

PERMISSIBLE SPITE: KIN SELECTION, DEMOGRAPHY, AND THE INVERSE HAMILTONIAN EQUATION

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Abstract: This article revisits Hamilton's rule by proposing an inverted formulation to evaluate the evolutionary permissibility of spiteful behavior within kin-based populations. We formalize a reverse Hamiltonian equation and apply replicator dynamics to investigate the demographic and genetic conditions under which within-group aggression may become evolutionarily stable. The model shows that in low-fertility populations, even close kin may be treated as expendable, while high fertility expands the range of altruistic stability. These findings highlight a previously overlooked symmetry between altruism and aggression and reveal how reproductive demography critically influences the logic of inclusive fitness. The proposed framework provides new analytical tools for understanding kin-directed conflict and the shifting boundaries of social norms under demographic constraints.

Keywords: Inclusive fitness theory, spiteful behaviour, mathematical modeling, kin selection, demographic parameters, altruism and aggression, evolutionary game theory

1 INTRODUCTION

In an era of digital transformation and social innovation, kinship — once central in the social sciences — has gradually faded from scholarly focus. This shift is not surprising: over the past decades, the structure and function of the family have undergone significant changes. Families have become more compact, and there has been a growing diversity of kinship and affiliative bonds, many of which now extend beyond biological criteria (Becker, 2022). Ongoing societal transformations are prompting a rethinking of kinship even at its most fundamental levels. As a result, in some countries, social attachment—rather than biological connection—has begun to take precedence in family law (Semenova, 2025; Bedin, 2018). Legal frameworks increasingly support stable social ties, even in cases where these conflict with genetic relatedness (Almeida, 2017).

Nevertheless, despite the social transformation of the family, biological foundations of kin-directed care continue to manifest across diverse cultural contexts and call for explanation through formal, mathematical modelling. In evolutionary biology, genetic relatedness remains a powerful determinant of altruistic assistance and social investment among relatives — parents, grandparents, uncles and aunts, nieces and nephews — even in modern societies. Studies conducted in post-industrial European societies show that biological grandmothers continue to provide substantial support in caring for grandchildren. Demographic analyses confirm that such intergenerational investment significantly increases critical biosocial parameters — such as child survival and total fertility rates — when grandparents participate in child-rearing (Chapman et al., 2021; Lahdenperä et al., 2004). Similar effects of increased inclusive fitness due to kin proximity have long been observed by ethnographers in traditional societies and remain evident today (Sear & Mace, 2008). Data from modern post-industrial societies also reveal the strong involvement of extended kin in childcare. Kin support from older generations remains robust and, according to fieldwork conducted by the author, can at times even exceed parental involvement (Semenova et al., 2025).

A key factor underlying the expression of altruistic kin care is the degree of biological relatedness and the perceived certainty of genetic ties. For example, the hypothesis of preferential investment in a daughter's offspring (Daly and Perry, 2017) stems from the assumption that grandmothers are more certain of their biological relationship to grandchildren via the maternal line than the paternal. While the actual risk of non-paternity in contemporary societies is considered relatively low, consistent differences in grandparental care have nonetheless been documented between maternal and paternal kin (Semenova and Butovskaya, 2022).

These empirical observations are especially noteworthy because they demonstrate the universal applicability of core evolutionary paradigms to theories of parenting and kin investment (Hawkes and Jones, 1997). Still, one may ask a fundamental question: Why does discrimination against non-kin remain a dominant behavioral strategy? Why is kin-directed care so stable that flows of altruism and mutual aid continue to selectively bind genetically close individuals — even amid deep cultural and institutional transformations in modern societies? What underlies the persistence of these attachments, despite the profound restructuring of the family?

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Understanding the resilience of kin-based altruistic strategies requires revisiting one of the central concepts in evolutionary biology: the theory of kin selection. In 1964, William Hamilton introduced a rigorous mathematical formulation describing the condition under which altruistic behavior can be evolutionarily advantageous:

$$r \cdot B > C,$$

where r is the coefficient of relatedness between the altruist and the beneficiary, B is the fitness benefit to the recipient, and c is the cost to the altruist. According to this inequality, evolution may favor behaviors that reduce individual fitness if they increase the survival chances of genetically related individuals. For example, a behavior that benefits a full sibling by more than twice the cost to oneself (given $r = 1/2$) can be selected for. The same logic applies to more distant kin, adjusted proportionally for the degree of relatedness.

For decades, this simple yet powerful inequality has been regarded as the cornerstone of inclusive fitness theory. However, as with many universal principles, its mathematical development has remained partial. Hamilton himself did not provide a dynamic model or formal analysis of stability; his equation functioned as a heuristic rather than a predictive framework. Meanwhile, contemporary biology has increasingly turned to evolutionary game theory to simulate the dynamics of kin altruism in populations with defined selection parameters (Maynard Smith, 1982; Semenova 2024a, b; Semenova, Brazhnikov and Butovskaya, 2023). A key advantage of this approach lies in its ability to model iterative agent interactions, allowing researchers to explore selective forces acting within a population. These simplified population models are often used to approximate the emergence of economic, logical, or biosocial strategies in human societies (Semenova and Butovskaya, 2021).

In this article, we propose a visualization and mathematical analysis of an alternative interpretation of Hamilton's equation — not as a description of altruism per se (as in Preston, 2013), but as a tool for quantifying the threshold of permissible harm within kin groups. Hamilton's formula is logically symmetric: by inverting the sign of the interaction, one can reinterpret it to describe the evolutionary logic behind aggression, repression, or other forms of harm toward individuals with varying degrees of relatedness to the actor. This inversion allows us to ask: under what conditions could harming, or even killing, a relative become evolutionarily advantageous? And what demographic or social parameters — such as declining fertility — might shift the balance so that spite toward kin becomes a dominant evolutionary strategy?

The idea of inverting Hamilton's rule was inspired by the work of Andy Gardner and Stuart West (Gardner and West, 2004), who proposed applying Hamilton's inequality not as a model of altruism, but as a framework for analysing spiteful or harmful behavior. In formalizing such aggression, Gardner and West introduced the notion of negative relatedness. However, we argue that this construct, while mathematically convenient, is biologically and anthropologically problematic: all non-kin are, by definition, less related, and this distinction does not require a negative metric to be meaningful.

In our approach, we reinterpret the inequality itself and formalize a scenario in which the actor harms another individual — potentially even a relative — in order to preserve their own life or that of their descendants. This inverted model allows us to specify a threshold condition for permissible spite based on demographic and behavioral parameters, without resorting to the abstraction of negative kinship. At the same time, it retains the formal structure and conceptual logic of Hamilton's original equation.

The work of Alan Grafen (Grafen, 2009) also contributed to the revision of our model. Grafen proposed a critical clarification: to interpret Hamilton's rule not in terms of abstract fitness, but in terms of actual offspring count — in our case, fertility. This perspective makes the model operationalizable and empirically testable, especially in light of ongoing demographic shifts and declining birth rates in post-industrial societies. In this paper, particular attention is given to replicator dynamics and to the question of whether a "threshold" exists — what we term a fitness watershed — that separates the zone of permissible spite from the domain of altruistic constraint, and how this watershed shifts with demographic changes.

Thus, this study not only refines the quantitative boundary between altruism and aggression within kin groups but also reveals the conceptual ambiguity of traditional inclusive fitness logic. We propose a broader interpretation of Hamilton's rule — not solely as a model of helping behavior, but also as a tool for analysing harm, cost, and the evolution of social strategies.

2 METHODS

The original formulation of Hamilton's rule is expressed as:

$$r \cdot B > C,$$

where B represents the number of additional offspring produced by the recipient as a result of the altruist's help, C denotes the number of offspring the altruist sacrifices (i.e., the cost of helping), and r is the coefficient of relatedness between the two individuals.

Let us now assume that an individual causes spite rather than provides help. That is, the actor commits a harmful act toward another member of the social group (potentially even a killing), which can be quantified in terms of the victim's unrealized reproductive potential. The benefit in this case is the reward to the aggressor — namely, their own survival (e.g., through resource acquisition, reduced competition, etc.).

We define:

B' as the number of unborn offspring lost by the victim,
 C' as the value of the aggressor's survival,
 r as the genetic relatedness between the aggressor and the victim.
 The new inequality becomes:

$$r \cdot B' < C'$$

This implies that aggression is only evolutionarily justified if its benefit (i.e., the value of the aggressor's survival) outweighs the loss inflicted on the kinship structure (in the form of unrealized offspring). This defines an evolutionary threshold for permissible harm: "Do not kill your kin — even distant ones — unless the benefit to yourself is substantially greater." It provides an ethically and mathematically grounded boundary, derived directly from the logic of Hamiltonian inclusive fitness.

3 RESULTS

3.1 Inverse Hamilton's Equation

In our model, we assume that the benefit to the aggressor is fixed at $C = 1$, representing the preservation of their own life. Of particular interest is how this dynamic plays out under varying fertility conditions — specifically, the parameter B , which represents the number of potential offspring the victim would have had. We begin by calculating and visualizing the inverse Hamiltonian inequality under contemporary fertility conditions. According to the United Nations World Population Prospects (2022), the total fertility rate in most post-industrial countries ranges between 1.3 and 1.6 children per woman, reflecting sustained low fertility levels characteristic of these regions (United Nations, 2022). For modelling purposes, we adopt an approximate value of ≈ 0.7 children per individual, accounting for both sexes equally. This approach facilitates the integration of demographic parameters into our evolutionary model while acknowledging its simplified nature.

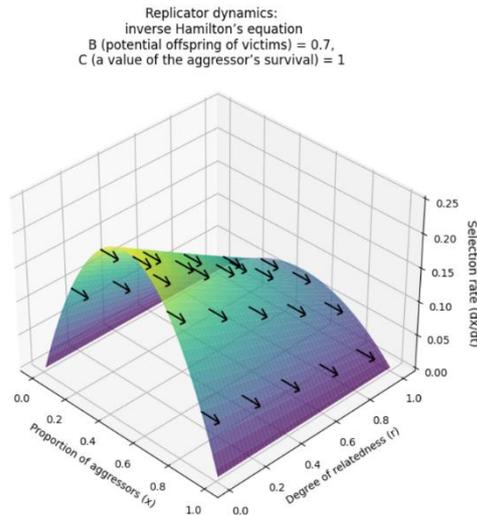


Figure 1: The three-dimensional surface represents the rate of increase in the frequency of the aggressive strategy in a population, under the following conditions: $B = 0.7$ (expected offspring per adult), $C = 1$ (fixed benefit of aggression), and r – relatedness from unrelated individuals to identical genetic self. The X -axis represents the frequency of aggressors, Z -axis the degree of relatedness, and Y -axis the selection gradient (rate of change in strategy frequency).

The simulation shows that under a modern fertility rate of $B \approx 0.7$, altruism is only evolutionarily stable if relatedness exceeds $r > 1.43$ — a biologically impossible value, as the theoretical maximum is $r = 1$ (complete self-relatedness). This means the inequality is never satisfied under current demographic conditions, and the selection gradient remains at or above zero — favoring the spread of spite and aggression. In other words, even close kin do not “pay off” the cost of altruism under low fertility. This could help explain the weakening of kin-based altruism in modern societies and the rise of individualism. To suppress aggression evolutionarily, either the reproductive value of the victim must be significantly higher (e.g., 4–6 offspring in pre-industrial settings), or the benefit to the aggressor (C) must be lower.

3.2 Scenario: Low Fertility with Altruistic Payoff

Another potential resolution is to introduce an exogenous fitness reward for altruists. In this variant, non-aggressive individuals receive a baseline fitness level of $W_2 = 0.6$. The dynamics of aggressor versus altruist under this condition are shown in Figure 2.

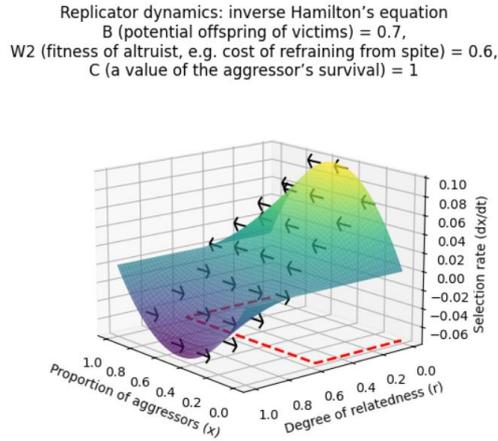


Figure 2: 3D surface of selection rate (dx/dt) under low fertility ($b = 0.7$), with altruist fitness $w_2 = 0.6$ and benefits for aggressors $c = 1$. Yellow area indicates selection for aggression; blue area indicates selection for altruism. Red dashed line shows the Hamiltonian threshold.

The graph illustrates a transition from positive to negative values along the vertical axis (Y), representing a shift from selection favoring aggression to selection acting against it. This is visualized by a blue-shaded region located below the zero level on the vertical axis, indicating a negative selection gradient for aggression. In this zone, the frequency of spiteful individuals declines — altruists begin to prevail. The deeper the surface dips below zero, the stronger the selective pressure against individuals who harm their kin.

We also observe that as relatedness increases along the Z -axis, the selection pressure favoring aggression diminishes and eventually becomes negative — signalling an evolutionary advantage for altruistic behavior.

3.3 High Fertility Scenario

To analyse how demographic changes — particularly declining birth rates in post-industrial societies experiencing the second demographic transition — affect evolutionary dynamics, we simulated two high-fertility conditions. In these models, each individual is assumed to have on average three (Figure 3) or five (Figure 4) offspring.

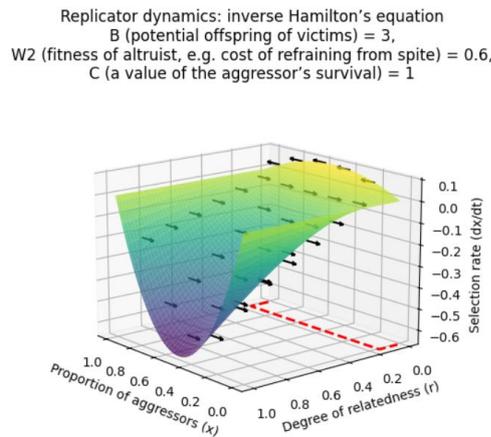


Figure 3: 3D surface with $b = 3$, $w_2 = 0.6$, and $c = 1$. As kinship increases (Z -axis), selection pressure shifts from aggression to altruism. The red dashed line marks the threshold where spite to kin becomes maladaptive.

Replicator dynamics: inverse Hamilton's equation
 B (potential offspring of victims) = 5,
 W_2 (fitness of altruist, e.g. cost of refraining from spite) = 0.6,
 C (a value of the aggressor's survival) = 1

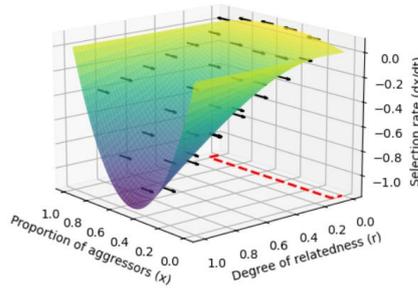


Figure 4: Simulation under high fertility conditions ($b = 5$). The yellow region, where spiteful behavior is adaptive, shrinks considerably. Natural selection favors altruism even at low kinship levels. The red dashed line indicates that the threshold has shifted to a lower relatedness value ($r \approx 0.08$)

These simulations show that when kinship is low (left side along the Z-axis), aggression is favored, especially when the proportion of aggressors in the population is moderate (see the red dashed line threshold on fig.1). As relatedness increases, the selection gradient decreases and turns negative — favoring altruism (see figure 3 and 4).

Across all graphs, we observe how the structure of the selection landscape changes when the expected number of offspring increases — from 0.7 to 3, and then to 5 per individual. As fertility increases, the yellow region — representing the evolutionary advantage of the spite — shrinks and the red dashed line shifts to a lower relatedness value. The selection gradient for aggression declines, and the protruding yellow surface becomes flatter. Meanwhile, the transition to altruism (the blue region) shifts toward lower levels of relatedness, meaning that altruistic behavior becomes evolutionarily stable even toward more distant kin. Moreover, the selection gradient for altruism — the depth and slope of the descending blue curvature — becomes more pronounced in high-fertility populations.

3.4 Threshold Relatedness Values

The red dashed line visible in each figure marks the Hamiltonian threshold — the point at which the cost of harming kin exceeds the evolutionary benefit. It appears visually as a sharp bend or “drop” in the selection surface, dividing the aggression-dominant zone from the altruistic one.

The position of this threshold — this “fitness watershed”— shifts based on demographic inputs. Our results show that under high-fertility conditions, only extremely distant relatives (those with near-zero relatedness) can be justifiably harmed. In contrast, under low modern fertility rates, even individuals with $r = 0.5$ (e.g., siblings) may fall below the altruism threshold, making harm toward them selectively advantageous —even with altruistic fitness benefits included.

Fertility Rate, (B) (offspring per individual)	Altruist Fitness (W_2)	Approximate Kinship Level
0.7	0	1.429 - Closer than identical twin (unrealistic)
0.7	0.6	0.571 - Closer than sibling ($1/2$)
3	0.6	0.133 - Between first cousin ($1/8$) and second cousin ($1/16$)
5	0.6	0.080 - Between second cousin ($1/16$) and third cousin ($1/32$)

Table 1: Threshold Relatedness Values (Fitness Watersheds) Under Varying Fertility Rates. The threshold value of relatedness r at which selection begins to favor altruism is calculated using the formula: $r^* = (C - W_2) / B$, where: $C = 1$ — benefit to the aggressor (e.g., survival), W_2 — fitness of the altruist, B — reproductive benefit (expected offspring) of the potential victim.

4 DISCUSSION AND LIMITATIONS

4.1 Insights from the Inverse Hamiltonian Model

Our visual simulations demonstrate that even the classical Hamilton's rule can be reinterpreted from the standpoint of the evolutionary stability of spite, rather than help. In the inverted formulation, where:

$$r \cdot B' < C',$$

we formalize a condition under which harming another individual is evolutionarily justified if the benefit to the actor exceeds the potential genetic loss from harming a relative. Thus, this inequality can be read not as a condition for altruism, but as a threshold for permissible spite within kin-based populations, analogous to the legal principle of necessary self-defense.

The models and surfaces we presented provide a quantitative and geometric interpretation of this inverse Hamiltonian framework, expanding the analytical horizon of the original equation. The conflict between altruism and individualism is thereby reframed not only as a moral dilemma, but as an analytical problem — determined by the parameters of relatedness, fertility, and payoff differentials, and shaped by the conceptual perspective (i.e., sign) we adopt in defining aggression versus cooperation.

Our study introduces a mathematical formulation of a "threshold of permissible spite," which may align not only with biological constraints but also with culturally embedded taboos in human societies. It is important to note that all versions of the Hamiltonian model exhibit disruptive selection: mixed strategies are unstable, and populations tend to evolve toward either 100% aggressors or 100% altruists, depending on initial conditions and the values of relatedness (r), benefit to the recipient (B), and cost to the actor (C).

This dynamic shift is the focus of our analysis toward demographic scenarios in which the expected loss of offspring for a potential victim varies—ranging from marginal to substantial (e.g., three or five children per individual). One of our central findings is that the balance between aggression and altruism is highly sensitive to demographic parameters. At low fertility levels, selection almost always favors the aggressor, even when the victim is a close relative.

Notably, the transition from harm to restraint is not gradual but threshold-like: on the modeled fitness surface, we observe a sharp discontinuity beyond which selection pressure for aggression rapidly collapses. This nonlinear behavior suggests the existence of an evolutionary watershed, analogous to phase transitions in physics.

Our results further indicate that for altruism to become evolutionarily stable, one of the following conditions must hold: (1) extremely high relatedness (biologically unrealistic), (2) substantially greater reproductive potential for the victim, or (3) reduced payoff for the aggressor. This implies that current low-fertility regimes in post-industrial societies may create evolutionary conditions in which even intrafamilial aggression becomes selectively advantageous.

An unexpected outcome of our model is the prediction that higher fertility can promote altruism, which contrasts with classical Life History (r/K selection) theory. While r -strategies (high fertility) are typically associated with increased competition and aggression, our model captures micro-dynamics within kin groups, whereas Life History theory concerns macro-evolutionary patterns of reproduction and survival — often overlooking kin-structured interactions.

In conclusion, we suggest that this inverted model offers a new analytical framework for exploring not only kin-directed altruism and aggression, but also the evolutionary logic of cannibalism, parasitism, punishment, and social norms, such as taboos against harming kin. It provides a scalable tool for integrating demography into models of ethical and evolutionary behavior in both biological and anthropological domains.

4.2 Limitations and Directions for Future Research

Despite the clarity and expressiveness of the visual results, the proposed model entails several simplifying assumptions. We employed the classical formulation of replicator dynamics, which assumes an infinitely large population and does not account for the stochastic nature of interactions. Furthermore, the model lacks a structural description of genetic or social networks: the degree of relatedness between individuals is treated as a smooth, continuous function (r), which does not reflect real-world population structures involving kin clusters, coalitions, or patterns of migration.

We also did not incorporate repeated interactions, memory of past behavior, or strategic responses such as coalition-based punishment of defectors. These elements can significantly affect the stability of both aggression and altruism in real communities. Nonetheless, our model provides a foundation for the quantitative analysis of permissible harm thresholds, depending on relatedness and fertility, and can serve as a useful framework for exploring social norms, sanctions, and institutions of altruism in the context of demographic contraction.

It is also worth addressing the logical vulnerability of Hamilton's original formulation. All three variables (r , B , and C) are presented as abstract and interchangeable numerical values. In practice, they may all derive from the same underlying metrics — relatedness and number of offspring — whether pertaining to the donor or the recipient of a harmful or altruistic act. This symmetry can be misleading: while it contributes to intuitive appeal, it may undermine

the explanatory power of the model when applied to complex social realities. For instance, if the average number of children per individual in a population is three, then the value of an individual's life could be estimated at three potential descendants. In such a framework, the costs and benefits appearing on either side of Hamilton's inequality become effectively equivalent, making the calculus of altruism versus harm analytically unstable unless additional constraints or context-specific interpretations of "life value" are introduced.

Even though our model inverts inequality and reinterprets the roles of the variables, it does not necessarily escape these conceptual limitations. Critics of classical kin selection theory have long noted that, despite its mathematical elegance, inclusive fitness theory often fails to account for the actual mechanisms of social evolution (Nowak et al., 2010; Wilson et al., 2023; Richerson et al., 2016). As a result, nowadays greater emphasis has shifted toward empirical approaches, multi-level selection theory, and evolutionary game-theoretic models of strategy development.

In recent years, attention in kinship research has increasingly moved toward more complex explanatory factors: colony stability, ecological constraints, behavioral plasticity, and multi-factorial interactions among individuals. This transition reflects a broader shift in evolutionary biology —from formal equations to interdisciplinary syntheses of data, observation, and modeling. Such logic extends beyond the classical aggressor-versus-victim dichotomy and demands a deeper theoretical integration of the drivers of social evolution, beyond the scope of simple adaptationist or cooperation-based frameworks.

5 CONCLUSIONS

The modeling reconstruction of the inverted Hamilton's equation enabled us to numerically identify the parameter space in which harmful behavior becomes evolutionarily advantageous. The fitness surface derived from replicator dynamics reveals a sharp transition from aggression to altruism as relatedness increases. This boundary — denoted in our visualizations as the "Hamiltonian threshold"—marks the point where the aggressor's benefit no longer compensates for the genetic loss incurred by harming a relative.

Visually, this transition appears as a pronounced break in the selection surface — a "drop" from the aggression-dominated region (yellow zone) to altruistic dominance (blue zone). The selection gradient favoring aggression is positive at low relatedness and moderate frequencies of aggressors in the population but decreases sharply and turns negative as relatedness increases. Thus, refraining from harm becomes an evolutionary stable strategy.

Particularly insightful were the simulations incorporating variable numbers of offspring for potential victims (B). The results indicate that as the expected fertility of the victim increases, the yellow aggression-favoring region shrinks, and altruism prevails even among relatively distant kin. Conversely, at contemporary post-industrial fertility rates (approximately 0.7 offspring per individual), even sibling-level relatedness ($r = 1/2$) fails to prevent selection favoring harmful strategies. In the extreme case where altruistic benefits are excluded entirely, no biologically plausible relatedness level can sustain altruism — r would need to exceed 1.43, which is impossible.

Hence, the inverted Hamiltonian equation offers not only a mathematical model for aggression and altruism but also an analytical tool for assessing social risks and the stability of ethical norms amid demographic decline. In high-fertility social groups, altruism can be evolutionarily stable even among distant relatives. In contrast, in the context of modern demographic depopulation, even close kinship loses evolutionary efficacy as a constraint on aggression. This finding opens avenues for further research ranging from anthropological modeling of social norms to applied biopolitics. Ultimately, our findings underscore the importance of integrating demographic realities into evolutionary models of social behavior, inviting future research that bridges mathematical modeling, cultural evolution, and ethical norm formation.

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