CHAPTER 2. Section 3.

THE BATTLE OF THE SEXES.

Sparing his mate may also bring the male a long-term advantage. If she does not become exhausted in one breeding season, she is more likely to survive to the next season, when he can mate with her again. Like human couples, experienced bird couples that have worked out a harmonious relationship are more successful at raising young than are bird newlyweds.

But generosity in anticipation of later repayment carries a risk, for male shorebirds as for humans. Once the male assumes sole parental responsibility, the road is clear for his mate to uso her free time in whatever way she chooses. Perhaps she'll choose to reciprocate and remain available to her mate, on the chance that her first clutch might be destroyed and he would require a replacement clutch. But she might also choose to pursue her own interests, seeking out some other male available immediately to receive her second clutch. If her first clutch survives and continues to occupy her former mate, her polyandrous strategy has thereby doubled her genetic output.

Naturally, other females will have the same idea, and all of them will find themselves in competition for a dwindling supply of males. As the breeding season progresses, most males become tied up with their first clutch and unable to accept further parental responsibilities. Although the numbers of adult males and females may be equal, the ratio of sexually available females to males rises as high as seven-to-one among breeding Spotted Sandpipers and Wilson's Phalaropes. Those cruel numbers are what drive sex-role reversal even further toward an extreme. Though females already had to be slightly larger than males in order to produce large eggs, they have evolved to become still larger in order to win the fights with other females. The female reduces her own parental care contribution further and woos the male rather than vice versa.

Thus, the distinctive features of shorebird biology— especially their precocial young, clutches of few but large eggs, ground-nesting habits, and severe losses from preda-tion—predispose them to male uniparental care and female emancipation or desertion. Granted, females of most shorebird species can't exploit those opportunities for polyandry. That's true, for instance, of most sandpipers of the high Arctic, where the very short breeding season leaves no time for a second clutch to be reared. Only among a minority of species, such as the tropical jacanas and southerly populations of Spotted Sandpipers, is polyandry frequent or routine. Though seemingly remote from human sexuality, shorebird sexuality is instructive because it illustrates the main message of this book: a species' sexuality is molded by other aspects of the species' biology. It's easier for us to acknowledge this conclusion about shorebirds, to which we don't apply moral standards, than about ourselves.

The remaining 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 coparent or the young, tend the young while the coparent 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 coparenthood 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 cuckolder's offspring. Males become justifiably paranoid about their mates' behavior.

An intensively studied and fairly typical example of those built-in tensions of coparenthood 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 humans but does not arouse the same moral indignation in us.

Here is how polygamy 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 polygamous 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. Polygamous 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 polygamous 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 polygamous 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 en route. The conclusion seems inescapable that polygamous 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 1 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 polygamous males, who spend much time in their other territory or commuting between their two territories. The polygamous 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.