Phylogenetic Modeling of Cultural Evolution under the Influence of Selection

The Origins and Maintenance of Female Genital Modification across Africa

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Abstract We present formal evolutionary models for the origins and persistence of the practice of Female Genital Modification (FGMo). We then test the implications of these models using normative cross-cultural data on FGMo in Africa and Bayesian phylogenetic methods that explicitly model adaptive evolution. Empirical evidence provides some support for the findings of our evolutionary models that the *de novo* origins of the FGMo practice should be associated with social stratification, and that social stratification should place selective pressures on the adoption of FGMo; these results, however, are tempered by the finding that FGMo has arisen in many cultures that have no social stratification, and that forces operating orthogonally to stratification appear to play a more important role in the cross-cultural distribution of FGMo. To explain these cases, one must consider cultural evolutionary explanations in conjunction with behavioral ecological ones. We conclude with a discussion of the implications of our study for policies designed to end the practice of FGMo.

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In many parts of the world the prevailing culture requires that women undergo genital cutting/modification prior to their marriage. These operations typically occur between infancy and late puberty, and they may be extremely costly in terms of health, survival, and reproduction; these operations thus constitute a major challenge for evolutionary explanation. The analyses presented herein test competing hypotheses for the distribution of this cultural trait, with a particular focus on how the conditions that may have selected for the emergence of the trait (arguments for origins) might differ from those that account for its persistence (arguments for maintenance). We first present a model that demonstrates how conditions selecting for the origins of female genital modification (FGMo)[1] might differ from those that select for its persistence. In particular, we model how wealth and/or status differences within social groups might select for the emergence of this potentially costly trait, and how subsequent frequency-dependent forces might keep the trait in the population, despite its costs. We then use empirical data from Africa to test whether status differences and social stratification are associated with the origins of FGMo. Our expectation (derived from the model) is that stratification will be associated with the *de novo* origins of FGMo and will increase the likelihood of the intercultural transmission of FGMo. We use our results to discuss the adaptive significance of apparently costly cultural traits, and to discuss the importance of differentiating explanations for the origins and the maintenance of cultural traits.

Our study lies at the intersection of several literatures. First is the substantial literature on how marriage markets affect a range of cultural practices, including marriage payments (Anderson 2003; Bell and Song 1994; Borgerhoff Mulder 1995) and other household outcomes (Chiappori et al. 2002; Quisumbing et al. 2000). Many of these insights are inspired by Becker (1981). Second, we develop hypotheses on the basis of a wide-ranging research literature on female "circumcision" (Ericksen 1989; Shell-Duncan and Hernlund 2000; Silverman 2004). While contributors to this literature span many different disciplines, there is considerable agreement over the hypothesized functions of FGMo and related practices, though less agreement with regards either to its specific geographical origins or to its function. Third, we draw indirectly on the insights of signaling (or handicap) theory, as developed in evolutionary biology and applied in anthropology (Grafen 1990; Smith et al. 2003), viewing FGMo as a signal demonstrating sexual fidelity and paternity certainty. Fourth, we use formalized evolutionary models to identify distinct hypotheses for the origins and maintenance of costly cultural traits, as these potentially differing dynamics are rarely separated in analysis (Borgerhoff Mulder et al. 2006). Fifth, a growing (albeit widely-dispersed) literature across academic venues and policy circles addresses the morality of, and challenges to, eradicating

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[1] Also known as Female Circumcision, Female Genital Mutilation (FGM), Female Genital Cutting (FGC), or a combination of these terms, such as FGM/C. The terminology one should use when discussing this practice is a matter of concern. We purposefully avoid using the term "mutilation" in the text of this paper, because we feel that it is unduly value-laden, as well as being insensitive to the women who have endured the practice. Likewise, we feel that it is wrong to distance the practice of female genital modification from male genital modification (circumcision), because such an action seems to validate one type of unnecessary, non-consensual amputation of genital tissue (common in "Western" culture), while stigmatizing a similar practice in other cultures. We use the more neutral term FGMo to contextualize the practice within the wider anthropological scope of body modification.

the practice of FGMo (Shell-Duncan and Hernlund 2000). We use our results to evaluate some of the debates in this complex area. Additionally, we argue that the statistical methods used in this case study have broad implications for cultural phylogenetic analysis.

Female Genital Modification

The prevalence of FGMo worldwide is unknown, but it is estimated that more than 125 million girls and women alive today have undergone some form of FGMo, with another 30 million at risk of being cut in the next decade (UNFPA-UNICEF 2013). It is most common in Africa, affecting up to 90% of women in Djibouti, Egypt, Eritrea, Mali, Sierra Leone and Somalia, over 50% of women in other African countries such as Benin, Ethiopia, Burkina Faso, Chad, Ethiopia, Gambia, Guinea Bissau, Kenya, Liberia, Nigeria, Sudan, and Togo. It occurs elsewhere across southern and central Africa and in the Middle East—for example, in Oman, Yemen, and the United Arab Emirates, as well as in some Asian countries, including Indonesia, Malaysia, Sri Lanka, and India (WHO 1998).

Little is known about the origins of the practice. Scholars have proposed a single origin in Egypt, on the basis of circumcised 5th century BC mummies (Little 2003), or ancient Meroe (Mackie 2000; Mackie and LeJeune 2009). In these highly stratified ancient empires, infibulation may have been practiced in the context of extreme resource inequality, with families cutting girls or women to signal their fidelity to highly polygynous wealthy males. Mackie has hypothesized that the practice diffused across social strata and spread along female slave trade routes. Others suggest a multi-source origin, arguing that as FGMo spread out of its original core areas, it encountered and merged with preexisting practices associated with initiation rites for both males and females (Dorkenoo 1994). Strong evidence for either claim is nevertheless lacking. Although the practice sometimes spread with Islam, many non-Islamic groups practice FGMo.

Types of operations vary in severity, entailing either the removal of the prepuce or hood of the clitoris (clitoridectomy), removal of the clitoris and all or part of the labia minora (excision), or removal of the complete clitoris, labia minora, and all or part of the labia majora followed by a sewing together of the labia (infibulation, or Pharaonic circumcision).

The health costs (and benefits) of FGMo are hotly disputed (e.g., Shell-Duncan and Hernlund 2000). Estimates are likely to be biased by concealed complications when the practice is illegal, exaggerated by prejudice and by proponents of elimination strategies, and impacted by lack of good data. Furthermore, Western observers tend to stress pain, reduced sexual enjoyment, and medical complications, whereas (some) Africans emphasize the cultural importance of the tradition; for example, a Kenyan woman commented that FGMo might be seen as "buying maturity with pain" (Davison 1996, p60). Nevertheless, the evidence is clear that these operations, and particularly the more severe forms, can cause extensive short- and long-term medical complications, with implications for maternal health, pregnancy loss and stillbirth, primary and secondary fertility, and child survival (Banks et al. 2006; Mackie 2003; Shell-Duncan and Hernlund 2000), as well as for mental health (e.g., Whitehorn et al. 2002), and HIV risk (WHO 2010).

Most pertinent to this paper are arguments regarding the function of FGMo, or similar practices with likely negative effects for women's health and well-being. There are three types of explanations. The first, and by far the most predominant, concerns the marriageability of women. Though specifics differ markedly in different parts of the world, virginity, "purity," and sexual restraint before marriage are highly regarded in many societies that practice FGMo. FGMo operations are seen as a way of protecting sexual propriety, morality, and paternity (Ericksen 1989; Little 2003; UNFPA-UNICEF 2013), or demonstrating the obedience and respect required for marriageability (WHO 2010). Furthermore, FGMo is often associated with veiling, child betrothal, virginity testing at marriage, a transfer of sexual and reproductive rights to the groom and his family at marriage, and the legitimacy of subsequent births. FGMo is sometimes found in groups that lack strong chastity and fidelity expectations—for example, the Rendille women of Kenya are free to engage in premarital sex but must undergo FGMo at marriage (Mackie 2000). Nevertheless, scholars investigating FGMo across multiple sites typically stress the theme of safeguarding female sexual purity, enhancing marriage chances, and preserving family honor (Shell-Duncan and Hernlund 2000; UNFPA-UNICEF 2013; WHO 2010). For instance, uninfibulated women in Sudan during the early 1970s were widely considered to be like prostitutes (Hayes 1975).

A second set of explanations is more heterogeneous. They include protecting the health of a baby, increasing the likelihood of conception, reducing (or increasing) sexual pleasure, achieving an aesthetic ideal, or becoming a fully adult member of society; these more proximate considerations are also linked to marriageability, albeit indirectly. Particularly idiosyncratic notions include the belief that FGMo prevents child mortality [through avoiding fatal connection between baby's head and the clitoris during delivery (Myers et al. 1985)], that FGMo cured certain "female psychological disorders" in Victorian England (Little 2003), and that genital cutting is a functionless fad, as witnessed recently in Chad. Although FGMo in southern Chad may have been adopted in the 19th century to deter slave raiders from taking women, adolescent girls in the 1990s reportedly sought out the operation, often without parental consent, as something "fun, rebellious and cool" (Leonard 2000, p190).

The third explanation stresses the importance of tradition, custom, and cultural identity. For instance, for the Kipsigis of Kenya their very name implies "we the circumcised," referring to the rebirth that is believed to occur at circumcision ceremonies, a central part Kipsigis identity vis-a-vis other ethnic groups (Daniels 1970). Even more strategically, the Kenyan Mukogodo appear to have adopted circumcision ceremonies to hasten their transition to becoming Maasai (Cronk 2004). In a compilation of studies on attitudes toward FGMo, more than half the respondents reported that tradition was their primary reason for undergoing the operation (Warzazi 1986). Some authors emphasize only the importance of following the ancestors; others note strong social pressure to conform to the behavior of others, and still others explicitly recognize the force of current social convention.

As many researchers on FGMo recognize, there are intricate interdependencies between these hypotheses, even in cases where marriageability is not the explicitly-stated motivation for FGMo [for example, as in the Senegambian region (Shell-Duncan and Hernlund 2007)]. It is extremely difficult to distinguish the more general motivations of social respectability and conformity from the motivation to be seen as a suitable wife (Mackie and LeJeune 2009). Furthermore, some of the

more idiosyncratic beliefs underlying the need for FGMo may also serve as a way of encouraging conformity to social norms. Accordingly Mackie (2000)—emphasizing the critical role of social convention in maintaining particular practices—notes how the belief that an uncut woman will be unfaithful fixes the custom, even if the conditions that first gave rise to the trait have changed: "As soon as women believed that men would not marry an unmutilated woman, and men believed that an unmutilated would not be a faithful partner in marriage, the convention was locked in place" (Mackie 2000, p264).

An Evolutionary Approach

Our evolutionary analysis of FGMo draws closely on the literatures reviewed above. Parents or other kin may choose to subject young female relatives to costly operations to enhance their marriageability. In other words, the trait may be sexually selected, functioning to enhance the access of females to favored mates. The intuition here is that in an initial non-FGMo population parents use FGMo to ensure and signal the virginity of their daughters at marriage. Insofar as women who have undergone FGMo observe more sexual restraint (whether as a consequence of the operation or of associated customs), FGMo also signals higher paternity certainty to a prospective groom. Where there is little difference in quality among prospective grooms, it is unlikely that parents would inflict this physiological cost on their daughters. However, where there is extensive competition among women to become the brides of particularly wealthy or powerful men, a costly trait such as FGMo could arise as a bargaining tool. The simple logic here parallels evolutionary arguments for the origin of another costly display—dowry, and its association with stratification (Dickemann 1979; Gaulin and Boster 1990, see also Fortunato et al. 2006) and has in fact been marshaled as an explanation for the origins of FGMo (Mackie 2000). Some support comes from evidence that female puberty rituals are more elaborate and costly as social complexity increases, although this is based on a non-random sample drawn from a selection of foraging societies deemed to be weakly stratified (Owens and Hayden 1997). Other support comes from comparative analysis that links public menarcheal ceremonies to strong fraternal interest groups, where it appears that powerful kin-based units are making explicit contractual negotiations over women (Ericksen 1989; Paige and Paige 1981).

As noted above, other functions can accrete to the practice of FGMo over time. For example, FGMo (at least when accompanied by ritual) can constitute a key rite of passage (Van Gennep 1960); it is also a cardinal symbol of ethnicity since groups that do not practice FGMo are sometimes seen as lower by groups that practice FGMo. There are also clear reasons why it is difficult to dislodge FGMo once it is in place as a marker of marriageability, since a family that abjures FGMo for their daughters may fail to find husbands and therefore fail to contribute to the next biological and cultural generation. Evolutionary scientists refer to this as a coordination game (e.g., Efferson et al. 2015) and it can strongly influence the payoffs to FGMo in some contexts. Without a critical mass of FGMo-rejecters, there can be a strong disincentive for families to reject the practice; additionally increased payoffs in the mating market as a function of FGMo use might also disincentivize abandonment of the practice.

This argument leads to the hypothesis that the *origins* of FGMo are likely to be linked to stratification, based on the rationale that where considerable variance among men in mate quality exists, and where men invest heavily in their offspring, parents will inflict physiological (and other) costs on their daughters to reap the benefits of a marriage to a high-ranking man. Conversely, the custom might *persist* purely as a consequence of the high cost of not conforming, irrespective of the presence of high variance in wealth or status among men.

Modeling the Emergence and Persistence of FGMo

We begin methodologically by providing formal theoretical models for the emergence and persistence of FGMo. We then use phylogenetic models of adaptive evolution to test the implications of the theoretical models using cross-cultural data.

Assumptions and Notations

The following assumptions and notations are constant across all models:

a. Mating assessment is universal. That is—each woman agrees on a mating value for each man, and each man agrees on a mating value for each woman. A given woman's mating value is denoted f (and a given man's, m). The distributions for the mating values of women and men are d_f and d_m, respectively. Mating values are reflective of the integrated suite of traits of interest to the opposite sex (Schacht and Grote 2015).

b. The symbols r_f and r_m denote the functions that map the mating value of an individual woman or man to her or his rank in the mating market. These functions lead to a ranking of all women where the woman with the highest mating value gets rank $r_f = 1$, the woman with the second highest mating value gets rank $r_f = 2$, and so on. The woman with rank $r_f = 1$ is then assumed to marry the man with rank $r_m = 1$, and so on. Thus, if f_1 is the woman with the highest mating value in the d_f distribution, then her rank is described as $r_f(f_1, d_f) = 1$; she will be paired with the male whose $r_m = 1$, the highest ranked male from the d_m distribution.

c. The marriage value of a given person in d_f or d_m can be returned as a function, V_f or V_m, of rank, such that $V_m(r_m(m_1, d_m))$, for example, is the marriage value of the highest ranked man. The marriage value function is order preserving but allows for a nonlinear relationship between rank order and marriage value; a unit change in rank may not significantly impact marriage value near the bottom of a ranking scale, but it might have a huge impact on marriage value near the top of a ranking scale—especially in stratified societies.

d. Everyone gets married.

e. FGMo comes at a constant cost, c.

f. FGMo gives a woman a higher mating value and, therefore, an opportunity to marry a more valuable man.

g. The sex ratio is balanced such that the number of women in the population, N_f, is equal the number of men in the population, N_m.

h. There is a benefit, s, to having the same behavior as the rest of the group. Generally, s is a function of the proportion of women, α, that have the FGMo behavior. We conceive of this pressure as resulting from frequency-dependent dynamics, such as conformist bias (Henrich and Boyd 1998; Henrich and Gil-White 2001; McElreath et al. 2003, and see Discussion).

i. Baseline fitness across women is described as $\bar{w}$.

The General Model

We will consider two models. In the first, FGMo gives an assurance of virginity, and therefore, a constant increase in mating value, i, to every woman who has FGMo. In the second model, FGMo acts as a costly signal of general fitness. In this model, we see the increase in mating value as a random variable, x, since different women can signal differential fitness in a nondeterministic way. Presumably, a woman will not know the effect of the signal before she undergoes the operation. Death, for example, is a possible, and not entirely uncommon, outcome of undergoing genital cutting (UNICEF 2013). Further, the signaling value of FGMo is likely to depend on the social context of the practice. For example, in the Kipsigis population (studied by Borgerhoff Mulder in the 1980s), FGMo was often practiced in semi-public ceremonies and girls were socially judged on their stoicism and ability to withstand the pain of the cutting. Additionally, recovery from the clitorectomy was the subject of discussion and social scrutiny, with considerable gossip (Power 1998; 2000) over who recovered quickly and who needed to be taken to the dispensary or hospital. The ability to tolerate pain and recover quickly are presumably signals of quality and immunocompetence that are impossible to fake. In contrast, FGMo in Egypt (studied by Ericksen in the 1990s) was conducted in private by midwifes; in such a context there is much less scope for FGMo to act as a costly signal. Figure 1 illustrates how the mathematical mechanisms outlined here function to produce the behavior of the model.

In both models, a woman who does not undergo FGMo has a payoff, P:

$$P = \bar{w} + V_m(r_f(f, d_f)) + s(1 - \alpha) \tag{1}$$

where α is the proportion of the population who undergo FGMo. Equation 1 says that the value she gets from marrying depends on the marriage value of the man she marries, which depends on her rank $r_f(f, d_f)$, which in turn depends on her value f and the distribution of mating values across all females d_f. The last term is the social payoff from having the same behavior as proportion $1 - \alpha$ of the population.
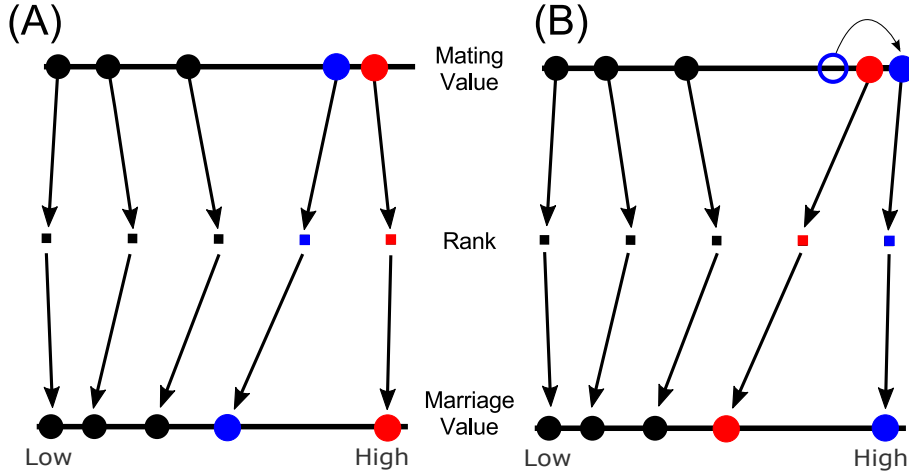
The Virginity Assurance Model

In the virginity assurance model, the payoff, P_{VA}, for undergoing FGMo is:

$$P_{VA} = \bar{w} + V_m(r_f(f + i, d_f)) + s(\alpha) - c \tag{2}$$

Under this condition, FGMo will emerge when, for any woman, $P_{VA} - P > 0$, for $\alpha = 0$. That is, when:

$$V_m(r_f(f + i, d_f)) - V_m(r_f(f, d_f)) - s(1) - c > 0 \tag{3}$$

Fig. 1 A simplified sketch of the mathematical model described in this section. In frame (A), we observe a distribution of mating values (on the real number line) for five women. We have highlighted two individuals in red (highest ranked) and blue (second highest ranked). The arrows from Mating Value to Rank are indicative of the rank function r_f and map mating values (on the real number line), to an ordered ranking. The arrows from Rank to Marriage Value are indicative of the value function V_m and map a woman's rank score on the marriage market to the marriage value of her husband (on the real number line). In frame (B), we imagine that the woman shown in blue has undergone FGMo and has thus added i or x to her mating value. This allows her to move from her previous position on the Mating Value scale (shown in the blue outlined circle) passed the woman labeled in red. This in turn increases her rank and allows her access to the marriage value of the highest ranked man.

So for FGMo to emerge, we need at least one (or a combination) of the following: low social control or conformity bias, s; a high value of FGMo, i; or a large difference in the marriage value of men, V_m. We will not elaborate on how FGMo spreads through the population, nor will we discuss all possible equilibria that can appear. Rather we focus on what is needed for an equilibrium where everyone in the population does FGMo. In the virginity assurance model, this occurs for cases such that when $\alpha = 1$, then $P_{\mathrm{VA}} - P > 0$ holds for all women in the population. That is when:

$$V_m(r_f(f + i, d_f)) - V_m(r_f(f, d_f)) + s(1) - c > 0 \qquad (4)$$

Here two things have changed from the emergence condition in Equation 3; the social effect has switched so that it now benefits FGMo, and also the value distribution of women d_f has changed since every woman has added i to her value. This means that when $\alpha = 1$ every woman is in the same position on the ranking scale as she would have been had no one undergone FGMo.

So Equation 4 can be reduced to:

$$s(1) - c > 0 \qquad (5)$$

Several interesting conclusions can be drawn from Equation 5. Whereas the marriage value function for males, V_m, is critical in explaining the origins of FGMo, it has no effect on the *maintenance* of the trait at fixation. Another conclusion is that strong social pressure is required to obtain an equilibrium where every woman

has undergone FGMo. Finally, we can see that the difference in payoff between being a woman in a society where everyone has FGMo and a society where no one has FGMo is strictly negative for every woman, since the rankings are unchanged between the FGMo and non-FGMo equilibria, but all women pay a cost c in the FGMo equilibrium.

The Costly Signaling Model

Here we assume that FGMo functions as a general costly signal of fitness, rather than a signal of virginity. It is unreasonable to imagine that this effect is the same for each woman or child, or that the effect is known before the decision to commit FGMo is taken. Therefore we model the mating value increase from having FGMo as a random variable x. The payoff, P_{CS}, to undergoing FGMo is thus:

$$P_{CS} = \bar{w} + V_m(r_f(f + x, d_f)) + s(\alpha) - c \tag{6}$$

And FGMo emerges in a population if the expected value of P_{CS} exceeds P for at least one woman in the population when $\alpha = 0$. That is, when:

$$E[V_m(r_f(f + x, d_f))] - V_m(r_f(f, d_f)) - s(1) - c > 0 \tag{7}$$

An equilibrium where everyone in the population undergoes FGMo is maintained if $E[P_{CS}] > P$ for every woman in the population when $\alpha = 1$. That is, when:

$$E[V_m(r_f(f + x, d_f))] - V_m(r_f(f, d_f)) + s(1) - c > 0 \tag{8}$$

And here the difference from the virginity assurance model becomes clear. If we again look at a case in which a low-ranking woman in a non-FGMo society considers FGMo, she can (depending on the distributions of x, d_f and d_m) still have:

$$E[V_m(r_f(f + x, d_f))] - V_m(r_f(f, d_f)) > 0 \tag{9}$$

Even though the probability of having a higher payoff after FGMo might be small, FGMo could have a high enough expected value to be worthwhile. This also means that there might be women who benefit from living in a society where everyone undergoes FGMo, which was not the case in the virginity assurance model. On average though, each woman still gets c less payoff.

For a better understanding of our results let's look closer at the implications of Equation 9. For the woman with lowest mating value before FGMo, Equation 9 can be expressed as:

$$\sum_{k=0}^{N} \Phi(k) V_m(N_f - k) - V_m(N_f) > 0 \tag{10}$$

where $\Phi(k)$ is the probability that undergoing FGMo gives her a higher value than k other women, and N_f is the number of women in the population. Note that as long as $\Phi(k)$ is not strictly zero for all k, then the left-hand side of Equation 10 is strictly positive, although it is neither necessarily greater than c nor necessarily large enough to move a woman up on the mating value ranking scale. Thus, FGMo could function to increase a woman's mating value relative to other women, though this is not guaranteed generally.

To further investigate the implications of this model, we make some reducing assumptions that d_f and x are normally distributed random variables. In this case, all that matters to our model are the variances of the respective distributions; to understand the impact of variance in x and d_f, let us note that the probability that a realization from $\text{Normal}(\mu_1, \sigma^2)$ is greater than a realization from $\text{Normal}(\mu_2, \sigma^2)$ is just the probability that $\text{Normal}(\mu_1 - \mu_2, 2\sigma^2) > 0$, which is determined by the difference between μ_1 and μ_2 and by σ. In our model, the difference between μ_1 and μ_2 is determined by the variance in the mating value of women, d_f, and σ is the variance of the random variable x.

An increasing variance of d_f decreases the chance that a low-ranking woman can move up on the rank scale as a function of FGMo adoption. An increase in the variance of x increases the chances that a low-ranking woman can move up on the mating rank scale. Finally, as V_m becomes an accelerating function of increasing rank, it increases the value for a woman of moving up on the mating rank scale.

Conclusions of the Model

In conclusion, our evolutionary models show that variance in male mating value should be associated with the origins of FGMo. The costly signaling model suggests that some women can benefit from FGMo at fixation, whereas under the virginity assurance model no women benefit from FGMo at fixation. Further, we show that variance in male mating value is not strictly required for the maintenance of FGMo at fixation, so long as social pressure is intense enough to maintain FGMo after it originates. Finally, we show that variance in male mating value may, however, factor into the maintenance of FGMo when the prevalence of FGMo is below fixation. This finding helps to explain the empirical observation by Efferson et al. (2015) that, in some cases, FGMo persists in populations at levels well below fixation—a situation that is unlikely to arise under a purely coordination-based model of FGMo persistence that does not also account for the effects of the differential value of males on the marriage market. We provide a much more thorough discussion of our model-based findings in light of Efferson et al. (2015) in the ESM Section 9.

Methods

Adaptive Phylogenetic Analysis of Empirical Data

Data Sources and Sample Selection

To test whether variance in male value is associated with the distribution of FGMo across cultures, we use an extensive coding of data on female genital modification in Africa, the continent in which the custom is largely concentrated. The sample consists of 112 cultural clusters geographically distributed across Africa, drawn from Murdock's *Ethnographic Atlas* (Murdock 1969). For this sample, Ericksen (1989) examined all available ethnographic sources for evidence of FGMo. Following Ericksen (1989), clusters that contained more than one culture are represented by the culture with the best coverage on the topics being coded; in cases where more

than one culture had good source materials, the choice was determined randomly. Interested readers are directed to Ericksen (1989) and Paige and Paige (1981) for detailed discussion of the included cultural clusters, sample construction, citations to primary sources, and ethnographic details; methodological details concerning the standard cross-cultural sample can be found in Murdock and White (1969).

Female genital modification, $FGMo$, was coded as present if the practice was mentioned as occurring by at least one ethnographer, either present or past, irrespective of how much detail was given; inter-coder reliability between 3 independent readers using English and non-English sources was 0.79 (Ericksen 1989). Recognizing that our analysis could be biased by considering FGMo as being practiced in cultural groups where the frequency of practice is actually quite low, we conduct a secondary analysis based on classifying FGMo as present only if contemporary FGMo prevalence is $> 50\%$ (ESM Section 8); the results of this analysis were qualitatively the same as those of our main analysis.

We use the existence of economic and/or social stratification as our measure of variation in male quality, on the assumption that in more stratified societies there are greater differences in male resource holdings, and greater power and prestige differences; stratification is coded using Variable 67 (class stratification) in Murdock (1957). This variable contains four categories:

1. Absence of significant class distinctions among freemen, ignoring variations in individual repute achieved through skill, valor, piety, or wisdom.
2. Wealth distinctions based either on the possessions or distribution of property, present and socially important but not crystallized into distinct and hereditary social classes, or on hereditary aristocracy and lower class of ordinary commoners of freemen, where traditionally ascribed noble status is at least as decisive as control over scarce resources.
3. Dual or elite stratification in which an elite class derives its superior status from, and perpetuates it through, control over scarce resources, particularly land, and is therefore differentiated from a property-less class.
4. Complex stratification into social classes correlated in large measure with extensive differentiation of occupational statuses.

In our model, we use a binary variable for stratification in which categories 2, 3, and 4 are collapsed, yielding a variable that distinguishes cultural groups with wealth and class distinction from cultural groups without such distinctions. For a small number of cultural groups, the *Ethnographic Atlas* had missing information; we investigated the primary ethnographic literature to obtain equivalent data for these groups. The Supplementary Materials (*FGMoData.csv*) contains our data and the relevant citations to supplementary primary sources. In total, we have data from 63 stratified cultural groups and 49 non-stratified groups; 44 groups practice FGMo and 68 do not.

Full Bayesian Phylogenetic Modeling of Adaptive Evolution

To model the effect of stratification on the evolution of FGMo, we utilize a Bayesian phylogenetic model of adaptive evolution (based on an Ornstein-Uhlenbeck process) in the spirit of Butler and King (2004). The methods advanced by Butler and King (2004) conceptualize evolution across a phylogeny as a function of both

selective processes and drift. This approach thus constitutes critical progress in phylogenetic analysis insofar as it allows for adaptive hypotheses to be evaluated with phylogenetic models that include selection dynamics explicitly. The methods advanced by Butler and King (2004) allow us to (1) investigate the extent to which the likelihood of a cultural group practicing FGMo is conditioned on the state of that cultural group as stratified versus non-stratified, and (2) contrast the strength of selection for FGMo based on stratification with the strength of drift (and selective forces operating orthogonally to stratification).

Standard tools for phylogenetic inference concerning the evolution of discrete traits (Ives and Garland 2010; Ives and Garland Jr 2014; Pagel 1994; Pagel and Meade 2006) represent an alternative analytic strategy. In the main text, we focus on the adaptive phylogenetic analysis, as we find the model dynamics to more elegantly match the empirical processes we wish to understand. For thoroughness, we present the results from various other discrete trait phylogenetic models in the ESM Section 7; our findings are consistent across all approaches.

Butler and King (2004) developed a software package (OUCH, Ornstein-Uhlenbeck for Comparative Hypotheses) for adaptive phylogenetic analysis in the R software environment (R Core Team 2013). This software package, however, treats phylogenies as known data, deals poorly with parameter constraints, and relies on a fragile maximum likelihood estimation procedure, which fails to function reliably in many contexts, as detailed in Butler and King (2004).

To improve on the software introduced by Butler and King (2004), we wrote our own full Bayesian implementation of the adaptive phylogenetic model using Hamilton Markov Chain Monte Carlo (HMC) simulation (Hoffman and Gelman 2014) in C++, using the Stan 2.2.0 library (Stan Development Team 2013a). Our Bayesian implementation allows us to integrate over phylogenetic uncertainty, impose parameter constraints, and use prior information to identify parameters that are not necessarily identifiable under maximum likelihood estimation.

Following Butler and King (2004), we imagine trait evolution over a phylogenetic tree occurring as an Ornstein-Uhlenbeck process where a trait, X, evolves under a regime composed of both selection and drift such that:

$$\partial X(t) = \alpha[\beta(t) - X(t)]\partial(t) + \sigma\partial B(t) \tag{11}$$

where $\partial X(t)$ is the change in the character trait X over the course of a small increment of time, α is the strength of selection, $\beta(t)$ is the optimal trait value, and σ mediates the intensity of "white noise" fluctuations, $\partial B(t)$.

Below we describe the phylogeny utilized in our analysis and then outline the mathematical details of our statistical model, which uses the phylogenetic generalized linear model structure discussed by Ives and Helmus (2011) and Ives and Garland Jr (2014)—with appropriate modifications to implement the adaptive process model introduced by Butler and King (2004).

A Phylogeny of Language Families Based on Lexical Similarity

We begin our phylogenetic analysis with a hierarchical clustering of the selected cultural groups ($N = 112$) in Africa (Murdock 1969) according to the linguistic divergences postulated in Ethnologue (Lewis 2009). Following Walker et al. (2012), we then utilize the estimated dates of lexical divergence produced by the

ASJP (Automated Similarity Judgment Program) to define the prior expected proportionality of branch lengths (Holman et al. 2011). Neither the clustering of languages in Ethnologue nor the estimated times of language divergence produced by the ASJP are free of controversy (see peer commentary in Holman et al. 2011). There are two critical issues with the use of linguistic data to infer the splitting of cultural groups: (1) linguistic evolution, as with any form of cultural evolution, is not necessarily treelike. There is, however, some treelike structure to linguistic and cultural evolution, and we believe accounting for this structure is better than ignoring it completely (Gray et al. 2010). And (2) assumptions of constant rates of language evolution have been shown to be in conflict with empirical data (Gray et al. 2007). ASJP estimates of divergence dates, however, are not based on constant evolutionary rates, and are estimated using empirical calibration on the basis of historical, archaeological, and other evidence, as suggested by Gray et al. (2007).

Despite the fact that the phylogenetic tree used in our analysis is only of limited accuracy, in the Bayesian interpretation of the model fit in our analysis, phylogenetic information is utilized to construct prior beliefs concerning the expected covariance of the preferences for the FGMo trait across cultural groups resulting from shared ancestry. The fact that there is error in the ASJP estimates of divergence times is not necessarily a problem for our analysis. So long as the errors of estimated divergence times based on lexical similarity are roughly proportional across cultural groups, and do not vary as a function of stratification or FGMo prevalence, our inferences are unlikely to be biased (the actual calender dates of linguistic divergences do not matter for our analysis).

Furthermore, we know of no other published phylogenies that estimate the divergence times (branch lengths) of all African languages in a unified framework; the ASJP phylogeny is also derived under more theoretical and empirical rigor than standard Bayesian approaches to phylogenetic reconstruction that utilize a simple binary coding procedure of cognate classes from Swadesh lists. Future studies will surely improve inference concerning the nature and dating of the somewhat treelike, somewhat reticulated river-network-like cultural evolutionary pasts of extant human groups (Towner et al. 2012). When such data become available, our inferences herein should be reinvestigated.

Figure 2 displays our phylogeny with prior branch lengths scaled to the ASJP estimates. In the ESM Section 3, we detail how exactly we bring the ASJP divergence times into our analysis, and how we model uncertainty in these values.

Modeling Adaptive Evolution

At each MCMC (Markov Chain Monte Carlo) iteration, a random painting of divergence times onto the branches of the phylogenetic tree is proposed. We then standardize the phylogeny to the unit interval such that $t = 0$ is the time of the deepest divergence and $t = T = 1$ is the present. We then calculate two matrices, S and C, from the phylogeny. The S matrix is an N by N matrix (N=number of cultures included in this analysis=112) of the time points when cultural group n split from each and every other cultural group. The C matrix is an N by Γ matrix of the cut-points/transitions in epochs within a lineage, where $\kappa(n)$ is the total number of epochs in lineage n, and $\Gamma = \max(\kappa(n)) = 12$ is the maximum number of epochs in a cultural lineage observed in our data. A cultural lineage is defined as
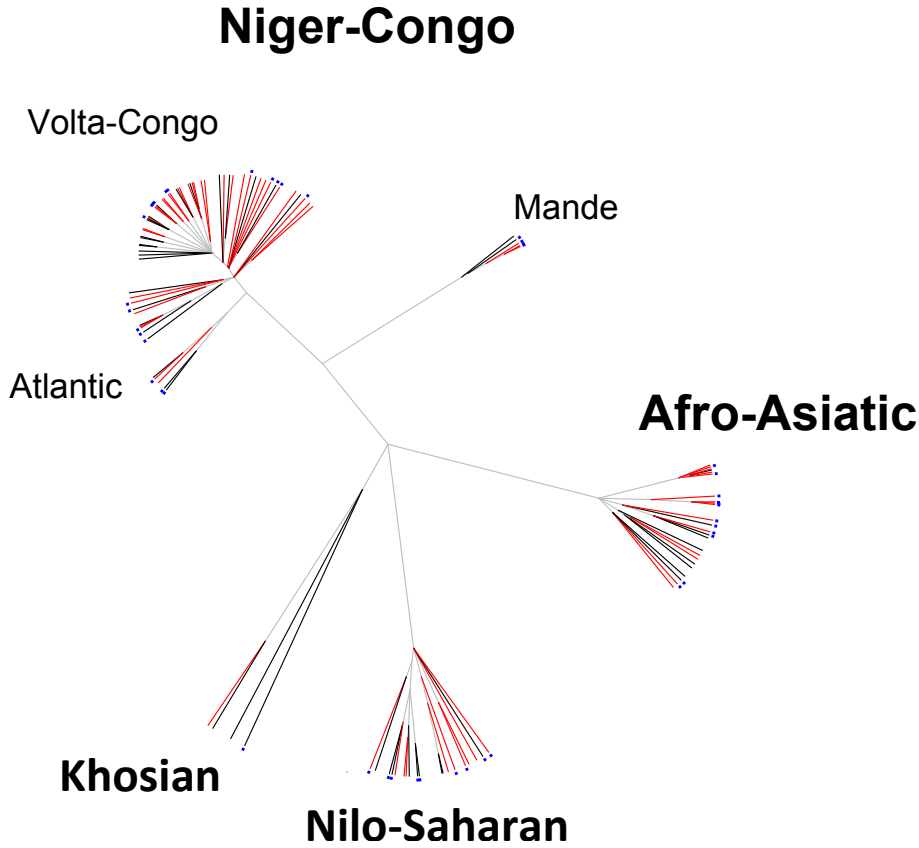
Fig. 2 The phylogeny of African languages used in this analysis. In this figure, branch lengths are presented as proportional to maximum likelihood AJSP divergence estimates; the actual phylogenetic tree implemented in the model, however, is a constrained random variable, allowing Bayesian integration over uncertainty in phylogenetic information. Black branches on the tree indicate non-stratified selection regimes. Red branches indicate stratified selection regimes. Gray branches indicate a mixture of stratified and non-stratified selection regimes. This mixture modeling allows for integration over uncertainty in deeper, nonterminal branches. The blue points on the edge of the phylogenetic tree indicate the presence of the practice of FGMo.

the path from the tip of the phylogenetic tree to its most basal node. The history of the nth lineage is then a series of $\kappa(n)$ branch segments demarcated by epochs $0 = t_n^0 < t_n^1 < t_n^2 < ... < t_n^{\kappa(n)} = T$, where each epoch constitutes a single kind of selective regime, to be defined more thoroughly later.

Equation 11 describes a stationary, Gaussian, and Markovian process with well-defined moments; following, Butler and King (2004), we make a reducing assumption that in every lineage, evolution of a cultural trait, X, occurs along piecewise-constant selection regimes. Accordingly, the expected value of a trait

524 evolving along a cultural lineage, n, can be defined as:

$$\mu_{[n]} = \mathrm{E}[X_n(T)|X_n(0) = \beta_{[n,1]}] = e^{-\alpha T}\beta_{[n,1]} + \sum_{\gamma=2}^{\kappa(n)} e^{-\alpha T}(e^{-\alpha C_{[n,\gamma]}} - e^{-\alpha C_{[n,\gamma-1]}})\beta_{[n,\gamma]}$$

(12)

525 where $\beta_{[n,1:\kappa(n)]}$ is a parameter vector of length $\kappa(n)$ painted with θ parameters.
526 The first cell of this vector, $\beta_{[n,1]}$, is defined to be equal to θ_{anc}, the estimated trait
527 value of the most basal node in the phylogeny, and all other cells are populated
528 with differing θ parameters that describe the hypothesized selective regime acting
529 on the γth epoch in lineage n. The specific way that other θ parameters are painted
530 on to the phylogenetic tree will be made clearer when we describe the exact models
531 being compared in this study.

532   Regarding covariance, we assume that when $t < S_{[n,m]}$, lineages n and m
533 evolved as a single group, and when $t > S_{[n,m]}$ the two lineages evolve indepen-
534 dently. Accordingly, the covariance matrix $V_{[n,m]}$ can be defined as:

$$V_{[n,m]} = \mathrm{Cov}[X_n(T), X_m(T)|X_n(0) = X_m(0) = \beta_{[n,1]}] = \frac{\sigma^2}{2\alpha}e^{-2\alpha(T-S_{[n,m]})}(1 - e^{-2\alpha S_{[n,m]}})$$

(13)

535 To complete the basic model definition, we define regularizing priors on the α and σ
536 parameters, which concentrate prior probability density near zero. We considered
537 both half-Gaussian and half-Cauchy (Gelman 2006) priors (see ESM Sections 5
538 for more information on these priors). In our final analysis, we used the following
539 half-Gaussian priors:

$$\alpha \sim \mathrm{Normal}(0, 5)T[0, \infty]$$

(14)

540

$$\sigma \sim \mathrm{Normal}(0, 5)T[0, \infty]$$

(15)

541 We use regularizing unit normal priors on each cell of the θ parameter vector.
542 These priors can be understood as imposing the Bayesian corollary of Tikhonov
543 regularization (Tikhonov and Arsenin 1977), or ridge regression (Hoerl and Ken-
544 nard 1970), and aid in the identification of θ and α, which are not necessary well
545 identified otherwise:

$$\theta \sim \mathrm{Normal}(0, 1)$$

(16)

546 We then model the data using a multivariate normal distribution parameterized to
547 accept a Cholesky factor, L_V, from the decomposition of the variance-covariance
548 matrix, V, in place of the variance-covariance matrix itself. This parameterization
549 of the model improves the performance of the HMC estimation process for technical
550 reasons that are outlined in the Stan manual (Stan Development Team 2013b). To
551 link μ and L_V to the outcomes, we use a parameter vector, Ψ, which represents
552 the strength of evolving social preferences for FGMo:

$$\Psi \sim \mathrm{Multivariate\ Normal\ Cholesky}(\mu, L_V)$$

(17)

553 and then use the statement:

$$FGMo_{[n]} \sim \mathrm{Bernoulli}(\mathrm{Logistic}(\Psi_{[n]}))$$

(18)

554 to return the log probability of the data, $FGMo$, conditioned on the estimated
555 social preferences for FGMo; $FGMo$ is a vector of binary indicators of the practice
556 of FGMo.

Model Construction

In this paper, we fit two models to the data. In the first, we conceive of the evolutionary dynamics as an Ornstein-Uhlenbeck process with a single global optima for all cultural groups, an OU(1) model. This model serves as a null model, where stratification plays no role in the adaptive evolution of FGMo. In this case, we paint every branch of the phylogeny other than the most basal node, θ_{anc}, with a single parameter that represents a single global selection regime, θ_{gsr}.

In the second model, we conceive of the evolutionary dynamics as an Ornstein-Uhlenbeck process with separate optima for stratified and non-stratified cultural groups, an OU(2) model. In this case, we paint the phylogeny using two θ parameters, with one corresponding to a stratified selection regime, θ_{ssr}, and one corresponding to a non-stratified selection regime, θ_{nssr}.

Deep ancestral branches are not easily classifiable as stratified or non-stratified, but the phylogenetic tree contains information on the probability of stratification in deeper branches conditional on the state of the branch tips and the strength of selection for stratification along the branches. Accordingly, at each MCMC iteration, we estimate the probability of stratification in deep branches by using the Butler and King (2004) method to model the culture-group specific evolution of stratification with an OU(15) model (See ESM Sections 2 and 6 for details and model diagnostics). Following this, we model the evolution of FGMo, conditioned on the estimated state of stratification at every node in the phylogeny.

More formally, in the OU(2) model, at each MCMC iteration, we run an adaptive phylogenetic model on stratification using the observed binary data variable *Strat*. We model:

$$\Psi_{strat} \sim \text{Multivariate Normal Cholesky}(\mu_{strat}, L_{V_{strat}}) \tag{19}$$

where μ_{strat} and $L_{V_{strat}}$ are corollaries to μ and L_V and are derived from Equations 12 and 13 in the same way; Ψ_{strat} is a parameter vector representing the log odds that a given cultural group is stratified, and:

$$Strat_{[n]} \sim \text{Bernoulli}(\text{Logistic}(\Psi_{strat[n]})) \tag{20}$$

provides the log probability of the observed stratification data conditional on the proposed parameter values.

The β_{strat} matrix for the stratification model is painted with θ parameters such that the branches for each language family and subfamily have unique parameters (e.g., language family parameters are $\theta_{Nilo-Sahran}$, $\theta_{NigerCongo}$, etc., and language subfamily parameters are θ_{Omotic}, θ_{Mande}, etc.). The way in which these parameters are painted onto the branches is made clear in the Supplementary Stan code, using variables $GID2$ and $GID3$ from the Supplementary Data.

Under such a model it is straightforward to calculate the probability of stratification in any epoch in any lineage, $\Lambda_{[n,\gamma]}$, from Equation(12) as:

$$\Lambda_{[n,\gamma]} = \text{Logistic}(e^{-\alpha T}\beta_{strat[n,1]} + \sum_{\gamma=2}^{\kappa(n)} e^{-\alpha T}(e^{-\alpha C_{[n,\gamma]}} - e^{-\alpha C_{[n,\gamma-1]}})\beta_{strat[n,\gamma]}) \tag{21}$$

To model the evolution of FGMo as a function of stratification, we then paint the tips of the phylogeny (in the FGMo model) with parameters using observed data:

$$\beta_{[n,\kappa(n)]} = \begin{cases} \theta_{ssr}, & \text{if } Strat_{[n]} = 1 \\ \theta_{nssr}, & \text{if } Strat_{[n]} = 0 \end{cases} \tag{22}$$

and paint all nonterminal epochs (e.g., where $\gamma \neq \kappa(n)$) across all lineages (in the FGMo model) as a mixture of θ_{ssr} and θ_{nssr} with mixing proportions determined by Λ:

$$\beta_{[n,\gamma]} = \theta_{ssr}\Lambda_{[n,\gamma]} + \theta_{nssr}(1 - \Lambda_{[n,\gamma]}) \tag{23}$$

Software Environment

Each complete model was fit using the Stan 2.2.0 C++ library, using the No-U-Turn sampler, a variant of Hamiltonian Monte Carlo (Stan Development Team 2013a). We ran multiple small chains to ensure that the models were well-defined and converged to similar posterior regions. Our final results are based on the results from a single long chain, run for 20,000 warm-up iterations and 400,000 sampling iterations, thinned at an interval of 20. We found that our model was well identified for all θ parameters, for α, and effectively identified for σ, although σ itself is not numerically well identified. Convergence diagnostics and model identification are discussed in detail in the ESM Sections 4 and 6.

All pre-processing of data and post-processing of MCMC samples was conducted using the R environment for statistical computing (R Core Team 2013). The package *RStan* was used to communicate between the C++ model and the R statistical environment.

Model Comparison

We compare models using the Watanabe-Akaike information criterion (WAIC) (Gelman et al. 2014), which is a more fully Bayesian generalization of the standard Akaike information theoretic criteria, AIC. Computed WAIC is defined as:

$$\text{WAIC} = -2(lppd - p_E) \tag{24}$$

The computed log pointwise posterior predictive density, *lppd*, is defined as:

$$lppd = \sum_{n=1}^{N} \log\left(\frac{1}{Q} \sum_{q=1}^{Q} Pr(FGMo_{[n]}|\Psi_{[n,q]})\right) \tag{25}$$

where $q = 1...Q$ references the index of simulations from the posterior distribution. The effective number of parameters, p_E, is computed as:

$$p_E = \sum_{n=1}^{N} \text{Var}_{q=1}^{Q} \log(Pr(FGMo_{[n]}|\Psi_{[n,q]})) \tag{26}$$

where the symbol $\text{Var}_{q=1}^{Q}$ represents the function to calculate the sample variance over the posterior simulations.

Results

Analysis of the data with Ornstein-Uhlenbeck process models and information theoretic model comparison methods shows that while stratified cultural groups are on average slightly more likely to practice FGMo than non-stratified groups, there is little evidence that the stratification model provides a better fit for the data than the null model.

Table 1 presents the key parameters of our models, showing the posterior mean and medians estimates, as well as the central 95% posterior confidence intervals (95PCIs) from the fitted OU(1) and OU(2) models. Table 2 presents the results of model comparison using WAIC.

Table 1 Key parameter estimates from our models, showing relative support for α (selection based on stratification) and σ (drift and/or orthogonal selective forces) in explaining the distribution of FGMo in Africa. The mean and median are point estimates of the posterior distribution; the 2.5% and 97.5% equal tail posterior confidence intervals (PCI) present the dispersion of the posterior distribution. The top set of parameter estimates is from the OU(2) model, and the bottom set of estimates is from the OU(1) model. The symbols prefixed by θ indicate the estimated optimal trait value (log odds) under the ancestral, global, stratified, or non-stratified selection regime, as indicated by the subscripts. We note that σ dominates α in both the OU(1) and OU(2) models, which is indicative that the distribution of FGMo in Africa is better explained by drift and/or selective forces operating orthogonally to stratification than by stratification itself. In the OU(2) model, however, we find that stratification relative to non-stratification is weakly, but positively, associated with elevated social pressure for FGMo.

	Model	Mean	Median	2.5% PCI	97.5% PCI
θ_{anc}	OU(2)	-0.075	-0.078	-1.974	1.853
θ_{ssr}	OU(2)	-0.04	-0.042	-1.868	1.761
θ_{nssr}	OU(2)	-0.278	-0.289	-2.106	1.56
α	OU(2)	2.781	2.636	0.412	6.105
σ	OU(2)	6.891	6.712	2.234	12.502
θ_{anc}	OU(1)	-0.047	-0.039	-1.994	1.889
θ_{gsr}	OU(1)	-0.18	-0.212	-1.789	1.547
α	OU(1)	2.652	2.496	0.337	5.88
σ	OU(1)	7.404	7.102	2.701	14.023

Inspection of the θ_{ssr} and θ_{nssr} parameter estimates from the OU(2) model in Table 1 shows a moderate difference in the mean estimated strength of social preferences for FGMo as a function of stratification. Converting these parameter estimates to the probability scale, we find that stratified cultural groups are about 6% more likely, on average, to practice FGMo than non-stratified cultural groups. Although the confidence intervals on these estimates are wide and largely overlap one another, the estimates of θ_{ssr} and θ_{nssr} are in the direction predicted by our evolutionary models.

Model comparison with WAIC, however, shows that the OU(1) model is preferred over the OU(2) model. So while increased stratification appears to be weakly associated with increased odds of FGMo, accounting for stratification does not improve predictions sufficiently to compensate for the increased model complexity in an information theoretic framework.

In conclusion, although we present evidence that social stratification places positive selection pressure on social preferences for FGMo, it is evident that σ

Table 2 Results of formal model comparison using WAIC. WAIC, p_E, and lppd are defined in the text. The symbol dWAIC indicates the difference in WAIC between the best model and the second model, and the symbol wWAIC indicates the weight in probability that the specified model will make the best predictions on new data, conditional on the set of models being considered. We note that the OU(1) model outperforms the OU(2) model. This result indicates that the distribution of FGMo across our sample of African cultural groups can be most parsimoniously explained by a drift model with a single global optima, as opposed to a model with separate optima for stratified and non-stratified societies. However, these wWAIC values are very close, and the application of WAIC to these models is not completely justified given the relative strength of drift; as such, we argue that both models are important to consider. See ESM Section 5 for a discussion of methodological issues that arise with WAIC, or any information criterion, as σ increases relative to α in adaptive phylogenetic models.

Model	p_E	lppd	WAIC	dWAIC	wWAIC
OU(1)-Null	28.099	-28.409	113.017	0	0.848
OU(2)-FixedBranchTips	27.407	-30.821	116.458	3.441	0.152

(which accounts for drift and/or selection dynamics operating orthogonally to stratification) plays a more important role in explaining the cross-cultural distribution of FGMo. Future research is needed to disentangle the effects of drift from other possible selective drivers of FGMo.

Since our variables for both stratification and FGMo are binary, use of continuous measures of resource inequality (e.g., a Gini coefficient) or FGMo prevalence might yield more informative results. However, we do not as of yet have access to such data. Future comparative work in anthropology might benefit from using higher-resolution cultural data (where such data exist) or, even better, individual-level measures (e.g., Borgerhoff Mulder et al. 2009; Hill et al. 2011). For example, if we had cross-cultural, individual-level data on FGMo prevalence and male wealth, we could estimate FGMo prevalence and calculate a Gini coefficient on wealth, which would likely be more informative than the simple binary coding scheme used in this analysis. Likewise, as methods of estimating cultural-group divergences through language information become more refined, the effectiveness and accuracy of cultural phylogentic methods may improve substantially.

Discussion

This paper offers four principal contributions. First we develop explicit evolutionary models for the origin and maintenance of FGMo. In so doing we provide formal justification for an existing hypothesis that the practice is related to social stratification (Mackie 2000), and a novel set of predictions regarding the distinction between trait origins and maintenance [albeit also recognized by Mackie (2000)]. Second, we consider two generative models for FGMo based on virginity assurance and costly signaling, and we find that both lead to similar macro-level model dynamics and could therefore be responsible for the emergence of FGMo when there is inequality in male mating or marriage value. Third, we fit an empirically grounded model that includes the two main effects from the theoretical model: a selective effect based on the inequality in mate value (operationalized in the empirical analysis using stratification as a proxy), and a social transmission effect (operationalized in the empirical model using a term orthogonal to the proposed

selective regime based on stratification). Finally, we provide a Bayesian implementation of the Ornstein-Uhlenbeck process model developed by Butler and King (2004).

We use mathematical models to show the importance of differentiating explanations for cultural trait origins from those for persistence; the importance of this distinction for explaining trait distributions has been made previously (Borgerhoff Mulder 2001) but has not, to our knowledge, been formally modeled or investigated with empirical data. The results of our adaptive phylogenetic analysis suggest that stratification is associated, though only weakly, with selection pressure on the uptake of FGMo. However, the fact that σ dominates α in explaining the evolutionary dynamics of the FGMo trait in Africa indicates that drift and/or selective forces operating orthogonally to social stratification play a very significant role in explaining the current cross-cultural distribution of the FGMo trait. This is entirely consistent with the view of earlier scholars who suggest that FGMo became decoupled from the signaling of marriageability and chastity as it spread into less stratified populations (Mackie 2000).

Historical records, albeit largely speculative, that place the origins of FGMo in ancient Egypt, or the strongly Egyptian-influenced and fabulously wealthy trading city of Meroe, are consistent with our model-based findings that variance in male mating value and social stratification should be causally linked to the *de novo* origins of FGMo, since ancient Egyptian society was marked by complex stratification (Murdock 1957).

Although our model-based results indicate that stratification is needed for the *de novo* origins of FGMo, once the trait has arisen in a single cultural group its adoption in any subsequent cultural groups does not require stratification. Once FGMo has arisen in a cultural group, and the system has equilibrated such that s—a measure of frequency-dependent or conformist biases (Boyd and Richerson 1985; Henrich and Boyd 1998; Henrich and Gil-White 2001)—functions to increase pressure on individuals to undergo FGMo, the genesis of FGMo in subsequent groups can occur strictly as a function of s, irrespective of stratification. Thus, the dynamics of the *de novo* origins of FGMo differ from the subsequent dynamics of intercultural transmission. Though our adaptive phylogenetic model illustrates that the evolution of FGMo is not strictly dependent on stratification, the model still suggests that stratification increases the likelihood of intergroup transmission or adoption of FGMo.

Most intriguingly, our model shows how ordinary adaptive processes over ecological time can lead to the emergence of a trait that leads individuals to accept huge fitness costs in their pursuit of mates. This, of course, is not unusual in the animal world (e.g., the costs of mating for female fruit flies; Chapman et al. 1995; Wigby and Chapman 2005). However, as a result of the biases that influence the spread of culturally transmitted traits (conformity and/or imitation of prestigious individuals), such traits can stabilize over evolutionary time and, because of the strength of cultural norms and social stigma against deviation, hold in place institutions that severely damage women. Our modeling therefore shows how ordinary adaptive processes, combined with cultural evolutionary feedbacks, can generate stable evolutionary outcome states in which sexual conflict is not resolved (Borgerhoff Mulder and Rauch 2009). Such outcome states may possibly set in place systems of gene-culture evolution where genetic variants arise due to culturally specific sexual selection pressures (Ross and Richerson 2014). Futhermore, our

modeling demonstrates the futility of thinking of cultural evolutionary and ordinary adaptive processes as alternative explanations since they are jointly required to explain the evolutionary dynamics of FGMo.

In our theoretical models, we focused mainly on differentiating the evolutionary forces responsible for the *de novo* origins of FGMo and its subsequent maintenance in a population. The results of our phylogenetic analysis, however, show that a holistic characterization of the cross-cultural origins of FGMo requires more explicit treatment of the dynamics underlying intergroup transmission as well; these dynamics are investigated elsewhere in an empirical case study of intergroup transmission of the FGMo trait in the African diaspora and indigenous populations of Colombia (Ross et al. 2015).

The relationship between s and the intercultural transmission of FGMo is complex and will be structured by culturally and historically particular processes. For instance, imagine that migrants from a non-FGMo culture enter an FGMo cultural area. In such a case, s and conformist biases can now act to place selective pressure on the uptake of FGMo by these intercultural migrants, even if stratification was not present in the migrants' cultural group. Such an effect would be exacerbated if there were perceived prestige differences between the FGMo-practicing cultural group and the non-FGMo-practicing migrant group that cause migrants to copy the behaviors of the prestigious group (Richerson et al. 2015). This pattern would be likely if FGMo is associated with the prestigious class in stratified areas.

A similar pattern would be observed if adoption of the cultural traits of a dominant or prestigious cultural group is an essential step in successfully integrating into that culture; such dynamics might partially underlie the observation by Cronk (2004) that Kenyan Mukogodo appear to have adopted FGMo to hasten their transition to becoming Maasai, or the observation by Ericksen (1989) that the Fur appear to have adopted FGMo to marry with their nomadic, stock-owning, and more wealthy Zaghawa neighbors. Similarly, non-practicing displaced ethnic communities in Darfur (Sudan) have adopted FGMo when moving to cities, just as in the state of Khartoum, where migrants from West Africa now cut their daughters to gain acceptance in their new host community (DFID 2013). If successful intercultural migrants are emulated or held in high esteem, or if migration events involve a large portion of a cultural group, then frequency-dependent, conformist, and prestige biases can result in the propagation of FGMo back into the migrants' natal cultural group.

Different patterns of transmission are also possible. We know, for example, that during the intense military turmoil in the Great Lakes region of central Africa that refugee segments of Bantu-speaking Abaluhyia lineages, subsequently known as the Tiriki, adopted the age set organization of their Niolotic Terik neighbors. In return for asylum with the more military-prepared Terik, Tiriki elders accepted the full set of initiation rituals for their sons, including circumcision and seclusion, in a bid to obtain protection (Boyd et al. 1997; Levine and Sangree 1962).

Contrarily, in many contexts the practice of FGMo may mark an ethnic boundary (McElreath et al. 2003) between groups that practice FGMo and those that do not. In such contexts, s could militate against adoption of the cultural traits of out-groups and work against the intercultural transmission of FGMo to neighboring population. Case studies in which such socially or behaviorally marked ethnic boundaries function to prevent the transmission of information and behavior across groups are well described in the literature (Barth 1998; Van den Berghe 1987).

As such, we expect that the dynamics governing the transmission of FGMo and other costly traits will be historically and locally contingent based on the nature of intercultural contact. We suspect that the mechanisms underlying these intercultural dynamics are likely to include frequency-dependence or conformist learning biases—as outlined in our introductory review of how FGMo is embedded in deeply held societal conventions—as well as prestige-biased learning, whereby adopting FGMo may facilitate inclusion in a more powerful or prestigious population. Similarly, we note that the decline in FGMo is particularly striking in countries such as Kenya and Tanzania, where FGMo is less prevalent across constituent ethnic groups (UNFPA-UNICEF 2013), suggesting that abandonment is more tolerable, even practicable, with non-practitioners as neighbors. Future research should investigate in more detail the socioecological circumstances that aid in the intercultural transmission of FGMo and those that hinder transmission and hasten abandonment.

Our conclusions are generally consistent with those of Murdock (1959), who argues that the trait of FGMo—in his terminology, excision—largely spread across Africa through cultural diffusion. For example, in East Africa, southern Nilotes and Bantu are thought to have adopted the custom from Cushitic neighbors, given that there is little evidence of FGMo among other Nilotes and the apparent Cushitic roots to the linguistic term used for the operation (Murray 1974). In West Africa too there is strong inferential evidence that FGMo was adopted by some of the neighbors of the FGMo-practicing Mande—for example, the Kissi and the Kran, but not the Kpelle, Guro, and Gbande—but the details of the adoption during this historic period of diffusion are unclear (Ericksen 1989). Furthermore ethnographic reports (Stannus 1919) indicate that the Yao of northwestern Mozambique and southern Tanzania appear to have adopted female "circumcision" during their close collaboration with Swahili and Arab slave traders in the nineteenth century, although now it is largely dropped. We note, however, that these conclusions regarding the historical diffusion of the trait are based largely on the observation that FGMo appears in populations that do not necessarily share a common language, geography, and cultural history, and that our methods (like those of Towner et al. 2012) provide a significant improvement in inference.

Implications for Policy

Here we sidestep ethical arguments regarding whether or not FGMo should be abandoned, as well as the debates over who has the moral authority to take the lead in such initiatives, recognizing that this can only be locally adjudicated. As Shell-Duncan and Hernlund (2000, p126) observe for the Rendille of Kenya, "awareness of the fact that female 'circumcision' is associated with adverse health consequences is widespread, yet the Rendille view the risks as worth taking in light of the implications for marriageability." There are clear social, psychological, and physical consequences to the practice of genital cutting, and these need to be weighed very carefully in each case. But, if abandonment is viewed as appropriate, the question of how to achieve such a goal remains. Many strategies are currently discussed, including medicalization of the practice (for example, the use of less extreme procedures in hospitals by specially trained practitioners), mass education campaigns, formal legislation with criminalization of operators and their

clients, withdrawing of foreign aid programs, developing ritual alternatives, or simply relying on the processes of development and the erosion of traditional culture (Shell-Duncan and Hernlund 2000).

Many scholars argue that knowledge of the origins of FGMo will not contribute to a determination of its current significance; others maintain that understanding the historical roots of the tradition helps justify the persistence of the custom to disapproving outsiders, and still others insist that the origins and maintenance of the practice cannot be conceptually separated from development of strategies for its elimination (Mackie 2000). The present analysis, with its implications for the importance of frequency-dependent biases in the maintenance of FGMo, supports this third viewpoint. Specifically, it points to the potential value of programs that foster contracts within small communities whereby all parties make a pact not to send their daughters for the operation; our model suggests that such pacts may be especially effective in cultural groups who have acquired FGMo via social transmission, or in cultural groups where there no longer exists sufficient heterogeneity in the value of men on the marriage market to create the selective pressures that would eclipse the effects of such pacts. Mackie (1996) has made precisely this point, drawing an analogy between successful campaigns to eradicate footbinding in China through fostering of such local contracts. Furthermore, the most recent evaluation of the status of FGMo globally suggests that public declarations, or collective announcements of abandonment by village delegates, have for the most part been very successful in supporting change (UNFPA-UNICEF 2013), especially if the initiative is supported by locally respected leaders (WHO 2010).

There is nevertheless huge variation within and between communities in the rate of abandonment (Shell-Duncan and Hernlund 2007), which begs further study. Recent observations by Efferson et al. (2015) that FGMo is not purely a coordination norm might help to explain this heterogeneity. While community-based pacts might be effective in abating FGMo in contexts where FGMo is driven primarily by coordination problems or other frequency or prestige-based social norms, in cases where FGMo is maintained at intermediate levels by selective pressures related to heterogeneity in the value of men or ranking of women on the marriage market, abatement pacts which assume that FGMo is maintained by a coordination system are unlikely to be effective. Future empirical study of the relative cross-cultural effectiveness of FGMo abatement programs as a function of male wealth inequality in each cultural group may help to validate this hypothesis.

Appendix

Following cautions raised in Efferson et al. (2015), we emphasize that our model does not assume that the social transmission bias arises purely from a coordination game; a wide range of social pressures, be they based on religious obligation (Gruenbaum 2001), gender marking (Gruenbaum 2001), coordination (Mackie 2000), or cultural identity (Daniels 1970), can all mutually interact to yield the net effects accounted for by $s(\alpha)$. Again following Efferson et al. (2015), our model formalizes the assumption that some males may hold considerable power in the mating market and explicitly considers the effects of providing these men with virginity assurance or costly signals of sexual fidelity, via the functions $V_m(r_f(f+i, d_f))$ or

$V_m(r_f(f+x, d_f))$. Our model also integrates information on the costs, c, of FGMo, but we did not consider inter-individual variation in these costs in the main text.

These costs, however, are likely to be heterogeneous across individuals, and could possibly contribute to the empirical observation by Efferson et al. (2015) that, in some cases, FGMo occurs in populations at levels well below fixation. To see how, let us consider the behavior of the model when there are two classes of men, rich and poor, and the cost of undergoing FGMo depends on the wealth class of men to which a given woman is paired, with wives of the rich men paying cost c_r and wives of poor men paying the cost c_p.

Although we limit the analytical exploration of our model in the main text to special cases describing the origins ($\alpha = 0$) and maintenance ($\alpha = 1$) of the FGMo cultural trait, our model provides a framework for understanding the dynamics leading to intermediate frequencies of FGMo, such that $0 < \alpha < 1$. Given the generality of our model, we can define the marriage value function for males, V_m, such that for some arbitrary fraction of males, $\hat{\alpha}$, $V_m(r_f(f+i, d_f)) - V_m(r_f(f, d_f)) > s(1 - \hat{\alpha}) - s(\hat{\alpha}) + c_r$, and for $1 - \hat{\alpha}$ of males, $V_m(r_f(f, d_f)) = V_m(r_f(f+i, d_f))$. This condition formalizes an empirical observation that in many populations the majority of male wealth values are similar, with a few outliers being responsible for the majority of the inequality (Borgerhoff Mulder et al. 2009), and leads to a situation where there is wealth-based incentive for the highest-ranked fraction of women, $\hat{\alpha}$, to practice FGMo, and there is no wealth-based incentive for the lowest-ranked $1 - \hat{\alpha}$ fraction of women to practice FGMo, since there is no difference in marriage value as a function of undergoing FGMo, due to $V_m(r_f(f+i, d_f)) - V_m(r_f(f, d_f)) = 0$.

However, for the lowest ranked woman paired with one of the wealthy men, her marriage partner will be the same with or without her undergoing FGMo, so for her not to switch strategies, social pressures must be responsible; she will not switch strategies so long as $s(\hat{\alpha}) - s(1 - \hat{\alpha}) > c_r$. For the highest ranked female paired to one of the poor males, she will not undergo FGMo when $P - P_{VA} > 0$, which holds so long as $s(\hat{\alpha}) - s(1 - \hat{\alpha}) < c_p$; this condition implies that all lower-ranked women will also not engage in FGMo.

Because c_r, c_p, and s are arbitrary, we can always find parameter values to satisfy both critical conditions—specifically, $c_r < s(\hat{\alpha}) - s(1 - \hat{\alpha}) < c_p$—so our model is thus capable of producing a stable FGMo distribution for all values of $\hat{\alpha} \in [0, 1]$. Thus, while a pure coordination game may not be able to explain the frequency distribution of FGMo in some groups, as shown by Efferson et al. (2015), even if s was determined solely by a coordination game, our model demonstrates how consideration of FGMo in a mating market operating under under a system of mating payoffs coupled with coordination payoffs and variation in costs of FGMo could produce the empirical outcomes documented by Efferson et al. (2015). Following this line of logic, and much previous emprical research, we argue that it may be more nuanced to argue that FGMo is not *purely* a social coordination norm, than to argue that it is not a coordination norm; depending on the parameters of the model, there could be very strong coordination norms driving FGMo, even when FGMo is practiced at intermediate levels.

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