Fitness and Power: The Contribution of Genetics to the History of Differential Reproduction

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Abstract

Textual evidence from pre-modern societies supports the prediction that status differences among men translate to variance in reproductive success. In recent years, analysis of genetic data has opened up new ways of studying this relationship. By investigating cases that range over several millennia, these analyses repeatedly document the replacement of local men by newcomers and reveal instances of exceptional reproductive success of specific male lineages. These findings suggest that violent population transfers and conquests could generate considerable reproductive advantages for male dominants. At the same time, this does not always seem to have been the case. Moreover, it is difficult to link such outcomes to particular historical characters or events, or to identify status-biased reproductive inequalities within dominant groups. The proximate factors that mediated implied imbalances in reproductive success often remain unclear. A better understanding of the complex interplay between social power and genetic fitness will only arise from sustained transdisciplinary engagement.

Keywords
differential reproduction, reproductive success, darwinian history

Accounting for Differential Reproduction

In humans, as in many other species, males experience higher variance in reproductive success than females for reasons rooted in physiologically determined sex-specific differences in parental investment. Human males may increase their reproductive success and fitness by depriving competitors of mating opportunities: this can be achieved by a variety of means, such as the removal or subordination of other males, the capture and sexual coercion of females, and the accumulation of resources (in terms of material goods and prestige) that attract mates and sustain child rearing. For human males, we would expect status (in terms of dominance and wealth) to be positively correlated with access to procreative sexual opportunities and thus, at least prior to the Demographic Transition, also with actual reproductive success. In practice, proximate mechanisms mediate this correlation in complex and culturally idiosyncratic ways, whether by enhancing variance in male reproductive success (e.g., under conditions of despotism or socially accepted polygyny) or by curtailing it (e.g., under conditions of democracy, normative monogamy, or modern family planning) (cf. in general Heyer et al., 2005). Very broadly speaking, for much of recorded history, societies tended to experience the former rather than the latter effect (for complications arising from the latter, see e.g. Sear et al., 2016). This allows us to predict that male status should indeed have translated to variance in male reproductive outcomes.

This prediction has been supported by a large body of empirical research. Back in the 1980s, Laura Betzig published a pioneering study of the relationship between stark asymmetries in socio-political power and commensurate asymmetries in male sexual opportunities and reproductive success: a wide range of historical and ethnographic data document powerful men who enjoyed disproportionate access to fecund women and out-reproduced lower-status competitors (Betzig, 1986). These findings have since been greatly enriched and augmented.
Betzig herself has gathered a wealth of additional evidence from different historical settings to buttress her case (Betzig, 1993, 1995, 1997, 2002, 2005, 2012), and so have others (Betzig, 2021a, 2021b provide the latest surveys). In earlier work, I have sought to explain imperialist behavior in pre-modern cultures in terms of mate competition and differential reproduction (Scheidel, 2009).

Most of this work has been based on textual evidence: statistical data at best, circumstantial evidence and qualitative impressions at worst. Slowly but surely, however, ongoing advances in genetics have expanded the evidentiary base. Over the last two decades, a growing number of increasingly sophisticated studies of both aDNA (genetic data retrieved from human remains) and the genetic properties of contemporaries have generated evidence of biased reproductive outcomes that can be linked to historical events such as migrations, conquests and enslavement. These data frequently point to the replacement of local males by male newcomers, and on occasion reveal instances of exceptional reproductive success of particular male lineages over time. In so doing, genetic analysis not only complements but at times also corroborates findings derived from more traditional sources such as historical texts and archaeological artifacts.

To the best of my knowledge, the contribution of this line of research has never been summarized from the vantage point of evolutionary psychology and with a focus on the history of differential reproductive success. (Reich, 2018b, ch.10; Krause & Trappe, 2021, ch.5 are engaging surveys but cover only some of the work referenced below). While a comprehensive critical review of the relevant scholarship is beyond the scope of this article, I hope to convey a sense of the richness, potential and limitations of this approach for the study of differential reproductive success.

Genetic Case Studies

In Homo sapiens, variance in reproductive success has always been greater for males than for females, even if this effect has not been particularly strong for much of our species’ history (Lippold et al., 2014; Poznik et al., 2013). This points to more muted forms of mate competition and polygynous practice than those that have been attributed to our more sexually dimorphic hominin ancestors (Schacht & Kramer, 2019). In various parts of the world, in a signal suggestive of increased male variance, the onset of the Holocene coincided with an expansion of the female population that has contributed to the current gene pool relative to its male counterpart (Lippold et al., 2014). More specifically, there are signs of a genetic bottleneck that caused far fewer males than females to pass on their genes in the mid-Holocene, a phenomenon likely to be associated with changes in social structure arising from the spread and maturation of farming, growing economic complexity and the emergence of larger polities, all of which supported hierarchies and enlarged the potential for variance in reproductive outcomes among males (Karmin et al., 2015).

The most dramatic processes of male-biased population replacement around that time have been linked to migratory movements of steppe populations associated with the Yamnaya culture of the Pontic and Volga regions north of the Black Sea and Caspian Sea. These movements took place after 3000 BCE, affecting populations from Europe to Siberia and South Asia and spreading the earliest forms of Indo-European languages. aDNA data from Germany, Poland, Hungary, Denmark and Sweden were the first to illuminate the massive demographic consequences of these transfers, which involved widespread replacement of local male chromosomal lineages with those carried by the newcomers (Allentoft et al., 2015; Haak et al., 2015). It soon became clear that this turnover not only extended to Britain but may even have been particularly severe: according to various samples, steppe-related lineages replaced some 90% of earlier male ancestry within a few centuries after the mid-third millennium BCE (Goldberg et al., 2017; Olalde et al., 2018). A similarly dramatic rupture was then observed on the Iberian peninsula, where individuals with steppe ancestry likewise began to appear in the mid-third millennium BCE. By the early second millennium BCE, 40 percent of genetic ancestry and almost all Y-chromosomes had been replaced by inflows from the steppe (Olalde et al., 2019). In all these cases, even though females of steppe origin were involved in these processes, incoming males consistently made a much larger contribution to the gene pool.

Several centuries later, analogous displacements took place in South Asia. While populations associated with the Harappan civilization of the Indus basin (which flourished especially in the second half of the third millennium BCE) lacked genetic steppe ancestry (Shinde et al., 2019), inflows from the steppe left a strong mark from about 2000 BCE onward (Narasimhan et al., 2019; Silva et al., 2017). Once again this contribution was mostly made by males: while female chromosomal lineages in present-day India mostly go back much further, between 50 and 90% of Y-chromosomal ancestry is of West Eurasian origin and reflects the immigration inflow of early Indo-European speakers from the steppe, much as it had occurred in Europe during the preceding millennium. Moreover, male steppe ancestry is correlated with elevated status: thus, upper-caste groups that speak Indo-European languages today, especially Brahmins, tend to have stronger steppe-derived genetic admixture than others (Debortoli et al., 2020; Narasimhan et al., 2019; Silva et al., 2017).

How did this happen? This question is more difficult to address than in instances in which we are able to link genomic change to textually documented historical events, as is the case in much of the remainder of this survey. We do know that these processes differed considerably from earlier Neolithic migrations of farmers from the Middle East, which involved males and females (or rather their respective genetic contributions) in a more balanced fashion (Goldberg et al., 2017). The spread of a few select male lineages of steppe origin points to more narrowly circumscribed operations characterized by considerable power asymmetries both within the migrants and between them and local populations. The
Yamnaya culture of the steppe is known for material remains suggestive of male-centered martial traditions and the pioneering use of wagons alongside domesticated livestock. Yet while this furnished these migrants with a package of mobility and coercive capabilities that would have been conducive to violent expansion, the fact that large parts of Europe as well as South Asia had been settled by growing populations of agriculturalists for thousands of years suggests that very considerable effort ought to have been required to produce the observed demographic turnover.

Conjectures that plague (Y. pestis) introduced by the steppe groups may have contributed population replacement (Rascovan et al., 2019; Rasmussen et al., 2015) rest on shaky foundations (Immel et al., 2020; Susat et al., 2021). Nor would they properly explain the strong sex differences in ancestry shifts, unless we were to assume that exposure to plague sufficiently weakened local populations for (more plague-resistant?) steppe invaders to displace the remaining local men and procreate with the remaining local women: although this is not an impossible scenario—given what happened in the New World after 1492—, it would seem hard to substantiate and does not currently seem particularly persuasive. With or without plague, it would seem hard to come up with a narrative that does not to some extent involve the violent takeover of resources and mates: accounts of war-chariots and warrior culture in the hymns of the Rig Veda, which were composed roughly during the period when steppe DNA entered India, may conceivably echo dislocations and innovations connected to that inflow.

A recent archaeological and aDNA study of two cemeteries in southern Germany dating from the late third millennium BCE offers a snapshot of the kind of communities created by these migrations (Sjögren et al., 2020). In these samples, all males with usable genetic information belonged to a single Y-chromosome lineage, which was the principal lineage associated with the movement of steppe ancestry after 2500 BCE. The genetic make-up of the females was much more diverse, reflecting a mixture of earlier local settlers and recent steppe ancestry. These communities practiced female exogamy and patrilocality but not polygamy, as the absence of half siblings suggests. This raises the question whether the newcomers sustained the kind of inequality among males which appears to have been typical of their ancestral Yamnaya culture and may also help explain why these migrations resulted in the spread of such a small number of types of Y-chromosomes (Reich, 2018a).

The question of inequality brings us to another phenomenon that made an appearance at around that time: the formation of so-called “star clusters”—instances of a high-frequency Y-microsatellite haplotype with close mutational neighbors that reflect an exceptionally strong contribution of a particular person to the gene pool later on. This process critically depends on continued reproductive success over generations: the reproductive performance of the founder alone cannot account for the presence of such explosive lineages. A large-scale survey of Y-chromosomes from 127 Asian populations has identified a number of star clusters (Balaresque et al., 2015). The genesis of the oldest examples—from Laos between 2100 and 1500 BCE and from somewhere near in Tibet around 1300 BCE—remains opaque. The Fertile Crescent region (perhaps northeast Anatolia) produced one star cluster around 700 BCE—the heyday of the Neo-Assyrian empire—and another one originated in India around 300 BCE, when the Maurya empire rose.

The lack of contextual information makes it impossible to tell if those clusters were meaningfully connected to the formation of large empires. All we can see is that these early instances occurred predominantly in agrarian societies that would have supported stratification and hierarchy. In general we lack tangible genetic data for differential reproduction in the first great empires, from the Achaemenids to Rome and the Caliphate. For instance, we do not know if genetic signals of substantial migration from the Eastern Mediterranean and the Middle East to the imperial city of Rome and its environs (Antonio et al., 2019) can be linked to slavery and how this might have affected the reproductive success of slaveholders. And while Y-chromosomal evidence from North Africa and Lebanon duly shows the introduction of Arab (and in the latter case also western European Crusader) lineages (Nebel et al., 2002; Zalloua et al., 2008) we are left wondering about male variance in reproductive outcomes in the context of conquest and elite formation. It is also unclear where the star cluster from the Fertile Crescent or Iran around 1100 CE came from (Balaresque et al., 2015).

Viking activity in the northeastern Atlantic from the ninth to the eleventh century is a promising candidate for the introduction of new Y-chromosomal material by means of male-biased migration, violent predation and colonization. Moreover, the genetic landscape of this region (the British Isles and Iceland) has been particularly well researched. Despite the hybrid nature of the Vikings, they were dominated by Norse elements from Scandinavia. The most recent survey consequently documents major inflows of Danish ancestry into England and of Norwegian ancestry into Ireland and Iceland (Margaryan et al., 2020).

Although substantial injection of Y-chromosomal lineages from Denmark into eastern England has long been attested (Weale et al., 2002), it has proven challenging to distinguish earlier Anglo-Saxon immigration from later Danish conquests that led to the creation of the Danelaw, or indeed to locate a clear genetic signal of the latter (Leslie et al., 2015; Margaryan et al., 2020). A recent report of possible traces of male-specific genetic contributions specifically in the Danelaw region (Lall et al., 2021) may point to a way forward. Even so, more work is required to establish male differential reproduction in the wake of the Danish occupation.

The study by Margaryan et al. (2020) confirms earlier findings of significant Norwegian admixture into Ireland (Gilbert et al., 2017) against a report of a lower contribution (Gilbert et al., 2019). Yet once again the question remains whether or to what extent this Norse presence interfered with reproduction by local (Gaelic) males or otherwise increased male variance in reproductive success. The modern paucity of Norse-derived
chromosome haplotypes may but need not point to a relatively modest impact of Viking activities (contra McEvoy et al., 2006): genetic drift due to small patrilineal effective population size or an abatement of Norse status after their early successes offer alternative explanations (Byrne et al., 2018). The last point is particularly worth considering: the genetic legacy of aggressive invaders and settlers depends not only on their initial impact but also on the continued preservation of competitive advantage, which was not always the case.

At first blush, Iceland presents a clearer scenario of Norse male dominance and Gaelic subordination. Among present-day Icelanders, about three quarters of male ancestry is Scandinavian (alongside 20–25% Gaelic, i.e. Scottish and Irish) whereas close to two thirds of female ancestry is Gaelic (Helgason et al., 2000a, 2000b). This situation may have come about in various ways: predominantly Gaelic women may have followed predominantly Norse men to Iceland, whether compelled by force or attracted by male resources; higher-status Norse men may have out-reproduced non-Norse settlers; or both. But as so often the devil lies in the details: an aDNA study of 25 individuals (20 men and 5 women) from a first-generation settlement reveals no significant difference between male and female ancestry shares (Ebensersdóttir et al., 2018). To be sure, we cannot expect any one community—and especially one so deprived of women—to reflect overall averages: even so, it would be helpful to obtain additional information from similar settings in order to compare historical conditions to the genomic profile derived from the current population. (By the authors’ own admission, the latest basiracranial study of settlement-era human remains by Plomp et al., 2021 that suggests sex-balanced ancestries cannot control for potential effects of male variance in reproductive success.)

From the perspective of this survey, the most striking finding from that period concerns the reproductive consequences of home-grown stratification rather than of foreign takeovers. Thus, a star cluster in Ireland that goes back some 1,500 years reflects a lineage of unusual long-term fitness (Moore et al., 2006). It has been tentatively linked to the Uí Néill, the “ancestors of Niall,” a Gaelic royal lineage of the seventh to eleventh century, a period when polygyny and concubinage were practiced by elite men. Members of this lineage continued to enjoy high status, and up to the early modern period, most ruling families in the northern parts of Ireland were connected to it. Thanks to emigration to America, some two to three million men today descend from that lineage.

The movement of Mongol and Turkic groups of out Central Asia represents some of the most notable (and frequently violent) migrations of the medieval period. Given cultural tolerance of polygyny in these populations, these transfers provided ample opportunity for differential reproduction. The Mongol invasions, which routinely involved mass slaughter, left their genetic mark on the current populations of Central Asia and Russia (Bai et al., 2014). Due to strong Turkic involvement in the Mongol expansion, the spread of Turkic ancestry may to some extent have been a function of the same process (Yunusbayev et al., 2015). However, it remains unclear to what extent language replacement via elite dominance—whereby more powerful Turkic immigrants spread their language across local populations—was accompanied by analogous genetic expansions. Genetic studies of present-day Turkey point to similar rates of male and female Turkic admixture, a finding inconsistent with the notion of male-biased immigration and reproductive success (Di Benedetto et al., 2001; Hodoglugil & Mahley, 2012). Near the end of the Ottoman period, polygyny was far less common in Anatolia than in the Arab provinces: it is possible that the same had already been true in previous centuries.

As with medieval Ireland, the strongest support for differential reproductive outcomes comes from elite contexts. The most famous finding is that some 8% of all men in Central Asia today belong to a Y-chromosome lineage that originated in Mongolia about a millennium ago (Zerjal et al., 2003). This proliferation was originally linked to the paternal ancestors of Genghis Khan and the extraordinary reproductive success he enjoyed and that would continue for his male descendants who inherited high status and attendant reproductive opportunities. This scenario has more recently been questioned: Wei et al. (2018) find that this cluster originated (some 900 years ago) more broadly from the Mongol Niru’un clan rather than narrowly from Genghis Khan’s own patriline. Yet even this revision is fully consistent with the notion that imperial expansion was associated with privilege and reproductive advantage.

Two other star clusters from between 700 and 1100 share the same background of Altaic-speaking steppe populations. One of them, centered on the Amur basin, awaits specification. The other, spreading out of northern Manchuria and Inner Mongolia, was initially dated to the sixteenth century and attributed to the paternal ancestors of the founder of the Manchu Qin dynasty, whose descendants enjoyed hereditary elite status: their ranks swollen to 80,000 members by the end of the dynasty, they received emoluments and engaged in concubinage (Xue et al., 2005). This reconstruction was undermined by a re-dating of the lineage’s origin to around 700, which requires a different explanation (Balaresque et al., 2015). In view of their timing, geographical origin and subsequent spread, either one or both of these clusters might be associated with the Mongol empire of the Liao dynasty that was established in 916 and controlled Manchuria and Mongolia. Whatever their precise circumstances, these star clusters represent a shift away from the earlier instances mentioned above, which were rooted in agrarian societies, and toward steppe populations as their political systems scaled up and produced more stable elite lineages.

The pandemics and violent interventions that accompanied the European takeover of the Americas caused massive Indigenous die-offs, and colonialism, chattel slavery and other forms of bondage created and sustained extreme inequalities of status, wealth and power. Taken together, these processes offered European settlers extraordinary opportunities for procreation by means of resource-biased mating practices and sexual predation. Genetic studies have revealed the scale of differential reproduction.
In Mexico, the male European contribution to Mestizos ranges from 50 to 80% whereas women’s ancestry is on average more than 90% Native American (Martínez-Cortés et al., 2012; Martínez-Cortés et al., 2013 for an even stronger signal than Kumar et al., 2011). In Panama, merely 22% of male ancestry is indigenous, as opposed to most female ancestry (Grugni et al., 2015). However, chronology can complicate the picture: Spanish genetic admixture in Peru seems to date primarily from after 1800 (Harris et al., 2018).

As a particularly intense form of subordination, New World slavery served as a conduit of status-biased male reproductive success. In the United States, male European admixture into the African-American gene pool appears to have occurred prior to the abolition of slavery, a finding that is consistent with the historical record regarding sexual coercion by slaveholders and concubinage with enslaved women. Going beyond earlier work that showed a much higher European genetic contribution for the Y chromosome than for the X chromosome or the mtDNA of contemporary African-Americans (e.g., Lind et al., 2007), a large study of data gained from the personal genomics company 23andMe found that African-American ancestry is on average 73% African and 24% European. Yet those means conceal large sex imbalances: about 5% of the ancestors of African-Americans were European women and 19% were European men (Bryc et al., 2015).

The scale of European male genetic contributions vary across the Americas. Among people of African descent, female ancestors from Africa generally outnumber males ones: the genetic contribution of male ancestors of European descent replaced the latter’s. The scale of this phenomenon differs greatly between regions, from a relatively modest bias in British-colonized America (of 1.5 to 2 African women for every African man contributing to the current gene pool) to more extreme ratios of anywhere from 5 to 17 African women for every African man in Latin America (Micheletti et al., 2020). This reflects both demographic and cultural variation, including male death rates, incentives for reproduction under slavery and “whitening” marriage policies, all of which differed by region. Once again, this highlights the importance of understanding the proximate mechanisms that mediated the overall trend of European male genetic hegemony.

The primary take-away lesson of this rapid survey is that the genetic evidence is extraordinarily rich and promising, that ever more sophisticated research techniques are making it yield ever more detailed information, and that its historical interpretation poses big challenges. While violent population transfers and conquests repeatedly generated reproductive advantages for male dominants that resulted in the observed male-biased replacement of genetic ancestry, this was not always the case. It is hard to identify status-biased reproductive inequalities within dominant groups.

The proximate mechanisms that precipitated shifts in genetic ancestry are often opaque, especially in pre-literate settings such as the putative Yamnaya expansion. Among geneticists, that particular process has prompted anodyne truisms such as “males from populations with more power tend to pair with females from populations with less” and “[t]he Yamnaya expansion also cannot have been entirely friendly” (Reich, 2018b, pp. 137–8, 239). Across the disciplinary divide, archaeologists, desperate to avoid any perceived association with noxious pre-1945 images of a superior “Aryan” warrior race, call for nuance and caution in assessing the underlying historical dynamics (e.g., Furbolt, 2018). As a result, we lack a coherent transdisciplinary narrative of what actually happened.

For later periods, connections between genetic shifts and documented historical events tend to become more apparent. However, as the debates over several star clusters show, even fairly dramatic examples of status-biased male fitness can prove difficult to tie to specific historical characters or events. Rarely are the historical sources as clear about the drivers of ancestry shifts as in the case of New World slavery: yet even for Blacks in the Americas, massive variation in ancestry ratios highlights the need to understand the regionally specific configurations of circumstances.

In most contexts, the relative significance of coercion (of male competitors and females mates) and resource concentration (in outcompeting fellow males and attracting females or those who made arrangements on their behalf) is impossible to gauge. It may be true that this distinction matters more to historians than to evolutionary psychologists who are more likely to focus on the shared fitness-related functions and effects of these strategies. Even so, we need to strive for properly consilient historical accounts of differential reproductive success, an aspiration thwarted by the self-defeating disengagement of the academic Humanities from the Life Sciences.

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