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## 'From Man to Bacteria': W.D. Hamilton, the theory of inclusive fitness, and the post-war social order

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### ABSTRACT

W.D. Hamilton's theory of inclusive fitness aimed to define the evolved limits of altruism with mathematical precision. Although it was meant to apply universally, it has been almost irretrievably entwined with the particular case of social insects that featured in his famous 1964 papers. The assumption that social insects were central to Hamilton's early work contradicts material in his rich personal archive. In fact, careful study of Hamilton's notes, letters, diaries, and early essays indicates the extent to which he had humans in mind when he decided altruism was a topic worthy of biological inquiry. For this reason, this article reconsiders the role of extra-scientific factors in Hamilton's early theorizing. In doing so, it offers an alternative perspective as to why Hamilton saw self-sacrifice to be an important subject. Although the traditional narrative prioritizes his distaste for benefit-of-the-species explanations as a motivating factor behind his foundational work, I argue that greater attention ought to be given to Hamilton's hope that science could be used to address social ills. By reconsidering the meaning Hamilton intended inclusive fitness to have, we see that while he was no political ideologue, the socio-political relevance of his theory was nevertheless integral to its development.

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First summarized in 1963 and more fully articulated in 1964, William Donald Hamilton's theory of inclusive fitness used a mathematical equation to universally explain the evolution of social behaviours. Viewing such behaviour from the level of the gene, Hamilton concluded that even characters that appeared self-sacrificing could be understood to be ultimately selfish. Altruism, as he saw it, was not an action performed randomly; it tended to benefit relatives. For this reason, Hamilton concluded that the existence of altruism was logical inasmuch as it represented a survival strategy that did not discount but rather intensified Darwin's emphasis on competition: by benefiting relatives, altruistic behaviours allowed shared genes to be passed to future generations, thus maximizing the effect of an individual's genetic contribution not only directly but also indirectly.

Owing primarily to the success of inclusive fitness, Bill Hamilton's name is well established within biology departments. When students are taught Hamilton's theory of inclusive fitness, they are also privy to a common narrative surrounding his life and work that traditionally depicts a young, ideologically untouched student with telltale signs of genius. While this story took root within Hamilton's lifetime, it appropriated a new potency after his tragic death in 2000. Immediately, scientists heralded him as evolutionary biology's "greatest practitioner since Charles Darwin" (Emlen, 2001). What is more, prominent biologists such as Alan Grafen (2005, 2004) gave Hamilton a "prophet-like status" and claimed that when the history of biology is brought up to date, Hamilton will be recognized among the three greatest evolutionary theorists, next to Charles Darwin and R.A. Fisher. In addition, David Hughes, who was once a student of Hamilton's, characterized his teacher according to the traditional conception of the scientific genius as an outsider, pitted against the backward beliefs of his society. In this way, Hughes (2002) imagined Hamilton to have "cut a lonely, paradigm-shifting path through science that others would follow". In positioning his work as extraordinary, these articulations rely on a

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central assumption that Hamilton's major contributions to science were derived from observations of nature and confirmed by the rigour of mathematics.

The above assumption has pervaded depictions of Hamilton's life and work to this point. Although Marek Kohn (2004, p. 23–24) recognized that the Darwinism of both Hamilton and Fisher was deeply impacted by their "right-wing" views on human heredity, more recent narratives, especially those penned by scientists, have overshadowed Kohn's work. In 2006, for example, biologist Lee Alan Dugatkin went as far as to claim that, unlike previous theorizers, "Hamilton appears to have [had] no philosophical, political, or religious leanings that influenced his opinion about whether natural selection worked via kinship to produce altruism". Negating the impact that society could have exercised on Hamilton, scientists have thus seen him to have been "more at home with insects than people".<sup>3</sup> Following this line, we are told that it was only owing to Hamilton's acute understanding of social insects that he could confidently conclude that his theory "was real" (Dugatkin, 2006, pp. x, 106, 94). Such images of objectivity have caused many to believe that however controversial sociobiology was from 1975 onwards, its intellectual foundations were essentially devoid of ideological preconceptions.

In 2013, sociologist Ullica Segerstrale, who had previously written extensively on the sociobiology debates (Segerstrale, 2000), attempted to underline Hamilton's place in history as 'Nature's Oracle'. Although she did not discount Hamilton's interest in human evolution, especially as evidenced through his intense study of R.A. Fisher's account of the rise and fall of civilizations in *The Genetical Theory of Natural Selection* (1930) (Segerstrale, 2013, p. 46), she stopped short of declaring that man played a major role in Hamilton's early theorizing. Key to her position, and the established narrative surrounding Hamilton's life more generally, are two points: first that Hamilton, through careful study of Fisher's book, was able to reject the idea that traits harmful to individuals could evolve so long as they in some way lessened the chance of extinction at the species level and second that it was his precocious understanding of Fisher's mathematical defence of natural selection that inspired him to reframe altruistic behaviour in terms of individual benefit via shared genes.<sup>4</sup>

Still, the view that prevalent 'group selection' thinking within biology had caused Hamilton's dissatisfaction with his undergraduate lecturers at Cambridge remains unsubstantiated. The evidence that Hamilton (1996, pp. 21–22) and others (Segerstrale, 2013, p. 45) have previously supplied is a declaration by Cambridge professor of entomology Sir Vincent Wigglesworth (1964), in which he claimed that the lives of insects are "devoted to the survival of the species whose representatives they are". This passage in particular, however, could not have provoked Hamilton as an undergraduate, as it was published in 1964, four years after Hamilton had left Cambridge. In fact, the only complaint Hamilton made explicit while attending the Cambridge lectures on evolution was the fact that C.O. Carter's course was "a trifle slow going" since "after two lectures he is still surveying the evidence that evolution & not creation is responsible for the origin of species".<sup>5</sup> The idea that

Hamilton's Cambridge lecturers were all "unreflective group selectionist[s]", as Segerstrale has maintained (2013, p. 45), is also complicated by the fact that while Hamilton was at Cambridge, there remained an active research group that was not only personally connected to Fisher but also dedicated to furthering his fundamental theorem of natural selection. This group included three of Fisher's students, Walter Bodmer, A.W.F. Edwards, and Peter Parsons, each of whom, in turn, lectured to Hamilton.

In light of these difficulties with the current narrative, it may be worth working from a new perspective in examining why Hamilton was motivated to take up the topic of altruism for biological study. In this paper, I wish to consider whether it may have been the lack of serious weight given to Fisher's chapters on man that was a major point of contention between Hamilton and his lecturers in these early years. When, in 1965, Hamilton privately discussed the relevance of his theory to human evolution and the fact that "the hope of arriving at some new understanding of human social evolution was a major incentive in this work" on inclusive fitness, he also revealed that "Most of my thought in this field is inspired by that amazing book of Fisher's", which he lamented had been "rather too severely disregarded just because he proved wrong in his interpretation of contemporary population trends, and therefore also in certain parts of the theory he based on this interpretation". Ultimately, Hamilton believed that it would "have to be recognised eventually that a lot of the ideas in this section of the book are basically correct".<sup>6</sup>

What is more, Hamilton's focus on Fisher's understanding of human evolution and the extent to which it placed him at odds with those around him is substantiated by the fact that his strong views regarding the meaning of evolution for human society were something he often espoused, even when family, friends, and colleagues met them with deep-seated disapproval. In contrast, group selection was not something Hamilton criticized at length until 1965<sup>7</sup>; well after his theory of inclusive fitness was published and his efforts turned towards defending his ideas against competing views. It is thus worth contemplating whether it was the meaning of inclusive fitness, especially inasmuch as it would contribute to the advancement of an evolutionary understanding of man, more than it was its method—a gene's eye view of natural selection—that Hamilton so ardently supported while a student, so much so that it placed him at odds with his supervisors. In fact, what he resented most about the guidance he had been given up to 1963 was that his professors denied that inclusive fitness had "much relevance to sociology".<sup>8</sup> He lamented that John Hajnal at the London School of Economics, in particular, "was as discouraging as any-one to my Fisherian views". Hajnal believed inclusive fitness had "no relevance to biology (leave alone human sociability) at all".<sup>9</sup>

To further explore Hamilton's desire to produce a theory that had meaning for human societies, we must address the assumed relationship between the theory of inclusive fitness and the particular case of social insects that is commonplace in histories of biology.<sup>10</sup> That Hamilton's theory was near completion before he understood the importance of haplodiploids remains an under-

<sup>3</sup> For example, Grafen (2005, p. 424) found Hamilton's leaving a formal dinner during his National Service to be "characteristic [of] Bill who found a formal social event tiresome, and fled to huddle under the bushes for the night, close to the natural world he loved".

<sup>4</sup> This narrative is reiterated in Grafen (2005), although even Grafen admitted that beyond the fundamental theorem Hamilton was "enthused" by Fisher's account of human evolution.

<sup>5</sup> Hamilton, W.D. to B. Hamilton (21 November 1957), W.D. Hamilton archive, British Library, Z1X42/1/16. 200 boxes of articles belonging to Hamilton were given to the British Library upon his death in 2000, and soon after, they began to be sorted, catalogued, and conserved (Summers & Leighton John (2001)). Although Dugatkin and Segerstrale accessed some of Hamilton's papers when preparing their books, the archive was not made fully accessible until April 2013.

<sup>6</sup> Hamilton, W.D. to Pfeiffer (19 February 1965), Z1X89/1/1.

<sup>7</sup> Hamilton, W.D. (5 November 1965), 'Why Society is Not an Organism', Z1X90/1/18.

<sup>8</sup> Hamilton, W.D. to B. Hamilton and A. Hamilton [n.d., c. November 1963], Z1X42/1/13.

<sup>9</sup> Hamilton, W.D. to B. Hamilton and A. Hamilton (3 September 1963), Z1X42/1/13.

<sup>10</sup> See, for example, see Bowler, P.J. (1989), p. 329; Ruse, M. (1996), p. 458; Brown, A. (1999), p. 83; Ruse, M. (2006), p. 48.

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