The general form of Hamilton's rule makes no predictions and cannot be tested empirically

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Hamilton's rule asserts that a trait is favored by natural selection if the benefit to others, B , multiplied by relatedness, R , exceeds the cost to self, C . Specifically, Hamilton's rule states that the change in average trait value in a population is proportional to $BR - C$. This rule is commonly believed to be a natural law making important predictions in biology, and its influence has spread from evolutionary biology to other fields including the social sciences. Whereas many feel that Hamilton's rule provides valuable intuition, there is disagreement even among experts as to how the quantities B , R , and C should be defined for a given system. Here, we investigate a widely endorsed formulation of Hamilton's rule, which is said to be as general as natural selection itself. We show that, in this formulation, Hamilton's rule does not make predictions and cannot be tested empirically. It turns out that the parameters B and C depend on the change in average trait value and therefore cannot predict that change. In this formulation, which has been called "exact and general" by its proponents, Hamilton's rule can "predict" only the data that have already been given.

evolution | cooperation | kin selection | sociobiology

Hamilton's rule is a widely known concept in evolutionary biology. It has become standard textbook knowledge and is encountered in undergraduate education. For many, Hamilton's rule expresses the intuition that cooperation evolves more easily when there are frequent interactions among relatives, because relatives are likely to share the cooperative trait. However, Hamilton's rule goes beyond this intuition by positing a quantitative condition, $BR - C > 0$, which is said to predict whether or not a trait will be selected. Specifically, it is claimed that the change in average trait value from one time point to the next is proportional to $BR - C$.

We immediately encounter the question of how the "benefit," B , the "relatedness," R , and the "cost," C , are calculated for a given system. Surprisingly, there is no consensus about the correct method. A variety of derivations have been proposed over the years (1–10), which define B , R , and C in distinct (nonequivalent) ways. In the empirical literature, peer reviewers often disagree over which method should be used in a particular manuscript (11).

A number of recent papers (7, 9, 10) have endorsed a particular formulation (4, 5) as the exact, general, and even "canonical" version of Hamilton's rule. This formulation, called "Hamilton's rule—general" (HRG) (12, 13), is claimed to be as general as natural selection itself (7, 14). The derivation, which we recapitulate below, is simple and contains only a few steps.

The mathematical investigation of HRG reveals three astonishing facts. First, HRG is logically incapable of making any prediction about any situation because the benefit, B , and the cost, C , cannot be known in advance. They depend on the data that are to be predicted. At the outset of an experiment, B and C are unknown, and so there is no way to say what Hamilton's rule would predict. Once the experiment is done, HRG will produce B and C values in retrospect such that $BR - C$ is positive if the trait in question has increased and negative if it has decreased. But these "predictions" are merely rearrangements of the data that have been collected and already contain information about

whether or not the trait has increased. In particular, the parameters B and C depend on the change in average trait value.

The second astonishing fact of HRG is that the prediction, which exists only in retrospect, is not based on relatedness or any other aspect of population structure. A common interpretation of the terms in Hamilton's rule is that R quantifies the population structure, whereas B and C characterize the nature of the trait. But the derivation shows that this interpretation is wrong. All three terms, B , R , and C , are functions of population structure, whereas the overall value of $BR - C$ is functionally independent of population structure. Any information about who interacts with whom cancels out when calculating the value of $BR - C$.

The third fact of HRG is that no conceivable experiment exists that could test (or invalidate) this rule. All input data, whether they come from biology or not, are formally in agreement with HRG. This agreement is not a consequence of natural selection, but a statement about a relationship between slopes in multivariate linear regression. This relationship between slopes has been known in statistics at least since 1897 (15).

Derivation of HRG

We recapitulate the derivation of HRG given in refs. 4, 5, 7, 9, and 10. We also provide explicit algebraic formulas for B and C that result from this derivation.

We imagine a population of n individuals at a given point in time. Each individual i has a fitness value, w_i . The list $w = (w_1, w_2, \dots, w_n)$ is the collection of fitness values in the population, which can be interpreted as expected or realized number of offspring in the next generation. If the total population size is constant, which is assumed for simplicity, then the average fitness is $\bar{w} = 1$.

Significance

Hamilton's rule is a well-known concept in evolutionary biology. It is usually perceived as a statement that makes predictions about natural selection in situations where interactions occur between genetic relatives. Here, we examine what has been called the "exact and general" formulation of Hamilton's rule. We show that in this formulation, which is widely endorsed by proponents of inclusive fitness theory, Hamilton's rule does not make any prediction and cannot be tested empirically. This formulation of Hamilton's rule is not a consequence of natural selection and not even a statement specifically about biology. We give simple and transparent expressions for the quantities of benefit, cost, and relatedness that appear in Hamilton's rule, which reveal that these quantities depend on the data that are to be predicted.

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Fig. 2. The retrospective prediction of Hamilton's rule is based on the numerical value of the term $BR - C$. (A and B) The numerical value of $BR - C$ does not depend (functionally) on the h list, which specifies the trait values of the interaction partners. Any (generic) choice of numbers can be used for the h list, for example the digits of π , and the value of $BR - C$ remains the same. The prediction of this form of Hamilton's rule therefore does not use information about who interacts with whom or on whether interactions are between relatives or not. (C) The numerical value of R depends on the g and h lists. The numerical values of B and C depend on all three lists. In particular, B and C also depend on the change in trait value. Therefore, they cannot be used to predict that change in any meaningful way.

The formal correctness of HRG is established by Eqs. 1 and 5. Because the variance v_g must be positive for the formalism to make sense, the sign of $BR - C$ is the same as the sign of $\Delta\bar{g}$. But we have seen that B and C depend on $\Delta\bar{g}$. Therefore, $BR - C$ cannot predict or explain $\Delta\bar{g}$. The expression $BR - C$ is simply an extended form of writing the ratio $\Delta\bar{g}/v_g$, in which we add an arbitrary h list that subsequently cancels out again.

Slopes and Statistics

The relationship between the slopes of the various linear regressions, expressed by HRG (Eq. 5), is not a consequence of biology and not a discovery of inclusive fitness theory. It is a fact of multivariate statistical analysis, the proof of which we recall in *Appendix*.

In a linear regression of w vs. g , the slope of the line is $m_{wg} = c_{wg}/v_g$. Likewise, a linear regression of w vs. h gives slope $m_{wh} = c_{wh}/v_h$. Furthermore, the linear regressions of h vs. g and of g vs. h lead to the slopes $m_{hg} = c_{hg}/v_g$ and $m_{gh} = c_{gh}/v_h$, respectively.

In three dimensions, the multivariate regression of w vs. both g and h leads to a plane given by two slopes M_g and M_h . It is standard textbook knowledge (16) that the relationship between the slopes is given by the linear system of equations

$$m_{wg} = M_g + M_h m_{hg}; \quad [6a]$$

$$m_{wh} = M_h + M_g m_{gh}. \quad [6b]$$

See Fig. 1 for a graphical depiction of each term.

Inclusive fitness theorists call Eq. 6a "Hamilton's rule" by setting $B = M_h$, $C = -M_g$, and $R = m_{hg}$. These quantities are interpreted as benefit, cost, and relatedness (7, 9) and are used to classify behaviors as "altruistic," "mutually beneficial," "selfish," or "spiteful" (17). If B and C are positive, the situation is classified as altruism; if furthermore $BR - C > 0$, then it is concluded that the altruistic trait increases because interactions occur between close relatives.

However, it is well understood in statistics that relationships such as Eq. 6 do not themselves imply causality (18, 19). Whereas there can be causal relationships between dependent and independent variables in a linear model, these relationships cannot be deduced from linear regression alone (20, 21). Therefore, without further assumptions or information, the meanings attached to the terms in HRG have no basis in mathematics or statistics. Moreover, the derivation of HRG does not take into account any aspect of the mechanism that leads to a change in trait value and therefore cannot return a description of that mechanism (Fig. 3) (22). It merely defines quantities B , R , and C as functions of w , g , and h such that $BR - C$ is proportional to the change in trait frequency, $\Delta\bar{g}$.

Benefit and Cost Need Not Make Sense

Although HRG does not explain or predict the change in average trait value, it could be the case that the parameters B and C provide some biological insights. In a previous paper, we showed that it is easy to envisage biological processes that are mischaracterized by the resulting values of B and C (22). In Fig. 3, we provide further examples of this kind.

The parameters B and C also behave unbiologically in the following way: A small change in a single g_i or h_i value can make B and C jump from a very large negative value to a very large positive value (Fig. 4). For example, a small deviation in the measurement of an empirical system could change the assessment of a behavior from tremendously helpful (say, $B = 10^{10}$) to tremendously harmful ($B = -10^{10}$). Such quantities are not biologically meaningful.

Discussion

Hamilton's rule is commonly thought to capture the idea that cooperative behaviors can be selected if the benefits go to close relatives, because these relatives are likely to share genes for cooperation. In this understanding, Hamilton's rule is believed

Fig. 3. The parameters B and C mischaracterize the underlying biology in simple examples. In all four populations of size $N=8$, there are two types of individuals: blue, which indicates presence of a trait ($g=1$), and red, which indicates absence of the trait ($g=0$). Each individual is labeled by its fitness, which is later normalized to ensure constant population size. Arrows indicate interaction partners. (A) Both blue and red have baseline fitness 3. Blue harms blue by reducing its fitness by 2 at no personal cost. Blue helps red by increasing its fitness by 2 at no cost. Red does nothing to its interaction partners. The regression method yields $B, C > 0$, misclassifying blue as altruism. (B) Blue has baseline fitness 1, and red has baseline fitness 2. Blue increases the fitness of blue by 3 and decreases the fitness of red by 1, both at no cost. Red does nothing to its interaction partners. The regression method yields $B > 0$ and $C < 0$, misclassifying blue as mutually beneficial. This classification is incorrect because blue harms red. (C) Blue has baseline fitness 2, and red has baseline fitness 3. Blue increases the fitness of blue by 1 and decreases the fitness of red by 2, both at no cost. Red decreases the fitness of blue by 1 at no cost and does nothing to red. The regression method yields $B < 0$ and $C > 0$, misclassifying blue as spiteful. (D) Blue has baseline fitness 1 and red has baseline fitness 2. Blue does nothing to blue, and red increases the fitness of blue by 2 at no cost. Red does nothing to red. The regression method yields $B, C < 0$, misclassifying blue as selfish. In all four cases the regression method yields $R=7/15$. In A, C, and D, we have $BR - C < 0$ (blue decreases in frequency); in B, $BR - C > 0$ (blue increases in frequency).

to make important, testable predictions for the evolution of social behavior: A trait is selected if benefit times relatedness exceeds cost. Clearly, such a simple and seemingly plausible statement has great intuitive appeal.

However, any intuition can only be as good as its mathematical or biological underpinning. The purpose of this article has been to clarify the mathematical derivation of Hamilton's rule that has been endorsed as exact, general, and canonical by the inclusive fitness community (HRG) (4, 5, 7, 9, 10). The derivation of HRG is encapsulated in Eqs. 1–5. Any collection of triples can be used as input data and will turn out to be in "agreement with Hamilton's rule" as long as the relevant denominators are nonzero. If the denominators are zero, the quantities B and C are undefined. The data can come from any experiment, from any theory, from a deliberate or erroneous variation of either, or be completely imaginary. All such data, biological or not, will behave as "predicted by Hamilton's rule." Clearly, HRG is not a statement about biology and not a consequence of natural selection.

The predictive power of HRG is equivalent to the following example: If you give me the shoe sizes and heights of a group of people, then I can predict the heights. My algorithm also works if you gave me the wrong shoe sizes.

That HRG has no predictive power has been previously noted by ourselves (22) and others (12, 23, 24), yet HRG is credited with making a variety of empirical predictions (7, 9, 14).

Much like the Price equation (25–27), HRG provides a functional relationship between quantities that are obtained from a population at two successive points in time. Whereas the change in trait frequency, $\Delta\bar{g}$, need not be independent of h in a statistical sense, the derivation of HRG takes neither statistical relationships nor any information about suitability of a linear model into account (7, 22). Starting from three lists, w , g , and h , it fits a linear model of w vs. g and h and finds B , C , and R such that $BR - C$ is proportional to $\Delta\bar{g}$. Notably, B and C are themselves functions of $\Delta\bar{g}$. The result is an algebraic expression for $BR - C$ that is (functionally) independent of h (Fig. 2). In analogy to our previous example, although shoe size and height could be correlated, if we already know the heights, the shoe sizes are not needed to determine heights.

In short, there is a startling discrepancy between the common intuitive understanding of Hamilton's rule and the derivation of this rule that has been described as exact and general. In some cases, this discrepancy can be seen within a single paper. For example, ref. 7 uses 18 different variations of "Hamilton's rule correctly predicts..." in reference to HRG, which makes no prediction at all.

Although HRG is the only formulation of Hamilton's rule that is claimed to be exact and general, there are other approaches that define benefit, cost, and relatedness in different ways. For example, benefit and cost can be properties of individual phenotypes, and relatedness can be defined using common ancestry (1, 3, 12, 13, 24, 28). This approach, "Hamilton's rule—special" (HRS) (12, 13), has the advantage of making testable predictions, because the benefit and cost of a phenotype can be determined in advance. However, it is easy to show that HRS holds only for special cases and not in general (12, 28–31).

The existence of these conflicting definitions makes it impossible to meaningfully test or falsify Hamilton's rule. Any theoretical or empirical result that appears to violate Hamilton's rule can be reanalyzed using HRG to show that the outcome is "as predicted by Hamilton's rule." Indeed, this pattern has been repeated many times in the literature (7, 14, 28, 32–34). It appears that there are no real or hypothetical data that the inclusive fitness community would accept as a violation of Hamilton's rule.

Some papers attempt to empirically test Hamilton's rule (35–40). Tests of Hamilton's rule are typically done by experimentally determining the benefits and costs of a phenotype and quantifying relatedness using genetic markers or pedigree. But such a procedure—while scientifically reasonable—tests only HRS, which is not the exact and general version of Hamilton's rule. We are aware of only one paper (23) that attempts to apply HRG to an empirical system. They find, as we have shown here, that HRG does not predict any aspect of their system, but yields only a value of $BR - C$ that coincides with the result they have already obtained.

The biological question at hand is how population structure affects the evolution of social behavior, which is a deep and important question that has been studied extensively (41–49).

$$m_{hg} = \frac{g \cdot h}{g \cdot g}; \quad [10c]$$

$$m_{gh} = \frac{g \cdot h}{h \cdot h}. \quad [10d]$$

Moreover, we also see from Eq. 9 that

$$\begin{pmatrix} n & 0 & 0 \\ 0 & g \cdot g & g \cdot h \\ 0 & g \cdot h & h \cdot h \end{pmatrix} \begin{pmatrix} 0 \\ M_g \\ M_h \end{pmatrix} = \begin{pmatrix} 0 \\ w \cdot g \\ w \cdot h \end{pmatrix}, \quad [11]$$

which, together with Eq. 10, gives Eq. 7. $\square$

Note that Eq. 7 can be written in matrix form as

$$\begin{pmatrix} m_{wg} \\ m_{wh} \end{pmatrix} = \begin{pmatrix} 1 & m_{hg} \\ m_{gh} & 1 \end{pmatrix} \begin{pmatrix} M_g \\ M_h \end{pmatrix}. \quad [12]$$

Provided $m_{hg} m_{gh} \neq 1$, we can invert this matrix to see that

$$M_g = \frac{m_{wg} - m_{wh} m_{hg}}{1 - m_{hg} m_{gh}}; \quad [13a]$$

$$M_h = \frac{m_{wh} - m_{wg} m_{gh}}{1 - m_{hg} m_{gh}}. \quad [13b]$$

Because $B = M_h$ and $C = -M_g$ in HRG, we have Eq. 3.

The only situation in which we cannot solve explicitly for M_g and M_h in Eq. 7 is if $m_{hg} m_{gh} = 1$, which happens if and only if there exist constants k_1 and k_2 (not both zero) for which $k_1 (g_i - \bar{g}) = k_2 (h_i - \bar{h})$ for each i . In this case, the values of M_g and M_h , and therefore also the values of B and C in HRG, are undefined.

Introducing $R' = m_{gh}$, we can write

$$B = \frac{c_{hw} - R \Delta \bar{g}}{v_h (1 - R R')}; \quad [14a]$$

$$C = -\frac{\Delta \bar{g} - R' c_{hw}}{v_g (1 - R R')}, \quad [14b]$$

which gives a symmetric alternative to Eq. 4.

It is interesting to note that the relationships between linear regressions with one and two explanatory variables, which are captured in Eq. 13 and give rise to HRG, appeared in the statistics literature as far back as 1897 (15).

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