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The Hamiltonian view of social evolution

The philosophy of social evolution, Birch Jonathan. Oxford University Press, Oxford (2017). 224 pp., Hardcover, ISBN: 9780198733058

1. Introduction

In the obituary of her mentor Bill Hamilton, the American entomologist and evolutionary biologist Marlene Zuk wrote that the difference between Hamilton and everyone else was “not the quality of his ideas, but their sheer abundance” (Zuk, 2000). The proportion of his ideas that were actually any good was about the same as anyone else, “the difference between Bill and most other people was that he had a total of over one hundred ideas, with the result that at least ten of them were brilliant, whereas the rest of us have only four or five ideas as long as we live, with the result that none of them are”. Hamilton indeed had many good ideas. Over the years he made substantial contributions to the study of the origin of sex, sex ratios, genetic conflicts, and the evolution of senescence (Ågren, 2013). His best idea, and the one that bears his name, is about the evolution of social behaviour, especially altruism. Hamilton's Rule, and the related concepts of inclusive fitness and kin selection, have been the bedrock of the study of social evolution for the past half century (Fig. 1).

Jonathan Birch's recent book *The philosophy of social of evolution* is a superb exploration of philosophical implications of Hamilton's work. The philosophy of biology has a long-standing close relationship with evolutionary biology (maybe too close, some have argued (Pradeu, 2017)). Within evolutionary biology, the study of social evolution has been especially important. In a recent interview (Marshall, 2016), Elliot Sober, one of the founders of the field, described how he came to the philosophy of biology after being intrigued by William Wimsatt's review of George C. Williams's classic critique of group selection *Adaptation and natural selection* (Williams, 1966; Wimsatt, 1970). Pioneering books in the field of philosophy of biology, like Sober's *The nature of selection* (Sober, 1984), Elizabeth Lloyd's *The structure and confirmation of evolutionary theory* (Lloyd, 1988), and Daniel Dennett's *Darwin's dangerous idea* (Dennett, 1995) all dedicated large chunks to the issues of causality, altruism and selfishness, and the levels of selection, raised by influential books on social evolution, especially Williams' *Adaptation and natural selection* and Richard Dawkins' *The selfish gene* (Dawkins, 1976). These authors belong to the finest tradition in the philosophy of science. They are deeply informed about the biology in question and their work contributed to the advancement of not only philosophy of biology but practice as well. Early on in *The philosophy of social evolution* (p. 9), Birch aligns his book to this tradition, to which Brandon (1990), Okasha (2006), and Godfrey-Smith (2009) also belong, and in my view the book fits squarely in that company.

In *The philosophy of social Evolution* Birch provides a comprehensive introduction to the conceptual foundations of the Hamiltonian view of social evolution, and a passionate defence of its enduring value in face of recent high profile criticism. The book is divided into two parts: Foundations (five chapters) and Extensions (three chapters). The early parts lay out the Hamiltonian approach to social evolution. In particular, Birch takes his starting point in David Queller's formulation of Hamilton's Rule (Queller, 1992), dubbed Hamilton's Rule General (HRG). This version is central to the arguments throughout the book and in this review essay I will therefore first outline HRG and its derivation. With this in place, I will then navigate through the intense disagreements that Hamilton's Rule, including HRG, generates and evaluate Birch's central argument of the book that HRG serves as an organizing framework for social evolution research under which we can compare and interpret more detailed causal models. The book also contains novel insights on group vs. kin selection models, conceptions of social fitness, and recent developments in the study of the origin of multicellularity and cultural evolution. These chapters are all stimulating, but in the interest of space I will spend the remainder of the review on what I take to be three of the most exciting implications of Hamilton's thinking raised by Birch: (1) the extension of Hamilton's Rule to mobile genetic elements, (2) maximization of inclusive fitness models and the idea of adaptation as organism design, and (3) the relationship between Hamilton's approaches to social behaviour and the gene's-eye view of evolution.

2. Defining Hamilton's rule

One of the most famous anecdotes in evolutionary biology involves the Orange Tree pub, once located around the corner from the University College London at the intersection of Gower Street and Euston Road.[1] In it, sometime in the 1950s, JBS Haldane is meant to have proclaimed (after “calculating on the back of an envelope for some minutes”) to his graduate student John Maynard Smith that “he was prepared to lay down his life for eight cousins or two brothers” (Maynard Smith, 1975). This quip is often used to summarize the essence of our modern understanding of social evolution: costly social behaviour (altruism) can evolve if it is preferentially directed towards relatives. Independently of Haldane, Hamilton formalized this insight in two papers: a short note in The American Naturalist in 1963 and then a majestic two-part paper in The Journal of Theoretical Biology the following year (Hamilton, 1963, 1964). And while Maynard Smith would be instrumental in getting the 1964 paper published, their relationship never really recovered from what Hamilton considered a gross oversight by Maynard Smith in repeatedly attributing the basic insight to Haldane (Segerstrale, 2013).

[1] In a fantastic piece of detective work, Birch reveals that after the Orange Tree was demolished in 1963, the rubble was used for the photo on the cover of the Beatles' EP Twist and Shout.

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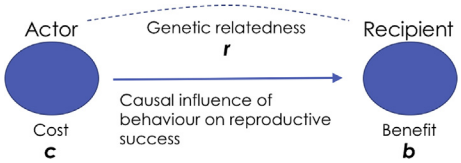

Fig. 1. Hamilton's Rule in its simplest form. Hamilton's Rule says that a costly social behaviour can evolve if and only if $rb>c$, where r is the coefficient of relatedness between the actor and the recipient, b is the fitness benefit to the recipient of the social behaviour, and c is the fitness cost to the actor. Adopted from Fig. 2.1 in Birch (2017).

The current controversy over Hamilton's Rule can be illustrated by contrasting two quotes from leading authors on each side of the debate. One the one hand, in the paper that kicked it all off, Nowak, Tarnita, and Wilson (2010) write that Hamilton's Rule "almost never holds". On the other, Gardner, West, and Wild (2011) describe the Nowak et al. statement as "simply incorrect" and go on to argue that Hamilton's Rule has "the same generality and explanatory power as the theory of natural selection itself". More recently, the sceptical attitude is clearly laid out in van Veelen, Allen, Hoffman, Simon, and Veller (2017), and the enthusiastic case receives a book-length treatment in Marshall (2015).

While the informal version of Hamilton's Rule ($rb>c$; Fig. 1) will make an appearance in most introductory evolution courses, the version subject to current debate takes a bit more getting used to. Birch's introduction to this version, David Queller's (1992) 'general model' referred to as 'HRG', is very instructive. In particular, it does an excellent job highlighting the key assumptions that make HRG simultaneously so attractive for its supporters and so unbearable for its critics. The following passage outlining the HRG derivation will therefore largely follow Birch's lead.

Queller's derivation of Hamilton's Rule takes its starting point in the Price equation (Frank, 2012; Price, 1970). The Price equation is a simple abstract statement about evolutionary change from one generation to the next, such that

$$\Delta\overline{p} = \frac{1}{\overline{w}}[Cov(w_i, p_i) + E(w_i \Delta p_i)] \tag{1}$$

The change in population frequency of a given allele ($\Delta\overline{p}$), where p_i is the individual gene frequency of the i^{th} individual for the allele under consideration, is the sum of two population statistics. The first is the selection term, given by $Cov(w_i, p_i)$, the covariance between individual fitness (w_i) and individual gene frequency (p_i), and the second is the transmission term, $E(w_i \Delta p_i)$, the expected change in p_i between parent and offspring. They are both weighed by the population mean fitness $\overline{w}$. With this in place, Birch outlines the three key assumptions made by Queller in deriving HRG from the Price equation.

First, p_i is reinterpreted as a breeding value, as used in quantitative genetics. This is possible because p_i can be thought of as not just an individual gene frequency, but as a linear combination of frequencies across multiple alleles of multiple loci. From this, $\Delta\overline{p}$ becomes the change in a quantitative polygenic trait. Next, the transmission term $E(w_i \Delta p_i)$ is assumed to be 0. This has two biological implications. Number one is that processes like segregation distortion, gametic selection, and genetic drift are ignored. Number two is that the average effects of alleles on the considered phenotype are constant. Because dominance and epistasis can both cause this assumption to be violated, one way to conceptualize it is to think of the 'genic environment' being held fixed. (An assumption one might recognize from discussions of Fisher's (1930) fundamental theorem of natural selection (Ewens, 2010; Okasha, 2008).) Both assumptions are quite substantial and I will return to them later in the review. Finally, with $E(w_i \Delta p_i)$ dropped, $Cov(w_i, p_i)$ is conceived as the effect of natural selection on the evolutionary change of the trait under study and we are left with

$$\Delta\overline{p} = \frac{1}{\overline{w}}[Cov(w_i, p_i)] \tag{2}$$

To get from this to the familiar $rb>c$, the selective covariance term must be partitioned into rb and c. Queller achieves this by making use of the Lande–Arnold regression model of fitness (Lande & Arnold, 1983) and therefore first stating the fitness of the of the i^{th} individual using a linear regression model, such that

$$w_i = \alpha + \beta_1 p_i + \beta_2 \hat{p}_i + \varepsilon_{w_i} \tag{3}$$

The linear function considers the gene frequency of a given individual (p_i), as well as the average individual gene frequency of its social partners ($\hat{p}_i$). It then captures the partial regression of an individual's fitness on that individual's gene frequency (β_i), accounting for the that of the social partners' and the partial regression of an individual's fitness on the gene frequency of social partners', this time accounting for that individual's gene frequency. α is the non-social part of fitness and taken to be the same for all individuals. ε_{w_i} is the traditional error term of linear regressions; here it represents the discrepancy between actual and predicted fitness of the i^{th} individual. This regression model is then substituted into the Price equation (2), leading to

$$\overline{w}\Delta\overline{p} = Cov(\alpha, p_i) + \beta_1 Var(p_i) + \beta_2 Cov(\hat{p}_i, p_i) + Cov\left(\varepsilon_{w_i}, p_i\right) \tag{4}$$

Simplifying and rearranging to state the condition for the population mean of the trait of interest to increase ($\Delta\overline{p}>0$ gives

$$\Delta\overline{p}>0 \Leftrightarrow \frac{Cov(\hat{p}_i, p_i)}{Var(p_i)}\beta_2 > -\beta_1 \tag{5}$$

Then, because r, b, c, in Hamilton's Rule can be defined as

$$r = \frac{Cov(\hat{p}_i, p_i)}{Var(p_i)}, \quad b = \beta_2, \text{ and } c = -\beta_1$$

this notation means that (5) can be rewritten as

$(\Delta\overline{p})>0 \Leftrightarrow rb>c$ (HRG)

This is the formulation of Hamilton's Rule that Birch, following a previous paper of his (Birch, 2014a), calls Hamilton's Rule General (HRG).

At this point, it is worth pausing and reflecting on what the variables in HRG actually mean. Because there is no such thing as a regression coefficient for a single data point, r, b, and c are not actually properties of individual organisms or of any given social interaction (which for example a first look at Fig. 1 may have you believe). Instead, they are population statistics: r is the slope of the line of best fit plotting $\hat{p}_i$ against p_i for every individual in the population, and b and c can be calculated from the plane of best fit after adding w_i to the $\hat{p}_i$ against p_i plot. This formulation may at first seem strange, but it leads to a flexibility that can be a great strength, or a great weakness depending on who you ask.

3. Hamilton's rule as an organizing framework in social evolution

The heart of Birch's defence of the Hamiltonian approach to social evolution is the proposition that HRG can act as an organizing framework that allows us to identify common mechanisms in the origin of social behaviours. It offers a classificatory scheme and common vocabulary to translate between models, which means that more detailed theoretical models can be interpreted, compared, and contrasted in a

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