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GENETIC DIVERSITY IN THE MATRILINEAL WHALES: MODELS OF CULTURAL HITCHHIKING AND GROUP-SPECIFIC NON-HERITABLE DEMOGRAPHIC VARIATION

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ABSTRACT

Cultural hitchhiking is the process by which cultural selection reduces the diversity of genes that are being transmitted in parallel to selective cultural traits. I use simulation models to investigate cultural hitchhiking in geographically unstructured populations of culturally homogeneous tribes. Substantial reduction of genetic diversity required: a reasonably low mutation rate; that tribes split fairly frequently when they constitute a substantial part of the population; a fairly low migration rate ($<\sim10$ migrants per tribe per generation); only a low rate of cultural evolution (mean culturally determined fitness change $>\sim0.005\%$/generation); and that cultural assimilation from other tribes change the fitness of a tribe less than cultural innovation within it. Cultural hitchhiking tends to increase mean tribe size. Measures of genetic and cultural variation among tribes poorly indicate past cultural hitchhiking. Demographic effects, in which tribal fitness varies but is not heritable, can also reduce a population's genetic diversity if the fitness varies very considerably, or tribal extirpation is added. In such cases populations frequently become extinct. Four species of matrilineal whales have remarkably low mitochondrial DNA diversity. Knowledge of the population and social structure of these species is consistent with the conditions for cultural hitchhiking. However, there remain important information gaps.

Key words: cultural evolution, gene-culture coevolution, genetic diversity, whale, matriline.

Population substructure can reduce genetic diversity below the level expected in a panmictic population of the same size (Whitlock and Barton 1997). Attributes which may structure a population include culture, where culture may be defined as information or behavior shared by members of a population or subpopulation and transmitted by some form of social learning (Rendell and Whitehead 2001). Culture can reduce the diversity of genes which are being transmitted in parallel ("symetrically" in the terminology of Boyd and Richerson 1985) with selective and heritable cultural traits (Whitehead 1998). I have called this process "cultural hitchhiking" (Whitehead 1998), as it is analogous to genetic hitchhiking in which selectively advantageous genes spread neighboring linked neutral alleles, reducing diversity at a neutral locus (Maynard Smith and Haigh 1974).

I have suggested that cultural hitchhiking caused the remarkably low diversity in the mitochondrial DNA (mtDNA) of four species of whale that have matrilineal social systems (Whitehead 1998). These species are "matrilineal" in the sense that females generally remain grouped with their mother while she is alive. Cultural hitchhiking may also have caused a low diversity in Y-chromosome genes, and possibly also mtDNA, of *Homo sapiens* (Whitehead *et al.* 2002).

Cultural hitchhiking is a form of gene-culture coevolution in which both the transmission of genes and cultural traits affect genotypes (Feldman and Laland 1996). Among others, Feldman and Laland (1996) consider gene-culture coevolution to be restricted to humans. Thus, its presence in the matrilineal whales would be particularly significant.

The model that investigated the feasibility of cultural hitchhiking in humans used current conceptions of the societies and cultures of late Pleistocene hunter-gatherers (Whitehead *et al.* 2002). It included tribe-based demography with extinctions, territoriality, competition for resources between neighboring tribes, intertribe flows of genes and culture, genetic mutation, and cultural evolution.

In contrast, the earlier model which introduced the idea of cultural hitchhiking in reference to the matrilineal whales (Whitehead 1998) was much simpler. It ignored territoriality—reasonable as the matrilineal whales are not territorial—, cultural evolution, and the sizes of the social entities with homogeneous cultures. In this model, just one, advantageous, cultural innovation promulgated in a simple matrilineal fashion. This model was overly simple, and some of its implications have been used to argue against cultural hitchhiking in these species. To produce cultural hitchhiking, it required an innovation which had substantial effect on fitness, and transmitted faithfully between generations with low rates of assimilation outside the matrilineal line. Critics questioned whether such an innovation could be sufficiently constant over time for the process to operate (Deecke *et al.* 2000), and whether the whale societies were stable enough so that the innovation would be maintained largely within matrilineal lines (Mesnick *et al.* 1999, Tiedemann and Milinkovitch 1999). The major simplification of the original model was the inclusion of just one innovation, while cultural evolution more likely proceeds by a series of small steps.

As an alternative, several authors have suggested that the low mtDNA diversity of the matrilineal whales may result from purely demographic, non-heritable processes, if animals within matrilineal groups tend to have correlated fitness (Siemann 1994, Amos 1999, Tiedemann and Milinkovitch 1999). I have argued that such models make assumptions or predictions that are not consistent with the known natural history of the species (Whitehead 1998, 1999*a*), but have not formally compared demographic models with cultural hitchhiking.

Here, I look generally at the possibility of cultural hitchhiking in geographically unstructured populations divided into social entities that have distinctive cultures. I will call these social entities "tribes," following the anthropological definition of culturally homogeneous entities (*e.g.*, Birdsell 1966). The model allows both genes and culture to evolve, and both to move between the tribes. While based upon the information available for the matrilineal whales, the model has sufficient generality that it can indicate the feasibility of cultural hitchhiking at any locus in a geographically unstructured population socially divided into entities that have distinctive cultures. Secondarily, I examine whether measures of genetic or cultural divergence among tribes can be used to assess the likelihood of past cultural hitchhiking. I also adapt the model to investigate the feasibility of purely demographic, non-heritable, processes reducing genetic diversity in a socially structured population (following Siemann 1994, Amos 1999, Tiedemann and Milinkovitch 1999).

METHODS

I stochastically simulated the progress of genetic and cultural evolution in a geographically unstructured haploid population of individuals each of which possesses a haplotype, *h.* As noted below, the results of the model can be adapted to consider diploid genes. The population is socially structured into tribes, which may have distinctive cultural phenotypes. This fits with knowledge of the matrilineal whales where social structures include permanent groups which travel together and, at least in some cases, have distinctive behavior (*e.g.*, Whitehead 1999*b*, 2003*b*; Ottensmeyer and Whitehead 2003; Yurk 2003). Thus the population can be described by $\{n(t, h, c)\}$, the number of individuals in the population which are members of tribe c and have haplotype h at generation t. Each tribe possesses a mean fitness $w(c, t)$ which can change with time through cultural evolution, but mean fitness does not vary between haplotypes within a tribe. The following events can take place (in this order) at each simulated generation: reproduction, genetic mutation, cultural evolution, cultural assimilation, intertribe migration, and tribe fission.

Reproduction

I represent reproduction by a Poisson process, so that the number of individuals with any haplotype in a tribe depends on the number in the previous generation, adjusted for the culturally determined relative fitness of the tribe ($w(c, t)$) and the total population size relative to the carrying capacity of the environment, K. So:

$$n(t+1,h,c) = \mathrm{Po}\left[\frac{n(t,h,c)\cdot w(c,t)\cdot K}{\sum_h \sum_c n(t,h,c)\cdot w(c,t)}\right] \qquad (1)$$

where Po(x) is a Poisson random variable with mean x. This leads to density dependence, and a total population size that approximates K.

Genetic Mutation

Following reproduction, each individual has probability μ of mutating into a totally new haplotype, different at one base-pair from the parent haplotype. There are no back mutations.

Cultural Evolution

Two parameters define cultural evolution: the frequency (ρ) and magnitude (σ) of fitness changes due to cultural innovations (which are assumed to spread through a tribe within a generation). Thus:

$$w(c,t+1) = \begin{array}{c} w(c,t) \quad \text{with probability } 1-\rho \\ |w(c,t)\cdot \mathrm{N}(1,\sigma)| \quad \text{with probability } \rho \end{array} \tag{2}$$

where $\mathrm{N}(1,\sigma)$ represents a normal random variable with mean 1.0 and standard deviation σ. Thus, roughly once every $1/\rho$ generations, a tribe produces a cultural innovation which changes its fitness by a factor with mean 1.0 and standard deviation σ. In this formulation, σ represents the approximate significance of the cultural innovations (high σ indicating that cultural innovations have a major effect on fitness), and cultural innovations can have positive or negative effects on fitness. Then $\rho \cdot \sigma$ approximates the proportional absolute change in fitness per generation. I also ran the model with a modification so that all innovations had a positive effect on fitness: in equation 2, the fitness with an innovation was $w(c,\ t)\cdot(1+|\mathrm{N}(0,\sigma)|)$.

Cultural Assimilation

I added cultural assimilation between tribes in some runs of the model. In this scenario culture itself moves across tribal boundaries, as when a tribe adopts a behavior pattern characteristic of another tribe and, in consequence its fitness converges towards that of the donor tribe. At each generation, each tribe, *c*, has a probability α of receiving cultural input from another, randomly chosen, tribe, *d*:

$$w(c,t+1) = \begin{array}{c} w(c,t) \quad \text{with probability } 1-\alpha \\ (1-\beta)\cdot w(c,t) + \beta \cdot w(d,t) \quad \text{with probability } \alpha \end{array} \tag{3}$$

Thus, α represents the frequency of cultural assimilation, and β its magnitude; β being less than 1.0 represents situations when only some cultural traits are assimilated.

Intertribe Migration

At the start of each generation, a proportion, *m*, of individuals in each tribe leave and then each moves to a randomly chosen tribe (which could include their original tribe), and then adopts the culturally determined fitness of the receiving tribe.

Tribe Fission

At each generation, each tribe *c* has a probability, $q(c,\ t)$, of splitting into two separate tribes:

$$q(c,t) = \frac{\sum_h n(t,h,c)}{K\cdot P + \sum_h n(t,h,c)} \tag{4}$$

Thus, the probability of a tribe splitting rises as the tribe's population increases towards $K\cdot P$. After a split, a proportion *p* of the members of the tribe with a particular haplotype are assigned randomly to the first daughter tribe, and a proportion $1-p$ to the other, where *p* is chosen randomly from the [0 1] uniform distribution. The fitness of both daughter tribes initially equal that of their parent, but subsequently they evolve independently.

Table 1. Combinations of parameters used in model runs. Ten runs were made with all combinations of parameters in each vertical column.

Carrying capacity	$K = 1{,}000$	$K = 10{,}000$	$K = 100{,}000$
μ, mutation rate per generation	10^{-3}*	10^{-3}, 10^{-4}	10^{-4}, 10^{-5}
m, migration rate per generation	10^{-1}, 10^{-2}, 10^{-3}, 10^{-4}, 0	10^{-1}, 10^{-2}, 10^{-3}, 10^{-4}, 0	10^{-2}, 10^{-3}, 10^{-4}, 0§
P, splitting parameter per generation	1, 10, 100, 1,000	1, 10, 100, 1,000	100, 1,000¶

* For small populations, low mutation rates produced no genetic diversity so analyses were redundant.

§ For large populations, a very high migration rate ($m = 0.1$) produced too much genetic diversity within tribes to be reasonably modeled.

¶ For large populations, a low splitting parameter produced too many tribes to be reasonably modeled.

Procedure for Running Model

This model then has parameters K, μ, ρ, σ, α, β, m, and P, as well as the option of using either positive/negative innovations (as in equation 2) or just positive innovations.

First, I produced "baseline" populations, with the degree of genetic diversity expected given the carrying capacity, K, (which will be very close to mean population size because of the density-dependent nature of the formulation), the mutation rate (μ), the intertribe migration rate (m), and the tribe fission parameter (P). To do this, I ran the model without cultural innovation ($\rho = 0$) on a population initially consisting of K genetically and culturally identical individuals in one tribe. I noted when, at T_E generations, the overall haplotype diversity first exceeded the expected equilibrium genetic diversity given an infinite allele model (Birky *et al.* 1983):

$$\frac{M(T_E)^2 - \sum_h \left[\sum_c n(T_E, h, c)\right]^2}{M(T_E)(M(T_E) - 1)} > \frac{2\mu K}{(1 + 2\mu K)} \tag{5}$$

where M is the population size ($M(t) = \sum\sum n(t,h,c)$). I then ran the model for another T_E generations to produce an approximate "equilibrium" population. At this stage, I saved the genetic structure of the culturally undifferentiated population (given by $\{n(2T_E, h, c)\}$).

Using this procedure, I produced baseline populations for combinations of three carrying capacities: $K = 1{,}000$, 10,000, or 100,000; mutation rates so that $K \cdot \mu = 1$ or 10; splitting parameters $P = 1$, 10, 100 or 1,000; and migration rates, $m = 10^{-1}$, 10^{-2}, 10^{-3}, 10^{-4}, or 0.0. A few combinations of these parameters were not used because they were unrealistic or not computationally feasible (Table 1). I produced ten different baseline populations for each of the combinations of K, μ, P, and m given in the columns of Table 1.

I then "tested" each of these baseline populations for 200 generations in situations first (as a control) with no cultural innovation ($\rho = 0$), and then with all combinations of the following parameters governing cultural innovation (but no cultural assimilation, *i.e.*, $\alpha = 0$):

(1) Cultural innovations positive/negative, or just positive;
(2) Cultural innovation rate: $\rho = \{10^{-1}, 10^{-2}, 10^{-3}, 10^{-4}\}$;
(3) Cultural innovation magnitude: $\sigma = \{0.0125, 0.05, 0.2\}$.

I investigated the effects of cultural assimilation by making test runs with positive or negative innovations, all combinations of the cultural innovation parameters $\alpha = \{0, 0.01, 0.05, 0.1, 0.5\}$ and $\beta = \{0.2, 0.5, 0.8\}$, and each of the following sets of other parameters:

$K = 1{,}000$; $\mu = 10^{-3}$; $P = 1$; $m = 10^{-4}$; $\rho = 0.1$; $\sigma = 0.05$
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Output from each test run included the number of tribes in the population, the mean tribe size at the end of the test run (N), and the approximate number of migrants entering or leaving a tribe per generation, estimated by $N \cdot m$, and the haplotype and nucleotide diversities. Haplotype diversity (left side of equation 5) refers to the number and distribution of haplotypes in the population; nucleotide diversity also incorporates the number of base-pair differences between haplotypes. For the runs which included cultural assimilation, I calculated the ratio of the sum of the absolute changes in fitness that were due to assimilation to those that were due to innovation, as well as the variation in fitness among tribes (given by the coefficient of variation of $w(c)$), and the genetic divergence among tribes (G_{ST}).

Non-heritable Demographic Variation

In order to investigate whether purely demographic processes could reduce genetic diversity in a socially structured population, I amended the model for the testing phase in two ways. In both cases tribal fitness varies but this variation is not heritable, a contrast with the cultural models. In the first version, which follows the outline of Tiedemann and Milinkovitch's (1999) model (except for spatial structuring), the fitness of a tribe at any generation is given by:

$$w(c,t) = \mathrm{N}(1, \nu) \tag{6}$$

In this formulation tribal fitness is not heritable but varies with time and has an overall mean of 1.0 and standard deviation of ν for all tribes. Tribes with zero or negative fitness are automatically extirpated. Such non-heritable variation in fitness could arise from several causes including tribe-specific habitat use, tribe-specific disease epidemiology, or short-term "horizontal" cultures (transmitted among members of the same generation).

In the second version, using the basic model of Siemann (1994), tribes disappear through mass mortality at a rate of δ per generation. This is modeled by:

$$w(c,t) = \begin{matrix} 0 & \text{with probability } \delta \\ 1 & \text{with probability } 1-\delta \end{matrix} \tag{7}$$

The mass stranding mortalities of some whale species, especially the pilot whales (*Globicephala* spp.), suggested such a scenario (Siemann 1994).

For each of the combinations of K, μ, m, and P given in the columns of Table 1, and each of the ten equilibrium populations, each of these models was run for 200

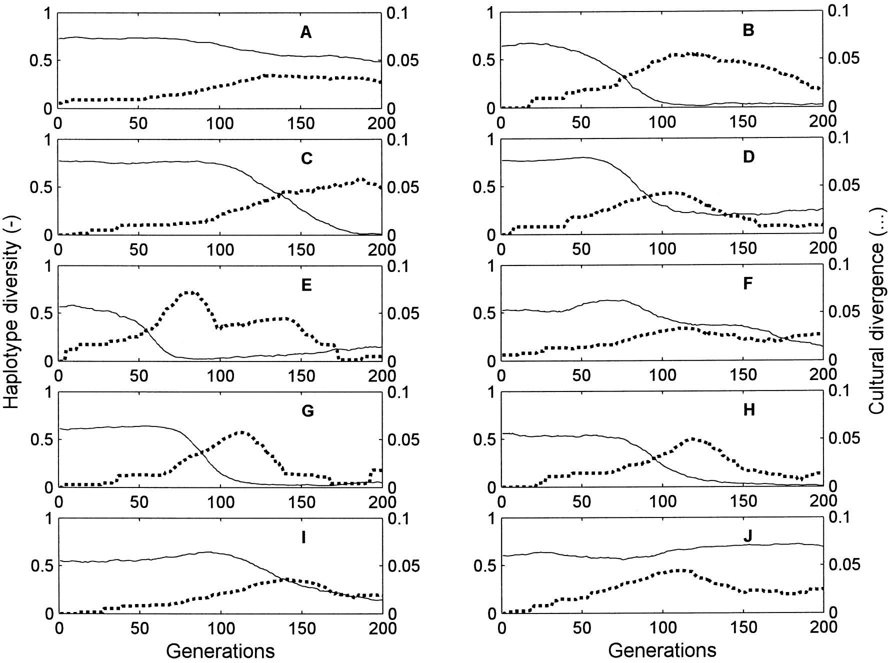

Figure 1. Ten runs of the model showing changes in haplotype diversity (-, left axes) and cultural divergence among tribes, given by CV(w), (· · ·, right axes) over 200 generations with the same parameters ($K = 10{,}000$, $P = 1$, $\mu = 0.0001$, $m = 0.0001$, $\rho = 0.001$, $\sigma = 0.05$, with just positive cultural innovations).

generations, with $\nu = \{0.4, 0.2, 0.1, 0.05\}$ in the first case, and $\delta = \{0.1, 0.05, 0.025, 0.0125\}$ in the second.

RESULTS

The Process of Cultural Hitchhiking

The model runs shown in Figure 1 illustrate the process of cultural hitchhiking. They use a set of parameters that sometimes, but not always, reduced genetic diversity. In the initial fifty-or-so generations, with little cultural divergence (equivalent to little variation in fitness) among tribes, genetic diversity remained fairly constant, but once the coefficient of variation of tribal fitness reached about 0.02 (*i.e.*, roughly a 2% difference between the fitness of different tribes), then genetic diversity often began to change. Sometimes (*e.g.*, Fig. 1F, I) there was an initial rise, indicating that the fitter tribes were initially smaller. Later on, genetic diversity usually fell, sometimes to very low levels (Fig. 1B, E, G, H), and at others to intermediate values (Fig. 1A, D). With low genetic diversity, indicating a population descended from just one or two culturally successful tribes, cultural divergence among tribes also declined (Fig. 1B, D, E, G, H, I). However, results of these model runs show much variation; sometimes, using the same set of parameters that produced substantial cultural hitchhiking, genetic diversity was not reduced

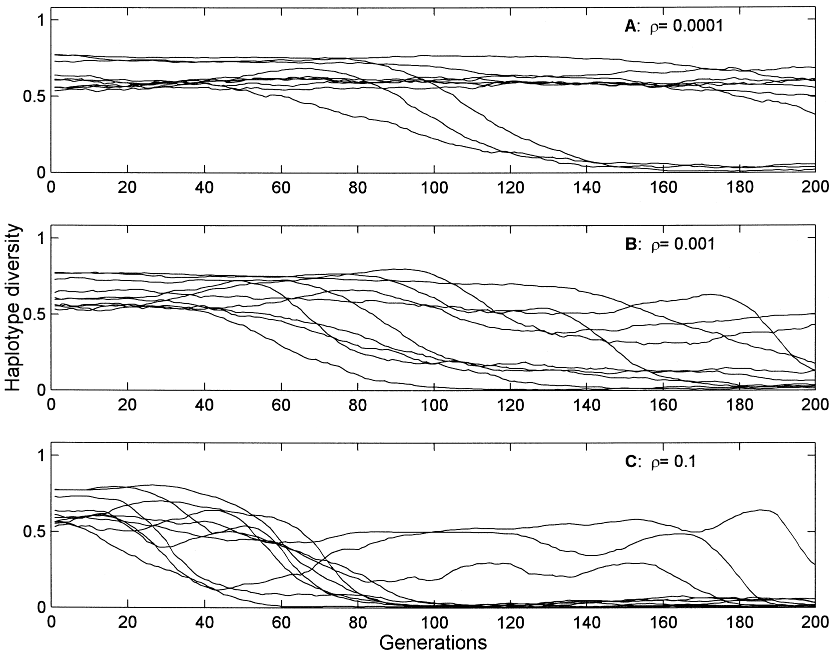

Figure 2. Examples of test runs of model using the same ten "equilibrium" populations (produced with $K = 10{,}000$, $P = 1$, $\mu = 0.0001$, $m = 0.0001$), and three rates of cultural innovation (A: $\rho = 0.0001$; B: $\rho = 0.001$; C: $\rho = 0.1$; $\sigma = 0.05$ with just positive cultural innovations in all cases).

within 200 generations despite a cultural divergence among tribes of greater than 0.02 (Fig. 1J).

Incidence of Cultural Hitchhiking

Under some parameter combinations, cultural evolution usually made little impact (*e.g.*, Fig. 2A), while in other circumstances the introduction of cultural evolution usually decimated genetic diversity within only a few tens of generations (*e.g.*, Fig. 2C). However, especially at intermediate parameter combinations, cultural hitchhiking was unpredictable, with genetic diversity sometimes plummeting and at others remaining unaffected (*e.g.*, Fig. 1, 2B). The values of K and P used to generate the results in Figure 2 result in populations consisting of about 100 tribes before cultural hitchhiking, so Figure 2C corresponds to about 2,000 innovations in the population per run during the 200 test generations, whereas in the runs of Figure 2B only approximately 20 innovations occurred per run, and in Figure 2A about two innovations per run. So, even with very few innovations (Fig. 2A), cultural evolution sometimes greatly reduced genetic diversity.

The models contain a number of parameters and produce several output measures. I have tried to organize this information in Figures 3 and 5 by displaying the rates of achieving moderate (50%–90%) or severe (>90%) reductions in genetic diversity after 200 generations for each parameter and output measure, over combinations of other parameters, for both haplotype and nucleotide diversity.

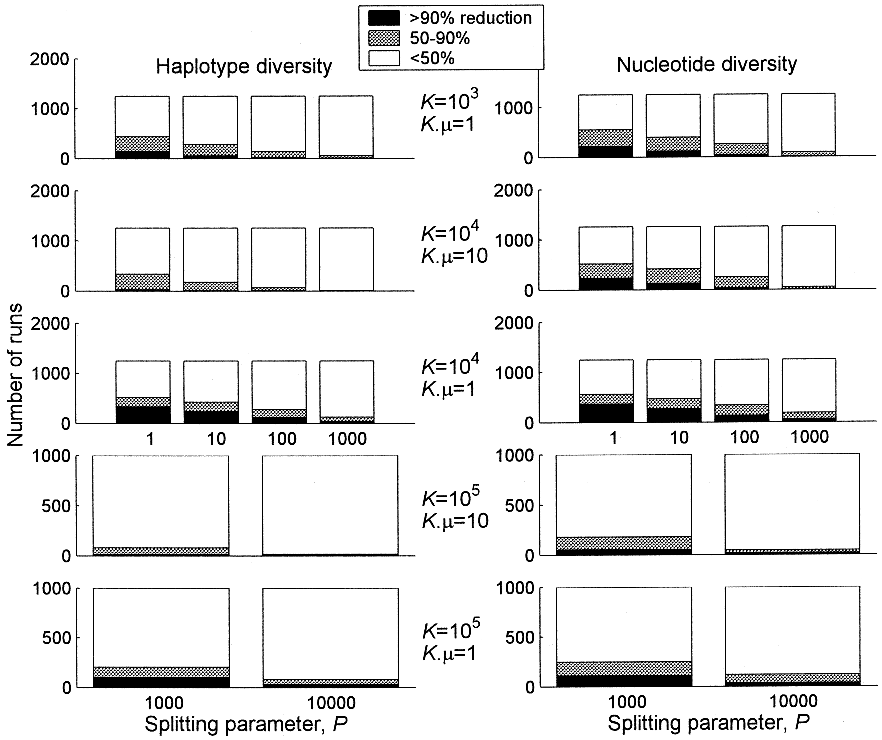

Figure 3. Frequencies of model runs producing different reductions in haplotype and nucleotide diversity compared over the range of the splitting parameter, P, for each combination of carrying capacity (K) and mutation rate (μ) listed in Table 1.

Below, I group results from related parameters and output measures, displaying only one representative measure when the pattern of reduction in genetic diversity is similar among parameters and measures.

Mutation Rate

For a given total population size, as indicated by K, cultural hitchhiking in haplotype diversity was more likely at $K \cdot \mu = 1$ than $K \cdot \mu = 10$ (Fig. 3). This is intuitively reasonable, as high mutation rates quickly counter reductions in genetic diversity from other causes. The reduction in nucleotide diversity was not so clearly affected by higher mutation rates as that of haplotype diversity (Fig. 3). This contrast is also expected as each new mutation generally increases haplotype diversity more than nucleotide diversity.

Population Size

Cultural hitchhiking did not obviously become more or less important over the range of population sizes investigated (Fig. 3). Although cases of reduced genetic diversity became less frequent at the highest population sizes ($K = 100{,}000$), this may well be related to the relatively higher values of the splitting parameter (P)

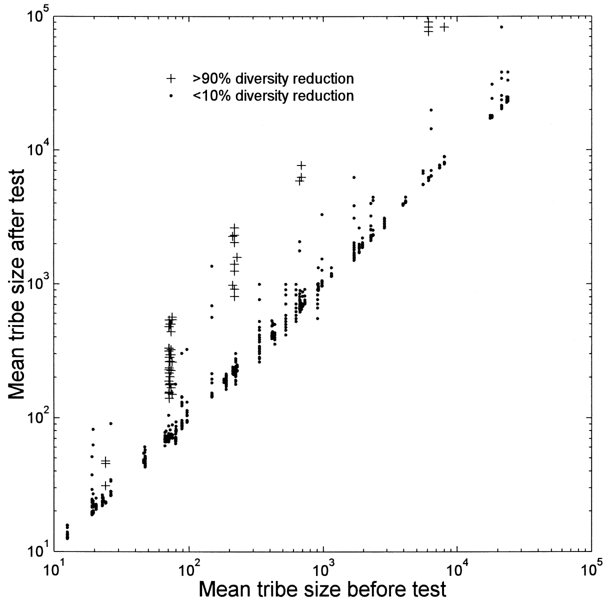

Figure 4. Mean (over 10 runs with a particular set of parameters) tribe size after 200 generations of cultural evolution plotted against the initial mean tribe size in cases where haplotype diversity was reduced by more than 90% (+) or less than 10% (•).

used with this population size (see Table 1, Fig. 3). It was impracticable to use lower splitting parameters at this population size, as large numbers of tribes were produced and computer run-times became prohibitively long.

Tribe Size

Reduction in genetic diversity depended on having reasonably low values of the splitting parameter, P, (Fig. 3) so that the population was initially divided into quite a number of small tribes. However, at the end of the 200 generations, and especially with the larger populations sizes (K), large tribe size (N) better indicated cultural hitchhiking (Fig. 4). The process of cultural hitchhiking, in which culturally fitter tribes overwhelm those with lower fitness, tends to increase mean tribe size (Fig. 4). Over all tests runs which did not include cultural assimilation, tribe size increased by a mean factor of 3.3 when nucleotide diversity was reduced by 50%–60% and a factor of 5.2 when nucleotide diversity was reduced by more than 90%.

Migration Rate

As the migration rate between tribes (m) and the number of migrants per tribe per generation (Nm, Fig. 5A) increased, a reduction in genetic diversity became less likely, because intertribe migration tends to reduce genetic divergence among tribes. However, cultural hitchhiking was still present at rates of about 10 migrants per generation per tribe (Fig. 5A).

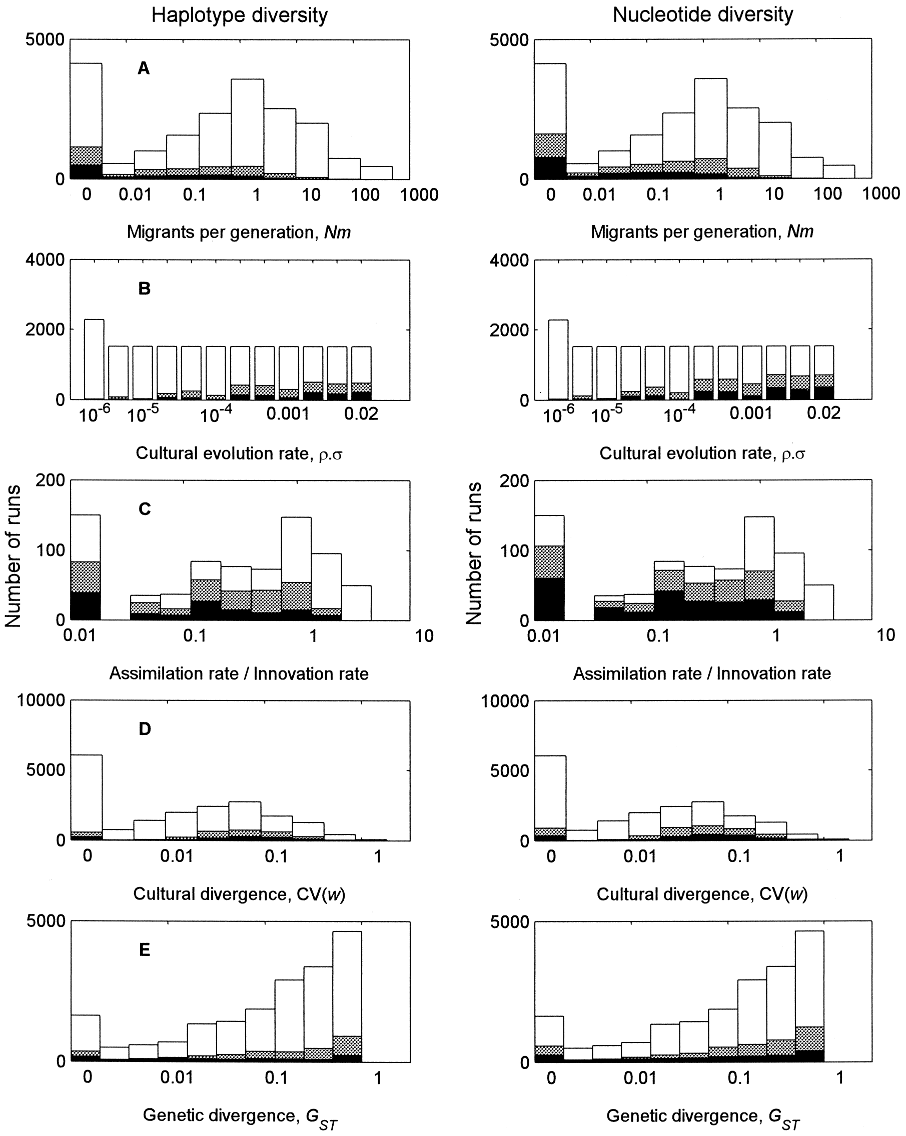

Figure 5. Frequencies of model runs producing different reductions in haplotype and nucleotide diversity (>90% reduction in black; 50%–90% reduction in gray; <50% in white) compared over the range of: A, estimated migrants per tribe per generation (*Nm*); B, cultural evolution rates ($\rho \cdot \sigma$; approximate mean change in fitness per generation); C, cultural assimilation rates (given by the ratio of the total change in fitness due to assimilation from neighboring tribes to that due to innovation from within tribes); D, the cultural divergence among tribes at the end of the test runs (given by CV(w)); and E, the genetic divergence among tribes at the end of the test runs (given by G_{ST}). The distributions use outcomes of runs with all combinations of input parameters, with the exception of that for cultural assimilation (C) when only a reduced selection of parameters, more likely to show cultural hitchhiking, was used (see text).

Rate of Cultural Evolution

In Figure 5B, the incidence of cultural hitchhiking is plotted against the cultural evolution rate ($\rho \cdot \sigma$), the proportional change in fitness per generation. It is clear that genetic diversity was increasingly likely to be reduced as the cultural evolution rate increased, and that the process rarely operated if cultural evolution changed fitness by less than 0.005%/generation. Plots of the likelihood of cultural hitchhiking against ρ and σ separately showed the same pattern as in Figure 5B.

Positive or Negative Innovations

Models with just positive, or positive and negative, cultural innovations gave similar rates of moderate and severe cultural hitchhiking. Genetic hitchhiking can operate on purely deleterious mutations (Charlesworth *et al.* 1993). So, although a system of purely deleterious cultural innovations would seem unlikely, I checked to see whether cultural hitchhiking could result from purely negative innovations by making runs with the parameter combinations used in Figure 2, and just negative innovations. Although the highest rate of cultural innovation ($\rho = 0.1$) produced some reduction in genetic diversity, this (mean reduction of 77%) was less than with purely positive innovations (mean of 91% for the runs in Fig. 2C). The lower rates of cultural innovation ($\rho = 0.001, 0.0001$) gave no reduction at all. Therefore negative innovations seem to have less impact on genetic variation than positive ones. This is reasonable, as elevating the fitness of one tribe above all others is likely to produce a selective sweep more easily than lowering fitness in just some tribes.

Cultural Assimilation

The addition of cultural assimilation reduced the effects of cultural hitchhiking (Fig. 5C). As the amount of fitness change due to cultural assimilation from other tribes approached that due to innovations within the tribe, marked reductions in genetic diversity became less frequent, and when fitness was more affected by assimilation than innovation, cultural hitchhiking virtually disappeared. The likelihood of cultural hitchhiking decreased with increasing values of both α, the frequency of cultural assimilation, and, to a lesser extent, β, its magnitude.

Cultural and Genetic Divergence among Tribes

Although cultural divergence among tribes is a prerequisite for cultural hitchhiking to reduce genetic variability (Fig. 1), the amount of cultural divergence among tribes remaining ($\mathrm{CV}(w(c))$) after 200 generations varied considerably (Fig. 1, 5D). Cultural hitchhiking also needs genetic divergence among tribes; initial values of G_{ST} exceeded 0.5 in most instances of substantial cultural hitchhiking (Fig. 6). However, after 200 generations G_{ST} was often reduced below 0.2 (Fig. 5E, 6). Thus, although cultural hitchhiking needs genetic and cultural differentiation among tribes to operate, it can substantially reduce both.

Non-heritable Demographic Variation

Table 2 summarizes the results of running the model with non-heritable variation in tribal fitness (as given by Eq. 6 or 7). In the first scenario, variation in

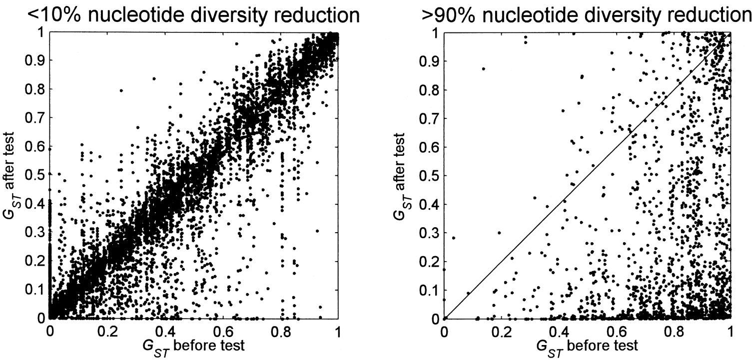

Figure 6. Genetic diversity among tribes (G_{ST}) before and after 200-generation test runs with little (left) and substantial (right) cultural hitchhiking.

fitness had to be quite substantial (CV $\geq \sim 0.2$) to obtain even a low diversity reduction (8% of runs showing >50% reduction in diversity and 0.4% having >90% reduction with CV = 0.2). With very substantial tribal fitness variation (CV = 0.4), reduced genetic diversity was more frequent, but in these runs the total population frequently went extinct. In the second scenario, with mass mortality of tribes, fairly low rates of tribal extirpation (1.25% per generation) produced some reductions in genetic diversity (7% of runs showing greater than 50% reduction in genetic diversity), but population extinction was even more prevalent (22% of runs, Table 2). To reduce genetic diversity substantially using non-heritable variation in tribal fitness, a reasonable proportion of the tribes in a population must be extirpated within not too many generations, but, if this happens, then the population itself is at considerable risk.

DISCUSSION

Generality and Validity of Results

The results suggest that cultural hitchhiking will reduce genetic diversity if: (1) genetic mutations are not too frequent (relative to tribal turnover); (2) tribes split fairly frequently when they constitute a substantial part of the population so that, before cultural evolution comes into play, there are quite a number of small tribes; (3) individuals rarely move between tribes ($Nm < \sim 10$); (4) cultures evolve at least slowly (with the culturally determined contribution to the fitness of a tribe changing by a mean of more than about 0.005%/generation); and (5) cultural assimilation changes fitness less than cultural innovation. These results are consistent with those from more general theory of subdivided populations (*e.g.*, Whitlock and Barton 1997), especially that as connections between subpopulations are reduced, expected genetic diversity decreases.

Although much more realistic than its predecessor (Whitehead 1998), the model used here still simplifies the social, demographic, genetic, and cultural dynamics of a real population of matrilineal whales, or any other animals. So how likely are these results to indicate whether genetic diversity has been reduced by cultural evolution in real populations?

Table 2. Results of running model with non-heritable variation in tribal fitness in control conditions (no variation), different levels of normally distributed variation in tribal fitness (given by the standard deviation of the tribal fitness, ν) and with mass tribal mortality (at a rate of δ per generation). Shown are the number of runs with little (<50%), moderate (50%–90%) or severe (>90%) reductions in haplotype diversity after 200 generations, as well as the number of runs in which the total population went extinct.

	Reduction in haplotype diversity			
Conditions	<50%	50%–90%	>90%	Extinction
Control	756	4	0	0
$\nu = 0.05$	757	3	0	0
$\nu = 0.10$	745	14	1	0
$\nu = 0.20$	700	57	3	0
$\nu = 0.40$	473	130	65	92
$\delta = 0.0125$	544	29	21	166
$\delta = 0.0250$	285	46	18	411
$\delta = 0.0500$	132	35	13	580
$\delta = 0.1000$	71	38	29	622

The patterns found over a wide range of parameter estimates and model variants usually agreed, and the general results concord with those of the quite differently structured territorial model used to investigate cultural hitchhiking in humans (Whitehead *et al.* 2002). Conditions for cultural hitchhiking were similar between the results of the two models for migration rates among tribes and the amount of permissible cultural assimilation between tribes. However, rates of cultural evolution as low as 0.005%/generation led to reduced genetic diversity in the geographically unstructured model used here, whereas the territorial model for humans set a lower limit at about 0.3%/generation. This difference may relate to the increased importance of stochastic events in the highly structured human model.

The model assumes that innovations spread through tribes within a generation. This may not be realistic, especially with large tribe sizes. However, a gradual change in tribal fitness over a few generations, rather than the sudden step modeled here, would seem unlikely to change the results of the modeling in any substantial way. In killer whales, *Orcinus orca*, (Table 3), and humans, there are cultural differences at several levels of social structure, which could allow multilevel cultural hitchhiking, where innovations spread quickly through "subtribes" and then more slowly, or perhaps never, into the wider tribe. Modeling such situations would be complex, but I can see no reason why the results should not be basically similar to those found here.

The model used in this paper is conservative in several respects. For practical reasons, it only considered 200 generations of cultural evolution, and, especially with low rates of cultural evolution (*e.g.*, Fig. 2), the process may take longer to operate. Additionally, when tribes split, the model randomly assigns individuals to the two daughter tribes. In reality, the tribal division is likely to occur, at least partially, along kinship lines (*e.g.*, in killer whales; Ford *et al.* 2000) so that the daughter tribes will have less internal genetic diversity and more genetic divergence than envisioned by the model, thus providing a better substrate for cultural hitchhiking. Similarly, intertribe migration may be preferentially directed to genetically, and/or culturally, similar tribes, in contrast to the random movement modeled.

Table 3. Possible cultural "tribes" in matrilineal whales.

Species	"Tribe"	Tribe size	Intertribe migration rate of females	Mating within tribe?	Cultural attributes of tribe
Killer whale	"Type" ("resident", "transient")	~1,000–10,000	None	Yes	Vocal repertoire, foraging patterns, habitat use, social system, diet
"Resident" killer whale	"Community"	~100	Low	Yes, usually	Vocal repertoire, habitat use, greeting ceremonies
	"Clan"	~50	Very low	Usually no	Vocal repertoire
	"Pod"	~10	High	No	Vocal repertoire, foraging patterns
	"Matrilineal group"	~4	Very low	No	Vocal repertoire
Sperm whale	"Social unit"	~10	Some	No	Vocal repertoire, movement patterns
	"Clan"	~10,000	Probably low	?	Vocal repertoire, habitat use, movement patterns
Longfinned pilot whale	"Unit"	~10	?	?	?
	"Pod"	~100	?	Very rare	?
Shortfinned pilot whale	"Pod"	~10	?	?	?

References:
Killer whales: Baird 2000, Barrett-Lennard 2000, Ford *et al.* 2000, Hoelzel *et al.* 2002, Yurk 2003.
Sperm whales: Whitehead 1999*b*, 2003*b*, Whitehead and Weilgart 2000, Rendell and Whitehead 2003, Whitehead and Rendell 2004.
Longfinned pilot whale: Amos 1993, Ottensmeyer and Whitehead 2003.
Shortfinned pilot whale: Heimlich-Boran 1993, as interpreted by Ottensmeyer and Whitehead 2003.

For all these reasons I believe that the model gives useful indications as to the conditions in which genetic diversity in a haploid gene may be reduced by cultural evolution.

The results can easily be extended to diploid genes, simply by replacing the term "individuals" by "gene copies" in the formulation of the model. Thus the equilibrium population contains $K/2$ individuals, and an average of $m/2$ individuals migrate between tribes or mate across tribes per generation.

Relationship to Other Models

Gene-culture coevolution has been explored from a number of perspectives, using a wide range of models (*e.g.*, Feldman and Cavalli-Sforza 1984, Boyd and Richerson 1985, Laland 1992, Bull *et al.* 2000). A general result of this work is that in a dual-replicator system, cultural evolution may, under some circumstances, affect genetic evolution, and *vice versa.* Among the results most relevant to the cultural hitchhiking hypothesis are Whitlock and Barton's (1997) general conclusion that population subdivision, resulting from any mechanism, tends to reduce genetic diversity, and Bull *et al.*'s (2000) model of meme-gene coevolution which found that cultural evolution can have a "significantly detrimental effect on the evolution of genes." However, as far as I know, the only other models that have specifically addressed the effects of cultural evolution on the diversity of neutral genes are the original, and greatly simplified, presentation of cultural hitchhiking (Whitehead 1998), and the territorial model developed to explore the issues in humans (Whitehead *et al.* 2002).

Detecting Cultural Hitchhiking

Cultural hitchhiking depends on culturally determined fitness differences between tribes, and genetic divergence among them (Fig. 1, 6). Thus, I had hoped that assessments of genetic and cultural diversity among tribes might be used to indicate whether cultural hitchhiking had operated. Unfortunately, the process of cultural hitchhiking often reduces both cultural and genetic divergence among tribes (Fig. 1, 6), and so this hope was not fulfilled. There are both theoretical and empirical grounds (in humans) for believing that cultural evolution may homogenize populations (*e.g.*, Laland *et al.* 2000).

However, the process may leave other distinctive genetic or cultural traces. If the fitness-influencing culture transmits in parallel with one set of genes but not another, we might expect reduced diversity in the former but not the latter. So, if culture transmits, and tribes are formed, along matrilineal lines, then mtDNA diversity may be reduced, but not that of patrilineally-transmitted genes, such as those in the Y-chromosome of mammals. Measures of the relative diversity of genes with different transmission systems can thus indicate the presence of cultural hitchhiking in populations with reduced genetic diversity (Schlötterer 1999). They may allow us to distinguish between cultural hitchhiking and population bottlenecks as causes of reduced diversity, as a bottleneck reduces the diversity of all genes (although not equally, see Amos 1996, and assortative mating may complicate the picture). However, such measures of relative gene diversity cannot distinguish between cultural hitchhiking and molecular hitchhiking (Maynard Smith and Haigh 1974). Also, when mating is within tribes, all genes are transmitted in parallel with the culture.

Another approach is to look at the dynamics of the population; instead of G_{ST}, we could examine intertribe migration directly; instead of CV(w), study cultural evolution within tribes, and cultural assimilation between them. Unfortunately, these dynamic studies are generally much harder to address than the "snapshot" measures.

Cultural Hitchhiking in Matrilineal Whales

So can I say more about the original hypothesis (Whitehead 1998), that cultural hitchhiking has reduced the mtDNA diversity of four species of matrilineal whale, the killer whale, the sperm whale (*Physeter macrocephalus*), the shortfinned pilot whale (*Globicephala macrorhynchus*), and the longfinned pilot whale (*G. melas*)? In all these species, mtDNA diversity is many-fold below that found in other species of Cetacea with similar population sizes (Whitehead 1998) and geographic ranges (Whitehead 2003*a*). Here I will reassess the likelihood of cultural hitchhiking within these species in the light of the results presented in this paper and new results on the social, genetic, and cultural structures of their populations.

Firstly, cultural hitchhiking, at least in haplotype diversity, requires that the mutation rate should be less than about ten times the inverse of the population size. Mutation rates in the part of the control region of the mitochondrial genome of cetaceans that is usually sequenced are of the order of 10^{-7}/generation (Whitehead 1998), which means that, even with population sizes of 1,000,000 whales as is reasonable for sperm and pilot whales, the mutation rate lies well below the inverse of the population size.

We need "tribes" to assess the other four conditions for cultural hitchhiking suggested by the modeling: that tribes split when they become large; that movement between tribes is limited; that tribal cultures evolve, and that innovation within tribes is more important than assimilation. Table 3 lists potential candidates for tribes in the matrilineal whales under the names ("pods," "clans," "units," . . .) which have been used in the primary literature for these species.

The killer whale is the best known of the four species, especially from studies in the vicinity of Vancouver Island off the west coast of North America. A range of matrilineally based and hierarchically organized social structures are recognized, each mapped onto cultural distinctions (Table 3; Baird 2000). Any of these could have been subject to cultural hitchhiking, although all have some drawbacks as candidates for the "tribes" of my model. At one extreme, the "types" are so different that they may well be subspecies and do not appear to compete for resources (Baird 2000) and, at the other, "matrilineal groups" are very small and so less indicative of cultural hitchhiking (Table 3). The best candidates may be "clans" or "communities." Killer whale communities are at least sometimes geographically based (Ford *et al.* 2000), and so the results of the model described in this paper may be less applicable than those of the territorial model developed for humans (Whitehead *et al.* 2002). Non-vocal culture is not well recognized at the level of the clan, but it may exist. We do know that some killer whale social entities split when large (Ford *et al.* 2000), that killer whale cultures evolve (Deecke *et al.* 2000), and we can infer from the cultural distinctiveness of the social structures (Table 3) that assimilation does not overwhelm innovation. Thus, data on killer whales are generally consistent with the conditions for cultural hitchhiking, although I have some doubts as to whether there are suitable tribes. Both nuclear and mtDNA diversity are low in killer whales (Hoelzel *et al.* 2002), indicating that, if cultural hitchhiking has operated in this species, it did so at a level at which mating occurs predominantly within tribes, such as "communities" or "types." Of course, cultural hitchhiking may have operated at more than one of the levels of killer whale social structure, simultaneously or sequentially.

There are two currently known candidates for tribes in sperm whales (Table 3). "Social units" may be too small and unstable (Christal *et al.* 1998) to support cultural hitchhiking (Mesnick *et al.* 1999). The recently discovered "clans," which are large, sympatric, and distinctive in vocal and non-vocal cultures, seem excellent candidates (Rendell and Whitehead 2003, Whitehead and Rendell 2004), but the rates of migration among them and cultural evolution within them have yet to be estimated. In sperm whales, nuclear DNA, unlike mtDNA, seems diverse (Lyrholm *et al.* 1999), consistent with cultural hitchhiking in a population with at least some mating between tribes.

The social and population structures of pilot whales are less well known, and there have been no published studies of cultural attributes in these species. The two potential tribe structures suggested for longfinned pilot whales, "units" and "pods" (Table 3), come from very different types of study, and are in some ways mutually incompatible (Ottensmeyer and Whitehead 2003). However, pilot whale societies seem, in some ways, comparable to those found in killer and sperm whales, and there may be other tribe-like structures not listed in Table 3; it took many years of work before "clans" were uncovered in either killer or sperm whales (Ford 1991, Rendell and Whitehead 2003).

What kinds of culture could drive cultural hitchhiking in these species? They would need to be quite stable across generations, affect fitness, and be hard to assimilate. As in the case of humans (Whitehead *et al.* 2002), elements of social behavior and foraging strategies may be the best candidates. For killer and sperm whales there is good evidence that cultural variation in foraging strategies exists among the putative tribes listed in Table 3 (Boran and Heimlich 1999, Whitehead and Rendell 2004), and in sperm whales at least these translate into differences in foraging success, and so probably fitness (Whitehead and Rendell 2004).

Thus, the results of the modeling in this paper, and empirical research in the past five years, have strengthened the case for cultural hitchhiking in the matrilineal whales. In particular, the modeling in this paper and new empirical results largely resolve concerns about the constancy of innovations (Deecke *et al.* 2000) and the stability of whale societies (Mesnick *et al.* 1999, Tiedemann and Milinkovitch 1999) raised by the results of the original simple model (Whitehead 1998). The results in this paper substantially widen the conditions under which cultural hitchhiking may occur compared with the previous model; for instance, by allowing cultural evolution in many small steps, by allowing negative as well as positive innovations, by increasing the amount of allowable intertribe migration, and by considerably lowering the minimum rate of cultural evolution that is consistent with cultural hitchhiking.

The results of this paper further weaken the case for demographic, non-heritable processes as the sole cause of the low mtDNA diversity of the matrilineal whales. Although such processes can reduce a population's genetic diversity, in the version with varying fitness, the variation must be substantial, a mean of at least 20% per generation compared with a lower limit of about 0.005% per generation for heritable cultural variation, and such populations are very likely to be driven extinct (Table 2). In the tribal extirpation model, population extinction is even more likely (Table 2). Variations of the demographic models could possibly be introduced to safeguard the total population from extinction but allow frequent tribal extirpations (perhaps by having a lower tribal extirpation rate if a tribe is the only one left in the population, or the spatial effect mentioned by Tiedemann and Milinkovitch 1999). If tribes split along matrilineal lines, or intertribe migrations are principally between genetically similar tribes, then, as in the case of cultural hitchhiking, reductions in genetic diversity may be more readily achieved by demographic processes than is indicated by the models used here. However, with the results now available, the purely demographic models do not appear to be very promising alternatives to cultural hitchhiking.

It seems likely that combinations of non-heritable and heritable tribal fitness can effectively reduce genetic diversity. Thus, the demographic and cultural hitchhiking explanations for the low mtDNA diversity of the matrilineal whales are not mutually exclusive.

Other explanations for the reduced mtDNA diversity of the matrilineal whales, such as genetic bottlenecks (Lyrholm *et al.* 1996, Hoelzel *et al.* 2002) and selection (Janik 2001), should not be discarded, although they also seem to make assumptions or predictions that are inconsistent with what we know of the biology of the species (Whitehead 1999*a*, Rendell and Whitehead 2001).

Cultural Hitchhiking in Other Species

The phenomenon modeled here could have occurred in other animals, but they would need to possess a rather unusual combination of characters: little geographically based population structure, social structuring into tribes with distinctive cultures, and low intertribe gene flow. Little-studied cetaceans, especially among the larger odontocetes, such as false killer whales (*Pseudorca crassidens*) and narwhals (*Monodon monoceros*), are perhaps the best candidates, and both of these species have low mtDNA diversity (Palsbøll *et al.* 1997, Chivers *et al.* 2003[1]). In both elephants and bats there are sympatric social structures which seem to have distinctive cultures (Moss and Poole 1983, Boughman and Wilkinson 1998, McComb *et al.* 2001), but in these species geographical barriers probably usually prevent species-wide cultural hitchhiking (see *e.g.*, Georgiadis *et al.* 1994).

Conclusion

The models developed in this paper considerably widen the known conditions under which cultural processes may reduce genetic diversity through cultural hitchhiking. Within geographically unstructured populations, considerable reduction of genetic diversity requires only low levels of cultural evolution, and diversity is still reduced with moderate levels of intertribe migration and cultural assimilation. Knowledge of the population and social structure of the matrilineal whales is largely consistent with the conditions for cultural hitchhiking. The results invalidate some previous criticisms of cultural hitchhiking in the matrilineal whales and indicate the implausibility of alternative scenarios using purely demographic models, although non-heritable and heritable fitness variation may work together to

[1] Chivers, S. J., R. G. LeDuc and R. W. Baird. 2003. Hawaiian island populations of false killer whales and shortfinned pilot whales revealed by genetic analysis. Abstract. 15th Biennial Conference on the Biology of Marine Mammals. Greensboro, NC. December 2003. Page 32.

reduce genetic diversity, and it would be worth examining the effects of revising the models so that tribes split along matrilineal lines and/or intertribe migrations are principally between genetically similar tribes. Thus, I have strengthened the case for cultural hitchhiking in the matrilineal whales, but it is still far from proven. Unfortunately, this study also shows that measures of genetic and cultural variation among tribes are not good indicators of past cultural hitchhiking.

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