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SOCIOBIOLOGY

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Sociobiology is relevant to sociology for a number of important reasons. First, and foremost, sociobiology claims to be a general science of social behavior embracing all organisms, not just humans. This means that sociology is at least a subfield of this wider discipline, and at best a parallel one, mirroring at the human level social behavior seen throughout nature. Second, sociobiology is important because methodologically it has taken a quite different line to traditional sociology and has seen itself as a branch of evolutionary science enshrining a “bottom-up,” reductive approach to social behavior rather than the “top-down,” more holistic approach traditional in sociology. Finally, sociobiology is important because its theories and findings, however they may be regarded, have challenged sociology to respond to them, just as sociology, in its own way, has challenged sociobiology to respond to it.

SOCIAL THEORY IN SOCIOBIOLOGY

The term *sociobiology* first came to notice when the entomologist E. O. Wilson published his great work *Sociobiology: The New Synthesis* (Wilson 1975). Although associated with Wilson ever since, the movement now known as sociobiology was in fact based predominantly on the insights of the English evolutionary geneticist, W. D. Hamilton (1936–2000). Hamilton had read genetics at Cambridge in the early 1960s and at a time when Darwin’s work was still very much under a cloud as far as undergraduate-level studies were concerned. Although Darwin’s great work on the origin of species had been published in 1859, acceptance of his theories by the biological establishment

had been very slow in coming. The principal reason was that Darwin himself had professed a “Lamarckian” theory of “inheritance of acquired characteristics” (he called it *Pangenesis*, after a Greek precedent) that failed to accord well with his crucial mechanism of natural selection. Because naturally selected traits must be inherited to have any effect on evolution, Darwin’s failure to correctly account for inheritance was a serious obstacle to the acceptance of his theory. Furthermore, it was an obstacle that got considerably more serious when Gregor Mendel’s (1822–1884) discovery of the laws of inheritance finally came to general notice at the turn of the twentieth century. At first it seemed as if Mendelian inheritance contradicted evolution by natural selection, and it was not until the 1930s that R. A. Fisher (1890–1963) and others proved the contrary and established Darwinism on a firm genetic and mathematical foundation. This, in the subtitle of another famous book, J. S. Huxley’s *Evolution*, became known as the “modern synthesis” (Huxley 1942).

Ironically, in view of his association with sociobiology, Wilson himself always retained a link with an alternative tradition of evolutionary thinking that stemmed from Herbert Spencer (1820–1903), also of course the founder of British sociology. Spencer was responsible for popularizing the term *evolution*—used by Darwin only once in *The Origin of Species*, where “evolved” is the final word of the book. Part of the reason for Darwin’s reluctance was that his concept of evolution was very different from Spencer’s. Whereas Spencer saw evolution as a cosmic process of progressive development toward larger, more complex, and more integrated entities culminating ultimately in Victorian industrial society, Darwin spoke of

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“descent with modification” and interpreted evolution simply as a process of gradual change whose antithesis was *revolution* (sudden change), by contrast to the *dissolution* that Spencer’s understanding of evolution implied. Specifically, Darwin denied that evolution was inherently progressive, and his theory contrasted with Spencer’s in being scientific, and based on observable facts, rather than being philosophical in inspiration, and founded on a belief in the inevitability of progress. However, confusion of Spencer’s and Darwin’s concepts of evolution remains common, especially in the social sciences (Freeman 1974).

One of Spencer’s central concepts was that of the *superorganism*. According to this way of looking at it, just as an organism is made up of cells, so a superorganism is made up of individual organisms. Examples quoted by Spencer include insect and human societies, and it is this concept of the superorganic that E. O. Wilson has continued to endorse—particularly in relation to his principal interest: the social insects, and ants in particular (Wilson 1971). Spencer’s holistic, superorganismic concept of society powerfully influenced Émile Durkheim (1859–1917) and via such sociological predecessors many subsequent sociologists, such as Talcott Parsons (1902–1979). Indeed, it remains to this day a defining paradigm for the subject: Society is an entity in itself, greater than the sum of its parts.

Spencer had coined the phrase “survival of the fittest” to epitomize what he believed to be Darwin’s theory of natural selection. But “survival of the fittest” was not a phrase Darwin himself used very often, and with hindsight, it is easy to see why. First, “survival of the fittest” creates the impression that natural selection selects for fitness understood in medical or sporting terms. But this fails to take account of the fact that, as far as natural selection is concerned, it is reproductive success, not individual fitness that matters. Looked at from the ultimate point of view of evolution, survival is only a means to reproductive success, and an organism, no matter how “fit” it might be, can only contribute to evolution by passing on its traits to its offspring. Human males, for example, live longer and suffer less from most types of pathology if they are castrated, but males without testes have not been selected for obvious reasons. Again, “survival of the fittest” also raises the question of the fittest *what*—individual, group, society, or species? Inevitably, Spencer’s slogan implied social Darwinism: The belief that, just as the fittest individual organism was favored by natural selection, so the fittest group, class, society, or race would be. This, combined with the belief that “fitness” could be promoted by eugenics, did much to bring social Darwinism into disrepute in the twentieth-century (Dawkins 1982).

Spencer’s survival-of-the-fittest social Darwinism, along with his ever-on-and-upward-toward-something-bigger-and-better view of evolution made the social superorganism seemingly inevitable and unproblematic. However, Darwin’s more sober view of evolution by natural selection created serious difficulties where accounting

for social behavior was concerned. For example, if only natural selection is invoked, how can it account for the fact that the vast majority of workers in insect societies are sterile females? Surely, a fertile worker would have greater reproductive success by definition than a sterile one, and so sterility would soon be selected out (particularly in view of the fact that females of such species can reproduce without males). Indeed, a simple “thought experiment” seems to prove the evolution of any kind of altruism impossible. The term *altruism* was first introduced by another founder of sociology, Auguste Comte (1798–1857), but can be defined objectively and quantitatively in biology (another term we owe to him) as *any contribution to the reproductive success of the recipient at a cost to the reproductive success of the altruist*. Consider an altruistic species where every individual acts to benefit the others: a single selfish mutant will have more reproductive success than the altruists because by definition, whereas they will make sacrifices of their reproductive success for the benefit of the reproductive success of the selfish mutant, the mutant itself will never make such a sacrifice for them. After a while, altruists will be driven to extinction and the species invaded by the selfish mutants. Now consider the converse: Imagine that in a species of selfish organisms an altruistic mutant appears. By definition, the mutant will promote the reproductive success of the selfish at a cost to itself and become extinct in no time. Nevertheless altruism, even when defined in this wholly objective way, is very common in nature, as Darwin was the first to realize (Badcock 2000:72–79).

This so-called problem of altruism was the subject chosen by Hamilton for his Ph.D. thesis, partly supervised in the Department of Sociology at the London School of Economics. Based on the mathematics of population genetics developed by Fisher and others, Hamilton developed a mathematical model devised to explore the paradox of how natural selection acting on individual genes could select for altruism as defined above. The simplest expression of what turned out to be a complex and recondite piece of mathematics is what is now known as *Hamilton’s inequality*. This states that altruism will evolve by natural selection acting on individual genes if $Br > C$, where B is the benefit to the reproductive success of the recipient, C is the cost to the reproductive success of the altruist, and r is the coefficient of relatedness of the two (Hamilton 1963).

This insight explained worker sterility in insect societies because the peculiarities of their genetic system meant that a worker ant or bee was more closely related (had higher r in other words) to her sisters, the other offspring of the queen, than she was to any offspring she might have of her own. But for Hamilton, this was an afterthought, and his insight does not rely on insect genetics fundamentally. For example, suppose I have a gene for self-sacrifice in the interests of my offspring. Because each of my offspring has a 50 percent chance of inheriting such a gene, saving three of them would preserve 150 percent of it on average, whereas sacrificing myself in doing so

would lose 100 percent of it—a clear gain in terms of the gene's reproductive success (Hamilton 1964).

The implications of this insight were controversial and often misunderstood in biology for a long time, so it is not surprising that the situation was a lot worse in sociology. Here, it is worth pointing out that George Price (1923–1975)—a real altruist if ever there was one, who died penniless after spending his considerable means on helping others—set out to disprove Hamilton and to refute his theory (Kohn 2004). But in the event Price discovered a much more elegant mathematical expression than Hamilton's original one and ended up wholly endorsing it (Price 1970). In short, Price's attempt to refute Hamilton in fact corroborated the theory, and today the Hamilton-Price equations remain the uncontested mathematical foundation of modern Darwinism (Frank 1995). This was "The New Synthesis" of Wilson's subtitle to *Sociobiology* recalling "The Modern Synthesis" of Darwin and Mendel alluded to in the title of Huxley's earlier book. Essentially, it is a synthesis of Darwinism and population genetics based on Hamilton's central insight. Hamilton had answered the *fittest what?* conundrum by showing that natural selection is ultimately a question of the survival of the fittest genes. However, because identical genes can be shared by relatives, he solved the problem of altruism by showing that behavior that appeared to harm a gene in one organism could more than compensate by promoting the same gene's survival in another: so-called inclusive fitness. Richard Dawkins later popularized the idea in his best seller *The Selfish Gene*, and many words have been wasted arguing against it (Dawkins 1978). But protestations against Dawkins's and others' purely verbal metaphors carry no weight with the fundamental science of Hamilton's theory, which is based on the Hamilton-Price equations, and on what is now a vast array of factual findings, most of which would be unintelligible otherwise.

Sociological reactions to the selfish gene metaphor have often been confused by sociologists' own Spencerian, superorganic assumptions, for example, the charge of "reductionism" or "individualism," which is often brought against sociobiology. Sociologists often assume that a top-down, holistic approach is inherently social, virtuous, and correct, by contrast to a bottom-up, reductionistic one, which is implicitly antisocial, vicious, and wrong. In Durkheim's case this was enshrined in a Hobbesian approach to the problem of social order: The belief that what Hobbes called "the state of nature" was one of murderous anarchy, only remedied by constraint imposed from above. Although Durkheim substituted society in the form of the *conscience collective* for Hobbes's absolute monarch, the solution was essentially the same, and explains the anathematization of individualism in such top-down, holistic thinking. However, one of Hamilton's other important insights was that social behavior in general, and group membership in particular, need not be imposed on recalcitrant individuals by preexisting social wholes such as societies, classes, or groups. In a paradigmatic paper,

Hamilton presented a mathematical model that showed that individuals have an incentive to join a group if their personal vulnerability to predation, for example, can be reduced by so doing. Subsequent studies have confirmed that much group behavior in animals can be explained by the simple insight that hiding behind the other members of the group pays all the members. This is particularly so if the group is a large one, and applies to temporal clustering also (female wildebeest, for example, synchronize giving birth because, although newborn calves are highly vulnerable to predators, the chances of any individual female's calf being attacked are greatly reduced by the vast numbers born at the same time) (Hamilton 1971).

In other words, Hobbes was wrong about the "state of nature," which is not one of "war of all against all," but often one of surprising cooperation. Nevertheless, sociobiology was able to correct earlier errors on the part of ethologists such as Konrad Lorenz (1903–1989), who had claimed that violence is instinctively inhibited in animals for the benefit of the species—particularly in those armed with lethal weapons, such as canines. Such top-down, biological holism had earlier been enshrined in the official, Soviet Marxist biology of Trofim Lysenko (1898–1976), whose *law of self-thinning out* held that if planted in thick clusters, saplings would "sacrifice themselves for the benefit of the species," adding that "the death of individual saplings in the group occurs not because they are crowded, but for the express purpose of ensuring that in the future they will not be crowded" (Medvedev 1969:162–70). About a billion old rubles was wasted on such plantings in the then USSR, where the vast majority of all the trees planted according to this "law" of Marxist biology died.

In Western biology, such top-down, holistic thinking was more implied than practiced until the Scottish biologist Wynne-Edwards explicitly articulated the theory in a well-known book (Wynne-Edwards 1986). However, overwhelming factual evidence soon accumulated against Wynne-Edwards's idea that species, for example, control their reproduction to prevent eating themselves out of existence. Meticulous field studies by David Lack (1910–1973) in particular showed that in birds many species that can normally raise only one chick per season habitually lay two eggs. For example, in one species of eagle, 200 nests with clutches of two eggs were found, but in only one did both chicks survive to fledge. This means that 99.5 percent of second eggs was wasted by the species, representing a very considerable squandering of scarce resources. The explanation, of course, is more individualistic: If natural selection is a question of the reproductive success of parents' genes jointly invested in offspring, in species where only one offspring can normally be raised per season it is critical to the parents' reproductive success to have one to raise. The second egg is a backup, so to speak, usually ignored if the first to hatch thrives, but ready if it fails (and, of course, a second also retains the opportunity of doubling the parents' reproductive

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success in that season if exceptionally good resources happen to be available) (Magrath 1989).

These findings illustrate what is often seen as *the fallacy of group selection*. However, since natural selection can undoubtedly act on entire groups—and even species—as well as on individuals, a better way of highlighting the fallacy involved here might be to say that it is not so much group selection as such that is fallacious as the belief that natural selection will automatically favor traits that benefit the group at a cost to the individuals who make it up. Here the problem is enshrined in what is often called *the free rider theorem*: Individuals will always have an incentive to gain a benefit of group membership without paying the cost, or alternatively not to pay an additional cost from which they will gain no more benefit than any other member. Either way, it is naïve to believe that merely citing the benefits of group membership is enough to explain why groups exist, and this essentially is the root of the so-called fallacy of group selection (Badcock 2000:77).

The same issue of cooperation with a mutual benefit or defection in the individual's self-interest is epitomized in the *Prisoner's Dilemma* (so called after the common practice of interrogating a suspect in a crime committed with another alone but with the incentive to incriminate the other suspect). Prisoner's Dilemma could be seen as the atom of society: Two individuals have the choice of either cooperating in their mutual benefit or defecting in their self-interest. However, payoffs are weighted so that selfish defection where the other cooperates (usually denoted as T) is more than mutual cooperation (R), while mutual defection (P) is better than the worst outcome of all: cooperating when the other defects (S): $T > R > P > S$ (additionally $R > (T + S)/2$, otherwise Prisoner's Dilemma is a game of chance, or could be resolved by players taking turns defecting). In a one-shot Prisoner's Dilemma, the rational choice is, of course, to defect because this may win you the biggest payoff (T) and protects you against the worst (S); but because both players ought to know this, one-shot interactions hardly encourage cooperation. However, the situation is transformed if Prisoner's Dilemma is iterated or repeated indefinitely. In the early 1980s, the political scientist Robert Axelrod announced an international tournament for computer programs to play iterated Prisoner's Dilemma. The winner was the simplest strategy entered: TIT-FOR-TAT, one which cooperated on the first round but thereafter repeated the other player's previous choice. Axelrod comments that "expert strategists from political science, sociology, economics, psychology and mathematics made the systematic errors of being too competitive for their own good, not being forgiving enough, and being too pessimistic about the responsiveness of the other side" (Axelrod 1984:40). He adds that TIT-FOR-TAT won, not by doing better than any other player, but by eliciting cooperation from the other player. In this way TIT-FOR-TAT does well by promoting the mutual interest rather than by exploiting the other's weakness. A moral person could not do better (Axelrod 1984:137).

Iterated Prisoner's Dilemma, in other words, proved that cooperation could evolve spontaneously in a world of self-interest and from bottom-up two-person interactions, not simply from top-down, holistic social forces such as those popular with sociologists. Like Hamilton's insight into groups, it explained how social behavior could be naturally selected at the most basic level and how mutuality could be a robust evolutionary strategy. Above all, it gave the lie to the common caricature of sociobiology as a form of social Darwinism, with individuals and groups set against each other in a merciless struggle for survival. Indeed, Robert Trivers, Hamilton's chief American collaborator, went on to show that reciprocity of this kind could become the basis of cooperation between organisms of different species, as in the so-called cleaning symbioses (Trivers 1971).

FAMILY CONFLICT AND COOPERATION

In the bird species such as eagles mentioned earlier that lay two eggs but normally hatch only one, the second hatchling is often consumed by its thriving sibling, causing natural revulsion to human beings and appearing to reinforce the common sociological caricature of sociobiology as endorsing rapacious violence and mindless murder. But of course this is a caricature, as can be seen by considering another, parallel example with an exactly opposite inference: infanticide in langur monkeys. Dominant male langur monkeys who take over harems of females habitually murder all infants under six months of age and still suckling at the time. This has been claimed to be "population control" for the benefit of the species because it dramatically affects population growth thanks to the fact that over a third of all infants can die this way (Hrdy 2000). If such dominant males were capable of it, presumably they would cite authorities such as Lysenko or Wynne-Edwards in justification! Nevertheless, mothers attempt to protect their infants from being murdered, apparently against the interests of the species. Furthermore, population control would be more effective if only young, nubile females were culled (because population growth is critically constrained by their numbers), yet the carnage is indiscriminate. Again, dominant males often control groups for several years, but only murder offspring in the first six months, evidently losing their interest in population control thereafter. The true reason is that since gestation lasts about six months in this species, any offspring under that age will have to be the progeny of the previous dominant male. Furthermore, any females who stop suckling because their existing infants have been killed by the new male quickly come into estrus again and so can be quickly remated by him. Langur infanticide, in other words, favors the reproductive self-interest of the dominant males who carry it out; it most emphatically does not serve the interests of the females who lose their offspring or that of the infants who die. As Robert Trivers (1981), Hamilton's principal American follower, remarked,

When critics argued that sociobiology tended to justify existing social arrangements, they were, of course, imputing to sociobiology a pre-Darwinian, species-advantage perspective . . . Arguments in terms of natural selection only appear to justify that which has evolved when one imagines—incorrectly—that traits evolve for the benefit of the species . . . such reasoning . . . tends to distract attention from the self-interest of the subordinate actors. No one analyzes how selection acts on them. Thus counter-strategies are overlooked, and resistance tends to be minimized. Conflict is overlooked or explained away as serving some larger function . . . Our destruction of group-selection thinking has removed the chief prop from the comfortable belief that the dominant interests naturally rule in everybody's self-interest . . . Those who took up the cry against sociobiology because it appeared to slight the interests of the oppressed failed to appreciate that the foundations of sociobiology have precisely the opposite effect: they call attention to the self-interest of all subordinated actors. (Pp. 36–39)

In many ways, the most striking human applications of sociobiological insights—not least by Robert Trivers—have been into family conflict and cooperation. For example, Daly and Wilson (1988) studied homicide as a corollary of Hamilton's key insight, reasoning that inclusive fitness would be promoted not merely by kin positively benefiting one another but by kin avoiding harming one another. They showed that in 1972, 75 percent of all murders of relatives in Detroit were of those where there was no actual blood tie between the family members. Furthermore, they argued that coresidence could not be the explanation: Coresidents with no blood tie were 11 times more likely to be murdered than coresidents who were related by blood. Again, they showed that 30 percent of comurderers in Miami were blood relatives, but only 2 percent of victims were blood relatives of their murderers. Nor are such findings peculiar to modern societies or to North America: On the contrary, there is no known society, nor has there ever been one, where violence between blood-related relatives even approaches the level seen between nonblood relatives.

The same authors showed that much the same is true of stepparents and stepchildren as compared with biological parents and their natural children. In one survey, only 53 percent of stepfathers and 25 percent of stepmothers claimed “parental feelings” toward their stepchildren, and statistics on child abuse show that a child living with one or more stepparents in the United States in 1976 was 100 times more likely to be murdered by them than was a child living with both biological parents. They conclude that “step-parenthood per se remains the single most powerful risk factor for child abuse . . . yet identified” (Daly and Wilson 1988:87–88).

Nevertheless, perhaps the most counterintuitive insights of the selfish gene approach have been into conflict and cooperation within the biological family. At first sight, parent-offspring conflict looks impossible from a biological point of view, because parents and offspring normally

share the same proportion of genes: 50 percent. But Trivers showed that if what is at issue is the readiness of offspring to make sacrifices for one another, then the situation is asymmetric. This is because parents are equally related to all their full, joint offspring: Each invests exactly half its genes. Therefore, any sacrifice by any offspring for any other that produces a net benefit, no matter how small, promotes the reproductive success of the parents. Offspring, on the other hand, are only related by 50 percent of their genes at most (and less if they only share one parent in common). Therefore, the offspring's genetic self-interest is only to perform an act of altruism toward a full sibling where $Br > C$: In other words, where benefit to the siblings is more than twice the cost to itself. To put it another way, *parents are selected to favor at least twice as much altruism—or half as much selfishness (which comes to the same thing)—as offspring are selected to favor* (Trivers 1974).

As Trivers (1981) himself points out, the implication of this is that “it is clearly a mistake to view socialization in humans as only, or even primarily, a process of ‘enculturation’ by which parents teach offspring their culture.” He adds that

one is not permitted to assume that parents who attempt to impart such virtues as responsibility, decency, honesty, trustworthiness, generosity, and self-denial are merely providing the offspring with useful information on the appropriate behavior in the local culture; for all such virtues are likely to affect the amount of altruistic and egoistic behavior impinging on the parent's kin, and parent and offspring are expected to view such behavior differently.

On the contrary,

socialization is a process by which parents attempt to mould each offspring in order to increase their own inclusive fitness, whereas each offspring is selected to resist some of the molding and to attempt to mould the behavior of its parents (and siblings) in order to increase its own inclusive fitness. Conflict during socialization need not be viewed solely as conflict between the culture of the parent and the biology of the child, it can also be viewed as conflict between the biology of the parent and the biology of the child. . . . Since teaching (as opposed to molding) is expected to be recognized by offspring as being in their own self-interest, parents would be expected to overemphasize their role as teachers in order to minimize resistance in their young. According to this view, then, the prevailing concept of socialization is to some extent a view that one would expect adults to entertain and disseminate. (Pp. 30–32)

Furthermore, that “prevailing concept of socialization” is of course also that of sociology: It is one that, by contrast to the sociobiological view, sides with the parents against the child and again exemplifies the force of Trivers's (1981) observation that sociobiology “uncovered the submerged actors in the social world, for example, . . . offspring, whose separate self-interest . . . we emphasize” (p. 39).

SEX AND PARENTAL INVESTMENT

Darwin did not invoke only natural selection in his attempt to explain evolution. From the beginning, he also appealed to what he came to call *sexual selection* understood as selection for traits that promoted the reproductive success of individual members of a species in competition with other members of the same sex. Although Darwin's 1872 book *The Descent of Man, or Selection in Relation to Sex* was a best seller at the time it was published, sexual selection remained a largely rejected idea for a century. Even Alfred Russel Wallace (1823–1913), who independently discovered evolution by natural selection and was a life-long collaborator, refused to accept the concept of sexual selection, along with just about all other naturalists and biologists—not to mention lay opinion. But like so much else associated with sociobiology, it was R. A. Fisher who made the first major step in rehabilitating the idea when he began to examine sexual selection quantitatively. Building on his work, Robert Trivers (1972) published a chapter in a book marking the centenary of Darwin's *Descent of Man* in which he established the basis of the modern theory of sexual selection. Following Fisher, Trivers defined the sexes in terms of the concept of *parental investment* defined as *any contribution to the reproductive success of an offspring at a cost to the remainder of the parent's reproductive success* (Trivers 1972). The trade-off implied here is illustrated by lactation in mammals, which contributes to the existing offspring at a cost to future ones by making the mother temporarily infertile (human mothers included). The sexes can in turn be defined in terms of their characteristically different pattern of parental investment. In modern biology, *female* is defined as *the sex with maximum investment in sex cells and/or offspring*, whereas *male* is *the sex with minimum investment in sex cells and/or offspring*. Male sex cells are *pollen* in plants or *sperm* in animals, usually microscopic and mobile, and in the human case, the smallest in the body. Female sex cells are *ovules* or *ova*, and are the largest in human body.

Where organisms such as mammals make further investment in offspring beyond the original sex cells, the disparity between male and female parental investment can reach staggering proportions. In human beings, for example, the energetic cost to the mother of a pregnancy amounts to about 80,000 calories (which equals 300 hamburger meals), or enough for a run of 800 miles; while in the United States, recently the going rate for egg donation was \$5,000 to 80,000, but for sperm donation only \$100! Finally, in terms of risk of death during pregnancy, childbirth, or abortion, the figure is a staggering 1 in 21 in sub-Saharan Africa, and 1 in 9,850 in the West (Potts and Short 1999:134). The risk to the father, by contrast, is exactly zero wherever he may be, and his only biologically obligatory contribution—a single sperm—is billions of times less than that of the mother as a proportion of the body weight of a newborn!

Of course, fathers can and do make impressive investments in their offspring in other ways than the directly biological. But even in this respect, the theory of parental investment explains facts that otherwise find no real explanation. Here, the relevant finding is that although remuneration of unmarried people of both sexes is broadly similar, a striking difference is observed when people marry, and especially when they have children. Typically, married men who have children increase their working hours, incomes, and pursuit of promotion, whereas women with children typically decrease all these things, just as the theory of parental investment would predict (Budig and England 2001).

If we ask what consequences follow from the fundamental difference between the sexes defined in terms of parental investment, we could immediately predict that, if one sex produces many more sex cells and invests much less in them than the other, that sex ought potentially at least to be able to engender many more offspring. A striking example of the cumulative effect of male, as opposed to female, reproductive success is provided by the members of the modern Saudi Arabian royal family who now number several thousand but are all descendants of Ibn Abd al-Rahman al-Saud (1880–1953) and his brother Faisal (1906–1975). Both monarchs had hundreds of official wives and an unknown but large number of concubines. The Saudi example may, admittedly, be exceptional, but it is nevertheless a simple fact of arithmetic that where individual men number their wives in tens, their offspring may number hundreds by the end of their lives, and where they have wives by the hundred there is nothing to stop them having offspring numbered in thousands. Nor is this effect limited to royalty. In modern Ghana, where men often marry several wives, the average father has twice as many children as the average mother (Konotey-Ahulu 1980). However, the corollary of this is that, given an equitable sex ratio, if some men have more women, other men are going to have fewer, or none. To put the matter in technical terms, the essential point is that males typically have greater *variance* of reproductive success than females normally do.

Sociological writers often take the sex ratio for granted, assuming that a more or less equal number of males to females in a society is an obvious expression of the essential equality of the sexes, but in the animal world as a whole, sex ratios can vary surprisingly, and accounting for them was another mystery Darwin could not solve, but Fisher could. Essentially, Fisher proved that even in a highly polygynous species where only 1 in 10 males mate, the successful males who do mate are 10 times more rewarding to parental resources invested in them, thereby compensating parents for investing equally in each sex (Fisher 1999). But the assumption is that parents have no way of knowing which of their offspring will be the successful ones. Trivers and Willard showed that if parents had some indication of the likely reproductive success of their offspring, they should invest preferentially in males if

their reproductive outlook was favorable but in females if not. The reason is that in all mating systems, females usually get mated, but where males compete—and they usually do—only the successful are likely to mate (Trivers and Willard 1973). In numerous animal species, the Trivers-Willard effect as it is known has been documented, and there are also some remarkable human parallels. One of the most horrifying was the finding that, following relatively expensive prenatal sex-determination tests in modern India (amniocentesis) by parents wealthy enough to be able to afford it, 430 of 450 women carrying a female fetus (95.5 percent) had it aborted, whereas every 1 of 250 carrying a son went to term, despite some being diagnosed defective (Ramanamma and Bambawale 1980). Indeed, historical studies show that some Rajput warrior castes in nineteenth-century India had no females whatsoever (Dickemann 1979)!

A common sociological reaction to such findings is to invoke purely cultural and economic factors, such as the desirability of receiving dowries. No one doubts for one moment that such explanations have their place, but the point is that such cultural, proximate mechanisms nevertheless seem to fit the larger, natural picture. Indeed, sometimes findings directly contradict sociological expectations, as in the case of eighteenth to nineteenth-century Schleswig-Holstein, where a study of a socially stratified farming community found that 7 percent of both girls in farmers' families at the top of the social scale and 7 percent of boys in laborers' families at the bottom died in their first year of life—suggesting that affluence was not a factor in child survival. However, the corresponding figure for their opposite-sex siblings was almost exactly 4 percent in each case, suggesting that irrespective of living conditions, the wealthiest members of the populations preserved more sons, and the poorest, more daughters, just as the Trivers-Willard principle would predict (Volland 1988). Again, a study of 1,314 Mormon women married to men born between 1821 and 1834 in Utah showed that those married to the highest-status men as defined by the church hierarchy had significantly more males (Mealey and Mackey 1990). In traditional American Indian society, high-status Cheyenne "peace bands" had more males than low status "war bands" (Cronk 1993), and in the modern United States, a study of 906 mothers found them more likely to nurse daughters in low-income households and sons in high-income ones. As the authors of the latter study conclude, "No simple model of sexist behavior can explain these findings" (Gaulin and Robbins 1991:69).

SOCIOBIOLOGY, EVOLUTIONARY PSYCHOLOGY, AND THE FUTURE

Of course, such findings raise the issue, not only of ultimate causes but also of proximate ones. In other words, quite apart from the fundamental biological principles involved in issues such as sex and parental investment,

there is the question of exactly how human beings have evolved to act in ways that may—or may not—put them into effect. More recently, so-called evolutionary psychology has emerged as a "kinder and gentler" variant of sociobiology in which particular emphasis is placed on the issue of proximate cause (Janicki 2004). A principal assumption of evolutionary psychology is that, to the extent that human behavior is controlled by human minds, such minds can be seen as having evolved to facilitate selected behavior (Barkow, Cosmides, and Tooby 1992). Where sexual selection is concerned, there is certainly a great deal of evidence now that patterns of human mating preferences found throughout the world accord with basic principles of evolutionary biology.

The largest study ever undertaken of human mating preferences covered all major religious, racial, and ethnic groups in 37 samples drawn from 33 countries and surveyed 10,047 people in all. It found that in 36 out of the 37 samples, women place roughly twice as much value as men do on good financial prospects in a partner (Buss 1997). In a comment that epitomizes the approach of evolutionary psychology, David Buss (1994), who carried out this research, explains the finding as follows: "Because ancestral women faced the tremendous burdens of internal fertilization, a nine-month gestation, and lactation, they would have benefited tremendously by selecting mates who possessed resources." He adds that "these preferences helped our ancestral mothers solve the adaptive problems of survival and reproduction" (p. 25).

Indeed, predicted sex differences are also found in sexual fantasy. A survey concludes that male sexual fantasies tend to be more ubiquitous, frequent, visual, specifically sexual, promiscuous, and active. Female sexual fantasies tend to be more contextual, emotive, intimate, and passive—just as theory would predict (Ellis and Symons 1990). Again, because paternity is much less certain than maternity, but can still be critical to a man's reproductive success, men should be more concerned with the biological details of insemination than women, who should instead be more concerned with a man's level of emotional commitment. This difference is reflected in jealousy, where men are much more disturbed by the physical details of their partner's activity with another male than are women in the corresponding situation. Women, by contrast, are much more disturbed by the emotional dimension of infidelity and its implications about their partner's feelings for them (Daly, Wilson, and Weghorst 1982).

A standard riposte by sociologists is to dismiss most such findings as simply the result of differential socialization of the sexes, but there is now overwhelming evidence for important innate sex differences in the one area that sociologists cannot afford to ignore: social behavior. From birth, girls attend more to social stimuli, such as faces and voices, while boys attend more to nonsocial, spatial stimuli, such as mobiles (Pierce et al. 2001). Studies conclude that contrary to the beliefs of many sociologists, there is little consistency between child-rearing practices and adult

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outcomes, and that parents' attitudes about sex stereotypes are poor predictors of their children's sex-typed behaviors. Others find that gender stereotypes are robust over cultures, show little change over time, and are reasonably accurate (Campbell 1998). Anne Campbell (1999) concludes that

girls are more concerned with developing shared norms and cohesion within the group and more frequently resolve conflict through discussion than do boys . . . evidence from both children and adults suggests that females are less competitive than males, show less . . . hierarchical organization, are less interested in achieving leadership within the group, and are more concerned with maintaining relationships of mutuality and reciprocity. (Pp. 208–209)

Women are found to exceed men in facial expressiveness, interpretative skill, gazing, smiling, and expressiveness of body language (Hall 1984). Meta-analysis of numerous studies shows that women exceed men on measures of anxiety, trust, tender-mindedness and gregariousness, whereas men exceed women on assertiveness. Furthermore, these differences are invariant across ages, educational levels, and nations (Feingold 1994). According to another meta-analysis, men are more aggressive and restless, are more likely to lead groups, and to contribute more in small groups. Women, on the other hand, make greater social and emotional contributions to small groups and are more easily influenced by them (Eagly 1987).

One of the most robust findings is that males take more risks than females in almost every species where males compete for reproductive success. As a consequence, it has been claimed that

because of women's greater involvement in childbearing . . . it would have been to their selective advantage to inhibit behaviors that would conflict with the best interests of children . . . The single interpretation that best describes the research findings across a wide range of tasks is that women have greater inhibitory abilities than men on most tasks involving sexual, social, emotional and some behavioral content (Bjorklund and Kipp 1996:167).

However, "because the male psyche is biased towards risk taking, the number of situations in which men demonstrate consistently superior inhibitory abilities to women will be few" (p. 168). For example, a study of Israeli kibbutzniks found that even after three generations of socialization aimed at eliminating sex differences in behavior, males still took more risks than females. The only exception was in defense of their own children, where women were more likely to endanger themselves than men (Lampert and Yassour 1992). Indeed, these findings have even persuaded some sociologists of religion that they explain the universal tendency for women to be more religious than men much better than sociology's stock-in-trade explanation of differential socialization (Miller and Stark 2002; Stark 2002).

Nevertheless, violence represents the starkest difference between the sexes in social behavior and is one that, even more than religious behavior, simply cannot be accounted for by differences in socialization. For example, a study of 35 societies throughout the world showed that a man was 20 times more likely to be murdered by another man than was a woman by a woman (despite excluding war and other group conflicts). Men in the United States commit 86 percent of simple assaults, 87 percent of aggravated assaults, and 88 percent of murders. Indeed, "*Intra-sexual competition is far more violent among men than among women in every human society for which information exists*" (Daly and Wilson 1988:161, authors' emphasis). According to a recent account,

these differences are understandable if, in evolutionary history, women have enhanced their reproductive success by cooperating in the familial sphere, with female relatives and co-wives—that is, in situations in which they could not gain through open conflict, or in attempting to change coalitions. Men, on the other hand, have enhanced their reproductive success by cooperating to get greater resources and power with both related and unrelated men—situations in which open assertions of dominance (with greater risk) may frequently gain. (Low 2000:196–97)

Reduced temporo-limbic and frontal brain areas have been found to be linked with psychopathy and antisocial behavior, but these same parts of the brain have recently been found to be larger in women (Gur, Gunning-Dixon, Bilker, and Gur 2002). As one authority comments, "This study affords us neurobiological evidence that women may have a better brain capacity than men for actually censoring their aggressive and anger responses" (Cohen 2002:7).

Evolutionary psychologists have criticized what they call the *Standard Social Science Model* for its exclusion of insights from biology (Tooby and Cosmides 1992), and sociologists such as Lee Ellis have castigated sociology for its so-called biophobia (Ellis 1996). Indeed, according to Lopreato and Crippen (1999), "Sociology will never get anywhere but farther out of the scientific course as long as it adheres to the banality that the fundamental cause of behavior resides exclusively in the immediate influence of culture and social structure." They add that "at present sociology offers a shallow and distorted view of human nature that prevents it from understanding the real world and thus from the likelihood of demonstrating its utility to society" (pp. 34, 43).

Part of the reason for sociology's phobic reaction to sociobiology and evolutionary psychology may be fear of so-called genetic determinism. This is specially so in relation to issues such as sex, which sociologists prefer to call *gender* (perhaps because, strictly speaking, whereas there are just two sexes, male and female, there are three genders, masculine, feminine, and neuter). But, notwithstanding the universally agreed definition of the sexes in terms of parental investment outlined above, it is important to realize that sociobiological insights (again springing

mainly from the work of Hamilton) suggest not simple genetic determinism but complex genetic conflict where sex is concerned, with every possible variation and mixture of maleness and femaleness being predictable.

The reason for this is that the male-defining Y chromosome in mammals such as human beings contains very few genes, meaning that the vast majority that are characteristically expressed in males are carried on the remaining 22 pairs of chromosomes, also present in females. This means that masculinization of female mammals can readily occur in a way in which it never could if all male-defining genes were carried on the Y, which is present only in males. Female mammals have two X sex chromosomes, by contrast to the male's single one (paired with the Y in males). But as Hamilton was one of the first to point out, this means that any gene on an X finds itself in a female body twice as often as in a male, meaning that selection will act on X chromosome genes to benefit females twice as much as it will to benefit males (Hamilton 1967). As a result, males might be feminized—or at least, their masculinity compromised by selection pressure favoring their female relatives. For example, a gene on the X chromosome called *DAX1* acts as an antagonist to the gene on the Y that initiates male development. Normally, this gene, *SRY* (for *Sex-determining Region of the Y*) transforms what would otherwise develop as ovaries into testes, with subsequent masculinization of the whole body (largely thanks to the male sex hormones produced by the testes). However, otherwise normal XY males with a duplication of part of the short arm of the X chromosome that contains *DAX1* show male-to-female sex reversal. It seems likely that the dose of *DAX1* carried on a normal male's single X chromosome is not enough to reverse male development, but a double dose provided by duplication of the *DAX1* region of the X chromosome is, and so sex reversal occurs. At the very least, this finding shows that particular genes on the X and Y chromosomes can be in conflict with one another. Indeed, *DAX1* has been described as more of an “anti-testis gene” than a “pro-ovary” gene (Swain et al. 1998).

Again, recent research has revealed that although each parent contributes half the offspring's genes, certain key genes are only expressed when inherited from one parent rather than the other. The paradigmatic example is *Igf2*, which codes for a growth factor. Normally *Igf2* is only expressed from the paternal copy, and in human beings, expression of the mother's copy too results in Beckwith-Wiedemann syndrome, an overgrowth condition with many symptoms, among which is birth weight more than one and half times normal (Reik and Maher 1997). Larger size is normally advantageous to mammals, and in the case of human beings, larger babies live longer, suffer less disease, and have better all-round health; while coronary heart disease, stroke, and non-insulin dependent diabetes are associated with low birth weight (Barker 1998). Taller men do better in most occupations, are preferred by women, and have more sexual partners and children than shorter ones (Pawlowski, Dunbar, and Lipowicz 2000). So

size definitely benefits a man's genes invested in his children (particularly if they are male), but as any woman who has ever been pregnant knows, larger babies also impose greater costs on the mother, and without recourse to Caesarean delivery, many Beckwith-Wiedemann babies in the past killed their mothers during childbirth simply because they were so large. This may explain why *Igf2* is paternally active and why *Igf2r* is maternally active: the latter being a gene that (at least in mice) creates receptors that act as a sink for the growth factor and reduce offspring size (Moore and Haig 1991). In other words, it looks as if *Igf2* serves the father's interests in promoting growth of his offspring, but that *Igf2r* represents the mother's point of view and tones down its effects to something more manageable for her. In maize, for example, paternal genes are associated with larger kernel size, whereas maternal genes produce smaller kernels (Domínguez 1995).

Maternity is certain: A woman always knows that half her genes are present in any child that issues from her body. But paternity is uncertain in the sense that fathers normally have no direct way of knowing whether it was one of their sperms or that of another man which fertilized a particular egg. Of course, life-time monogamy, virginity on marriage, and strict observation of sexual fidelity can lessen the uncertainty of paternity, but in most mammalian species—and in most human societies throughout most of history, not to mention the modern world—these ideals are seldom found. On the contrary, in the modern Western world, estimates of the extent to which a man who believes he is the father of a child is in fact not so vary between 1 and 30 percent (Baker and Bellis 1995; Heyer et al. 1997; Sasse et al. 1994; Wenk et al. 1992). In plants, a grain of pollen could come from practically any other plant within range of the one that it fertilizes, and so here even more than in mammals, complete uncertainty of paternity is the rule. The result is that paternal genes do not have the same vested interest in not exploiting the mother that maternal ones have. A woman's genes rely entirely on her own body to produce offspring once she is fertilized, so they have an interest in conserving her resources and protecting her future reproductive potential. However, a man can in principle count on the gestational services of as many women as he can successfully inseminate, and unless he is tied to one by lifelong monogamy, can regard his mates' reproductive potential as much more expendable than his own.

In humans, mainly paternal genes are expressed in the *placenta*: an organ designed primarily to extract resources for the growth and development of a fetus from its mother. Indeed, an abnormal conceptus with a double set of paternal genes without any genes whatsoever from the mother results in a massive proliferation of the placenta without any associated fetus (Newton 2001). The human placenta is the most invasive of all mammalian placentas and in some cases can perforate the uterus, killing the mother. The fact that anemic mothers have heavier placentas than nonanemic ones despite giving birth to lower-weight babies suggests that the placenta can actively respond to

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deficits in the mother's provision of nutrients by becoming larger. Cells originating in the placenta aggressively widen the mother's arteries that feed it by breaking down their walls and weakening them, so that they sag and distend, thereby increasing blood supply to the cavities that the placenta excavates to receive it. A paternally active gene within the fetus/placenta manipulates the mother's glucose economy by secreting *human placental lactogen*, a hormone that reduces the mother's sensitivity to her own insulin, causing the so-called gestational diabetes. This means that the mother's blood sugar level stays higher for longer, giving the fetus more time to consume glucose despite the mother's best efforts to prevent this by escalating her output of insulin. There is also evidence that the fetus heightens maternal blood pressure to decrease blood flow to the mother's peripheral circulation and to increase it to the placenta. Blood pressure in mothers appears to correlate with birth weight in both directions: Women with lower than normal blood pressure during pregnancy tend to have lighter babies, and those with hypertension probably have heavier ones than they would otherwise. In any event, women with higher blood pressure tend to lose fewer babies than average (Haig 1993).

Furthermore, conflict between maternal and paternal genes can continue after birth. *Prader-Willi syndrome* affects about 1 in 15,000 births, and is caused by the loss or silencing of paternal genes on chromosome 15 through inheriting both copies of this chromosome from the mother, or losing part of the paternal copy (Nicholls, Saitoh, and Horsthemke 1998). Symptoms include lack of appetite, poor suckling ability, a weak cry, inactivity and sleepiness, high pain threshold, and reduced tendency to vomit (Franke, Kerns, and Giacalone 1995)—all features that, interestingly enough, could be seen as benefiting the mother by making the baby less demanding on her resources (Haig 1997, 2000; Moore and Haig 1991). By contrast to Prader-Willi, in *Angelman syndrome* only the paternal chromosome 15 is present in its entirety and the critical maternal genes involved in Prader-Willi syndrome are missing (Nicholls et al. 1998). Symptoms include prolonged suckling, hyperactivity, and frequent waking—every mother's worst fear—and according to the conflict theory not coincidentally associated with paternally expressed genes (Badcock 2000:192–226)!

It is now possible to produce mice in the laboratory that express mainly the father's or the mother's genes and to stain cells in such a way that you can see exactly where the paternal or maternal genes are going in the developing body. The result is striking: Fetal mice with a father but no mother are larger than normal and have a bigger placenta but reduced brains; those with a mother and no father are the opposite—they are smaller than usual, have reduced placentas, but have larger brains than normal (Keverne et al. 1996). Of course, you could not carry out such an experiment on human fetuses, but naturally occurring human equivalents mirror these findings. Abnormal human

fetuses with a double set of their father's genes and a single set of the mother's (rather than a single set from each parent) are well grown except for the head and have a large placenta. By contrast, those with a double set of the mother's genes and one of the father's are small except for the head, show a retardation of growth, and have small placentas (Hannah et al. 2002; Newton 2001).

In mice, cells with only maternal genes are found in large numbers in the cerebral cortex and forebrain but very few are found in the lower brain, and especially the *hypothalamus*, a center concerned with basic drives and instincts. This is true both of mature, fully grown mice but even more so of fetuses, where there is a complete absence of maternal cells from the hypothalamus. In both cases, mother-only cells are found to be particularly clustered in the frontal lobes of the cortex. Father-only cells, by contrast, are the exact opposite: These are found in the hypothalamus and lower brain but not in the cerebral cortex. The few that are found in the forebrain tissue of embryos do not proliferate and are subsequently eliminated. However, no such difference is found in the brain stem, which appears to be equally the work of maternal and paternal genes (Allen et al. 1995).

As I pointed out earlier, *Igf2r* is the classic maternally active gene found in mice, effectively contradicting the growth-enhancing demands of *Igf2*. However, in humans, *IGF2R* has been found to be associated with high IQ (Chorney et al. 1998). As the authors of the study in question point out, the fact that *IGF2R* has been found to be statistically associated with high IQ in their sample does not mean that the gene is in fact contributing to intelligence. What they have found may simply be a genetic marker that is close to other genes that do directly contribute to measures of IQ. To this extent, the finding may be coincidental. However, there is evidence that insulin may play a role in spurring neuronal growth that contributes to learning and memory in the brain (Wickelgren 1998), and we have already seen that in mice *Igf2r* builds an insulin-like growth hormone receptor. So it is not entirely far fetched to think that the human version of the gene has become associated with mental functioning in the very parts of the brain built by maternal rather than paternal genes.

As the principal provider of parental investment during pregnancy and breast-feeding and almost always during childhood, a mother clearly has a vested interest, both in nurturing her child and enabling it to control its demands for further investment in her own and her other children's self-interest. The father, however, need make no biologically obligatory contribution beyond his single sperm, and so perhaps understandably relies on his genes alone and the lower brain centers they evidently build to motivate his offspring to compete for resources within a family where other children may not be related to him at all. Genetic conflict, in other words, appears to be built into the brain before birth and fought out in the mind for ever afterward (Badcock 2000:204–22, 2004).

As Hamilton (1996) himself confessed,

The genome wasn't the monolithic data bank plus executive team devoted to one project—keeping oneself alive, having babies—that I had hitherto imagined it to be. Instead, it was beginning to seem more a company boardroom, a theatre for a power struggle of egoists and factions. Emergent from the potential strife I was having to imagine, in parallel with others, a kind of parliament of the genes, and the signs suggested a rowdy parliament at that. (Pp. 133–34)

The fundamental insight of sociobiology, in other words, is not genetic determinism, but genetic conflict,

not robotic control by all-powerful genes, but ambivalence about how to respond to contrary wishes and mutually exclusive motivations. This in turn suggests that human beings evolved their enormous brains in large part to be able to arbitrate such internal conflicts and to make the difficult choices that result. Sociobiology is an attempt to understand how and why this extraordinary situation could have come about. Ultimately, its value lies in the extent to which it can help us make sense of our own selves and thereby perhaps even master the evolved basis of our own behavior (Badcock 2000:69–71).

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