CHAPTER 2. Section 2.

THE BATTLE OF THE SEXES.

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 vi-vipary (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 that 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 hung 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.

A second type of exception to the predominant pattern of male post-copulatory desertion involves a remarkable phenomenon with a long name: sex-role-reversal polyandry. As the name implies, this behavior is the opposite of the common polygamous breeding systems in which big males compete fiercely with each other to acquire a harem of females. Instead, big females compete fiercely to acquire a harem of smaller males, for each of which in turn the female lays a clutch of eggs, and each of which proceeds to do most or all of the work of incubating the eggs and rearing the young. The best known of these female sultans are the shore birds called jacanas (alias lily-trotters), Spotted Sandpipers, and Wilson's Phalaropes. For instance, flocks of up to ten female phalaropes may pursue a male for miles. The victorious female then stands guard over her prize to ensure that only she gets to have sex with him, and that he becomes one of the males rearing her chicks.

Clearly, sex-role-reversal polyandry represents for the successful female the fulfillment of an evolutionary dream. She wins the battle of the sexes by passing on her genes to far more clutches of young than she could rear, alone or with one male's help. She can utilize nearly her full egg-laying potential, limited only by her ability to defeat other females in the quest for males willing to take over parental care. But how did this strategy evolve? Why did males of some shorebird species end up seemingly defeated in the battle of the sexes, as polyandrous co-"husbands," when males of almost all other bird species avoided that fate or even reversed it to become polygamists ?

The explanation depends on shorebirds' unusual reproductive biology. They lay only four eggs at a time, and the young are precocial, meaning that they hatch already covered with down, with their eyes open, and able to run and find food for themselves. The parent doesn't have to feed the chicks but only has to protect them and keep them warm. That's something a single parent can handle, whereas it takes two parents to feed the young of most other bird species.

But a chick that can run around as soon as it hatches has undergone more development inside the egg than the usual helpless chick. That requires an exceptionally large egg. (Take a look sometime at a pigeon's typically small eggs, which produce the usual helpless chicks, to understand why egg farmers prefer to rear chickens with big eggs and precocial chicks.) In Spotted Sandpipers, each egg weighs fully one-fifth as much as its mother; the whole four-egg clutch weighs an astonishing 80 percent of her weight. Although even monogamous shorebird females have evolved to be slightly larger than their mates, the effort of producing those huge eggs is still exhausting. That maternal effort gives the male both a short-term and a long-term advantage if he takes over the not too onerous responsibility of rearing the precocial chicks alone, thereby leaving his mate free to fatten herself up again.

His short-term advantage is that his mate thereby becomes capable of producing another clutch of eggs for him quickly, in case the first clutch is destroyed by a predator. That's a big advantage, because shorebirds nest on the ground and suffer horrendous losses of eggs and chicks. For example, in 1975 a single mink destroyed every nest in a population of Spotted Sandpipers that the ornithologist Lewis Oring was studying in Minnesota. A study of jacanas in Panama found that forty-four out of fifty-two nests failed.