

The Evolutionary Roots of Familial Altruism: Paternity Uncertainty Shapes Patterns of Kindness

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Abstract

We investigated how paternity uncertainty (PU) shapes perceptions of familial kindness. We predicted that relatives with lower PU would be rated as kinder than those with higher PU. A total of 9,128 participants rated the kindness of specific relatives in their families. Main analyses focused on parents and maternal/paternal grandparents, who differ in their typical levels of PU. Siblings were included for broader within-family comparisons, while step-relatives, all having identical (maximal) PU, served as negative controls. Controlling for sex, age, and random effects of raters and targets, results supported PU predictions: PU showed a negative correlation with rated kindness ($\beta = -0.148$, $t_{(31,910)} = -6.23$, $p < 0.001$, with the full model (including PU) significantly outperforming a reduced model ($\chi^2_{(2)} = 42.84$, $p < 0.001$). Post-hoc tests revealed significant differences between adjacent PU levels (0 vs. 1: $p < 0.001$, $d = 0.15$; 1 vs. 2: $p = 0.0002$, $d = 0.08$). Mothers and maternal grandmothers (no PU) were rated the kindest, while the paternal grandfather (two PU) was rated lowest. Daughters consistently rated their biological parents higher than sons, possibly reflecting lower PU through female offspring. Maternal grandfathers were rated kinder than fathers, despite identical PU, perhaps due to redirected investment by non-reproducing elders. Furthermore, mothers were rated kinder than maternal grandmothers, possibly due to “insider knowledge” of their children’s paternity. Step-relatives showed minimal variation, suggesting that observed differences among biological kin reflect genetic relatedness and PU, rather than non-genetic factors. Overall, our findings support kin selection theory and suggest that paternity uncertainty subtly yet systematically shapes perceptions of familial kindness.

Keywords

kin selection theory, stepfamily, kindness, altruism, grandmothers, paternity certainty

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Introduction

Kin Selection

Kin Selection Theory suggests that individuals are inclined to support those to whom they are more genetically related, as this investment aids in propagating shared genes (Hamilton, 1964). This concept is encapsulated in Hamilton’s rule, which states that altruistic behavior is favored by natural selection when the product of the genetic relatedness (r) and the benefit to the recipient (B) exceeds the cost to the altruist (C). Assistance to closer kin is preferred over aid to more distant relatives because closer kin are likely to share a greater proportion of identical genes than those more distantly related. Beyond the immediate family, recent findings indicate that altruistic behaviors towards more distant kin, such as cousins, are also influenced by varying degrees of paternity

uncertainty. Jeon and Buss (2007) showed that individuals are more willing to act altruistically towards maternal relatives (e.g., mother’s sister’s children) compared to paternal relatives (e.g., father’s brother’s children), reflecting evolved psychological adaptations sensitive to differences in genetic certainty. The evidence for kin selection theory is robust and spans various species, demonstrating behaviors that

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support the survival and reproductive success of relatives. Observations in social insects like bees, ants, and wasps are often cited, where workers, who are genetically related to the queen and her offspring, sacrifice their own reproduction to support the colony (e.g., Nowak et al., 2010). Similarly, in mammals, including humans, behaviors such as altruism, cooperative breeding, and other forms of kin-directed help support the theory (Silk, 2009).

Focusing on parental investment, Trivers (1972) posits that parents are biologically predisposed to allocate resources in a manner that maximizes the reproductive success of their offspring. This theory has been empirically supported by studies such as Bereczkei et al. (2004), which found that parents tend to invest more resources in children who possess traits suggesting higher reproductive value. Geary (2000) further explores this concept, highlighting how parental investment strategies are influenced not only by available parental resources but also by factors such as offspring health and their potential for future reproductive success.

Recent research has expanded these findings by showing that parental investment is highly responsive to ecological and social conditions. For example, Sear and Coall (2011) reviewed how kin support and cooperative breeding strategies vary across different stages of the demographic transition. Anderson (2006) emphasized that paternal investment decisions are influenced by paternity confidence, with men being more likely to invest in children when they believe they are the biological fathers. Scelza and Bliege Bird (2008) demonstrated that female cooperative networks can substantially impact resource allocation patterns in subsistence societies. Additionally, Kaptijn et al. (2010) found that grandparental investment varies by lineage, which may reflect adaptations to sex-specific reproductive strategies. These studies, together with findings by Salmon and Daly (1998) and Pashos (2017) on differential caregiving biases, underscore that parental and grandparental investment strategies are flexible and shaped by both biological and cultural factors. Altogether, these findings support the view that parental investment is adaptively calibrated to maximize inclusive fitness based on biological relatedness, reproductive potential, and socioecological context.

Regarding grandparental investment, inclusive fitness theory suggests that grandparents may enhance their genetic success by investing resources in their grandchildren, thereby increasing the survival and well-being of their direct descendants. Euler and Weitzel (1996) demonstrated that grandparental investment is significantly influenced by the certainty of genetic relatedness. Cross-cultural evidence further supports the idea that grandparental investment is influenced not only by genetic relatedness but also by cultural norms. For example, Pashos (2000) demonstrated that in traditional patrilineal societies, such as rural Greece, paternal grandparents can be more involved than predicted by models based solely on paternity uncertainty, contrasting with patterns observed in Western societies. Pollet et al. (2009) further

investigated this phenomenon, revealing that grandparents' investment strategies are also shaped by cultural and socio-economic factors, indicating a multifaceted approach to supporting their grandchildren. Additionally, emotional closeness between grandparents and the parents of their grandchildren has been identified as a significant predictor of grandparental investment. Michalski and Shackelford (2005) found that relational uncertainty and emotional bonds with adult children substantially mediate the level of grandparental support, further refining evolutionary models of kin investment.

Research on grandparenting often focuses on the investment of resources, yet contemporary literature calls for broader investigations, particularly regarding the influence of grandparents on grandchildren's health (Sari, 2023). Studies indicate that a strong and positive relationship with grandparents can lead to lower levels of risky behaviors, such as substance use or nutritional outcomes, and contribute to better overall health outcomes (Sadrudin et al., 2019).

Beyond grandparents, evolutionary perspectives highlight the roles of other kin, such as siblings, aunts, and uncles, in supporting offspring. For instance, aunts and uncles, sharing approximately 25% genetic relatedness with their nieces and nephews, may invest in them to enhance their inclusive fitness. Studies have shown that maternal aunts and uncles often invest more than paternal ones, possibly due to greater certainty of genetic relatedness through maternal lines (McBurney et al., 2002).

Siblings, who share approximately 50% of their genes, can contribute to one another's reproductive success, albeit indirectly, through support, care, or cooperative behavior. Research indicates that individuals are more likely to invest in full siblings compared to half-siblings, reflecting the higher genetic payoff (Pollet et al., 2009). Moreover, in cooperative breeding models, it has been suggested that helping behavior toward siblings and contributions to kin may influence individuals' reproductive trajectories, potentially delaying independent reproduction as resources and care are directed toward family needs (Kramer, 2005; Hames & Draper, 2004). These findings highlight that sibling relationships can function as essential components of cooperative kin networks.

These findings underscore the importance of considering the broader kin network in studies of familial investment, as various relatives contribute differently based on genetic relatedness, cultural norms, and socio-economic contexts.

Paternity Uncertainty and Its Evolutionary Implications

Paternity uncertainty is a key biological factor influencing the strategies individuals employ for allocating resources among offspring and other family members. Originating from the basic premise that males face an inherent challenge in confirming the biological paternity of their offspring, this theory underscores a fundamental discrepancy in reproductive certainty between the sexes. Unlike maternity, which is visibly

confirmed through pregnancy and childbirth, paternity lacks direct physiological evidence, fostering a unique set of psychological and behavioral responses in males (Buss, 1995; Daly & Wilson, 1982).

The evolutionary implications of paternity uncertainty are profound, influencing male mating strategies and paternal investment. It has been suggested that men may exhibit behaviors such as mate guarding, increased jealousy, and a preference for certain cues of fidelity in partners as adaptive responses to mitigate the risks associated with paternity uncertainty (Buss, 1988; Symons, 1979). This concept is further elaborated, for example, by Anderson et al. (1999), who highlighted the evolutionary implications of extrapair paternity (EPP) and the ensuing paternity uncertainty on sexual selection and the coevolutionary arms race between males and females. These include behaviors such as mate guarding and repeated mating with one's partner, aimed at mitigating paternity uncertainty. Additionally, previous research has demonstrated that cues of physical resemblance can significantly influence paternal behaviors. Burch and Gallup (2000) found that perceived paternal resemblance was associated with lower rates of partner-directed violence, suggesting that men may respond to cues of genetic relatedness with behavioral adjustments. Similarly, Platek et al. (2002) showed that facial resemblance cues activate specific neural circuits linked to reward and parental motivation, emphasizing the biological basis of kin detection mechanisms. This line of research demonstrates that paternity uncertainty operates not only at a cognitive or social level but also involves deep-rooted psychological and neurobiological processes.

Considerable attention has also been given to the role of female infidelity in shaping male psychological adaptations related to paternity certainty. The extensive volume edited by Platek and Shackelford (2006) offers numerous empirical and theoretical contributions on how male mating strategies, including jealousy, mate guarding, and investment patterns, have evolved as responses to risks of female infidelity.

The prevalence of extra-pair paternity (EPP) — the conception of offspring outside of monogamous pairings — varies widely across species and human societies. This variation depends on biological predispositions and cultural practices. Earlier sources reported a relatively high presumed level of extra-pair paternity typically ranging from 1% to 10%, though these figures can be higher or lower depending on the specific community and social norms (Anderson, 2006). It was assumed that the rates were higher in the past, partly due to the lack of contraceptive use and lower awareness of sexually transmitted diseases. However, more recent studies suggest that even in the past, EPP in various human societies was around 1–2% (see Larmuseau et al., 2016). Nevertheless, it remains unclear what the rates of EPP were in the environment of evolutionary adaptedness (EEA), where the psychological mechanisms related to paternal investment are presumed to have evolved (Flegr, 2023; Tooby & Cosmides, 1990).

Genetic studies and paternity tests have provided direct evidence for these rates (Voracek et al., 2008). Considering the evolutionary background of the human species, evidence suggests that non-monogamous mating strategies were common among early humans and our hominin relatives. This is inferred from comparative analyses of testes size, mating behaviors observed in closely related primates, and the genetic diversity within human populations (Potts, 1999). Such analyses suggest a mixed reproductive strategy in men and women, involving both intra- and extra-pair matings. These findings challenge the notion of strict monogamy in human evolution and highlight the role of EPP in shaping genetic diversity and influencing social dynamics. Further studies enriching this discussion include Hrdy (2009), who examines the role of all parents in human evolution, and Hill and Hurtado (1996), who provide insights into the cooperative breeding strategies among the Ache hunter-gatherers. They demonstrate that understanding human and non-human animal social structures requires considering a broad spectrum of reproductive strategies and kinship behaviors.

Societal and Cultural Dimensions of Paternity Uncertainty

Beyond individual mating strategies and distribution of parental care, paternity uncertainty also significantly influences social structures, as well as legal and cultural norms (Geary, 2000). Higher paternity certainty is associated with greater paternal involvement across different societies (e.g., Anderson, 2006; Sear & Coall, 2011; Scelza & Bliege Bird, 2008).

Research has also demonstrated that PU significantly affects the allocation of resources within families, with paternal care often being contingent upon the degree of certainty regarding biological relatedness (Geary, 2005; Platek, 2003). Several studies have stated that maternal kin tend to both give and receive greater levels of investment than paternal ones, which could be explained by the potential paternity uncertainty associated with the latter (Colclasure, 2021; Bishop et al., 2009; Gaulin et al., 1997; Tanskanen et al., 2023). Similarly, grandparents typically have greater certainty regarding their biological relatedness to their daughter's children than with their son's children and, therefore, are expected to invest more in the former (Sear & Coall, 2011). This differential investment might lead to differences in perceptions between maternal and paternal family members.

Patterns of kin investment are also reflected in inheritance practices and lineage systems across cultures—core elements of human social organization that are also deeply intertwined with PU. The assurance of paternity has historically influenced inheritance laws and the transmission of wealth and status, highlighting the importance of lineage continuity in various cultures (Hartung, 1985; Volland, 1998). Empirical evidence further supports the idea that individuals tend to allocate resources preferentially based on perceived

relatedness, emphasizing the evolutionary rationale behind kin selection and altruistic behavior toward relatives (Burnstein et al., 1994). This can be exemplified by inheritance regulations, where property is passed from a man to his sister's offspring rather than to his own children, despite the assumption that his children would share a closer genetic relationship (e.g., Fortunato, 2012). The 'paternity threshold model' aligns this behavior with inclusive fitness theory, suggesting that as the rate of extra-pair paternity (EPP) rises, ensuring inheritance through female relatives becomes more advantageous. Similarly, it is often presumed that a man would prioritize investment for his sister's offspring, given the higher certainty of shared genetic ties through the maternal line.

Familial Evaluations and Kindness

The degree of genetic relatedness—shaped by factors such as paternity uncertainty—is expected to influence the extent of altruistic or spiteful behaviors exhibited among family members. Recipients perceive variations in the frequency and intensity of such behavior as differences in the kindness of individual family members. Thus, the rated kindness of individuals can serve as a proxy for altruistic or spiteful tendencies, as subjectively evaluated from the perspective of the behavior's recipient.

This reasoning builds on several prior studies that have examined kindness in the context of familial investment in offspring and relatives. For example, Eisenberg (2006) found a significant link between prosocial reasoning and behaviors towards family, suggesting kindness reflects familial investment motivations. Madsen et al. (2007) observed an increase in altruistic behaviors, which often manifest as kindness towards close relatives, thereby supporting the kin selection theory. Warneken and Tomasello (2009) showed that even young children display altruistic behavior towards family. Furthermore, the grandmother hypothesis (Hawkes et al., 1997) posits that grandmothers have played a crucial role in the evolutionary history of humans by providing invaluable support in the rearing of grandchildren. This would logically extend to grandmothers receiving very high ratings, reflecting their integral contribution to familial and social structures. Building on the theories of kin selection, mating strategies, and the grandmother hypothesis, we would expect maternal relatives—particularly maternal grandmothers—to receive the highest ratings in familial evaluations due to their greater certainty of genetic relatedness and historically significant caregiving roles.

Research consistently demonstrates a maternal advantage in the quality of grandchild–grandparent relationships. Bonds between grandchildren and maternal grandparents are generally closer, more meaningful, and more fulfilling compared to those with paternal grandparents (Matthews & Sprey, 1985; Somary & Stricker, 1998). Scholars often attribute this advantage to the role women play in maintaining

family ties and performing 'kinkeeping' activities (Hagestad, 1986, 1986; Rossi & Rossi, 1990).

Research also suggests that differences in the ratings of individual siblings could be influenced by their birth order, with first-borns often receiving more attention and resources, potentially leading to higher evaluations. Kramer (2005), for instance, examines the contributions of older children to household economies in traditional societies, offering perspectives on the broader kin cooperation beyond direct parental care. Furthermore, younger siblings have a higher degree of uncertainty regarding their biological kinship with older siblings because they did not witness the births of their siblings from the same parents. Consequently, older siblings are more likely to have a stronger preference for younger siblings than vice versa. Studies by Sulloway (1996) and Salmon and Daly (1998) indicate that birth order can affect personality development, parental investment, and sibling rivalry, suggesting that these factors contribute to the varied perceptions and evaluations of siblings within families. Reflecting on these insights, a substantial sample size could reveal variations in sibling ratings.

Objectives

The aim of our study was to investigate how altruism varies among different family members and to interpret these variations through the prism of paternity uncertainty.

We introduced a novel, high-throughput method where the proxy for altruism—kindness displayed by various family members—was directly assessed by the recipients of such kindness. Instead of directly questioning family members about the support they receive or provide, which might lead to bias or discomfort, we asked participants to rate their agreement with statements like 'maternal grandmothers are kinder than other people.' This approach builds on the above-mentioned studies, which recommend focusing not only on resource allocation to grandchildren but also on the overall quality of the grandparent–grandchild relationship. The dimension of kindness may serve as a useful proxy for assessing this quality. In contrast to assessments of kindness or willingness to invest made by external observers, our method enables family members to utilize a broader spectrum of information, including subtleties not accessible to outsiders. Moreover, having observed their family members' behavior over long periods (their entire life), they are positioned to consider specific family dynamics, such as the extent to which kindness is expressed among all members. Family members are also able to interpret these expressions in light of each relative's objective capacity to provide support—such as their available resources or opportunities to help. In doing so, respondents can recognize not only material assistance but also more subtle forms of support, such as emotional backing. As a result, this method holds the potential to be more sensitive, capable of uncovering even the most delicate effects attributable to paternity uncertainty. Our research expands

beyond the usual focus on grandparents to examine a broader range of relatives, including parents and siblings of both genders, investigating how paternity uncertainty—alongside sex effects, sex-specific reproductive strategies, and matrilineal bias—may influence rated kindness within the family. To distinguish the effects of actual kinship from other factors such as cultural norms or resource access, we included step-relatives—who lack biological relatedness and have an identical (absolute) level of PU—as a negative control in our study.

Methods

Participants

We collected data using an internet questionnaire distributed as a Qualtrics survey. Respondents were recruited using a Facebook-based snowball method (Kaňková et al., 2015) by posting an invitation on the ‘Lab Bunnies’ (‘Pokusní králíci’ in Czech) Facebook page (www.facebook.com/pokusnikralici). This page is dedicated to Czech and Slovak volunteers interested in participating in various evolutionary psychological experiments and assisting with the recruitment of other participants. Initially, the community therefore consisted of scientific enthusiasts, who could be considered a specific research sample. These individuals then shared the questionnaire with their friends. As it continued to spread through their social networks, the sample gradually became more representative of the broader internet population. At the beginning of our study in 2016, the group had over 10,000 volunteers, and it grew to exceed 20,000 by the study’s conclusion in 2021.

Participants were invited by our team and community members to take part in an anonymous online study “examining personal and societal beliefs, attitudes, and opinions, including perspectives on various superstitions, prejudices, and conspiracy theories”. Participants were briefed about the study’s goals on the first page of the electronic questionnaire, where they received the following details: “The questionnaire is anonymous, and the data obtained will be used solely for scientific purposes. Your participation in this project is voluntary, and you have the liberty to withdraw at any moment by closing this web page. While you may opt to skip any questions you find uncomfortable, complete data sets are most valuable. If you consent to participate in the research, please click the ‘Next’ button.” Additionally, both during recruitment and at the start of the questionnaire, participants were informed that it would delve into topics such as sexuality, health, and religious beliefs. The sole incentive offered to participants was feedback on their performance in personality and aptitude tests. Only individuals who confirmed they had read the information and were at least 18 years old were allowed to participate.

This project, including the procedure for obtaining electronic consent for participation, was approved by the

Institutional Review Board (IRB) of the Faculty of Science at Charles University – No. 2015/30.

Questionnaire

The survey gathered data for several unrelated projects, investigating the effects of various biological and social factors on behavior, health, cognitive performance, and attitudes within the internet population. It comprised over one thousand items and took a median time of 127 min to complete.

For the present study, only participants’ sex and their ratings of the kindness of various family members were used. The relevant questions were located in the first quarter of the questionnaire, following demographic and family background questions, and preceding the sections on personality, health, and lifestyle.

The questionnaire asked respondents to evaluate the kindness of their various family members, including both biological and step-relatives. They were asked to rate their agreement with statements such as, ‘Is this person on average kinder than other people?’ (the full wording in Czech was: “Ohodnoťte následující charakteristiku pro ‘vlastní/nevlastní’ členy vaší rodiny. Jsou v průměru *hodněji* než ostatní lidé?”) followed by a list of family members (see Figure 1 for details). The concept of ‘kindness’ was intentionally left broad and undefined to allow participants to draw upon their own experiences and interpretations. This approach aimed to capture a holistic assessment of the overall prosocial behaviors they perceived from each family member, encompassing diverse aspects such as emotional support, material assistance, and positive social interaction, without constraining the evaluation to a single narrowly defined dimension. Ratings were given on a scale from 0 to 4, with 0 indicating strong disagreement and 4 indicating strong agreement. Respondents were guided to rate only the family members they genuinely had, which led to fewer ratings for step-relatives compared to biological ones.

Data Analysis and Statistics

Our primary hypothesis predicted that increasing levels of paternity uncertainty (PU) would be associated with lower kindness ratings toward close biological relatives. To test this, we analyzed ratings for six core kin members: two biological parents and four grandparents. Advanced statistical analyses, including linear mixed-effects modeling (LMM), were performed using R version 4.5.0. We analyzed the data using the LMM implemented in the lme4 package (Bates et al., 2015). The model was fitted using the lmer() function with maximum likelihood (ML) estimation to allow comparison between models differing in fixed-effect structure. Respondent ID (*respondent_ID*) was included as a random intercept to account for repeated ratings from the same individuals.

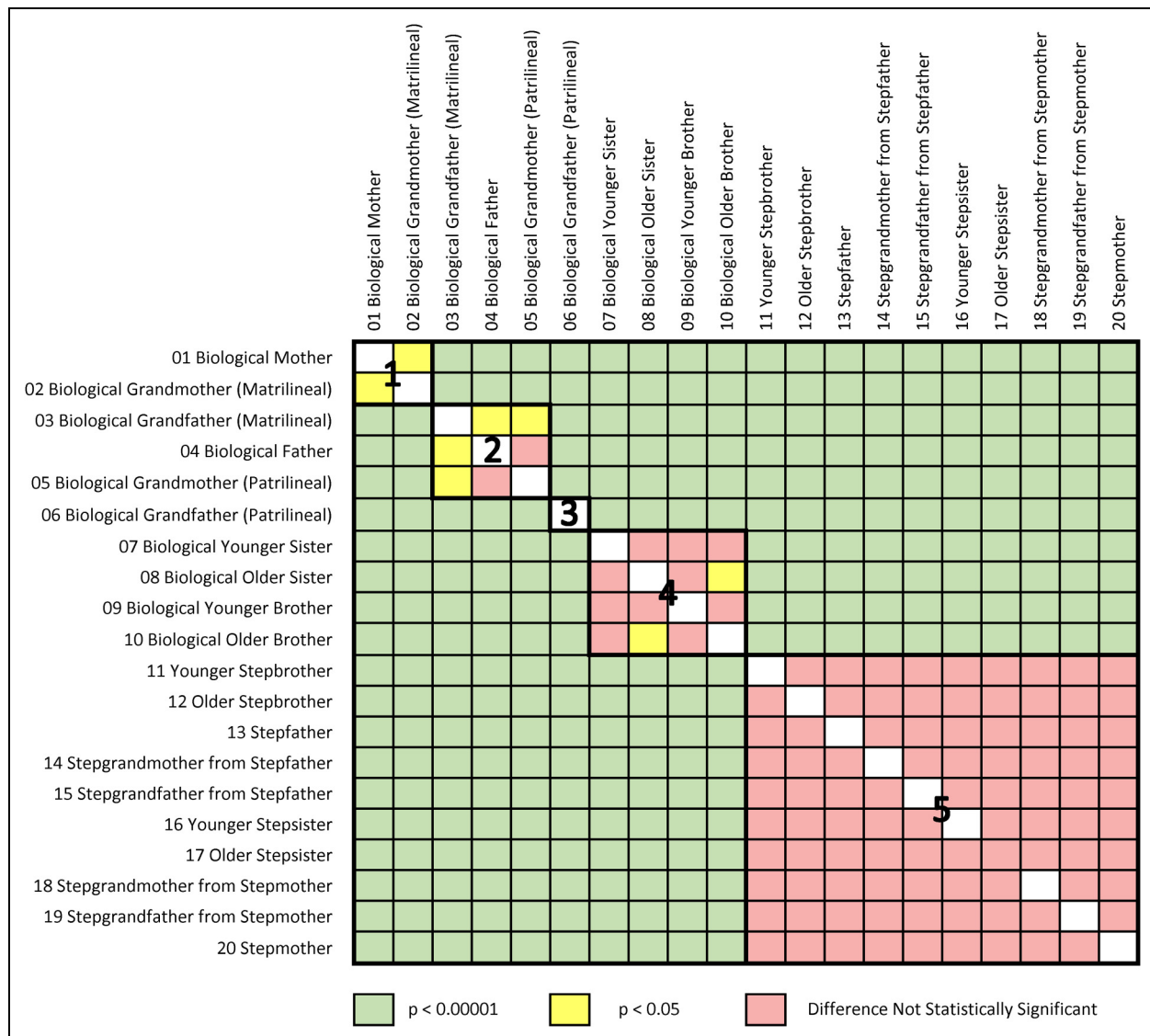


Figure 1. Matrix of Wilcoxon test results for all family member dyads. Ratings were aggregated across both male and female participants. Groups 1–5 represent family categories differing in their typical levels of paternity uncertainty (PU). The p-values were adjusted using the Bonferroni–Holm correction to control for multiple testing.

The dependent variable was *kindness*, treated as a continuous outcome. The fixed effects included *paternity_uncertainty_group* (three levels), *relative_rated* (six categories), their interaction, as well as *respondent age* and *sex*. Categorical predictors were coded using treatment contrasts (the default in lme4). Paternity uncertainty was operationalized as a three-level ordinal variable: Group 1 (no uncertainty): *biological mother* and *maternal grandmother*; Group 2 (one source of uncertainty): *paternal grandmother*, *biological father*, *maternal grandfather*; Group 3 (two sources of uncertainty): *paternal grandfather*.

Because the main effect of paternity uncertainty (PU) and its interaction with relative rated were each significant in the full model, we next asked whether the PU block as a whole adds

explanatory power beyond age, sex and relative rated. We therefore re-estimated a reduced model that is identical to the full model except that all PU terms (main effect + interaction) are removed, refitting both models with REML = FALSE. Comparing the two nested models isolates the variance uniquely attributable to PU. Model improvement was assessed via log-likelihood comparison, expressed as a likelihood-ratio χ^2 statistic—provides an omnibus test of PU's incremental contribution.

Furthermore, to clarify the specific pattern of the PU effect, we conducted targeted post hoc comparisons between levels of PU (0 vs. 1 and 1 vs. 2) using estimated marginal means and contrast testing within the mixed-effects framework in R.

After completing the main statistical analyses in R, we used IBM SPSS Statistics 21.0 to calculate the average ratings for each type of family member and to rank them accordingly. Due to the non-normal distribution of kindness ratings, non-parametric tests were employed for post hoc analyses. Specifically, the independent-samples Mann-Whitney U Test was used to examine gender differences in how participants rated family members. We also compared ratings between specific dyads of family members (e.g., biological mother vs. matrilineal biological grandmother) using paired-samples Wilcoxon signed-rank tests. Effect sizes were reported as Cohen's *d*. Given the extensive number of tests conducted, there was a potential for encountering false positive results. To mitigate and measure this risk, the Benjamini-Hochberg procedure (Benjamini & Hochberg, 1995) was applied for each of the five groups, setting the false discovery rate at 0.1. Additionally, the Bonferroni-Holm correction for multiple tests (Holm, 1979) was applied as a more conservative adjustment to further ensure the robustness and transparency of the reported findings.

Results

Descriptive Statistics

We collected data from a total of 14,817 respondents between June 4, 2016, and January 18, 2021. Prior to statistical analysis, less than 1% of the data was excluded due to implausible values (e.g., exceedingly high or low body height, body mass, age, or unusually short survey completion times). Approximately two-thirds of respondents reached the section involving family member ratings.

The analyses included only respondents who rated at least one family member, resulting in a final dataset of 9,128 respondents. This group comprised 3,503 men with an average age of 36.24 (*SD* = 12.21) and 5,625 women with an average age of 35.55 (*SD* = 12.72). The majority of respondents were highly educated, with 51.6% holding a university degree. Although 55.8% of respondents reported growing up in smaller settlements (towns with fewer than 50,000 inhabitants), they now primarily reside in larger settlements, with 59.2% living in cities with more than 50,000 inhabitants.

Figure 2 illustrates the distribution of respondents who rated each family member (biological or step) and their corresponding average kindness ratings. Furthermore, sibling relationship data showed that 22.1% of respondents reported having grown up without any biological siblings. About 55.6% of this subpopulation reported having only one sibling, 17.0% had two siblings, and 5.3% had three or more. In total, 47.5% reported having at least one biological brother and 44.1% at least one sister. Around 14.6% of respondents indicated they grew up with at least one stepsibling during their childhood. Male respondents reported having, on average, 0.60 brothers and 0.53 sisters, while female respondents reported an average of 0.55 brothers and 0.52 sisters.

Statistical Evaluation of the Predicted Effects of Paternity Uncertainty

We first tested the core hypothesis that increasing paternity uncertainty (PU) would lead to lower kindness ratings toward biological relatives. To this end, we analyzed ratings of six key biological relatives (biological parents and grandparents) using a linear mixed-effects model (LMM). The dataset comprised 38,292 observations from 6,382 unique raters. The random intercept for respondent ID had a variance of 0.779 (*SD* = 0.883), and the residual variance was 0.681 (*SD* = 0.825), indicating substantial between-subject variability.

The LMM showed significant main effects of *paternity_uncertainty_group*, *relative_rated*, and *age*, as well as a significant interaction between *paternity_uncertainty_group* and *relative_rated*. Kindness ratings decreased significantly as the degree of paternity uncertainty increased ($\beta = -0.148$, *SE* = 0.024, $t_{(31,904)} = -6.23$, $p < 0.001$). Ratings also varied across *relative_rated* ($\beta = -0.059$, *SE* = 0.009, $t_{(31,904)} = -6.74$, $p < 0.001$), and older participants gave slightly lower ratings ($\beta = -0.006$, *SE* = 0.001, $t_{(6,379)} = -6.34$, $p < 0.001$). Based on the model results, *sex* of the respondent did not significantly predict kindness ratings ($p = 0.922$). The interaction between *paternity_uncertainty_group* and *relative_rated* was statistically significant ($\beta = 0.013$, *SE* = 0.004, $t_{(31,904)} = 3.25$, $p = 0.00115$), indicating that the influence of paternity uncertainty differed across types of relatives.

The model's marginal R^2 (variance explained by fixed effects) was 0.015, while the conditional R^2 (including both fixed and random effects) was 0.540. A comparison using likelihood ratio test with a reduced model, which excluded PU and its interaction, showed that the full model fit the data significantly better ($\chi^2_{(2)} = 42.84$, $p = 0.001$). However, it is important to note that the PU-related predictors in both models exhibited low and nearly identical marginal R^2 values (0.015 vs. 0.014), suggesting that PU and its interaction explain a very small amount of the variance in kindness ratings. Full results for both models are shown in Table 1.

To further explore the pattern of the PU effect, we conducted pairwise comparisons between the three paternity groups using estimated marginal means and contrast tests (emmeans package; Lenth, 2023). Group 2 was rated as significantly less kind than Group 1 (Estimate = -0.12, $p < 0.001$, $d = 0.15$), and Group 3 as significantly less kind than Group 2 (Estimate = -0.07, $p = 0.0002$, $d = 0.08$). Effect sizes (*d*) were calculated based on model-estimated marginal means and pooled standard deviations.

Post Hoc Testing of Dyadic Differences

Following the analyses presented in the previous section, we conducted additional post hoc testing by comparing kindness ratings between all individual pairs of family members. Pairwise comparisons were performed using Wilcoxon signed-rank tests. The results are presented in Figure 1.

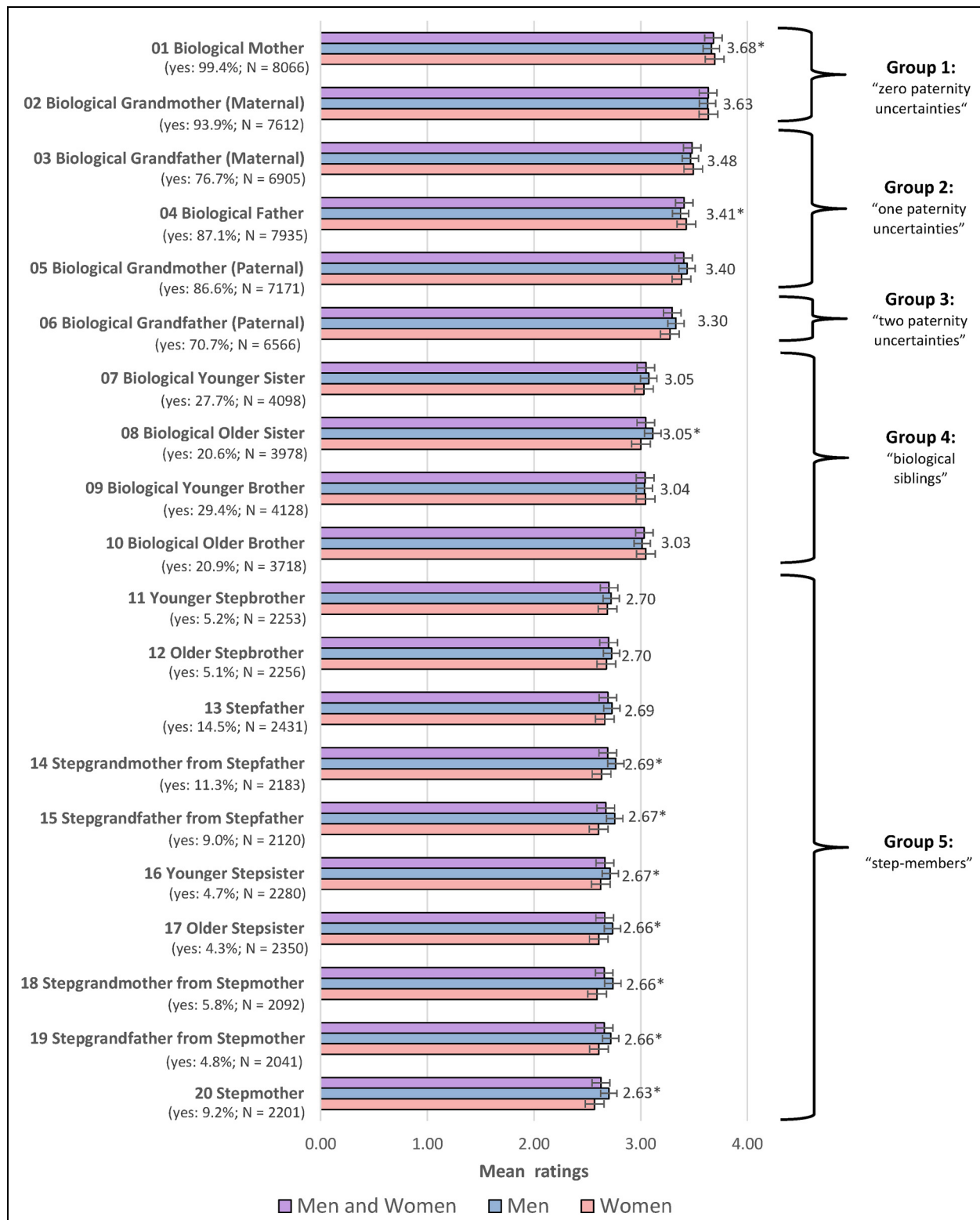


Figure 2. Average kindness ratings for different family members. Average kindness ratings, combined for male and female participants, are shown by numbers next to the bars. Statistically significant differences between male and female rater responses are marked with asterisks (*), based on a Benjamini-Hochberg correction (20 tests, FDR=0.10). Percentages under each label reflect the proportion of respondents who reported having that family member, while N values denote the number of raters. Error bars represent standard errors of the mean.

Table 1. Comparison of full and reduced linear mixed-effects models predicting kindness ratings.

Model	Type	Predictor	Estimate	Std. Error	df	t value	p value	Variance/SD	Marginal R ²
full	fixed	intercept	4.078	0.0599	9705	68.08	<0.001		0.015
		paternity_uncertainty_group	−0.148	0.0237	31,910	−6.23	<0.001		
		relative_rated	−0.0586	0.0087	31,910	−6.74	<0.001		
		sex	−0.0024	0.0242	6379	−0.10	0.922		
		age	−0.0061	0.00096	6379	−6.34	<0.001		
		paternity_uncertainty_group × relative_rated	0.0127	0.0039	31,910	3.25	0.00115		
	random	respondent_ID (intercept)						0.779/0.883	
		Residual						0.681/0.825	
reduced	fixed	intercept	3.954	0.05447	6712	72.58	<0.001		0.014
		relative_rated	−0.0732	0.00247	31,910	−29.63	<0.001		
		sex	−0.0024	0.0242	6379	−0.10	0.922		
		age	−0.0061	0.00096	6379	−6.34	<0.001		
	random	respondent_ID (intercept)						0.779/0.882	
		residual						0.682/0.826	

Note: The table compares two linear mixed-effects models predicting kindness ratings: a full model including *paternity_uncertainty_group*, *relative_rated*, their interaction, *age*, and *sex*; and a reduced model including only *age*, *sex* and *relative_rated*. Models were fitted using the `lmer()` function (lme4 package) with maximum likelihood (ML) estimation. Random intercepts were included for rater ID to account for repeated measures. The “Variance/SD” column lists the variance and standard deviation for random effects. Marginal R² represents variance explained by fixed effects alone. A likelihood ratio test confirmed that the full model provided a significantly better fit than the reduced model.

The results revealed patterns consistent with theoretical predictions: within groups of relatives sharing the same level of paternity uncertainty, differences in kindness ratings were generally small and mostly non-significant. By contrast, comparisons across different PU groups consistently yielded statistically significant differences in rated kindness.

Average Kindness Ratings and Prevalence of Family Members

Figure 2 illustrates the percentage and number of participants who reported having each type of family member. It also presents the average kindness ratings for each member, disaggregated by total, male, and female respondents. It also displays the results of statistical comparisons between male and female respondents.

Respondents rated their mother as the kindest family member (mean = 3.68), closely followed by their maternal grandmother (mean = 3.63). Although both belong to Group 1, characterized by no paternity uncertainty, the difference between them was statistically significant ($p < 0.0001$, $d = 0.05$).

In Group 2, which included biological relatives with one level of paternity uncertainty, the maternal grandfather received the highest kindness rating (mean = 3.48), followed by the father (3.41) and the paternal grandmother (3.40). Significant differences within Group 2 were observed only between the maternal grandfather and both the father and paternal grandmother (vs. father: $p < 0.001$, $d = 0.05$; vs. paternal grandmother: $p = 0.0001$, $d = 0.06$).

Group 3, characterized by two levels of paternity uncertainty, included only the paternal grandfather, who received

a mean rating of 3.30. No within-group comparisons were possible.

Group 4 consisted of younger and older brothers and sisters. All four sibling categories received nearly identical ratings (range: 3.03–3.05), with sisters rated slightly higher than brothers. The siblings were rated significantly lower than parents and grandparents, but significantly higher than all step-relatives (Group 5).

Group 5 comprised various stepfamily members, serving as a control group, since all members had uniformly low kinship ratings and identical paternity uncertainty (approximately 1.0). Compared to biological relatives, stepfamily members were rated significantly lower in kindness. Within this group, ratings varied only slightly: the younger stepbrother received the highest score (2.70), while the stepmother received the lowest (2.63). However, no within-group differences reached statistical significance.

Discussion

Our findings support the hypothesis that paternity uncertainty (PU) plays a small but statistically significant role in shaping perceptions of kindness: relatives with no PU received the highest kindness ratings, followed by those with one level of uncertainty, and finally those with two, with significant differences observed between each level. Consistent with theoretical expectations, no significant differences in kindness ratings were observed among step-relatives, who share no genetic relatedness and are assumed to have a comparable degree of PU.

These results, obtained through a novel participant-based method, align closely with predictions derived from paternity

uncertainty theory. Furthermore, they are broadly consistent with previously published data on kinship ratings, particularly regarding the general pattern of kindness assigned to various family members. This robust agreement across different methods and datasets underscores the consistent influence of PU on perceived familial kindness.

Parents and Grandparents

Mothers being rated as kinder than fathers are consistent with prior findings, particularly those emphasizing women's direct involvement in childcare (e.g., Hrdy, 2009). This pattern is reversed in stepfamilies, where stepfathers—typically less involved in childcare than stepmothers—receive higher kindness ratings. This divergence between biological and stepfamilies suggests that evolutionary mechanisms—especially genetic relatedness and paternity uncertainty—provide a more comprehensive explanation for these rating differences than caregiving roles alone.

Such interpretation is further strengthened by the observation that maternal grandparents, like mothers, consistently receive higher kindness ratings compared to fathers, and within stepfamilies, stepfathers are even viewed as slightly kinder than maternal grandparents, though this difference did not reach statistical significance.

Our results align with previous research on kinship ratings and paternity uncertainty, confirming that the maternal grandmother typically receives the highest kindness rating among grandparents, whereas the paternal grandfather (with two steps of PU) is usually rated the lowest (Bishop et al., 2009; Euler & Weitzel, 1996; Tanskanen et al., 2023). The fact that mothers received the highest ratings overall—followed by maternal grandmothers—might reflect the closer genetic relationship between mothers and their offspring compared to that between grandmothers and grandchildren. However, this can also be explained within the PU framework. While theoretically both have the same degree of PU, mothers possess “insider information” about their own paternity that their mothers (the grandmothers) lack. This allows a mother to be more certain of her children's paternity than her own mother can be.

The high kindness ratings of maternal grandmothers, compared to fathers, are consistent with the PU model and also align with the grandmother hypothesis proposed by Hawkes et al. (1997). This hypothesis emphasizes the critical role of post-reproductive individuals, especially grandmothers, in enhancing the survival and well-being of grandchildren. Empirical support for this hypothesis comes from Sear and Mace (2008), who found that grandmothers have a positive impact on child survival in traditional societies. This context likely contributes to the high rating of grandmothers (3.63), placing those second only to the biological mother (3.68) in rated kindness. A similar pattern was observed among male relatives as well. Maternal grandfathers receive higher kindness ratings than fathers, even though both face the same level

of paternity uncertainty. Their lower reproductive prospects may motivate increased investment in existing descendants, particularly grandchildren.

Siblings

As with parents and grandparents, lower kindness ratings—and gender differences—among siblings can be interpreted within the paternity uncertainty (PU) framework. In this case, uncertainty arises from the possibility that one or both siblings may not be the biological children of both parents, potentially due to extramarital relationships or adoption. This uncertainty is inherently greater among siblings because it applies to both individuals, thus doubling the potential for non-shared parentage. Essentially, when evaluating the shared parentage of oneself and a sibling, the opportunities for discrepancies in biological relation—whether through extramarital birth or adoption—are objectively doubled. This elevated uncertainty may result in reduced perceived kinship and, consequently, lower kindness ratings.

An alternative explanation for sibling ratings can be found in psychological and sociocultural theories of family dynamics. Sulloway (1996) suggested that sibling rivalry and competition shape personality and relational outcomes within families. According to the theory of family niches, oldest siblings often align more closely with parental roles, presumably receiving greater investment. Similarly, rivalry and competition tend to be less pronounced between siblings of opposite genders than between same-gender siblings (Conley, 2000; Kuo & Hauser, 1996; Minnett et al., 1983), likely due to culturally defined gender roles that limit overlap in interests and reduce direct competition. These dynamics could foster resentment in younger siblings toward their elders, which might be reflected in reduced kindness ratings for their older siblings. However, our findings of negligible differences between younger and older siblings (mean ratings 3.03–3.05) do not support strong birth order effects. Moreover, recent studies have shown that differences among siblings across various domains are generally minimal (e.g., Rohrer et al., 2015). Oldest siblings may align more closely with parental perspectives and receive greater investment, as suggested by family niche theory. However, contemporary evidence indicates that such differences have limited influence on sibling relationships.

Male and Female Family Members

Sex differences in caregiving tendencies and social behavior provide an important backdrop for interpreting patterns in kindness ratings across male and female family members. Research consistently shows that, on average, women exhibit higher levels of emotional attunement, nurturing behaviors, and prosociality compared to men (Eagly & Wood, 1999; Taylor et al., 2000). According to the Tend-and-Befriend Hypothesis (Taylor et al., 2000), women evolved stress

responses that favor social affiliation and caregiving, promoting social bonds and support networks.

Most prior work has lacked the sample size to examine whether men and women perceive kin kindness differently. Because our rater pool was unusually large, we could analyze kindness ratings separately for male and female respondents, allowing us to test whether male and female raters differ in their kindness assessments—and, if so, whether those differences accord with the predictions of the PU framework. Although the overall model (which included comparisons of all four grandparents and two parents) did not reveal a significant main effect of rater sex on kindness ratings, our data showed that daughters consistently gave higher ratings to their biological parents than sons did. This may reflect sex-specific reproductive strategies and kinship (e.g., Pashos, 2017; Salmon & Daly, 1998), but it can also be interpreted within the context of the paternity uncertainty (PU) framework. From an evolutionary perspective, investing in daughters secures indirect genetic returns via grandchildren with guaranteed relatedness. In contrast, investing in sons carries the risk that future grandchildren might not be biologically related to the grandparents due to uncertainty in paternity. The higher ratings of parental kindness by daughters are thus consistent with evolutionary strategies favoring the transmission of genetic material through more certain maternal lines.

A comparable asymmetry was observed among siblings, where patterns of perceived kindness varied depending on both the sex of the rater and the rated sibling. In our study, brothers tended to rate their older sisters as nicer than the sisters rate their older sisters. Unlike the previous findings related to parents, this pattern is not easily explained by paternity uncertainty. However, it can be explained by the theory of unequal returns of investment to male and female siblings. This theory posits that it is more adaptive to invest in the gender offering greater reproductive returns. In polygamous, economically stratified societies where a man's ability to acquire a wife significantly depends on his material resources, this means investing in males rather than females. Analytical models developed by Tureček et al. (2025) reach the same conclusion: under the demographic and inheritance conditions typical of these societies, directing help to older brothers yields the highest inclusive-fitness return for other siblings. Consistent with that result—and with Holden et al.'s (2003) ethnographic evidence—resources channelled to brothers boost their reproductive success, and thus the investor's genetic pay-off, more effectively than equivalent aid to sisters.

These investment patterns are further shaped by asymmetries in expected reproductive returns and family hierarchy. Such a type of resource transfer is especially expected from older sisters. Generally, daughters benefit more from transferring resources to any sibling compared to sons, who would likely diminish their own probable reproductive success through such transfers. At the same time, older siblings are typically better positioned to invest in their younger siblings than vice versa. Thus, the tendency of brothers to rate their

older sisters more favorably may reflect not just immediate social dynamics, but also evolved biases in perceived value of cross-sex investments within families.

Stepfamily Members

Our finding that stepfamily members receive lower kindness ratings aligns with existing studies indicating that relationships within stepfamilies are generally not perceived as stable or intimate as those within biological families (Ganong & Coleman, 2004). This is particularly true for stepmothers, who often receive the lowest ratings.

However, it is also essential to consider the potential influence of pervasive social stereotypes in shaping these evaluations. As Miller et al. (2018) highlighted, stepmothers are frequently viewed as less affectionate, committed, and competent than biological mothers, regardless of the lack of empirical evidence supporting such negative characterizations. Our results mirror previous research that demonstrates negative biases towards non-biological parents in evaluations of kinship. In our data, stepmothers were indeed rated lowest among step-relatives, but the difference was not statistically significant.

The consistently higher ratings of all stepfamily members by men compared to women (as depicted in Figure 2) remain unexplained. It's plausible that these disparities are unrelated to the paternity uncertainty theory and might require insights from disciplines beyond evolutionary psychology, such as sociology or psychological science. One speculative explanation is that step-siblings may be more motivated to maintain positive relations with male siblings due to perceived physical dominance, though this hypothesis remains untested and warrants further interdisciplinary exploration.

Beyond Paternity Uncertainty

A key advantage of our unusually large sample is that it allowed us to include a built-in negative control: the smaller subset of step-relatives, who share both zero genetic relatedness and the same (maximal) level of paternity uncertainty. The near-absence of variation in kindness ratings among these step-relatives—contrasting sharply with the stratified ratings observed among biological kin—points to expected genetic relatedness, modulated by paternity uncertainty, as the primary driver of the differences we report, rather than cultural norms, social expectations, or constraints tied to traditional parental roles. Notably, 98.5% of the total variance in kindness ratings lay in the random effects, underscoring that only very large, well-powered samples can detect generalizable evolutionary patterns amid substantial individual-level noise.

Having shown that pragmatic kin discrimination tracks expected relatedness modulated by paternity uncertainty (PU), we must next ask what ancestral force could have made humans so attuned to PU in the first place. A central

issue is whether extra-pair paternity (EPP) was common enough in ancestral populations to favour PU-sensitive altruistic heuristics. Reliable estimates are scarce: present-day EPP rates are low (Anderson, 2006; Larmuseau et al., 2016) yet rates in the environment of evolutionary adaptedness (EEA) may have been appreciably higher, creating stronger selective pressures. Even though EPP is infrequent today, the PU-linked biases we now observe could be non-adaptive echoes of a bygone reproductive ecology (Flegr, 2023). It is also worth remembering that a selective advantage well below one percent can drive an allele to high frequency within a few hundred generations (Crow & Kimura, 1970); consequently, EPP need not have been rampant to leave a lasting evolutionary imprint on kin-directed behaviour.

Although the paternity-uncertainty (PU) framework and, more broadly, kin-selection theory offer powerful evolutionary accounts of variation in kin altruism, they are not the field's only explanatory models. Proponents of group selection argue that altruistic traits can be favoured because they boost the success of entire groups, even when the beneficiaries are not close genetic relatives (Wilson & Wilson, 2007). Other lines of work—especially relevant for humans—emphasise socialisation and cultural norms: patterns of helping are learned, reinforced, and regulated by the surrounding society. The expectation that women should shoulder most family caregiving, for instance, reflects culturally transmitted gender roles rather than direct genetic relatedness (Eagly & Wood, 1999). Together, these perspectives remind us that PU-based kin discrimination is only one piece of a broader explanatory mosaic for human altruism.

The idea that human behavior is universally shaped by evolutionary pressures is nuanced by the variability of kinship systems and mating strategies across different cultures. For example, Orthodox Jewish communities, with their high paternity certainty due to strict social and marital norms, still follow matrilineal descent for religious identity and inheritance (Biale, 1995), indicating the strong influence of cultural and religious factors in addition to evolutionary logic in determining lineage.

Similarly, patrilineal biases in rural China and among the Kyrgyz, which support male-line inheritance of property and social status (Murphy, 2001; Werner, 2009), show how economic and environmental conditions can influence social structures, aligning with evolutionary strategies for resource distribution and kinship support. While the paternity uncertainty framework offers valuable insights, its explanatory scope remains limited—particularly when addressing the complex variability of caregiving behaviors across genders or within patrilineal social structures. In such contexts, it becomes evident that other powerful influences, notably ingrained social structures and prevailing cultural norms, significantly shape—and can even override—paternity-based predictions of caregiving.

This diversity in human social and kinship systems underlines the need for a multidisciplinary approach, integrating

both biological and cultural perspectives to fully understand human social organization. Studies highlight the importance of biological drives and social closeness in kin relationships (Pashos & McBurney, 2008; Pashos, 2017), challenging the reduction of kin caregiving to simple evolutionary narratives. Rather than contradicting evolutionary psychology, such findings extend its explanatory scope by highlighting the interplay between evolved psychological mechanisms and culturally mediated social dynamics.

Strengths and Limitations

One of the main strengths of this study is its large, diverse participant pool. We employed the Facebook-based snowball method, in which study participants and members of the Labbunnies community shared invitations across their social networks. This strategy resulted in a large and unusually diverse sample surpassing that observed in other studies addressing similar topics. Participants completed a lengthy questionnaire without any financial compensation, which effectively helped minimize participation by professional survey respondents and automated bots. Furthermore, the comprehensive nature of the two-hour questionnaire naturally weeded out less committed individuals, who typically abandon such surveys within the first 10 min. As participants were not informed in advance that the questionnaire included an assessment of their relatives' kindness, we successfully circumvented a significant potential source of bias—specifically, participant bias, where people with predominantly positive (or negative) attitudes towards their relatives might disproportionately participate.

While our study primarily focuses on paternity uncertainty and other evolutionary factors related to inclusive fitness, we acknowledge that the observed patterns may also reflect culturally shaped kinship norms, matrilineal biases, and biological or socioecological constraints, such as gendered divisions of labor or differential access to resources (e.g., higher male earnings or provisioning) (e.g., Pashos, 2017; Scelza, 2011). However, the absence of comparable differences among step-relatives—who do not vary in genetic relatedness—makes such interpretations less likely. A key strength of our high-throughput method is that it allowed the inclusion of a large number of step-relatives, enabling a critical control comparison. Data on biological relatives alone cannot determine whether perceived kindness differences stem from genetic relatedness or social roles. However, the absence of such differences among step-relatives—who differ in caregiving but not in genetic relatedness—makes non-genetic explanations less likely.

Nevertheless, the study has certain limitations. Although self-selection bias was unlikely among the rated individuals—who had no influence over their inclusion—the voluntary nature of rater participation may have introduced some degree of selection bias, the extent of which remains uncertain. Therefore, the patterns observed may predominantly apply

to families comprising individuals who are more curious or altruistic. Moreover, the sample is non-representative in terms of education and, consequently, possibly familiarity with evolutionary concepts. Compared to the general population, respondents were more highly educated and may have been more aware of evolutionary predictions, which could have influenced their responses. However, only a minimal proportion of participants had formal education in biology, and advanced evolutionary concepts are rarely covered in Czech curricula. Thus, a substantial bias due to prior familiarity with evolutionary hypotheses appears unlikely.

Kindness ratings were influenced not only by the actual behavior of the rated individuals, but also by their relationship with the raters—a relationship likely shaped by the rated individuals' past behavior toward them. This introduces a degree of subjectivity, as ratings may partly reflect prior personal experiences rather than objective assessments of kindness. Potential influencing factors, such as family constellation or age differences among the raters and rated individuals, that were not tracked, might also affect the results.

Our questionnaire aimed to cover a wide range of familial relationships, but did not specifically include half-siblings. This exclusion was based on practical considerations—half-sibling relationships are highly variable, and including them would have substantially increased the number of relationship categories, complicating the analysis. Exploring the dynamics with half-siblings in future research will be valuable.

While participants were asked to rate members of their own family, it is possible that some participants may have provided ratings based on assumptions rather than direct experience with a certain type of relative. However, the fact that differences in kindness ratings were observed only among biological relatives—and not among step-relatives, who serve as negative controls—strongly suggests that the observed pattern reflects paternity uncertainty rather than indirect effects or biases.

Similarly, participants were not explicitly instructed to assess kindness directed solely toward themselves. As a result, their evaluations may reflect a combination of personal experiences and general impressions of the family members' behavior. Although personal experience was likely the main source of evaluations, the lack of explicit instruction may have introduced some rating variability.

Conclusion

This study introduces a novel, sensitive, and high-throughput method for investigating how paternity uncertainty influences altruism within families, by examining how individuals rate the kindness of their various relatives. Despite modest effect sizes, our findings support the hypothesis that paternity uncertainty may shape the distribution of altruistic behavior within families. By employing a large and diverse sample, we were able to include less commonly studied step-relatives, whose inclusion as a control group proved essential for interpreting


differences among biological kin. The sample size also enabled us to examine sex-related patterns in kin altruism, which we interpret within the framework of paternity uncertainty theory. In particular, the higher kindness ratings of biological parents provided by female participants are consistent with our original PU-based hypothesis, which posits a greater likelihood of genetic relatedness to grandchildren when descent is traced through daughters rather than through sons.


Taken together, our results illustrate the utility of this new approach in capturing subtle, evolutionarily relevant asymmetries in family relationships. At the same time, they highlight the complexity of factors influencing kin-directed altruism and the substantial role of individual variability. We therefore emphasize the need for further studies to replicate and extend these findings, and to assess the generalizability and broader applicability of this method in future research within evolutionary psychology.

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Authors' Contributions

R.K. and J.F. conceived and designed the study and participated in data collection. R.K. (with substantial assistance from J.F.) performed the analysis and wrote the first draft of the manuscript. Both authors agree to be accountable for the content of this work.

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Data Accessibility

The datasets are available in the Figshare Digital Repository: <https://doi.org/10.6084/m9.figshare.23895888.v1>.

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