“How complex and even perverse the real world can be” W.D. Hamilton’s early work on social wasps (1964–1968)

Guido Caniglia

Center for Biology and Society, Arizona State University, PO Box 873301, Tempe, AZ 85287-3301, United States

ARTICLE INFO

Article history:
Received 27 December 2016
Received in revised form
10 May 2017

Keywords:
Kin selection
Inclusive fitness
Haplodiploidy
Sociobiology
Polistes
West-Eberhard

ABSTRACT

William D. Hamilton’s name is often connected to important theoretical accomplishments, from the theory of inclusive fitness and kin selection to the so-called Hamilton’s rule and the haplodiploidy hypothesis. This article asks: How did Hamilton attempt to test his theory and hypothesis against the complexity of the biological world? The article reconstructs Hamilton’s empirical work with social wasps between 1963 and 1968, the years before and after the publication of the groundbreaking “The Genetical Evolution of Social Behavior” in 1964. It points out the centrality of Hamilton’s work on wasps and shows how the British scientist attempted to test theories and hypotheses with naturalistic, developmental, and physiological observations as well as, at times, with experimental manipulations. The article offers a new perspective on the history of the scientific understanding of the evolution of social behavior. In contrast to existing narratives, this perspective emphasizes the importance of empirical work—e.g., natural history, physiology, comparative anatomy—which is often obscured by a nearly exclusive focus on theoretical developments in this field.

© 2017 Elsevier Ltd. All rights reserved.

1. Introduction

William D. Hamilton’s name is often connected to important theoretical accomplishments, from the theory of inclusive fitness and kin selection to the so-called Hamilton’s rule and the haplodiploidy hypothesis (Charnov, 1977; Hamilton, 1963, 1964a, 1964b). Inclusive fitness theory shows how the genetic relatedness of individuals affects their behavior towards one another. Hamilton’s rule points out that social behavior evolves under specific combinations of costs, benefits, and relatedness (Hamilton, 1963). The haplodiploidy hypothesis explains how self-sacrificing behaviors evolved in social insects of the order Hymenoptera, including wasps, bees and ants (Hamilton, 1964b). Rules, theory and hypothesis have dominated the attention of most scholars since the publication of “The Genetical Evolution of Social Behavior” in 1964 (Wilson, 1971; Grafen, 2004). This paper asks: How did Hamilton seek to test his theory and hypothesis against the complexity of the biological world? How did he attempt to see if the theory, the rule and the hypothesis could help explain the evolution of social behavior in specific biological systems?

In some notes for the preparation of a lecture in the late 1970s, Hamilton wrote: “I feel very strongly that a theorist ought not to become too detached from the things he theorizes about—at least I find it salutary to keep reminding myself by observation and experimentation of how complex and even perverse the real world can be” (Hamilton; Undated; Z1X90/1/18). Though mostly a theorist, Hamilton maintained that scientists should always pay close attention to the complexity and even perversity of real biological phenomena. Complex and perversive features of wasp societies posed challenges to Hamilton’s theory of inclusive fitness and to the haplodiploidy hypothesis (Hamilton, 1964b). In his work during the 1960s and early 1970s, though not always systematically, Hamilton addressed these challenges by investigating societies of tropical and non-tropical wasps.

Social wasps occupy a central place in Hamilton’s publications and notebooks as well as in his correspondence with colleagues, family and friends. Borrowing an expression from the evolutionary biologist M.J. West-Eberhard, wasps were for Hamilton a microcosm...
for the investigation of social life (West-Eberhard, 1996). There are two main reasons for Hamilton's interest in wasps. First, the human-like features of wasp societies fascinated him. For instance, Hamilton talked about the: “indescribable quality of the wasps' life itself—wayward, mysterious, almost human” (Hamilton to West-Eberhard; 5 October 1967; Z1X83/1/10). This feature distinguishes most wasp societies from the perfect organization of many ant and bee societies (e.g. Hölldobler & Wilson, 2009). The second reason was that wasps provided ‘touchstone puzzles’ to the theory of inclusive fitness and to the haplodiploidy hypothesis (Caniglia, 2016). According to this theory, altruistic acts, such as the self-sacrificing behavior of most workers and auxiliaries in wasp colonies, evolve because beneficiaries and self-sacrificing actors, under certain ecological conditions, share copies of the same genes (Hamilton, 1964). Therefore, the self-sacrificing individuals can pass on their genes to their offspring by helping their relatives, who carry copies of the same genes (Hamilton, 1963). However, most social wasps show behaviors that tend to lower the relatedness of the individuals in a colony and therefore challenge explanations in terms of inclusive fitness (e.g. Gadagkar, 2009).

This article reconstructs Hamilton's investigations on social wasps between 1963 and 1968. This reconstruction complements existing articles about Hamilton's work and about our scientific understanding of the evolution of social life. Such narratives have privileged the theoretical development of Hamilton's ideas and of the whole field (e.g. Grafen, 2004; Queller, 2001), as well as Hamilton's correspondence with important evolutionary theorists of his time from J. Maynard Smith to G. Price (Borrello, 2010; Harman, 2010; Segerstrale, 2013). They have often described Hamilton's empirical work as a compulsive tendency to follow his own "boyhood training" (Hamilton, 1996a, p. 117), a need to escape formal academic environments (Dugatkin, 2011), a necessity to feed his imaginative mind (Grafen, 2004) or even as derived from a political interest in "human society and his concern for man's future" (Swenson, 2015a, p. 47). With some exceptions (Hughes, 2002), such narratives have deprived Hamilton's empirical work of scientific interest and importance (Grafen, 2004, p. 119). By detailing Hamilton's early work on wasps, this article provides an alternative and complementary narrative to existing ones and brings Hamilton's empirical work to the foreground.

Hamilton's empirical work on wasps often did not reach the stage of publication (Wilson, 1971; Grafen, 2004). Yet, Hamilton's notebooks, loose papers, and correspondence stored in Hamilton's Archive at The British Library document the importance the British scientist attributed to empirical work. Archival material also shows that Hamilton's empirical work was nourished by a network of relationships with scientists, such as the Brazilian W.E. Kerr and the young evolutionary biologist M.J. West (later M.J. West-Eberhard), who made important contributions not only to the theory of social evolution but also to its empirical foundations. Though not in the form of published papers, Hamilton's empirical investigations influenced the way many scientists started looking for empirical evidence in order to understand whether abstract theories and models of social evolution could help explain why social life evolved (e.g. Strassmann 1979, 1981; West, 1967; West-Eberhard, 1973, 1975). Thus, the reconstruction of Hamilton's empirical work invites us to consider these empirically-oriented investigations as an important component in the historical development of scientific ideas on social evolution.

This article follows Hamilton's investigations in the years between 1963, when Hamilton's first publication in The American Naturalist came out, and 1968, when Hamilton left for his second trip to Latin America. First, it sketches the main features of Hamilton's theory of inclusive fitness (Hamilton, 1963, 1964a) and the haplodiploidy hypothesis (Hamilton, 1964b) as they emerged from Hamilton's publications of the time. Second, it details Hamilton's attempts to conduct empirical work on wasp societies during his first trip to Latin America from August 1964 to late summer 1965. Third, it reconstructs Hamilton's reflections about the value and meaning of his empirical investigations between 1964 and 1968. Finally, it provides an outlook on how Hamilton sought to evaluate inclusive fitness theory with empirical evidence after 1968.

### 2. The genetical theory of social behavior (1964)

Since his college years at Cambridge, Hamilton had worked strenuously on the problem of biological altruism (Hamilton, 1966a; Segerstrale, 2013). In order to approach this problem, he had engaged with earlier foundational works in evolutionary biology and population genetics, chiefly Fisher's The Genetical Theory of Natural Selection (1930) and Haldane's The Causes of Evolution (1932), in the development of his theories and ideas (e.g. Grafen, 2004; Segerstrale, 2013; Harman, 2010). Since 1962, Hamilton had unsuccessfully tried to publish his ideas in Nature (Hamilton, 1996a; Segerstrale, 2013). On March 7, 1963, he submitted what would become his first published article (Hamilton, 1963). In a letter to The American Naturalist with the title “The Evolution of Altruistic Behavior”, Hamilton sketched out his core ideas about the evolution of social behaviors (Hamilton, 1963). The news soon reached Hamilton's friends in North America, who had witnessed his struggle to get his research published. Later in 1963, Hamilton's friend and colleague, Colin Hudson wrote to him: “yesterday we received a copy of your letter to The American Naturalist [...] you must be pleased to have got your chief idea into print at last. It will be interesting to see what reactions it receives” (Hudson to Hamilton; Undated; ZIXUN/S).

In his letter to The American Naturalist, Hamilton presented his ideas about the evolution of altruistic behaviors, that is, those behaviors that are beneficial for the ones who receive them and detrimental for those who perform them (Hamilton, 1963). He explained the conditions favoring the increase in the frequency of a gene with altruistic effects in a population. According to Hamilton, under the right circumstances, it did not contradict Darwinian theory that some individuals direct altruistic behaviors towards their close relatives, who are more likely to share with them the same genes. Taking a gene's eye view, Hamilton explained that a gene with altruistic effects can spread in a population if it favors the fitness of those individuals who bear copies of that same gene (Hamilton, 1963). In order for a gene to transmit copies of itself in a population, it is not necessary that it be transmitted directly in the offspring of the individuals bearing it. The bearers can help members in the population that are related to them, who then transmit copies identical to itself in other members of the population (Hamilton, 1963).

A formula, which in the 1970s came to be called Hamilton's rule (Charnov, 1977), condensed Hamilton's ideas about the conditions favoring the evolution of altruistic traits in a population. Hamilton wrote: “If the gain to a relative of degree r is k-times the loss to the altruist, the criterion for positive selection of the causative gene is $k > 1/r$” (Hamilton, 1963, p. 355). If we substitute k with the ratio of benefits and costs (k = b/c) of the altruistic act, we obtain the more common formulation of Hamilton's rule: $br > c$, where r is a measure of the degree of relatedness between the altruistic actor and the recipient of the altruistic action as a result of common descent; b and c are respectively the benefits in fitness to the recipient and the costs in fitness to the actor (Charnov, 1977).

The publication in The American Naturalist boosted Hamilton's confidence that the scientific community, or at least the editors of some important journals, might be ready for his ideas. Yet, Hamilton had been working on a longer and more detailed article...
امکان دانلود نسخه تمام متن مقالات انگلیسی
امکان دانلود نسخه ترجمه شده مقالات
پذیرش سفارش ترجمه تخصصی
امکان جستجو در آرشیو جامعی از صدها موضوع و هزاران مقاله
امکان دانلود رایگان ۲ صفحه اول هر مقاله
امکان پرداخت اینترنتی با کلیه کارت های عضو شتاب
دانلود فوری مقاله پس از پرداخت آنلاین
پشتیبانی کامل خرید با بهره مندی از سیستم هوشمند رهگیری سفارشات