. For as this ought, or ought not, expresses some new relation or affirmation, it is necessary that it should be observed and explained; and at the same time that a reason should be given, for what seems altogether inconceivable, how this new relation can be a deduction from others, which are entirely different from it." This distinction between is and ought, which Hume found so mysterious, may not be a mark of moral conscience so much as the capacity to semantically distinguish past and future in the emergence of semantic language.

Proponents of biology have taken a variety of views about the relation between evolution and morality. Darwin ([R148](#) 500) developed the first complete theory of morality and ethics, in the following words: "Ultimately our moral sense or conscience becomes a highly complex sentiment-originating in the social instincts, largely guided by the approbation of our fellow men, ruled by self-reason, and confirmed by instruction and habit. It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet that an increase in the number of well-endowed men and advancement in the standard of morality will certainly give an immense advantage to one tribe over another. A tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good would be victorious over most other tribes; and this would be natural selection. At all times throughout the world tribes have supplanted other tribes; and as morality is one important element in their success, the standard of morality and the number of well-endowed men will thus everywhere tend to rise and increase".

Interestingly, this is a group selection model reflecting Darwin's lack of knowledge of exact genetic mechanisms. Since George Williams' argument that which alleles survive depends primarily on reproductive successes and failures of individual organisms, rather than of groups, group selection has become a more complex proposition to assert, however it does have particular application when dealing with the group competition and social fluidity that is concomitant with the emergence of moral systems. Darwin's model depends on confluences of interests within groups and does not deny the existence of countering conflicts of interest within groups in a manner predictive of Alexander's ideas below.

Julian Huxley ([R333](#) 132) states clearly that morality must be founded on evolution:

"the evolutionist is able to provide new general standards or criteria for ethics ... contributions from ... [other] fields have been either incomplete (as in theology) or limited in extent. It is only in relation to the evolutionary process as a whole that our ethical standards can be fully generalized, and the system be rounded out to completion."

He goes further setting an evolutionary paradigm for a valid ethic: ([R333](#) 142)

"evolutionary ethics must be based on a combination of a few main principles: that it is right to realize ever new possibilities in evolution, notably those which are valued for their own sake; that it is right both to respect human individuality and to encourage its fullest development; that it is right to construct a mechanism for further social evolution which shall satisfy these prior conditions as fully, efficiently, and as rapidly as possible".

By contrast, in the same work, Thomas Huxley, ([R333](#) 83) coming from a pessimistic view of violent nature argues, as Augustine might have, that the imitation of 'the cosmic [evolutionary] process by man is inconsistent with the first principle of ethics':

"Let us understand, once for all, that the future depends, not on imitating the cosmic process, still less in running away from it, but in combating it ... the practice of that which is ethically best - what we call goodness or virtue - involves a course of conduct which, in all respects, is opposed to that which leads to success in the cosmic struggle for existence. Ethical nature may count upon having to reckon with a tenacious and powerful enemy as long as the world lasts."

However he footnotes this statement with an evolutionary qualification:

"Of course, strictly speaking, social life, and the ethical process in virtue of which it advances toward perfection, are part and parcel of the general process of evolution, just as the gregarious habit of innumerable plants and animals which has been of immense advantage to them, is so. A hive of bees is an organic polity, a society in which the part played by each member is determined by organic necessities ... Even in these rudimentary forms of society, love and fear come into play, and enforce a greater or less renunciation of self-will. To this extent the general cosmic process begins to be checked by a rudimentary ethical process, which is, strictly speaking, part of the former, just as the 'governor' in a steam-engine is part of the mechanism of the engine".

In this statement Huxley too seems to see moral systems as an outcome of the 'general cosmic process' as well as something that combats, or opposes it.

There are major questions here about what is 'good' in terms of nature, amicability or sustainable survival. Many evolutionary arguments are not made on agreeableness or non-violence but an appeal to the innate principles of viability contained in evolutionarily stable strategies and their ecosystemic relationships. Society may thus need to learn to incorporate paradigms of violence and conflict in its ethical models to ensure its own survival. Indeed capitalistic free market models are based on overweening competition of a kind not even found in living ecosystems.

This means that some critiques of the so called 'naturalistic fallacy' are themselves fallacies. Steven Pinker ([R544](#) 162) critiques environmentalist conservation of predators: "We have already met the naturalistic fallacy, the belief that whatever happens in nature is good. One might think that the belief was irreversibly tainted by Social Darwinism, but it was revived by the romanticism of the 1960s and 1970s. The environmentalist movement, in particular, often appeals to the goodness of nature to promote conservation of natural environments, despite their ubiquitous gore. For example, predators such as wolves, bears, and sharks have been given an image makeover as euthanists of the old and the lame, and thus worthy of preservation or reintroduction." There is clearly a confusion here between 'good' in terms of a viable ecosystem, which generally does need predators ([p.507](#)) to avoid population boom and bust, and 'good' in the social sense of non-violent.

Pinker noting its converse, exacts the fallacy from the feminist movement:

"It would seem to follow that anything we have inherited from this Eden is healthy and proper, so a claim that aggression or rape is 'natural,' in the sense of having been favored by evolution, is tantamount to saying that it is good. The naturalistic fallacy leads quickly to its converse, the moralistic fallacy: that if a trait is moral, it must be found in nature. That is, not only does 'is' imply 'ought,' but 'ought' implies 'is.' Nature, including human nature, is stipulated to have only virtuous traits (no needless killings, no rapacity, no exploitation), or no traits at all, because the alternative is too horrible to accept. That is why the naturalistic and moralistic fallacies are so often associated with the Noble Savage and the Blank Slate. Defenders of the naturalistic and moralistic fallacies are not made of straw but include prominent scholars and writers. For example, in response to Thornhill's earlier writings on rape, the feminist scholar Susan Brownmiller wrote, 'It seems quite clear that the biologicization of rape and the dismissal of social or 'moral' factors will ... tend to legitimate rape.... It is reductive and reactionary to isolate rape from other forms of violent antisocial behavior and dignify it with adaptive significance.' Note the fallacy: if something is explained with biology, it has been 'legitimated'; if something is shown to be adaptive, it has been 'dignified'."

Edward O. Wilson the founder of sociobiology ([R752](#)) advances some curious evolutionary arguments, accepting homosexuality as having a possible offshoot genetic advantage in uncle parenting (such a tendency has by no means been demonstrated in gay men) and condemning incest as genetically deleterious, while introducing some intriguing personal moral interpretations of sexuality: "The primary functions of sexual behavior are pair bonding and the creation of genetic diversity, rather than reproduction per se. Thus the sexual revolution, but not promiscuity, is in concert with the innate learning rules." Alexander ([R6](#) 169) comments: "One is led to believe that he is implying by this that promiscuity somehow violates a 'natural law.' When asked following his oral presentation of this material if he meant that promiscuous people cannot be happy, he hesitated, but responded affirmatively, stating that in regard to questions of monogamy and fidelity he was conservative. After denying the validity of the naturalistic fallacy, Wilson is suggesting there are natural laws governing what is right and wrong about human behavior, and that only biologists, or those with extensive biological knowledge, are able to discover them".

This debate has manifest political dimensions. In supporting the purity of racial blood, Hitler quotes providence: "God having created races, it is therefore the noblest and most sacred duty for each racial species of mankind to preserve the purity of the blood which God has given it." At the same time he practised eugenics and evolutionary amorality "the most cruel methods are humane if they give a speedy victory" (Alexander [R6](#) 167).

Critical in human universals is innate violence. In 1963 Konrad Lorenz added, in his influential 'On Aggression' ([R426](#)) that our species unfortunately has not had time to evolve the same inhibitions we see in 'professional' carnivores, such as lions and wolves. As a result, we are dangerous to our own kind. This pessimistic view soon met with resistance. Social psychologists and anthropologists demonstrated that aggressive behavior can be learned, and they questioned the universality of human violence by cultures believed to be peaceful. However it later became clear that Chimpanzees, rather than being peaceful vegetarians, also shared characteristics of human violence, including predation on monkeys, lethal intercommunity aggression, infanticide and even occasional cannibalism. Richard Wrangham and David Peterson in 'Demonic Males' ([R764](#)) put it this way "That chimpanzees and humans kill members of neighbouring groups of their own species is ... a startling exception to the normal rule for animals. Add our close genetic relationship to these apes and we face the possibility that inter-group aggression in our two species has a common origin. This idea of a common origin is made more haunting by clues that suggest modern chimpanzees are not merely fellow time-travellers and evolutionary relatives, but surprisingly excellent models of our distant ancestors. It suggests that chimpanzee-like violence preceded and paved the way for human war, making modern humans the dazed survivors of a continuous 5-million year habit of lethal aggression."

De Waal ([R164](#)) notes that both our subsequent experience of bonobos, for which we have no evidence for intercommunity raiding, infanticide, cooperative hunting or any of the other lethal activities, stressed as the hallmark of our species, and the greater flexibility and processes of reconciliation we now associate with ape aggression, which are quite distinct from predation, means our ideas are no longer dependent on the Lorenzian drive concept and the killer ape myth, which did little justice to the complexity of our species and its many distinct features other than aggressiveness. Bonobos particularly associate sex with reconciling aggression, where chimpanzees would merely kiss and embrace ([p.66](#)). Inter-male aggression is also reduced by the cooperative attitude of female bonobos when two groups meet.

Kind vs Kin: The Eusociality - Relatedness Debate

In a recent development, Nowak, Tarnita and Wilson (Nowak, M; Tarnita, Corina; Wilson, E O 2010 The Evolution of Eusociality Nature 466/26 August 2010 doi:10.1038/nature09205 1057-62) have questioned the encompassing validity of inclusive fitness, centered on kin altruism and proposed instead that natural selection can go through a transition to 'eusociality' based only on central principles of natural and social selection, although replies in comment in Nature were almost universally critical (doi:10.1038/nature09831, doi:10.1038/nature09832, doi:10.1038/nature09833, doi:10.1038/nature09834, doi:10.1038/nature09835).

Nowak suggests five factors - kin selection, direct and indirect reciprocity and spatial and group selection as playing a part in a transition driven partly by relative confinement of small reproducing populations through processes such as nesting. They suggest that the full theory of eusocial evolution consists of a series of stages, of which the following may be recognized: (1) the formation of groups. (2) The occurrence of a minimum and necessary combination of pre-adaptive traits, causing the groups to be tightly formed. In animals at least, the combination includes a valuable and defensible nest. (3) The appearance of mutations that prescribe the persistence of the group, most likely by the silencing of dispersal behaviour. (4) Emergent traits caused by the interaction of group members are shaped through natural selection by environmental forces. (5) Multilevel selection drives changes in the colony life cycle and social structures, often to elaborate extremes.

However kin selection and group selection are not necessarily inconsistent. Hamilton's kin selection equation was extended to include group selection by George R. Price, confirming its evolutionary stability in terms of altruistic and free-loading individuals, a development both Hamilton and Price agreed on, some time before Price tragically cut his carotid with a pair of nail scissors in the midst of the winter blues. Thus both processes are alid and whether one or the other pertains is dependent on which model fits the actual process biologically (Michael Johnson "[The Good Fight](#)" Sci. Am. July 2012).

A difficulty with the group model is that it depends heavily on natural selection in a single gene locus in (3) with eusocial and autonomous alleles at one specific locus, to evade the necessity for individuals to be related to be altruistically cooperative in social species such as honey bees. If a eusocial habit is multi-gene based the process could be evolutionarily unstable.

The resurgence of group selection has led to a major controversy in the scientific community (Lehrer J 2012 Kin and Kind, Evolution and the Origins of Altruism New Yorker 5 Mar 36-43, Okasha S 2010 Altruism researchers must cooperate Nature 7 Oct 467 653) which still remains unresolved, and which has given creationists a wedge into yet further mindless claims against evolutionary theory. Nowak and Roger Highfield's book "SuperCooperators" (Simon & Schuster) has likewise led to accusations over name-dropping and 'wildul ignorance of the literature' amid a good presentation of the mathematical modeling behind the ideas of indirect reciprocity and group selection. At stake also is a hopeful point of view espoused by both Nowak and Wilson that science need not be in conflict with religious belief, in which espoused terms such as 'hopeful, generous and forgiving' can be seen by detractors as coloring evolutionary theory with a 'wishful' gloss.

Social hymenopteran insects such as bees, have haploid-diploid sexuality, in which the males are haploid and the females are diploid. A queen bee thus has diploid daughters, a few of which are fed with royal jelly and become fertile queen larvae, while the rest become sterile workers whose ovarian apparatus becomes instead a feeding organ for their sister larvae. This is the best genetic investment for the workers under Hamilton's rule because the workers share 75% of their genes, inheriting a full equal paternal 50% from their common father drone who originally fertilized the queen, and another 25% from the 50% mixed maternal inheritance arising from meiosis. Since this exceeds the 50% relatedness of their own offspring, it fulfils Hamilton's rule. Notice also in passing that haploid males are performing a stringent genuine indicator of fitness because all their single alleles must be functioning well enough to produce a drone who can fertilize the queen in flight, so the system is well-positioned to be optimally selective in males.

A 2012 experiment with bees however suggests that relatedness, i.e. kin altruism, IS key, consistent with traits involving behavior depending on the combined activity of a number of genes which are naturally selected as a group only in a context of familial relatedness. When the old queen migrates, leaving a daughter to hatch to become the new queen of the hive, the older 'aunt' workers are no longer closely enough related to their 'niece' worker daughters of the new daughter-queen and some rebel, becoming themselves fertile at the larval stage, when raised by their mature sisters. It is only when the 'nieces' grow numerous enough to contain such rebellions that order fully returns to the hive (BBC [Family disputes create rebel bees](#)).

On the other hand, it has been established that queens do not necessarily mate with only one drone, throwing the whole haploid-diploid arrangement into disarray, as half sister are only about 33% related.

Intriguingly the royal jelly which results in only one or a few bees becoming queens and the rest, who don't receive it become sterile workers, has proved to be a phenomenon of epigenetic modification of the DNA. A team used interfering RNAi to silence a gene for DNA methyltransferase - an enzyme necessary for adding methyl groups to DNA - in honeybee larvae. Most of these larvae emerged as queens, without ever having tasted royal jelly (Science, DOI: 10.1126/science.1153069).

Further reinforcing the viability of group selection is the discovery that bacterial colonies in the wild share a group altruism in which mutant bacteria possessing antibiotic resistance secrete indole to warn bacteria not loaded with resistance factors to turn on their toxin protecting pathways (Lee HH, et al 2010. Bacterial charity work leads to population-wide resistance. Nature, 467 82-5).

Group Cooperation and Social Competition

Alexander (R6 79) and others have developed the idea that human evolution and in particular the morality of intra-group cooperation, has been guided to some large extent by inter-group competition and aggression, which we shall explain in detail because it is the basis of some of De Waal's views and it neatly explains many aspects of the sexual paradox between cooperation and competition inherent in the Prisoners' Dilemma.

Group living entails automatic costs to individuals, which must be compensated by specific benefits if group living is to evolve. Larger groups involve greater costs to individuals. Even if cooperative group hunting was the original context of human grouping, it cannot explain much of the history of human sociality. As hunting weapons and skills improved, group sizes should have decreased. Cooperative group hunters among nonhumans tend to live in small groups (canines, felines, cetaceans, some fish, and pelicans). Large groups are typically what Hamilton called 'selfish herds', whose evolutionary raison d'être is security from predation. Even groups evidently evolved to cooperate against predators are typically small (chimpanzees, baboons, musk ox). The only adequately significant external threat is other groups of humans. This can explain any size of group (as results of balance-of-power races). It accords with recorded human history. It is consistent with the fact that humans alone play competitively group-against-group on a large and complex scale. It also accords with the ecological dominance of humans as a species. In effect, organized in competitive groups, humans have become their own principal 'hostile force of nature.' Most of the evolution of human social life and the human psyche, may thus have occurred in the context of within- and between-group competition, the former resulting from the latter. Without the pressure of between-group competition, within-group competition would have been mild, nonexistent - or else dramatically different - because groups would have been smaller and would have required less unity and cooperativeness. Strate (R669) has concluded from a cross-cultural study that defense against other human groups accounts for variations in social organization better than any alternative. No other sexual organisms compete in groups as extensively, fluidly, and complexly as humans do. No other organisms play competitively group-against-group. So far as we know, in no other species do social groups have as their main jeopardy other social groups of the same species - hence the unending selective race toward greater social complexity, intelligence, and cleverness in dealing with one another.

To make the above argument requires some way of distinguishing primary causes of social grouping and secondary responses to it. On the other hand, one must also consider that any cooperative cause of group living cannot be expected to last and be elaborated unless it leads to increased reproductive success among all participants, which by definition means in relation to members of other groups, thereby establishing at least an indirect inter-group competition. Although indirect reciprocity may be unique to humans, we cannot ignore the possibility that there may be a parallel to morality in many nonhuman social groups that cooperate. Rudimentary moral systems (indirect reciprocity) would thus be expected to appear where outside threats most powerfully dictate group cohesion, when such threats are combated best by complex social organization within the group, and when the actions of single individuals or small subgroups can threaten, from within, either the group as a whole or its most powerful elements.

Alexander's theory has the following key features: (1) Individuals seek their own interests. (2) Their interests are ultimately reproductive, so include the interests of relatives and other shared relationships such as partners (3) Interests of individuals can be furthered by cooperating with others (4) The mechanisms are direct and indirect reciprocity, the latter involving a very complex significance of reputation or status. (5) The rules consist of restraints on particular methods of seeking self-interests that impede the efforts of others to seek their own interests. What is new in this theory is that (a) interests are seen as reproductive, not as individual survival, and, accordingly, pleasure and comfort are postulated to have evolved as vehicles of reproductive success, and (b) the mechanism of indirect reciprocity is made explicit as the central feature. These are not trivial refinements, since together they can account for aspects of beneficence that have perplexed philosophers, theologians, and students of morality.

A variety of research results lend confirmation to the thrust of Alexander's theory as an explanation for why human altruism extends far further and in much larger groups than kin and reciprocal altruism would allow for alone. Ernst Fehr, in developing the concept of 'strong reciprocity' (R205) notes: "many people are willing to cooperate and to punish those who don't even when no gain is possible". Robert Trivers has suggested that small group cooperation might have been a feature of regular interactions between known parties based on reciprocal altruism, which might have become maladaptive and be dying out in our larger social structures, where one shot interactions have become more common. Gächter and Falk (R230) have demonstrated that repeated play more than doubles cooperation levels. However Joseph Heinrich has noted that one-shot versus repeated interactions would have also occurred in gatherer-hunter times (Buchanan R93). Rilling et. al. (p 378) have demonstrated cooperation activates areas involved in emotional rewards and de Quervain et. al. (p 378) similarly demonstrate that altruistic punishment of defectors also stimulates reward centres in an emotional form of 'sweet revenge'. Boyd et. al. (R73) using computer simulations have demonstrated that group competition encourages cooperation - punishing cheats increases the size of cooperative groups from 10 up to 30 the size of gatherer hunter bands. In a key extension of this idea, Fehr and Fishbacher (R204) have noted that punishing those who fail to punish cheats can increase cooperative group size to hundreds of individuals, effectively explaining in one stroke both large scale human social cooperativity and punitive moral codes. In another computer model Pamchanathan and Boyd (R528) have shown that such selection can be based more generally on coveting good reputations and punishing the bad.

Both the essential components of Alexander's theory of conflict between and within groups are manifest features of ape societies. Inter-group conflict is matched by mechanisms of reconciliation and mediation of aggression in intra-group conflict, noting that moral systems are produced by tension between individual and collective interests. Reconciliation is essential to maintain group cohesion against splinter defection and is widespread in animals societies, most often initiated by the 'victim' towards the 'aggressor' (p 67), as noted in "Natural Conflict Resolution" (Aureli and de Waal R27). The authors point out that reconciliation is even more important to individuals who have a long-standing cooperative relationship - the valuable friendship model. It is also worth a dominant individual reconciling to avoid debilitating stress at the top (Dugatkin R176).

In "Good Natured" De Waal (R162 38) notes "Philosophers tell us that there is an element of rational choice in human morality, psychologists say there is a learning component, and anthropologists argue that there are few if any universal rules. The distinction between right and wrong is made by people on the basis of how they would like their society to function. It arises from interpersonal negotiation in a particular environment, and derives its sense of obligation and guilt from the internalization of these processes. Moral

reasoning is done by us and not by natural selection". However he then goes on to make the argument that "Evolution has produced the requisites for morality: a tendency to develop social norms and enforce them, the capacities of empathy and sympathy, mutual aid and a sense of fairness, the mechanisms of conflict resolution, and so on. Evolution has also produced the unalterable needs and desires of our species: the need for the young for care, a desire for high status, the need to belong to a group, and so forth. How all these factors are put together to form a moral framework is poorly understood, and current theories of moral evolution are no doubt only part of the answer." In the remainder of 'Good Natured' De Waal investigates the extent to which aspects of morality are recognizable in other animals, and "how humanity may have moved from societies in which things were as they were to societies with a vision of how things ought to be" bringing to the surface instances of sympathy and empathy, guilt and shame, giving and taking, reconciliation, peacemaking and just getting along.



Left: The tooth and claw of predator and prey is a delicate dynamic which often helps preserve both. Too few predators and the prey may become epidemic and eat themselves to catastrophic extinction. Stragglers may die quickly from suffocation or a neck bite, although hunting play can become torment. Right: Crocodile guards its young in its mouth ([R30](#)).

Evolutionary Foundations of Original Sin and the Cultural Fall

The concept of original sin and its relation to free-will leads to major questions of the origin of good and evil and social responsibility, which have wracked religious thinking and moral imperatives throughout the millennia. There is no such thing as natural evil in any meaningful sense. Nature survives by tooth and claw. Homicide is natural as predation itself is an extension of the primary division between autotrophic plants and heterotrophic animals which must survive by consuming other life forms ([p 325](#)). This division leads in turn to herbivores and carnivores. Even parasites and diseases are an integral part of an ecosystem and must adapt to survive. Although some animals kill mercilessly, or toy with their injured victims for skill, predators and prey are in a dynamical sense interdependent ([p 507](#)). Too few predators and the herbivores may eat and reproduce themselves to starvation and population crisis. We need to learn from nature what are the true universals before attempting to exert moral or religious ideas of good and evil. We are taught "Thou shalt not kill" but every man woman and child was reputedly slaughtered in the fall of Jericho and Hazor, illustrating that this injunction was for the Hebrews but not apparently for the Canaanites or Philistines. Our ideas of social evil are thus relative.

However there is another dimension of human evil which in the development of culture and utopian visions and the capacity of psychopathic individuals to gain disproportionate power, can become unhinged from nature and diabolical in their manifestations, from the programmed genocide of Shoah through the nuclear insanity of MAD - mutually assured destruction of the Cold War. One can draw the similar conclusions about an expedient George Bush stoking the fires of industrial pollution while every man woman and child in the US uses up to 150 times more non-renewable resources than a person in a developing country, strategically denying symptoms of climate change, when a mass extinction of biodiversity caused by human impact is in full swing. Of course China is no angel in the piece either having already overtaken the US in CO₂ emissions.

We also have growing examples of genetic influences on criminality that lead to inferences that in some cases at least, anything from individual violence to compulsive gambling could be regarded as 'original sin' inherited in our genomes. Steve Jones' 'In the Blood' notes: "The law's basic assumption is that of autonomy: that everyone is liable for their deeds and is obliged to pay the price if they misbehave", based on the philosophy of the Greek Stoics of 300 BC who saw everyone as equally imbued with virtue and equally accountable for their misdemeanors. This makes a key distinction between the absence of natural evil in violent acts such as the predatory behaviour of carnivores, since this conforms to the natural processes of evolutionary selection and the human expedience of violence that comes from the exercise of free-will. This in turn is an affirmation for the pivotal role free will begins to have when sentient beings come of 'cosmic age' and begin to recognize how their intentionality can come to shape beneficent futures of abundance or agonizing unholy futures. of betrayal, attrition. competition and violence.

However the balance between nature and nurture is sensitive. Wild rhesus monkeys with low serotonin and aggressive behaviour were found to become socially adjusted when given supportive mothering (see Stephen Suomi Biological Psychiatry). A similar result has been found in the New Zealand serial study of the fate of 1037 children born in 1972 in Dunedin, New Zealand. They found that children were much more likely to grow up to be aggressive and antisocial if they had inherited a 'short' version the MAOA gene, which makes monoamine oxidase A, an enzyme which helps to break down neurotransmitters such as serotonin, and was less efficient in the individuals with the 'short' version. But carriers only went off the rails if they had had an abusive upbringing. Carriers with good mothering were usually completely normal ([R477](#)).

The classic view of accountability must have exceptions when the culprit's soundness of mind is compromised, genetically or otherwise. Just as genes can give us the power to love, some genetic 'profiles' predispose to depression, psychosis, or psychopathic behaviour. In a climate of genetic predisposition this predispositions can and do lead to the defence that the actions were genetically caused, effectively citing original sin as a plea of individual 'innocence' or at least mitigation. For example there are up to 100-fold variations in the activity of the monoamine oxidase A enzyme involved in processing neurotransmitters such as serotonin, associated with emotional confidence. The short-arm versions of the MAOA gene results in individuals much more likely to suffer from depression, apprehension under stress (Ridley [R580](#) 267). Chaotic behavior of people, particularly males, at the bottom of the social hierarchy, resulting from emotional dysphoria, may tend to give them more of a chance to break out of an invidious reproductive position and such 'delinquent' genes could thus be selected for. Schizophrenia also appears to have genetic correlates (Ridley [R580](#) 109) raising a further spectre of original genetic 'evil' causing insanity, but here again there may be a trade-off in creative genius being associated with borderline insanity. Corballis ([R133](#) 178) also considers 'magical thinking' to be a social adaption, possibly associated with reduced cerebral dominance, reinforced by a form of reproductive advantage.

Genetic and environmental factors interpenetrate in non-relative homicide. Detroit has a 40 times higher murder rate than the UK. However men commit about 30 times as many murders as women. Genes and cultures are not mutually exclusive explanations, but the trend towards male violence is incontestable. Genetic and cultural factors of family disintegration may combine here. Limiting weapons is an obvious social measure (Jones [R348](#) 213).

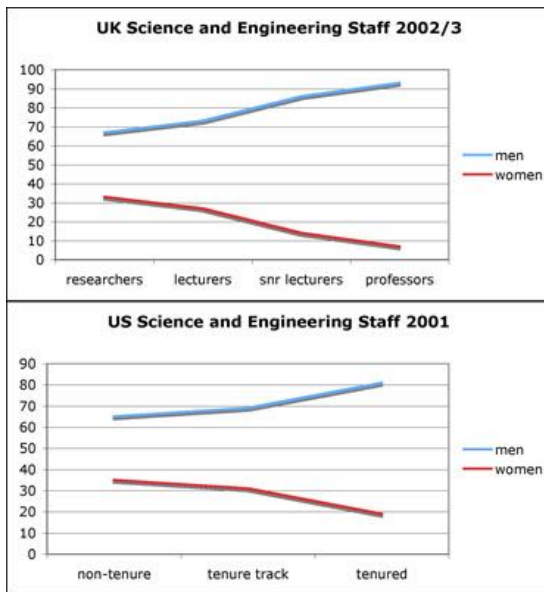
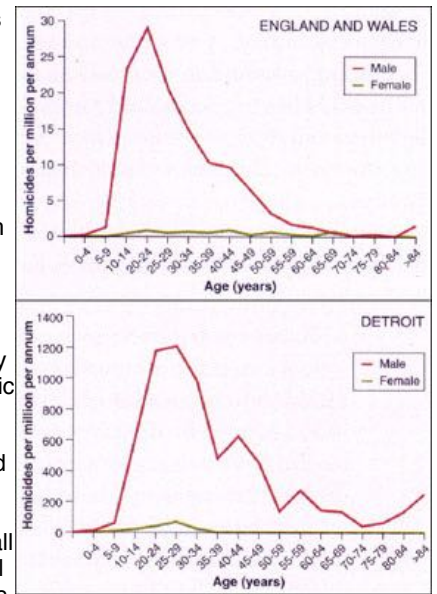
From an evolutionary point of view, the leading cause of violence is maleness. "Men have evolved the morphological, physiological and psychological means to be effective users of violence" - Daly and Wilson. Some Darwinists such as Randy Thornhill ([R689](#), [R690](#)) contend that rape may be a 'natural' and even effective means to the male reproductive imperative. In fact, rape is more likely to get a female pregnant than intercourse with a partner. Rape is also clearly to get women pregnant in times of war as in Bosnia, so the simple idea of sex a non-reproductive naked power ignores key realities. In a light and shade debate, Robin Dunbar suggests rape is an

evolutionarily viable reproductive strategy for a less attractive man, while Robin Baker counters this 'loser' theory stating that a woman selects for a rapist's genes because they have 'above average [reproductive] potential' (Taylor R683). However all human social actions are also influenced by social responses to them.

Feminists such as Anne Fausto-Sterling (R202) object that such work opens the door to frivolous exonerating pleas in the criminal justice system ('I beat my wife because it is man's nature to experience extreme sexual jealousy because of internal fertilization') (Campbell A R103 19). Robert Wright (R768) notes: "Of course, to call these things 'natural' isn't to call them beyond self-control, or beyond the influence of punishment. And it certainly isn't necessary to call them good. Evolutionary psychology might even be invoked on behalf of the doctrine of Original Sin: we are in some respects born bad, and redemption entails struggle against our nature". It is only by men understanding the biological roots of their violence and tendency to dominion over nature that society can become whole and the environment can survive. The key to undoing the negative endowment of the Fall is understanding ourselves and adopting an ethic which induces the unity of purpose required to coexist in a closing circle of life.

Wright (R769) continues: 'By Darwinian lights, the classic sins, such as gluttony, lust, greed and envy, are the unchecked expression of impulses that arose by natural selection, or worse still the calculated use of them in a newly unfeeling, menacing and expedient way. More than a century ago, Thomas Huxley, Darwin's popularizer, lamented the fact that evolution has given all children "the instinct of unlimited self-assertion - their dose of original sin." However as we shall see, evolutionary psychology asserts that our "ethical sentiments" likewise have an innate basis. Such impulses as compassion, empathy, generosity, gratitude and remorse are genetically based. These impulses, with their checks on raw selfishness, helped our ancestors survive and pass their genes to future generations'.

In Asia there are 100 million more men than women and this excess of men, particularly in China, has led to fears of "macho militarism and imperialism". These concerns portray a violent, socially unstable world, caused by a glut of testosterone-driven, unmarried men. However a 2014 review of violence in different societies found that violence was equally likely to be associated with extra women as with extra men (Trends in Ecology & Evolution, vol 29, p 214). Out of 20 studies, nine showed violence increasing with more men, but nine showed the opposite. Two were inconclusive. "Mating market models", based on the principle of supply and demand, suggest the rarer sex has more bargaining power in the marketplace. If not pleased with the terms of the relationship, they have little trouble going elsewhere. But the more abundant gender has few options, and therefore must cater to the preferences of the rarer gender. When there are extra women, men have the upper hand – behaving promiscuously, offering little parental investment, and yet still being able to obtain partners. On the other hand, when women are in short supply, men will find that marriage and a commitment to family are necessary to attain mating opportunities. In this situation, the best strategy for the average man is to secure and maintain a single partner.



Patriarchy is still a major force in informed human society, in the upper echelons of academia (New Scientist 2 Oct 2004 45). Compare fig (p 392).

The U.S. Centers for Disease Control and Prevention reported in 2005 that homicide is a leading cause of traumatic death among new and expectant mothers, accounting for 31% of maternal injury deaths, second, after auto accidents (44%), other unintentional injuries (13%) and suicide (10%) among trauma deaths of pregnant women and new mothers. Black women had a maternal homicide risk about seven times that of white women. At ages 25 to 29, black women were about 11 times as likely as white women to be killed, although the age factor is more prominent. Using 617 cases, the CDC calculated a ratio of 1.7 homicides per 100,000 live births, but Chang, the lead author, acknowledged the ratio is understated because homicides are so poorly tracked. In Maryland, researchers found 11.5 homicides per 100,000 live births. In two other state studies, the figures were much higher in other studies. These figures suggest male jealousy is a significant factor in the pregnant female death rate.

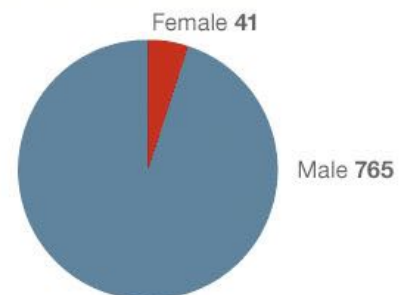
Some human societies, such as the Yanomamo (p 148) and Jivaro (p 156) are avowedly violent and practice levels of warfare lethal to 25% to 60% of adult males (p 149), in pursuing practices of wife capture and abduction driven by clearly reproductive imperatives. Martin Daly and Margo Wilson (R144) have also found suggestive evidence that male infanticide of competitors seen in apes (p 65) also exists among humans. Surveying crime statistics, they noted that when an adult

male murders a child he is 65 times more likely to be a stepfather or live-in boyfriend than the child's biological father.

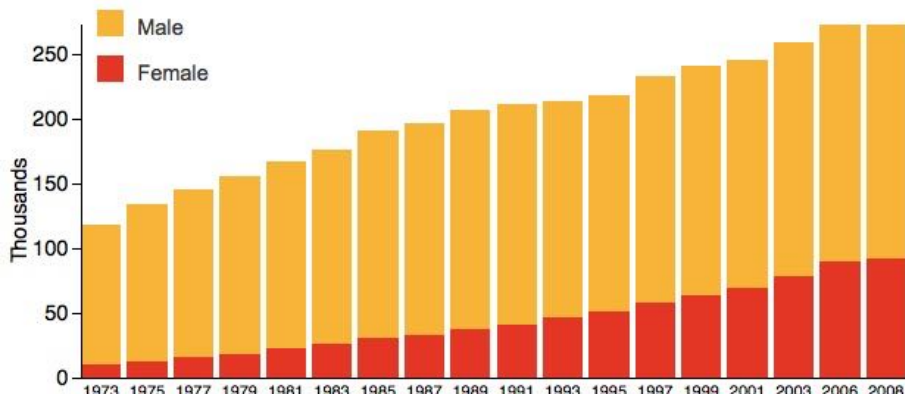
[Gender Analysis of Nobel Winners 2010](#). Does this reflect sexual difference at the upper extreme, differing opportunities or bias on the part of the Nobel judges?

In an analysis of 25,000 studies involving 8 million people, Susan Fiske concludes (Science 306) that almost anyone was found to be capable of torture, not just psychopathic people, if a peer group and/or commanding figures of authority were also condoning it. Stress of war, and alienation towards the 'other', were also factors conducive to torture. It is notable that even in such situations the study also found there was often a moral, defecting whistle blower who bucked the trend. Culture thus acts strongly enough on the average human genetic makeup to be capable of generating acts of atrocity. This is not a genetic form of 'original sin' but rather a cultural product of the 'fall'. To a large extent, it is culture which has to be accountable for many aspects of human violence, and patriarchy is human culture's classic alienation, across the sexual divide. Unlike genes, which are conserved over many generations and thus both trustworthy and slow to change, culture can be creatively transformed for the better by an informed act of choice.

Nobel Prize Winners by Gender



GENDER BREAKDOWN BY FIELD OF STUDY FOR US SCIENTISTS AND ENGINEERS WITH PHDS EMPLOYED IN ACADEMIA



Geoffrey Miller ([R475](#)) claims our propensity for generosity is also a product of selection, albeit sexual, rather than natural, leading to compassion for others and agreeable good nature. When starving people watch on television, the public respond and are often moved with great emotion by their empathy with situations of human plight. Throughout the world organizations like Amnesty International and Greenpeace receive their grass roots vitality from an emotional force that flows like a river towards an altruism which underlies our very will to survive in a world of light and life. It is clearly within the power of human communication to give a common sense of purpose to the human family, so that in reaching to the desire of humanity to live "creatively, intensively and successfully in the world" we all gain a measure of the blessing of fulfillment. The need to balance forgiveness

with firm but fair responses to exploitation and aggression is part of our evolutionary endowment. To "Love your enemies, bless them that curse you, do good to them that hate you, and pray for them which despitefully use you, and persecute you", is conducive to mutual coexistence but not practiced in a one-sided way that let's them hang us accursed on a tree, or more innocent blood will flow. Evolution appears to have struck this balance well.

Does Religious Spirituality have an [Evolutionary Basis](#)?

Beyond [sexual differences in the brain](#) is a development, connecting the emotional areas giving peak ecstatic significance in the limbic emotional and memory systems on the one hand and the closely adjacent ultimate centres of meaning and significance in the temporal lobes on the other, which the neuroscientist Ramachandran called the "God spot". These associated areas, when excited by psychedelic hallucinogens, meditation, prayer, incantation or sensory deprivation can give rise to a peak spiritual experience. They are also intimately involved in expressions of deep religious significance experienced by people in temporal lobe epilepsy.

However more recent studies of Carmelite nuns and meditating Buddhist monks have revealed very different and diverse forms of brain activity associated with different forms of religious feeling and practice (Biello, David 2007 Searching for God in the Brain Scientific American Oct 38-45), demonstrating that there is no one brain process, or "God module" involved in the diversity of religious experience.

One reading of religious reverence is that it is a confluence of higher evolution, leading to societies which can express feelings and behaviour in ways which promote social harmony. These do not necessarily have to involve the moral imperatives of conservative religious edict to induce a world order, but emotional and perceptual experience. To be effective they need to be naturally and autonomously expressed and in a way which reflects the dynamics of both sexes, not the coercion of religio 'binding again'.

Spiritual experience is also claimed to have a strong genetic basis. Dean Hamer ([R282](#)) asked volunteers 226 questions in order to determine how spiritually connected they felt to the universe. The higher their score, the greater a person's ability to believe in a greater spiritual force and the more likely they were to share the more active allele of VMAT2 a transport protein for serotonin, dopamine and other monoamine neurotransmitters. Studies on twins showed that those with this gene, a vesicular monoamine transporter that regulates the flow of mood-altering chemicals in the brain, were more likely to develop a spiritual belief. Growing up in a religious environment was said to have little effect on belief. Hamer laconically remarks: "Religious believers can point to the existence of god genes as one more sign of the creator's ingenuity - a clever way to help humans acknowledge and embrace a divine presence". Neurotransmitter differences have also been associated with subjects' readiness to perceive 'synchronistic' unseen influences between events. However Hamer's findings have been criticized as lacking scientific validity (Zimmer Carl 2004 Faith-Boosting Genes A search for the genetic basis of spirituality Scientific American Oct 110-114). VMAT2 is a very general neurotransmitter transport protein and the kind of religiosity measured, 'self transcendence' is as much associated with general feelings of connectedness to the world as it is to any form of religious practice and there was little corresponding evidence for a genetic component in any specific form of worship or religion.

Another type of evolutionary basis for religious inclination is as a cultural facilitator of social cohesion and ingroup solidarity often at the expense of rival groups, which facilitated vastly larger social communities than would be possible based on reciprocal altruism alone through the intervention of moral deities. This coincides with [Alexander's](#) theory of the biology of morality. In a far ranging review of several studies (The Origin and Evolution of Religious Prosociality, Ara Norenzayan and Azim Shariff Science 322 58-62 2008) evidence was put forward for a possible evolutionary role for religious thinking in terms of prosociality - the engendering of mutual trust and in a more bounded way the maintaining of a good personal reputation through acts which are costly to the participant and relatively hard to fake. Religious communities were found to have a lifetime proportional to the costliness in terms of commitments to its members, religious people were found to be more inclined to act as good Samaritans, but only when it would enhance their personal reputation and subjects were found to act more generously and cheat less when an unseen supernatural agent was said to be present.

An idea of how religiosity might function to produce ordered social structures is gleaned from closely watching chimp societies and the hierarchies topped by an alpha male. Helen Fisher ([R209](#)) notes: "The ruler has an important job - sheriff. He steps into a brawl and pulls the adversaries from one another. And he is expected to be a non-partisan referee. When this alpha male keeps fights at a minimum his chimp underlings respect him, support him, even pay him homage. They bow to him, plunging their heads and upper bodies repeatedly. They kiss his hands, feet and neck and chest. They lower themselves to make sure they are beneath him. And they follow him in an entourage. But if the leader fails to maintain harmony, his inferiors shift their allegiance ... subordinates create the chief." The leader of the hierarchy has an investment in keeping the peace, diffusing quarrels and reducing intra-group violence. These spontaneous expressions of reverence are precisely those we display in bowing down to God in expressing a deep inner reverence for a mystery which we believe brings a more harmonious and meaningful order to our lives. We can also see in the Draconian invoking of order by many religions under pain of diabolical punishment in the name of God a runaway example of ape society invoking the strong sheriff who keeps keeping the peace by threat of retribution of the high and mighty upon the weak. The compensating factor in ape society is egalitarian instability - that the alpha male can be deposed by a male coalition ([p 63](#)), or in bonobos by an alliance of females in support of a ranking son ([p 66](#)).

It is notable here that the females bear allegiance to this 'world order' only in so far as it is consistent with their reproductive choices. Fisher somewhat idealistically describes female chimps by contrast as good networkers: "Female chimps do not establish this kind of status ladder. They form cliques instead - laterally connected subgroups of individuals who care for one another's infants and protect and nurture one another in times of social chaos. Females are less aggressive, less dominance oriented and this network can remain stable - and relatively egalitarian for years. Moreover the most dominant female generally acquires this position by sheer personality, charisma if you will, as well as by age rather than by intimidation." While female bonobos do form large loose coalitions, female chimps spend much more time alone than the sociable males, foraging in their local terrains, or mothering. They do also have a hierarchical ranking although less precisely defined and will drive off outside females who come on to their feeding domains.