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Introduction

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One contribution of 12 to the Special Feature '50 Years on: the legacy of William Donald Hamilton' organized by Joan Herbers and Neil Tsutsui.

Evolutionary biology

50 Years on: the legacy of William Donald Hamilton

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W. D. Hamilton was one of the twentieth century's intellectual giants, and with this Special Feature we note the 50th anniversary of his seminal contributions [1,2] that established inclusive fitness as a central element of Darwinian evolution. The authors contributing to this Special Feature present work that traces in some way to Hamilton's oeuvre; looking back further, Costa's contribution [3] links Hamilton's work to Darwin's and shows how he not only extended Darwin's concept of natural selection but also provided the framework within which it could ramify. The 1963–1964 papers that we celebrate here provide an elegant solution to a nagging problem, the evolution of altruistic behaviour. Darwin himself had worried about how to explain traits that benefitted others at the expense of the bearer. Costa describes how the next century of thought provided a few genetic propositions for altruistic evolution, but became dominated by misguided arguments invoking group selection. Focusing exclusively on genetic mechanisms, Hamilton developed a new algebra that incorporated and formalized suggestions in the literature. A testimony to his genius is that he worked virtually in isolation, unable to convince others of his work's import [4]. Furthermore, reaction to his first papers was somewhat tepid until E. O. Wilson championed Hamilton's formulation, especially with reference to the evolution of sterile castes in hymenopteran insects [4,5]. Further attention from Williams in his influential book [6] sparked widespread appreciation, positioning Hamilton's work as a major advance.

The catalogue of problems Hamilton treated with his gene's-eye view includes the evolution of social behaviour, sexual selection, sex ratio evolution, evolution of sex, levels of selection theory and evolution of ageing. His contributions are noteworthy in many ways; not least, Hamilton was formidable both as a mathematical biologist and as a naturalist. Indeed, he credited his ability to formulate theories about the world to his fascination with natural history, which started in childhood [4].

We typically judge scientific theory with two yardsticks. The first measure is whether a theory represents a reasonable description of the world: are its assumptions valid? Does it include the most important variables? Does the mathematical structure match the biological reality it seeks to understand? Are the results reasonable within our current knowledge? In addition to meeting those criteria, theories must strike an appropriate balance among three characteristics. Levins [7] described how biological theories can have at most two of the three attributes of reality, precision and generality. Theory that reflects reality and is precise cannot be general as well; theory that reflects reality and is general cannot be precise; theories that are general and precise are rarely realistic. Hamilton excelled in producing mathematical constructions of the world that solved long-standing evolutionary problems, and also struck a balance among Levins' three axes.

The second yardstick by which we measure theories is their fertility. Do they inspire additional research? Do they open up new fields of endeavour? One easy measure of any work's fertility is its citation record. Papers cited decades after their appearance clearly have left a long legacy. By that reckoning, Hamilton is certainly an intellectual patriarch; his last paper (posthumous) was published

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in 2003, and the 1964 papers continue to be cited by authors today. Hamilton's publications number fewer than 60, but his h-index is nearly the same as the number of his papers (the h-index is the *N* of papers that have been cited *N* times). Perhaps the most compelling evidence of his influence is the compendium of his papers in three volumes, books still in print today [8–10].

Our Special Feature focuses on this second yardstick of intellectual fertility, and brings together authors whose work was inspired by Hamilton's thinking. The papers traverse a broad scale of current topics in evolutionary biology and represent but a fraction of Hamilton's intellectual legacy. The seminal 1964 papers on inclusive fitness have been particularly influential and fruitful. In those papers, Hamilton's formulation of inclusive fitness showed that Darwinian genetic evolution was but a special case of a broader framework. His theory starts with survival and reproduction, the focus of Darwinian theory, and adds a component derived from the fitness of relatives. By formalizing how additional contributions from the effects of relatives on the individual's fitness affect the long-term fitness of a focal individual, Hamilton was able to solve long-difficult questions. In particular, inclusive fitness reasoning provided a mechanism to explain the origin and spread of altruism, a central problem in evolutionary biology. Indeed, his famous equation, now known as Hamilton's rule, is prominently featured in every evolution textbook. This equation sets a fundamental condition for the evolution of traits that disadvantage the bearer while benefiting a relative: ($r > c/b$), where r is the proportion of alleles shared between interactants, c is the cost in fitness to the bearer of expressing the trait, and b is the fitness advantage gained by the relative. We still know very little about what kinds of genes might underlie altruistic behaviour, and Thompson *et al*.'s [11] contribution in this Special Feature provides guidelines for that quest.

Hamlton's development of the fundamental concept, that individual organisms share genes with relatives and thus the gene's ability to propagate depends in part on the success of those relatives, opened up entirely new ways of thinking about the natural world. For example, social behaviour had to be examined with reference to kin structure, and the possibility of selective pressures to recognize kin gave rise to a new field of kin recognition. In this Special Feature, Tsutsui [12] shows how the advent of genomic and proteomic techniques has provided insight to this phenomenon, while Queller & Strassmann [13] point out that incomplete knowledge about kinship can in fact promote cooperation.

Although Hamilton's original exposition gave insight to the evolution of cooperation, authors quickly extended inclusive fitness thinking to study the evolution of conflict within social groups as well. Indeed, studies of conflict that arose from Hamiltonian thinking have tied kinship to sex ratio theory, sexual selection and parental investment, among others. Most importantly, analysis of inclusive-fitness-driven conflict furthered the development of multilevel selection theory. In this Special Feature, conflict is explored by Haig [14], Hall *et al*. [15] and Wenseleers *et al*. [16], with special emphasis on genic-level conflict.

Fifty years on, the literature inspired by Hamilton's work shows important biases. First, his emphasis on genetic relatedness caused the field to focus heavily on the relatedness component r and consigned the terms b (benefit) and c (cost) to relative obscurity. A cottage industry arose with methodologies to estimate r, development of markers that are useful to estimate r and analysis of how r varied among family members, across populations, between species, etc. Yet, relatively little progress has been made on estimating the costs and benefits of altruistic behaviour. We recognize that the components b and c are equally, if not more, important for making predictions about evolutionary trajectories via inclusive fitness, but they are substantially harder to measure: relatedness is easily calculated from genetic data, whereas costs and benefits can only be measured from laborious and hard-won field data, and surely are context-specific. Current research is attempting to redress the balance for a fuller understanding of how all components of Hamilton's rule work together to direct evolutionary change. In this Special Feature, Tsuji [17] examines this problem, and then ties relatedness structure to broader ecological questions of community structure.

Second, the literature shows a strong taxonomic bias, also evident in our Special Feature. Many of our authors focus on the haplodiploid Hymenoptera, for which Hamilton's theory seemed especially apt. Indeed, haplodiploidy was initially considered the primary mover of altruism for the Hymenoptera; while that stance has become tempered, social insect studies have certainly explored furthest the ramifications of Hamilton's rule. Thus, we welcome the contribution from Kamel & Grosberg [18], who describe numerous frontiers for future work on altruistic evolution in marine ecosystems.

The very success of Hamilton's inclusive fitness construct also generated ideas that now appear to be blind alleys. The success of kin recognition studies suggested that helping behaviour should be biased towards relatives. Thus, considerable effort was expended to study the possible existence and mechanisms of such nepotistic behaviour. Despite some successes, researchers have documented a prevailing pattern that kin-biased helping behaviour does not exist, even within species for which strong kin recognition is known. Boomsma & D'Etorre's [19] contribution explains why nepotism is rare and suggests alternative research agendas.

A second apparent blind alley emanating from Hamiltonian inclusive fitness theory is the hypothesis of reproductive skew. This idea considers how social contracts that apportion direct reproduction within groups are driven by their degree of relatedness and environmental factors such as availability of nesting sites, predation pressure and the like. Dominance of reproduction by one or a few produces high variance, or high skew; egalitarian reproduction with low variance produces low skew. A considerable body of theory explains how reproductive skew should result under an array of conditions. Despite its appeal, however, the field remains largely the realm of theoreticians: empirical evidence to support predictions of skew theory has been slow to appear [20].

Biases and blind alleys notwithstanding, the catalogue of Hamilton-inspired ideas still under active investigation bears ample testimony to his influence. The contribution by Zuk & Borello [21] shows how two of Hamilton's interests, parasites and altruism—at first blush seemingly distinct—can be synthesized to open up new avenues of research, and I feel sure that future scholars will examine other intersections among Hamilton's narrow roads of gene land. We are pleased to offer this Special Feature to honour his legacy, and look forward to seeing how his ideas continue to influence the field over the coming 50 years.

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