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Hamilton's rule in economic decision-making

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Hamilton's rule [W. D. Hamilton, *Am. Nat.* 97, 354–356 (1963); W. D. Hamilton, *J. Theor. Biol.* 7, 17–52 (1964)] quantifies the central evolutionary ideas of inclusive fitness and kin selection into a simple algebraic relationship. Evidence consistent with Hamilton's rule is found in many animal species. A drawback of investigating Hamilton's rule in these species is that one can estimate whether a given behavior is consistent with the rule, but a direct examination of the exact cutoff for altruistic behavior predicted by Hamilton is almost impossible. However, to the degree that economic resources confer survival benefits in modern society, Hamilton's rule may be applicable to economic decision-making, in which case techniques from experimental economics offer a way to determine this cutoff. We employ these techniques to examine whether Hamilton's rule holds in human decision-making, by measuring the dependence between an experimental subject's maximal willingness to pay for a gift of $50 to be given to someone else and the genetic relatedness of the subject to the gift's recipient. We find good agreement with the predictions of Hamilton's rule. Moreover, regression analysis of the willingness to pay versus genetic relatedness, the number of years living in the same residence, age, and sex shows that almost all the variation is explained by genetic relatedness. Similar but weaker results are obtained from hypothetical questions regarding the maximal risk to her own life that the subject is willing to take in order to save the recipient's life.

Hamilton's rule | experimental economics | altruism | evolution

Significance

Kin selection—helping genetically related individuals even at a cost to oneself—can be evolutionarily advantageous. This is the main theoretical explanation for altruism in the natural world. Hamilton's rule provides a simple algebraic relationship that captures this profound idea. While behavior consistent with Hamilton's rule has been observed in many species, a direct and sharp test of this rule has not yet been performed. In this paper, we employ techniques borrowed from experimental economics to test the predictions of Hamilton's rule. We find strong support for the rule. This result sheds light on the dominant role played by evolutionary biology in explaining human behavior.

The fundamental idea of kin selection states that natural selection takes place at the level of the gene rather than at the level of the organism (1). It may therefore be evolutionarily advantageous for an individual to take an action that imposes a fitness cost to itself, if this action yields a sufficiently large fitness gain to a genetically related recipient. For a given fitness gain to the recipient, the higher the degree of genetic relatedness, the higher the personal cost the individual should be willing to pay. Hamilton's rule formalizes this idea by stating that an altruistic act is evolutionarily advantageous if $rB > C$, where C is the fitness cost to the altruist, B is the fitness gain to the recipient, and r is the genetic relatedness between them (2, 3). Evidence consistent with this rule covers a diverse range of species, including bees (4–6), wasps (7, 8), birds (9, 10), shrimp (11), monkeys (12, 13), and even plants (14). Hamilton's rule is widely accepted as the principal explanation for altruistic behavior in the natural world (15, 16) and is considered "one of the greatest theoretical advances in evolution since Darwin's time" (17).

Hamilton's rule yields a precise prediction of the maximal fitness cost, C^*, that an individual would be willing to "pay" for a given fixed benefit B to its relative: $C^* = rB$. This is the cutoff cost: For any cost smaller than C^*, the altruistic action is evolutionary advantageous, while, for any cost larger than C^*, it is disadvantageous. Hamilton's rule yields a very precise prediction for the cutoff cost: For a given benefit B, C^* is proportional to the genetic relatedness r. Observational studies typically estimate B, C, and r for a given behavior, and determine whether the observed behavior is consistent or inconsistent with Hamilton's rule (18). However, they do not allow for a sharp test of the rule, because they do not reveal the cutoff cost. In this study, we employ standard methods of experimental economics to find the cutoff cost, C^*, and to examine whether it is proportional to r, as predicted by Hamilton's rule.

Hamilton's rule is fundamentally about the evolution of genetically determined traits. One can think of Hamilton's rule having operated in the past at the level of the decision-making mechanism, shaping human behavior observed today (19, 20). This leads to the prediction that the proximate guides of behavior should be the marginal cutoff rule $C^* = rB$. Hamilton's rule is stated in terms of fitness gain and cost. However, to the extent that economic resources confer survival benefits, several authors have established possible links between economic decisions and Hamilton's rule (21, 22). Here we propose to test the cutoff predicted by Hamilton's rule in an economic decision-making context involving monetary transfers between individuals of varying degrees of genetic relatedness.

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In economic terminology, our application of Hamilton's rule can be viewed as a "reduced form" equilibrium result emerging from possibly complex population genetics dynamics (18–20, 23). In such dynamics, physical proximity may serve as a proxy for genetic relatedness, and demography plays an important role. In humans, kin recognition is based not only on explicit information transmission from parents to offspring but also on facial resemblance and olfactory cues (17). In this study, we directly examine Hamilton's rule, abstracting from the potentially complex underlying dynamics leading to it.

While it is established that people tend to help their relatives the more closely they are genetically related (24–28), surprisingly few studies have attempted to directly investigate Hamilton's rule in humans. Madsen et al. (29) experimentally measure the amount of time that subjects are willing to bear physical pain, with a reward paid to the subject's relatives proportional to this time. They find that subjects are willing to bear pain for longer times for more closely related individuals. While they observe a link between the relatedness of the subject to the individual and the amount of time the subject is willing to suffer pain, the relation is qualitative, and not very strong. Their design does not allow a direct examination of Hamilton's rule, because the cost to the subject and the reward to the relative are both proportional to the amount of time that the subject suffers pain.

Experimental Design

In our setup, we ask subjects a primary question: "What is the maximal amount of money that are you willing to pay in order for a recipient to receive \$50 from us?" This question is repeated with different recipients, in randomized order. The recipients are sibling ($r = 0.5$), half-sibling ($r = 0.25$), cousin ($r = 0.125$), nonidentical twin ($r = 0.5$), identical twin ($r = 1$), and a student randomly chosen by the computer ($r = 0$). This is then enacted with real money, the subject's reported cutoff values having substantial monetary consequences. Crucially, the experiment is set up so that the subject is best off by indicating his true cutoff value in each case; that is, there is no place for strategic behavior on the subject's part (for further details, see *Methods*).

We also ask the following hypothetical question: "Suppose that the recipient is in a life-threatening situation. If you do not take action, s/he will surely die. If you take action, s/he will be saved with certainty, but there is a probability p that you will lose your own life. What is the maximal value of p for which you will still take the action?" The question is repeated, each time with a different recipient (sibling, cousin, etc.). The details of the experimental procedure and the description of the subject population ($n = 256$) are provided in *Methods*.

Assumptions and Hypotheses

The hypothesis we set out to examine is $C^* = rB$. This requires an estimation of the fitness benefit, B, and the cutoff fitness cost, C^*. Several past studies have assumed that fitness is proportional to wealth (30, 31). This assumption may be too strong, however, as the biological concept of fitness is more closely related to the economic concept of utility than it is to wealth (32). In our analysis, involving concrete financial payoffs, we use a much weaker assumption. Since the amounts of money in the experiment are small compared to the subject's total wealth, we need only to assume that the marginal change in wealth is a proxy for the marginal change in fitness. For marginal changes in wealth, the changes in utility are approximately linear (33). The marginal change in wealth may therefore serve as a reasonable proxy for the marginal change in fitness. Namely, in our experiment, the \$50 gain to the recipient takes the role of B, and C^* is determined experimentally as the maximum amount the subject is willing to pay in order for the recipient to receive the \$50.

The marginal change in fitness may also depend on other parameters, such as the age, health, sex, and fertility of both the subject and the recipient. While we control for some of these factors, we cannot control for all of them. As we aggregate our data across many pairs of subject and recipient, however, because these factors are nonsystematic, most of these effects are expected to cancel out.

Finally, in our hypothetical questions, the proxy for fitness is life itself. Again, this is not a perfect proxy, as fitness depends on other factors, some of which we cannot control. In the aggregate, however, we expect most of the effects of these factors to cancel out.

To differentiate between genetic relatedness and social proximity, in our multivariate analysis, we control for the years the subject and recipient shared the same residence. We also use a control for the "most favorite" and "least favorite" recipient of a given type. A natural concern in our experimental setup is the possibility of "side payments," that is, the possibility that the subject will request some part of the money from the recipient. To address this concern, all subjects sign a formal statement in which they commit not to take such action. To eliminate possible reciprocity, we also do not allow recipients to participate as subjects; for example, we do not allow both siblings in the experiment as subjects.

Results

Fig. 1 illustrates our main results. Fig. 1*A* shows the mean maximal willingness to pay as a function of the genetic relatedness. The diagonal line represents the theoretical prediction of Hamilton's rule, $C^* = rB$. The experimental results are in very good agreement with the theoretical prediction ($R^2 = 0.94$). One notable exception is the mean willingness to pay in the case of identical twins. While higher than for all other cases, it is still substantially lower than the theoretical prediction.

Fig. 1*B* shows the average results for the hypothetical questions about a life-threatening situation. Again, the diagonal line presents the theoretical prediction of Hamilton's rule. The willingness to take risk increases with the genetic relatedness, as expected by theory ($R^2 = 0.87$). However, in most cases, the willingness to take risk exceeds the theoretical prediction. This is likely due to "cheap talk," that is, as the subject's responses have no real consequences, subjects may inflate their reported willingness to take risk. As before, there is an exception in the case of identical twins, where the results are lower than predicted by Hamilton's rule.

An alternative hypothesis to Hamilton's rule states that altruism is driven by social proximity, rather than by genetic relatedness. To differentiate between these two competing hypotheses, we estimate a multivariate mixed-effect regression where the dependent variable is the willingness to pay (or the willingness to take risk), and the explanatory variables are genetic relatedness, the number of years that the subject and recipient lived in the same home, and the age and sex of both subject and recipient. If the subject has more than one recipient of the same type (e.g., the subject has two or more siblings), we repeat the questions for both the "most favorite" and the "least favorite" recipient. This explanatory variable takes the value of 1 for "most favorite," -1 for "least favorite," and 0 in the case where there is only one recipient of a given type. As each subject answers several questions, subject identity is

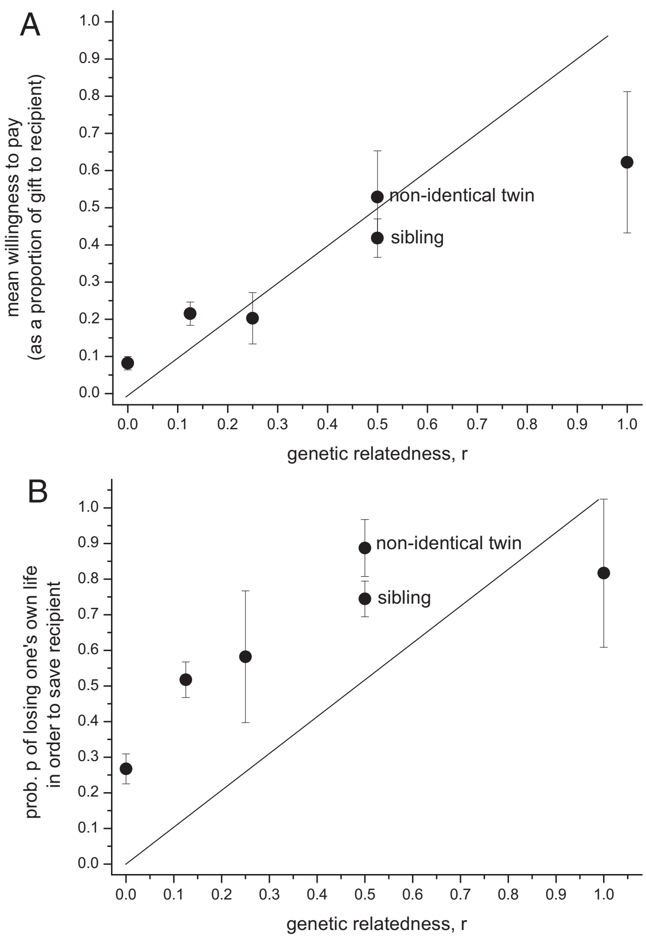

Fig. 1. Willingness to pay and willingness to take on personal risk as a function of genetic relatedness to the recipient. The diagonal line depicts the predictions of Hamilton's rule, $C^* = rB$. Mean results are reported, with the error bars indicating two SEs. When money is involved (*A*), the results are very close to the theoretical predictions ($R^2 = 0.94$), except in the case of identical twins. When the questions are hypothetical (*B*), the willingness to take risk increases with the genetic relatedness ($R^2 = 0.87$), but subjects are generally more altruistic than predicted by theory, consistent with the "cheap talk" argument.

treated as a random effect (see *Methods* for further details). An additional possible way to disentangle pure kin selection from social proximity could be to compare willingness to pay when the recipient is a genetically unrelated friend versus the case where the recipient is a stranger. This alternative is not explored here, and is left for future work.

Table 1 reports the results when the dependent variable is the willingness to pay, and Table 2 reports the results when the dependent variable is the willingness to take risk. In both cases, genetic relatedness is highly significant. In stepwise ordinary least squares (OLS) regressions, it is the first variable included. The addition of all the other explanatory variables only increases the R^2 from 0.313 to 0.346 for willingness to pay, and from 0.250 to 0.258 for willingness to take risk (note that these R^2 s, which are obtained for individual-level regressions, are lower than the R^2 values in Fig. 1, which are for the aggregate-level results). The most/least favorite variable is significant in the case of willingness to pay (Table 1) but not in the hypothetical case of willingness to take risk (Table 2).

Discussion

The methodology of experimental economics offers a sharp test of Hamilton's rule applied to a specific economic decision-making context by eliciting the maximal cost a subject is willing to bear, either in terms of money or mortality risk, for another individual to receive a given benefit. Hamilton's rule predicts that this cutoff is proportional to the genetic relatedness between the subject and the recipient. When the questions are hypothetical, the willingness to take risks increases with the genetic relatedness, but the subjects appear to be overaltruistic relative to the rule, presumably because their answers have no real consequences ("cheap talk"). However, when real and substantial financial consequences are involved, we find very good agreement with the theoretical predictions of Hamilton's rule.

There is one notable exception to this close agreement, in the case of identical twins, in which the results are visibly lower than those predicted by Hamilton's rule. One possible explanation is that identical twins are rare (~0.4% of births) (34), and it is likely that survival rates for twins were lower than for single births in human evolution. The evolutionary forces toward altruism may therefore be weaker than expected in the case of identical twins. Moreover, individuals feel their own pleasure and suffering more keenly than the emotions of others, even of an identical twin. Thus, even if the evolutionary break-even cost–benefit ratio is 1:1, as in the case of identical twins, individuals may not be completely indifferent to their own cost–benefit compared to that of their identical twin.

Shaped by nurture, education, culture, social norms, and religious belief, human behavior is highly complex and adaptive. People are organized in complex social networks, embedded in multiple dimensions (kinship, professional ties, geographic proximity, etc.) (35, 36). Resource sharing, reciprocity, and competition play important roles in these networks (20, 37–39).

Table 1. Multivariate regression with willingness to pay as the dependent variable

	(1)	(2)
Const	0.010	0.156
	(9.69)	(4.21)
r	0.647	0.455
	(14.68)	(3.91)
Age difference		−0.0005
		(−0.44)
Years together		0.003
		(1.15)
Sex–subject		−0.001
		(−0.08)
Sex–recipient		−0.042
		(−0.86)
Same sex		−0.014
		(−0.80)
Most/least favorite		0.038
		(3.78)

The sex variable is defined as 1 for male, 0 for female, and 0.5 if unknown, as in the case of a random recipient. The same sex variable is defined as 1 if both subject and recipient are of the same sex, 0 if they are of the opposite sex, and 0.5 if the recipient's sex is unknown. Const is the regression constant. Age difference is the subject's age minus the recipient's age, in years (and 0 if the recipient's age is unknown). As each subject makes several choices, the number of observations, $n = 515$, is larger than the number of subjects. To address possible dependence between the answers of the same subject, we employ a linear mixed-effect regression model treating subject identity as a random effect. The regression fixed-effect coefficients are given in the table, with their *t* values in parentheses. Column 1 provides the results when the genetic relatedness, *r*, is the only explanatory variable, and column 2 provides the results when all explanatory variables are employed; *r* is highly significant in both cases. The only other significant variable is the most/least favorite variable. In a stepwise OLS regression analysis, the first explanatory variable included is the genetic relatedness, *r*, and the second explanatory variable included is the most/least favorite variable. None of the other variables are included. When *r* is the only explanatory variable, the OLS R^2 is 0.313; when all explanatory variables are included, the R^2 increases only to 0.346.

Table 2. Multivariate regression with willingness to take risk as the dependent variable

	(1)	(2)
Const	0.340	0.442
	(15.63)	(4.46)
r	0.820	0.366
	(17.68)	(2.68)
Age difference		0.002
		(1.39)
Years together		0.005
		(1.66)
Sex—subject		−0.032
		(−0.79)
Sex—recipient		−0.033
		(−0.23)
Same sex		−0.015
		(−0.56)
Most/least favorite		0.013
		(0.96)

The explanatory variables are defined as in Table 1. The table shows results of linear mixed-effect regressions when using r as a single explanatory variable (column 1), and with all explanatory variables included (column 2). The fixed-effect regression coefficients are given in the table, with the t values in parentheses (n = 515). Genetic relatedness, r, is the only significant explanatory variable. It is interesting to note that the age difference coefficient is positive (albeit not significant), consistent with theories of kin detection in humans. In a stepwise OLS regression analysis, the only explanatory variable included is the genetic relatedness, r. When r is the only explanatory variable, the OLS R^2 is 0.250; when all explanatory variables are included, the R^2 increases only to 0.258.

Therefore, one may be surprised by the strong explanatory power of the forces of evolutionary biology on such complex human behavior. It is perhaps possible that these ancient forces are acting indirectly and under the surface on human behavior, by shaping social networks, norms, and morality to exert their influence.

Moreover, we cannot rule out the possibility that our subjects have been exposed to Hamilton's rule through educational or media channels, and are therefore reflecting that preconditioning rather than innate behavior arising from natural selection. Whether such preconditioning would give rise to the exact numerical trade-offs that Hamilton's rule implies is a question that we cannot answer with our study design. However, an experiment to quantify the impact of preconditioning—in which a group of volunteers is deliberately exposed to a lecture on Hamilton's rule and then asked to participate in our study along with a control group that receives no preconditioning—may be able to shed light on the magnitude of preconditioning. Our experimental results provide a more nuanced conclusion: Economic decision-making and monetary reward does provide one proximate manifestation of Hamilton's rule.

Methods

All subjects completed a questionnaire in four parts. The first part was composed of informational questions, including family composition (e.g., "Do you have siblings?"). The second part included questions involving real money payments (e.g., "What is the maximal amount of money that are you willing to pay in order for your sibling to receive $50 from us?"), while the third part included questions about hypothetical life-threatening situations. The last part asked a question that tested rationality (see below), used to verify that the subject had paid attention to the questionnaire. The experiment was approved by the Hebrew University Ethics Committee. All participants provided informed consent. The full questionnaire is available at https://huji.az1.qualtrics.com/jfe/preview/SV_6M8PKRDriO9kBmZ?Q_SurveyVersionID=current&Q_CHL=preview.

Subjects (n = 256) were 42.4% male and 57.8% female. The average subject age was 26.3 y (SD 6.6 y). The experiment was conducted during 2019–2020 in two locations: the Massachusetts Institute of Technology (MIT) Laboratory for Financial Engineering (85 subjects) and the Hebrew University Rationality Lab (171 subjects). Subjects filled out the survey on laboratory computers. As the experiment was conducted in two different countries, the monetary payoffs were denominated differently in the two locations: at MIT, the recipient of the altruistic action received $50, and, at the Hebrew University, she received 100 new Israel shekels (NIS) (at the time of the experiment, 100 NIS ≈ $28.) In both cases, the subjects' willingness to pay is reported as a proportion of the benefit to the recipient. Subjects received an up-front show-up fee of $50/100NIS in cash. The results were similar for the two subject groups–see *SI Appendix* and *Dataset S1*–and, therefore, in our main analysis, we report the aggregate results.

Crucially, the experimental setup was designed such that the subject would be motivated to reply truthfully, that is, to report the true maximal value he is willing to pay. This was achieved by the following procedure: After the subject stated her cutoff value X, the computer generated a random number Y between 1 and 50 (or between 1 and 100 in the Hebrew University setting). If $Y > X$, no "deal" was made; that is, nothing happened. If $Y < X$, the "deal" was executed at Y: The subject paid Y, and her relative received $50 (or 100 NIS), sent by the researchers via mail. This setup gave subjects an incentive to state their true cutoff X: If a subject reports a number that is larger than her true cutoff, she may end up executing deals that she does not want; if she reports a number that is smaller than her true cutoff, she may give up deals that she does want.

This mechanism was explained to the subjects in detail. Before introducing the questions involving real money, the subjects were given two "training" questions, to verify that they understood the experimental setup. If they answered a training question incorrectly, they were given the correct answer and an additional explanation of the setup.

As with any experiment involving human subjects, it is possible some subjects may not understand the experiment, and others may want to receive their fee and to finish the experiment as quickly as possible, without paying serious attention to the questions. In order to screen these subjects, in our analysis, we only included subjects who answered the second training question correctly, and who also answered the very last question in the survey, which is a test of rationality, correctly. This last question is as follows: Consider the two lotteries A and B in Table 3. If you had to choose one of these lotteries, which one would you choose?

Table 3. Test of rationality

Lottery A		Lottery B	
Probability	Prize, $	Probability	Prize, $
1/3	120	1/3	90
1/3	100	1/3	115
1/3	80	1/3	130

Note that lottery B dominates lottery A by first-degree stochastic dominance; therefore, all rational subjects who prefer more money over less money should choose lottery B (40); 151 (59%) of the subjects answered both the second training question and the rationality question correctly: 44 from MIT (average age 29.4, 72.7% female) and 107 from the Hebrew University (average age 25.0 y, 51.4% female). The reported results are for these 151 subjects.

A possible concern is that subjects were knowledgeable about Hamilton's rule and consciously tried to follow it to fulfill normative expectations. However, most subjects (86.3%) had no educational background in either biology, psychology, or medicine, and hence were not likely to have studied Hamilton's rule. Moreover, as the subjects' choices had rather substantial monetary consequences, they were motivated to answer truthfully, rather than according to normative expectations. Nevertheless, we cannot rule out the possibility of such preconditioning without additional controls and more-sophisticated experiment designs with much larger sample sizes.

Data Availability. All study data are included in the article and/or supporting information.

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