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Kinship, Marriage, and the Genetics of Past Human Dispersals

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Abstract

The extent to which colonizing farmer populations have overwhelmed or "replaced" indigenous forager populations, as opposed to having intermarried with them, has been widely debated. Indigenous-colonist "admixture" is often represented in genetic models as a single parameter that, although parsimonious and simple, is incongruous with the sex-specific nature of mtDNA and Y-chromosome data. To help interpret genetic patterns, we can construct useful null hypotheses about the generalized migration history of females (mtDNA) as opposed to males (Y chromosome), which differ significantly in almost every ethnographically known society. We seek to integrate ethnographic knowledge into models that incorporate new social parameters for predicting geographic patterns in mtDNA and Y-chromosome distributions. We provide an example of a model simulation for the spread of agriculture in which this individual-scale evidence is used to refine the parameters.

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Abstract   The extent to which colonizing farmer populations have overwhelmed or "replaced" indigenous forager populations, as opposed to having intermarried with them, has been widely debated. Indigenous-colonist "admixture" is often represented in genetic models as a single parameter that, although parsimonious and simple, is incongruous with the sex-specific nature of mtDNA and Y-chromosome data. To help interpret genetic patterns, we can construct useful null hypotheses about the generalized migration history of females (mtDNA) as opposed to males (Y chromosome), which differ significantly in almost every ethnographically known society. We seek to integrate ethnographic knowledge into models that incorporate new social parameters for predicting geographic patterns in mtDNA and Y-chromosome distributions. We provide an example of a model simulation for the spread of agriculture in which this individual-scale evidence is used to refine the parameters.

Understanding the processes through which populations grow and disperse is crucial to the study of human history and diversity and forms a major topic in anthropology and other related disciplines. A key problem is determining the extent to which colonizing populations (e.g., modern humans, Neolithic farmers, European colonists) overwhelmed or "replaced" native populations (e.g., Neanderthals, hunter-gatherers, non-European indigenous societies), as opposed to having integrated into or intermarried with them. These issues have been debated by numerous researchers in a variety of different historical and regional contexts, but no consensus has yet been reached about whether or not it is possible to discern any general patterns. Here, we aim to contribute to a more sophisticated understanding of human migratory activity by integrating data drawn from several disciplines, namely, archaeology, ethnography, and human genetics.

Our critique focuses on the highly influential wave of advance model of human dispersals, as first developed by Ammerman and Cavalli-Sforza (1984). We argue that this model is not equipped to consider complex intermarriage between indigenous and colonizing groups (cf. Armelagos and Harper 2005). Although the

parsimony and simplicity of the wave of advance model were its big advantages in the era of analytical modeling by means of differential equations, the availability of computer simulation (cf., Barbujani et al. 1995; Thomas et al. 2006) makes it possible to introduce simple sex-specific parameters for intermarriage and reproductive success into more realistic models, with crucial effects on the predictions for geographic patterns in mtDNA and Y-chromosome distributions.

Wave of Advance Model

The wave of advance model describes both the diffusion of a novel mode of subsistence and the genetic impact made by immigrant groups. Simple and generalizable, the model was originally developed by Fisher (1937) to represent the spread of advantageous genes, and it has been attractive to modelers of past human dispersals because it provides mathematically detailed predictions about demographic spread over time, with equations that unambiguously characterize the hypothesized migratory activity (see Armelagos and Harper 2005).

Used to explain the demic diffusion of prehistoric populations, the engine for dispersal by the wave of advance has two components. The first component, logistic growth, is expressed as

$$\frac{dp}{dt} = ap\left(1 - \frac{p}{M}\right) \tag{1}$$

(Ammerman and Cavalli-Sforza 1984: 154), where p is the population density, a is the intrinsic growth rate of the population, and M is the maximum population density that can be reached. Over time, logistic growth forms an S-shaped curve, that is, one that begins exponentially, slows to nearly linear growth, and then asymptotically approaches a constant population.

The second component of the wave of advance is random movements of the individual components—mathematically analogous to the diffusion of particles in a gas—which are combined with logistic growth to predict the change in population density p over time. For a one-dimensional distance x, this component can be expressed as

$$\frac{dp}{dt} = ap\left(1 - \frac{p}{M}\right) + m\frac{d^2p}{dx^2} \tag{2}$$

where m is a measure of migratory activity (distance/time). This partial differential equation models an advancing wave of population (Figure 1) with no net change in population density at the origin (where out-migration balances in-migration) and the most rapid growth in the wave front (out-migration exceeds in-migration), which advances from the origin at a rate of $2(ma)^{1/2}$ (Ammerman and Cavalli-Sforza 1984: 154; Fisher 1937). Hence the spread rate increases as either migration activity m or growth rate a increases (or both m and a increase).

Most varieties of the wave of advance model, also known as demic diffusion, use an equation basically equivalent to Eq. (2), whether exploring solutions
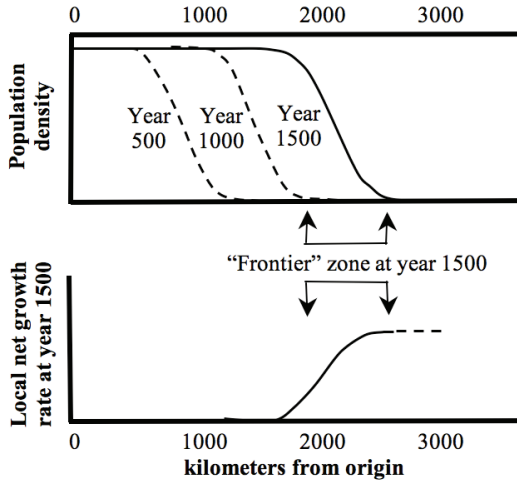
Figure 1. Relationship between distance and local population growth in the wave of advance model. The diagram shows how population densities increase primarily within the "frontier" zone. Behind the wave front, population densities are stable and high. After Ammerman and Cavalli-Sforza (1984, Figure 5.5).

in one dimension (Aoki et al. 1995; Pinhasi et al. 2005) or performing computer simulations in multiple dimensions [e.g., Davison et al. 2006, Eq. (2); Eswaran 2002, Eq. (1)]. Concerning human genetic data and models, demic diffusion has become a basic null hypothesis (e.g., Barbujani and Goldstein 2004; Chikhi et al. 2002; Cordaux et al. 2004; Currat and Excoffier 2005; Ray et al. 2005; Semino et al. 2004; Wen et al. 2004). Other genetic models use subtly different modes of movement (e.g., Figure 2), but in general the underlying rule is that populations spread through short undirected movements of asexual individuals.

The wave of advance model makes testable predictions given changes in initial population density p_0, intrinsic growth rate a, and migratory activity m. For example, if the growth rate a is such that a population doubles every 18 years and if the migratory activity m is 18 km per 25-year generation, then the predicted advance rate is 1 km/year (Renfrew 1987: 129). In terms of its advance in linear, radial distances on the continental scale, this rate roughly fits the radiocarbon record for Neolithic Europe (Pinhasi et al. 2005). On a more detailed scale, however, the fit is much worse. The Neolithic spread 1,000 km from western Hungary to the Rhine in a few centuries (e.g., Dolukhanov et al. 2005), and along the Mediterranean coast of southern Europe the spread was even faster (Di Giacomo et al. 2004; Zilhão 2001). Although m or a or both might be adjusted to fit the wave of advance model to dispersals in each specific region, this fine-tuning could be argued to compromise the explanatory power and predictive utility of the model.
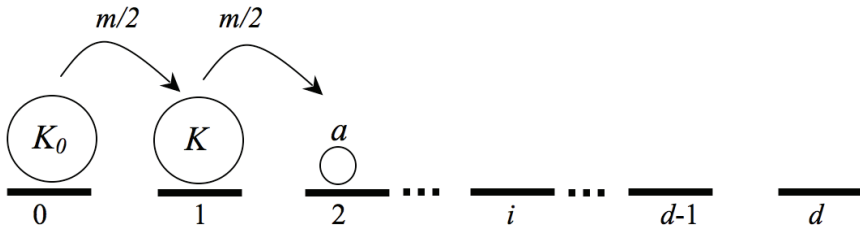
Figure 2. A single time step in the colonization model of Liu et al. (2006). The model begins with an ancestral population at location 0, which has carrying capacity K_0. At each time step, this population sends a proportion of $m/2$ migrants to the neighboring site. The individuals in this neighboring deme reproduce by logistic growth, with a growth parameter a. Once a population i has reached the carrying capacity K_i of its deme, it starts sending migrants to its two neighboring sites. After Liu et al. (2006, Figure 1).

Some investigators argue that archaeological evidence for Neolithic population densities and growth rates do not really fit the wave of advance model. Demographic analyses of skeletal samples indicate population growth at the arrival of the Neolithic in various places (Bocquet-Appel 2002) but not with the timing or a rate sufficient for a wave of advance. Bocquet-Appel (2002) demonstrated a clear demographic transition, characterized by an increase in fertility rates, at the onset of the Neolithic. However, skeletal samples analyzed by Bocquet-Appel (2002) were lacking from the first part of the Neolithic dispersal (Anatolia to southeastern Europe), and Bocquet-Appel (2002: 646) acknowledged the difficulty in resolving a range of possible mechanisms that have been suggested by archaeologists, such as leapfrog colonization, elite predominance, infiltration, and folk migration (e.g., Andel and Runnels 1995; Zvelebil 2006; Zvelebil and Lillie 2000).

On a more general level, wave of advance models are not helpful in resolving what it was that actually spread. The population growth expressed in Eq. (1) could just as well involve native groups as incoming colonists. An increase in farming settlements, for example, could indicate the aggregation of indigenous groups converting to agriculture rather than intrinsic growth of colonizing populations. In particular, the availability model (Zvelebil 2006; Zvelebil and Rowley-Conwy 1984) for the adoption of agriculture by foragers, in contact along a frontier with farmers, predicts the logistic growth of Neolithic assemblages (as opposed to population in the wave of advance model). The model involves slow adoption during an initial availability phase followed by a rapid substitution phase and finally a slow consolidation phase [Zvelebil and Lillie 2000; but see Shennan (2009) (this issue) for an alternative interpretation of the evidence used to support this model]. In other words, the exact same archaeological pattern predicted by the wave of advance—an S-shaped curve in the increase of Neolithic remains over time—could just as easily fit a model of indigenous adoption, as originally suggested by Ammerman and Cavalli-Sforza (1984: 134–135), who pointed out

that "these two models of explanation need not be mutually exclusive; their combination is indeed possible, and in some areas both are likely to have contributed to the process" (134–135).

To resolve these issues, Renfrew (2001) has called for a "second generation of wave of advance model" that explicitly incorporates the demographic consequences of contact and intermarriage between incoming and local populations. Specifically, he proposes that the spread of the Neolithic occurred through a series of stages, whereby the input of the "original" farmer genes tails off exponentially the farther the wave advances. This is because each "new" farming group will include not only converted foragers who married into the community but also the descendants of hunters and gatherers converted in the adjacent source area from which farming spread. To some extent, these ideas were anticipated by Ammerman and Cavalli-Sforza in their 1984 book, which included simulations of the effects of gene flow and acculturation among populations on the "demic cline" of the frequencies of genes associated with original farming groups over geographic space (Ammerman and Cavalli-Sforza 1984: 116–130). However, these models represented colonist-indigenous admixture as a single parameter that now, 25 years later, needs to be elaborated on in light of growing evidence for the sex-specific and culture-specific character of intermarriage patterns.

Ethnographic, archaeological, and genetic data show that movement and mating strategies of men and women in foraging and farming societies are inevitably different. These differences can be captured by introducing separate parameters for the reproductive success of incoming males, indigenous males, incoming females, and indigenous females. We construct a quantifiable grid of predictions about the relative values of these four parameters, which we believe provides a useful basis for future models of genetic admixture among farmers and foragers in prehistory.

Archaeological and Ethnohistorical Evidence

As Bellwood (2005: 27) showed with data from Murdock (1967), the world's societies have overwhelmingly relied on either farming or hunting and gathering, as opposed to transitional values such as 60% farming and 40% hunting-gathering. For this reason, archaeologists have hypothesized that forager-farmer "frontiers" existed in prehistory, where such groups were relatively distinct. Evidence from prehistoric and historic Europe suggests that farmer-forager frontiers have often been stable and long-lasting. Examples include the coexistence of Germanic people and the Fenni mentioned in Tacitus's *Germania*, Danubian Neolithic and Mesolithic Ertebølle groups (Verhart and Wansleeben 1997), Scandinavians and Lapps (Mulk and Bayliss-Smith 1999: 385), and Mesolithic and Neolithic communities in Iberia (Arias 1999). In the Black Sea region, a frontier between the Bug-Dniester Mesolithic and the Cris-Körös Neolithic lasted perhaps 1,500 years, from about 6100 BC to 4300 cal. BC (Dolukhanov et al. 2005; Zvelebil and Lillie

2000), although in fact the Cris-Körös farmers themselves may been descended from local foragers.

Outside Neolithic Europe, forager-farmer frontiers are evident in many regions and time periods, such as the Torres Strait (Davidson 1989), Iron Age Africa (Denbow 1984; Thorp 2000), North America (Schrire 1984: 14–17), and Southeast Asia (Griffin 1984; Headland and Reid 1989; Junker 1996). In the ethnographic record, discrete farmer-hunter boundaries have been observed with the San Bushmen (Gordon 1984; Parkington 1984) and the Australian Aborigines in contact with Europeans (Davidson 1989).

As well as being relatively stable, forager-farmer frontiers were also permeable, with farmers and foragers often engaged in mutually beneficial exchanges of goods, services, and people (e.g., Zvelebil 2006). Indeed, because hunter-gatherer groups were typically highly mobile and maintained social networks over large geographic areas, they were well placed to exploit the new opportunities that arose as farming communities appeared and actively sought trade in newly settled areas (Zvelebil 2006). For example, it appears that hunter-gatherers of the Philippines did not move into the tropical forest until they had established a symbiotic relationship with cultivators, trading wild produce with local farmers and overseas traders (Bailey et al. 1989; Headland and Reid 1989; Junker 1996: 390). Pastoralists in particular benefit from exchange links with groups practicing other forms of production, including farmers and/or foragers (Kassam and Bashuna 2004). Under particularly difficult conditions, pastoralists in Africa have been observed to join hunter-gatherers, with subsequent generations returning to pastoralism (Hodder 1982: 97–98; Kassam and Bashuna 2004: 204). In the Kalahari of southern Africa, exchange between hunter-gatherers and agropastoralists was such that neither group evolved independently of the other, yet their separate identities apparently lasted for 1,500 years, into the 19th century (Denbow 1984), when Kalahari foragers made new trade links with Western traders (Gordon 1984). Hence the forager-farmer frontier may have actually enhanced interethnic distinctions, groups specialized in complementary modes of production for trade across it (e.g., Griffin 1984; Headland and Reid 1989; Hoffman 1984; Junker 1996).

Genetic Evidence

In samples of modern Europeans, early genetic studies worked with gene markers such as blood groups, plasma proteins, enzymes, and antigens, which were interpreted to reflect demic diffusion from the Middle East into Europe [e.g., Sokal et al. (1991) and reviews by Armelagos and Harper (2005) and Cavalli-Sforza (1998)]. Most evidence from Y-chromosome DNA, which is inherited paternally, was also interpreted in terms of demic diffusion from the Near East (Chikhi et al. 2002; King and Underhill 2002). In contrast, studies of mitochondrial DNA (mtDNA), which is maternally inherited, point to six distinct phylogenetic lineages in Europe, five of which have been interpreted to originate

in late Upper Paleolithic Europe (e.g., M. Richards 2003; M. Richards et al. 2000; Sykes 1999).

On one hand, the different results may just be methodological, as these mtDNA studies used a phylogeographic approach, which has been strongly criticized (e.g., Goldstein and Chikhi 2002; Nielsen and Beaumont 2009). The issue is broader than just complications regarding mutation rates and nonrecombination (e.g., Eyre-Walker 2006). The basis of this critique is that, strictly speaking, phylogeography is merely a method of reconstructing a tree or network of genetic relations. This reconstruction becomes highly misleading if what is essentially a random outcome of a stochastic population genetic process is directly equated with real geographic population movements (Nielsen and Beaumont 2009). Tests of a popular phylogeographic method against simulated data sets suggested that the method can falsely identify a geographic pattern (such as isolation by distance or demic diffusion) from what was actually an entirely randomly mating simulated population (Panchal and Beaumont 2007). The further back in time the phylogeographic reconstructions are made, the more uncertain their resolution from real-world genetic data becomes (e.g., Chikhi et al. 2001).

On the other hand, taken at face value, much of the mtDNA evidence, repeatedly presented to root European maternal ancestry in the European Mesolithic or before (e.g., M. Richards 2003), has been invoked to support indigenous adoption of farming by hunter-gatherers, whereas the Y-chromosome evidence suggests farming borne by colonizers. The probable solution to this apparent discrepancy was noted more than ten years ago by Cavalli-Sforza and Minch (1997: 250), who explicitly considered the roles of matrilocality and patrilocality.

> One of them is a tendency, at marriage, for women to migrate more than men . . . in anthropological terminology, marriage is more often than not patri- or virilocal. . . . This makes women, on average, genetically more mobile than men, even though their average daily displacement may be less than that of men. Another factor that may have been especially active during the spread of farmers is female hypergamy. . . . Both patrilocality and hypergamy, as well as abduction of women . . . can increase the gene flow tied to women's migration and hence of mtDNA, over that of autosomes or Y chromosomes. Most probably for the same reasons, Y chromosomes seem to show a greater geographic clustering than is seen in mtDNA trees.

Cavalli-Sforza (1998) pointed out that genetic inferences extrapolate backward from modern populations and are sensitive to sex-specific biases in intermarriages between genetic groups. This accords well with what archaeologists have found (e.g., Bellwood 2005: 260; Bentley et al. 2003), but many geneticists have tended to dismiss consideration of prehistoric kinship as more or less ad hoc with respect to genetic modeling (e.g., M. Richards et al. 1997). Admixture between farmers and hunter-gatherers is still often characterized simply as a single variable

between 0 and 100%, without reference to sex differences (e.g., Belle et al. 2006; Currat and Excoffier 2005; Eswaran 2002).

Recently, however, there have been exciting new explorations of kinship effects on genetic patterns. To characterize long-term sex-specific behaviors, an increasing number of research groups have compared the diversity of Y chromosomes and mtDNA in the same populations or at least in the same regions (e.g., Hamilton et al. 2005; Kayser et al. 2001; Pérez-Lezaun et al. 1999; Quintana-Murci et al. 2004; Seielstad et al. 1998). Seielstad et al. (1998) concluded that patrilocality has prevailed over much of Europe's prehistory, because modern Y-chromosome variants are more geographically localized than mtDNA variants are; as geographic distance is increased, differences in Y chromosomes increase, whereas mtDNA tends to remain similar [although see Thomas et al. (2002) for a contrary example in Jewish populations]. Similar geographic comparisons of mtDNA versus Y-chromosome distributions have indicated that males participated more highly in the spread of Han Chinese and Iranian Parsi migrations (McElreavey and Quintana-Murci 2005; Wen et al. 2004), whereas women played a greater role in central Asian migrations (Calafell et al. 2000; Pérez-Lezaun et al. 1999). Quintana-Murci et al. (2004), for example, found that mtDNA haplogroup M, which is associated with Indian populations, has a high frequency among modern Parsis (55%) yet is rare in the combined Iranian sample (>2%). This finding suggests asymmetric mating between Iranian males and local Gujarati women, leading ultimately to the loss of Iranian mtDNA in Gujarat (Quintana-Murci et al. 2004).

With the aim of informing genetic models, we now discuss, using evidence from archaeology, genetics, and ethnography, how kinship rules affect the movements of men and women.

Inherited Property Rights and Marriage.   Inheritance and marriage systems can be divided into numerous types, the most basic of which are patrilineal and matrilineal. Patrilineality is usually associated with female exogamy, particularly in well-documented African societies such as the pastoralist Nuer (Evans-Pritchard 1940) and the cultivator Tiv (Nigeria), where the changing residence of women upon marriage serves to ally communities.

Matrilineality falls into two important categories. The first consists of matrilineal systems in which men still retain rights to their natal descent group, such as the Bemba and Asante of Africa (Fortes 1970; A. Richards 1939) and the Hopi of the U.S. Southwest (Eggan 1950). Both men and women may change residence under this system, but on marriage a man is required to live in his wife's village for a period, whereas women frequently remain in their natal group all their lives (Eggan 1950: 54; Titiev 1972: 46). In the second category of matrilineality, men depend on their wives for rights to land, as in Yuan villages of Lampang Province, northern Thailand (Pannengpetch 1984), and the Iroquois of North America (Snow 1994). Because residence is matrilocal and land is evenly divided among daughters, men have no reason to sustain ties with their natal group and tend to travel widely to hunt, trade, and conduct war.

Cross-cultural studies indicate that these systems are closely linked to patterns of resource exploitation and accumulation [an oft-quoted statistic is that women control the labor in 50% of horticultural societies, whereas men do so in more than 80% of agricultural societies (Martin and Voorhies 1975: 283)] such that matrilineal inheritance is more common among subsistence cultivators and hunter-gatherer-fisherfolk (Hage and Marck 2003; Marlowe 2004) and patrilineality is strongly favored among pastoralists and intensified cultivators (Holden and Mace 2003; Marlowe 2004). For this reason, inheritance rules can change over time as conditions change, as when matrilineality gave way to patrilineality as pastoralism spread into African horticultural societies (Holden and Mace 2003).

Inheritance systems also have specific effects on the movement of men and women. Among farmers, inheritors of land have little incentive to move, leaving noninheritors to be more mobile. Because kinship-based wealth inheritance correlates with reproductive success (e.g., Mace 1996), it is genetically relevant. Patterns can be archaeologically visible: Unigeniture (in which all property passes to a single heir) is characterized by dispersed farms (Rogers 1991: 88), whereas partible inheritance is more likely to result in nucleated villages (Friedl 1974; Layton 2000; Netting 1981).

A More Flexible Genetic Model.   It is possible to develop several hypotheses to account for the persistence of forager mtDNA and farmer Y-chromosome DNA in Europe, and there is much to be gained from a systematic consideration of the possible permutations. As a general model, we find great promise and flexibility in the model proposed by Thomas et al. (2006). It begins with two populations, A ("incoming") and B ("indigenous"), and several parameters: S, the reproductive advantage of population A with respect to population B; D, the proportion of people (per generation) in population A that marry into population B, and U, the proportion of population B that marry into population A.

This model is highly flexible and can cover many different situations. For simplicity and by parsimony, Thomas et al. (2006) assumed that $U = D$, which together become the intermarriage rate, which is then varied to produce their simulation results (Figure 3a). The results show convincingly that when there is a significant reproductive advantage to being in the elite class, the predominance of incoming genes persists, even with relatively high intermarriage rates. By assuming that $U = D$, Thomas et al. (2006) essentially tested their model in the same way as previous models: by means of a universal intermarriage (admixture) rate, which is both symmetric between colonists and indigenous groups and symmetric between sexes. Their model, however, provides an excellent framework for testing asymmetries. Thomas et al. (2006) did test cases where $D > U$ and $U > D$ and found that the reproductive parameter rather than the intermarriage rate determined the time to reach a near-ceiling value (Figure 3b), although "the ceiling value itself is strongly affected by the intermarriage rate" (p. 2564).

Following Cavalli-Sforza (1998), we advocate that model parameters be made sex-specific, i.e., A_f and A_m and B_f and B_m for females and males in the incoming and
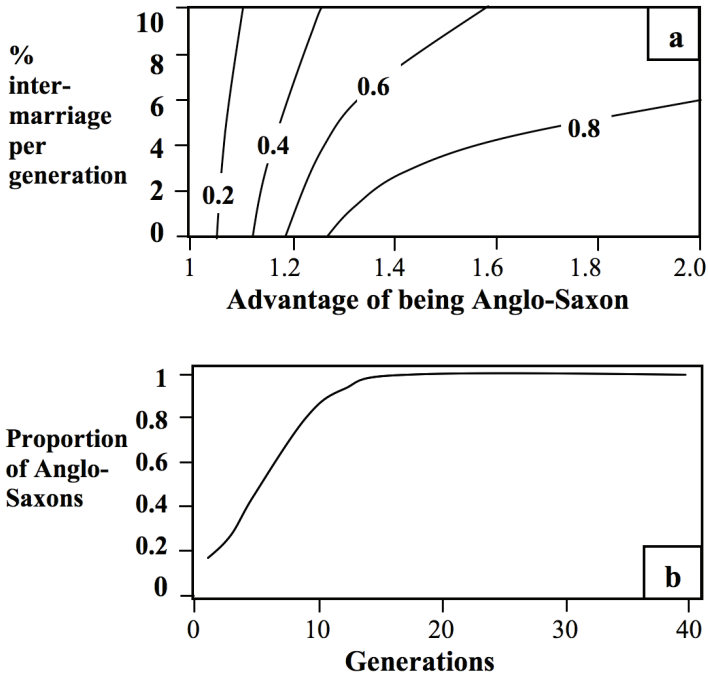
Figure 3. Predicted genetic consequences of Anglo-Saxon "apartheid" as modeled by Thomas et al. (2006). (a) Assuming an initial population of 10% immigrants, each curve represents a combination of intermarriage and selective advantage values that result in the proportion of "Anglo-Saxon" Y chromosomes after 15 generations, as labeled on each curve. (b) Change through time in the proportion of the "Anglo-Saxon" ethnic group, assuming a selective advantage of 1.5. After Thomas et al. (2006, Figures 1b and 4b).

indigenous populations, respectively. Similarly, we would suggest that U and D be sex-specific, with U_f and U_m for indigenous females and males, respectively, marrying into the incoming population and D_f and D_m for incoming females and males, respectively, marrying into local groups. These are a lot of parameters, but rarely would we need to use all of them because various forms of evidence allow generalization about kinship in particular settings. For example, by using historical evidence concerning Anglo-Saxons, Thomas et al. (2006) could assume that the majority of intermarrying individuals represented by population A were males and that those represented by population B were females; that is, the predominant form of intermarriage was between incoming males and indigenous females. In fact, hypergyny (a situation in which women try to marry into the more advantaged class) has arguably prevailed in many past human dispersals, as we discuss later. Concerning the other possibilities (Table 1), we will attempt to make simplifying generalizations based on ethnographic evidence.

Table 1. Four Categories of Sex-Specific Colonization Processes[a]

Predominant Intermarriage	*S*	U_f	U_m	D_f	D_m	*Cultural Example*
Indigenous females enter colonizing population	≤1	High	Low	~0	~0	Neolithic Europe; Anglo-Saxons in Britain; colonial Australia
Colonist males enter indigenous population	>1	Low	~0	~0	High	Norse of the Viking era; French colonists in North America; (pre)historic traders in Thailand
Indigenous males enter colonizing population	<1	Low	High	~0	~0	Hunter-gatherers working for farmers
Colonist females enter indigenous population	?	Low	Low	High	~0	Iroquois

a. With reference to the model of Thomas et al. (2006), S is the reproductive advantage of colonizers with respect to indigenous groups, U_f and U_m are the proportions of indigenous females and males, respectively, marrying into the incoming groups, and D_f and D_m are the proportions of incoming females and males, respectively, marrying into local groups.

Four Permutations: Ethnographic and Archaeological Evidence

As discussed, the ethnographic and archaeological evidence demonstrates that forager-farmer frontiers are fluid not just in terms of objects of exchange across the divide but also in terms of people (Headland and Reid 1989; Spielmann and Eder 1994). This exchange can occur in both directions, based on marital choices, ecological constraints, and economic incentives. The key for genetic models is any regularity in intermarriage pattern. If we assume, for simplicity's sake, that movement of members of one sex into the other population reduces the reproductive success of the sex "left behind," four permutations, each with different consequences, can be envisaged: (1) indigenous females enter the colonizing population, (2) male colonists (or their genes) enter the indigenous population, (3) indigenous males enter the colonizing population, or (4) female colonists enter the indigenous population. We consider each permutation separately.

Indigenous Females Enter the Colonizing Population.   The case of colonizing men marrying indigenous women is arguably the most common type of intermarriage in the prehistoric spread of agriculture. The reason is that men are often mobile in colonizing situations, and forager-farmer frontiers often favor forager women marrying farmer men. Furthermore, if small groups of colonizing populations were commonly short of women of reproductive age, then those groups that did intermarry with indigenous women would have had a reproductive advantage

and may even have been the only groups to produce a surviving line of descendants. In terms of an adaptation of the model by Thomas et al. (2006), this would mean that U_f was greater than U_m and that D_f and D_m were potentially negligible.

In terms of reproductive advantage (parameter S), agricultural groups can benefit directly from forager women marrying into the community, both demographically and politically. Sahlins (1961) famously argued that segmentary patrilineages facilitated territorial expansion at the expense of smaller lineages, and Evans-Pritchard (1940) recorded that, among East African pastoralists, small Dinka lineages could become incorporated into a Nuer tribe (see also Kelly 1985). Women, particularly young women, were captured and given in marriage to other Nuer to gain their bride wealth, with few Dinka (less than 2,000) actually killed in the process (Kelly 1985). Dinka men were thus deprived of the women's reproductive capacity. Kelly (1985: 61) estimated that this capacity augmented the Nuer population by 23,250. However, four times as many Dinka of both sexes were incorporated into Nuer tribes as their territory was annexed, losing their Dinka identity through acculturation within two generations (Evans-Pritchard 1940: 221–224).

Southern African oral history records numerous cases of incoming Bantu chiefs making strategic marriages with San hunter-gatherer wives (Jolly 1996). Turnbull (1965) described how sometimes male villagers of the Ituri Forest took a Mbuti wife, but never the reverse. The offspring were considered villagers, and the Mbuti wife "was in a good position to attract meat and honey" (Turnbull 1965: 49). This intermarriage bias changed the political and demographic balance, and Zvelebil and Lillie (2000) argued that as time passed, farmers began to exploit hunter-gatherer territory and procured their own raw materials rather than trading with foragers. The flow of material goods tended to increase over time in the direction from farmers to foragers, as overexploitation typically pushed foragers into unsustainable use of high-ranking resources in competition for prestige materials traded by farmers (Cronk 1989; Layton et al. 1991; Spielmann and Eder 1994; Thorp 2000). In southern Africa in the early 1900s, as Muckogodo hunter-gatherer women married non-Muckogodo pastoralists, livestock became an increasing element of bride wealth. Muckogodo men then became pastoralists in order to get married or traded women to become wealthy. Muckogodo men had to obtain livestock in order to marry (Figure 4). It was less expensive and more common for a Muckogodo woman to marry a non-Muckogodo man than vice versa (Figure 4). Over about half a century, the Muckogodo adopted the Masaii language, built houses, and became pastoralists themselves (Cronk 1989).

As Shennan (2009) (this issue) has shown, ethnographic case studies of demographic processes in contemporary foraging and farming communities can provide useful models for interpreting archaeological data. The studies we have cited support archaeological evidence that suggests that intermarriage with indigenous women may have been the predominant form of marriage altogether for the men in the first colonist groups (Gronenborn 2003). Isotopic analyses of skeletal remains from Linearbandkeramik (LBK) sites in central Europe (Bentley et al. 2002, 2008) indicate that residence patterns among the newly arrived populations
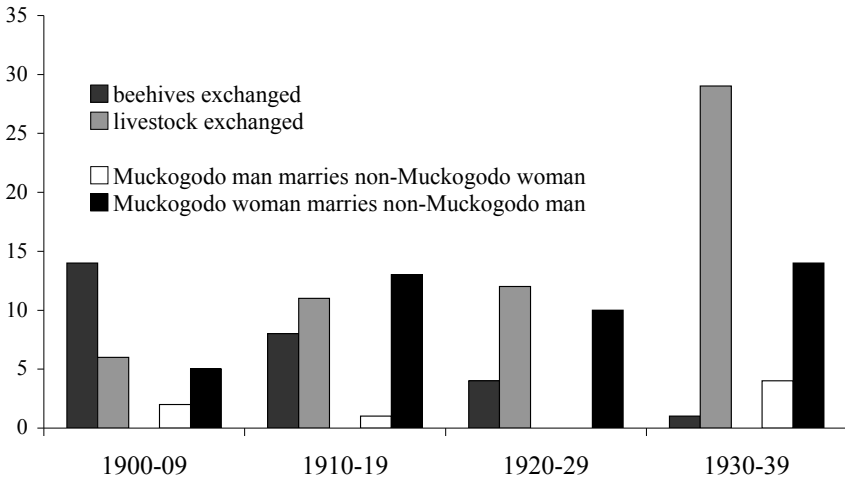
Figure 4. Muckogodo-Masaii marriages in early decades of the 20th century showing the parties involved and the type of bride wealth paid. After Cronk (1989, Figures 2 and 3).

were patrilocal and that some households may even have been nuclear families (Bentley et al. 2008). Evidence of dietary differences between men and women at some of these sites is consistent with the introgression of native hunter-gatherer females into newly arrived farming communities, perhaps reflecting a pattern of intermarriage similar to that observed by Cronk (1989) among the Muckogodo and Masaii (Figure 4).

In Europe, studies of European Y-chromosome and mitochondrial DNA data generally suggest that male lineages are closer to a Near Eastern origin than female lineages, albeit against a pattern of a general decline in the Y-chromosome Near Eastern contribution to less than 20% in Central Europe and to 5–10% in the Baltic region and northern Europe (Zvelebil 2006). Among the range of possible intermarriages, it seems that the greatest reproduction may have occurred between incoming males and indigenous hunter-gatherer females in many areas of early Neolithic Europe (Ammerman and Cavalli-Sforza 1984; Ammerman et al. 2006; Bentley et al. 2002). Ancient DNA studies have been interpreted to suggest that "farmer" females (haplogroup N1a) and "forager" males (lacking haplotype N1a) of early LBK Germany contributed little to the genetic makeup of modern European populations (e.g., Burger et al. 2006; Haak et al. 2005). If we accept that haplogroup N1a is associated with incoming farming populations [but see Barbujani and Chikhi (2006) for cautions, which should include possible random extinction of haplogroup N1a], then this would mean that U_f was greater than U_m and that D_f and D_m were often close to negligible in model terms.

Isotopic analyses are also beginning to support the contention by Cavalli-Sforza and Minch (1997) that prehistoric abduction of women could be significant

to the human genetic history of Europe. At the Neolithic site of Talheim in Germany, where the remains of 34 individuals indicate a community killed in an attack (Wahl and König 1987), isotope signatures suggest that the local community contained no adult females, only males and children (Bentley et al. 2008). It appears that the women of the local community were captured and carried away by the attackers (Bentley et al. 2008). This evidence suggests that patrilocality was firmly a part of LBK kinship by latest LBK time (Talheim dates to ca. 4900 BC) and that patrilocality thus appears likely for the earlier LBK dispersal phase.

Such exploitation does not necessarily lead to hybridization. In Australia an almost womanless European pioneer population exploited (often brutally) an Aboriginal society that allowed the ceremonial exchange of women and treated the offer of sexual favor as a means of hospitality or method of diplomacy (e.g., Roberts 2006). Such offers were misconstrued as prostitution by the settlers who had no intention of recognizing Aboriginal rights to land and were therefore not interested in negotiating alliances (Reynolds 1982: 70; Ryan 1981: 78). As a rule, therefore, Aboriginal women were not incorporated into the dominant society and colonial men were rarely incorporated into the indigenous community. The children born to white fathers and Aboriginal mothers were excluded from elite colonial society, and this coincided with a dramatic decline in the indigenous birth rate [as low as only 6–8 children in three years among about 100 local women, by one 19th-century account (Reynolds 1982: 126)]. By 1863 the Aboriginal population of the state of Victoria had plummeted from 11,500 to less than 2,000 (AAL 1985: 17). Hence, despite the exploitation of native women, their relative lack of reproductive success (high S_f in terms of the model) left them a small genetic legacy compared with colonial women. In the Australian case it did not really matter what U_f, U_m, D_f, and D_m were because whenever intermarriage occurred, ostracism usually meant low reproductive success for any resulting children.

Male Colonists (or Their Genes) Enter the Indigenous Population.   Unlike females, a small number of incoming males can transfer their genes into an indigenous population even though they are in the numerical minority (e.g., Thomas et al. 2006). Contemporary gene frequencies indicate that Genghis Khan has a large number of descendants in continental Asia (e.g., Zerjal et al. 2003). This may have been due either to his personal success in fathering many children or to a lesser but cumulative success among his descendants. Thomas et al. (2006, Figure 3a) showed that, by modeling their reproductive advantage at about 1.4, just 5% Anglo-Saxon immigrants could achieve 50% "Anglo-Saxon" genes in modern England after only 10 model generations. The Norse colonists of the Viking era (ca. AD 800–1200) are another example. Among the Greenlandic Inuit, Bosch et al. (2003) found Y chromosomes typical of European populations, which, combined with non-European mtDNA, indicates "strongly male-biased European admixture" (p. 353) involving Icelandic Norse and/or Danish-Norwegian males. In Ireland, analysis of surnames (which are paternally inherited like Y chromosomes) indicates that only a relatively small number of Viking settlers migrated

to Ireland, presumably intermarrying with indigenous Irish (McEvoy et al. 2006; Moore et al. 2006).

The degree of this kind of intermarriage varies by subsistence and kinship system. In colonial North America, French traders were more likely than English colonists to marry native women because the French depended on native hunting and gathering expertise (Snow 1994: 120–1), whereas English colonists moved as complete families. In 19th-century Taiwan, where the native Taiwanese Saisiyat practiced hunting and gathering within a patrilineal-patrilocal descent system, many famous Saisiyat headmen were adopted Han Chinese, who presumably provided valuable political links with the colonizing population (Hu 2006: 86–87). In Thailand, where a matrilineal kinship prevailed, foreign traders were a source of male marriage partners, often temporary, for the months between the incoming and outgoing monsoon sailing winds, as observed in Pattani (southern Thailand) in 1604.

> When foreigners come there from other lands to do their business . . . men come and ask them whether they do not desire a woman; these young women and girls themselves also come and present themselves, from whom they may choose the most agreeable to them, provided they agree what he shall pay for certain months. Once they agree about money . . . she comes to his house, and serves him by day as his maidservant and by night as his wedded wife. He is then not able to consort with other women or he will be in grave trouble with his wife, while she is similarly wholly forbidden to converse with other men, but the marriage lasts as long as he keeps his residence there, in good peace and unity. When he wants to depart he gives her whatever is promised, and so they leave each other in friendship, and she may even look for another man she wishes, in all propriety, without scandal. [Van Neck (1604: 225), cited in Reid (1988)]

The matrilocal setting for this pattern may extend back several millennia, as indicated by the geography of mtDNA and Y-chromosome distributions (Oota et al. 2001) and strontium isotope analysis of archaeological skeletons (Bentley et al. 2007). Interestingly, genetic evidence indicates that there has been considerable female migration in northern Thailand, even under matrilocality (Hamilton et al. 2005). At Khok Phanom Di (ca. 2000–1500 BC), near the coast by modern Bangkok, a shift to local isotope signatures among female archaeological skeletons is observed at a phase corresponding to about 1700 BC (Bentley et al. 2007). At Khok Phanom Di, the export of pottery made by women, probably by means of maritime trade, could well have instigated a long tradition of local women marrying trader men.

Indigenous Males Enter a Colonizing Population.   We are not aware of any ethnographic cases that describe significant intermarriage of indigenous males into a colonizing group, although male foragers often enter into clientage relations with farmers that might include herding or hunting services in exchange for

agricultural products, working in agricultural fields, or acting as porters for farmer trade (Spielmann and Eder 1994; Thorp 2000). There is often a gender difference in how forager labor is allocated by farmers, such that, for example, women work in farmers' gardens or homes and men clear vegetation or herd animals (Spielmann and Eder 1994). Although foragers may enter into these relationships on an opportunistic basis, they do so on unequal terms and rarely, if ever, establish the sort of long-term reciprocal relationships that might enable them to acquire brides from the host group.

Female Colonists Enter an Indigenous Population.   This scenario has not been frequently observed but could apply to the expansion of the matrilineal Iroquois in prehistoric North America (Sahlins 1961; Snow 1994: 15). Early Iroquois pottery style uses the same technique as that used by earlier people, perhaps indicating absorption of women from the time of the Iroquois' arrival (Snow 1994: 17). The Iroquois raided their neighbors in historic times to capture women, and from the seventeenth century the Iroquois confederation absorbed "hundreds, probably thousands, of refugees and captives from other Indian nations of the north eastern North America" (Snow 1994: 1). With their matrilineal political organization, Iroquois women were not inclined to marry Frenchmen (Snow 1994), yet the Iroquois did capture white and native women. Snow writes that captured white women often preferred to stay with their adoptive Iroquois families because, although white society regarded them as "ruined," as women they had high status among the Iroquois.

Conclusions

Given the potentially incongruous sex-specific nature of mtDNA versus Y-chromosome data from modern populations, it is no longer appropriate to model prehistoric colonist-indigenous intermarriage with a single admixture parameter, as has long been done in demic diffusion (wave of advance) models. Fortunately, computer simulations can potentially incorporate basic aspects of kinship and socioeconomic interaction. Incorporating such new social parameters requires the integration of ethnographic and archaeological evidence, inviting collaboration with anthropologists and archaeologists. As an example, we demonstrated a model (after Thomas et al. 2006) that is adequately specific but still quite flexible and generalizable.

In any case, such models, being extremely general, are not meant to be specific answers but platforms for more focused questions regarding the social contexts of forager-farmer gene exchanges. For example, scenarios in which male or female colonists enter an indigenous population assume, mostly on ethnographic grounds, that colonists entered as elite groups, socially superior to the foragers. However, as Zvelebil (2006) has argued, it may be possible that contacts were not made by elite male groups but by people as traders, negotiated marriage partners, even perhaps social outcasts from their original communities, or individuals unable

to find partners in their home regions. Such population movements would have been much more individualized and socially less damaging to foraging groups, and they would have produced genetic admixtures more balanced between the "Near Eastern" and "European" genetic signatures. Such socially balanced exchanges would also have allowed the local hunter-gatherer communities to adopt farming more readily and undergo population growth typical of the early stages of Neolithic transition and to effect population dispersal themselves, but it would have been the indigenous forager-turned-farmer genes, not the "Near Eastern colonist farmer" genes, that would have spread across Europe (Zvelebil 2006; also see Renfrew 2001). The graduated pattern of Y-chromosome gene variation across Europe would certainly support such a scenario.

Of course, we should not underestimate the difficulties of inferring demographic processes in prehistoric communities from present-day genetic patterns [see Ray and Excoffier 2009 (this issue)]. Indeed, such an exercise is likely to require study of other markers apart from the mtDNA and Y-chromosome data that have been the focus of this paper. Nevertheless, it is exciting to begin incorporating kinship-related parameters in models of human dispersals to differentiate male from female population histories. Archaeological and ethnographic evidence suggests that the relative numbers of foragers and farmers in a given locality are determined by adaptive decision making within the context of co-existing symbiotic subsistence regimes. Cross-cultural evidence suggests that patterns of kinship organization often favor the introgression of female foragers into farming communities. The genetic consequences are not, however, necessarily uniform. Where the farming population is politically dominant, forager males suffer a reproductive disadvantage, but focus on the history of European colonial expansion has perhaps biased our view of the relative status of foragers and farmers where they interact. A stable symbiosis may arise in which hunter-gatherers have comparable reproductive success for many generations, because in fact foragers do not always have lower population densities than neighboring farmers. There are many possibilities, but each is situation-specific. As Cavalli-Sforza (1998) advocated a decade ago, to understand the genetic legacy of human dispersals on a continental scale, we need sex-specific models that accurately represent the individual scale.

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