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Trends of Pathogen Overload and the Influence on Social Behavior

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Abstract: *A review of the literature has been undertaken showing that higher levels of pathogen stress have been positively correlated with multiple aspects of social structure: non-sororal polygyny (Ember et al. 2007; Low 1990), exogamy and bride capture (Low 1990), resource defense (Barber 2008; Hames 1996), and male-female body alteration (Singh and Bronstad 1997). Non-sororal polygyny is the most effective reproductive strategy to defend against pathogen stress, as it promotes much genetic variability within gene pools, allowing for more pathogenic resistance in individuals because of heterozygous alleles. In order to secure mates while faced with ecological extremes, individuals will modify their bodies to increase the attractiveness, an indicator of pathogen resistance (Low 1990; Gangestad and Buss 1993). Intra-societal data are needed to test the direct relations between pathogenically debilitated individuals and likelihood of obtaining a mate (Low 1990). Intra-societal data are also needed to test the direct relations between pathogenically debilitated individuals and intensity of body modification (Singh and Bronstad 1997).*

This paper analyzes the impact of pathogen prevalence in local populations as it relates to marriage patterns and other associated social behaviors. Pathogen stress within societies has been shown to increase rates of polygyny and polyandry, with non-sororal as opposed to sororal polygyny being the most common form (Low 1990; Ember et al. 2007). At a population level, of the forms of polygamy, polygyny will provide the most variability within a population's gene pool. This is so because males can spread their genes more quickly than can females. After insemination, a man has the option of staying with his mate and investing in the child, finding another mate, or both. The inseminated female must wait through at least nine months of gestation before she can reproduce again. Even though non-sororal polygyny produces the most genetic variability within a population and is thus the most effective reproductive strategy in thwarting deleterious effects of heritable diseases, its testability is extremely difficult and complicated. In tribal contexts, it becomes difficult to know who fathered a particular child. On the other hand, it is much easier to know who actually gave birth to the child. As such, maternity is more certain and more easily testable than paternity (Gangestad and Buss 1993).

Pathogen overload within a community can be viewed as one ultimate cause of polygyny, which serves as an adaptation developed over time to protect and defend against disease. However, localized pathogen prevalence is not the most common reason why individuals engage in polygynous marriage or other multi-mate reproduction strategies. Therefore, other proximate causes of polygyny will be reviewed. Pathogens and parasites can significantly reduce populations, and as a result, potential mating partners also become reduced in numbers. It has been shown in non-human species that individuals will develop biological adaptations to overcome the obstacles in securing mates that are posed by pathogen prevalence, serving as a "display" of reproductive fitness (Hamilton and Zuk 1982). In human populations, however, individuals have been shown to utilize cultural strategies to overcome mating obstacles, such as tattooing and scarification, as a means to increase attractiveness (Singh and Bronstad 1997). Also, the number of societies with polygynous marriage is decreasing cross-culturally; so the implications of this trend and the social behaviors elicited by pathogen overload will be reviewed. Finally, the implications of pathogen overload itself will be discussed as it relates to the future of these societies.

Why Non-Sororal Polygyny?

Although there are multiple species that have life-long mates, only humans have the institution of marriage (Low 1990); and marriage can take on many different forms. What is more, every society has certain rules dictating who individuals can or cannot marry and how many partners they are allowed (Pasternak, Ember, and Ember 1997). Within each society, how much dictation is due to culture and how much is due to environmental constraint is difficult to ascertain. Is there really a difference? It is likely that many societies initially create marriage restrictions based on what has or has not been reproductively successful. As time passes, rules are followed and practiced for so long that they become embedded in the culture, becoming something they just do out of habit as opposed to something they *must* do. Perhaps marriage is where culture and genetics overlap (Low 1990). On the other hand, does cultural determinism play any role in the explanation of polygyny? This question will be revisited.

While living in the environment of evolutionary adaptedness (EEA), early humans certainly had to deal with much ecological extremity and unpredictability in terms of climate change, the availability of resources, and exposure to pathogens. Today many societies still deal with these issues of uncertainty. However, they may not do so in the same way as in the past, especially when faced with disease overload. Prior thought dominating the literature proffers that early hominids likely dealt with such environmental threats with rather reactionary behavior, like fission and homicide, while anatomically modern humans began to incorporate more long-term strategies that better defend against the deleterious effects of environmental threats. Such strategies include multi-mate procreation (Ember et al. 2007; Low 1990; Gangestad and Buss 1993). Such supposition is difficult to test. In any regard, the environment was and is constantly changing, as are cultures; so human groups must either keep up or die out.

Matt Ridley's (1995) Red Queen Hypothesis suggests that all species are in an evolutionary arms race with pathogens and parasites. With parasites, these guests try everything they can to survive *on* the hosts and the hosts try everything they can to survive these guests. Thus, individuals must utilize efficient techniques to stave off the deleterious effects of such stressors in order to survive and perpetuate the species in their area. They do so by producing viable, variable offspring that will have high reproductive success. However, as noted by Low (1990), a parent's resistance to disease is not indicative of the offspring's resistance. Therefore, the most effective technique is not necessarily to have as many offspring as possible, but to have as much variability in the population's gene pool as possible. The more genetic combinations there are in a population the more difficult it becomes for pathogens to survive and thrive within the population, an idea championed by Hamilton (Low 1990; Barber 2008).

Since men are able to produce more offspring throughout their lives than women, the most effective strategy for maintaining and enhancing genetic variance in a population would be for males to procreate with as many different females as they can. One way to do this is by marrying polygynously (Low 1990). In this regard, it would not behoove individuals to marry monogamously, as one or both individuals within a marriage may have recessive genes that continually get passed on to subsequent offspring. However, it is difficult to test the heritability of pathogen resistant genes, especially in tribal contexts (Low 1990). Polygyny allows males to increase their reproductive fitness by passing on more of their genes to the next generation and with more combinations.

Non-sororal polygyny allows for more genetic variability than sororal polygyny because sisters are related to each other by 50 percent. If a set of sisters are all procreating with the same man, there will be little variation in the genetic makeup of their offspring- the children will all be related to each other by fifty percent. A set of unrelated women, however, will produce much more genetic variation in the offspring because there will be many more combinations of genes being expressed- these children will be related to each other by 25 percent.

In terms of genetic fitness, women may benefit more from being second or third wives of healthy men resistant to pathogens than from marrying pathogenically debilitated men with no wives. A trade-off arises where women must take a chance: Even though a woman must take on the risk of receiving less attention and resources from the husband (this has been refuted; see Hames 1996), a woman will have more time to invest in her offspring (Trivers 1972; Hames 1996) and these offspring are more likely to receive the man's pathogen-resistant genes, thus increasing her reproductive fitness (Barber 2007; Low 1990). These are the kind of risks that tend to work out in the long run, because, as noted by Hamilton (Low 1990), variance in mate fitness is unlikely to deplete with time. However, a woman's fertility is decreased by marrying a man with multiple wives, wherein she will have fewer offspring than she typically would with a monogamous man, though she is likely to have higher quality children that will give her more grandchildren, enhancing her inclusive fitness (Barber 2007).

Other Determinants of Polygyny

While this human ecological approach helps explain why polygyny has been positively selected for in disease ridden contexts, other more proximate, cultural explanations must be addressed. Certainly many individuals are not thinking about the long-term benefit of the group as they make individual decisions, but it turns out that what is good for the individual can actually good for the group (Pasternak et al. 1997). Many times, a man will acquire multiple wives to increase his wealth within the society (White 1988). Multiple wives will provide a man with more children than he could have with only one wife. In many pastoral societies, such as the Bantu of Equatorial Africa, a wealthy man who owns many cattle is able to obtain multiple wives, who, in effect, provide him with the progeny necessary to work and tend to the cattle. This is how a Bantu man can obtain economic and reproductive success (Murphy 1974).

Whiting (Ember 1974) suggests that polygyny is a result of men not being able to remain abstinent during a post-partum sex taboo, which is a dubious claim on the grounds that men need not marry extra women to fulfill their sexual appetite when they can simply have extramarital affairs. Ember (1974) states that polygyny in non-state societies is due to high male mortality rates in warfare, leaving an unbalanced sex ratio in favor of women; more deaths in a society create a shortage of marriageable men and an abundance of reproductively available women (Ember 1974). In effect, a shortage of available males in a society has been shown to increase female-female competition over access to the limited numbers of healthy males (Singh and Bronstad 1997).

Barber (2008) states that resource-defense is a specific predictor of polygyny, but only in more sedentary societies where resources are stored. Such societies tend to be less egalitarian, as resources become more privatized and kept under lock and key. Wealthy males are not only able to monopolize the resources, such as the little available farmland and cattle, but the reproductive access to women (Barber 2008). This leaves less privileged men at a disadvantage. So how are they to compete?

Low (1990) indicates that the pathogen resistance of a procreating couple, while indicative of attractiveness (Gangestad and Buss 1993), is not necessarily indicative of resistance in their offspring because of their potential of being homozygous recessive for a harmful disease. However, Low (1990) is contradictory in her claim by proffering Hamilton's idea that resistant genes are likely to prevail in a population. Singh and Bronstad (1997) claim that physical attractiveness is still a significant determinant in mate choice and disadvantaged individuals will consciously alter their physical appearance to attract mates. After all, is it plausible that individuals will simply give up the idea of mating just because they are carriers of a particular disease?

Singh and Bronstad (1997) state that severe pathogen overload will limit the number of healthy males, which will increase female-female competition and rates of body modification. They note that women will "display" themselves (i.e., attempt to gain sexual attention from the opposite sex) by scarring parts of the body indicative of fertility, like the breasts and stomach, and leave these parts exposed while covering other parts of their body with clothing, as is the case in much of sub-Saharan Africa. Men will display by scarring parts of the body indicative of maturity and strength, such as the face, chest, shoulders, and arms. For example, among the Nuer of southern Sudan, males will carve six lines on their foreheads to display themselves. In any regard, scarification is done by both sexes in a symmetrical fashion: Scarring draws attention to the parts of the body that reveal reproductive capabilities and the symmetry in scarring bolsters the attractiveness of the individual. Indeed, Singh and Bronstad (1997) found that physical attractiveness became more important to individuals as pathogen rates increased, a finding consistent with the prediction of Gangestad and Buss (1993). However, it was found that scarification played more of a role in the lives of females as a means to attract male mates, suggesting that males are better able to attract female mates by sheer behavior and competency in obtaining resources (Sing and Bronstad 1997).

Reduction in Polygyny

Polygyny has traditionally been the most common type of marriage in societies cross-culturally (Pasternak et al. 1997). In more modern contexts, this form of marriage has been on the decline (Ember et al. 2007), except for in certain Islamic and African cultures (Barber 2007). One viewpoint of the transition from polygyny to monogamy suggests that men give up their wives to other men who, in return, will give them political support. Kanazawa and Still (1999) state that democracy has no effect on polygyny, but more division of labor will create a reduction in polygyny. Moreover, these authors state that women will marry polygynously if there is economic inequality between men in a society. In this scenario, women will choose to marry men with more economic resources, assuming that it is better to marry a wealthy man with multiple wives than to marry a poor man with no wives. This may be so on the grounds that a wealthy man will, regardless of how many wives he has, be able to provide resources for her and her children. On the other hand, women will marry monogamously if there is little economic inequality between men (Kanazawa and Still 1999). In this scenario, there is an even economic playing field. By being the only wife to a man, a woman can expect that she will not have to compete with other women over her husband's affection and resources. In effect, the gradual decline of inequality among men has led to the gradual decline of polygyny.

Discussion

Among many others characteristics, humans are separate from other species in that we not only have ecological factors shaping our behavior, we have culture. This complicates our ability to accurately assess the determinants of social behavior. One of the most distinct differences between humans and other species in terms of social dynamics is the concept of marriage. Taking a look at how societies regulate marriage lets one get a glimpse into how they deal with unpredictability and environmental extremity. It is true that not all societies regulate marriage in the same way or enforce dissentions of marriage codes. It is likely that societies will punish more severely for breaking the rules if there are higher levels of pathogen stress present. Severe punishment may likely occur in areas where there is an extension of the incest taboo to cousins, indicating that more variation in the gene pool is needed.

Pathogen prevalence is one of the most consistent ecological threats faced by all species. The literature on pathogen stress and human society indicates that non-sororal polygyny is the most common technique used by humans to keep enough genetic variability in a population to stave off the deleterious effects of pathogens. Rates of polygyny increase in areas with high pathogen stress (Ember et al. 2007; Low 1990), high rates of exogamy and bride capture (Low 1990), high levels of resource defense (Barber 2008; Hames 1996), and high rates of male-female body alteration through tattooing and scarification (Singh and Bronstad 1997). Hamilton and Zuk (1982) have shown that, among birds, females look at secondary sexy characteristic of males (i.e., attractiveness) when selecting potential mates. However, among humans, attractiveness is not always a clear sign of pathogen resistance (Low 1990) and can be altered to attract potential mates (Singh and Bronstad 1997). Further research needs to be done to investigate and establish a more detailed connection between mate choice and pathogen resistance. Further research also needs to be done to divulge other variables that are related to pathogen stress. As individuals are genetically related to their first cousins by 12.5 percent, areas with high levels of pathogens may not favor cousin marriage because of potential reproductive failure. These societies may not just restrict men from marrying their cousins, but may prefer or require them to obtain marriage partners from outside villages.

Future research should also look at the use of the levirate and sororate as they relate to pathogen stress in societies. Similar to cousin marriage, a man marrying his brother's wife or woman marrying her sister's husband may not be the most suitable in societies that require much genetic variation. Finally, further research should take an in depth look at how Western civilization has influenced nonstate societies with high levels of pathogen stress. Among the Nuer and Dinka of southern Sudan, who both experience a high rate of trichiasis, European missionaries have converted many individuals to Christianity, which requires them to be monogamous. In effect, this has altered the traditional social structure of these pastoral groups. While wealthy Nuer men would take on multiple wives to provide them with children to tend to increasing cattle herds, having only one wife limits the amount of help they will potentially have (Evans-Pritchard 1972).

Other societies have been introduced to state-level methods of mitigating disease, such as the Yanomamo of lowland Amazonia in South America, which entail the use of modern medicine as opposed to indigenous herbs and plants (Chagnon 1997). Ironically, many indigenous groups are introduced to disease by the very individuals who came to provide medicinal assistance. To obtain more medicine, they not only pay exceedingly high costs to travel far distances to cities where they must visit a hospital, they have to pay for seeing the doctor as well (Chagnon 1997). In terms of outside contact, it is more detrimental to have limited contact than full-blown or no contact at all. Limited contact introduces pathogens into a population that native peoples have not developed medicines for or resistances to, making treatment difficult because hospitals are far away. Full-blown contact introduces pathogen into a population, but at least in this scenario help is close by. Of course, no contact is preferred because there is no introduction to pathogens whatsoever.

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