Social evolution and genetic interactions in the short and long term

CrossMark

Jeremy Van Cleve

Department of Biology, University of Kentucky, Lexington, KY 40506, USA

ARTICLE INFO

ABSTRACT

The evolution of social traits remains one of the most fascinating and feisty topics in evolutionary biology even after half a century of theoretical research. W.D. Hamilton shaped much of the field initially with his 1964 papers that laid out the foundation for understanding the effect of genetic relatedness on the evolution of social behavior. Early theoretical investigations revealed two critical assumptions required for Hamilton's rule to hold in dynamical models: weak selection and additive genetic interactions. However, only recently have analytical approaches from population genetics and evolutionary game theory developed sufficiently so that social evolution can be studied under the joint action of selection, mutation, and genetic drift. We review how these approaches suggest two timescales for evolution under weak mutation: (i) a short-term timescale where evolution occurs between a finite set of alleles, and (ii) a long-term timescale where a continuum of alleles are possible and populations evolve continuously from one monomorphic trait to another. We show how Hamilton's rule emerges from the short-term analysis under additivity and how non-additive genetic interactions can be accounted for more generally. This short-term approach reproduces, synthesizes, and generalizes many previous results including the one-third law from evolutionary game theory and risk dominance from economic game theory. Using the long-term approach, we illustrate how trait evolution can be described with a diffusion equation that is a stochastic analogue of the canonical equation of adaptive dynamics. Peaks in the stationary distribution of the diffusion capture classic notions of convergence stability from evolutionary game theory and generally depend on the additive genetic interactions inherent in Hamilton's rule. Surprisingly, the peaks of the long-term stationary distribution can predict the effects of simple kinds of non-additive interactions. Additionally, the peaks capture both weak and strong effects of social payoffs in a manner difficult to replicate with the short-term approach. Together, the results from the short and long-term approaches suggest both how Hamilton's insight may be robust in unexpected ways and how current analytical approaches can expand our understanding of social evolution far beyond Hamilton's original work.

© 2015 Elsevier Inc. All rights reserved.

1. Introduction

The theory of evolution by natural selection as first fully elucidated by Darwin (1859) is so profoundly elegant and comprehensive that truly new additions to theory have been extremely rare. In 1963, W.D. Hamilton began publishing his seminal work on how natural selection can shape social behavior (Hamilton, 1963, 1964a,b), which is often either referred to as the theory of "kin selection" (Maynard Smith, 1964) or "inclusive fitness" (Frank, 2013). It is a tribute to the importance of this work that upon his untimely death in 2000 Hamilton was called "one of the most influential Darwinian thinkers of our time" (Eshel and Feldman, 2001) and a candidate for the "most distinguished Darwinian since Darwin" (Dawkins, 2000).
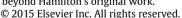
In this article, we will review how the tools of population genetics and evolutionary game theory can be used to formalize Hamilton's insight. We will begin with a summary of classic analyses of Hamilton's approach and will then introduce the population genetic and game theoretic tools that currently provide a complete framework for studying social evolution under weak selection and weak mutation (Lehmann and Rousset, 2014b). Using these tools, we will see how two general timescales for analysis emerge: a short-term timescale where evolution proceeds among a finite set of alleles, and a long-term timescale where populations evolve continuously among a continuum of alleles. These notions of short and long-term derive from a broader attempt to reconcile population genetic methods with evolutionary game theory (Eshel, 1996; Hammerstein, 1996; Weissing, 1996).

Using the short-term approach, we show how genetic interactions between individuals (e.g. Queller, 1985) can affect selection for cooperation in deme or group-structured populations

(Ladret and Lessard, 2007). These results extend previous analyses of stochastic evolution that have shown conditions such as "risk dominance" (Harsanyi and Selten, 1988; Blume, 1993; Kandori et al., 1993) and the "one-third law" (Nowak et al., 2004; Ohtsuki et al., 2007) to be important determinants of evolutionary stability. Using the substitution rate approach to long-term evolution (Lehmann, 2012; Van Cleve and Lehmann, 2013), we describe a diffusion equation that approximates the long-term change in monomorphic trait values. We show how peaks in the stationary distribution of this diffusion captures classic notions of evolutionary and convergence stability. Moreover, the location of these convergence stable states can be calculated using the classic direct-fitness approach of kin selection (Taylor and Frank, 1996; Rousset and Billiard, 2000; Rousset, 2004). Applying this long-term approach to a simple non-additive social interaction, we find surprisingly that the long-term analysis can capture these non-additive effects even though the diffusion integrates over only additive interactions. Moreover, the long-term approach appears to reproduce results from some strong selection models, which suggests an unexpected robustness of the long-term diffusion. Together, the results from the short and long-term approaches reveal the usefulness of these approaches for integrating Hamilton's original insight with recent results from population genetics and evolutionary game theory.

1.1. Hamilton's rule

The core insight in Hamilton's work is often summarized with his eponymous rule (Hamilton, 1964a, 1970): an allele for a social behavior increases in frequency when the "inclusive fitness effect" is positive, namely

$$-c + b\,r > 0. \tag{1}$$

In Hamilton's rule (1), b is the increase in fitness (benefit) of a social partner from the behavior of a focal individual, c is the decrease in fitness (cost) of a focal individual that performs the behavior, and r measures genetic relatedness between focal and recipient individuals (Frank, 1998). More generally, $-c$ is called the "direct fitness effect" and b the "indirect fitness effect". Hamilton (1964a) initially emphasized that genetic relatedness is generated by a genealogical process that produces alleles identical by descent (IBD) among a group of socially interacting individuals. Another general definition of genetic relatedness says that it is the regression of the genotypes of social partners on the genotype of the focal individual (Hamilton, 1970; Grafen, 1985). Hamilton's rule crystallized the notion that natural selection depends both on the effect of an individual's genes on its own fitness and also on the indirect effect of those genes on the fitness of social partners. Although Darwin (1859), Fisher (1930), and Haldane (1955), among others, had expressed this idea in relation to how evolution would lead one individual to sacrifice its fitness for another, Hamilton was the first to present a compelling framework applicable to social evolution more generally.

Within Hamilton's inclusive fitness framework, behaviors that decrease the fitness of a focal individual ($c > 0$) but increase the fitness of social partners ($b > 0$) are "altruistic". Well-known examples of altruism include worker sterility in eusocial insects (Andersson, 1984), stalk cells that give up reproduction to disperse spore cells in *Dictyostelium discoideum* (Strassmann et al., 2000), and costly human warfare (Hamilton, 1975; Lehmann and Feldman, 2008). Other behaviors can also be classified in Hamilton's framework (Hamilton, 1964a), and Table 2: (i) behaviors are "mutualistic" when they increase the fitness of the focal individual and its social partners, (ii) "selfish" when they increase the fitness of the focal at the expense of the fitness of social partners, and

(iii) "spiteful" when they decrease the fitness of both the focal individual and its social partners. Although there are other potential definitions of altruism and other behaviors (see Kerr et al., 2004; Bshary and Bergmuller, 2008), Hamilton's classification based on direct and indirect effects has proven useful for distinguishing different kinds of helping behaviors (mutualisms and altruisms) and for showing how different biological mechanisms can promote or inhibit the evolution of these behaviors (Lehmann and Keller, 2006a; West et al., 2007).

Though Hamilton's approach was initially accepted among empiricists (Wilson, 1975) and some theorists (Maynard Smith, 1964; Oster et al., 1977), other theorists were concerned about the generality of the approach due to its emphasis on fitness maximization and optimality modeling (Cavalli-Sforza and Feldman, 1978; Williams, 1981; Karlin and Matessi, 1983). Fitness maximization was viewed as untenable because examples where it is violated are well known (Moran, 1964). Optimality models were additionally viewed with skepticism because, by neglecting gene frequency dynamics, they cannot study genetic polymorphisms; in effect, such models must assume that mutant alleles that invade a population also reach fixation. An initial wave of population genetic studies in response to these concerns showed that Hamilton's rule was generally a correct mutant invasion condition so long as selection is weak and fitness interactions between individuals are additive (Cavalli-Sforza and Feldman, 1978; Wade, 1979; Abugov and Michod, 1981; Uyenoyama and Feldman, 1981; Uyenoyama et al., 1981). However, these models were family structured where cooperation occurs between close relatives and could not address the applicability of Hamilton's rule in populations with more generic structure, such as deme structure in island (Wright, 1931) and lattice models (Kimura and Weiss, 1964; Malécot, 1948, 1967).

1.2. The Price equation and the individually-based approach

Part of the difficulty with the population genetic methods used to analyze family-structured models is that they use genotypes as state variables. This quickly increases the dimensionality of the model as the number of loci, family size, or demes increases and makes approximation difficult. An important alternative approach was introduced to population genetics by George Price (Price, 1970, 1972). The core of that approach, the Price equation, uses the distribution of allele frequencies in each individual in the population as the set of state variables and tracks the first population-level moment of this distribution, which is the mean allele frequency. If $\mathbf{p} = (p_1, \ldots, p_{N_T})$ represents the allele frequency distribution for N_T haploid individuals ($p_i = 0$ or 1 for individual i), the Price equation yields

$$\mathrm{E}\left[w\Delta p | \mathbf{p}\right] = \mathrm{Cov}\left[w_i, p_i\right] + \mathrm{E}\left[w_i \Delta p_i\right] \tag{2}$$

where $\mathrm{E}\left[w\Delta p | \mathbf{p}\right]$ is the expected change in mean allele frequency p weighted by mean fitness w and conditional on $\mathbf{p}$ in the parental generation. The first term on the right hand side, the covariance between individual fitness w_i and allele frequency p_i, measures the effect of selection on the change in mean allele frequency in the population. The second term, $\mathrm{E}\left[w_i \Delta p_i\right]$, measures the effect of non-selective transmission forces, such as mutation and migration (and recombination for changes in genotype frequencies), on the change in mean allele frequency. When selection is the only force on allele frequencies and the population size remains fixed ($w = 1$), the Price equation simplifies to

$$\mathrm{E}\left[\Delta p | \mathbf{p}\right] = \mathrm{Cov}\left[w_i, p_i\right]. \tag{3}$$

Calculating higher-order moments of the allele frequency distribution $\mathbf{p}$ is necessary to measure the exact dynamics of the distribution over time; thus, moment-based approaches like the Price equation are not necessarily more tractable than directly tracking