It's a Man's World: Mate Guarding and the Evolution of Patriarchy

During human evolution the prevention of cuckoldry has been an adaptive problem for the human male, solved in many other species by intensely quarding females during fertile periods. Signs of estrus in human females are much subtler than in many other species meaning that there is less certainty of the exact timing of the fertile period. This necessitates extended mate quarding which potentially reduces male fitness due to the loss of extra-pair fertilization opportunities and other fitness-compromising costs. such as reduction in the time spent acquiring status and resources. Patriarchy is a system of implicit and explicit rules of conduct, of power structures, and of belief systems that support male control over women's reproduction and has existed for thousands of years. We examine the manifestations of patriarchy as a unique form of mate guarding which is able to function even in the absence of males. We explore historical and contemporary patriarchal practices such as rape, foot-binding, honor-killing and female genital mutilation and argue that males use patriarchy to increase the costs associated with female extra-pair copulation to increase their certainty of paternity. At the same time patriarchy functions to enforce in-pair childbearing by discouraging contraception and abortion. We propose that this form of control of females evolved to avoid an evolutionary trade-off between the benefits of monogamy and those of promiscuity for human males and that there has been selection on females for those compliant with patriarchy, who tended to have more surviving offspring. We also discuss patriarchy in the context of niche construction and propose that patriarchy is a cultural niche which has functioned to maximize individual males' fitness. When viewed from an evolutionary perspective, the persistence of patriarchy into the 21st century is unsurprising.

Cuckoldry occurs in a number of socially monogamous species including birds (Birkhead et al., 1987; Griffith et al., 2002; Westneat & Stewart, 2003), rodents (Goossens et al., 1998; Solomon et al., 2004), and primates (Fietz et al., 2000; Reichard, 1995). While socially monogamous mates may form long-term partnerships and exhibit biparental care, they also often engage in extra-pair copulations (EPC). Where males invest in parental care or allocation of resources, cuckoldry, where males unknowingly raise another male's offspring, is an adaptive problem (Neff, 2003; Shackelford et al., 2006; Trivers, 1972).

Mate guarding is a common reproductive strategy to overcome the possibility

of cuckoldry and ensure certainty of paternity in socially monogamous species (birds: Hasselquist & Bensch, 1991; Komdeur et al., 1999; Møller & Birkhead, 1991; Petrie & Kempenaers, 1998; rodents: Schubert et al... 2009: primates: Anzenberger, 1992). Mate guarding by males takes the form of preventing the female of the pair from engaging in EPCs by various tactics ranging from vigilance to violence (Buss & Shackelford, 1997; Komdeur et al., 1999: Møller & Birkhead, 1993: Reichard & Boesch, 2003: Schubert et al., 2009). In *Homo sapiens*, a socially monogamous and partly polygynous primate, mate guarding is a common strategy aimed to solve the problem of genetic cuckoldry and lessen the likelihood of mate defection (Buss. 1988, 2002, 2003; Shackelford et al., 2006). Cuckoldry is a concern in humans with estimates of occurrence being between 1% and 30% (Anderson, 2006; Bellis et al., 2005; Cerda-Flores et al., 1999). Early data on human nonpaternity was taken from paternity testing laboratories and may not be representative of the general population, being drawn from a sample with low confidence of paternity (Larmuseau et al., 2016). Interestingly, recent estimates infer historical and contemporary human nonpaternity to be in the lower part of this range (~1%) (Greeff & Erasmus, 2015; Larmuseau et al., 2016) making cuckoldry rates in humans considerably lower than those of some other socially monogamous primates. For example, cheirogaleid lemurs, a primitive pairbonding lineage with obligate paternal care, are considered to represent a plausible model for social systems of humans' ancestors (Schülke et al... 2004). High levels of extra-pair paternity are seen in the fat-tailed dwarf lemur, Cheirogaleus medius (~44%) (Fietz et al., 2000) and the masoala fork-marked lemur. Phaner furcifer (75%) (Schülke et al., 2004). Whitehanded gibbons, Hylobates lar, one of the only extant socially monogamous ape species, also have relatively high (7-12%) extra-pair copulation rates (Barelli et al., 2013; Reichard, 1995). The reason for the rarity of cuckoldry in human populations is not clear but could potentially point to the effectiveness of mate guarding strategies. One form of mate guarding in human societies is patriarchal control of female sexuality and reproduction. In this paper we develop the argument

1. Patriarchy as a form of mate guarding

monogamy and those of promiscuity for human males.

Males have a greater potential variance in fitness than females (Wilson &

for an evolutionary and biological, rather than sociological, explanation for the development and persistence of patriarchy, which may have arisen as a

means of avoiding evolutionary trade-offs between the benefits of

Daly, 2009), and because of the low cost of sperm production, males could maximize their reproductive success by fertilizing as many females as possible (Bateman, 1948; Trivers, 1972), however social monogamy or limited polygyny is the norm in humans. The benefits of monogamy include increased certainty of paternity and access to the entire reproductive potential of at least one female (Schuiling, 2003), reduction in infanticide (Opie et al., 2013) and greater survival of offspring due to higher parental investment (Geary, 2000). Despite the advantages of monogamy, mate guarding imposes a high cost on males; they are restricted to one location and they must invest time and resources which could be spent performing other activities.

Costs of mate guarding in primates include increased levels of stress. increased amounts of time spent in vigilance, costly aggressive encounters and reduced time spent in food gathering (Alberts et al., 1996; Girard-Buttoz et al., 2014). In most socially monogamous species, extra-pair fertilizations (EPF) make an important contribution to a male's reproductive success and therefore direct fitness (Hill et al., 1994; Palombit, 1994; Webster et al., 1995). This leads to an evolutionary conflict between natural selection favoring males pursuing EPFs on the one hand and ensuring certainty of paternity on the other (Hasselquist & Bensch, 1991; Kappeler & van Schaik. 2004: Schuiling, 2003). This realization has led to a focus on sperm competition and its behavioral manifestations, such as mate guarding (Kappeler & van Schaik, 2004; Schuiling, 2003). In many species, females' fertile periods are short, meaning that it is realistic for males to intensely mate guard at this time, and in species with obvious fertile periods guarding is indeed intensified, or only carried out, at this time (e.g. birds: Birkhead, 1979; Hasselquist & Bensch, 1991; mammals: Poole, 1989; Schubert et al., 2009; Watts, 1998). In human females, however, the signs of estrus are subtle and may have become hidden during human evolution to encourage paternal care and allocation of resources in stable monogamous relationships (Burt, 1992; Strassmann, 1981; Turke, 1984) or as a paternity confusion strategy to reduce infanticide (Hestermann et al., 2001). Alternatively, conspicuous estrus may have just never evolved in human primates (Laland & Brown, 2011).

However, despite the signs of human estrus being subtle, it has been reported that there are cues relating to an increase in general female attractiveness during fertile times which males can detect (Havlíček et al., 2006; Kirchengast & Gartner, 2002; Krug et al., 1999; Kuukasiarvi et al., 2004; Roberts et al., 2004; Singh & Bronstad, 2001; Symonds et al., 2004),

and males display greater mate guarding behaviors when females are fertile (Gangestad et al., 2002). Nevertheless, the prevalence of menstrual taboos in many religions as a way of detecting the resumption of estrus after pregnancy (Strassman et al., 2012), and the use of ovulation test kits in couples trying to conceive (Miller & Soules, 1996), suggests that signs of estrus may be too subtle to be used as an accurate indication of females' fertile periods. In addition, ancient philosophers and scholars such as Soranus incorrectly identified the female fertile period and its timing was not correctly established until the 20th century (Freundl et al., 2010), so it is unlikely that ancient people were able to detect it with any accuracy.

Human sexual intercourse results in conception only from around 5/6 days before ovulation to the day of ovulation (Gangestad et al., 2005; Gangestad & Thornhill, 2008; Wilcox et al., 1995). Although females are continuously receptive to sex throughout their cycle (Gangestad et al., 2005), the chance of fertilization is low in any one cycle, compared with other primates (Cahill & Wardle, 2002).

Females are thought to display psychological changes during their fertile period such as being motivated to enhance their attractiveness (Beall & Tracy, 2013; Eisenbruch et al., 2015; Haselton et al., 2007). In addition, fertile females report greater attraction to extra-pair males, and less commitment to their partners (Gangestad et al., 2002; Haselton & Gangestad, 2006; Jones et al., 2005). Recent evidence, however, suggests that this effect does not occur with women who are very committed to their partners (Grøntvedt et al., 2017). In addition, this attraction to extra-pair males could alternatively have a mate switching, rather than a cuckoldry function (Buss et al., 2017).

In primates with concealed ovulation, where males cannot distinguish perfectly between a female's fertile and non-fertile periods, it is very difficult for a single male to sexually control a receptive female (Dubuc et al., 2012; Kappeler & van Schaik, 2004). Human primates face this situation due to the lack of conspicuous physical signs of ovulation in females (Gangestad & Thornhill, 2008). This means that human males have a problem not faced by the males of most other socially monogamous species – the need for extended periods of mate guarding to ensure certainty of paternity. This mate guarding reduces fitness due to the loss of extra-pair fertilization opportunities and other fitness costs, such as reduction in the time spent acquiring status and resources (Kruger et al., 2014).

Mate guarding in humans manifests in various ways and much has been written about human sexual jealousy, mate concealment, vigilance, violent and possessive behavior, monopolization of time, verbal and physical symbols of possession, and derogation of competitors (Barbaro et al., 2015; Buss, 1988, 2002; Kaighobadi et al., 2009; Sela & Barbaro, 2017; Shackelford et al., 2005). However, less attention has been given to another very powerful form of mate quarding: patriarchy.

Patriarchy has been defined in a variety of ways over time and throughout the literature. Definitions of patriarchy include "a hierarchical social system" that functions in such a way to uphold men and their needs while subordinating and oppressing women according to male desires" (Friedman et al., 1987, p. 8) or "a system of kinship relations which is organized in terms of the rule of the father and endorses a set of social and economic values that promote young motherhood and large families" (Lerch, 2013, p. 135). In this paper, we focus in particular on a reproductive definition of patriarchy i.e. the control by males of female sexuality (Lerner, 1986: MacKinnon, 1987) in the form of a system of implicit and explicit rules of conduct, of power structures, and of belief systems that support male control over women's reproduction. Patriarchy relies on concepts such as morality, guilt, shame and family honor to maintain it (Schneider, 1971), is ubiquitous and exists in the social structure of almost all human cultures. although its forms and its severity vary historically, ethnographically and geographically (Potts & Campbell, 2008).

Patriarchy is also embedded in most religions (Potts & Campbell, 2008) which is thought to be for the express purpose of ensuring certainty of paternity (Strassman et al., 2012). What is unique about patriarchy, in comparison to other mate guarding strategies, is that it can function even in the temporary absence of males. We argue that patriarchy has an evolutionary origin and has arisen as a mate guarding strategy and a way of avoiding fitness-reducing evolutionary trade- offs. This biological theory of patriarchy remains underdeveloped and has not yet received enough attention in the literature, which focuses primarily on sociological explanations for patriarchy.

Although other primate species show co-operative aggression towards or control of females (Smuts, 1995; Watts, 1998), males have to be present for this to occur. While coalitionary aggression shown by nonhuman

primates towards females to either prevent or ensure future sexual access (Smuts & Smuts, 1993) could be termed a simple patriarchy, here we use the term patriarchy to refer to aggression to and control of females through a system of values, beliefs, cultural norms and religious or civic laws. Using this definition, patriarchy appears to be unique to human primates and it seems likely that the complex cognitive and linguistic capacities of humans have facilitated this particular form of female control.

Smuts (1995) discusses the evolutionary origins of patriarchy, putting forward six hypotheses, which detail the mechanisms by which male control of female sexuality could have evolved in humans. These six hypotheses relate to a weakening of female and strengthening of male alliances leading to greater male control of resources and hierarchy building, coupled with female acceptance and reinforcement of patriarchy and, finally, the ideology of patriarchy arising from the use of language (Smuts, 1995). The ultimate question of why male control of female sexuality is critical in maximizing males' reproductive success is not fully addressed.

Smuts (1995) argues that patriarchy evolved as an extension of sexual coercion, of the type found in many non-human primates, where coercion is defined as aggression used to lower the costs of sexual access to females. Because humans are socially monogamous, (and in fact many monogamous primates do not use coercion at all (Smuts 1995)), we argue that coercion is relevant only in that coercive cuckoldry attempts from extrapair males make mate guarding necessary to ensure paternity certainty, and that mate guarding is the primary driver of the evolution of the human patriarchal system.

Ultimate evolutionary causes can be examined in two ways, firstly by outlining a series of evolutionary steps which may have occurred to lead to a particular characteristic and secondly by detailing how the behavior has been favored by natural selection by increasing individuals' fitness. We will explore both of these in this paper.

2. Historical and current manifestations of patriarchal mate guarding

We define patriarchal mate guarding as mate guarding which has been socialized and integrated into society, culture, religion and law. Unlike mate guarding in non-human species, patriarchal mate guarding is community-enforced and can therefore function even in the absence of male spouses

or kin. It has occurred through the ages in all geographical regions, but varies in form and intensity.

In China the practice of footbinding mutilated the feet of women and severely restricted their movements, by breaking the bones of the feet and binding them to prevent the bones healing. This practice persisted for more than 1000 years, affecting millions of women (Blake, 1994). With bound feet, women could neither travel far, escape from marriage or concubinage, nor gain financial independence (Mackie, 1996; Wilson & Daly, 2009). The primary function of footbinding was thought to be to ensure female fidelity (Mackie, 1996). It has been described as "a voluntary ordeal undertaken by mothers to inform their daughters how to succeed in a world authored by men" (Blake, 1994, p. 676) and "Mothers constantly informed their daughters that binding was necessary to find a good family in which to marry" (Blake, 1994, p. 683). Meanwhile in Europe, tight-lacing of corsets, causing ill health and bone deformation (Stone, 2012), combined with strict codes of morality restricted the movement and independence of women to a similar degree. Purdah and female genital mutilation (FGM) are contemporary examples of patriarchal mate guarding, and affect hundreds of millions of women worldwide (Wilson & Daly, 2009).

FGM refers to clitoridectomy and infibulation, mutilations which ensure virginity up to marriage and remove the capacity for sexual enjoyment (Shaw, 1985; Wilson & Daly, 2009). FGM is a major human rights problem thought to affect as many as 100 million women in Africa (Mackie, 1996). Mackie (1996) suggests that Chinese footbinding and FGM are equivalent in many ways, as both are for the purpose of control over chastity and reproduction and both are claimed to enhance male sexual pleasure. Both are also extreme, painful, debilitating life- long mutilations, the severity and persistence of which, in our opinion, require explanation.

Purdah is another contemporary form of mate guarding practiced widely in Asia which can involve segregation of the sexes, sequestering of women, veiling women and / or expectations of chaste behavior and comportment in order to prevent sexual access by extra-pair males (Khan, 1999). The fact that strict purdah requirements are only applied to women of reproductive age and in front of unrelated males (Khan, 1999) is evidence that purdah is a form of mate guarding. Women in many contemporary patriarchal societies have other restrictions which limit their mobility and economic independence such as restrictions on voting, travelling without the

permission of male relatives, and working (Doumato, 1991). In rural Pakistan for example, female work or education can be seen as "a threat to the honor code" (Khan, 1999, p. 30). Even in industrialized and economically advanced Western nations, patriarchy is not absent (Ortner, 2014) although it may be more covert. This takes the form of double standards in acceptable sexual behavior between genders (Allison & Risman, 2013), unequal sharing of domestic work and childcare limiting females' economic potential, societal pressure to marry and bear children, gender pay gaps and workplace harassment (Cortina & Leskinen, 2013; Ortner, 2014). There is also considerable objectification of women in the media which is linked to mental health problems such as anorexia (Moradi et al., 2005).

The gender gap report (Bekhouche et al., 2013) analyzes four measures of gender inequality caused by patriarchy in 130 countries, including occupational opportunities, access to education, political empowerment, and health and survival. According to this report, there are no countries where complete gender equality exists (Bekhouche et al., 2013). Similarly the World Bank's (2016) report on legal restrictions which limit women's economic activity showed that 155 economies out of 173 had at least one law which impeded women's economic progress. The evidence suggests that patriarchy appears to be ubiquitous in both historical and contemporary human society.

Another example of patriarchal guarding relates to parental control. Apostolou (2007) looked at data from 190 hunting and gathering societies, finding that while parents exhibited influence over mating of both sons and daughters, much greater control was shown with daughters. In addition fathers were more frequently the decision makers regarding daughters' mating choices. This study suggests that historically, parental control has been important in constraining female sexuality. Parental control is also important in a contemporary context. Parents will control their daughters' behavior and mating decisions, including such as enforcing curfew, influencing clothing choices, approval of partner choice and not allowing daughters to spend the night with a partner (Apostolou, 2007). Daughters' sexual behavior and mate choice are controlled more than that of sons (Perilloux et al., 2008).

In addition, parents will attempt to manipulate their children's mating choices and are willing to use more manipulation to control their daughters' mate choices than their sons' (Apostolou, 2012; Apostolou & Papageorgi, 2013). Parental control may be an additional evolutionary driving force of

patriarchy due to conflicts between parents and offspring over offspring mating choices. Offspring may trade off resource-based advantages such as family status for indicators of good genes to maximize their own, but not necessarily their parents' inclusive fitness (Apostolou, 2013). As females' investment in offspring is greater than that of males, control over mating decisions is more effective when directed at daughters (Apostolou, 2013). In particular, the patriarchal practices of footbinding and FGM, usually carried out when females are very young, may be driven by a need not only to enforce chastity before marriage and fidelity after marriage, but also to further parents' genetic interests in controlling which spouse is chosen. While the practices of FGM, footbinding and purdah, and control of mate choice may appear to have little in common, they all restrict the movements and independence of females for the purpose of male control over chastity and reproduction (Mackie, 1996).

While a discussion of all of the various contexts in which patriarchy can occur is beyond the scope of this review, it is clear that there are large differences in how patriarchy is manifested both currently and historically. and the severity of patriarchy appears to be context dependent (Apostolou, 2007: Figueredo et al., 2001). For example, while the patriarchal Catholic Church is evidence for the long persistence of patriarchy in a monogamous system, footbinding and FGM are thought to have arisen in an environment of hierarchical polygyny (Mackie, 1996). Wilson & Daly (2009) point out that while there are many varying systems of patriarchy, there is a cross-cultural consistency of sexual proprietariness by males that underlies all its varied manifestations. For example, despite large cultural differences, adultery is universally viewed as a crime against the husband and the male adulterer's marital status is largely irrelevant (Wilson & Daly, 2009). Therefore it is important to realize that context-dependent differential expressions of patriarchal mate guarding have the same underlying motivation (Wilson & Daly, 2009).

3. Role of patriarchy in preventing female EPFs

Natural selection is thought to favor female extra-pair fertilizations (EPFs) to increase the genetic quality of offspring, as long as the benefits of increased genetic quality outweigh the costs associated with the extra-pair copulation (EPC) (Thornhill & Gangestad, 2008). It is clear that males have traditionally inflicted, and still do inflict, severe measures to increase the costs to females of EPCs and thereby minimize EPFs and increase certainty of paternity. So crucial is this for the maximization of male

reproductive success that it has become literally a life and death matter. Traditional penalties have always been much harsher for female than for male adultery, and this is still the case in many countries where women adulterers face the death penalty (Schabas, 2000). So-called "honor killings" (killing of women who have violated religious and cultural standards of chastity) are common in highly patriarchal societies such as those in the Middle East (Kulczycki & Windle, 2011; Kulwicki, 2002). Women may be killed for alleged or actual adultery, being in a relationship deemed inappropriate, refusing a pre- arranged marriage or being raped (e.g. Mirza, 2008; Sela et al., 2016; Spolar, 2005). In some countries, such as Pakistan, honor killings can occur at a rate of 300 per year when sexual activity outside of marriage is suspected (Sev'er & Yurdakul, 2001) although generally the crime is concealed and under-reported so real figures are likely to be considerably higher (Arnold, 2000).

The woman concerned is killed by the father, brother or other members of the extended family or in-laws and the killing is pre-meditated (Sev'er & Yurdakul, 2001). Interestingly, honor killings are often treated more leniently than other forms of murder and there has been some debate about whether they are actually murder, with sentences being typically a fraction of those given for non-honor homicide (Arin, 1996; Feldner, 2000), Men who have carried out the crime of honor killing will usually mourn the victim but frequently defend their actions which they view as justified, unavoidable and necessary to restore family honor or cleanse the stigma associated with the woman's actions (Arnold, 2000; Mirza, 2008; Sela et al., 2016). In many Arab countries in particular, a woman's character is almost wholly dependent on her sexual morality and maintaining virginity until marriage (Arnold, 2000), whereas a man's character is dependent on his not being cuckolded, and if such an occurrence exists, the only way he can repair his tarnished and emasculated reputation is by honor killing (Buss. 2005: Daly & Wilson, 1988). This rather extreme manifestation of patriarchy clearly supports the mate-quarding hypothesis.

4. Why women comply with patriarchy

Smuts (1995) in her essay on the biological origins of patriarchy suggests that female compliance with patriarchy was instrumental in its evolution and we agree with this evaluation. The ultimate reason for female compliance with patriarchy is worth exploring. Many of the more severe manifestations of patriarchy are inflicted on young women not by males but by other women, often mothers and sisters. Women, not men, usually broke the

bones in daughters' feet in China and bound them, and women usually carry out FGM in Africa. Women are also instrumental in maintaining patriarchy in many Arab and Middle Eastern countries: the "honor" of every female in the family can be affected by the behavior of female relatives. This is also seen when parental control over daughters' mating decisions is considered. Mothers are more willing than fathers to use manipulation to control their daughter's mate choices (Apostolou & Papageorgi, 2013). This perpetuation of patriarchy by women can be easily explained: inside a highly patriarchal system where men control resources and female sexuality, marriage is the only option for women. Daughters' marriage prospects will be almost non-existent if the patriarchal mandate such as footbinding or genital mutilation is not carried out (Blake, 1994; Mackie, 1996).

Parental control of daughter's mate choices and sexual behavior is also important in facilitating marriage. The 'Daughter Guarding Hypothesis' proposes that parents will attempt to preserve their daughter's mate value. protect her sexual reputation and also prevent sexual victimization. This control can attempt to ensure that their daughter can gain a high quality partner (Perilloux et al., 2008). Mothers and sisters, operating within an established patriarchal system where they have little or no power, are, to their knowledge, acting in their relative's best interests by ensuring their relative will not be rejected in the marriage market (Blake, 1994; Mackie, 1996). A woman who has children outside of marriage in a highly patriarchal society receives fewer resources and her offspring are disadvantaged. punished or killed (Sev'er & Yurdakul, 2001; Smart, 1996), meaning noncompliance with patriarchy leads to a decrease in direct fitness. For example, in Indonesia child mortality is 12% higher when the child's parents are divorced, when compared to an intact monogamous marriage (Geary, 2000). In Turkey, illegitimacy is dishonorable and children born out of wedlock are often killed (Sev'er & Yurdakul, 2001).

Even in developed, less patriarchal countries such as Sweden, children growing up in single parent families have increased risk of mortality, severe morbidity and injury (Weitoft et al., 2003). In a UK study, children growing up with economically inactive single mothers suffered a substantially higher increase in mortality risk compared with higher socio-economic groups (Judge & Benzeval, 1993). As recently as 1945, in the UK, unmarried motherhood was highly stigmatized, with women often being known as "fallen women" and punished by having their child removed; in fact, the best

fate an unmarried mother could hope for was to be taken into live-in domestic service (Kunzel, 1995). Patriarchal practices which may seem maladaptive, such as FGM, which often has negative health consequences that could be assumed to reduce fitness, clearly serve an adaptive purpose in some contexts. Recent evidence (Howard & Gibson, 2016) shows that female genital cutting increases direct fitness in areas where most of the population carries out the practice. This is the reason that many women, throughout human history, have complied with patriarchy and still do: non-conforming females are culturally stigmatized, have lower socio-economic status and decreased reproductive success.

The implications of this are clear. If the survival of illegitimate children is low due to infanticide, neglect or poverty, and survival of offspring is higher within monogamous marriage, then there must have been selection favoring female acceptance of patriarchy, including traditional gender roles and family structures. There is clear evidence for this: Kaufman (2000) studied egalitarian versus traditional families and found that women in egalitarian families were less likely to intend to have a child and less likely to actually have a child, suggesting contemporary ongoing evolution of psychological adaptations for patriarchy, expressed as preferences, value systems, ideologies and behavior.

Smuts (1995) suggests that women may voluntarily undergo FGM and purdah in order to secure a high-quality spouse, highlighting that women, as well as men, engage in behaviors that support patriarchy. Buss (1996) also posits that women participate in reinforcing their own oppression by "espousing an ideology that reinforces men's control" (Buss, 1996, p.300). Buss & Duntley (1999) argue that patriarchy arose through co-evolution: women prefer men with status and resources, which causes men to become more competitive and status/resource/power seeking. Thereby. women have actively participated in creating patriarchy. We suggest, however, that an equally plausible explanation for women's compliant behavior is that it is a survival strategy in an already patriarchal environment. Women's preference for men with status and resources, and other forms of compliance with patriarchy, may have arisen very early in human evolution, out of a situation in which violence and unbalanced allocation of high-protein food was already being used to control females (Stanford, 1999). Perhaps this preference would never have arisen in an early environment of equally shared resources.

5. Female resistance to patriarchy

The question of whether women have historically resisted patriarchal mate guarding is worth considering. Female resistance to mate guarding, if it existed, may have been instrumental in intensifying mate guarding and in the evolutionary development of patriarchy.

Female coalitions have been observed in some non-human primates such as baboons, chimpanzees and bonobos, where females band together to counter male aggression (Newton-Fisher, 2006; Smuts, 1995; Tokuyama and Furuichi, 2016). However, patriarchy is subtler than this kind of overt aggression and we hypothesize that one of the reasons patriarchy is so effective and has endured for such a long time is that it has created an embedded system from which it is extremely difficult to escape from the inside

There is little evidence for resistance to mate guarding in the literature on humans (Cousins et al., 2015). The evidence that does exist is contemporary, drawn from Western, less patriarchal societies. Cousins et al. (2015) report several resistance tactics including avoiding contact with partners and resisting public displays of affection. An interesting finding is that contemporary, Western women are more likely to resist mate guarding tactics when there are lower costs involved and there is less chance of punishment or retaliation from partners (Cousins et al., 2015). These examples are, however, in the contemporary Western context and such low costs of resistance would have been very unlikely in historical societies and indeed in contemporary highly patriarchal societies. Furthermore, it is important to consider that the study looked specifically at overt mate guarding tactics which are only a small part of patriarchal mate guarding, due to the latter's societal and community-enforced nature.

One historical example of the consequences of resistance to patriarchy is the witch hunts which took place between the 11th and 17th centuries in Europe. Women who resisted patriarchal norms (marriage and childbearing) were viewed with extreme suspicion, tortured to extract confession and usually killed (Hester, 1990; Levack, 2006). Witch hunting targeted primarily single women (Levack, 2006). Women could also be branded as witches and killed as scapegoats for misfortune occurring in communities, or for the "crime" of being sexually abused and made pregnant outside marriage (Hester, 1990). This persecution of females was legitimized by both the Church and the state and is thought to be an example of sexual and social control of women by inducing fear of torture, imprisonment and death (Hester, 1990).

In primitive societies both inequalities in physical strength between the sexes and male control over the allocation of protein-rich food resources may have meant there was little opportunity for women to resist mate guarding by males (Apostolou, 2007; Stanford, 1999). Males in both traditional hunter-gatherer societies and non-human primate species use access to meat to control females and Stanford (1999) considers control of food instrumental in the early development of patriarchy. As patriarchy developed, women who resisted would, at best, have had reduced direct fitness due to rejection in the marriage market (Blake, 1994; Mackie, 1996). and at worst, been killed for violating societal norms pertaining to chastity (e.g. Hester, 1990; Mirza, 2008; Sela et al., 2016; Spolar, 2005). Another reason that resistance is unlikely is that women born into societies where patriarchy is already embedded into religious and legal frameworks would not realize that patriarchy was anything other than "the way things are". Women either do not understand that they are being controlled, often against their own interests, or they perceive that there is no other option. For example, it is reported that women who have undergone FGM think that genital pain and the length of time taken for urination (15 minutes) are "normal" (Horowitz & Jackson, 1997:Morrone et al., 2002).

Also, many highly patriarchal practices which are contrary to the interests of individual females, such as FGM, promote patriarchal myths and cultural "traps" to ensure that women comply (Mackie, 1996). In parts of Africa, girls are told that if the clitoris touches the baby's head during childbirth the baby will die, therefore girls are taught to believe that clitorectomy is necessary (Mackie, 1996; Morris, 2008). Mackie (1996) makes the point that FGM and footbinding "are practiced even by those who oppose them" due to the embeddedness of patriarchy into socially approved codes of behavior.

Even if females did not gain fitness by extra-pair copulations and were never motivated to cheat on their mates, there could still be a need for patriarchy as males would still be likely to pursue EPCs. For example, Buss & Schmitt (2011) showed that men are much more likely than women to be unfaithful to their partners, to seek one night stands, to have multiple partners and to seek short term sex partners who are already married.

The question of whether human mate guarding is needed primarily to prevent females from pursuing extra pair liaisons or to guard them from cuckoldry attempts of other males is an interesting one. Probably both

factors were at play in the evolution of patriarchy. The burden of maintaining chastity, however, has usually been placed firmly on female shoulders: in patriarchal societies, women often take the blame for being victims of sexual coercion (Pollard, 1992). Mackie (1996) suggests that, although the primary reason for Chinese footbinding was to control females' fidelity, it would have also made capture for the purposes of sexual coercion by extra-pair males such as marauding barbarians very difficult, as females would need to be carried as they could not walk far.

6. Control of female fertility by patriarchy

It is interesting to note that, despite recent advances in human rights for other discriminated groups, women are still very much entrenched in patriarchy in much of the world to greater or lesser degrees including Africa (Essien & Ukpong, 2013), Asia (Brown, 2014; Samarasinghe, 2012), the Middle East (Joseph & Slyomovics, 2001), Europe (Lerch, 2013) and the USA (Ortner, 2014).

Brown (2014) points out that patriarchal culture in Asia is "resistant to change" and Mackie (1996) reports that education, anti-FGM laws and modernization have failed to halt the practice in much of Africa. In post-Soviet Central Asia, many decades after the introduction of laws to improve women's rights and a legislative ban on bride abduction, this practice has recently been reinstated using a culture of shame and tradition to coerce women into remaining with their abductors. Women who resist the practice of kidnapping, rape and forced marriage are branded "traitors to their ethnicity" (Kleinbach et al., 2005; Werner, 2009). In several countries bride kidnapping and subsequent rape are viewed as a usual and justified practice in obtaining a wife and, like other forms of patriarchal violence against women, the perpetrators of bride abduction are rarely prosecuted (Human Rights Watch, 2006; McLaren, 2001).

Another example of the endurance of patriarchy is that, despite the advent of medical advances which make contraception and abortion virtually risk free, there are still religious and civil laws preventing women from taking up these options in many highly patriarchal countries (Campbell et al., 2013). For example, contraception is outlawed by Catholic bishops in the Philippines, and in much of the Sahel and Indian subcontinent women marry very young and simply do not have the autonomy to make decisions about their own fertility (Campbell et al., 2013). The World Health Organization estimates

that "225 million women in developing countries would like to delay or stop childbearing but are not using any method of contraception" and that one of the reasons for this is "cultural and religious opposition" as well as "gender based barriers" (WHO factsheet No. 351, 2015). For example, Khan (1999) reports that in rural villages in Pakistan many women are unable to access family planning resources.

It is clear that patriarchy is about more than merely preventing females from engaging in EPCs, it also controls women's fertility by enforcing in-pair childbearing and discouraging contraception – again for the purpose of increasing males' fitness. In her excellent discussion on deconstructing motherhood Smart (1996) explains how, through the ages, women seeking to terminate unwanted pregnancy have been criminalized and harshly punished by prison sentences or even the death penalty.

Even in less patriarchal social systems such as those found in the USA and Western Europe, abortion was only legalized relatively recently, and in fact, it can be argued that even this legalization has occurred primarily for reasons unconnected with the rights of women to control their own fertility (Jesani & Iyer, 1993). Campbell et al. (2013) argue that patriarchy is the main reason for large families in less economically developed countries. When contraception is freely available and women are more empowered to control their own reproduction, fertility will always fall (Campbell et al., 2013).

If this is the case, and patriarchy enforces high in-pair fertility while increasing the cost to women of EPFs, it would be expected that in matriarchal societies where women have complete control over their reproduction, fertility would be considerably lower. Patriarchal societies would be expected to expand over time and matriarchal ones decline. The Moso are a matrilineal, matriarchal group living in Southwest China, with a very low rate of population expansion. They came to the attention of the Chinese government which was concerned about the high rate of population growth in other groups such as the Han (Johnson & Zhang, 1991). Unlike the Han and other groups the Moso do not practice a patriarchal system. In the Moso, sex occurs by mutual consent and women stay in their own household and are visited by men who must return to their own household in the morning (Shih & Jenike, 2002). Women are completely in control of their own fertility and limit it accordingly. Children produced belong to the mother and illegitimacy does not exist. Since no

individual female bears the responsibility for providing offspring for the household, the pro-natalist pressure found in patriarchal societies is completely absent for the Moso women (Shih & Jenike, 2002). The practice of limiting fertility by the Moso has led to the decline of the population, so much so that Johnson & Zhang (1991) advised the Chinese government to be tolerant of matriarchal polyandrous societies in order to achieve their goal of zero population growth. In matrilineal polyandrous societies, male certainty of paternity is low and, in the absence of patriarchy, males would be expected to change their behavior accordingly - indeed, in as many as 10% of matrilineal societies property is passed by males to a sister's sons rather than a man's own presumed offspring as there is more confidence in the level of relatedness (Fortunato, 2012).

7. Patriarchy and religion

The world's major religions are highly patriarchal (Sadiqi, 2014; Stopler, 2008; Uchem, 2015). For example, the five great world religions are far more emphatic regarding the importance of chastity and virginity in marriage for females than males (Strassman et al., 2012). Although several authors have recognized the usefulness of religion in mate guarding and ensuring certainty of paternity (Sela et al., 2016; Strassmann et al., 2012), we propose that religion is not a cause of patriarchy, but is rather a very convenient and effective way of enforcing it. A number of practices that enforce male control over female sexuality are justified by religious doctrines, e.g. discouraging the use of contraception and endorsing rape of women in certain contexts (Sela et al., 2016). Rape has been prevalent throughout our evolutionary history (McKibbin et al., 2008; Thornhill & Thornhill, 1983) and is not caused by religion, however tacit approval by some religions in certain situations, for example during war (Sela et al., 2016), helps enforce patriarchal control.

Strassman et al. (2012) show, by comparing cuckoldry rates in three coexisting religions which vary in the degree of patriarchal control, that religions with greater control over female sexuality lower cuckoldry rates. This can be taken as evidence that patriarchy, but not necessarily religion per se exists primarily for the prevention of cuckoldry. While practices such as FGM and honor killing are principally religious practices encouraged by a number of sacred texts and, in some cases, religious authorities (Sela et al., 2016; Slack, 1988), other practices such as footbinding are primarily cultural yet have affected millions of women over thousands of years, showing that extreme patriarchy also exists independently of religion. Nevertheless, religion, being vertically transmitted in families, is highly reinforcing to patriarchy. It is quite likely that surviving religions persist because they have been the most pronatalist. For example, fundamentalist Christians and ultra-orthodox Jews have much greater fertility (25% and 200% respectively) than other, more secular, members of their religions (Kaufmann, 2010). As women become more educated and fertility rates fall in many areas of the world, so religious fundamentalism undermines this by sheer demographics due to the production of greater numbers of offspring (Kaufmann, 2010). The "human population will not dwindle to zero, precisely because of the 'counter-entropic' religiously-committed populations whose fertility remains above replacement even in societies experiencing general population decline" (Kaufmann, 2010, p. 7).

8. The evolutionary development of patriarchy

Patriarchy is the integration of mate guarding into society, law and religion. We will now speculate on the possible evolutionary stages which might have led to the widespread and embedded patriarchal societies that exist today.

In ancestral populations, aggression and violence would probably have been used to control females. In extant non-human primates, male aggression is used to force females to mate, to punish them for mating with lower-ranking males, and even towards non-estrous females to ensure future sexual access (Smuts & Smuts, 1993). Recent studies of chimpanzees show that females mate with the male that is aggressive to them and behaves coercively even when they are not fertile (Muller et al., 2011), and as previously discussed, coalitionary mate guarding is common in nonhuman primates.

This behavior in nonhuman primates could indicate the beginnings of a basic patriarchal system, where females are not guarded only when fertile, but at other times as well, and by more than one male. Another way of controlling females in ancestral populations could have been through allocation of high-protein food resources, namely, meat (Stanford, 1999).

In more modern humans, aggressive mate guarding could have been carried out by the male of a (socially) monogamous pair or the male of a polygynous group. However, this would have been onerous, preventing him from pursuing other fitness enhancing activities. Males who spent too much

time away from home pursuing extra-pair copulations or acquiring status or resources would risk being cuckolded.

The next stage in the evolution of patriarchy, requiring only a multi-male community, the presence of monogamous pair bonding and sufficient language to narrate events, could have been the participation of other community members who would observe the behavior of wives, and gossip about any activity which would threaten certainty of paternity. Initially these were likely to have been extended family members, who had a genetic interest through kin selection. At this stage punishment of the wife may still have been the domain of the husband and close male family members (see honor killings in section 3).

In many monogamous primate societies, males defend territories and females have a low probability of encountering males outside their group (Smuts & Smuts, 1993). However, humans live in multi-male communities. Their growing mobility and expanding population would have increased cuckoldry risk within the group and even with out-group males. The next stage would have been the creation among a community of shared views of what was moral and immoral behavior for society as a whole, in the form of customs, honor codes and societal norms. This would have been essential as ever-larger communities were formed, and males could not always rely on their own and their kin's powers of observation.

At this point, sanctioning the wayward wife would also be a community affair, in the form of ostracism, formal punishment or even the death penalty. Evidence for this stage of patriarchy comes from the morality police which are active in several highly patriarchal cultures, such as Iran and orthodox Jewish neighborhoods of Israel, who act violently towards women who are not conforming to prescribed standards of modesty and chastity regarding dress and behavior (Sela & Barbaro, 2017). It is interesting to note that the beginning of the extreme patriarchal practice of footbinding (960-1279) coincided with a period of strong urban expansion, monetization and commercialization of agriculture in China (Mackie, 1996). These factors could also have been influential in the development of patriarchy generally.

As societies tended to become larger and more diverse and made up of more unrelated individuals, so the threat of paternity uncertainty grew, as did the need for males to travel outside of their communities to acquire resources (i.e. work), increasing the need for a culturally embedded form of female control still further. The growth of monotheistic patriarchal religion may have fulfilled this role. Embedding of patriarchy into religion attributed what was once biological to the supernatural — now, even if the neighbors weren't watching, God still would be. Indeed, Sela and Barbaro (2017) propose that the concept of God is, in fact, an extension of the alpha male of a primate group. Finally, patriarchy was extended to all females, rather than only wives. Daughters and other female family members now had to abide by similar rules to ensure the honor of the family or ethno-cultural group was not tarnished.

We predict that patriarchy will arise in a species when the following conditions are satisfied:

- 1. Females with concealed ovulation. We propose that concealed ovulation is a necessary condition for the evolution of a patriarchy. Species with short unconcealed fertile periods could easily be guarded at those times only. Without patriarchy, concealed ovulation would "force" males into extended mate guarding with a high cost and therefore natural selection would favor any change which relieved males of this cost.
- 2. Social, but not genetic, monogamy (or polygyny). A wholly monogamous species would have no need of a patriarchy.
- 3. Males and females both gain fitness from EPFs, or males use coercion. For patriarchy to evolve, there has to be a risk of females being fertilized by sperm outside the monogamous pair. This could be because of females gaining better genes from EPFs or because of male coercion, or a combination of the two.
- 4. Male uncertainty of paternity / cuckoldry risk. This is a direct consequence of the previous points.
- 5. Smuts (1995) argues that the evolution of language was instrumental in expanding the range and scope of patriarchy. Language and cultural transmission of information between generations are therefore needed for patriarchal mate guarding to evolve. While language is not a prerequisite for the type of coercive violence seen in many primates, language would facilitate the socialization of mate guarding into a sophisticated system of beliefs and customs, which is its current form. It is costly to use physical violence when other, non-physical methods of aggression are equally effective.
- 6. Advanced cognitive functioning and "self-conscious emotions" (Lewis, 2000) such as guilt, shame, pride and honor. Patriarchy relies on these self- conscious emotions, which make it, to some extent, a self-regulating system.

9. Patriarchy as a constructed niche

The premise of this paper is that patriarchy has an evolutionary origin and functions to prevent female extra-pair fertilizations (cuckoldry) while maximizing in-pair fertility and avoiding fitness reducing trade-offs, primarily the costs associated with mate guarding. Niche construction is the process by which organisms alter their environment or niche and by doing so drive evolutionary change by altering the selection pressures which they themselves are exposed to, and is a cyclical process (Krakauer et al., 2009; Laland et al., 2004; Laland & Sterelny, 2006). Niche construction can be defined as "the process whereby organisms, through their metabolism, their activities, and their choices, modify their own and/or each other's niches" (Odling-Smee et al., 2003, p. 419). During evolution, *Homo sapiens* has transmuted its physical, ecological, biological, social and informational milieu through niche construction and this engineering is experienced by each subsequent generation differently, through the new selection pressures created (Sterelny, 2007).

Culture is a very powerful way in which humans can niche construct, and cultural niche construction can drive rapid evolutionary change (Odling-Smee et al., 2003) by imposing selection pressures on future generations. Examples include the co-evolution of the gene for lactase with human pastoralism and dairy farming (Gerbault et al., 2011) and the persistence of the gene for sickle cell anemia as a consequence of yam cultivation (Durham, 1991).

However, many niche constructed traits do not involve single genes, so cultural niche construction can be difficult to test empirically although there is a theoretical body of work which has modelled niche construction and gene-culture co-evolution (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Durham, 1991; Feldman & Laland, 1996). Laland et al. (2001) modelled cultural niche construction to show that it has the potential to overtake natural selection in the speed and magnitude of evolutionary change that it causes, and they describe culture as "an extra-genetic 'knowledge-carrying' inheritance system" (p.24).

We propose that patriarchy is a cultural niche which has had, throughout the evolutionary history of the species, significant and comprehensive effects on the behavior of human females, both through cultural inheritance and also through genetic change and selection for females tolerant of

patriarchal family systems. The movements, behavior, chastity, fertility and economic independence of women have been controlled through the ages for the purpose of male reproductive advantage. Patriarchy has arisen from the reproductive environment and also creates it.

Laland et al. (2000) discuss, in a niche construction framework, the possibility of exploitation by powerful individuals in a culture-using population to promote their own interests at the expense of weaker members through the inheritance of cultural practices. This may be amplified by, for example, religious propaganda which "can be used to...coerce conformity from others against their own individual interests, yet in favor of the interests of a dominant class of cultural transmitters" (Laland et al., 2000, pp. 143-144).

As gene-culture coevolution is much faster than genetic evolution in natural ecosystems (Kumm et al., 1994), it should be possible to observe niche construction operating over only one or two generations. A recent and ongoing example of niche constructing patriarchy comes from female infanticide in Asia, where up to 80% of females die prematurely in some countries (Kumm et al., 1994). In many Asian societies sons are strongly favored over daughters and this appears to be a direct consequence of patriarchy, as preference for sons has been shown to be highly negatively correlated with women's status and economic potential and positively correlated with patriarchal family systems (Das Gupta et al., 2003; Huiying, 2016; Larsen et al., 1998; Winkvist & Akhtar, 2000). While certain countries such as India have practiced female infanticide for centuries, recent advances in reproductive technology such as prenatal sex determination have made it possible to abort female fetuses (Jha et al., 2006) with only minimal effects on overall lifetime fitness.

Presumably extreme female infanticide had historically been kept in check by the consequent reduction in fitness that would result from killing half of one's offspring (Kumm et al., 1994). Now that this cost has been greatly reduced by the availability of pre-natal screening and abortion, and the Chinese one child policy which limited fitness anyway, there has been a consequent increase in female infanticide (Jha et al., 2006; Kumm et al., 1994). This culturally-induced biasing of sex ratios has now led to an adult sex ratio imbalance in countries such as India and China, creating "involuntary bachelors" with ensuing negative psychological and health consequences (Zhou & Hesketh, 2017). It would be expected that mating

systems are under pressure to change to counter this extreme bias in adult sex ratio, and it will be interesting to see how and when a new equilibrium is established and whether fraternal polyandry, a historical solution to bride shortages in India, will re-emerge (Kaur, 2004). Already, the adult sex ratio imbalance has dramatically influenced patterns of mating, migration and dispersal and is even cutting through religious and social stratifications which have been in place for centuries (Kaur, 2004).

10. Suggested testable hypotheses for patriarchal mate guarding

If patriarchy is an evolved mate guarding strategy, it should be possible to test falsifiable hypotheses in relation to it.

- 1. Fertility should be higher and cuckoldry rates lower in more patriarchal versus less patriarchal communities within the same ethnic / religious group. In Albania, a study of 2001 census data on fertility intentions and reproductive histories showed that patriarchal kinship organization explained much of the variation in fertility, with those geographical areas where patriarchal rule was respected having a far higher fertility (Lerch, 2013). Further studies could look directly at cuckoldry rates.
- 2. Fertility should be higher and cuckoldry rates lower in more fundamentalist and patriarchal religious groups compared to more secular members of the same religions. This has been confirmed by Kaufmann (2010). Again, this looks at fertility rather than cuckoldry though.
- 3. Fertility should decline when women are allowed complete control over it. This has been demonstrated by the matriarchal Moso who limit their fertility (Shih & Jenike, 2002).
- 4. In the same ethno-geographic region, more patriarchal religions or systems should lead to lower cuckoldry rates. This was tested by Strassman et al. (2012), who compared cuckoldry rates in three religions coexisting in the same ethno-geographic area. Cuckoldry rates varied depending on the level of patriarchal control shown by the religion.
- 5. Countries or communities with the highest levels of patriarchy should have the fastest growing populations, but this would be hard to disentangle from other factors which influence population growth.
- 6. Patriarchy will be more severe in polygynous mating systems as cuckoldry risk will be higher, both due to the difficulty of controlling multiple females and large inequalities in male mating success, possibly driving cuckoldry attempts by extra-pair males. The relationship between polygyny and the development of extreme patriarchy would be an interesting hypothesis to test.

Conclusion

Although coalitionary mate guarding and violence against females are carried out by many primates, presently, only the human species satisfies the outlined conditions for the development of patriarchy. Women comply with patriarchy because the costs of not doing so are extremely high both in proximate terms (male violence, cultural and religious pressure) and also in ultimate terms of reduced direct fitness. When viewed from a biological perspective, reinforced with cultural and religious aspects, there is a potent evolutionary force maintaining patriarchy, and its persistence into the 21St century is not surprising.

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