



## NEW BIOLOGICAL BOOKS

*The aim of this section is to give brief indications of the character, content and cost of new books in the various fields of biology. More books are received by The Quarterly than can be reviewed critically. All submitted books, however, are carefully considered for originality, timeliness, and reader interest, and we make every effort to find a competent and conscientious reviewer for each book selected for review.*

*Of those books that are selected for consideration, some are merely listed, others are given brief notice, most receive critical reviews, and a few are featured in lead reviews. Listings, without comments, are mainly to inform the reader that the books have appeared; examples are books whose titles are self-explanatory, such as dictionaries and taxonomic revisions, or that are reprints of earlier publications, or are new editions of well-established works. Unsigned brief notices, written by one of the editors, may be given to such works as anthologies or symposium volumes that are organized in a fashion that makes it possible to comment meaningfully on them. Regular reviews are more extensive evaluations and are signed by the reviewers. The longer lead reviews consider books of special significance. Each volume reviewed becomes the property of the reviewer. Most books not reviewed are donated to libraries at SUNY Stony Brook or other appropriate recipient.*

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## THE SCIENCE THAT DARE NOT SPEAK ITS NAME

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A review of  
NARROW ROADS OF GENE LAND: THE COLLECTED PAPERS OF W. D. HAMILTON. *Volume 2: The Evolution of Sex.*

*By W D Hamilton; Foreword by Richard Dawkins. Oxford and New York: Oxford University Press. \$85.00 (paper). lvi + 872 p; ill.; name and subject indexes. ISBN: 0-19-850336-9. 2001.*

*The Evolution of Sex*, the second volume of *Narrow Roads of Gene Land*, was in the final stages of preparation at the time of Bill Hamilton's death in March 2000. Its 800-plus pages contain 18 republished papers (including eight book chapters) from the years 1981 to 1991 and Hamilton's discursive commentaries on

these papers. Most of the papers are concerned with the evolution of sex and mate choice, but other subjects make an appearance, including Hamilton's classic paper with Robert Axelrod, *The Evolution of Cooperation* (1981). The commentaries are part intellectual argument, part autobiography, part prose poem, part settling of scores, and part jeremiad, written in an allusive, parenthetical style that sometimes approaches a stream of consciousness.

Hamilton appears to have had two major goals in preparing this volume. The first was to present a convincing case that he had solved the problem of the maintenance of sex, and that his solution had not been given

the credit it deserved by the community of evolutionary theoreticians. The second was to present his views on the implications of natural selection for human affairs and to initiate a debate on subjects that he considered to have been treated as taboo, particularly eugenics. In pursuit of this second goal, Hamilton saw himself as a voice crying in the wilderness, speaking simple truths against the falsehoods of demagogues. The two goals were interrelated, but it will be convenient to treat them separately.

THE RED QUEEN'S REALM:  
PARASITES AND SEX

Most of the republished papers in this volume chronicle Hamilton's groping toward an explanation of sex that he calls the Parasite Red Queen (PRQ) theory. The earlier papers present limited results that do not satisfy their author, let alone his readers, but they chart Hamilton's progress toward the antepenultimate paper of the volume, *Sexual Reproduction as an Adaptation to Resist Parasites* (a review) (1990). Hamilton considered this to be his second most important paper, presumably ceding first place to *The Genetical Evolution of Social Behaviour I and II* (1964). Despite his own high estimation, the paper (written with Robert Axelrod and Reiko Tanese) was twice rejected by *Nature*, once by *Science*, and its submission to the Royal Society journals was discouraged. The paper finally appeared in the *Proceedings of the National Academy of Sciences, USA* when Axelrod used his membership in the Academy to obtain favorable reviews. Since the paper appeared, PRQ has been treated as one hypothesis among many, rather than as a solution to the problem of why so many species are sexual. At the time of writing his commentaries, Hamilton clearly still felt bitter about the multiple rejections of the paper and its subsequent unenthusiastic reception by his peers.

What then was his solution to the problem of sex and why has it failed to achieve the unqualified assent of the evolutionary community? In Hamilton's vision, host gene pools contain a large number of polymorphisms that determine resistance to parasites. Parasites evolve to specialize on the most common

genotypes and, as a consequence, these genotypes decrease in frequency and rarer genotypes take their place, only to be hammered down in turn by the force of selection from the ever-evolving parasites. The currently disfavored variants are not lost from the gene pool because, as they become rare, selective mortality declines as parasites switch to the new most frequent variants. "The essence of sex in . . . [this] theory is that it stores genes that are currently bad but have promise for reuse. It continually tries them in combination, waiting for the time when the focus of disadvantage has moved elsewhere" (pp 656–657).

PRQ is a model of seething gene frequencies that never come to rest, of a constant obsolescence of antiparasite adaptations, and of the chance of redemption for variants that once conferred resistance, and may do so again. It is a model in which linkage disequilibrium retards the efficacy of natural selection and thus helps to maintain polymorphism, in which slow, nonsynchronized cycles maintain substantial variance and heritability of fitness, and thus provide an advantage for female mate choice. It is a model that seeks to find an evolutionary role for males other than as mere parasites on the parental investment of females.

Probably the principal reason for discontent with PRQ is the complexity of the underlying model (in this, it reminds me of Sewall Wright's shifting balance hypothesis). Early versions did not achieve stable maintenance of sex for biologically plausible conditions, and Hamilton responded by adding more and more features to his models. Later versions increased the number of resistance loci and the number of types of parasites, incorporated soft truncation selection in which a genotype's fitness depended on its ranking relative to all other genotypes, and added a variable life history in which births and deaths depended on habitat saturation. Clearly, Hamilton had an underlying faith that parasites can maintain sex and that this would emerge if only the models could be made realistic enough. His models were analytically intractable, so he relied increasingly on computer simulations. He admitted that simulation is not understanding, but he was

prepared to settle for the partially understandable. If simple analytical models had all failed to find a robust short-term advantage of sex, this might mean that the advantage would only emerge in models that included multiple loci and a complex ecology.

By the time that Hamilton achieved his epiphany in *Sexual Reproduction as an Adaptation to Resist Parasites*, the simulations incorporated a population of 200 hosts beset by up to 12 species of asexual parasites (also with populations of 200 individuals). Host chromosomes contained up to 14 resistance loci and a sex locus, whereas parasite chromosomes had up to seven virulence loci. All loci were subject to mutation. In each cycle, births were assigned at random to surviving adults (individuals that had survived at least 13 cycles) to compensate for the elimination of the 14 hosts that ranked lowest on a scale determined by the number of matches between host and parasite chromosomes. The number of matches also determined a parasite's relative fecundity, with parasites culled at random in each cycle to reduce their numbers to 200. This is not a simple model—Hamilton describes it as a group pursuit around the vertices of a multidimensional hypercube—but the simulations had achieved an impressive result: the stable maintenance of sex in an outbred population, with very low fecundity, frequent mutation to parthenogenesis, and broadly overlapping generations.

Has host-parasite coevolution solved the problem of the maintenance of sexual reproduction? *The Evolution of Sex* makes a strong case, but the lack of transparency of the simulations cannot dispel all lingering doubts. Every simulation makes simplifying assumptions. What if the hosts had been diploid rather than haploid? What if mutation rates, or recombination frequencies, had been different? And so on. Hamilton believed that the strength of PRQ was its ability to explain the ecological patterns of sexuality. The theory will rise or fall on the basis of these patterns, and of studies that compare related sexual and asexual forms.

In Hamilton's view, the main rival to PRQ was the hypothesis that sex facilitates the clearance of deleterious mutations, a hypothesis that he called the Mutation Black Queen

(MBQ). Hamilton believed that purging deleterious mutations was indeed a function of sex, albeit distinctly subsidiary to its function of shuffling resistance genes to stay one step ahead of parasites. He saw the major weakness of MBQ, relative to PRQ, however, as its inability to say anything much about the ecology of sex. All populations everywhere should benefit about the same from mutation clearance, but Hamilton believed that the various ecological correlates of sex showed that they do not. He believed that sex allowed mutation rates to be higher than they would otherwise be: “[i]f the PRQ alone is really powerful enough to cause sex to be stable, as I believe, sex's retention means that *individuals* have the opportunity to cream extra advantages from higher genome mutation rates than they would otherwise be expected to tolerate—that is, given so inevitably restless a population state as PRQ describes, such rates may exist at little extra cost to the *organisms*. I have not worked out this idea in detail but it seems plausible that if a *species* is changing its defences all the time to keep pace with rapid parasite coevolution, then the same selection that is facilitating escape from current parasites can eliminate bad mutations simultaneously at little extra cost” (p 619, emphasis added). In this quotation, I have added italics to indicate my uncertainty about the level at which selection on the mutation rate is envisaged as acting. Perhaps Hamilton is referring to a relaxation of selection for lower mutation rates, rather than positive selection for higher rates. Hamilton believed that if all organisms were switched “magically to a condition of no parasites, sex would indeed die out and as it did so mutation rates would start to fall” (p 752).

#### THE BLACK QUEEN'S REALM: EUGENICS AND THE HUMAN GENOME

Hamilton's task, when he turns to apply evolutionary theory to the human condition, is to strip away comforting illusions, to expose the cant and hypocrisy that dominate discourse, peddled by intellectual charlatans who play to the gallery, offering comforting bromides and short-term palliatives in the

place of a serious discussion of alternatives. He views culture as a braggart that is always overstating its own importance relative to our evolved nature, but sees himself as able to bring clarity and honesty to issues that are treated as taboo, because the oddities of his own mind have rendered his ears deaf to the prevailing propaganda.

The preface describes two occasions, more than 30 years apart, when Hamilton considered himself silenced and pushed aside because of attempts to speak hard truths. The first occurred in the mid-1960s when he was a junior lecturer at Imperial College and an almost unknown participant in a Population Study Group of the Royal Society. Hamilton suggested that evolutionary biology might have something to say about the psychology of intergroup conflicts, particularly about how different rates of population growth exacerbate tensions between groups, but his topic for discussion was met with silence, except for its dismissal as fanciful and off limits by Lord Florey, then President of the Royal Society.

The second occasion occurred in 1998 at a meeting in the Vatican of the Pontifical Academy of Sciences. Hamilton had been invited to speak on a subject in the general area of evolution, and he chose as his topic how modern medicine is causing long-term deleterious changes in the genome and how these changes make desirable a program of eugenics and selective abortion. After a written version of his presentation had been submitted to the organizers, Hamilton found that his talk had been rescheduled to the end of the meeting. Various commentators on earlier talks then ran out the clock to leave only 20 minutes, including questions, for his paper. Hamilton's own commentator then took the floor to say that he so disagreed with the paper that he would not even try to address it and talked about other issues. That Hamilton should choose to speak on such a topic at the Vatican, and should be upset at its stony reception, is symptomatic of his intellectual fearlessness and political naïvety.

The topic of intergroup relations occupies only a minor part of *Narrow Roads of Gene Land*. Hamilton's vision is not completely bleak. He believed that in recent human evo-

lution there has been selection against some of the more extreme forms of nepotism, because of the distinctively human division of labor and the associated advantages of trade. "Definitely on all fronts it has become imperative not to bristle with hostility every time you encounter a stranger. Instead, observe him, find out what he might be. Behave to him with politeness, pretending that you like him more than you do—at least while you find out how he might be of use to you. Wash before you go to talk to him so as to conceal your tribal odour and take great care not to let on that you notice his own, foul as it may be. Talk about human brotherhood. In the end don't even just pretend that you like him (he begins to see through that); instead, really like him. It pays" (p 359).

Despite this evolved sense of fellow feeling, however, our attitudes to others remain strongly ambivalent, and can readily spill over into hatred and intergroup conflicts. "We must cease to pretend with cries of 'brotherhood' and other nonsense, that there is one ideal way of life, one dominant culture, one right or inevitable programme of evolution of our species, whether claiming a way of a noble savage, a Marxist, a Christian, an Englishman, or any other. Then, still countering less-liberal views, there follows one rule that most different cultures should be willing to enforce, however varied and individualistic their practices may be in other ways: that no race or genotype has the right to unlimited numbers, and yet every race has the right to be protected against extinction" (p 362). Hamilton has little to say on how such consensus could be achieved or on how such a rule would be enforced.

The author's major social concern is with the deterioration of the human genome. He is an unabashed advocate of what he is not afraid to call eugenics, but his eugenics has a distinctive flavor in its preoccupation, not with race nor class, nor even intelligence, but with health. If our current state of perfection has been achieved by the selective elimination of the slightly less perfect, then this perfection cannot be indefinitely maintained if such selective elimination is removed. Hamilton warns of the Mephistophelean gifts of modern medicine, of a coming genetic dystopia in which every one of our descendants has sev-

eral lethal genes that require medication all of the time. It is far kinder, he believes, to let nature take its course with the continued elimination of the less fit. This could be most efficiently and humanely achieved by the selective elimination of zygotes and embryos, but he is willing to countenance the killing of defective neonates. This, he believes, is the course of true compassion, and that “[b]y kidding ourselves about some weird kindness to embryos, to neonates, and the like now, we are actually being very unkind to numerous far more sentient persons of the future” (p 476). He feels that an “evolutionary understanding will make us less cowardly about death and will deter the cant of claiming it is dogmatically and unequivocally right to cure disease, save lives, or fix infertility” (p 532).

On first reading, Hamilton’s insistence on the preeminence of the Parasitic Red Queen in the evolution of sex appears inconsistent with his focus on the Mutational Black Queen in his concerns for the human genome. The inconsistency is perhaps more apparent than real. Under the Red Queen hypothesis, currently disfavored genes are not new; they were favored by natural selection in the past; and may be so favored in the future. Fluctuation in their frequency does not contribute to a long-term deterioration of the genome, as long as the genes are not lost altogether. By contrast, the deleterious alleles generated by mutation arise anew in each generation and will accumulate if not effectively purged by selection. Consequently, Hamilton has relatively little to say on the role of parasites in his eugenic pronouncements. Resistance genes are scattered throughout the human population. Therefore, he is an advocate of wide outbreeding, and, in matters of mate choice, his advice is simple: “follow your senses of beauty and love wherever they lead” (p 276).

Hamilton has much more to say about the dangers of genetic deterioration than about specific eugenic interventions. Often, his eugenics seems limited to the promotion of an ethos in which medical treatment is withheld, but sometimes he promotes more active measures. The part of Hamilton’s vision that many readers will find most disturbing is his promotion of infanticide. He sees this as a

natural extension of prenatal selection of embryos. They feel no pain and have no fear because this would be of no adaptive use. That is, fear and pain are adaptations that prompt an organism to avoid some threat. If the organism can do nothing to avoid the threat, fear and pain have no utility and therefore should be absent. In this argument, one wonders about the ontogeny of pain. Could developmental constraints ensure that nervous functionings are present before they have utility? Although Hamilton concedes that human neonates can feel pain, he believed that they have no fear of death and virtually no “soul” until reaching an age when they start to bond with particular adults. “If early signs of a coming severe handicap can be detected during that early postnatal period, I hold that the kindest thing for the family in which the defective child is to be dependent, and for the child itself, may well be to kill it” (p 477). These ideas are most fully developed in Chapter 12 and are structured around his thoughts on the deaths of two brothers, Jimmy at two days and Alex at 18 years, and the death in late puppyhood of Freya, the family dog. Hamilton would have done nothing to prevent the first death, but still mourned the others.

There is much that is thought provoking in Hamilton’s reflections on eugenics. The author believes that his previous attempts to raise eugenical questions have been passed over in embarrassed silence, or have been dismissed with facile remarks that did not engage the real issues. He clearly hoped that this book would open debate on these questions. In that spirit, I will present some of my own inconclusive thoughts that were stimulated by reading his book.

It is a trivial result in population genetics that, if selection against mutations is relaxed, mutant alleles will increase in frequency until they attain an equilibrium frequency that is determined by the rate of mutation and the remaining selective pressures. If all selection were removed, all gene copies would be non-functional at equilibrium. Further, most people would agree, if they stopped to reflect, that the birth of a child without a genetic disease is preferable to the birth of a child with the disease. Two questions need to be addressed. First, what is the magnitude of the problem

posed by relaxed selection? Second, what (if anything) should be done?

I do not believe we have a good answer to the first question. Rather, the question raises subsidiary questions. First, how much is selection relaxed? I have heard eugenics dismissed because mutation accumulation affects only a small part of the world population. This is not comforting. There should be no consolation in the view that selective mortality in the developing world is keeping the gene pool healthy, while the developed world enjoys the benefits of modern medicine. But, if we restrict our consideration to the developed world, how effective is modern medicine in reducing fitness differentials? Does the child with phenylketonuria (PKU) who is treated with a phenylalanine-free diet have the same fitness as a child without PKU, when all components of fitness (both fertility and survival) are considered? If a selective differential remains, and the mutation rate stays low, PKU will increase in frequency, but will never affect a major proportion of the population.

Second, how much of genetic ill health is due to new mutation? Some genetic disease may be due to balancing selection—consider sickle-cell anemia. If selective mortality due to malaria is relaxed, the frequency of the “wild type” allele would tend to increase because of continued selection against sickle-cell homozygotes (who still have low fitness). This effect, however, will be partially opposed by the decreased frequency of homozygotes due to genetic admixture of populations with different gene frequencies. Some genetic disease may be caused by alleles that are at high frequency because of selection in past environments (e.g., the proposed association of type II diabetes with “thrifty genotypes”). Medical treatment might slow the rate at which these genes decline in frequency, due to the changed selective forces, but it will not promote the accumulation of the disease-causing alleles by mutation.

Finally, how rapidly will genetic load accumulate given modern medical interventions? A typical textbook figure for loss-of-function mutations is one new mutant per 100,000 gene copies per generation. Therefore, the accumulation of mutant alleles at a single

locus is likely to be slow. But if the genome contains 35,000 to 100,000 loci, each present in two copies, then the same mutation rate would mean that most individuals will carry a new loss-of-function mutation somewhere in their genome. How rapidly such a genome-wide mutation rate would translate into a marked deterioration in genetic health is unclear. This will depend on the poorly understood mapping of genotype onto phenotype. Some mutations will have little health cost, whereas others will have effects so severe that modern medicine makes little difference (early embryonic lethals combine little health cost with severe effects). Only mutations for which medical care causes a substantial increase in reproductive fitness are relevant to this question.

My usual response, when asked what should be done about the accumulation of deleterious mutations, has been to argue that deterioration is probably taking place, but the process is slow, and the world faces far more urgent problems. Hamilton would have considered this to be moral and intellectual cowardice because the same response could be made at every stage of deterioration. He appeared to believe, however, that the problem was pressing, and predicted that “in two generations the damage being done to the human genome by the ante- and postnatal life-saving efforts of modern medicine will be obvious to all and be a big talking point of science and politics” (p. xlvi). To me, this seems too rapid, unless Hamilton is referring to the rapidity with which politics and what is “obvious to all” can change. That is, if the change Hamilton predicts comes about, it is likely to be the result of a political debate about who gets health care and who pays, rather than a rapid change in the load of genetic disease.

When it comes to the second question of what should be done, a variety of positions could be taken. One might deny any problem. If selection is relaxed, this is just another way of saying that mutant alleles have become less deleterious, or more fit, in the new selective environment. Why should we be concerned about maintaining adaptations for past environments? Hamilton worried about our ability to survive future catastrophes and his response to this question would have been

that sooner or later past adaptations would be useful again. Of more immediate concern is the potential confusion between two meanings of fitness. Human well-being is measured more by bodily fitness than by reproductive fitness. One might propose that the problem be fixed by technological means. Hamilton is scathing in his rejection of gene therapy as a practical solution, and I am inclined to agree with his analysis. One might propose that selection should be maintained—this was Hamilton's position. Or, one might decide that, even though there is a problem, nothing should be done, either because none of the options are practical, or because all of the options are even less desirable than the problem they are designed to solve.

For purposes of discussing the eugenical option, a useful distinction can be made between what I will call public-good eugenics and private-good eugenics. A reduction in the future load of genetic disease is a remote public good that may come into conflict with the immediate, and intense, private good of having a desired child. Public-good eugenics corresponds to a policy of discouraging designated persons from having children. Political science and experience suggest that attempts to provide a public good tend to be ineffective when these come into conflict with private goods, especially if the public good is delayed to some future generation. Hamilton dismisses the dreams of communism as "hopeless—silvery dreams of the centralized, all-singing, all-protecting, all-predictive economy" (p 470), but seems to have similar dreams for a state-sanctioned program of eugenics.

One possible route to public-good eugenics would be a policy of direct physical coercion, such as involuntary sterilization. The historical precedents are well known, and Hamilton does not propose such a route. Another way would be to convert the public good into a private good. This is essentially what Hamilton proposes in his schemes of "state rewards" and "reproductive disincentives" (discussed below in the context of caesarean sections). To me, rewards seem completely impractical. Even if rewards for nonreproduction could be made large enough, this would merely shift the public-good problem to funding the

rewards, presumably by taxation. Disincentives seem politically more feasible (I am not saying more desirable). For example, parents could be made to bear the full costs of health care for their children, and perhaps be made to contribute to some form of "genetic social security" to offset costs in future generations. Apart from issues of equity and differential ability to pay, there is a more fundamental problem of visiting the "sins" of parents on their children. Liberal democracies are based on the principle that rights and obligations belong to individuals, not to genetic lineages. Genome deterioration will itself be democratic, with most individuals carrying a share of the genetic load. Demanding sacrifices from a large proportion of the population is less feasible than imposing sacrifices on a small minority. For these reasons, I believe public-goods eugenics is neither practical nor desirable.

By contrast, private-good eugenics is driven by market mechanisms, although sometimes funded from a public purse. Private-good eugenics involves facilitating women, or couples, to have the children they want. It includes various forms of embryo selection, both before and after implantation, as well as the care that is taken in selecting attributes of sperm and ovum donors. The latter procedures seem to be on an ethical and logical continuum with normal processes of partner choice. I do not have any objections in principle to private-good eugenics, but question whether it would ever be effective at halting the accumulation of deleterious mutations.

Private-good eugenics shares the market with private-good dysgenics (Hamilton places much of modern medicine in the latter category). As one example, many infertile men who conceive by intracytoplasmic sperm injection have microdeletions of the Y chromosome, or carry cystic fibrosis mutations, which are transmitted to their offspring in Mendelian frequencies. In the case of Y-chromosome deletions, the deletion and consequent infertility will be transmitted to all sons. The couples involved usually accept this risk with the hope that technology will have improved by the time their sons reach reproductive age. One might debate the ethics of parents choosing risks for their unborn chil-

dren, but similar issues arise in nonassisted conceptions, in which case the ethical dilemma has been left to parents rather than social policy.

An evil of modern medicine to which Hamilton obsessively returns is the high rate of caesarean sections. He sees this as relaxing the action of natural selection on the width of the female pelvis, favoring narrower hips. His passage on the evolution of sexual dimorphism of the pelvis, and of the male aesthetic response, is a characteristic Hamiltonian juxtaposition of beauty and death: "Selection by this death in childbirth, without a shadow of doubt, has produced the present wide feminine hips: if you had not thought of this before I am sorry to shock you, but every time a man looks at that shape of the female torso that so attracts him, it has to be faced that he is looking at consequences of hundreds of thousands of adult women's deaths—in a sense a graveyard shimmers behind that subtle and, to us, so beautiful hourglass curve" (p 486). The evolutionary argument of this quotation is, I believe, basically sound, although it is embedded in a discussion that emphasizes mate choice—big heads desired by women and wide hips by men—rather than mother-offspring conflict.

But what does Hamilton suggest should be done to reverse this dysgenic trend? He writes: "Evolving back from a commitment to Caesareans will be difficult but not impossible and will need to be begun before matters have gone too far. It will involve, however, the very sorts of eugenics measures that are typically most strongly rejected. Caesareans would, of course, continue to be performed where necessary, but each would be a notifiable event entailing negative marks recorded in some government records with such marks being applied to both of the parents and also to the offspring. The marks would be used in state-organized counselling and reproductive disincentive schemes" (pp 503–504). He later makes a similar suggestion: "Mothers' lives obviously must be saved by Caesareans when necessary; but perhaps operations that are done in true necessity could be followed by an offer of a state reward for a pledge by the woman not to bear more children" (p 531).

These proposals appear neither desirable, practical, nor effective. Moreover, assisted

delivery appears a poor choice as an example of the dangers of relaxed selection. No evidence is presented that the incidence of dystocia has increased, and Hamilton refers to hundred and thousands of deaths in our evolutionary past. Obstructed delivery is not principally a problem due to recent deleterious mutations, although such mutations will undoubtedly make a contribution, but rather a problem of conflicting selective pressures on mothers and fetuses during human evolution. Babies determine when to be born, and the tightness of the birth passage possibly reflects the evolutionary brinksmanship of fetuses remaining in the safety of the womb until almost the last moment at which it is safe to emerge.

If we are to predict the effects of relaxed selection on the future of birth, we should consider all the selective forces that are relaxed. Here, Hamilton is strangely inconsistent. He argues that caesarean sections will favor narrowing of female hips because of the biomechanical advantages of a masculine pelvis. This seems to imply continued selection for these advantages. Nor does he consider that modern medicine is reducing selection against earlier deliveries, which seemingly would act to favor easier births. Given all these considerations, I do not know what to predict.

In the *Archiv für Rassen- und Gesellschaftsbiologie* (Archive for Racial and Social Biology) of 1912, Agnes Bluhm worried that medical assistance at delivery was allowing women to survive and reproduce who would otherwise have been unable to give birth. These practices, she feared, were contributing to an increased incidence of birth complications due to narrower birth passages (cited by Proctor 1988:18). After the Great War, German Jews "were accused of promoting hospital births (versus birthing by midwives) and Caesarean sections (versus natural childbirth)" (Proctor 1988:164) and the Nazi regime was successful in shifting assistance at birth from physicians to midwives (Proctor 1988:241–243). Thus, Hamilton's concerns about medicalized childbirth have historical precedents. I raise them, not to invoke the knee-jerk equation of sociobiology/eugenics with fascism that is a common response to all attempts to

apply evolutionary biology to modern human concerns, but rather the opposite. Playing the "Nazi card" is a rhetorical ploy that usually stifles further discussion, beyond the mouthing of pious platitudes and ad hominem invective. The historical record *is* important, but it would be an injustice to summarily dismiss the arguments of modern proponents of natural childbirth, or of breast-feeding (another Nazi priority), by simply accusing them of fascism. Their case should be judged on its merits. The same consideration should apply to the arguments of evolutionary biologists, and even to those of modern eugenicists.

On most complex subjects, a single person cannot come to a balanced position alone, without the open debate that helps to separate good from bad arguments. I think that many of Hamilton's ideas on eugenics are naïve and misguided, but I support his plea that this should be a question on which one could have a reasoned, nonacrimonious exchange of

views. The extent to which the human genome is deteriorating is an important question that should be squarely faced, rather than side-stepped.

On reading *The Evolution of Sex*, I found myself in the presence of a passionate and idiosyncratic mind. I regret that Hamilton will not be around to write commentaries for the projected Volume 3. Natural selection was central to his view of the world, and he clearly recognized that natural selection has a bright and a dark face. The bright face reflects all the beauties, and exquisite adaptations, of the living world. The dark face hides the selective culling of the less fit, in parasite-ridden lives that are often nasty, brutish, and short. In Hamilton's essentially tragic (far from Panglossian) vision, the bright face is the product of the dark face and is dependent for its continued existence on the dark face. Out of his love for the bright face he was prepared to embrace the dark.

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