Hitchhiker's guide to genetic diversity in socially structured populations

L. S. PREMO[1,2]*

[1] Department of Anthropology, Washington State University, Pullman, WA 99164-4910, USA

[2] Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany

Abstract   When selection increases the frequency of a beneficial gene substitution it can also increase the frequencies of linked neutral alleles through a process called genetic hitchhiking. A model built to investigate reduced genetic diversity in Pleistocene hominins shows that genetic hitchhiking can have a strong effect on neutral diversity in the presence of culturally mediated migration. Under conditions in which genetic and cultural variants are transmitted symmetrically, neutral genes may also hitchhike to higher frequencies on the coattails of adaptive cultural traits through a process called cultural hitchhiking. Cultural hitchhiking has been proposed to explain why some species of matrilineal whales display relatively low levels of mitochondrial DNA diversity, and it may be applicable to humans as well. This paper provides a critical review of recent models of both types of hitchhiking in socially structured populations. The models' assumptions and predictions are compared and discussed in the hope that studies of reduced genetic diversity in humans might improve our understanding of reduced genetic diversity in other species, and *vice versa* [*Current Zoology* 58 (1): 287–297, 2012].

Keywords   Cultural group selection, Cultural hitchhiking, Culturally mediated migration, Diversity, Evolution, Genetic hitchhiking

Culture is information acquired through social learning that can lead to variation in behavior (Boyd and Richerson, 1985). Socially transmitted information can affect fitness. For example, culture plays such an influential role in human survival and reproduction that one is hard-pressed to identify another species so dependent upon culturally transmitted information. But cultural traits are not inherently adaptive. Although selectively neutral cultural variation does not affect fitness, it can lend structure to a population, and culturally (or socially) mediated population structure can influence evolutionary dynamics. While the importance of considering the effects of culturally mediated population structure on neutral genetic diversity is apparent for the case of humans, here I argue that it may be important to consider the effects of culturally mediated population structure for a wider range of social animals, including some species of whales and birds.

There is considerable debate over the extents to which cultural transmission and genetic transmission explain regional behavioral variation in some social non-human animals (e.g., see Lycett et al., 2007; Langergraber et al., 2010; Lycett et al., 2010; Langergraber and Vigilant, 2011; Lycett et al., 2011). The present paper does not weigh in on the ultimate cause of regional variation in animal behavior. I work from the generally accepted assumption that cultural transmission plays at least some role in explaining the behavioral diversity we see in some species. I focus on the role that regional variation can play in structuring a population and how socially mediated population structure can, in turn, affect neutral genetic diversity. My goal here is to introduce, and provide context for, a new perspective for explaining reduced neutral genetic diversity in animal populations structured by regional variation in culturally transmitted behavior.

Reduced genetic diversity has been interpreted variously as resulting from bottlenecks in census size, from genetic hitchhiking, or from cultural hitchhiking. The following section provides some background on these processes. Sections 2 and 3 provide a critical review of hitchhiking models that consider the effects of culturally transmitted variation on genetic diversity in structured populations. The models' assumptions, results, and interpretations are compared and discussed. I conclude with a discussion of how a model built to investigate the effects of culturally mediated migration in Pleistocene hominins might help explain reduced genetic diversity

in any species in which the population is structured by selectively neutral behavioral variation.

1   Background

Homo sapiens (and Neandertals) display a lower level of neutral genetic diversity than living great apes (Wise et al., 1997; Gagneux et al., 1999; Kaessman et al., 2001; Stone et al., 2002; Noonan et al., 2006; Briggs et al., 2009; Green et al., 2010). Although this signal varies among genetic markers (see Hey, 1997; Harris and Hey, 1999a; Harris and Hey, 1999b; Harpending and Rogers, 2000), generally speaking, the neutral genetic diversity displayed by chimpanzees, gorillas or orangutans is at least 2–6 times greater than in modern humans. This finding is especially surprising given the fact that the census population size of humans is many orders of magnitude greater than that of any other great ape species. Population genetic theory predicts that, holding all else equal, larger populations will display greater neutral genetic diversity than smaller ones, yet *H. sapiens* shows the least neutral genetic diversity among extant, large-bodied apes. Obviously, all else was not held equal. How can we best explain reduced neutral genetic diversity in living humans and Pleistocene hominins?

A number of demographic models have been proposed to explain why humans are marked by reduced genetic diversity, and many invoke a bottleneck in census population size followed by a rapid expansion beginning sometime between 30,000 and 130,000 years ago (for review, see Harpending and Rogers, 2000). Although details concerning the onset and duration of the population bottleneck vary, all of these models arrive at the same conclusion: mutation has had insufficient time to keep pace with a drastic and relatively recent increase in census size. Indeed, it appears as though our population has undergone what can be described as exponential-like growth since at least the beginning of the Holocene, with the most notable increases occurring only within the last 200 years.

As it currently stands, a rapid expansion from a relatively small census population size beginning sometime between 30,000 and 130,000 years ago cannot be rejected as a possible explanation for the observation that modern humans display a lower level of genetic diversity than any great ape species. However, a relatively recent expansion in the census size of modern humans does little to explain reduced neutral genetic diversity in some now-extinct Pleistocene hominins, including Neandertals and the most recent common ancestor of Ne-

andertals and modern humans (Noonan et al., 2006; Briggs et al., 2009; Green et al., 2010). What is more, modern humans, Neandertals, and their most recent common ancestor are all associated with a similar effective population size ($N_e \sim 10,000$), suggesting that perhaps a more parsimonious explanation of the modern human condition is that low genetic diversity may be characteristic of (at least) the latter portion of our lineage, not just our species. This is not a new idea. Li and Sadler (1991) and Takahata and Satta (1998) suggested that the human lineage may have been marked by low genetic diversity for at least 500,000 years (see also Harpending et al., 1998). Their hypothesis finds support in recent discoveries that Pleistocene hominins other than anatomically modern *H. sapiens* display reduced genetic diversity.

A second family of explanations for low genetic diversity in modern humans invokes the effects of natural selection. Population geneticists have identified two related, yet distinct, processes—called background selection and selective sweep—by which natural selection can reduce variation at neutral loci (Hartl and Clark, 2007). Both are based on the understanding that the fate of a neutral variant depends (to varying degree) on the fate of the variant(s) at a selected locus (or selected loci), and that adjacent loci are more tightly "linked" to one another than distant loci. Unless recombination breaks the association between a neutral locus and selected one, the variant at the neutral locus will be lost along with a deleterious gene substitution at the selected locus (background selection) or it will increase in frequency along with a beneficial gene substitution at the selected locus (selective sweep).

Note that background selection and selective sweeps both reduce diversity at neutral genetic loci. But selective sweeps deserve additional attention here because they play a more important role than background selection in hitchhiking models. Consider a scenario in which a highly beneficial gene substitution appears in a panmictic population. Assuming the beneficial variant is not lost to drift soon after it appears, selection increases its frequency in the population because carriers of the beneficial mutation enjoy higher relative fitness than non-carriers. Selection favoring the beneficial variant over all others reduces diversity at the selected locus. In the process, however, selection also "sweeps" away diversity in the neutral or nearly neutral loci that surround the selected gene via *genetic hitchhiking* (Maynard Smith and Haigh, 1974).

Maynard Smith and Haigh (1974) were among the

first to demonstrate that a neutral allele can "hitchhike" to a higher frequency in a population as a consequence of being linked to a beneficial gene substitution, and, thus, that selection can reduce heterozygosity not only at the selected locus but also at thousands of neutral loci that surround it. Subsequent work has shown that the size of the affected region of the genome is a function of the strength of selection (s) (i.e., the fitness advantage associated with the beneficial mutation), the recombination rate (c), and the effective size of the population (N_e) (Stephan et al., 1992; Kim and Stephen, 2002). Holding all else equal, a highly beneficial gene substitution—one with a large value of s—requires relatively few generations to spread throughout a panmictic population, thus providing recombination with relatively few opportunities to rearrange the genome. Genetic hitchhiking can reduce neutral diversity over a relatively large region of the genome when s is large. In contrast, weak selection (small value of s) and high recombination rates (large value of c) both reduce the size of the region affected by genetic hitchhiking. Genetic hitchhiking generally has a weaker effect in populations with larger effective sizes (Stephan et al., 1992). Spatial population structure can also weaken the effect of genetic hitchhiking because migration between partially isolated groups slows the spread of the beneficial variant, providing more time for recombination to erode the association between a beneficial gene substitution and surrounding loci (Barton, 2000).

Whitehead (1998) describes a related process called *cultural hitchhiking*, whereby neutral genetic alleles "hitchhike" to higher frequencies in a population, not because of an association with a beneficial genetic mutation, but because they are "linked" to a beneficial cultural innovation. In this context, genes and cultural traits are "linked" to the extent that they are passed symmetrically—or, in other words, to the extent that genes and cultural traits are transmitted in parallel from parent(s) to offspring (Boyd and Richerson, 1985). Although Whitehead (1998, 2005) introduced cultural hitchhiking to explain reduced mitochondrial DNA (mtDNA) diversity in matrilineal whales, his hypothesis may help explain reduced genetic diversity in Pleistocene hominins—organisms for which claims of the cultural transmission of fitness-enhancing strategies are less controversial.

2 Cultural Hitchhiking in Socially Structured Populations

2.1 Whitehead's 1998 model

Pilot whales, sperm whales, and killer whales have mtDNA nucleotide diversities that are approximately ten-fold lower than those of other whales and dolphins (Whitehead, 1998). The whale species with low genetic diversities also display "matrilineal" (or matrifocal, in the case of norwhals) social systems, in which females commonly live in groups that contain close female relatives (Whitehead, 1998). What is more, there is evidence to suggest that, in some of these species, traits such as specialized feeding strategies (Boran and Heimlich, 1999; Whitehead and Rendell, 2004), vocal dialects (Whitehead et al., 1998), and migration strategies (Whitehead, 1996) might be culturally transmitted with high fidelity between members of the same matrilineal group. Whitehead (1998) hypothesized that, if some of the cultural traits transmitted along matrilines—effectively, in parallel (i.e., symmetrically) with mtDNA haplotypes—affect individual fitness, then beneficial cultural innovations might reduce mtDNA diversity through the process of cultural hitchhiking. Whitehead's suggestion provoked a number of interesting alternative hypotheses for explaining reduced mtDNA diversity in matrilineal whales (see Amos, 1999; Mesnick et al., 1999; Schlotterer, 1999; Tiedemann and Milinkovitch, 1999; Deecke et al., 2000). Tiedemann and Milinkovitch (1999), authors of the most salient and parsimonious alternative hypothesis, demonstrate that matrilineal social organization, alone, may account for reduced mtDNA diversity. In societies structured along matrilines, stochastic heterogeneity in the reproductive success among females increases the variance in the success of haplotype matrilines (Tiedemann and Milinkovitch, 1999). Increased variance in the success of matrilines strengthens the effects of genetic drift on the number and frequency of unique mtDNA haplotypes (or, put differently, it decreases the effective population size), reducing neutral genetic diversity at the level of the population.

Whitehead (1998) provides a proof of his cultural hitchhiking concept. His 1998 model represents a large, constant-sized, haploid population (n=200,000 females) structured along matrilines. Daughters inherit their mother's mtDNA haplotype with a high probability ($1-\mu$). A small proportion (μ) of females display a haplotype that differs at one base pair from their mothers' haplotype. Thus, μ represents the mutation rate. Each individual also possesses a single, adaptive cultural trait, for which there are two possible variants—ancestral and beneficial. At birth, an offspring learns its cultural variant either from its mother or from an individual outside the matriline. The beneficial cultural variant, which is

introduced to populations at the same point in simulated time in each run, provides carriers with a very large (10%) fitness advantage. Assuming the beneficial variant is not lost to drift soon after it appears, individual selection increases its frequency in the population.

Whitehead's results show that the magnitude of the negative effect of cultural hitchhiking on mtDNA diversity in matrilineal populations is positively correlated with the degree to which cultural traits are transmitted matrilineally. Cultural hitchhiking regularly reduces mtDNA nucleotide diversity even if 5% of the females whose mother possessed the beneficial cultural trait nevertheless acquire the less fit variant from an individual outside of their matriline, via oblique or horizontal transmission. But the negative effect of cultural hitchhiking in a matrilineal society disappears if little more than just 0.5% of the females whose mother does not display the beneficial trait acquire it through non-matrilineal transmission (Whitehead, 1998: 1710).

2.2   Whitehead's 2005 model

In response to critics of the cultural hitchhiking hypothesis, Whitehead (2005) conducted a thorough analysis of a more complete model (see also Whitehead, 1999). While some aspects of the 2005 model are the same as before—for example, μ still represents the mutation rate—others are quite different. Perhaps most strikingly, reproductive fitness is defined by "the culturally determined relative fitness of the tribe" (Whitehead, 2005:60) rather than by individual fitness.

Whitehead also represents socially mediated population structure differently in the 2005 model. Here, the population of haploid individuals is structured by social groups (called "tribes"), rather than by matrilines. Individuals (i.e., genes) are allowed to migrate between tribes. During each generation, a proportion m of the individuals in each group randomly choose a group from among all groups (including their own) to join. Each émigré immediately adopts the cultural trait displayed by the group it joins. The probability that a group will fission is a function of its size relative to the product of the carrying capacity of the environment, K, and a "tribe splitting" parameter, P (Whitehead, 2005). During group fission, a proportion p (randomly chosen from a uniform distribution bound by 0 and 1) of the members of the "parent" group is randomly assigned to one "daughter" group, and those that remain are assigned to the other "daughter" group. Both daughter groups start with the same cultural fitness, but not necessarily the same size.

The 2005 version of the model also includes a more complete representation of cultural evolution. Innovation occurs with probability ρ per individual per generation. With each innovation, a real number drawn randomly from a normal distribution with a mean of 1 and a standard deviation of σ is added to the individual's previous cultural fitness value (Note: Whitehead's 2005 model can also be run such that all innovations have only positive or only negative fitness effects). Each cultural innovation is assumed to spread through the social group in which it appears during a single generation. Thus, every member of a "tribe" displays the same cultural variant and fitness. This results in cultural homogeneity within groups and cultural heterogeneity between groups. In addition, because all members of a group immediately adopt each innovation that appears in its group, larger groups effectively have a higher innovation rate than smaller groups despite the fact that every individual in the metapopulation is characterized by the same innovation rate.

Cultural traits can be transmitted across group boundaries by a process Whitehead (2005) calls "cultural assimilation." Each generation, each group has probability α of receiving "cultural input" from a randomly chosen group in the metapopulation. The magnitude of the effect on the cultural fitness of the group receiving cultural input is a function of β, a real number bound by 0 and 1. When $\beta=0$, there is no effect on the recipient group's fitness. When $\beta=1$, the cultural fitness of the receiving group is set equal to the transmitting group's cultural fitness (for more details, see Whitehead, 2005:61).

Whitehead's simulation results illustrate a number of important points. First, the likelihood that cultural hitchhiking will substantially reduce genetic diversity is positively correlated with both the innovation rate (ρ) and the magnitude of the effect (σ) of innovation on fitness. Second, high mutation rates (μ) replenish neutral genetic diversity, negating much of the effect of cultural hitchhiking. Third, higher rates of migration (m) and higher rates of intertribal cultural transmission (α) relative to innovation weaken the effect of cultural hitchhiking because both create asymmetries in the transmission of genetic haplotypes and cultural traits. Because the model includes the assumption that each group is culturally homogeneous, migration ensures that an individual that moves into a new group is likely to pair a "new" (i.e., not inherited at birth) cultural trait with the haplotype it inherited from its parent. The same assumption also means that an individual is likely to

pair the haplotype it inherited from its parent with a "new" cultural trait as a result of intertribal cultural transmission.

2.3 Whitehead, Richerson, and Boyd's model

Whitehead, Richerson, and Boyd's (2002) cultural hitchhiking model was designed with an eye towards Late Pleistocene human hunter-gatherers rather than whales. Their model is similar in many respects to the model described in Whitehead (2005): the population is structured by culturally homogeneous tribes; innovations occur with a probability ρ, incur a fitness effect with a magnitude σ, and each spreads within the tribe in which it appears during a single generation; larger groups effectively have a higher innovation rate than smaller groups; fitness is a group-level characteristic that is based largely on a cultural trait (genes are selectively neutral); and mutations occur with a probability μ. Both models include migration and cultural assimilation.

Nevertheless, Whitehead et al.'s (2002) cultural hitchhiking model is unique. For example, it is spatially explicit: a single tribe inhabits every cell on a 6 × 6 (or 10 × 10) array. As a result, processes such as migration and cultural assimilation occur at the local scale of a Moore (or von Neumann) neighborhood of groups rather than at the scale of the entire metapopulation. The number of migrants that move among neighboring groups is proportional to the geometric mean of their sizes. As a consequence, proportionally more individuals move out of (and into) smaller groups than larger groups. Cultural assimilation also occurs only among neighboring groups. Here, the parameter α represents the probability per group per generation of receiving cultural input from the adjacent tribe with the *highest* cultural fitness. Thus, Whitehead and colleagues' model includes the assumption that intergroup cultural transmission is biased, not only by spatial scale (Premo and Scholnick, 2011), but, also, by cultural fitness. Put simply, groups preferentially choose to copy the fittest group in their local Moore neighborhood.

In addition, Whitehead et al. (2002) allow neighboring tribes to compete with each other over locally available resources. The parameter f represents the importance of resources in neighboring tribes' cells relative to the importance of resources in ego's cell. Larger values of f correspond to fiercer competition between tribes. When $f>0$, each tribe's reproductive success depends in part on how well it can compete with its neighbors (Whitehead et al., 2002:117). Because the

size of a group surrounded by fitter groups tends to shrink while the neighboring groups grow, inter-tribal competition increases the rate at which beneficial cultural traits spread via cultural group selection. Groups that are less fit than their neighbors can become extinct. In the wake of a local extinction event, a genetically representative sample of the members of the neighboring group marked by the *highest* net fitness (cultural fitness * group size) colonizes the cell left vacant by the unsuccessful tribe. These rules ensure that colonization will aid the spread of the fittest cultural variant in the neighborhood, just as the rules governing cultural assimilation ensure that intergroup cultural transmission aids the spread of the fittest cultural variant in the neighborhood.

As in Whitehead (2005), the conditions of Whitehead et al.'s (2002) model are favorable to cultural hitchhiking via cultural group selection. Whitehead et al. find that the effect of cultural hitchhiking is greater when (1) cultural evolution is relatively rapid (that is to say, when $\rho*\sigma$ is relatively large), (2) migration between groups is rare, and (3) intergroup cultural transmission rates are low enough that innovation plays a more important role than cultural assimilation in determining changes in fitness. However, even in a model that is generally favorable to cultural hitchhiking by cultural group selection, the results show that genetic diversity was "substantially" reduced (i.e., reduced by more than 50%) in only a fraction of the simulation runs, most regularly when the migration rate was less than 0.6 genes per tribe per generation; cultural evolution had a large fitness effect, changing tribe fitness by *more than* 2.8% per generation; and the fitness effects of cultural transmission between tribes was "considerably less important" than innovation within tribes (Whitehead et al., 2002:120). Eliminating intergroup cultural transmission and assuming that all innovations are associated with positive fitness effects increase the likelihood that cultural hitchhiking will reduce genetic diversity, though neither measure guarantees reduced genetic diversity in any given simulation run. Whitehead and colleagues conclude that Late Pleistocene forager societies marked by sufficiently rapid cultural evolution, very little migration between groups, and a low rate of intergroup cultural transmission would have been susceptible to the effects of cultural hitchhiking on neutral genetic diversity. It remains unclear to what extent such conditions, let alone many of the model's more fundamental assumptions, apply to Late Pleistocene hominin hunter-gatherers.

3   Genetic Hitchhiking in Socially Structured Populations

Cultural hitchhiking requires culturally transmitted traits that (1) have large fitness effects and (2) are not easily transmitted to other groups. One can identify cultural traits in living humans that satisfy these conditions, but the task becomes much more difficult for the case of Pleistocene hominins. Whitehead et al. (2002:122) nominate social structure and foraging strategies as good candidates for the types of adaptive cultural traits that may have facilitated cultural hitchhiking in Pleistocene hunter-gatherers, while ruling out traits related to technological innovations in the use of fire or weaponry. They reason that the former might be contained within groups over many generations by conformist biased transmission, while the latter is likely to be associated with high rates of intergroup cultural transmission. Unfortunately, the archaeological record of the Pleistocene is largely silent on issues of social structure. Below I introduce another way that culturally transmitted behavioral variation can affect neutral genetic diversity.

Even in humans, many cultural variants do not differentially affect individual fitness. But selectively neutral cultural variation can still influence evolutionary dynamics in a population. For example, selectively neutral behavioral variation can play an important role in creating and maintaining population structure in the presence of *culturally mediated migration* (Premo and Hublin 2009).

Humans often base decisions about which groups to join or which set of individuals to consider as possible mates on the degree to which others display cultural variants in language, diet code, dress, socio-economic class, religion, etc. that are similar to one's own. Although all living humans exhibit some degree of culturally mediated migration, it appears that great ape species do not. This suggests that selectively neutral behavioral variation may have played a role in mediating gene flow between groups within Pleistocene hominin populations but not between groups within Pleistocene hominoid populations. This difference may be responsible for the differing levels of genetic diversity observed in their living descendants. Or, restated in the form of a testable question: could a primitive form of culturally mediated migration explain why the genetic diversity estimates of modern humans and some now-extinct Pleistocene hominin populations are lower than those of any living great ape species?

Premo and Hublin (2009) use a spatially explicit agent-based model to investigate how selection might affect neutral genetic diversity in the presence of a rudimentary version of culturally mediated migration. In Premo and Hublin's model, cultural traits *and* genes define individual fitness. Each individual carries 100 cultural traits and 1,000 genetic loci. A proportion ε (some simulations were run with $\varepsilon=0.3$ and some with $\varepsilon=0.7$) of cultural traits and a proportion $\eta=0.98$ of genetic loci are selectively neutral, and the rest contribute additively and independently to an individual's fitness. Individual relative fitness is calculated by scaling each individual's fitness to the maximum fitness value in the metapopulation. To maintain a nearly constant population size, each individual's relative fitness is then scaled by a coefficient that is sensitive to the difference between the number of individuals needed to increase the current population size to carrying capacity and the number of offspring the population expects to produce (the latter is given by the sum of all individual relative fitness values). Death is stochastic: each individual experiences a constant probability of mortality per time step ($\delta=0.15$) regardless of its individual fitness.

Each offspring inherits its selectively neutral cultural variants from one of its parents (chosen randomly). For each selective trait, each offspring adopts the variant with the highest fitness among those displayed by the offspring's parents and a "teacher" that is chosen randomly from within the Moore neighborhood of the offspring's group (including the offspring's group but excluding the offspring itself). Genetic variants are passed via sexual reproduction (mates are chosen at random from within groups) with recombination, as if contained on a single chromosome. At birth, each cultural trait undergoes single stepwise innovation with probability ι and each genetic locus undergoes single stepwise mutation with probability μ.

A group is defined as the set of individuals that occupy the same cell at the same time. Group membership is dynamic, but each individual can belong to just one group per time step. In the model, as is in biological populations of modern humans, great apes, and (presumably) now-extinct Pleistocene hominins, groups do not maintain a constant size nor do they contribute an equal number of progeny to the metapopulation. In the model, a group fissions when its membership exceeds the maximum group size of $\varphi=50$ individuals. During fission, a group splits and sends half of its members (chosen randomly) to a neighboring cell that contains fewer than 25 individuals. In the rare case that all eight

of the neighboring cells are inhabited by at least 25 individuals, the group does not fission during that time step. Group fission is the only instance in which a group may compete directly with other groups over resources. Although most of the competition in this model occurs between individuals—or, more precisely, individual relative fitness values—group membership and group-level population dynamics are important for understanding changes in genetic diversity. In the presence of culturally mediated migration, the success of a beneficial gene substitution can become bound to the success of a group (see more below).

Premo and Hublin's model includes culturally mediated migration. During each time step, each individual attempts to move to a nearby group with probability ν=0.05. But an individual can move only if the degree of cultural similarity between a prospective target group and its current group exceeds the cultural similarity threshold (CST) (see Premo and Hublin, 2009:37). When CST=0, simulated populations are structured by geographic distance only. The role culturally mediated migration plays in structuring a population along discontinuities in culturally transmitted variation increases as CST approaches 1.

Premo and Hublin's model does not include a process analogous to Whitehead's (2005) or Whitehead et al.'s (2002) "cultural assimilation." Including a process of intergroup cultural transmission would likely weaken the negative effect of CST on neutral genetic diversity, just as Whitehead shows that increasing the relative importance of cultural assimilation weakens the negative effect of cultural hitchhiking on neutral genetic diversity. However, it is important to note that the extent to which intergroup cultural transmission negates the effect of CST is likely to be dependent upon the topology of the social network that connects members of different groups (Premo, in press).

Simulation results show that selection can reduce neutral genetic diversity when CST is sufficiently high (Premo and Hublin, 2009: Fig. 1). Increasing the innovation rate (ι) or increasing the proportion of selectively neutral cultural variants (ε) strengthens the effect of CST on neutral genetic diversity. Holding CST constant, decreasing the number of traits in the cultural repertoire is also likely to strengthen the effect of CST, although this has yet to be demonstrated. With sufficiently high CST, selection suppresses the average gene diversity of neutral loci over thousands of generations via a recursive, two-phase cycle that is composed of a "collection" phase and a "sweep" phase (see Premo and Hublin,

2009: Fig. 2). It is important to understand how this process works.

When CST is sufficiently high, groups become reproductively isolated with time, as the cultural differences that accumulate between groups deter gene flow. Reduced gene flow, in turn, leads to greater genetic and cultural differentiation among groups. The recursive relationship between increased group differentiation and reduced gene flow is characteristic of the collection phase. Culturally mediated migration drives the accumulation (or "collection") of genetic and cultural differences *between* groups by reducing gene flow. Of course, reduced gene flow also has the effect of decreasing genetic and cultural diversity *within* groups.

In a structured population, gene flow is required for a beneficial gene substitution to spread beyond the boundaries of the group in which it first appears (Barton, 1993). But because culturally mediated migration reduces gene flow, the fate of each beneficial mutation—measured as its frequency in the whole population, not just in one group—comes to depend to a greater extent upon the rate at which the group that "contains" carriers of the beneficial mutation fissions relative to the rate at which groups composed of non-carriers fission. Variability among group fission rates depends upon the way in which relative individual fitness is partitioned within and between groups. A group-level selective sweep requires low within-group variance and high between-group variance in relative individual fitness (Whitlock and Barton, 1997). When CST is sufficiently high, even a relatively rudimentary version of culturally mediate migration can structure the genetic variation of a population such that it meets this requirement, setting the stage for a group-level sweep (see Premo and Hublin, 2009: Fig. 3).

During the sweep phase, the population's genetic (and cultural) diversity is reduced as a relatively small number of individuals—those carrying the beneficial mutation, who also tend to be members of the same culturally and spatially defined group—produce disproportionately more offspring than others. The cultural differences that emerge during the collection phase and create effective barriers to gene flow, disintegrate during the sweep phase. The between-group genetic differences that accumulate during the collection phase and then fuel the selective sweep also largely disappear because, as a result of the selective sweep, a large proportion of the members in the population coalesce to a very recent common ancestor. As soon as a sweep ends, the collection phase begins anew.

In sum, like Whitehead et al. (2002) and Whitehead (2005), Premo and Hublin (2009) find that the process of cultural group selection is responsible for reduced neutral genetic diversity, but this form of cultural group selection is different from that observed elsewhere. Premo and Hublin relax the assumptions that cultural innovations spread throughout the group in a single generation, that there is no variation between individual fitness within each group, and that reproductive fitness is a function of a single cultural trait and group size. Instead, cultural innovations may take many generations to spread throughout a group (if they spread at all), individual relative fitness can vary within groups, and reproductive success is a function of individual relative fitness rather than group fitness. The transient group-level cultural identities that emerge during the collection phase allow culturally mediated migration to partition genetic variation such that individual selection can reduce neutral genetic diversity in the population by way of a group-level sweep.

4   Discussion

Whitehead and colleagues have shown that cultural hitchhiking reduces genetic diversity in structured populations when genes and cultural traits are transmitted symmetrically, gene flow is low, intergroup cultural transmission is rare, and cultural evolution is rapid. However, their model of Late Pleistocene humans assumes that cultural traits define group-level reproductive fitness, such that "culturally advanced" groups directly outcompete other groups. By allowing for a proportion of cultural traits to be selectively neutral and for a small proportion of genetic loci to directly affect individual relative fitness, Premo and Hublin show that cultural hitchhiking is not the only avenue through which cultural variation can affect genetic diversity. Selection can suppress neutral genetic diversity for tens of thousands of generations through a recursive two-stage process that involves (1) the accumulation of between-group differences in cultural and (then) genetic variation via culturally mediated migration and (2) the selective sweep of beneficial gene substitutions.

Culturally mediated migration assumes that behavioral variation plays a role in regulating gene flow between groups. While true of humans, does this assumption hold for other species, such as the matrilineal whales that served as the motivation for Whitehead's models of cultural hitchhiking? A number of researchers have argued that vocal dialects provide examples of culturally transmitted variation in some whale species

(e.g., Deecke et al., 2000; Noad et al., 2000; Rendell and Whitehead, 2001; Rendell and Whitehead, 2003). This type of variation can lend structure to a population if individuals who belong to groups marked by different dialects interact and—more importantly—mate with each other less frequently than individuals that use similar dialects. Unfortunately, it remains unknown what the real CST value might be for any of the matrilineal whale species studied by Whitehead. Indeed, it would be interesting to know whether (or to what extent) matrilineal whales engage in culturally mediated migration. Until those data are available, I can only suggest that because different cultural variants need not affect fitness differentially in order for selection to reduce neutral genetic diversity in the presence of culturally mediated migration, Premo and Hublin's model may provide a more parsimonious explanation of reduced mtDNA in matrilineal whales than cultural hitchhiking does—at least until the type of selectively advantageous, matrineally transmitted traits required by Whitehead's cultural hitchhiking hypothesis are identified.

Of course, models that include culturally mediated migration may be applicable beyond humans and whales. A decades-old hypothesis predicts that variation in songbird dialects may inhibit gene flow between groups (Mayr, 1942; Marler and Tamura, 1962), assuming that birds preferentially disperse to groups marked by culturally transmitted dialects (Marler and Tamura 1964) that sound similar to their own. Empirical tests of this hypothesis have yielded mixed results. Studies of a few songbird species have found that genetic variation corresponds with variation in dialects (Kroosdma et al., 1985; Balaban, 1988). Indeed, this is the type of association one would expect to observe during the collection phase described above. However, studies of other species have found evidence that imply relatively high levels of gene flow across dialect boundaries (Fleischer and Rothstein, 1988; Payne and Westneat, 1988; Lougheed and Handford, 1992; Wright and Wilkinson, 2001). These findings suggest that the boundaries between culturally dissimilar groups are porous, which is inconsistent with the notion that genetic variation is structured by variation in dialects, at least in these species.

Wright and Wilkinson (2001) note that dialect variation is likely to play less of a role in structuring genetic variation in species in which individuals disperse while they are still highly sensitive to vocal learning. In such cases, an unfamiliar dialect does not discourage an individual from joining a group. Instead, an individual sim-

ply learns the dialect of the group it joins, as appears to be the case for yellow-naped Amazon parrots (Wright and Wilkinson 2001). Assuming that some species of songbirds do in fact prefer to disperse to groups with familiar dialects once their own dialect is set, Premo and Hublin's model predicts reduced neutral genetic diversity for songbird species that disperse when they are no longer sensitive to vocal learning.

The above review of hitchhiking models raises two larger questions. First, to what extent does regional behavioral variation beget population structure and to what extent does population structure beget regional behavioral variation? This question may prove difficult to answer, especially for highly social animals. But it is worth recognizing that whenever the type or frequency of interactions between individuals or migrations between groups is based on an assessment of the degree to which socially transmitted behaviors are similar, regional behavioral variation may play an important role in structuring a population along lines that resemble cultural boundaries. A number of studies have shown this to be true of modern humans (Barbujani and Sokal, 1990; Chen et al., 1995; Cavalli-Sforza, 1997), but I submit that it may also hold for other species, such as matrilineal whales and some birds.

Second, what methods can be employed to distinguish cultural hitchhiking from genetic hitchhiking in socially structured populations? As Whitehead (2005) correctly notes, it is futile to attempt to diagnose cultural hitchhiking by searching for differences between cultural diversity and genetic diversity because both are reduced as a result of a selective sweep. The same is true in Premo and Hublin's model, even though the group-level selective sweep is driven by beneficial mutations rather than by beneficial innovations. Thus, it may be more useful to concentrate solely on genomic data.

Both forms of hitchhiking cause reduced neutral genetic diversity and increased linkage disequilibrium at the metapopulation-level. As in the case of a population bottleneck, cultural hitchhiking reduces diversity more-or-less equally across all genetic loci. This is because the genome (or at least large parts of it) is pulled to a higher frequency in the population by a beneficial cultural trait that, while "linked" to the genome when genes and cultural traits are transmitted symmetrically, is nonetheless equally "linked" to all loci. Genetic hitchhiking is associated with a different prediction. Because, with genetic hitchhiking, neutral loci can ride the coattails of a beneficial gene substitution at a se-

lected locus as long as recombination fails to sever the association, diversity should be lowest at the selected locus and increase as recombinational distance from the selected locus increases. Thus, genetic hitchhiking often leaves a telltale signature in heterozygosity across loci, a spatial pattern which resembles the cross-section of a river valley. Kim and Stephen (2002) demonstrate that the floor of the valley (i.e., the point of the least diversity) is often—though not always—situated near the selected locus, while the overall shape, width, and symmetry of the valley walls vary with the strength of selection and the recombination rate, among other factors. Kim and Stephen (2002) show that a similar pattern of local reduction can arise due to stochastic change along recombining chromosomes in the absence of selection, and this should give pause for concern. Nevertheless, methods designed to identify and test the significance of local regions of genetic reduction (see Galtier et al., 2000; Kim and Stephen, 2002) provide great promise for discerning cultural hitchhiking from genetic hitchhiking.

In the final analysis, any attempt to identify whether cultural hitchhiking *or* genetic hitchhiking *or* census population bottlenecks is responsible for patterns in genetic polymorphism data collected from social animals may not be the best course for action. In many cases, available methods may simply lack the power required to identify which of these alternatives is best supported by empirical polymorphism data. But it is also worth considering whether the reduced genetic diversity observed in modern humans and in some now-extinct Pleistocene hominin populations may be better explained as a combined effect of all three (and possibly other) processes. In other words, the best explanation may be one that describes how cultural hitchhiking, genetic hitchhiking, social network topology, *and* local demographic bottlenecks/expansions in different places at different times influenced genetic diversity in Pleistocene hominins in a different way than they influenced genetic diversity in the Pleistocene ancestors of living great apes. Future paleodemographic research could benefit from employing a perspective that does not hold cultural hitchhiking, genetic hitchhiking, and demographic bottlenecks to be mutually exclusive explanations of reduced genetic diversity.

The story behind reduced genetic diversity in living humans and some now-extinct Pleistocene hominin populations is likely to be more complicated—and, thus, more interesting—than previously thought. The same may be true of other species in which culturally trans-

mitted behaviors affect fitness and/or lend structure to a population. Independent of the current debate over the extent to which regional behavioral variation in nonhuman animals is grounded in genetic versus cultural transmission, continued animal culture research is likely to provide a more comprehensive catalog of the myriad ways in which behavioral variation not only arises from population structure but also helps to create (and recreate) it. Such insights are necessary if we are to construct more comprehensive models of demographic history, models that will expand and ultimately improve our understanding of why some species, such as our own, are marked by reduced genetic diversity.

References

Amos W, 1999. Culture and genetic evolution in whales. Science 284: 2055a.

Balaban, E, 1988. Cultural and genetic variation in swamp sparrows *Melospiza georgiana*. I. Song variation, genetic variation and their relationship. Behaviour 105: 250–291.

Barbujani G, Sokal RR, 1990. Zones of sharp genetic change in Europe are also linguistic boundaries. Proc. Natl. Acad. Sci. USA 87: 1816–1819.

Barton NH, 1993. The probability of fixation of a favoured allele in a subdivided population. Genet. Res. 62: 149–157.

Barton NH, 2000. Genetic hitchhiking. Phil. Trans. R. Soc. Lond. B 355:1553–1562.

Boran JR, Heimlich SL, 1999. Social learning in cetaceans: Hunting, hearing and hierarchies. In: Box HO, Gibson KR ed. Mammalian Social Learning: Comparative and Ecological Perspectives. Cambridge: Cambridge University Press, 282–307.

Boyd R, Richerson PJ, 1985. Culture and the Evolutionary Process. Chicago: University of Chicago Press.

Briggs AW, Good JM, Green RE, Krause J, Maricic T et al., 2009. Targeted retrieval and analysis of five Neandertal mtDNA genomes. Science 325: 318–321.

Cavalli-Sforza LL, 1997. Genes, peoples, and languages. Proc. Natl. Acad. Sci. USA 94: 7719–7724.

Chen J, Sokal RR, Ruhlen M, 1995. Worldwide analysis of genetic and linguistic relationships of human populations. Hum. Biol. 67: 595–612.

Deeke VB, Ford JKB, Spong P, 2000. Dialect change in resident killer whales: Implications for vocal learning and cultural transmission. Anim. Behav. 40: 629–638.

Fleischer RC, Rothstein SI, 1988. Known secondary contact and rapid gene flow among subspecies and dialects in the brown-headed cowbird. Evolution 42: 1146–1158.

Gagneux P, Wills C, Gerloff U, Tautz D, Morin P et al., 1999. Mitochondrial sequences show diverse evolutionary histories of African hominoids. Proc. Natl. Acad. Sci. USA 96: 5077–5082.

Galtier N, Depaulis F, Barton NH, 2000. Detecting bottlenecks and selective sweeps from DNA sequence polymorphism. Genetics 155: 981–987.

Green RE, Krause J, Briggs AW, Maricic T, Stenzel U et al., 2010. A draft sequence of the Neandertal genome. Science 328: 710–722.

Harpending HC, Batzer MA, Gurven M, Jorde LB, Rogers AR et al., 1998. Genetic traces of ancient demography. Proc. Natl. Acad. Sci. USA 95: 1961–1967.

Harpending HC, Rogers AR, 2000 Genetic perspectives on human origins and differentiation. Annu. Rev. Genomics Hum. Genet. 1: 361–385.

Harris EE, Hey J, 1999a. X chromosome evidence for ancient human histories. Proc. Natl. Acad. Sci. USA 96: 3320–3324.

Harris EE, Hey J, 1999b. Human demography in the Pleistocene: Do mitochondrial and nuclear genes tell the same story? Evol. Anthropol. 8: 81–86.

Hartl DL, Clark AJ, 2007. Principles of Population Genetics. Sunderland: Sinauer Associates, Inc.

Hey J, 1997. Mitochondrial and nuclear genes present conflicting portraits of human origins. Mol. Biol. Evol. 14: 166–172.

Kaessmann H, Wiebe V, Weiss G, Paabo S, 2001. Great ape DNA sequences reveal a reduced diversity and expansion in humans. Nat. Genet. 27: 155–156.

Kim Y, Stephen W, 2002. Detecting a local signature of genetic hitchhiking along a recombining chromosome. Genetics 160: 765–777.

Krings M, Capelli C, Tschentscher F, Geisert H, Meyer S et al., 2000. A view of Neandertal genetic diversity. Nat. Genet. 26: 144–146.

Kroodsma DE, Baker MC, Baptista LF, Petrinovich L, 1985. Vocal dialects in Nuttall's white-crowned sparrow. In: Johnston RF ed. Current Ornithology, Vol 2. New York: Plenum Press, 103–133.

Langergraber KE, Boesch C, Inoue E, Inoue-Murayama M, Mitani JC et al., 2011. Genetic and 'cultural' similarity in wild chimpanzees. Proc. R. Soc. B 278: 408–416.

Langergraber KE, Vigilant L, 2011. Genetic differences cannot be excluded from generating behavioural differences among chimpanzee groups. Proc. R. Soc. B 278: 2094–2095.

Lougheed SC, Handford P, 1992. Vocal dialects and the structure of geographic variation in the morphological and allozymic characters in the rufous-collared sparrow *Zonotrichia capensis*.

Evolution 46: 1443–1456.

Lycett SJ, Collard M, McGrew WC, 2007. Phylogenetic analyses of behavior support existence of culture among wild chimpanzees. Proc. Natl. Acad. Sci. USA 104: 17588–17592.

Lycett SJ, Collard M, McGrew WC, 2010. Are behavioral differences among wild chimpanzee communities genetic or cultural? An assessment using tool-use data and phylogenetic methods. Am. J. Phys. Anth. 142: 461–467.

Lycett SJ, Collard M, McGrew WC, 2011. Correlations between genetic and behavioural dissimilarities in wild chimpanzees *Pan troglodytes* do not undermine the case for culture. Proc. R. Soc. B 278: 2091–2093.

Li W-H, Sadler LA, 1991. Low nucleotide diversity in man. Genetics 129: 513–523.

Marler P, Tamura M, 1962. Song 'dialects' in three populations of white-crowned sparrows. Condor 64: 368–377.

Marler P, Tamura M, 1964. Culturally transmitted patterns of vocal behavior in sparrows. Science 146: 1483–1486.

Maynard Smith J, Haigh J, 1974. The hitch-hiking effect of a favourable allele. Genet. Res. 23: 23–35.

Mayr E, 1942. Systematics and the Origin of Species. New York: Columbia University Press.

Mesnick SL, Taylor BL, Le Duc RG, Trevino SE, O'Corry-Crow GM et al., 1999. Culture and genetic evolution in whales. Science 284: 2055a.

Noad MJ, Cato DH, Bryden MM, Jenner M-N, Jenner KCS, 2000. Cultural revolution in whale songs. Nature 408: 537.

Noonan JP, Coop G, Kudaravalli S, Smith D, Krause J et al., 2006. Sequencing and analysis of Neanderthal genomic DNA. Science 314: 1113–1118.

Payne RB, Westneat DF, 1988. A genetic and behavioral analysis of mate choice and song neighborhoods in indigo buntings. Evolution 42: 935–947.

Premo LS, in press. Local extinctions, connectedness, and cultural evolution in structured populations. Adv. Complex Syst. DOI: 10.1142/S0219525911003268.

Premo LS, Hublin J-J, 2009. Culture, population structure, and low genetic diversity in Pleistocene hominins. Proc. Natl. Acad. Sci. USA 106: 33–37.

Premo LS, Scholnick JB, 2011. The spatial scale of social learning affects cultural diversity. Am. Antiquity 76: 163–176.

Rendell L, Whitehead H, 2001. Culture in whales and dolphins. Behav. Brain Sci. 24: 309–382.

Rendell L, Whitehead H, 2003. Vocal clans in sperm whales *Physeter macrocephalus*. Proc. R. Soc. B 270: 225–231.

Schlotterer C, 1999. Culture and genetic evolution in whales. Science 284: 2055a.

Stephen W, Wiehe THE, Lenz MW, 1992. The effect of strongly selected substitutions on neutral polymorphism: Analytical results based on diffusion theory. Theor. Popul. Biol. 41: 237–254.

Stone AC, Griffiths RC, Zegura SL, Hammer MF, 2002. High levels of Y-chromosome nucleotide diversity in the genus *Pan*. Proc. Natl. Acad. Sci. USA 99: 43–48.

Takahata N, Satta Y, 1998. Footprints of intragenic recombination at HLA loci. Immunogenet. 47: 430–441.

Tiedemann R, Milinkovitch MC, 1999. Culture and genetic evolution in whales. Science 284: 2055a.

Whitehead H, 1996. Variation in the feeding success of sperm whales: Temporal scale, spatial scale and relationship to migrations. J. Anim. Ecol. 65: 429–438.

Whitehead H, 1998. Cultural selection and genetic diversity in matrilineal whales. Science 282: 1708–1711.

Whitehead H, 1999. Culture and genetic evolution in whales. Science 284: 2055a.

Whitehead H, 2005. Genetic diversity in the matrilineal whales: Models of cultural hitchhiking and group-specific non-heritable demographic variation. Mar. Mammal. Sci. 21:58–79.

Whitehead H, Dillon M, Dufault S, Weilgart L, Wright J, 1998. Non-geographically based population structure of South Pacific sperm whales: Dialects, fluke-markings and genetics. J. Anim. Ecol. 67: 253–262.

Whitehead H, Rendell L, 2004. Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. J. Anim. Ecol. 73: 190–196.

Whitehead H, Richerson P, Boyd R, 2002. Cultural selection and genetic diversity in humans. Selection 3: 115–125.

Whitlock MC, Barton NH, 1997. The effective population size of a subdivided population. Genetics 146: 427–441.

Wise CA, Sraml M, Rubinsztein DC, Easteal S, 1997. Comparative nuclear and mitochondrial genome diversity in humans and chimpanzees. Mol. Biol. Evol. 14: 707–716.

Wright TF, Wilkinson GS, 2001. Population genetic structure and vocal dialects in an amazon parrot. Proc. R. Soc. B 268: 609–616.