Culture and Genetic Evolution in Whales

H. Whitehead (*1*) explains low nucleotide diversities in the control region of the mitochondrial DNA (mtDNA) of matrilineal whale species with the use of a theory developed for molecular "hitchhiking," in which diversity at a neutral locus is reduced by selection at a linked locus. As appealing as this idea is, we question the strength of the evidence presented to support a connection between whale culture and genetic variation.

In the proposed model [figure 1 in (*1*)], if nonmatrilineal transmission is greater than 0.5%, then mtDNA diversity is little reduced [figure 1D in (*1*)]. We agree that killer whales, pilot whales, and sperm whales show the best evidence for matrilineal social structure (*2*), yet even in these species the parameters of the model are likely not met. This is especially so in the case of sperm whales, where recent studies show that sperm whale units (*3*) and groups (*4*) are composed of both related and unrelated individuals, at numbers significantly above the 0.5% threshold (*1*) at which mtDNA diversity is little reduced. If unrelated individuals co-occur within a group, then the cultural transmission of advantageous information must be done in such a way that members outside a particular matriline are not privy to it.

The model is presented to demonstrate the feasibility of a cultural trait that devastates mtDNA diversity. After such a trait sweeps through the population, molecular diversity should regenerate. Even if continual cultural innovation suppresses regeneration of diversity within geographic populations, one would not expect divergence among isolated populations to remain low. A good example of this problem would be short-finned pilot whales, whose distribution is generally thought to be restricted to warm waters. It is difficult to imagine selective sweeps, cultural or otherwise, acting to maintain low inter-ocean diversity. To us, the finding of low inter-ocean mtDNA diversity suggests continuing selection.

The data summarized to support the report's hypothesis [table 1 in (*1*)] deserve close scrutiny. In comparative studies, it is necessary that the playing field be level. Samples need to be collected over comparable scales (geographic, temporal, and numerical), which is no trivial task in ocean-dwelling species. Moreover, the unsettled nature of cetacean alpha level taxonomy affects our ability to accurately compare estimates of molecular diversity across taxa. For example the "killer whale" and the "bottlenose dolphin" are names given to what we now understand to be complexes comprised of genetically distinct inshore and offshore taxa and suggested to be separate species (*5*). Table 1 in the report may be presenting diversity levels calculated both within species and within genera.

There is strikingly low control region diversity in some cetacean species, all the more remarkable given the vast geographic ranges of these animals. With the above concerns in mind, we advocate the investigation of a more general question: What factors could reduce mtDNA diversity in whales, and how does their marine existence affect this pattern?

Sarah L. Mesnick
Barbara L. Taylor
Richard G. Le Duc
Sergio Escorza Treviño
Greg M. O'Corry-Crowe
Andrew E. Dizon
Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanographic and Atmospheric Administration, La Jolla, CA 92038, USA
E-mail: sarahlyn@caliban.ucsd.edu

References

1. H. Whitehead, *Science* **282**, 1708 (1998).
2. R. C. Connor *et al*., *Trends Ecol. Evol.* **13**, 228 (1998).
3. J. Christal, thesis, Dalhousie University, Halifax (1998).
4. K. Richard *et al*., *Proc. Natl. Acad. Sci. U.S.A.* **93**, 8792 (1996); J. Bond, thesis, Cambridge University (1999); S. Mesnick *et al*., in preparation.
5. B. Curry, thesis, Texas A & M University, Galveston, TX (1997); A. R. Hoelzel, M. Dahlheim, S. J. Stern, *J. Hered.* **89**, 121 (1998); R. Hoelzel, C. W. Potter, P. B. Best, *Proc. R. Soc. London B.* **265**. 1177 (1998).

12 February 1999; accepted 10 May 1999

Whitehead (*1*) found low mtDNA diversity in whales with a matrilineal social structure. He interpreted this finding as resulting from "hitchhiking" of neutral mtDNA alleles through selection on maternally transmitted cultural traits.

The matrilineal structure of *Globicephalas melas*, the long finned pilot whale, has been studied in great detail by the use of molecular markers (*2*). Thus, one might ask if the current knowledge about the social structure in this species is compatible with the predictions and requirements for transmitted cultural traits. Are cultural traits transmitted through females only? Both sexes are observed in the social groups, and thus an advantageous behavior may be rapidly adapted from males. With the use of polymorphic microsatellite loci, Amos *et al.* (*2*) demonstrated that males in a social group (pod) are related to the females, but do not reproduce in their natal group. It is generally assumed that, during the mating period, males temporarily leave their group, mate with females from a different group, and return to their natal group. Thus, in pilot whales, cultural transmission need not be limited to females and could still result in a reduced mtDNA variability.

While the behavior of pilot whales is fully consistent with the proposed cultural transmission, more scrunity should be applied to the molecular data on which the hypothesis is based. Whitehead calculated Tajima's "D" statistic (*3*) to exclude the possibility that the reduced mitochondrial variability is the result of an advantageous base substitution in the mtDNA that is sweeping through the population. The absence of a significant value of D was taken as evidence against a putative nonneutral behavior of mtDNA causing the observed low mtDNA variability. Although this conclusion may be correct, the alternative scenario of maternally transmitted cultural traits does not differ qualitatively. In both cases, it is assumed that the target of selection resides outside the sequenced part of the mtDNA. Thus, hitchhiking of the sequenced DNA region together with the target of selection is assumed. The effect on the sequenced mtDNA region is expected to be the same, whether or not a base substitution in the mtDNA or cultural transmission through the bearer of the mtDNA is causing the selective advantage. Consequently, the predictions for Tajima's D are identical in both cases. A nonsignificant value of D could also be regarded as a rejection of the cultural transmission hypothesis of Whitehead.

In summary, the data presented by Whitehead do not provide evidence for or against the hypothesis of maternally transmitted cultural traits that confer selective advantage. Low mtDNA diversity could be a result of the effective population size of these species simply being smaller than that of the other species surveyed. Census population sizes are known to be an inaccurate estimator of effective population sizes (*4*), thus, data from nuclear sequences are needed for an independent estimate of the effective population size. Microsatellites, for which some data have been already collected (*2*, *5*, *6*), may not be the most appropriate genetic marker to test this hypothesis, given the well-documented problem of ascertainment bias (*7*) as well as large differences between individual microsatellite loci (*8*).

Christian Schlötterer
Institut für Tierzucht und Genetik, Josef-Baumann Gasse 1, A-1210 Wien, Austria
E-mail: christian.schloetterer@vu-wien.ac.at

References and Notes

1. H. Whitehead, *Science* **282**, 1708 (1998).
2. B. Amos, C. Schlötterer, D. Tautz, *ibid.* **260**, 670 (1993).
3. F. Tajima, *Genetics* **123**, 585 (1989). Briefly, Tajima's D is a popular test statistic used to infer selection from DNA sequences.
4. R. Frankham, *Genet. Res.* **66**, 95 (1995).
5. A. R. Hoelzel, M. Dahlheim, S. J. Stern, *J. Hered.* **89**, 121 (1998).
6. P. J. Palsbøll *et al.*, *Nature* **388**, 767 (1997).
7. H. Ellegren, C. R. Primmer, B. C. Sheldon, *Nature Genetics* **11**, 360 (1995).
8. B. Harr, B. Zangerl, G. Brem, C. Schlötterer, *Mol. Biol. Evol.* **15**, 176 (1998).
9. I thank R. Bürger for helpful comments. The laboratory of C.S. is supported by Fonds zur Förderung des wissenschaftlichen Forschung (FWF) and the European Union.

12 December 1998; accepted 10 May 1999

Whitehead notes (*1*) that mtDNA variation is about tenfold lower in matrilineal whales than in whales without that specific social structure. He interprets this correlation as selection of maternally transmitted cultural traits on which neutral mtDNA alleles "hitchhike." His hypothesis requires that selection of cultural traits occurs in whales, as well as the questionable additional assumption that lateral transmission of the behavior to unrelated females is below 0.5%. We suggest, rather, that lower variability of mtDNA in matrilineal whales does not require selection of mtDNA haplotypes or linked cultural traits because any stochastic heterogeneity in fecundity through space and time will cause a drastic reduction of mtDNA variability in matrilineal populations.

To test our hypothesis, we used sperm whale life history parameters and simulated the effect of (i) matrilineal social structure and (ii) stochastic heterogeneity in fecundity on mtDNA variation (*2*). Our results show that a large drop in mtDNA diversity occurred only when matrilineal structure was implemented (Fig. 1). Stochastic differences in reproduction through time and space increase the variance in reproductive success among haplotype matrilines—causing a decrease in mtDNA variation observed in the whole population—only if these haplotype matrilines are spatially associated through the existence of *individual* matrilines (that is, matrilineal social structure).

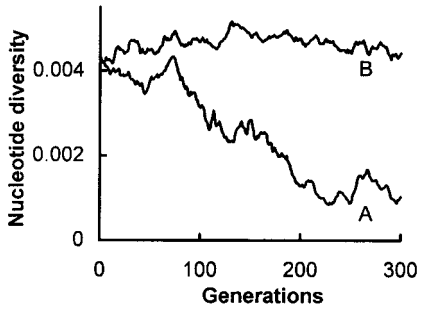


Fig. 1. Mitochondrial DNA nucleotide diversity (mean of 10 replicates) over 300 simulated generations with (A) and without (B) matrilineality.

It is unlikely that the environment will be so homogeneous as not to contribute to variation in reproductive success through evolutionary time and across the whole range of the species distribution. At any time, variations in the environment will slightly increase the reproductive success of animals in some areas as compared with others. However, this heterogeneity will cause rapid extinction of some haplotypic matrilines, while others will flourish, only if individuals bearing haplotypes from the same mitochondrial lineage are spatially associated; that is, if their *social* organization is matrilineal. This principle holds even if matrilineal groups migrate a great deal. As simulated here, the heterogeneity in reproductive success is stochastic in the sense that specific mtDNA haplotypes and cultural traits can be perfectly neutral in respect to variations in fecundity of individuals. Even if one would assume perfect neutrality of all characters (morphological, molecular, and behavioral), matrilineality itself is sufficient to cause low genetic variability when the environment (thus, the fecundity) is heterogeneous through time and space.

Our hypothesis does not require any character that produces differential fitness to be transmitted from one generation to the next. It fits the data in the report (*1*) more closely and parsimoniously than does the idea of hitchhiking of neutral mtDNA alleles through selection on maternally transmitted cultural traits.

Ralph Tiedemann
Michel C. Milinkovitch
Unit of Evolutionary Genetics, Institute of Molecular Biology and Medicine, CP 300, Free University of Brussels (ULB), B-6041 Gosselies, Belgium
E-mail: rtiedemann@ifh.uni-kiel.de
E-mail: mcmilink@ulb.ac.be

References and Notes

1. H. Whitehead, *Science* **282**, 1708 (1998).
2. Generation length, sequence length, and mutation rate were as in the report (*1*). Simulations started at mutation-drift-equilibrium. Fecundity is the annual probability of a conceptive female to mate successfully. For any of 5000 simulated subregions, fecundity values were taken randomly and independently from a normal distribution with a mean of $\mu = 0.60$ and a standard deviation of $\sigma = 0.1$. μ and σ were derived from the duration of gestation (16 months), the minimum calving interval (4 years), and estimates on the percentage of pregnant females (25% to 33%) in sperm whales. With an annual probability of 10%, any fecundity specific to a subregion was randomly altered throughout the simulations. Details of our individual-based model will be published elsewhere.

Received 11 January 1999; accepted 10 May 1999

Whitehead proposes that natural selection, acting on maternally transmitted cultural traits, can account for the remarkably low mitochondrial diversity in cetaceans that live in matrilineal groups (*1*). One of the alternative explanations dismissed by Whitehead, however, may also be important. If dispersal from natal group is rare or absent, each group can be thought of as a life history unit capable of "birth" and "death," and the genetic effective population size could be as small as the true population size divided by mean group size.

Whitehead cites simulations which indicate that 1% group mortality per year would be required to account for the observed genetic diversity if group size were the primary factor, and he considers this rate too high relative to documented numbers of mass strandings and fisheries mortality. However, in equilibrium populations, birth and death rates must balance, such that a death rate below 1% implies a birth rate below 1%, far smaller than known cetacean recruitment rates, which range up to 10% per year. This apparent contradiction could be resolved if not all groups were equally successful; that is, while some prosper, grow, and split, others decline and are eventually lost. Such "stochastic death" is often overlooked because, as with most other cetacean deaths, it would not result in countable bodies on beaches. Correlation between group members could then be maintained by predictable splitting along matrilines at some critical group size, rather than by whole-group mortality.

To examine evidence for matrilineal cohesion as an explanation for the low diversity of group-living species, I reanalyzed Whitehead's data (Table 1), looking for a match between the genetic population size and either census size or census size/mean group size (= "adjusted"). For comparability, I chose a single source for both population and social group size estimates, the *Red Data Book* (*2*). In essentially every case, there is good agreement between the genetic size and population size estimates. Those species with a good fit between the genetic and adjusted sizes include all species classified as matrilineal by Whitehead, along with several other highly social dolphins that are plausibly matrilineal. Some dolphins, such as the Pacific white-sided dolphin, swim in large groups, but have a genetic size close to their census size, which suggests that these species are social, but not strictly matrilineal.

Thus, there are two ways to account for the low mitochondrial diversity of some cetaceans. The "cultural inheritance" hypothesis of Whitehead can act independently of group size, while the "groups as life history units" hypothesis requires a strong relationship between effective group size and the observed shortfall in variability. Good agreement between shortfall and group size in a range of species, including all those classed as matrilineal by Whitehead, suggests that in some cetaceans, dispersal between matrilineal units is rare enough for these groups to be equiv-

Table 1. Comparison between genetic effective population size, census size and social group size for the same species analyzed by Whitehead (*1*). Gen = log(genetic effective size), taken from (*1*). Cen = log(census size), from the *Red Data Book* (*2*), multiple estimates presented as log (geometric mean). Adj = log(census size) − log(group size), group size taken from reference (*2*). Grp = group size. Fit = minimum difference between genetic and either census or adjusted size (in bold, except for species with group size = 1). Geographic abbreviations: N = north, W = west, E = east, A = Atlantic, Ant = Antarctic, Am = American, P = Pacific, I = Indian, BS = Black Sea, M = Mediterranean, and NZ = New Zealand. In most cases, fit < 0.2, equivalent to a factor of 1.58, which is a good agreement given the uncertainty associated with both the genetic and census estimates.

Species	Gen	Cen	Adj	Grp	Fit	Interpretation
Minke whale NA	4.79	4.70	4.70	1	0.09	Nonsocial
Minke whale Ant	4.99	5.85	5.85	1	0.86*	Nonsocial
Humpback whale NA, NP, Ant	5.39	5.30	5.30	1	0.09	Nonsocial
Humpback whale NA, Ant	5.39	5.23	5.23	1	0.16	Nonsocial
Beluga NAm	4.56	**4.85**	3.15	50	0.19	Social, nonmatrilineal
Bottlenose dolphin A, P	4.75	5.85	**4.54**	20	0.20	Matrilineal
Northern right whale dolphin NP	4.85	**4.23**†	2.03	160	0.62	Social, nonmatrilineal
Long-beaked common dolphin NP	4.59	5.70	**4.22**	30	0.39	Matrilineal
Short-beaked common dolphin P, BS	4.79	6.10	**4.62**	30	0.17	Matrilineal
Harbour porpoise NP, BS, NA	5.19	**5.18**	4.70	3	0.01	Nonsocial
Hector's dolphin NZ	4.43	**3.70**†	3.22	3	0.73	Nonsocial
Pacific white-sided dolphin NP	4.84	**5.00**	2.70	200	0.16	Social, nonmatrilineal
Striped dolphin EP, WM, Wa	4.64	6.00	**4.30**	50	0.34	Matrilineal
Narwhal Greenland	3.85	4.70	**3.40**	20	0.45	Matrilineal
Sperm whale NA, NP Ant	4.18	5.70‡	**4.22**	30	0.04	Matrilineal
Sperm whale P, A, I	4.04	5.70‡	**4.22**	30	0.16	Matrilineal
Killer whale NP	4.11	4.75§	**3.75**	10	0.36	Matrilineal
Short-finned pilot whale A, P	3.48	4.70	**3.30**	25	0.18	Matrilineal
Long-finned pilot whale A	3.30	5.11‡	**3.30**	65	0.00	Matrilineal

*This large difference probably results from population sub-structure in the Antarctic Oceans. †These census estimates are unlikely to be reliable. ‡These are the only large discrepancies in census size between those in the *Red Data Book* and Whitehead's report. In each case, Whitehead sets an upper limit of 10^7, about tenfold greater than estimates based on surveys {without access today to the two Ph.D. dissertations Whitehead uses as his sources [references 8 and 34 in (*1*)], I cannot comment on why his estimates are so large}. §Estimate is from Whitehead (*1*) because no appropriate estimate was given in the *Red Data Book*.

alent to mitochondrial super-individuals. This does not exclude the possibility that cultural inheritance operates alongside.

William Amos
Department of Zoology,
University of Cambridge,
Cambridge, CB2 3EJ, United Kingdom
E-mail: w.amos@zoo.cam.ac.uk

References

1. H. Whitehead, *Science* **282**, 1708 (1998).
2. M. Klinowska, *Dolphins, Porpoises and Whales of the World, The IUCN Red Data Book* (International Union for Conservation of Nature and Natural Resources, Gland, Switzerland, 1991).

27 May 1999; accepted 16 June 1999

Response: **Mesnick *et al*.** question some of the evidence I presented (*1*) in support of my hypothesis that selection on cultural traits may have reduced mtDNA diversity by cultural hitchhiking in four species of matrilineal whale: the sperm whale (*Physeter macrocephalus*), the killer whale (*Orcinus orca*), and the two species of pilot whale (*Globicephala melas* and *G. macrorhynchus*). First, they note that sperm whale social structure is not perfectly matrilineal: unrelated individuals co-occur within groups. Consequently, Mesnick *et al*. imply, transmission of information between matrilines will be sufficiently common to reduce the stability of any group-specific cultural trait below that needed for cultural processes to affect genetic evolution. However, the one (presumably) cultural trait of sperm whale groups whose stability has been examined (although in a study with small sample size), the repertoire of "coda" vocalizations, seems to have stability greater than the minimum bound necessary for cultural hitchhiking (*1, 2*).

How is this stability possible in a society where matrilineal units frequently group for periods of days, occasionally exchange members, and sometimes contain unrelated individuals (*3*)? Christal (*3*) suggests three possible factors: (i) that the results on nonmatrilineality of sperm whale units, which are based on studies of just a few units in Galapogos and Ecuadorean waters, may be artifacts of the fragmentation of matrilineal units caused by intense whaling from Peru [studies over large geographical scales generally support matrilineality in sperm whale groups (*4*)]; (ii) that the transfer of individuals between units may occur within larger, currently unrecognized, cultural trait-groups, such as have been found in killer whales (*5*); and (iii), that transferring individuals may have low reproductive success. The two particularly unstable female units that Christal studied in detail contained no animals less than about 6 years of age (*3*). Additionally, conformist traditions can maintain cultural stability within groups in situations where groups frequently interact (*6*).

Mesnick *et al*. also note that the four matrilineal whale species have low mtDNA diversity on oceanic scales, and suggest that this indicates continuous selection within the mtDNA. Their argument includes the assumptions that oceanic populations are isolated, and that diversity of unselected characters should have regenerated since isolation. However, three of the four species of matrilineal cetacean have globally continuous distributions of females (*7*), mtDNA diversity of the fourth, the long-finned pilot whale, has only been measured in its continuous, North Atlantic, range, and groups of all four species move widely. Additionally, regeneration of diversity following a selective sweep is slow, at a rate of approximately twice the mutation rate. Thus, with a mutation of 7.5×10^{-9} per year (*8*), a whale population's depauperate nucleotide diversity of 0.003 will double in about 200,000 years, within which period isolation is unlikely to have been maintained.

Mesnick *et al*. are concerned about the quality of the data indicating reduced mtDNA diversity in the matrilineal whales. The difficulties of collecting genetic samples from cetaceans, and the very different ranging patterns of the species, mean that estimates of cetacean mtDNA diversity, of necessity, come from disparate types of samples. For example, samples from Hector's dolphin (*Cephalorhynchus hectori*), which is endemic to New Zealand waters, cannot be collected over comparable geographical scales to those used for the wide ranging sperm whale. However, the studies of cetacean mtDNA diversity that I could find [listed in table 1 of (*1*)] have identical median sample sizes (66 individuals) for matrilineal and nonmatrilineal species and the samples for the matrilineal species come from generally wider geographical ranges (*1*). Therefore, sampling artifacts are unlikely to be the cause of the substantial differences in mtDNA diversity between the two sets of species (*1*).

A more important point raised by Mesnick *et al*. concerns uncertainties in cetacean taxonomy: some of the estimates of mtDNA diversity may refer to diversity within genera. Of the species listed, two particular concerns are one matrilineal "species," the killer whale, and one nonmatrilineal "species," the bottlenose dolphin (*Tursiops* spp.). I agree with Mesnick *et al*. that diversity estimates in these "species" should be treated cautiously. In the case of the killer whale, I adopted the conservative approach of listing the estimated diversity for killer whales as a whole. Diver-

sities of each of the two forms are much lower (*9*) than given in table 1 of my report.

In their final paragraph, Mesnick *et al*. seem to discount these methodological difficulties, apparently accepting "the strikingly low control region diversities" of the matrilineal species. I presented (*1*) one possible evolutionary scenario for this phenomenon, but the data are not conclusive, and I strongly support their call for an exploration of all feasible explanations.

Schlötterer makes two principal comments on my hypothesis (*1*) that selection of matrilineally transmitted cultural traits, on which neutral mtDNA alleles "hitch-hike," may have reduced mtDNA diversity in four species of matrilineal whale.

First, for the process to work, males must not be a conduit for culture between matrilineal groups of females. Schlötterer notes that male long-finned pilot whales seem to stay largely within their natal groups throughout their lives (*10*), so allowing cultures of matrilineal groups to remain distinctive. Killer whales have a similar social system (*11*), while male sperm whales, after leaving their natal groups at about the age of puberty, thereafter visit groups of females for only very brief periods (*12*). Thus, in three of the four matrilineal species considered in my report, male behavior is consistent with the cultural hitchhiking hypothesis. In the fourth species, the short-finned pilot whale, patterns of male dispersal have not been well documented.

Second, Schlötterer notes that nonsignificant values of Tajima's D statistics (*13*), which I use to support the hypothesis of little selection in the mtDNA control region, also do not support the cultural hitch-hiking hypothesis, as both processes would be expected to have similar effects on the sequenced mtDNA region. This is a potentially important point and one that I had not properly considered. Thus, I calculated Tajima's D statistic using the results of simulations (*14*) of cultural hitchhiking shown in my report. Only 28% (17/60) of the tests on data produced by models of cultural hitchhiking showed statistically signficiant ($P < 0.05$) evidence of selection. These results reinforce an emerging consensus that, in many circumstances, such tests have little power to detect selection (*15*). Thus, they provide little insight as to the significance of selection either within the mtDNA control region or within matrilineal cultures.

I endorse Schlötterer's conclusions that analyses of nuclear DNA diversity may help discriminate between possible causes of the low mtDNA diversity in the matrilineal cetaceans (*1*), and that microsatellites may not be the most suitable genetic markers for this. However, his suggestion that these species have low effective population sizes seems at odds with their moderate to large actual population sizes (relative to non-matrilineal cetaceans of similar body size) and widespread distributions (*1*). After humans, killer whales and sperm whales are the most widely distributed mammal species on Earth. That they possess abnormally low mtDNA diversities presents a significant puzzle, to which cultural hitch-hiking provides a feasible solution.

Tiedmann and Milinkovitch use an interesting model to suggest that stochastic variation in fecundity through space and time, combined with a matrilineal social system, can result in reduced diversity of mitochondrial DNA of animals like sperm whales, without the need to invoke any form of selection. Key elements of their model are that matrilineal groups independently experience different environmental conditions, which result in differential fecundities between matrilines at any time, and that these matriline-specific environments persist for the order of a decade. Such a situation is most readily represented by a population with a great deal of geographical structure, so that matrilines effectively inhabit independent environments. However, sperm whale populations are characterized by remarkably little geographical structure at spatial scales less than an ocean basin in size (*2, 14*). For example, during the late 1980's, about 4000 female and immature sperm whales (about 300 groups) visited the waters off the Galápagos Islands, and these animals had ranges spanning at least 1000 km (*16*). Furthermore, the groups frequently met and associated for periods of days (*17*). Thus groups of sperm whales do not usually experience independent, geographically-based environmental conditions which persist for the order of a decade.

However, the model of Tiedemann and Milinkovitch can still hold for a population in which matrilines intermingle and make substantial movements, if the animals carry important elements of their environment with them. It is perhaps possible that some non-spatial factor or factors could cause differences in fecundities between matrilines to be autocorrelated over several years. A disease which affects fecundity, is largely transmitted within matrilines, and persists within a matriline for a decade or more, would be such a factor. In light of Tiedemann and Milinkovitch's model, it could be worth exploring the likelihood that this kind of mechanism is present in the matrilineal whale species, as well as examining data sets which indicate the variabiality of fecundity between matrilines. In killer whales, the only one of the four matrilineal species with reduced mtDNA diversity (*1*) where group-specific fecundity has been examined, little variation between matrilines was found (*18*).

Amos suggests that, for some species of Cetacea—especially those with a matrilineal social system—the apparent shortfall between actual population size and effective population size estimated from mtDNA diversity may be explained if population dynamics operates at the level of the group, rather than the individual. This could happen either if members of a group reproduce or die, or both, in a correlated fashion, or if groups possess characteristics that give their members consistently better, or worse, fecundity or survival, and these differences persist over many generations.

The first of these mechanisms requires mass reproductive or mortality events, or both. There is no evidence of correlated reproduction in any of the matrilineal cetacean species (except for synchrony of oestrus over scales of weeks (*19*), which is irrelevant for this discussion). In the population where the question has been most closely examined, the "resident" killer whales off Vancouver Island, substantial group-specific demographic effects were not found (*19*). Siemann (*20*) (not myself, as suggested by Amos) modeled the effects of mass mortalities on genetic diversity in pilot whales. In her models, there was an individual mortality rate of 5% per year (explaining the "apparent contradiction" of Amos' second paragraph) as well as a variable group extinction rate. Siemann (*20*) found that only at group extinction rates of 1% per year (or, presumably, higher) was mtDNA diversity substantially reduced. Such rates of group extinction seem unlikely for any of the populations of matrilineal cetacean, with the possible exception of North Atlantic long-finned pilot whales (*1*).

The second mechanism for group-specific demography requires that differences between the reproduction or survival of members of different groups persist over many generations. Although the groups of some cetacean species are matrilineal (*1*), in these species mating almost always seems to be between groups (*9, 10, 12*). Therefore, systematic differences in reproduction or survival would have to lack paternal inheritance. Purely maternal genetic inheritance of such characters is theoretically possible, either on the mitochondrial genome or as maternally-expressed nuclear genomic imprinting (*21*), as is the perpetuation of nongenetic, noncultural "maternal" effects [for example, mothers in good condition raising daughters in good condition, (*22*)]. However, it would be highly unusual if either mechanism was sufficiently strong so as to affect genetic diversity, and I see no reason why they should have such effects only in species with matrilineal social systems. Other causes of consistent differences between the survival or reproduction of matrilineal groups are persistent group-specific environmental conditions, discussed above, and the presence of group-specific cultural traits maintained by conformist traditions (*1*).

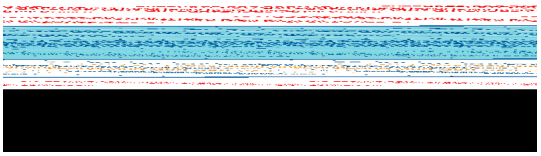
Amos notes that under the group-specific demography hypothesis, the shortfall between observed and expected mtDNA diversities should be related to group size, whereas no such relationship is predicted for cultural hitchhiking. He suggests that there is such a relationship for cetaceans. But the transition from individual-based to group-specific demography involves more than dividing the census population size by the group size and comparing this result with the effective population size calculated from the genetic diversity and mutation rate. The mutation rate of a group (which could be defined as the rate of change of the most frequent allele among members of a group at a locus) is not the same as the mutation rates of its constitutent individuls (*10*), and so the effective population size also needs recalculating. Furthermore, the sizes of stable long-term groups (which would be the units in a group-specific demography) are unknown for most species of Cetacea and, where known, bear little resemblance to the observed size of short-term aggregations (*23*), as listed in table 1 of the comment by Amos. Scientists are currently collecting and analyzing long-term data on the social structure of a number of species of cetaceans (*24*). Among the many insights provided by these data could be a useful test of these competing hypotheses based on the ideas of Amos.

Hal Whitehead
Department of Biology,
Dalhousie University,
Halifax, Nova Scotia B3H 4J1, Canada
E-mail: hwhitehe@is.dal.ca

References and Notes

1. H. Whitehead, *Science* **282**, 1708 (1998).
2. H. Whitehead *et al.*, *J. Anim. Ecol.* **67**, 253 (1998).
3. J. Christal, thesis, Dalhousie University, Halifax (1998).
4. M. C. Dillon, thesis, Dalhousie University, Halifax (1996); T. Lyrhom and U. Gyllensten, *Proc. R. Soc. London B* **265**, 1679 (1998); S. Dufault and H. Whitehead, *J. Mammal.* **79**, 514 (1998).
5. J. K. B. Ford, *Can. J. Zool.* **69**, 1454 (1991).
6. R. Boyd and P. Richerson, *Culture and the Evolutionary Process* (Univ. of Chicago Press, Chicago, 1985).
7. T. A. Jefferson, S. Leatherwood, M. A. Webber, *Marine Mammals of the World* (United Nations Environmental Programme, Rome, 1993).
8. A. R. Hoelzel, J. M. Hancock, G. A. Dover, *Mol. Biol. Evol.* **8**, 475 (1991).
9. A. R. Hoelzel, M. Dahlheim, S. J. Stern, *J. Hered.* **89**, 121 (1998).
10. B. Amos, C. Schlötterer, D. Tautz, *Science* **260**, 670 (1993).
11. M. A. Bigg *et al.*, *Rep. Int. Whal. Comm.* (*special issue*) **12**, 383 (1990).
12. H. Whitehead, *Can. J. Zool.* **71**, 689 (1993).
13. F. Tajima, *Genetics* **123**, 585 (1989).
14. Simulations were made as in figure 1 of my report (*1*), using the same starting conditions (four populations, each of 200,000 females with stable mtDNA haplotype diversities, 300 base pairs sequenced, generation length of 15 years, mutation rate of 7.5×10^{-9} per year), and the same four protocols: without cultural selection (control); with selection (10% advantage) on a matrilineally transmitted cultural trait; with cultural selection, but 5% of daughters not learning the selected trait from their mother; and with cultural selection and 0.5% of transmission going to daughters of mothers lacking the trait. At the end of each run of 300 generations, Tajima's D was calculated for five samples of approximately 231 animals [the largest real sample size for matrilineal whales in table 1 of (*1*)] chosen using random binomial sampling from the population. Thus, there were 60 tests of data sets produced by a process of cultural selection and showing clearly reduced mtDNA diversities (3 protocols X 4 runs X 5 tests of different random samples).
15. M. L. Wayne and K. L. Simonsen, *Trends. Ecol. Evol.* **13**, 236 (1998).
16. H. Whitehead, J. Christal, S. Dufault, *Conserv. Biol.* **11**, 1387 (1997).
17. H. Whitehead, S. Waters, T. Lyrholm, *Behav. Ecol. Sociobiol.* **29**, 385 (1991).
18. S. Brault and H. Caswell, *Ecology* **74**, 1444 (1993).
19. P. B. Best and D. S. Butterworth, *Rep. Int. Whaling Comm.* (*special issue*) **2**, 137 (1980).
20. L. Siemann, thesis, Massachusetts Institute of Technology, Cambridge, MA (1994).
21. D. P. Barlow, *Science* **270**, 1610 (1995).
22. J. B. Wolf *et al.*, *Trends Ecol. Evol.* **13**, 64 (1998).
23. Simulations with an individual mutation rate of 0.01, birth rate of 0.05. mortality rate of 0.046, and groups splitting randomly into two when reaching twice the mean population group size, produced group mutation rates of approximately 0.001 for populations with mean population group size of either 10 or 50.
24. R. C. Connor *et al.*, *Trends Ecol. Evol.* **13**, 408 (1998); *ibid.*, p. 228.
25. Thanks to R. Tiedemann and M. C. Milinkovitch for providing additional information about their model, and to R. Latta for reading my response to their comment. Thanks to W. Amos for helping to clarify my thoughts on the issues raised in his comment.

29 March 1999; accepted 16 June 1999



Culture and Genetic Evolution in Whales
Sarah L. Mesnick, Barbara L. Taylor, Richard G. Le Duc, Sergio Escorza Treviño, Greg M. O'Corry-Crowe and Andrew E. Dizon (June 25, 1999)
Science **284** (5423), 2055. [doi: 10.1126/science.284.5423.2055a]

Editor's Summary

Science (print ISSN 0036-8075; online ISSN 1095-9203) is published weekly, except the last week in December, by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005.