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Genetic markers of cousin marriage and honour cultures

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ABSTRACT

Honour cultures, characterized by violent responses to perceived threats to personal or family honour, are widespread. Honour killings, one of the manifestations of honour cultures, claims the lives of thousands of women each year, often at the hands of close relatives, representing not only a social problem but also an evolutionary puzzle. They typically follow accusations of sexual impropriety and are the most extreme manifestation of a range of punishments that control the sexual and marital choices of women. The origins of such practices remain unclear, though honour cultures frequently occur where cousin marriage is common. We propose that cousin marriage offers kin benefits through wealth consolidation yet may also generate parent-offspring conflict over marriage choices. In response, norms and punitive measures, including aspects of honour codes, may have evolved to enforce cousin marriage. To test this, we use the average genomic inbreeding coefficient of an ethnic group, as a measure of the historical practice of cousin marriage, to show that this is associated with the likelihood of endorsing honour killings across 52 ethnic groups. We interpret our findings within the context of parent-offspring conflict over consanguineous marriage and we contribute to the growing body of research exploring the relationship between intensive kinship and cultural traits.

1. Introduction

Honour cultures occur cross-culturally and are characterized by the belief that individuals must respond to threats to their honour with violence (Cohen, 2007). While all honour cultures emphasise norms of retribution that can lead to violence, they vary in the extent to which this violence is directed towards men compared to women. Some examples of features of honour cultures include Albanian blood feuds and the Italian vendetta system, which lead to cycles of retaliatory violence between families, clans or other groups. In these examples, both the victims and perpetrators of violence tend to be men who are unrelated. By contrast, among the honour cultures of North Africa, the Middle East, and Central and South Asia (hereafter referred to as the Greater Middle East), women are also victims of honour-based control and violence. There is often great value placed on female virginity, with numerous regulations related to sexual behaviour and marriage. Honour-based controls and violence against women range from limitations on female movement, veiling, the requirement of male chaperones, gender segregation, female seclusion, physical violence, and at its most extreme, honour killings (Gill et al., 2014). Honour killings typically follow

accusations of sexual impropriety, the victims are usually young women, and they are often perpetrated by the victim's agnates, such as her brothers, uncles, cousins or father (D'Lima et al., 2020; Kressel et al., 1981; Kulwicki, 2002). Today, kin-perpetrated honour killings of women are principally but not exclusively reported from the Middle East and South Asia, such as from Afghanistan (Gibbs et al., 2019), Pakistan (Nasrullah et al., 2009) and also India (D'Lima et al., 2020). However, historically they also occurred in the Southern Mediterranean such as in present-day Albania (Önal, 2008), Italy (Cottino, 1999), and Greece (Safilios-Rothschild, 1969).

That the female victims are harmed by *blood* kin presents something of an evolutionary puzzle, since one would expect, given a kin selection framework, that this behaviour would harm an individual's inclusive fitness. This is a very unusual behaviour, across both humans and other species. It is relatively unstudied from an evolutionary perspective, and hypotheses are few. It is somewhat akin to infanticide, but occurs when a child is just reaching adulthood, and the relatives involved in the murder are not just parents. It also has characteristics of punishment-related killing. This suggests conditions unique to humans, such as the inheritance of wealth, are playing some role. Some have hypothesised that a

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history of pastoralism and herding drives honour-based violence, as groups at risk of raiding develop norms of revenge and retaliation (Nisbett & Cohen, 1996). This literature has focussed on honour-based violence between unrelated men in the southern states of the USA, rather than kin-perpetrated violence in the Greater Middle East, which is the focus of this research. Others have proposed that female inheritance and cousin marriage co-evolve as a means to control the behaviour of women when they have access to wealth, which in turn drives honour-based violence against women (Tillion, 1983). Here, we test a hypothesis that cousin marriage is associated with kin-perpetrated honour killings, using the average genomic inbreeding coefficient as a measure of a society's historical practise of cousin marriage.

It has been noted that honour killings tend to occur in societies with a strong preference for cousin marriage and intensive kinship (Tillion, 1983). Intensive kinship systems emphasise relatedness-increasing norms, such as marriages among relatives and endogamy, creating dense, often co-resident kin networks (Walker & Bailey, 2014). In contrast, extensive kinship systems tend to practise exogamy with unrelated individuals forming dispersed kin networks. Cousin marriage is a key feature of intensive kinship, and societies differ in their preferences. Some favour cross-cousins - the offspring of opposite sex siblings i.e. a daughter marrying her mother's brother's or father's sister's son. Others, particularly in the Greater Middle East, prefer patrilineal parallel cousin, i.e. a son marrying his father's brother's daughter (FBD). Both types increase relatedness equally, in terms of the likelihood that an allele is identical by descent, but FBD marriage will be endogamous in patrilineal societies, whereas cross-cousin marriage is exogamous. Furthermore, FBD marriage often forms part of a broader preference for consanguinity and within lineage endogamy (Ayoub, 1959). If the preferred cousin is not available, then a second cousin on the father's side will be found, and failing that, a cross-cousin or more distant relative. Societies that prefer cross-cousins, however, often view FBD marriage as incestuous. This contributes to the assumption that FBD marriage is more kinship intense than practising cross-cousin marriage (Schulz et al., 2019), which is supported by genetic evidence of higher consanguinity in FBD-practising societies, though strong signals are also evident in cross-cousin marriage societies (Laurent et al., 2024; Marchi et al., 2018; Pemberton et al., 2012).

The rationale behind an association between intensive kinship and honour cultures has been verbally theorised. On the one hand staying with close kin may increase cooperation within families due to high relatedness and increased female bargaining power (Chen et al., 2023). This could protect women from family violence (Campbell & Mace, 2022), suggesting a negative relationship between consanguinity and honour-based violence. On the other hand, competition between relatives is common and can cancel out any benefits of increased relatedness (Grafen, 1984; Taylor, 1992). Examples from humans and other species of individuals competing with and harming kin include the policing systems of eusocial insects (Ratnieks & Wenseleers, 2005), siblicide in spotted hyenas (Hofer & East, 2008), infanticide in banded mongooses (Cant et al., 2014), and conflicts over reproduction between Mosuo sisters (Ji et al., 2013). Such behaviours benefit individuals by reducing the number of competitors, but they also deter others from engaging in individually selfish behaviour that would be harmful to the fitness of the overall group, to whom, given cousin marriage, an individual may be significantly related. We hypothesise that cousin marriage in humans may benefit parents and the wider kin group but increase parent-offspring over marriage. Honour cultures, with their many prescriptions around marriage and sex, may arise to enforce parental marriage choices and prevent individually selfish behaviour.

What are the benefits of cousin marriage? Firstly, there are financial benefits of increasing intergenerational wealth concentration among families, through preventing wealth escape (Johow et al., 2019; Joshi et al., 2018). These wealth escape effects may be particularly pronounced if women inherit some of the patrimony in patrilineal societies. In these instances women will take their inheritance to their husbands

home unless she is married to her patrilineal parallel cousin, in which case her inheritance never leaves the lineage (Tillion, 1983). Indeed, female inheritance and patrilineal parallel cousin marriage are associated cross culturally (Korotayev, 2000) and evidence from India indicates that cousin marriage increased following the introduction of a legal amendment that meant that daughters became entitled to inherit (Bahrami-Rad, 2021). This is one reason that is proposed to explain the high rates of patrilineal parallel cousin marriage in Islamic societies, since Islam brought with it the Koranic law of female inheritance whereby daughters receive an inheritance worth half the value of their brother's. Even in societies without female inheritance, daughters may still inherit when they have no brothers, in which case she is also married to her father's brother's son, a pattern observed in ancient Greece (Goody, 1983), historical Germany (Johow et al., 2019), and contemporary Bangladesh (Shenk et al., 2016). Cousin marriages also tend to have reduced bride price or dowry, simplifying negotiations financially, and frequently named as a chief reason for cousin marriage (Aswad, 1971; Bittles & Hamamy, 2010; Do et al., 2013; Kressel, 1986; Mobarak et al., 2018).

Secondly, the production of well-defined kin groups with high group relatedness may benefit those who are required to cooperate on issues such as warfare and migration (Keddie, 1990). This may be particularly true among pastoralists, who face frequent raids and warfare (Nisbett & Cohen, 1996). Cousin marriage, particularly of the FBD type, should consolidate the patrilineal group through binding brothers together through the marriage of their daughters. Beyond pastoralist groups, non-foragers in general have higher rates of violence than foragers (Wrangham et al., 2006) and may have adopted more intensive kinship practices for that reason. In line with this, modelling has shown that honour cultures emerge where the rule of law is weak and the environment is tough (Nowak et al., 2016) and where reputations are well known and there are resource benefits of engaging in conflict (McElreath, 2003). Arguably reputation is more easily tracked in societies featuring kinship-intense tight knit social networks and possible resource gains are large in agro-pastoral societies.

While cousin marriage benefits kin, offspring may suffer the costs of inbreeding depression. These costs are well documented among humans, albeit the size is contested. These include increased child mortality (Álvarez et al., 2015; Ceballos & Álvarez, 2013; Dalzero et al., 2023), higher risks of diseases such as diabetes and cancer (Bener & Mohammad, 2017), reduced fertility (Swinford et al., 2023), and higher mortality throughout the lifespan (Hwang et al., 2023). Furthermore, genetic purging, is inefficient in human populations (Laurent et al., 2024). In line with the idea that there is a trade-off between the social and material benefits of cousin marriage and the biological costs, fitness peaks have been documented for cousin marriage among the Yānomamō, the Dogon, historical Icelanders, and the European nobility (Bailey et al., 2014; Chagnon, 1980; Dalzero et al., 2023; Helgason et al., 2008).

Parents also bear the reproductive cost of cousin marriage, as they are related to their grandchildren. However, there may be asymmetries since parents consider the summed costs and benefits to all their children. For instance, one child may marry a cousin, while others do not, allowing parents to reap the material and political benefits of some consanguineous marriages, whilst avoiding the costs in others (Kressel, 1986; Payton, 2015). Additionally, parent-offspring conflict may be sex-biased if the costs of a child deviating from the norm are sex-biased. For example, if cousin marriage prevents wealth escape when women inherit some of the patrimony, then it is particularly important that daughters marry cousins, whereas sons can marry unrelated women without wealth escape. Conflict could also be sex biased if the costs or benefits of consanguinity flow predominantly to one sex. For example, if men are able to marry polygynously having both related and unrelated wives, if brothers gain fitness benefits from their sisters marrying relatives through marriage exchanges, and if cousin marriage allows sons to marry younger women or avoid a shortage of mates (Aswad, 1971;

Chagnon et al., 2017; Dalzero et al., 2023). At the individual level there is some evidence that cousin marriage is associated with honour-based violence (Payton, 2015), although there may be variation in this risk depending on the type of cousin (Campbell & Mace, 2022).

In line with the reasoning outlined above and summarised in Fig. 1, we use a variety of data sources, including a genetic measure of cousin marriage rarely used in the social science literature, to show that higher rates of cousin marriage are indeed associated with honour-based violence against women at two levels: 1) across ethnicities and 2) between regions within countries.

2. Methods A: attitudes towards honour killings and genetic measures of consanguinity

2.1. Participants

To examine cross-cultural variation in honour-based violence, we use survey data from the Pew Research Centre, collected between 2011 and 2012 (Pew Research Centre, 2013). Respondents are all Muslim and come from 26 countries. They were asked how much they agreed with the statement: “Some people think that if a woman engages in premarital sex or adultery, it is justified for family members to end her life in order to protect the family’s honour. Others believe that this practice is not justified, no matter the circumstances. Do you personally feel that this practice is often justified to defend the family honour, sometimes justified, rarely justified, or never justified?” The same question was asked about honour killings of men. In Afghanistan, Iraq, and Uzbekistan, the question was altered to remove references to sexual behaviour due to cultural sensitivities. Instead, the question reads “Some people think that if a woman brings dishonour to the family, it is justified for family members to end her life in order to protect the family’s honour”. This broader wording could inflate responses endorsing honour killings, since dishonour could be interpreted more widely than premarital sex and adultery. However, the ambiguity could also deflate responses if respondents felt many dishonourable situations would not warrant such a punishment. Individuals were scored 1 if they believed violence was often or sometimes justified and 0 if they believed it was rarely or never justified or if did not know.

Respondents also reported their sex, ethnicity, education, religiosity, urban or rural residence, and age. Education was transformed into four levels: no education, some or all of primary, some or all of secondary, and some or all of higher. Religiosity was measured by asking “on average, how often do you attend the mosque for salah and Jum’ah Prayer?”. Responses included: never, seldom, a few times a year especially for the Eid, once or twice a month, once a week, and more than once a week. For all covariates individuals who responded they did not know or refused to answer were coded as missing and excluded from analyses.

2.2. Calculating runs of homozygosity

We calculate population-level average genomic inbreeding coefficients (F_{ROH}) using genome-wide single nucleotide polymorphism

(SNP) data from the publicly available Human Origins dataset described in Lazaridis et al. (2014) - a standard genetic panel purpose built for between population comparisons. Runs of homozygosity (ROH) are regions of the genome where an individual is homozygous across all sites due to common ancestry between said individuals’ parents. They are currently the best and most well-established means of detecting parental relatedness and consanguinity with significant improvements on pedigree data. Genetic measures calculate the realised rather than expected homozygosity, while also associating strongly with known pedigrees (Ceballos et al., 2018; Kirin et al., 2010; McQuillan et al., 2008; Ringbauer et al., 2021).

We calculate the mean F_{ROH} per population (hereafter referred to as mean F_{ROH}) by averaging the F_{ROH} estimates of the individuals within each population. Mean F_{ROH} can be considered as an estimate of total inbreeding relative to an unknown base generation, approximately tens of generations past (Clark et al., 2019). ROH and their lengths were analysed using published methods (Ceballos et al., 2018; Clark et al., 2019; Joshi et al., 2015). See the Supplementary Information for further details.

Inbreeding coefficients were calculated for each individual as follows:

$$F_{ROH} = \frac{L_{ROH}}{L_{AUT}}$$

Where L_{ROH} is the total length of an individual’s genome in ROH of the specified minimum length and L_{AUT} is the total length of the autosomal genome, or in this case, the length between the first SNP and the last SNP per chromosome for all autosomal chromosomes (in base pairs). We vary the minimum length of ROH from ROH >0.5 Mb to >10 Mb to show that our results are robust to more conservative lengths of ROH that we can be sure is demonstrative of consanguinity and secondly, to demonstrate what length has the strongest association with our outcome of interest. Generally, longer ROH (>1.5 Mb) are seen as evidence of consanguinity, whilst shorter runs are thought to reflect the demographic history of populations (in particular, recent population bottlenecks) (Clark et al., 2019; Kirin et al., 2010), although it has been shown that demonstrably outbred individuals for at least 10 generations, can harbour ROH of up to 4 Mb in length but no longer (McQuillan et al., 2008). We report results for $F_{ROH>1.5}$ in the main manuscript and additional results for the full range of F_{ROH} in the SI.

2.3. Matching genetic samples to self-reported ethnic groups

We match the mean F_{ROH} of the genetic samples to self-reported ethnicity. There were 27 exact matches where the self-reported ethnicity and the genetic sample names were the same or ethnonyms (e.g., Pashtun and Pushto matched to Pathan). For ethnicities without an exact genetic match, we selected the closest match using sources including eHRAF, D-PLACE, Glottolog, Joshua Project, other academic sources and Encyclopaedia Britannica. Matches were made based on geographic and linguistic closeness, given similar marriage practises. Matches were avoided if one group practised cousin marriage while the other did not, even if they were geographically and linguistically close.



Fig. 1. Summary of why cousin marriage is hypothesised to be related to honour killings.

In some cases, no suitable proxy match was available due to lack of information on marriage practises. In two cases we averaged the F_{ROH} of multiple groups. For example, Kurds live in Turkey, Iran, Iraq, and Syria, and speak Kurdish, related to Persian. The F_{ROH} for Kurds was an average of the Turkish, Iranian, and Syrian F_{ROH} (no data for Iraqis), all of whom practice cousin marriage. This method resulted in 25 additional matches, bringing the total sample to 52 ethnic groups from 25 countries. See the Supplementary Information for a list of matches and a map of the ethnic groups and genetic samples.

2.4. Calculating the kinship intensity index

Previous research has also demonstrated associations between an omnibus measure of kinship intensity called the Kinship Intensity Index (KII) and global psychological variation and economic or political development (Bahrami-Rad et al., 2022; Schulz, 2022; Schulz et al., 2019). We calculate the KII for each ethnicity using categorical variables on cousin marriage preference, polygamy, co-residence of extended families, lineage organisation, and community organisation from D-PLACE (Kirby et al., 2016). These are used to create a score which is then standardised across the range of ethnic groups to create a relative index of kinship intensity. Where there was no exact match between a self-reported ethnicity and society in D-PLACE, the closest possible match was used and where data on the variables that make up the KII were missing in D-PLACE we used information from eHRAF. All matches and information on how the KII is calculated is found in the Supplementary Information. We repeat our analyses using the KII to demonstrate that when comparing societies that are similar the KII is unable to capture variation in kinship intensity.

2.5. Other data sources

GDP data was taken from the Penn World Table for 2012. Preference for patrilineal parallel cousin marriage was coded using variable EA026 from D-PLACE. Ethnic groups received a score of 1 if they had a preference for FBD marriage, and 0 otherwise. Missing cousin marriage data was filled in using eHRAF or other academic sources. Language was coded using Glottolog v 3.0 (Hammarström et al., 2024). A linguistic proximity matrix was calculated using a global language phylogeny from Bouckaert et al., 2022, with pairwise distances between languages calculated using the `cophenetic.phylo` function from the R package *ape* (Paradis et al., 2024). The latitude and longitude of ethnic groups were sourced from D-PLACE or, if missing, from eHRAF or Glottolog. See the Supplementary Information for a table of all data sources.

2.6. Analysis

We fit multi-level logistic regression models in R (R Core Team, 2021) using the *spaMM* package (Rousset et al., 2023). This allowed us to fit random effects, including the language proximity matrix and the Matern covariance function, to control for shared cultural history and spatial autocorrelation, respectively (Claessens et al., 2023). We also fit random intercepts for ethnic groups to account for the data's nested structure. Ethnic groups with fewer than 10 respondents are removed from the dataset. The binary outcome variable was whether an individual believed honour killings are ever justified and our variable of interest is the average F_{ROH} . Two sets of models were fit depending on whether the outcome was an honour killing against a woman or a man. Individual level controls include sex, religiosity, education, age, and rural residence.

3. Results A

3.1. Higher inbreeding coefficients explains honour-based violence across ethnicities

Fig. 2 presents the proportion of individuals that justified an honour killing against men and women across ethnicities. Some groups, like Karakalpaks, Balkarets, and Circassians, never justify honour killings for either sex, while in others the majority believe it is justified. The proportion justifying honour killings against each sex also varies by group. For example, Jordanians are more likely to endorse murdering a woman than a man, whereas among Pashtuns and Nuristani's more endorsed killing men. Note that these two ethnicities are from Afghanistan where respondents were given a broader question about whether honour killings were justified, which may have inflated responses for men (see section 2.1.1). Overall, more respondents believed that honour killings were justified against a woman (28 %) than a man (23 %).

Justification of honour-based violence is generally strongly positively associated with $F_{ROH>1.5}$ at the ethnicity level, with Pearson correlations (R) of 0.45, 95 % CI [0.20–0.64] and 0.34, 95 % CI [0.08–0.56] between $\log(F_{ROH>1.5})$ and the proportion of individuals who justify an honour killing against women and men, respectively (Fig. 3). For male honour killings, this association appears to be driven by Pashtun and Nuristani respondents. Removing these groups reduces the association, rendering it non-significant ($R = 0.26$, 95 % CI [−0.02–0.51]). However, the association with female honour killings remains significant ($R = 0.41$, 95 % CI [0.15–0.62]).

As expected, societies that prefer patrilineal parallel cousin marriage tend to have higher and more variable values of $F_{ROH>1.5}$ than those that prefer cross-cousins or do not practice cousin marriage. This aligns with evidence that FBD marriage is often practised at higher rates. In our sample, average $F_{ROH>1.5}$ ranges from 0.63 % among Egyptians to 6.75 % among Balochi. For context, an 6.25 % increase in F_{ROH} is equivalent to the difference between the offspring of first cousins and those of unrelated parents (Clark et al., 2019).

In the multi-level logistic regression models, which controlled for respondent characteristics including sex, education, age, religiosity, and urban/rural residence, and accounted for clustering at the ethnicity level, a 1 % increase in $F_{ROH>1.5}$ was estimated to increase the odds of justifying honour killings by 27 % for women (OR = 1.27, 95 % CI [1.08–1.49]) and 17 % for men (OR = 1.07, 95 % CI [0.98–1.39]), though the latter was not statistically significant (Table 1, Model 2). To address potential confounding from shared phylogenetic ancestry and spatial autocorrelation (Claessens et al., 2023; Mace & Pagel, 1994), models incorporated a language proximity matrix and a Matern function to control for spatial dependencies. The inclusion of spatial controls did not alter the relationship between F_{ROH} and the justification of honour killings for either women or men, suggesting that the observed association is not driven by spatial proximity (Table 1, Models 2 & 4). However, accounting for shared cultural history through the language proximity matrix attenuated the association for women (OR = 1.20, 95 % CI [1.03–1.41]), implying some degree of co-transmission of cousin marriage and honour-based violence against women (Table 1, Model 3). In contrast, the odds ratio for men remained unchanged with the inclusion of the language proximity matrix, indicating a distinct pattern of justification for honour killings across sexes (Table 1, Models 2 & 3).

Interestingly our associations hold for honour killings against women at all levels of F_{ROH} ranging from a minimum length of 0.5 Mb to 10 Mb and get stronger with increasing length. An increase of 1 % in $F_{ROH>10}$ is associated with a 45 % higher likelihood of endorsing an honour killing against a woman (OR 1.34, 95 % CI [1.06–1.69], Table S1). This suggests that cousin marriage, rather than other population dynamics that could produce ROH, is the primary driver of the association.

Odds ratios remain positive, although significance is lost, when we exclude respondents from Afghanistan, Iraq, and Uzbekistan - where the honour question omitted reference to premarital sex and adultery. The

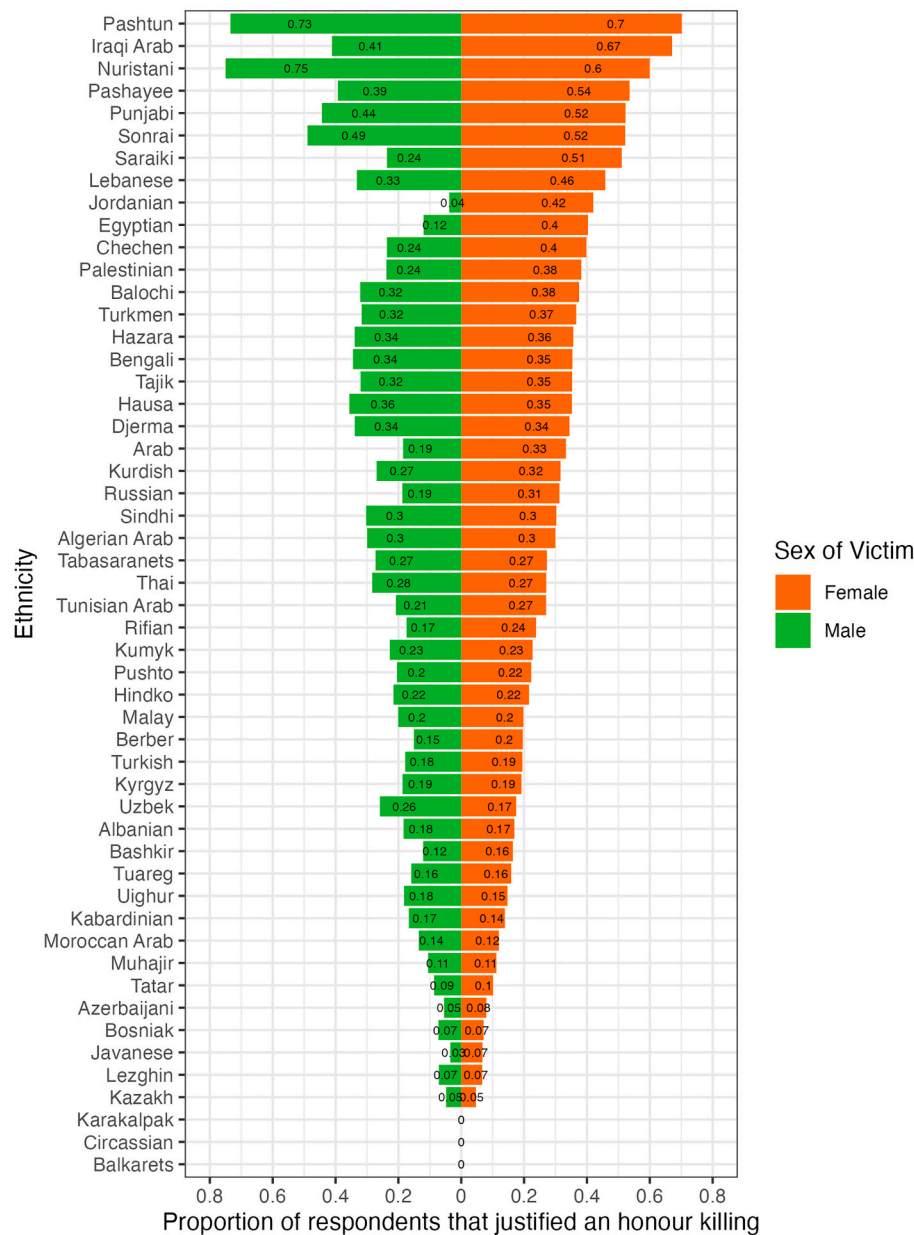


Fig. 2. Proportion of respondents for each ethnicity in our sample who justified an honour killing against either a man or a woman.

same occurs when we exclude imperfect ethnicity matches, which reduces the number of ethnicities from 50 to 27 (Table S3). Across all model specifications, the associations with honour killings against men are consistently weaker and non-significant (Table S5–S8). Nevertheless, while the results are stronger for women, the estimates for men are not substantially different, indicating that groups endorsing violence against women often also endorse violence against men, as suggested in Fig. 1.

As mentioned, FBD marriage is linked to female inheritance, since it is hypothesised to consolidate wealth within the patriline more effectively than cross-cousin marriage. FBD marriage returns a woman's inheritance to her natal patriline, unlike cross-cousin unions. Additionally, FBD marriage is hypothesised to strengthen patrilineal kin groups by bonding brothers through their children's marriage. If honour-based violence serves to prevent wealth escape and the disintegration of patrilineal networks, FBD marriage should be more strongly tied to such violence than cross-cousin marriage. Indeed, FBD marriage is more strongly associated with the justification of honour-based violence against women, controlling for the same level of consanguinity using

F_{ROH} (OR 1.80, 95 % CI [1.07–3.04]) (Table 2, Model 2). This is not the case for honour killings against men (OR 1.08, 95 % CI [0.59–2.00]).

Interestingly, the kinship intensity index (KII) does not show a significant association with the likelihood of justifying honour killings against either women (OR 1.04, 95 % CI [0.80–1.33]) or men (OR 1.11, 95 % CI [0.85–1.45]), though the coefficients are positive (Table S9 & Fig. S8). Additionally, KII does not correlate with $F_{ROH} > 1.5$ ($\beta = 0.002$, 95 % CI [−0.002, 0.005]), suggesting it is ineffective at capturing kinship intensity differences among closely related societies, which are similar across the broad categories comprising the KII (Table S10 & Fig. S9).

4. Methods B: honour-based proxies and regional proportions of cousin marriage

4.1. Participants

To address concerns about omitted country-level variables and

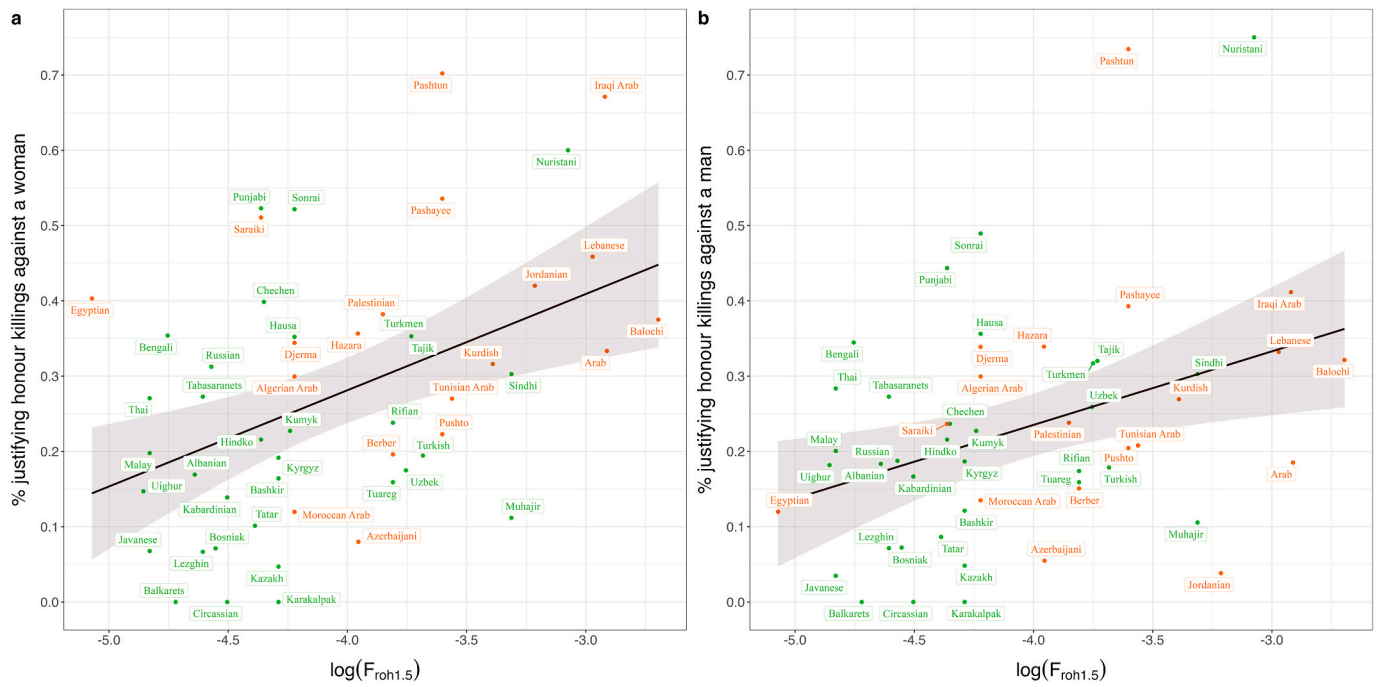


Fig. 3. Correlation plots between the log average $F_{ROH>1.5Mb}$ and the percentage of individuals who justify honour killings against a) women and b) men, coloured by whether the society is reported to practice FBD marriage. Shaded areas are the 95 % CI of a linear regression.

Table 1

Odds ratios (OR) and 95 % confidence intervals (CI) of multi-level logistic regression of average ethnicity-level $F_{ROH>1.5}$ on the likelihood of justifying an honour killing against a woman or a man. All models include a random intercept for ethnicity. Additional random effects include the language proximity matrix to control for shared cultural history and a Matern covariance function to control for spatial autocorrelation. Individual level controls include sex, education, urban/rural living, and religiosity. Education data is missing for Moroccans, so Moroccan Arabs and Rifians are lost from the model when education is added as a control. *** $p < 0.001$ ** $p < 0.01$ * $p < 0.05$ • $p < 0.1$.

	(1) OR (CI)		(2) OR (CI)		(3) OR (CI)		(4) OR (CI)		(5) OR (CI)	
	Women	Men	Women	Men	Women	Men	Women	Men	Women	Men
$F_{roh1.5} \times 100$	1.33*** (1.12–1.58)	1.23* (1.03–1.47)	1.27** (1.08–1.49)	1.17• (0.98–1.39)	1.20* (1.03–1.41)	1.17• (0.98–1.39)	1.27** (1.08–1.49)	1.17• (0.98–1.39)	1.20* (1.03–1.41)	1.17• (0.98–1.39)
GDP	–	–	Yes	–	Yes	–	Yes	–	Yes	–
Individual Level Controls	–	–	Yes	–	Yes	–	Yes	–	Yes	–
Language proximity matrix	–	–	–	–	Yes	–	–	–	Yes	–
Spatial control	–	–	–	–	–	–	Yes	–	Yes	–
Observations	29,068	29,142	27,182	27,261	27,182	27,261	27,182	27,261	27,182	27,261
Ethnicities	52	–	50	–	50	–	50	–	50	–

unaccounted cultural history, we conducted a second analysis, focusing on within-country regional variation. We utilized data from the Demographic Health Surveys ([The DHS Program, 2022](#)) for the following countries and years: Jordan 2007, 2012, 2018; Egypt 2014; Pakistan 2012 and 2017; and Turkey 2013.

Respondents, all of whom are women, were asked whether they were related to their husbands by blood, and if so, the degree of relatedness. We calculated the proportion of first-cousin marriages at the regional level. Two binary proxies were used to assess honour-related behaviours: 1) whether respondents justified domestic abuse if a wife “goes out without telling him” and 2) whether the woman was employed outside the home. These variables capture key features of honour cultures, particularly female seclusion and gender segregation. A binary variable for justifying violence was created by coding individuals as 1 if they justified violence and 0 if they did not justify violence, or said they did not know. Employment outside the home was coded as 1, while respondents who were unemployed or worked within the home were

coded as 0.

4.2. Analysis

We fit multi-level logistic regression models in R ([R Core Team, 2021](#)) using *lme4* ([Bates et al., 2015](#)), including random intercepts for region and country. Controls were included for a respondent’s education, wealth, year of birth, and urban/rural residence. Education was categorised as no education, primary, secondary, or higher, while wealth was measured using the DHS derived wealth index, which classifies individuals into five categories ranging from poorest to richest based on household assets.

Table 2

Odds ratios (OR) and 95 % confidence intervals (CI) of multi-level logistic regression testing the association between whether an ethnic group practises patrilineal parallel cousin marriage (compared to cross-cousin marriage), also known as father's brother's daughter marriage (FBD) on the likelihood of justifying an honour killing against a woman or a man. The sample size is reduced as ethnic groups that do not practise any kind of cousin marriage are removed from this analysis since we wish to compare only patrilineal parallel cousin marriage to other types of cousin marriage. Individual level controls include sex, education, urban/rural living, and religiosity. *** $p < 0.001$ ** $p < 0.01$ * $p < 0.05$ • $p < 0.1$.

	(1) OR (CI)		(2) OR (CI)	
	Women	Men	Women	Men
FBD Marriage (Ref = Cross-Cousin marriage)	1.80*** (1.07–3.04)	1.08 (0.59–1.99)	1.80*** (1.07–3.04)	1.08 (0.59–2.00)
F _{ROH>1.5}	Yes		Yes	
GDP	Yes		Yes	
Individual Level Controls	Yes		Yes	
Language proximity matrix	–		Yes	
Spatial control	–		Yes	
Observations	22,509	22,580	22,509	22,580
Ethnicities	35		35	

5. Results B

5.1. Higher rates of cousin marriage associate with honour-related behaviours across regions within countries

Fig. 4 shows an association between the frequency of cousin marriage and the prevalence of honour-related behaviours among women across regions. Specifically, a 1 % increase in the proportion of marriages between first cousins corresponds to a 5 % increase in the odds of justifying violence against a woman if she goes out without informing her husband (OR 1.05 95 % CI [1.03–1.08]) (Table 3). Conversely, this increase is associated with a 3 % decrease in the odds of women being employed outside the home (OR 0.97 95 % CI [0.96–0.99]) (Table 3). The association between cousin marriage and the honour-based proxies

Table 3

Odds ratios (OR) and 95 % confidence intervals (CI) from multi-level logistic regressions of the association between the regional proportion of marriages that are between first cousins and the likelihood of 1) justifying violence against a woman if she goes out without telling her husband and 2) being employed outside the home. Random intercepts for region and country. Controls include year of birth, education, wealth, rural living. Jordan and Turkey are excluded from model 2 due to missing data for female employment. *** $p < 0.001$ ** $p < 0.01$ * $p < 0.05$ • $p < 0.1$.

	(1) Justification of violence OR (CI)	(2) Employed outside the home OR (CI)
% of marriages between first cousins	1.05*** (1.03–1.08)	0.97*** (0.96–0.99)
Observations	97,024	49,597
Regions	57	33
Country	4	2

is unclear for Pakistan. This ambiguity may stem from the limited number of administrative regions in Pakistan or an asymptotic effect resulting from the notably high rates of consanguinity compared to Egypt, Jordan and Turkey.

6. Discussion

Why does honour-based violence perpetrated by kin emerge? We hypothesised that a preference for cousin marriage generates parent-offspring conflict, fostering the emergence of an honour culture and honour-based violence as mechanisms for policing marriage choices among offspring. For parents and kin, cousin marriage prevents wealth escape and creates closely related groups that may be advantageous in contexts requiring collective decision-making, such as migration and warfare. In contrast, offspring suffer the costs of inbreeding depression, including higher infant mortality and overall mortality, as well as other less overtly deleterious traits (Bittles, 2008; Dalzero et al., 2023; Hedrick & Garcia-Dorado, 2016; Hwang et al., 2023). Parents can offset these costs by not marrying all their children consanguineously, which can lead to sibling conflict regarding who should shoulder the cousin

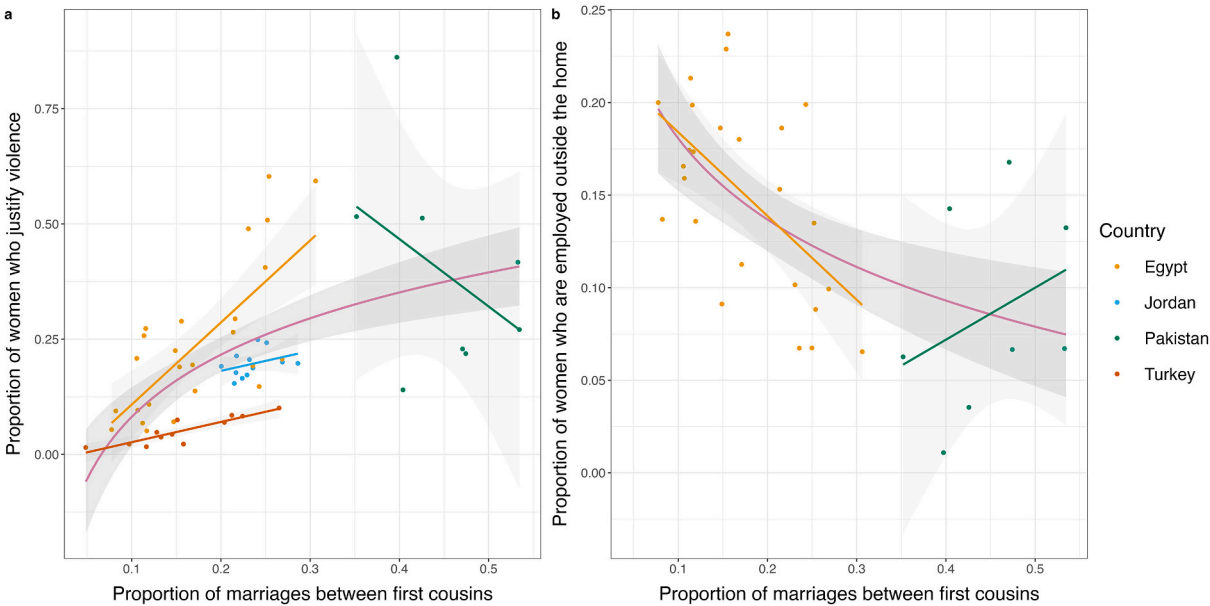


Fig. 4. Correlation plots between the regional proportion of marriages that are between first cousins and a) the proportion of women who believe violence is justified when a wife goes out without telling her husband and b) the proportion of women employed outside the home, coloured by Country. Dark grey shaded area presents 95 % CI of a linear-log regression across the whole sample. Light grey shared areas present 95 % CI of a linear regression for each individual country.

marriage duty (Kressel, 1986; Payton, 2015).

Supporting this hypothesis, we find a positive association between our genetic measure of cousin marriage and honour-based violence against women, across ethnic groups located across the Middle East, North Africa and parts of Central and South Asia. This association strengthens with increasing lengths of ROH, from 1.5 Mb to 10 Mb. Given that longer ROH (>1.5 Mb) are seen as evidence of consanguinity, this indicates two things about what is driving the association: 1) that it is cousin marriage and not other population dynamics and 2) that it is *recent* as well as historical cousin marriage events, given that more recent cousin marriage events will produce ROH of greater length than more distant cousin marriage events. This distinction is important as we compare a genetic measure reflecting several generations of cousin marriage practises with attitudinal data collected in 2012. This speaks to a literature that suggests that cultural traits that stabilised several generations ago persist over time because of cultural inertia, even when the original functional rationale has disappeared (Alesina et al., 2013; Baranov et al., 2023). Our results suggest that it is not merely inertia but may also depend on the ongoing normative acceptance of cousin marriage.

Interestingly, we observe a weaker relationship between cousin marriage and the endorsement of honour killings of men, suggesting a potential sex-bias in parent-offspring conflict. This bias may arise if the costs of deviating from cousin marriage norms are greater for daughters than sons. For instance, if daughters inherit in an otherwise patrilineal and patrilocal society, their deviation from the cousin marriage norm could result in greater wealth loss than if sons do. This result may tell us something about the ultimate cause of cousin marriage and the honour code in these populations. If cousin marriage's primary purpose is to prevent wealth escape, this differential targeting makes sense. If, however, the purpose is to strengthen kin groups in harsh environments by binding brothers together through the marriages of their children, then we would not expect to see this. Indeed, analysis of ancient DNA from Pakistan reveals that cousin marriage was likely not present in the Middle Ages or prior, whereas it is common today (Ringbauer et al., 2021), suggesting that it is linked to changes in inheritance rules, such as the spread of the Koranic law of female inheritance, rather than a harsh environment.

This sex-bias in violence may also arise if the costs and/or benefits of cousin marriage flow unevenly to one sex. This inequality would occur if men can offset the cost of inbreeding depression through polygyny, if brothers gain fitness benefits from their sisters marrying relatives through marriage exchanges, and if cousin marriage allows males to marry a younger women or avoid a shortage of mates, all of which have been documented (Aswad, 1971; Chagnon et al., 2017; Dalzero et al., 2023). Another possibility is that punishing women is less costly for families than punishing a man. Murdering a man could initiate a blood feud (Robertson Smith, 1885), men are stronger and more likely to resist, and the strength of a lineage may depend on the number of men, where the loss of one might weaken it (Barth, 1986).

Nevertheless, many individuals did justify honour killings against men, and it makes sense that among groups that strictly regulate marriage choices, there will also be a degree of control over male behaviour. Certainly, honour codes also attempt to limit the sexual behaviour of men. Among the Awlad-Ali, an Egyptian Bedouin group, men who pursue women do not have *aql*, the virtue of self-control, and they will be ridiculed and described as *bita sabāya*, literally meaning 'belonging to women' (Abu-Lughod, 2016). Fulani men who fall in love too deeply are ridiculed as lacking *pulaaku* - the set of qualities appropriate to a Fulani, a form of honour (Riesman, 1998). More broadly, norms around honour, such as the concept of *ghairat* in Iran, ensure male commitment to their family (Atari et al., 2020). The underlying sentiment is that if the marital bond becomes too strong, men will neglect their kinship bonds to the detriment of the wider group (Abu-Lughod, 2016). Analogously, the rise of 'romantic' love in literary history occurs in tandem with economic development, possibly because development changes the environment

that would have made cousin marriage beneficial, breaking down extended family ties and limiting the ability of family to control the marriage choices of offspring (Baumard et al., 2022).

We can also find many examples of enforcement of and resistance to cousin marriage in both historical and contemporary reports. In many groups of the Greater Middle East men have historically had a right to marry their female cousins. One case quoted in the Aghani – a 10th century Arabic collection of poems and songs – describes a father who is scolding his daughter for resisting to marry his brother's son: "He is your uncle's son and of all men has first claim to you" (quoted in Levy, 1957). This cousin right exists widely among Kurds, Arabs and Turks (Aswad, 1971; Barth, 1986; Patai, 1955) and when parents wished to arrange their daughter's marriage to someone other than said cousin, they required the permission of the cousin and his father (Barth, 1986; Patai, 1955). They may also have had to pay an additional forfeit (Aswad, 1971). Today in Pakistan, some men will still claim this right and force girls into marrying them (Gauhar, 2014) and many honour killings follow resistance to a cousin marriage (Kressel et al., 1981; Payton, 2015). Most recently in the UK, the 2022 murder of Somaiya Begum, followed her resistance to a cousin marriage.

Of course, honour killings do not *always* follow conflict over a cousin marriage. Nevertheless, there is broad consensus that they do follow accusations of sexual impropriety such as consorting with or dating an inappropriate individual (see Sev'er & Yurdakul, 2016 for several case studies from Turkey), indicating that there is strong parent-offspring conflict over marriage choice in general. This is not inconsistent with our overall hypothesis. Societies structured by cousin marriage and intensive kinship tend to be those where there is considerable gain to consolidating wealth, or where the environment is harsh, possibly with a risk of warfare, and with a lack of institutional policing. Marrying cousins helps to solve these risks, but so too does strategic marriage choice more broadly. It is intuitive that the societies that place great weight on marrying consanguineously will, when an appropriate cousin is unavailable, place great weight on the next best option. Indeed, cousin marriage within the Greater Middle East is often seen as one end of an overall pattern of within lineage endogamy (Ayoub, 1959).

While we have highlighted wealth consolidation and inbreeding depression as a clear benefit and cost of cousin marriage, we also speculate beyond this. Cooperation among kin is highly correlated with conflict among kin as those most likely to be sharing resources also have the most to fight about (Mace, 2013; Wu et al., 2013). Murphy & Kasdan (1959) highlight the fission fusion dynamics common to groups structured by cousin marriage where agnates benefit from pooling resources and joining in conflict against other groups. However, at some point the lineage becomes too large and segments because of increased competition, often over division of the patrimony. Similarly for women they may derive benefits from marrying kin, through increased bargaining power and social status (Abu-Lughod, 2016; Aswad, 1971), but at some point, perhaps due to increasing costs of inbreeding, it may benefit her instead to marry exogamously. In contemporary Bangladesh, for example, women report feeling controlled by their male relatives when married consanguineously and state that they are unable to speak out about grievances for fear of upsetting the family balance (Shenk et al., 2016). Thus, the dynamics of societies structured by high rates of cousin marriage may be such that for much of the time they operate as highly cooperative groups yet are occasionally punctuated with extreme violence. This might explain why previous research at the individual level has found unclear relationships between cousin marriage and honour-based violence (Campbell & Mace, 2022).

6.1. Strengths of using genetic data & the limitations of the KII

The use of genetic data to measure the practise of cousin marriage captures the realised inbreeding and marks a significant improvement on previous measures, such as pedigree-based measures or coarse ethnographic categorisations. Detailed pedigrees are unavailable for

large parts of the world and when available, often only reflect particular subsets of society. Furthermore, inbreeding coefficients derived from pedigree data are a measure of the expected level of inbreeding, whereas genetic data allows us to calculate the observed level of inbreeding. The improvement on using ethnographic categorisations is demonstrated by the lack of association found between the kinship intensity index and both honour-based violence and F_{ROH} itself. The KII suffers from a number of limitations. Firstly, the validity of variables drawn from the ethnographic record has been subject to critiques over data quality (Tobin, 1990), and while recent evidence suggests that ethnographic categories do hold contemporary validity, the effect sizes are small (Bahrami-Rad et al., 2021). Secondly, even if the variables that make up the KII are reliable, the KII is only relevant to studying variation across the whole range of human societies. In our case, small random variation in the sub-indicators is overweighted by the index as the societies tend to be similar across dimensions. Although it is possible that the KII does not associate with F_{ROH} because it weights patrilineal parallel cousin marriage higher than cross-cousin marriage yet both types of first cousin marriage will produce the same number of ROH and be indistinguishable genetically. Thirdly, the KII uses EA026 to code the cousin marriage sub-indicator, which reports a group's preferred cousin marriage partner. However, there are several societies that practise cousin marriage yet do not have a preferred type. These societies are coded as "no preference" in EA026 and are weighted the same as groups that practise no cousin marriage at all. An improvement would be to combine EA023 on whether cousin marriage is permitted with EA026. Fourthly, the KII weights each sub-dimension equally, in that it assumes that polygyny, cousin marriage, co-residence of extended families, descent patterns and community organisation all contribute equally to kinship intensity. This is a largely untested assumption, and we would argue that cousin marriage is likely to have a much stronger influence than unilineal descent, for example, on fostering dense kin networks and increasing group relatedness. In contrast to the KII, the genetic measurements are both continuous and allow us to infer the extent of cousin marriage in the past, whereas codes drawn from ethnography are synchronic observations made at the time ethnographers investigated each society.

6.2. Limitations

Firstly, while we show that intensive kinship is associated with higher rates of endorsement of honour killings, future work is needed to determine whether an honour killing increases the biological fitness of the kin group enough to compensate for the loss of a kin member. Therefore, whether fitness itself is optimised, or wealth consolidation, or a combination of the two. Furthermore, whether our explanation can extend to other regions of the world where honour killings are practised, such as India, remains to be seen. Hindus are known to practise consanguineous marriage, such as cross-cousin and uncle-niece marriage, alongside caste endogamy that could produce similar dynamics to the ones reported here. Secondly, the results are correlational, although we have attempted to make them more robust by controlling for shared cultural history, spatial autocorrelation, and showing that the results hold between regions within countries. However, residual confounding may remain. A second possibility is that our results are produced by selection effects: areas where women are treated poorly are more likely to adopt cousin marriage practises. This can produce results where cross-culturally the practise of cousin marriage looks detrimental, but at the individual level women married to their cousins have better outcomes, as has been found in other marital practises (Jacoby & Mansuri, 2010). Indeed, previous work has found that women married consanguineously are less likely to report violence (Campbell & Mace, 2022). Thirdly, the imperfect matching process between the genetic samples and the survey respondents may also affect results. Despite matching based on similar kinship systems it is known that two populations with similar systems can exhibit substantial variation in genetic estimates of inbreeding (Ly et al., 2019; Marchi et al., 2018). There are also limitations to using

multiple datasets and relying on survey data, in that the data are collected at different times by different researchers, and survey participants may conceal true beliefs. However, given the sensitivity of the topic there are severe limitations on what sorts of data collection are possible. Additionally, concealment of true beliefs around honour-based violence is likely to make the results more conservative, rather than inflating them. Lastly, we rely mostly on verbal models when hypothesising why we might expect to see an association between cousin marriage and honour-based violence. However, empirical tests of the hypothesis are novel in the honour literature, despite having been hypothesised decades ago (Tillion, 1983).

CRedit authorship contribution statement

Olympia L.K. Campbell: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Cecilia Padilla-Iglesias:** Writing – review & editing, Methodology, Formal analysis. **Grégory Fiorio:** Methodology. **Ruth Mace:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.evolhumbehav.2024.106636>.

Data availability

The data associated with this research are available from multiple publicly available sources listed in the SI. We also make available the F_{ROH} in the supplementary excel file.

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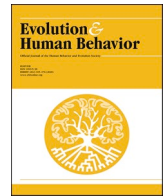
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Update

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Corrigendum to “Genetic markers of cousin marriage and honour cultures” [Evolution & Human Behaviour (2024) Volume 45, Issue 6, 106,636].

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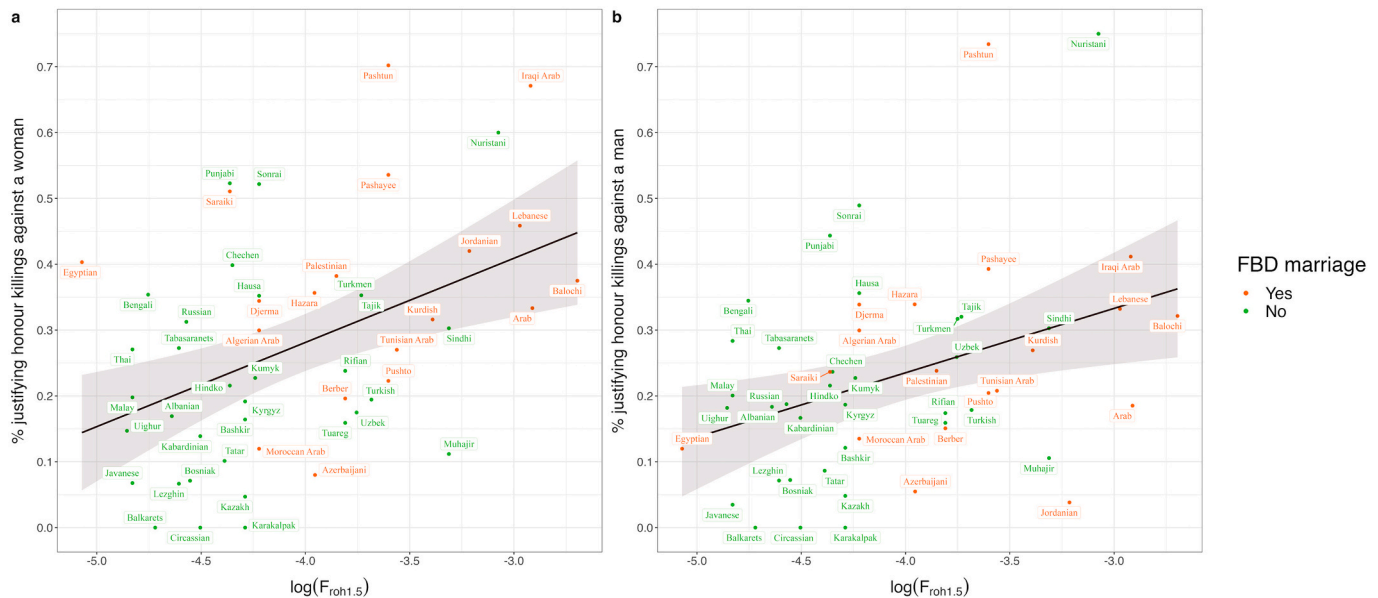
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The authors also regret that Fig. 3 was missing a legend. The correct Fig. 3 is below



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The authors would like to apologise for any inconvenience caused.

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