**CHAPTER 4.**

**WRONG TIME FOR LOVE.**

**The Evolution of Recreational Sex.**

**Section 3.**

There is no question that the many-fathers theory is plausible for those animal species (and perhaps those traditional human societies) in which infanticide is a big problem. But the theory seems hard to reconcile with modern human society as we know it. Yes, extramarital sex occurs, but doubts about paternity remain the exception, not the rule that drives society. Genetic tests show that at least 70 percent, perhaps even 95 percent, of American and British babies really are sired legitimately, that is, by the mother's husband. It's hardly the case that for each kid there are many men standing around radiating benevolent interest, or even showering gifts and dispensing protection, while thinking, "/may be that kid's real father!"

It therefore seems unlikely that protecting kids against infanticide is what propels women's constant sexual receptivity today. Nevertheless, as we'll now see, women may have had this motivation in our distant past, and sex may have subsequently assumed a different function that now sustains it.

How, then, are we to evaluate these two competing theories? Like so many other questions about human evolution, this one can't be settled in the way preferred by chemists and molecular biologists, a test-tube experiment. Yes, we'd have a decisive test if there were some human population whose women we could cause to turn bright red at estrus and to remain frigid at other times, and whose men we could cause to be turned on only by bright red women. We could then see whether the result was more philandering and less paternal care (as predicted by the daddy-at-home theory) or less philandering and more infanticide (as predicted by the many-fathers theory). Alas for science, such a test is presently impossible, and it will remain immoral even if genetic engineering ever makes it possible.

But we can still resort to another powerful technique preferred by evolutionary biologists for solving such problems. It's termed the comparative method. We humans, it turns out, aren't unique in our concealment of ovulation. While it's exceptional among mammals in general, it's fairly common among higher primates (monkeys and apes), the group of mammals to which we belong. Dozens of primate species show no externally visible signs of ovulation; many others do show signs, albeit slight ones; and still others advertise it flagrantly. The reproductive biology of each species represents the outcome of an experiment, performed by nature, on the benefits and drawbacks of concealing ovulation. By comparing primate species, we can learn which features are shared by those species with concealed ovulation but are absent from those species with advertised ovulation.

That comparison throws new light on our sexual habits. It was the subject of an important study by the Swedish biologists Birgitta Sillen-Tullberg and Anders Moller. Their analysis proceeded in four steps.

Step 1. For as many higher primate species as possible (sixty-eight in all), Sillen-Tullberg and Moller tabulated visible signs of ovulation. Aha!—you may object immediately—visible to whom? A monkey may give signals invisible to us humans but obvious to another monkey, such as odors (pheromones). For example, cattle breeders trying to perform artificial insemination on a prize dairy cow have big problems figuring out when the cow is ovulat-ing. Bulls, though, can tell easily by the cow's smell and behavior.

Yes, that problem can't be ignored, but it's more serious for cows than for higher primates. Most primates resemble us in being active by day, sleeping at night, and depending heavily on their eyes. A male rhesus monkey whose nose isn't working can still recognize an ovulating female monkey by the slight reddening around her vagina, even though her reddening is not nearly so obvious as in a female baboon. For those monkey species that we humans classify as having no visible signs of ovulation, it's often clear that the male monkeys are equally confused, because they copulate at totally inappropriate times, such as with non-estrous or pregnant females. Hence our own ratings of "visible signs" aren't worthless.

The result of this first step of the analysis was that nearly half of the primates studied—thirty-two out of sixty-eight—resemble humans in lacking visible signs of ovulation. Those thirty-two species include vervets, marmosets, and spider monkeys, as well as one ape, the orangutan. Another eighteen species, including our close relative the gorilla, exhibit slight signs. The remaining eighteen species, including baboons and our close relatives the chimpanzees, advertise ovulation conspicuously.

Step 2. Next, Sillen-Tullberg and Moller categorized the same sixty-eight species according to their mating system. Eleven species—including marmosets, gibbons, and many human societies—turn out to be monogamous. Twenty-three species—including other human societies, plus gorillas—have harems of females controlled by a single adult male. But the largest number of primate species—thirty-four, including vervets, bonobos, and chimpanzees—have a promiscuous system in which females routinely associate and copulate with multiple males. Again I hear cries of Aha!—Why aren't humans also classified as promiscuous? Because I was careful to specify routinely. Yes, most woman have multiple sex partners in sequence over their lifetimes, and many women are at times involved with multiple men simultaneously. However, within any given estrus cycle the norm is for a woman to be involved with a single man, but the norm for a female vervet or bonobo is to be involved with several partners.

Step 3. As the next-to-last step, Sillen-Tullberg and Moller combined steps 1 and 2 to ask: is there any tendency for more or less conspicuous ovulations to be associated with a particular mating system? Based on a naive reading of our two competing theories, concealed ovulation should be a feature of monogamous species if the daddy-at-home theory is correct, but of promiscuous species if the many-fathers theory holds. In fact, the overwhelming majority of monogamous primate species analyzed—ten out of eleven species—prove to have concealed ovulation. Not a single monogamous primate species has boldly advertised ovulations, which instead are usually (in fourteen out of eighteen cases) confined to promiscuous species. That seems to be strong support for the daddy-at-home theory.

However, the fit between predictions and theory is only a half-fit, because the reverse correlations don't hold up at all. While most monogamous species have concealed ovulation, concealed ovulation in turn is no guarantee of monogamy. Out of thirty-two species with concealed ovulation, twenty-two aren't monogamous but are instead promiscuous or live in harems. Concealed ovulators include monogamous night monkeys, often-monogamous humans, harem-holding langur monkeys, and promiscuous vervets. Thus, whatever caused concealed ovulation to evolve in the first place, it can be maintained thereafter under the most varied mating systems. Similarly, while most species with boldly advertised ovulations are promiscuous, promiscuity is no guarantee of advertisement. In fact, most promiscuous primates— twenty out of thirty-four species—either have concealed ovulation or only slight signs. Harem-holding species as well have invisible, slightly visible, or conspicuous ovulations, depending on the particular species. These complexities warn us that concealed ovulation will prove to serve different functions, according to the particular mating system with which it coexists.

Step 4. To identify these changes of function, Sillen-Tullberg and M0ller got the bright idea of studying the family tree of living primate species. They thereby hoped to identify the points in primate evolutionary history at which there had been evolutionary changes in ovulatory signals and mating systems. The underlying rationale is that some modern species that are very closely related to each other, hence presumably derived recently from a common ancestor, turn out to differ in mating system or in strength of ovulatory signals. This implies recent evolutionary changes in mating systems or signals.

Here's an example of how the reasoning works. We know that humans, chimps, and gorillas are genetically about 98 percent identical and stem from an ancestor ("the Missing Link") that lived as recently as nine million years ago. Yet those three modern descendants of the Missing Link now exhibit all three types of ovulatory signal: concealed ovulation in humans, slight signals in gorillas, bold advertisement in chimps. Hence only one of those descendants can be like the Missing Link in ovulatory signals, and the other two descendants must have evolved different signals.

In fact, most living species of primitive primates have slight signs of ovulation. Hence the Missing Link may have preserved that condition, and gorillas may have inherited it in turn from the Missing Link (see figure 4.1). Within the last nine million years, though, humans must have evolved concealed ovulation, and chimps must have evolved bold advertisement. Our signals and those of chimps thus di-verged in opposite directions from the cues of our mildly signaling ancestors. To us humans, the swollen derrieres of ovulating chimps look like those of baboons. However, the ancestors of chimps and baboons must have evolved their eye-catching derrieres quite independently, since the ancestors of baboons and of the Missing Link parted company around thirty million years ago.

By similar reasoning, one can infer other points in the primate family tree at which ovulatory signals must have changed. It turns out that switches of signals have evolved at least twenty times. There have been at least three independent origins of bold advertisement (including the example in chimps); at least eight independent origins of concealed ovulation (including its origins in us, in orangutans, and in at least six separate groups of monkeys); and several reappearances of slight signs of ovulation, from either concealed ovulation (as in some howler monkeys) or from bold advertisement (as in many macaques).

In the same way as we've just seen for ovulatory signals, one can also identify points in the primate family tree at which mating systems must have changed. The original system for the common ancestor of all monkeys and apes was probably promiscuous mating. But if we now look at humans and our closest relatives, the chimps and gorillas, we find all three types of mating system represented: harems in gorillas, promiscuity in chimps, and either monogamy or harems in humans (see figure 4.2). Thus, among the three descendants of the Missing Link of nine million years ago, at least two must have changed their mating system. Other evidence suggests that the Missing Link lived in harems, so that gorillas and some human societies may just have retained that mating system. But chimps must have reinvented promiscuity, while many human societies invented monogamy. Again, we see that humans and chimps have evolved oppositely, in mating systems as in ovulatory signals.

Overall, it appears that monogamy has evolved independently at least seven times in higher primates: in us, in gibbons, and in at least five separate groups of monkeys. Harems must have evolved at least eight times, including in the Missing Link. Chimps and at least two monkeys must have reinvented promiscuity after their recent ances-tors had given it up for harems. Thus, we have reconstructed both the type of mating system and the type of ovulatory signal that probably existed in primates of the remote past, all along the primate family tree. We can now, finally, put both types of information together and ask: what mating system prevailed at each point in our family tree when concealed ovulation evolved?

Here's what one learns. Consider those ancestral species that gave signals of ovulation, and that then went on to lose those signals and evolve concealed ovulation. Only one of those ancestral species was monogamous. In contrast, eight, perhaps as many as eleven, of them were promiscuous or harem-holding species—one of them being the human ancestor that arose from the harem-holding Missing Link. We thus conclude that promiscuity or harems, not monogamy, is the mating system that leads to concealed ovulation (see figure 4.3). This is the conclusion predicted by the many-fathers theory. It doesn't agree with the daddy-at-home theory.

Conversely, we can also ask: what were the ovulatory signals prevailing at each point in our family tree when monogamy evolved? We find that monogamy never evolved in species with bold advertisement of ovulation. Instead, monogamy has usually arisen in species that already had concealed ovulation, and sometimes in species that already had slight ovulatory signals (see figure 4.4). This conclusion agrees with the predictions of the daddy-at-home theory.

How can these two apparently opposite conclusions be reconciled? Recall that Sillen-Tullberg and M0ller found, in step 3 of their analysis, that almost all monogamous primates have concealed ovulation. We now see that that result must have arisen in two steps. First, concealed ovulation arose, in a promiscuous or harem-holding species. Then, with concealed ovulation already present, the species switched to monogamy

By combining facts about modern observed species with inferences about ancestral species, one can infer the mating system prevailing when ovulatory signals underwent evolutionary change. We infer that species 3 evolved concealed ovulation from a harem-holding ancestor with slight signs of ovulation, while species I and 2 preserved the ancestral mating system (harems) and slight ovulatory signs. Perhaps by now you're finding our sexual history confusing. We started out with an apparently simple question that deserved a simple answer: why do we hide our ovulations and have recreational sex on any day of the month? Instead of a simple answer, you're being told that the answer is more complex and involves two steps.

What it boils down to is that concealed ovulation has repeatedly changed, and actually reversed, its function during primate evolutionary history. It arose at a time when our ancestors were still promiscuous or living in harems. At such times, concealed ovulation let the ancestral ape-woman distribute her sexual favors to many males, none of which could swear that he was the father of her child but each of which knew that he might be. As a result, none of those potentially murderous males wanted to harm the ape-woman's baby, and some may actually have protected or helped feed it. Once the ape-woman had evolved concealed ovulation for that purpose, she then used it to pick a good caveman, to entice or force him to stay at home with her, and to get him to provide lots of protection or help for her baby—secure in the knowledge that it was his baby too.

On reflection, we shouldn't be surprised at this shift of function for concealed ovulation. Such shifts are very common in evolutionary biology. That's because natural selection doesn't proceed consciously and in a straight line toward a distant perceived goal, in the way that an engineer consciously designs a new product. Instead, a feature that serves one function in an animal begins to serve another function as well, becomes modified as a result, and may even lose the original function. The consequence is frequent reinventions of similar adaptations, and frequent losses, shifts, or even reversals of function, as living things evolve.

One of the most familiar examples involves vertebrate limbs. The fins of ancestral fishes, used for swimming, evolved into the legs of ancestral reptiles, birds, and mammals, which used them for running or hopping on land. The front legs of certain ancestral mammals and reptile-birds subsequently evolved into the wings, used for flying, of bats and modern birds, respectively. Bird wings and mammal legs then evolved independently into the flippers of penguins and whales, respectively, thereby reverting to a swimming function and effectively reinventing the fins of fish. At least three groups of fish descendants independently lost their limbs to become snakes, legless lizards, and the legless amphibians known as cecilians. In essentially the same way, features of reproductive biology—such as concealed ovulation, boldly advertised ovulation, monogamy, harems, and promiscuity—have repeatedly changed function and been transmuted into each other, reinvented, or lost.

The implications of these evolutionary shifts can lend

zest to our love lives. For example, in the last novel by the great German writer Thomas Mann, Confessions of Felix Krull, Confidence Man, Felix shares a compartment on a train journey with a paleontologist, who regales him with an account of vertebrate limb evolution. Felix, an accomplished and imaginative ladies' man, is delighted by the implications. "Human arms and legs retain the bones of the most primitive land animals! . . . It's thrilling! ... A woman's shapely charming arm, which embraces us if we find favor . . . it's no different from the primordial bird's clawed wing, and the fish's pectoral fin. . . . I'll think of that, next time. . . . Dream of that shapely arm, with its ancient scaffolding of bones!"

Now that Sillen-Tullberg and M0ller have unraveled the evolution of concealed ovulation, you can nourish your own fantasy with its implications, just as Felix Krull nourished his fantasy with the implications of vertebrate limb evolution. Wait until the next time that you are having sex for fun, at a nonfertile time of the ovulatory cycle, while enjoying the security of a lasting monogamous relationship. At such a time, reflect on how your bliss is made paradoxically possible by precisely those features of your physiology that distinguished your remote ancestors as they languished in harems, or as they rotated among promiscuously shared sex partners. Ironically, those wretched ancestors had sex only on rare days of ovulation, when they perfunctorily discharged the biological imperative to fertilize, robbed of your leisurely pleasure by their desperate need for swift results.