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Pillars of Biology: ‘The Genetical Evolution of Social Behaviour, I and II’

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1. Introduction

No celebration of landmark contributions to the *Journal of Theoretical Biology* is complete without a discussion of two papers by W. D. Hamilton that appear in Volume 7 (Hamilton, 1964a,b). Of all papers published in the journal to-date, these two are the most highly cited according to both Scopus and Web of Science databases. They have, undoubtedly, transformed the way biologists of all stripes approach their own corner of the discipline.

2. Hamilton’s Accomplishment

With his papers, Hamilton aimed to fill a gap left by the Neo-Darwinist pioneers who combined ideas about natural selection from *The Origin* with revelations brought about by the re-discovery of Mendel’s work on genetics (Hamilton, 1996). The Neo-Darwinists had neglected problematic social behaviours, like altruism, in their work. The significance of the omission was underscored by the popularity of dubious ‘survival of the species’ explanations for the advantage of these puzzling traits (e.g. Wynne-Edwards, 1963). By correctly predicting the change in the frequency of an allele whose expression altered social behaviour, Hamilton (1964a) achieved his aim and laid the genetical groundwork for future discussions of social behaviour and its evolution.

Hamilton expended considerable effort detailing how his theoretical insights might change the way we understand biology in a broader sense. His efforts were so considerable that he was asked to present them separately in a second paper (namely, Hamilton, 1964b) that served as companion to the first, more technical one. Hamilton applied his theoretical approach in the companion work

to to explain the evolution of warning colouration, mutual grooming, and nest parasitism. He also famously used his approach to suggest that haplodiploidy shapes the social tendencies of the Hymenoptera, though this particular idea remains rather contentious.

The significance of Hamilton's contribution goes well beyond connecting population genetics to the evolution of social traits or exposing the evolutionary accounting that underlies sociality in bees and ants. What Hamilton's idea really gives us is a way to make predictions about the evolution of behaviour by reasoning from analogy.

As many readers will know, Hamilton's theoretical insight is epitomized by a mathematical inequality (often called, 'Hamilton's rule') that appeared in the second of his two papers in Volume 7 (Hamilton, 1964b, but see Hamilton, 1963). The inequality tells us that an allele, whose expression reduces the fitness of its carrier by a small amount c and increases that of its carrier's neighbour by a small amount b , will rise in frequency under the action of selection whenever

$$-c + br > 0, \tag{1}$$

where r is the genetic relatedness between carrier and neighbour. As one might expect, when Eq (1) is reversed, the frequency of the allele will decrease over time, and when it is zero allele frequencies will be at equilibrium. The latter point is important, because $-c + br = 0$ is part of a suite of conditions that implies the primitive of $-c + br$ is maximized when selection on social behaviour reaches an adaptive peak. The primitive here is what (Hamilton, 1964a) called 'inclusive fitness.'

Unlike allele frequency, inclusive fitness is a property we can ascribe to an individual. Therefore, we can view adaptive social behaviour as an individual's solution to the goal of maximizing its inclusive fitness (West and Gardner, 2013). In this way, inclusive fitness gives purpose to social behaviour. It allows us to leave population genetics behind and generate predictions by thinking of individuals as agents intent on climbing a hill on an inclusive-fitness landscape. What's more, by unlocking this hill-climbing analogy, inclusive fitness captures our imagination and allow us to bring our creativity to bear on relatively complicated problems of evolution. It is hardly surprising, then, that inclusive-fitness-thinking has improved our understanding of traits that are not obviously connected to altruism. These traits include (but are not limited to) pathogen virulence, natal dispersal, sex allocation, spite, parental investment, and traits linked to various genetic conditions (Haig,

1997; Haig and Wharton, 2003; West et al., 2007; Abbot et al., 2011).

3. Key Developments Since 1964

Inclusive-fitness theory has been developed in at least three important ways since 1964. The first key development came on the back of the covariance approach to population genetics presented by Price (1970). The new covariance approach allowed Hamilton to re-formulate conditions like (1) with greater clarity (see Hamilton, 1970). This approach also connected Hamilton's inclusive fitness to the hierarchical nature of selection (Price, 1972), and resolved early confusion over the definition of genetic relatedness (Grafen, 1985). More recently, re-formulations of the covariance approach have aligned inclusive-fitness theory with discourse in mathematical population genetics by establishing that statements about inclusive fitness match ones about the fixation probability of an allele (Rousset and Billiard, 2000; Rousset, 2003; Wild, 2011).

The second key development appeared in Hamilton's own detailed look at social insects, published several years after his original ideas (Hamilton, 1972). The focus on social insects led Hamilton to combine relatedness coefficients, featured in the 1964 papers, and Fisher's reproductive value (Fisher, 1930) into a single 'life-for-life' coefficient. Life-for-life coefficients were instrumental in building a more complete understanding of social behaviour in haplodiploid Hymenoptera. They also opened the door to applications of inclusive-fitness theory to the study of sociality in populations with complicated demographic structure (Taylor, 1990).

A third development was contributed by Taylor and Frank (1996). These authors outlined a way of creating inclusive-fitness models for general ecological scenarios. Their 'direct-fitness' methodology gave users the power to discover analogues to Eq (1) using elementary calculus, as is done routinely in evolutionary game theory (e.g., Abrams et al., 1993). The systematic nature of the direct-fitness methodology allowed a wider range of researchers to provide their input on issues related to social behaviour and its evolution. While inclusivity is certainly a win, the direct-fitness method is not perfect. In particular, the method focuses on individuals affected by the actions of others (recipients) rather than on actors themselves. Thus, the method distracts from Hamilton's main insight, namely that individuals perform a particular behaviour because they value those affected by the behaviour itself. Misplaced focus might seem like a technicality, but the step-by-step nature of Taylor and Frank's approach gives the impression that their recipient-centred

view is more fundamental than the actor-centred formulation presented by Hamilton (Fromhage and Jennions, 2019). The broader implication here is that inclusive fitness exists only because it rests on a foundation of something basic, which is not actor-centred at all. I suspect future developments in inclusive-fitness thinking will show that Hamilton's actor-centred view can be applied as systematically as the recipient-centred one—that its application is justified for reasons other than the direct-fitness recipes.

4. Summary

Taken together, Hamilton's papers (Hamilton, 1964a,b) are an exemplary contribution to the *Journal of Theoretical Biology*. Hamilton's inclusive notion of fitness offered (and continues to offer) more than a gene's-eye-view of social behaviour. It also gave us a sociobiological shorthand that, in turn, transformed the way we understand nature. Though inclusive-fitness theory has been developed extensively, more work is needed. Future theoretical priorities include the creation of systematic, actor-centred methods for building inclusive-fitness models.

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