

Hamilton Symposium

Introduction to William D. Hamilton Symposium

On 7 March 2000, William Donald Hamilton died in Oxford, England, from malaria contracted during a field expedition to the Congo. With his death, the field of evolutionary biology arguably lost its greatest practitioner since Charles Darwin. W. D. Hamilton made major contributions to many areas of evolutionary biology, but perhaps his greatest impact was on the discipline of behavioral ecology. The topics that he focused his energies upon include kin selection, reciprocity, sex-ratio selection, the evolution of senescence, alternative reproductive strategies, selfish gains of group living, haplodiploidy and the evolution of eusociality, parasite–host arms races, and the role of parasites in both mate choice and the evolution of sex. His contributions formed a foundation for the new field of sociobiology, and his theories provide the bases for a good deal of the theoretical and empirical work currently being done in behavioral ecology.

Given the intellectual contributions of the man and the magnitude of the void caused by his loss, the International Society for Behavioral Ecology decided to honor the life of William Hamilton in two tangible ways. The first was to hold a symposium in his honor at the Eighth International Behavioral Ecology Congress in Zurich, Switzerland, on 10 August 2000. The proceedings of the symposium are published in the pages that follow. The second is to sponsor a William D. Hamilton Lectureship to be presented at each future ISBE Congress. The society's executive council will biennially select a distinguished evolutionary behaviorist to present this lecture.

William Hamilton was, first and foremost, a passionate natural historian. He traveled throughout the world, but especially loved its tropical regions. He repeatedly stated that he obtained many of his research ideas from simple observations made in nature. Yet Hamilton was no ordinary natural historian. He had the knack of selecting research topics that had broad evolutionary implications. He sought out unanswered questions—evolutionary paradoxes—that were not readily explicable by current natural selection theory. As Richard D. Alexander so aptly expressed it, “Bill's originality of mind often turned the barely articulated ideas of distinguished predecessors—ideas overlooked or neglected by all the rest of us—into magnificent theoretical edifices affecting our view of all life” (*Natural History*, vol. 6, 2000, pp. 44–46).

Hamilton may have taken his ideas from nature, but he developed his hypotheses in the form of rigorous mathematical models. In an interview with Frans Roes, he said: “Often I use mathematics because I need to straighten out my own ideas. I have a somewhat illogical brain, and unless I put it through the mill of mathematics, I can continue to believe in the impossible for a long time” (*International Society of Human Ethology Newsletter*, vol. 12, 1997, pp. 3–7). The math helped to make his assumptions clear and his predictions more precise. This, in turn, enabled others not only to understand his innovative ideas but also to design better empirical tests of his theories.

For our symposium, we selected three of the theoretical edifices that owe much to William Hamilton: kin selection and social evolution, sexual selection and parasites, and parasites and the evolution of sex. We asked David Queller, Manfred

Milinski, and Paul Schmid-Hempel to summarize and comment on Hamilton's contributions to each area. We trust that readers will find the symposium papers to be valuable personalized synopses, not only of Hamilton's contributions, but also of current unresolved issues in each area.

It is too soon to measure the full magnitude of William Hamilton's impact on evolutionary biology, but it is safe to say that it will be immense. We can state with certainty that his ideas on inclusive fitness and reciprocity have revolutionized the ways in which we view social conflict and cooperation. The jury currently is more mixed on the relative importance of his thoughts concerning parasite–host arms races as a primary cause for the evolution of sexual reproduction. But there can be little doubt that succeeding generations of evolutionary biologists in general, and behavioral ecologists in particular, will continue to find fertile ground in the innovative ideas first suggested or formalized by Hamilton. He will be sorely missed. We hope that the symposium papers that follow will help readers to put some of Hamilton's contributions into perspective.

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W. D. Hamilton and the evolution of sociality

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Bill Hamilton was always at his best in small groups, and I would like to open and close my reflections with some thoughts generated by two small scientific meetings that Bill Hamilton attended. I was not present at the first meeting, in Tvarminne, Finland, but a photograph from the meeting made an impression on me. In the foreground stood Pekka Pamilo, the organizer of the meeting, with a rather worried expression on his face. In the background was Bill Hamilton, skating across the ice. Bill had brought his ice skates, intent on taking every advantage of this visit to the north. It turned out, however, that the ice was quite thin, so the organizers attempted to dissuade Bill. They made a general request that speakers at the meeting should please not attempt any ice skating, at least until after they had delivered their talks. Bill followed the letter of this request, but did not follow its spirit. After giving his talk, he donned his skates and set off.

This picture brought to mind all sorts of associations. How can one not remember J. B. S. Haldane's musings about being willing to rescue two drowning brothers, or eight cousins. I hope Pekka will forgive me if I try to imagine his thoughts about the possibility of Bill falling through the ice. “Well, I do not think I am related to him . . . On the other hand, everyone in Finland is more or less related! But then, he is not from Finland, is he? Still, we may not share many genes, but we do share a great many memes.”

The other thought that comes to my mind is one that has been noted frequently since Bill's recent death from malaria. Bill Hamilton was a risk taker, not just in his life, but also in his science. In his work, too, he sometimes skated on thin ice, traveling where others would not. E. O. Wilson once used exactly this metaphor to describe a certain kind of scientist who is always drawn to the dangerous or to the forbidden: "They are the taboo breakers who enjoy the whiff of grape-shot and the crackle of thin ice" (Wilson, 1978: 283). When Bill skated on thin ice in Finland, the results were satisfactory: the ice may have crackled but it did not give way. When he skated on thin scientific ice, the results were usually not just satisfactory, but glorious.

Bill Hamilton's most glorious ideas were kin selection and inclusive fitness. Talking about Hamilton's contributions to inclusive fitness is a bit like talking about Isaac Newton's contributions to dynamics or Charles Darwin's contributions to natural selection. He invented the idea, and he developed most of its important implications. There were some forerunners, as there always are in science. I think of Hamilton's contribution as a fusing of two traditions. First, there was population genetics. Hamilton didn't completely invent the idea of kin selection. The idea was foreshadowed by Haldane (1955), Fisher (1958), and Williams (Williams and Williams, 1957). However, none of them developed it in any detail, perhaps because they did not appreciate its general importance in nature. For that we can thank animal behaviorists, particularly those like Wynne-Edwards (1962) and Emerson (1960), who believed that cooperation was very common in nature. Bill neatly hybridized the two traditions. If cooperation and altruism were important in nature, then we needed an explanation that was consistent with population genetics, and so inclusive fitness was born.

Hamilton was well suited to make this match. Those acquainted with Hamilton only through his best-known papers may think of him as a theoretician and might conclude that he had the theoretician's superficial knowledge of the natural world. But in fact it was his mathematical skills that were hard won, while as a natural historian he was, well, a natural. You can see evidence of this in many of his papers, but it comes out particularly in his lesser known papers on insects under bark (Hamilton, 1978) and on fig wasps (Hamilton, 1979).

So was Hamilton's contribution a simple merging of the insights of an ethologist and a population geneticist? No, it wasn't that simple, for several reasons. First, there was a lot of thin ice between these areas, and skating from one to the other was not encouraged in the early 1960s. Geneticists were leery of anything that smacked of eugenics. That included any application of population genetics to behavior. It included most of all applications to understanding social behavior, something we have always been a little touchy about. If nature was nasty, rude, or bawdy, better not to know about it, let alone let the public know. Let me illustrate the idea in an unconventional way, with a bit of verse that I call "Family Values":

Would I jump in a lake
To save my drowning cousin?
It's not a risk I'd take
For him plus half a dozen.
But if you raise the stake
And make the prize my brother?
Now that's a deal I'll make. . .
If you'll just toss in another.

If this poem, and the Haldane quip it is based upon, elicit chuckles, it is in large part because they treat a topic that is uncomfortable for us. Most humor is built on discomfort of one form or another. In this case, we recognize that we make unconscious judgments akin to these, with awkward balances

of self-interest and family interest, but we don't like to see ourselves as calculating self-servers. Now throw in a good dash of genetics, and the mixture becomes truly taboo. Perhaps that's why Haldane and others did not pursue the topic.

Bill's recollections of his graduate career (Hamilton, 1996) describe the price that he paid for his desire to be where the ice is thin. He had difficulty finding advisors. He had no desk. He had no invitations to talk about his work. It was not even clear that his thesis work, which would produce some of the most heavily cited papers in evolutionary biology (Hamilton, 1964a,b), would be acceptable for a Ph.D. For someone who was not socially outgoing in the first place, the effect of this isolation was severe. He feared that he might be a crank; why else would all these manifestly smart people fail to see the interest in what he was doing? He took to working in train stations and public parks simply to have some minimal level of human interaction.

Mary Jane West Eberhard made a telling point in her talk about Bill at a recent meeting (West-Eberhard, 2000). She noted that Bill's life serves as a counter-example to those critics who said that sociobiological knowledge was dangerous. He was proof that one can see all that is grim in the depths of our nature and still live a life of decency and kindness. Bill would have been uncomfortable with hagiography. His writings allude to a knowledge of the dark side of human nature, obvious to him through introspection, so clearly his thoughts were not always saintly. But whatever dark thoughts swirled in his mind, on the surface—and this is where it counts—he was basically a gentle man. Despite his highly critical mind, I never heard him criticize anyone in anything but the kindest, most self-effacing manner. He did not judge people by credentials and had time for people that others might consider to be amateurs or even crackpots, George Price being a notable example. And while he no doubt appreciated the recognition he eventually received, particularly given his lonely days as a graduate student, he did not seem to crave recognition excessively. Dawkins reported one example where Bill gave credit to someone else for an idea that was really his own and had to be confronted with the evidence from his own paper (Dawkins, 2000). Then, as Dawkins described it with an adverbial tour de force, Bill "eeyorishly" admitted that, yes, he'd had the idea, but the other fellow had put it much better.

I can give another small illustration from my own experience. In 1985 I published a paper using Price's rule to obtain a new expression for inclusive fitness (Queller, 1985). Alan Grafen then chided me (Grafen, 1985), quite rightly, for having neglected to cite Hamilton's paper using Price's rule (Hamilton, 1970). My only excuse is that Bill had read my paper in manuscript without ever pointing out the omission, which he must have noticed. For that matter, I had learned about Price's rule directly from Bill in seminars at the University of Michigan. If I remembered Price's rule well and forgot Bill's uses of it, it is partly because of the selfless way that Bill taught the subject.

There is another reason that Hamilton's contribution cannot be viewed as a simple merging of naturalist and theoretical traditions. He did not just come up with any old theoretical model. For example, one could model the evolution of altruism for some particular limited set of conditions (George and Doris Williams had already done this; Williams and Williams, 1957), but then one has to wonder how general the conclusions are. And it is also possible, as other modelers later showed, to add so many mathematical bells and whistles that we lose track of the general theme. In contrast, what Hamilton came up with was a theory that was not only basically true, but also beautiful and elegant. I'm not speaking of the mathematical derivation in his 1964 paper, which was actually rather gruesome. I'm speaking of the result, what has come to be

known as Hamilton's rule. It is so simple that even a non-mathematical mind can easily understand it and wield it, and so general that it can often be applied to new social evolution problems without any fresh mathematical modeling.

How was this simple elegance achieved? I think there are two main reasons. First, Hamilton was willing to make assumptions that allowed the result to be simple without seriously compromising the biology. For example, he assumed that selection would be weak. Stronger selection has the effect of distorting the relatednesses away from their familiar values, and it makes them dependent on genetic details such as dominance. Hamilton's assumption was justified because weak selection is presumably common. For that matter, it's probably not so bad an approximation for stronger selection. A little distortion of correlation coefficients doesn't matter too much to someone interested in the real world, where estimates of parameters are typically only good to about one significant digit anyway.

The second reason inclusive fitness is so useful is its inversion of fitness calculation methods. Instead of grouping together all effects of others on x 's fitness, it calculated all the inclusive effects of x on others' fitnesses. This actor-centered approach is what makes the method so easy to apply. In Hamilton's own words: "The social behaviour of a species evolves in such a way that in each distinct behaviour-evoking situation the individual will seem to value his neighbors' fitness against his own according to the coefficients of relationship appropriate to the situation" (Hamilton, 1964b: 19).

It has become clear in recent years that the same behaviors can also often be understood as a form of group selection—the old group selection of Wynne-Edwards, but nevertheless a method that involves partitioning of selection into within-group and between-group components (see Sober and Wilson, 1998). But the fact remains that almost no one uses these methods much to think about and solve interesting problems. Each of the two methods can dissect social evolution into component parts, but where inclusive fitness divides nature neatly at the joints, other methods seem to hack clumsily through the long bones.

Inclusive fitness and kin selection were important on several levels. First, of course, they provided an explanation for the evolution of altruism. We still don't know whether Hamilton's famous haplodiploid hypothesis, based on three-quarters relatedness (Hamilton, 1964b, 1972), explains the origin of eusociality. But it seems certain that the answer does lie within his more general framework of relatedness, costs, and benefits. For the study of social insects, another result of inclusive thinking was perhaps even more interesting. The theory did not simply explain the altruism that we already knew about. It also predicted something we did not know much about: conflicts within colonies. Because inclusive fitness interests often differ even among close relatives (Hamilton, 1972), there can be conflicts over who should be queen, conflicts over who should lay the male-destined eggs, and conflicts over sex ratios (reviewed in Queller and Strassmann, 1998). Studies in these areas have amply satisfied the requirement that a good theory should not just explain what is known, but also make novel and successful predictions.

I think a parallel phenomenon occurs in the world beyond social insects. Perhaps even more important than the explanation of altruism itself was the general validation given to selfish gene models. If selfish genes are to be of any value in explaining the evolution of social behavior, they simply must be able to explain the cases where the behavior is not phenotypically selfish. Otherwise the method must be counted as a failure. So kin-selected explanations of altruistic behavior gave life to selfish gene explanation in areas where kinship was not paramount. Hamilton's own work clearly shows this. He didn't stop with altruism. He made pioneering contributions in many other areas. The accompanying pieces in this issue describe his contributions to the study of sexual selection and parasites, but

his work also included important contributions to senescence theory (Hamilton, 1966), sex ratios (Hamilton, 1967), selfish herds (Hamilton, 1971), dispersal (Hamilton and May, 1977), tit-for-tat cooperation (Axelrod and Hamilton, 1981), and within-individual conflict (Hamilton, 1967). This truly formidable list of accomplishments, and the whole selfish gene tradition of which it is a part, emerged from a confidence based on Hamilton's success in solving the potentially fatal problem of altruism.

Finally, in recent years it has become increasingly clear that a theory of altruism and cooperation is important for a much grander reason than solving the annoying puzzle of the social insects. It is also needed to explain a much more pervasive kind of cooperation; the evolution of the organism itself (Maynard Smith and Szathmáry, 1995) Why do cells cooperate in a body? Why do formerly independent bacteria evolve into organelles? How did replicators get together in the first place? Organisms, though they compete selfishly with each other, are themselves cooperative entities. Cooperation is therefore fundamental to all of life.

I began with a small scientific meeting in Finland. Let me close with another one, in Castiglione, Italy. The highest scientific compliment I have ever received was one that Bill delivered there, actually to my wife and collaborator Joan Strassmann. Bill had, many years previously, done field work in Brazil on the troubling question of how sociality could be maintained in wasps with many queens. We had recently helped show, with molecular tools that had not been available to Bill, how relatedness was kept at levels consistent with kin selection (Queller et al., 1988, 1993; West Eberhard, 1978). What he said to Joan was "Now I will have to think up a different question to ask St. Peter when I meet him." Of course, this was ridiculously inflated praise, a reflection of Bill's generosity rather than his acumen. He was no doubt signaling this exaggeration by his use of the religious reference, since Bill did not seem to be a conventionally religious man. Instead, he is some one who saw his afterlife more in terms of burying beetles (Hamilton, 2000) than in terms of meeting St. Peter.

Still, I'd like to run with idea for just a moment. In the sad days after Bill died, the thought of him interrogating St. Peter gave me a certain amount of solace, and perhaps even pleasure. It's not that I can imagine what Bill's question was. Nor was it the thought of him receiving a satisfactory answer. Instead, what appeals to me is the impact on old St. Peter. I imagine him at first flummoxed because he couldn't answer the question, then annoyed because he had never thought of it himself, and finally intrigued by the implications. I imagine him spending his free moments over the next few centuries thinking about it, making new observations on the teeming life below, scribbling some population genetic equations in the margins of his heavenly register, and perhaps running some simulations on God's fastest supercomputer. Perhaps I overestimate St. Peter's curiosity, but Bill's questions have always had that kind of effect. That they will long continue to do so is his legacy to us.

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Bill Hamilton, sexual selection, and parasites

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Darwin (1871) first introduced the idea that males with elaborate ornaments have a net benefit because they are preferred as mates. Evidence for such preferences is now abundant (e.g.,

Andersson, 1994). A more troublesome problem has been to understand the evolution of female preferences for handicapped males. Until the early 1980s, there were mainly two theories: (1) Fisher's (1930) runaway process, which predicts that the male character and the female preference could, through genetic correlation in the offspring, advance together with ever-increasing speed. This was "easy to see," as Fisher wrote, and therefore he did not provide a formal proof. (2) Zahavi's (1975) handicap principle: a female prefers a male with a handicapping trait because this male must have high viability (i.e. good genes), to be able to survive with the handicap. Both hypotheses appeared to resist any theoretical proof that was based on conventional population genetics. For example, the problem with all good genes models is that if females prefer to mate with the males that have the good genes for high viability, then these genes become quickly fixed in the population and nothing will be revealed by the handicap except the handicap itself. So females should stop preferring handicapped males.

In the early 1980s both hypotheses suddenly received support. Lande (1981) and Kirkpatrick (1982) showed with elaborate genetic models that Fisher's runaway process can work [actually O'Donald (1980) had paved the way]. But it was Bill Hamilton and Marlene Zuk (1982; see also Hamilton, 1982) who proposed a new good genes hypothesis that predicted substantial additive heritability for viability genes ad infinitum. Hamilton and Zuk (1982) suggested that genes for resistance might have important effects on fitness and always remain heritable. The interaction between host and parasite is unusual because it produces cycles of coadaptation. These cycles can ensure a continual source of fitness variation in genotypes.

Imagine a host and a parasite population in which individual hosts differ in their resistance to different genotypes of the parasite. Some hosts are resistant to parasite A, some to parasite B. If a female chooses a male that is resistant to parasite A, when this is the more common parasite genotype, she is obviously getting a selective advantage because her offspring will be more likely to be resistant to the common disease. So the next host generation may be more resistant to parasite A. Now parasite B can successfully infect the host population, and females should prefer males that are resistant to B. The process will be cyclical because new resistant genotypes that arise in the host species will provoke the evolution of new parasite genotypes; these in turn will provoke the evolution of new host genotypes; and so on ad infinitum. This provides a plausible reason that a population may have substantial additive heritability for disease resistance. Then a male who is unmistakably outstanding in health and vigor offers females that mate with him an inherited healthiness in their offspring that is well above average (Hamilton and Zuk, 1982).

How do females detect the males that are resistant to the currently predominating parasite? Hamilton and Zuk's (1982) clever insight was that the method a female uses should have much in common with those of a physician checking eligibility for life insurance. The choosing animal should unclot the subject, weigh, listen, observe vital capacity, and take blood, urine, and fecal samples. Instead, if a male can present an elaborate bright plumage, produce a song that is energetically costly, and display with an exhausting athletic behavior, it likely has the currently needed genes for resistance because it so demonstrates that it is healthy.

In later generations, other resistance genes against other parasites need to be detected. Again, females can use the same preference for elaborate adornment to detect those males that are resistant to the new parasite. Hamilton and Zuk (1982) predicted for comparisons among species that species that show strongly developed epigamic characters should be subject to a wider variety of parasites. In species where disease