

Handout Chapter 10 Motivation

THE ANIMAL WITH THE WEIRDEST SEX LIFE:

From the book “Why is Sex Fun?” Chapter 1

If your dog had your brain and could speak, and if you asked it what it thought of your sex life, you might be surprised by its response. It would be something like this:

Those disgusting humans have sex any day of the month! Barbara proposes sex even when she knows perfectly well that she isn't fertile-like just after her period. John is eager for sex all the time, without caring whether his efforts could result in a baby or not. But if you want to hear something really gross-Barbara and John kept on having sex while she was pregnant! That's as bad as all the times when John's parents come for a visit, and I can hear them too having sex, although John's mother went through this thing they call menopause years ago. Now she can't have babies anymore, but she still wants sex, and John's father obliges her. What a waste of effort! Here's the weirdest thing of all: Barbara and John, and John's parents, close the bedroom door and have sex in private, instead of doing it in front of their friends like any self-respecting dog!

To understand where your dog is coming from, you need to free yourself from your human-based perspective on what constitutes normal sexual behavior. Increasingly today, we consider it narrow-minded and despicably prejudiced to denigrate those who do not conform to our own standards. Each such form of narrow-mindedness is associated with a despicable “ism”-for instance, racism, sexism, Eurocentrism, and phallocentrism. To that list of modern “ism” sins, defenders of animal rights are now adding the sin of **species-ism**. Our standards of sexual conduct are especially warped, species-ist, and human-centric because human sexuality is so abnormal by the standards of the world's thirty million other animal species. It's also abnormal by the standards of the world's millions of species of plants, fungi, and microbes, but I'll ignore that broader perspective because I haven't yet worked through my own zoo-centrism. This book confines itself to the insights that we can gain into our sexuality merely by broadening our perspective to encompass other animal species.

As a beginning, let's consider normal sexuality by the standards of the world's approximately 4,300 species of mammals, of which we humans are just one. Most mammals do not live as a nuclear family of a mated adult male and adult female, caring jointly for their offspring. Instead, in many mammal species both adult males and adult females are solitary, at least during the breeding season, and meet only to copulate. Hence, males do not provide paternal care; their sperm is their sole contribution to their offspring and to their temporary mate.

Even most social mammal species, such as lions, wolves, chimpanzees, and many hoofed mammals, are not paired off within the herd/pride/pack/band into male/ female couples. Within such a herd/pride/et cetera, each adult male shows no signs of recognizing specific infants as his offspring by devoting himself to them at the expense of other infants in the herd. Indeed, it is only within the last few years that scientists studying lions, wolves, and chimpanzees have begun to figure out, with the help of DNA testing, which male sired which infant. However, like all generalizations, these admit exceptions. Among the minority of adult male mammals that do offer their offspring paternal care are polygynous male zebras and gorillas with harems of females, male gibbons paired off with females as solitary couples, and saddleback tamarin monkeys, of which two adult males are kept as a harem by one polyandrous adult female.

Sex in social mammals is generally carried out in public, before the gazes of other members of the troop. For instance, a female Barbary macaque in estrus copulates with every adult male in her troop and makes no effort to conceal each copulation from other males. The best-documented exception to this pattern of public sex is in chimpanzee troops, where an adult male and estrous female may go off by themselves for a few days on what human observers term a “consortship.” However, the same female chimpanzee that has private sex with a consort may also have public sex with other adult male chimpanzees within the same estrus cycle.

Adult females of most mammal species use various means of conspicuously advertising the brief phase of their reproductive cycle when they are ovulating and can be fertilized. The advertisement may be visual (for instance, the area around the vagina turning bright red), olfactory (releasing a distinctive smell), auditory (making noises), or behavioral (crouching in front of an adult male and displaying the vagina). Females solicit sex only during those fertile days, are sexually unattractive or less attractive to males on other days because they lack the arousing signals, and rebuff the advances of any male that is nevertheless interested on other days. Thus, sex is emphatically not just

for fun and is rarely divorced from its function of fertilization. This generalization too admits exceptions: sex is flagrantly separated from reproduction in a few species, including bonobos (pygmy chimpanzees) and dolphins.

Finally, the existence of menopause as a regular phenomenon is not well established for most wild mammal populations. By menopause is meant a complete cessation of fertility within a time span that is much briefer than the previous fertile career and that is followed by an infertile life span of significant length. Instead, wild mammals either are still fertile at the time of death or else exhibit gradually diminishing fertility with advancing age.

Now contrast what I have just said about normal mammalian sexuality with human sexuality. The following human attributes are among those that we take for granted as normal:

1. Most men and women in most human societies end up in a long-term pair relationship (“marriage”) that other members of the society recognize as a contract involving mutual obligations.
2. The couple has sex repeatedly, and mainly or exclusively with each other. In addition to being a sexual union, marriage is a partnership for joint rearing of the resulting babies. In particular, human males as well as females commonly provide parental care.
3. Despite forming a couple (or occasionally a harem), a husband and wife (or wives) do not live (like gibbons) as a solitary couple in an exclusive territory that they defend against other couples, but instead they live embedded in a society of other couples with whom they cooperate economically and share access to communal territory.
4. Marriage partners usually have sex in private, rather than being indifferent to the presence of other humans.
5. Human ovulation is concealed rather than advertised. That is, women’s brief period of fertility around the time of ovulation is difficult to detect for their potential sex partners as well as for most women themselves. A woman’s sexual receptivity extends beyond the time of fertility to encompass most or all of the menstrual cycle. Hence, most human copulations occur at a time unsuitable for conception. That is, human sex is mostly for fun, not for insemination.
6. All women who live past the age of forty or fifty undergo menopause, a complete shutdown of fertility. Men in general do not undergo menopause: while individual men may develop fertility problems at any age, there is no age-clumping of infertility or universal shutdown.

Norms imply violation of norms: we call something a “norm” merely because it is more frequent than its opposite (the “violation of the norm”). That’s as true for human sexual norms as for other norms. Readers up to this point will surely have been thinking of exceptions to the supposed generalizations that I have been describing, but they still stand as generalizations. For example, even in societies that recognize monogamy by law or custom there is much extramarital and premarital sex, and much sex that is not part of a long-term relationship. Humans do engage in one-night stands. On the other hand, most humans also engage in many-year or many-decade stands, whereas tigers and orangutans engage in nothing except one-night stands. The genetically based paternity tests developed over the last half-century have shown that the majority of American, British, and Italian babies are indeed sired by the husband (or steady boyfriend) of the baby’s mother.

Readers may also bristle at hearing human societies described as monogamous; the term “harem,” which zoologists apply to zebras and gorillas, is taken from the Arabic word for a human institution. Yes, many humans practice sequential monogamy. Yes, polygyny (long-term simultaneous unions between one man and multiple wives) is legal in some countries today, and polyandry (long-term simultaneous unions between one woman and multiple husbands) is legal in a few societies. In fact, polygyny was accepted in the great majority of traditional human societies before the rise of state institutions. However, even in officially polygynous societies most men have only one wife at a time, and only especially wealthy men can acquire and maintain a few wives simultaneously. The large harems that spring to mind at the mention of the word polygamy, such as those of recent Arabian and Indian royalty, are possible only in the state-level societies that arose very late in human evolution and that permitted a few men to concentrate great wealth. Hence the generalization stands: most adults in most human societies are at any given moment involved in a long-term pair bond that is often monogamous in practice as well as legally.

Still another cause for bristling may have been my description of human marriage as a partnership for the joint rearing of the resulting babies. Most children receive more parental care from their mothers than from their fathers. Unwed mothers form a significant proportion of the adult population in some modern societies, though it has been much harder for unwed mothers to rear children successfully in traditional societies. But the generalization

again holds: most human children receive some parental care from their father, in the form of child care, teaching, protection, and provision of food, housing, and money.

All these features of human sexuality-long-term sexual partnerships, co-parenting, proximity to the sexual partnerships of others, private sex, concealed ovulation, extended female receptivity, sex for fun, and female menopause- constitute what we humans assume is normal sexuality. It titillates, amuses, or disgusts us to read of the sexual habits of elephant seals, marsupial mice, or orangutans, whose lives are so different from ours. Their lives seem to us bizarre. But that proves to be a species-ist interpretation. By the standards of the world's 4,300 other species of mammals, and even by the standards of our own closest relatives, the great apes (the chimpanzee, bonobo, gorilla, and orangutan), **we are the ones who are bizarre.**

However, I am still being worse than zoo-centric. I am falling into the even narrower trap of mammalo-centrism. Do we become more normal when judged by the standards of non-mammalian animals? Other animals do exhibit a wider range of sexual and social systems than do mammals alone. Whereas the young of most mammal species receive maternal care but no paternal care, the reverse is true for some species of birds, frogs, and fish in which the father is the sole caretaker for his offspring. The male is a parasitic appendage fused to the female's body in some species of deep-sea fish; he is eaten by the female immediately after copulation in some species of spiders and insects. While humans and most other mammal species breed repeatedly, salmon, octopus, and many other animal species practice what is termed big-bang reproduction, or semelparity: a single reproductive effort, followed by preprogrammed death. The mating system of some species of birds, frogs, fish, and insects (as well as some bats and antelope) resembles a singles bar-at a traditional site, termed a "lek," many males maintain stations and compete for the attention of visiting females, each of which chooses a mate (often the same preferred male chosen by many other females), copulates with him, and then goes off to rear the resulting offspring without his assistance.

Among other animal species, it is possible to point out some whose sexuality resembles ours in particular respects. Most European and North American bird species form pair bonds that last for at least one breeding season (in some cases for life), and the father as well as the mother cares for the young. While most such bird species differ from us in that pairs occupy mutually exclusive territories, most species of sea birds resemble us further in that mated pairs breed colonially in close proximity to each other. However, all these bird species differ from us in that ovulation is advertised, female receptivity and the sex act are mostly confined to the fertile period around ovulation, sex is not recreational, and economic cooperation between pairs is slight or nonexistent. Bonobos (pygmy chimpanzees) resemble or approach us in many of these latter respects: female receptivity is extended through several weeks of the estrus cycle, sex is mainly recreational, and there is some economic cooperation between many members of the band. However, bonobos still lack our pair-bonded couples, our well-concealed ovulation, and our paternal recognition of and care for offspring. Most or all of these species differ from us in lacking a well-defined female menopause.

Thus, even a non-mammalo-centric view reinforces our dog's interpretation: we are the ones who are bizarre. We marvel at what seems to us the weird behavior of peacocks and big-bang marsupial mice, but those species actually fall securely within the range of animal variation, and in fact **we are the weirdest of them all.** Species-ist zoologists theorize about why hammer-headed fruit bats evolved their lek mating system, yet the mating system that cries out for explanation is our own. **Why did we evolve to be so different?**

This question becomes even more acute when we compare ourselves with our closest relatives among the world's mammal species, the great apes (as distinguished from the gibbons or little apes). Closest of all are Africa's chimpanzee and bonobo, from which we differ in only about 1.6 percent of our nuclear genetic material (DNA). Nearly as close are the gorilla (2.3 percent genetic difference from us) and the orangutan of Southeast Asia (3.6 percent different). Our ancestors diverged "only" about seven million years ago from the ancestors of chimpanzees and bonobos, nine million years ago from the ancestors of gorillas, and fourteen million years ago from the ancestors of orangutans.

That sounds like an enormous amount of time in comparison to an individual human lifetime, but it's a mere eye-blink on the evolutionary time scale. Life has existed on Earth for more than three billion years, and hard-shelled, complex large animals exploded in diversity more than half a billion years ago. Within that relatively short period during which our ancestors and the ancestors of our great ape relatives have been evolving separately, we have diverged in only a few significant respects and to a modest degree, even though some of those modest

differences- especially our upright posture and larger brains-have had enormous consequences for our behavioral differences.

Along with posture and brain size, sexuality completes the trinity of the decisive respects in which the ancestors of humans and great apes diverged. Orangutans are often solitary, males and females associate just to copulate, and males provide no paternal care; a gorilla male gathers a harem of a few females, with each of which he has sex at intervals of several years (after the female weans her most recent offspring and resumes menstrual cycling and before she becomes pregnant again); and chimpanzees and bonobos live in troops with no lasting male-female pair bonds or specific father-offspring bonds. It is clear how our large brain and upright posture played a decisive role in what is termed our humanity-in the fact that we now use language, read books, watch TV, buy or grow most of our food, occupy all continents and oceans, keep members of our own and other species in cages, and are exterminating most other animal and plant species, while the great apes still speechlessly gather wild fruit in the jungle, occupy small ranges in the Old World tropics, cage no animal, and threaten the existence of no other species.

What role did our weird sexuality play in our achieving these hallmarks of humanity? Could our sexual distinctiveness be related to our other distinctions from the great apes? In addition to (and probably ultimately as a product of) our upright posture and large brains, those distinctions include our relative hairlessness, dependence on tools, command of fire, and development of language, art, and writing. If any of these distinctions predisposed us toward evolving our sexual distinctions, the links are certainly unclear. For example, it is not obvious why our loss of body hair should have made recreational sex more appealing, nor why our command of fire should have favored menopause. Instead, I shall argue the reverse: recreational sex and menopause were as important for our development of fire, language, art, and writing as were our upright posture and large brains.

The key to understanding human sexuality is to recognize that it is a problem in evolutionary biology. When Darwin recognized the phenomenon of biological evolution in his great book *On the Origin of Species*, most of his evidence was drawn from anatomy. He inferred that most plant and animal structures evolve-that is, they tend to change from generation to generation. He also inferred that **the major force behind evolutionary change is natural selection**. By that term, Darwin meant that plants and animals vary in their anatomical adaptations, that certain adaptations enable individuals bearing them to survive and reproduce more successfully than other individuals, and that those particular adaptations therefore increase in frequency in a population from generation to generation. Later biologists showed that Darwin's reasoning about anatomy also applies to physiology and biochemistry: an animal's or plant's physiological and biochemical characteristics also adapt it to certain lifestyles and evolve in response to environmental conditions.

More recently, evolutionary biologists have shown that animal social systems also evolve and adapt. Even among closely related animal species, some are solitary, others live in small groups, and still others live in large groups. But social behavior has consequences for survival and reproduction. Depending, for example, on whether a species' food supply is clumped or spread out, and on whether a species faces high risk of attack by predators, either solitary living or group living may be better for promoting survival and reproduction.¹

Similar considerations apply to sexuality. Some sexual characteristics may be more advantageous for survival and reproduction than others, depending on each species' food supply, exposure to predators, and other biological characteristics. At this point I shall mention just one example, a behavior that at first seems diametrically opposed to evolutionary logic: **sexual cannibalism**. The male of some species of spiders and mantises is routinely eaten by his mate just after or even while he is copulating with her. This cannibalism clearly involves the male's consent, because the male of these species approaches the female, makes no attempt to escape, and may even bend his head and thorax toward the female's mouth so that she may munch her way through most of his body while his abdomen remains to complete the job of injecting sperm into her.

If one thinks of natural selection as the maximization of survival, such cannibalistic suicide makes no sense. Actually, natural selection maximizes the transmission of genes, and survival is in most cases just one strategy that provides repeated opportunities to transmit genes. Suppose that opportunities to transmit genes arise unpredictably and infrequently, and that the number of offspring produced by such opportunities increases with the

¹ What he is saying is important. If the food supply is clumped and there are a lot of predators, those people that live in groups will thrive compared to living alone. So "social systems" will evolve in mammals.

female's nutritional condition. That's the case for some species of spiders and mantises living at low population densities. A male is lucky to encounter a female at all, and such luck is unlikely to strike twice. The male's best strategy is to produce as many offspring bearing his genes as possible out of his lucky find. The larger a female's nutritional reserves, the more calories and protein she has available to transform into eggs. If the male departed after mating, he would probably not find another female and his continued survival would thus be useless. Instead, by encouraging the female to eat him, he enables her to produce more eggs bearing his genes. In addition, a female spider whose mouth is distracted by munching a male's body allows copulation with the male's genitalia to proceed for a longer time, resulting in more sperm transferred and more eggs fertilized.

The male spider's evolutionary logic is impeccable and seems bizarre to us only because other aspects of human biology make sexual cannibalism disadvantageous. Most men have more than one lifetime opportunity to copulate; even well-nourished women usually give birth to only a single baby at a time, or at most twins; and a woman could not consume enough of a man's body at one sitting to improve significantly the nutritional basis for her pregnancy.

This example illustrates the dependence of evolved sexual strategies on both ecological parameters and the parameters of a species' biology, both of which vary among species. **Sexual cannibalism in spiders and mantises is favored by the ecological variables of low population densities and low encounter rates, and by the biological variables of a female's capacity to digest relatively large meals and to increase her egg output considerably when well nourished.** Ecological parameters can change overnight if an individual colonizes a new type of habitat, but the colonizing individual carries with it a baggage of inherited biological attributes that can change only slowly, through natural selection. Hence it is not enough to consider a species' habitat and lifestyle, design on paper a set of sexual characteristics that would be well matched to that habitat and lifestyle, and then be surprised that those supposedly optimal sexual characteristics do not evolve. Instead, sexual evolution is severely constrained by inherited commitments and prior evolutionary history.²

For example, in most fish species a female lays eggs and a male fertilizes those eggs outside the female's body, but in all placental mammal species and marsupials a female gives birth to live young rather than to eggs, and all mammal species practice internal fertilization (male sperm injected into the female's body). Live birth and internal fertilization involve so many biological adaptations and so many genes that all placental mammals and marsupials have been firmly committed to those attributes for tens of millions of years. As we shall see, these inherited commitments help explain why there is no mammal species in which parental care is provided solely by the male, even in habitats where mammals live alongside fish and frog species whose males are the sole providers of parental care.

We can thus redefine the problem posed by our strange sexuality. Within the last seven million years, our sexual anatomy diverged somewhat, our sexual physiology further, and our sexual behavior even more, from those of our closest relatives, the chimpanzees. Those divergences must reflect a divergence between humans and chimpanzees in environment and lifestyle. But those divergences were also limited by inherited constraints. What were the lifestyle changes and inherited constraints that molded the evolution of our weird sexuality?

From "Why is Sex Fun" Chapter 1 by Jared Diamond, 1997

Chapter 2

THE BATTLE OF THE SEXES

In the preceding chapter we saw that our effort to understand human sexuality must begin by our distancing ourselves from our warped human perspective. We're exceptional animals in that our fathers and mothers often remain together after copulating and are both involved in rearing the resulting child. No one could claim that men's

² What he is saying here is important. When we look at a species today and can't understand why they do what they do, we must realize that "what they do today" is a result of millions of years of adapting to a past environment that may or may not be different from today's environment. In other words within us are our evolved instincts that may or may not be optimal in our current environment.

and women's parental contributions are equal: they tend to be grossly unequal in most marriages and societies. But most fathers make some contribution to their children, even if it's just food or defense or land rights. We take such contributions so much for granted that they're written into law: divorced fathers owe child support, and even an unwed mother can sue a man for child support if genetic-testing proves that he is her child's father.

But that's our warped human perspective. Alas for sexual equality, we're aberrations in the animal world, and especially among mammals. If orangutans, giraffes, and most other mammal species could express their opinion, they would declare our child support laws absurd. Most male mammals have no involvement with either their offspring or their offspring's mother after inseminating her; they are too busy seeking other females to inseminate. Male animals in general, not just male mammals, provide much less parental care (if any) than do females.

Yet there are quite a few exceptions to this chauvinist pattern. In some bird species, such as phalaropes and Spotted Sandpipers, it's the male that does the work of incubating the eggs and rearing the chicks, while the female goes in search of another male to inseminate her again and to rear her next clutch. Males of some fish species (like seahorses and sticklebacks) and some amphibian males (like midwife toads) care for the eggs in a nest or in their mouth, pouch, or back. How can we explain simultaneously this general pattern of female parental care and also its numerous exceptions?

The answer comes from the realization that **genes for behavior, as well as for malaria resistance and teeth, are subject to natural selection. A behavior pattern that helps individuals of one animal species pass on their genes won't necessarily be helpful in another species.** In particular, a male and female that have just copulated to produce a fertilized egg face a "choice" of subsequent behaviors. Should that male and female both leave the egg to fend for itself and set to work on producing another fertilized egg, copulating either with the same partner or with a different partner? On the one hand, a time-out from sex for the purpose of parental care might improve the chances of the first egg surviving. If so, that choice leads to further choices: both the mother and the father could choose to provide the parental care, or just the mother could choose to do so, or just the father could. On the other hand, if the egg has a one-in-ten chance of surviving even with no parental care, and if the time you'd devote to tending it would alternatively let you produce 1,000 more fertilized eggs, you'd be best off leaving that first egg to fend for itself and going on to produce more fertilized eggs.³

I've referred to these alternatives as "choices." That word may seem to suggest that animals operate like human decision-makers, consciously evaluating alternatives and finally choosing the particular alternative that seems most likely to advance the animal's self-interest. Of course, that's not what happens. Many of the so-called choices actually are programmed into an animal's anatomy and physiology. For example, female kangaroos have "chosen" to have a pouch that can accommodate their young, but male kangaroos have not. Most or all of the remaining choices are ones that would be anatomically possible for either sex, but animals have programmed instincts that lead them to provide (or not to provide) parental care, and this instinctive "choice" of behavior can differ between sexes of the same species. For example, among parent birds, both male and female albatrosses, male but not female ostriches, females but not males of most hummingbird species, and no brush turkeys of either sex are instinctively programmed to bring food to their chicks, although both sexes of all of these species are physically and anatomically perfectly capable of doing so.

The anatomy, physiology, and instincts underlying parental care are all programmed genetically by natural selection. Collectively, they constitute part of what biologists term a reproductive strategy. That is, genetic mutations or recombinations in a parent bird could strengthen or weaken the instinct to bring food to the chicks and could do so differently in the two sexes of the same species. Those instincts are likely to have a big effect on the number of chicks that survive to carry on the parent's genes. It's obvious that a chick to which a parent brings food is more likely to survive, but we shall also see that a parent that forgoes bringing food to its chicks thereby gains other increased chances to pass on its genes. Hence the net effect of a gene that causes a parent bird instinctively to bring food to its chicks could be either to increase or to decrease the number of chicks carrying on the parent's genes, depending on ecological and biological factors that we shall discuss.

³ Do you see what he is saying here? If an egg has a 1 in 10 chance of surviving on his own and by deserting to inseminate 1,000 eggs, deserting leads to 100 surviving (1/10 times 1,000). So if you stay, you are giving up 100 surviving kids for making sure that 1 survives. That "staying" behavior would die out.

Genes that specify the particular anatomical structures or instincts most likely to ensure the survival of offspring bearing the genes will tend to increase in frequency. This statement can be rephrased: anatomical structures and instincts that promote survival and reproductive success tend to become established (genetically programmed) by natural selection. But the need to make wordy statements such as these arises very often in any discussion of evolutionary biology. Hence biologists routinely resort to anthropomorphic language to condense such statements—for example, they say that an animal "chooses" to do something or pursues a certain strategy. This shorthand vocabulary should not be misconstrued as implying that animals make conscious calculations.

For a long time, evolutionary biologists thought of natural selection as somehow promoting "the good of the species." In fact, natural selection operates initially on individual animals and plants. Natural selection is not just a struggle between species (entire populations), nor is it just a struggle between individuals of different species, nor just between conspecific individuals of the same age and sex. Natural selection can also be a struggle between parents and their offspring or a struggle between mates, because the self-interests of parents and their offspring, or of father and mother, may not coincide. **What makes individuals of one age and sex successful at transmitting their genes may not increase the success of other classes of individuals.**

In particular, while natural selection favors both males and females that leave many offspring, the best strategy for doing so may be different for fathers and mothers. That generates a built-in conflict between the parents, a conclusion that all too many humans don't need scientists to reveal to them. We make jokes about the battle of the sexes, but the battle is neither a joke nor an aberrant accident of how individual father or mothers behave on particular occasions. It is indeed perfectly true that behavior that is in a male's genetic interests may not necessarily be in the interests of his female co-parent, and vice versa. That cruel fact is one of the fundamental causes of human misery.

Consider again the case of the male and female who have just copulated to produce a fertilized egg and now face the "choice" of what to do next. If the egg has some chance of surviving unassisted, and if both the mother and the father could produce many more fertilized eggs in the time that they would devote to tending that first fertilized egg, then the interests of the mother and father coincide in deserting the egg. But now suppose that the newly fertilized, laid, or hatched egg or newborn offspring has absolutely zero chance of surviving unless it is cared for by one parent. Then there is indeed a conflict of interest. Should one parent succeed in foisting the obligation of parental care onto the other parent and then going off in search of a new sex partner, then the foister will have advanced her or his genetic interests at the expense of the abandoned parents. The foister will really promote his or her selfish evolutionary goals by deserting his or her mate and offspring.

In such cases when care by one parent is essential for offspring survival, child-rearing can be thought of as a cold-blooded race between mother and father to be the first to desert the other and their mutual offspring and to get on with the business of producing more babies. Whether it actually pays you to desert, depends on whether you can count on your old mate to finish rearing the kids, and whether you are then likely to find a receptive new mate. It's as if, at the moment of fertilization, the mother and father play a game of chicken, stare at each other, and simultaneously say, "I am going to walk off and find a new partner, and you can care for this embryo if you want to, but even if you don't, I won't!" If both partners call each other's bluff in that race to desert their embryo, then the embryo dies and both parents lose the game of chicken. Which parent is more likely to back down?

The answer depends on such considerations as which parent has more invested in the fertilized egg, and which parent has better alternative prospects. As I said before, neither parent makes a conscious calculation; the actions of each parent are instead programmed genetically by natural selection into the anatomy and instincts of their sex. In many animal species the female backs down and becomes sole parent while the male deserts, but in other species the male assumes responsibility and the female deserts, and in still other species both parents assume shared responsibility. Those varying outcomes depend on three interrelated sets of factors whose differences between the sexes vary among species: **investment in the already fertilized embryo or egg; alternative opportunities that would be foreclosed by further care of the already fertilized embryo or egg, and confidence in the paternity or maternity of the embryo or egg.**

All of us know from experience that we are much more reluctant to walk away from an ongoing enterprise in which we have invested a lot than from one in which we have invested only a little. That's true of our investments in human relationships, in business projects, or in the stock market. It's true regardless of whether our investment is

in the form of money, time, or effort. We lightly end a relationship that turns bad on the first date, and we stop trying to construct from parts a cheap toy when we hit a snag within a few minutes. But we agonize over ending a twenty-five-year marriage or an expensive house remodeling.

The same principle applies to **parental investment** in potential offspring. Even at the moment when an egg is fertilized by a sperm, the resulting fertilized embryo generally represents a greater investment for the female than for the male, because in most animal species the egg is much larger than the sperm. While both eggs and sperm contain chromosomes, the egg in addition must contain enough nutrients and metabolic machinery to support the embryo's further development for some time, at least until the embryo can start feeding itself. Sperm, in contrast, need contain only a flagellar motor and sufficient energy to drive that motor and support swimming for at most a few days. As a result, a mature human egg has roughly one million times the mass of the sperm that fertilizes it; the corresponding factor for kiwis is one million billion. Hence a fertilized embryo, viewed simply as an early-stage construction project, represents an utterly trivial investment of its father's body mass compared to its mother's. But that doesn't mean that the female has automatically lost the game of chicken before the moment of conception. Along with the one sperm that fertilized the egg, the male may have produced several hundred million other sperm in the ejaculate, so that his total investment may be not dissimilar to the female's.

The act of fertilizing an egg is described as either internal or external, depending on whether it takes place inside or outside the female's body. External fertilization characterizes most species of fish and amphibia. For example, in most fish species a female and a nearby male simultaneously discharge their eggs and sperm into the water, where fertilization occurs. With external fertilization, the female's obligate investment ends at the moment she extrudes the eggs. The embryos may then be left to float away and fend for themselves without parental care, or they may receive care from one parent, depending on the species.

More familiar to humans is internal fertilization, the male's injection of sperm (for example, via an intromittive penis) into the female's body. What happens next in most species is that the female does not immediately extrude the embryos but retains them in her body for a period of development until they are closer to the stage when they can survive by themselves. The offspring may eventually be packaged for release within a protective eggshell, together with an energy supply in the form of yolk—as in all birds, many reptiles, and monotreme mammals (the platypus and echidnas of Australia and New Guinea). Alternatively, the embryo may continue to grow within the mother until the embryo is "born" without an eggshell instead of being "laid" as an egg. That alternative, termed vivipaty (Latin for "live birth"), characterizes us and all other mammals except monotremes, plus some fish, reptiles, and amphibia. Vivipary requires specialized internal structures—of which the mammalian placenta is the most complex—for the transfer of nutrients from the mother to her developing embryo and the transfer of wastes from embryo to mother.

Internal fertilization thus obligates the mother to further investment in the embryo beyond the investment that she has already made in producing the egg until it is fertilized. Either she uses calcium and nutrients from her own body to make an eggshell and yolk, or else she uses her nutrients to make the embryo's body itself. Besides that investment of nutrients, the mother is also obligated to invest the time required for pregnancy. The result is that **the investment of an internally fertilized mother at the time of hatching or birth, relative to the father's, is likely to be much greater than that of an externally fertilized mother at the time of unfertilized egg extrusion**. For instance, by the end of a nine-month pregnancy a human mother's expenditure of time and energy is colossal in comparison with her husband's or boyfriend's pathetically slight investment during the few minutes it took him to copulate and extrude his one milliliter of sperm.

As a result of that unequal investment of mothers and fathers in internally fertilized embryos, it becomes harder for the mother to bluff her way out of post-hatching or post-birth parental care, if any is required. That care takes many forms: for instance, lactation by female mammals, guarding the eggs by female alligators, and brooding the eggs by female pythons. Nevertheless, as we shall see, there are other circumstances that may induce the father to stop bluffing and to start assuming shared or even sole responsibility for his offspring.

I mentioned that three related sets of factors influence the "choice" of parent to be caretaker, and that relative size of investment in the young is only one of those factors. A second factor is **foreclosed opportunity**. Picture yourself as an animal parent contemplating your newborn offspring and coldly calculating your genetic self-interest as you debate what you should now do with your time. That offspring bears your genes, and its chance of

surviving to perpetuate your genes would undoubtedly be improved if you hang around to protect and feed it. If there is nothing else you could do with your time to perpetuate your genes, your interests would be best served by caring for that offspring and not trying to bluff your mate into being sole parent. On the other hand, if you can think of ways to spread your genes to many more offspring in the same time, you should certainly do so and desert your current mate and offspring.

Now consider a mother and father animal both doing that calculation the moment after they have mated to produce some fertilized embryos. If fertilization is external, neither mother nor father is automatically committed to anything further, and both are theoretically free to seek another partner with whom to produce more fertilized embryos. Yes, their just-fertilized embryos may need some care, but mother and father are equally able to try to bluff the other into providing that care. But if fertilization is internal, the female is now pregnant and committed to nourishing the fertilized embryos until birth or laying. If she is a mammal, she is committed for even longer, through the period of lactation. During that period it does her no genetic good to copulate with another male, because she cannot thereby produce more babies. That is, she loses nothing by devoting herself to child care.

But the male who has just discharged his sperm sample into one female is available a moment later to discharge another sperm sample into another female, and thereby potentially to pass his genes to more offspring. A man, for example, produces about two hundred million sperm in one ejaculate—or at least a few tens of millions, even if reports of a decline in human sperm count in recent decades are correct. **By ejaculating once every 28 days during his recent partner's 280-day pregnancy--a frequency of ejaculation easily within the reach of most men—he would broadcast enough sperm to fertilize every one of the world's approximately two billion reproductively mature women, if he could only succeed in arranging for each of them to receive one of his sperm.** That's the evolutionary logic that induces so many men to desert a woman immediately after impregnating her and to move on to the next woman. A man who devotes himself to child care potentially forecloses many alternative opportunities. Similar logic applies to males and females of most other internally fertilized animals. Those alternative opportunities available to males contribute to the predominant pattern of females providing child care in the animal world.

The remaining factor is **confidence of parenthood**. If you are going to invest time, effort, and nutrients in raising a fertilized egg or embryo, you'd better make damn sure first that it's your own offspring. If it turns out to be somebody else's offspring, you've lost the evolutionary race. You'll have knocked yourself out in order to pass on a rival's genes.

For women and other female animals practicing internal fertilization, doubt about maternity never arises. Into the mother's body, containing her eggs, goes sperm. Out of her body sometime later comes a baby. There's no way that the baby could have been switched with some other mother's baby inside of her. It's a safe evolutionary bet for the mother to care for that baby.

But males of mammals and other internally fertilized animals have no corresponding confidence in their paternity. Yes, the male knows that his sperm went into a female's body. Sometime later, out of that female's body, comes a baby. How does the male know whether the female copulated with other males while he wasn't looking? How does he know whether his sperm or some other male's sperm was the one that fertilized the egg. In the face of this inevitable uncertainty, the evolutionary conclusion reached by most male mammals is to walk off the job immediately after copulation, seek more females to impregnate, and leave those females to rear their offspring—hoping that one or more of the females with which he copulated will actually have been impregnated by him and will succeed in rearing his offspring unassisted. Male parental care would be a bad evolutionary gamble.

Yet we know, from our own experience, that some species constitute exceptions to that general pattern of male post-copulatory desertion. The exceptions are of three types. One type is those species whose eggs are fertilized externally. The female ejects her not yet fertilized eggs; the male, hovering nearby or already grasping the female, spreads his sperm on the eggs; he immediately scoops up the eggs, before any other males have a chance to cloud the picture with their sperm; and he proceeds to care for the eggs, completely confident in his paternity. This is the evolutionary logic that programs some male fish and frogs to play the role of sole parent after fertilization. For example, the male midwife toad guards the eggs by wrapping them around his hind legs; the male glass frog stands watch over eggs in vegetation over a stream into which the hatched tadpoles can drop; and the male stickleback builds a nest in which to protect the eggs against predators.

(I removed one type of exception that was mentioned in the original chapter in the interests of shortening this reading)

Another type of exception to the predominant pattern of male desertion occurs in species in which, like us, fertilization is internal but it's hard or impossible for a single parent to rear the young unassisted. A second parent may be required to gather food for the co-parent or the young, tend the young while the co-parent is off gathering food, defend a territory, or teach the young. In such species the female alone would not be able to feed and defend the young without the male's help. Deserting a fertilized mate to pursue other females would bring no evolutionary gain to a male if his offspring thereby died of starvation. Thus, self-interest may force the male to remain with his fertilized spouse, and vice versa.

That's the case with most of our familiar North American and European birds: males and females are monogamous, and they share in caring for the young. It's also approximately true for humans, as we know so well. Human single-parenthood is difficult enough, even in these days of supermarket shopping and babysitters for hire. In ancient hunter-gatherer days, a child orphaned by either its mother's or its father's death faced reduced chances of survival. The father as well as the mother, desirous of passing on genes finds it a matter of self-interest to care for the child. Hence most men have provided food, protection and housing for their spouse and kids. The result is our human social system of nominally monogamous married couples, or occasionally of harems of women committed to one affluent man. Essentially the same considerations apply to gorillas, gibbons, and the other minority mammals practicing male parental care.

Yet that familiar arrangement of co-parenthood does not end the battle of the sexes. It does not necessarily dissolve the tension between the mother's and father's interests, arising from their unequal investments before birth. **Even among those mammal and bird species that provide paternal care, males try to see how little care they can get away with and still have the offspring survive owing mainly to the mother's efforts. Males also try to impregnate other males' mates, leaving the unfortunate cuckolded male to care unknowingly for the cuckold's offspring. Males become justifiably paranoid about their mates' behavior.**

An intensively studied and fairly typical example of those built-in tensions of co-parenthood is the European bird species known as the Pied Flycatcher. Most flycatcher males are nominally monogamous, but many try to be polygynous, and quite a few succeed. Again, it is instructive to devote a few pages of this book on human sexuality to another example involving birds, because (as we'll see) the behavior of some birds is strikingly like that of human but does not arouse the same moral indignation in us.

Here is how polygyny works for Pied Flycatchers. In the spring a male finds a good nest hole, stakes out his territory around it, woos a female, and copulates with her. When this female (termed his primary female) lays her first egg, the male feels confident that he has fertilized her, that she'll be busy incubating his eggs, and that she won't be interested in other males and is temporarily sterile anyway. Hence the male finds another nest hole nearby, courts another female (termed his secondary female), and copulates with her.

When that secondary female begins laying, the male feels confident that he has fertilized her as well. Around that same time, the eggs of his primary female are starting to hatch. The male returns to her, devotes most of his energy to feeding her chicks and devotes less or no energy to feeding the chicks of his secondary female. Numbers tell the cruel story: the male averages fourteen deliveries of food per hour to the primary female's nest but only seven deliveries of food per hour to the secondary female's nest. If enough nest holes are available, most mated males try to acquire a secondary female, and up to 39 percent succeed.

Obviously, this system produces both winners and losers. Since the numbers of male and female flycatchers are roughly equal, and since each female has one mate, for every bigamous male there must be one unfortunate male with no mate. The big winners are the polygynous males, who sire on the average 8.1 flycatcher chicks each year (adding up the contributions of both mates), compared to only 5.5 chicks sired by monogamous males. Polygynous males tend to be older and bigger than unmated males, and they succeed in staking out the best territories and best nest holes in the best habitats. As a result, their chicks end up 10 percent heavier than the chicks of other males, and those big chicks have a better chance of surviving than do smaller chicks.

The biggest losers are the unfortunate unmated males, who fail to acquire any mates and sire no offspring at all (at least in theory—more on that later). The other losers are the secondary females, who have to work much harder than primary females to feed their young. The former end up making twenty food deliveries per hour to the nest, compared with only thirteen for the latter. Since the secondary females thus exhaust themselves, they may die earlier. Despite her herculean efforts, one hardworking secondary female can't bring as much food to the nest as a relaxed primary female and a male working together. Hence some chicks starve, and the secondary females end up with fewer surviving chicks than do primary females (on the average, 3.4 versus 5.4 chicks). In addition, the surviving chicks of secondary females are smaller than the chicks of primary females, and hence are less likely to survive the rigors of winter and migration.

Given these cruel statistics, why should any female accept the fate of being the "other woman"? Biologists used to speculate that secondary females choose their fate, reasoning that the neglected second spouse of a good male is better off than the sole spouse of a lousy male with a poor territory. (Rich married men have been known to make similar pitches to prospective mistresses.) It turns out, though, that the secondary females do not accept their fate knowingly but are tricked into it.

The key to this deception is the care that polygynous males take to set up their second household a couple of hundred yards from their first household, with many other males' territories intervening. It's striking that polygynous males don't court a second spouse at any of dozens of potential nest holes near the first nest, even though they would thereby reduce their commuting time between nests, have more time available to feed their young, and reduce their risk of being cuckolded while enroute. The conclusion seems inescapable that polygynous males accept the disadvantage of a remote second household in order to deceive the prospective secondary mate and conceal from her the existence of the first household. Life's exigencies make a female Pied Flycatcher especially vulnerable to being deceived. If she discovers after egg-laying that her mate is polygynous, it's too late for her to do anything about it. She's better off staying with those eggs than deserting them, seeking a new mate from the males now available (most of them are would-be bigamists anyway), and hoping the new mate will prove to be any better than the former one.

The remaining strategy of male Pied Flycatchers has been dressed up by male biologists in the morally neutral-sounding term "mixed reproductive strategy" (abbreviated MRS). What this means is that mated male Pied Flycatchers don't just have a mate: they also sneak around trying to inseminate the mates of other males. If they find a female whose mate is temporarily absent, they try to copulate with her and often succeed. Either they approach her singing loudly or they sneak up to her quietly; the latter method succeeds more often.

The scale of this activity staggers our human imagination. In act I of Mozart's opera *Don Giovanni*, the Don's servant, Leporello, boasts to Donna Elvira that Don Giovanni has seduced 1,003 women in Spain alone. That sounds impressive until you realize how long-lived we humans are. If Don Giovanni's conquests took place over thirty years, he seduced only one Spanish woman every eleven days. In contrast, if a male Pied Flycatcher temporarily leaves his mate (for instance, to find food), then on the average another male enters his territory in ten minutes and copulates with his mate in thirty-four minutes. Twenty-nine percent of all observed copulations prove to be EPCs (extra-pair copulations), and an estimated 24 percent of all nestlings are "illegitimate." The intruder-seducer usually proves to be the boy next door (a male from an adjoining territory).

The big loser is the cuckolded male, for whom EPCs and MRSs are an evolutionary disaster. He squanders a whole breeding season out of his short life by feeding chicks that do not pass on his genes. Although the male perpetrator of an EPC might seem to be the big winner, a little reflection makes it clear that working out the male's balance sheet is tricky. While you are off philandering, other males have the chance to philander with your mate. EPC attempts rarely succeed if a female is within ten yards of her mate, but the chances of success rise steeply if her mate is more distant than ten yards. That makes MRSs especially risky for polygynous males, who spend much time in their other territory or commuting between their two territories. The polygynous males try to pull off EPCs themselves and on the average make one attempt every twenty-five minutes, but once every eleven minutes some other male is sneaking into their own territory to try for an EPC. In half of all EPC attempts, the cuckolded male flycatcher is off in pursuit of another female flycatcher at the very moment when his own mate is under siege. These statistics would seem to make MRSs a strategy of dubious value to male Pied Flycatchers, but they are clever enough to minimize their risks. Until they have fertilized their own mate, they stay within two or three yards of her and guard her diligently. Only when she has been inseminated do they go off philandering.

Now that we have surveyed the varying outcomes of the battle of the sexes in animals, let's see how humans fit into this broader picture. While human sexuality is unique in other respects, it is quite ordinary when it comes to the battle of the sexes. Human sexuality resembles that of many other animal species' whose offspring are internally fertilized and require biparental care. It thereby differs from that of most species whose young are externally fertilized and given only uniparental care or even no care at all.

In humans, as in all other mammalian and bird species except brush turkeys, an egg that has just been fertilized is incapable of independent survival. In fact, the length of time until the offspring can forage and care for itself is at least as long for humans as for any other animal species, and far longer than for the vast majority of animal species. Hence parental care is indispensable. The only question is, which parent will provide that care or will both parents provide it?

For animals, we saw that the answer to that question depends on the relative size of the mother's and father's obligate investment in the embryo, their other opportunities foreclosed by their choice to provide parental care, and their confidence in their paternity or maternity. Looking at the first of those factors, the human mother has a greater obligate investment than the human father. Already at the time of fertilization a human egg is much larger than a human sperm, though that discrepancy disappears or is reversed if the egg is compared to an entire ejaculate of sperm. After fertilization the human mother is committed to up to nine months of time and energy expenditure, followed by a period of lactation that lasted about four years under the conditions of the hunter-gatherer lifestyle that characterized all human societies until the rise of agriculture about ten thousand years ago. As I recall well myself from watching how fast the food disappeared from our refrigerator when my wife was nursing our sons, human lactation is energetically very expensive. The daily energy-budget of a nursing mother exceeds that of most men with even a moderately active lifestyle and is topped among women only by marathon runners in training. Hence there is no way that a just-fertilized woman can rise from the conjugal bed, look her spouse or lover in the eye, and tell him, "You'll have to take care of this embryo if you want it to survive, because I won't!" Her consort would recognize this for an empty bluff.

The second factor affecting the relative interest of men and women in child care is their difference in other opportunities thereby foreclosed. Because of the woman's time commitment to pregnancy and (under hunter-gatherer condition,) lactation, there is nothing she can do during that time that would permit her to produce another offspring. The traditional nursing pattern was to nurse many times each hour, and the resulting release of hormones tended to **cause lactational amenorrhea** (cessation of menstrual cycles) for up to several years. Hence hunter-gatherer mothers had children at intervals of several years. In modern society a woman can conceive again within a few months of delivery, either by forgoing breast-feeding in favor of bottle-feeding or by nursing the infant only every few hours (as modern women tend to do for convenience). Under those conditions the woman soon resumes menstrual cycles. Nevertheless, even modern women who eschew breast-feeding and contraception rarely give birth at intervals of less than a year, and few women give birth to more than a dozen children over the course of their lives. The record lifetime number of offspring for a woman is a mere sixty-nine (a nineteenth-century Moscow woman who specialized in triplets), which sounds stupendous until compared with the numbers achieved by some men to be mentioned below.

Hence multiple husbands do not help a woman to produce more babies, and very few human societies regularly practice polyandry. In the only such society that has received much study, the Tre-ba of Tibet, women with two husbands have on the average, no more children than women with one husband. The reasons for Tre-ba polyandry are instead related to the Tre-ba system of land tenure: "Tre-ba brothers often marry the same woman in order to avoid subdividing a small landholding.

Thus, a woman who "chooses" to care for her offspring is not thereby foreclosing other spectacular reproductive opportunities. A woman differs in that respect from a man, whose theoretical ability to impregnate all the women of the world we have already discussed. Unlike the genetic unprofitability of polyandry for Tre-ba women, polygyny paid off well for nineteenth-century Mormon men, whose average lifetime output of children increased from a mere seven children for Mormon men with one wife to sixteen or twenty children for men with two or three wives, respectively, and to twenty-five children for Mormon church leaders, who averaged five wives. Even these benefits of polygyny are modest compared to the hundreds of children sired by modern princes able to commandeer the resources of a centralized society for rearing their offspring without directly providing child care themselves. A nineteenth-century visitor to the court of the Nizam of Hyderabad, an Indian prince with an especially

large harem, happened to be present during an eight-day period when four of the Nizam's wives gave birth, with nine more births anticipated for the following week. The record for lifetime number of offspring sired is credited to Morocco's Emperor Ismail the Bloodthirsty, father of seven hundred sons and an uncounted but presumably comparable number of daughters. These numbers make it clear that a man who fertilizes one woman and then devotes himself to child care may by that choice foreclose enormous alternative opportunities.

The remaining factor tending to make child care genetically less rewarding for men than for women is the justified paranoia about paternity that men share with the males of all other internally fertilized species. A man who opts for child care runs the risk that, unbeknownst to him, his efforts are transmitting the genes of a rival. This biological fact is the underlying cause for a host of repulsive practices by which men of various societies have sought to increase their confidence in paternity by restricting their wife's opportunity for sex with other men. Among such practices are high bride prices only for brides delivered as proven virgin goods; traditional adultery laws that define adultery by the marital status only of the participating woman (that of the participating man being irrelevant); chaperoning or virtual imprisonment of women; female "circumcision" (clitoridectomy) to reduce a woman's interest in initiating sex, whether marital or extramarital; and infibulation (suturing a woman's labia majora nearly shut so as to make intercourse impossible while the husband is away).

All three factors—sex differences in obligate parental investment, alternative opportunities foreclosed by childcare, and confidence in parenthood—contribute to making men much more prone than women to desert a spouse and child. However, a man is not like a male hummingbird, male tiger, or the male of many other animal species, who can safely fly or walk away immediately after copulation secure in the knowledge that his deserted female sex partner will be able to handle all the ensuing work of promoting the survival of his genes. Human infants virtually need biparental care, especially in traditional societies. While we shall see in chapter 5 that activities represented as male parental care may actually have more complex function than meet the eye, many or most men in traditional societies do undoubtedly provide services to their children and spouse. Those services include: acquiring and delivering food; offering protection, not only against predators but also against other men who are sexually interested in a mother and regard her offspring (their potential stepchildren) as a competing genetic nuisance; owning land and making its produce available; building a house, clearing a garden, and performing other useful labor; and educating children, especially sons, so as to increase the children's chances of survival.

Sex differences in the genetic value of parental care to the parent provide a biological basis for the all-too-familiar differing attitudes of men and women toward extramarital sex. Because a human child virtually required paternal care in traditional human societies, extramarital sex is most profitable for a man if it is with a married woman whose husband will unknowingly rear the resulting child. Casual sex between a man and a married woman tends to increase the man's output of children, but not the woman's. That decisive difference is reflected in men's and women's differing motivations. Attitude surveys in a wide variety of human societies around the world have shown that men tend to be more interested than women in sexual variety, including casual sex and brief relationships. That attitude is readily understandable because it tends to maximize transmission of the genes of a man but not of a woman. In contrast, the motivation of a woman participating in extramarital sex is more often self-reported as marital dissatisfaction. Such a woman tends to be searching for a new lasting relationship: either a new marriage or a lengthy extramarital relationship with a man better able than her husband to provide resources or good genes.

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