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DISCERNING BETWEEN RECURRENT GENE FLOW AND RECENT DIVERGENCE UNDER A FINITE-SITE MUTATION MODEL APPLIED TO NORTH ATLANTIC AND MEDITERRANEAN SEA FIN WHALE (*BALAENOPTERA PHYSALUS*) POPULATIONS

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Abstract.—Genetic divergence among conspecific subpopulations can be due to either low recurrent gene flow or recent divergence and no gene flow. Here we present a modification of an earlier method developed by Nielsen and Wakeley (2001), which accommodates a finite-site mutation model, to assess which of the two models of divergence is most likely given the observed data. We apply the method to nucleotide sequence data collected from the variable part of the mitochondrial control region in fin whales (*Balaenoptera physalus*) from the Atlantic coast off Spain and the Mediterranean Sea. Our estimations strongly favor a model of recurrent gene flow over a model of recent divergence and zero gene flow. We estimated the migration rate at two females per generation. While the estimated rate is high by evolutionary standards, exchange rates of this order of magnitude is low from an ecological and conservation perspective and entirely consistent with the current paucity of fin whale sightings in the Strait of Gibraltar today. Intensive commercial shore-based whaling during the 1920s removed substantial numbers of fin whales in the Strait of Gibraltar and this local population has seemingly since failed to recover.

Key words.—*Cetacea*, divergence, nonequilibrium, reproductive isolation.

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The degree of reproductive isolation among conspecifics is a basic parameter in evolutionary biology and most commonly estimated by genetic analysis. However, different evolutionary models may yield a similar degree of genetic divergence among subpopulations. For instance, low levels of genetic differentiation are commonly observed among conspecific subpopulations and could be due to either low levels of ongoing gene flow or recent divergence with zero gene flow. Methods to discriminate between these two different models have been developed by Nielsen and Wakeley (2001) based on an infinite-site mutation model. However, estimation of genetic divergence among conspecific populations is usually based on loci that evolve at relatively high rates, such as the mitochondrial control region, and where the infinite-site mutation model is inappropriate. In this study, we present a modification of the approach presented by Nielsen and Wakeley (2001), which assumes a finite-site rather than an infinite-site mutation model. We apply the approach to fin whale (*Balaenoptera physalus*) samples collected off the Atlantic coast of Spain and in the Mediterranean Sea.

A recent study by Bérubé et al. (1998) aimed at North Atlantic and Mediterranean fin whales found a significant degree of genetic divergence (F_{ST} estimated at 0.097) at the mitochondrial control region loci between fin whales sampled off the Atlantic coast of Spain and in the Mediterranean Sea. In contrast, significant levels of genetic divergence at six nuclear microsatellite loci were only detected among the populations furthest away from the Mediterranean Sea, such as the Gulf of Maine and western Greenland. These results suggested that an isolation-by-distance model most appropriately describes the gene flow among North Atlantic and Mediterranean Sea fin whales. However, mismatch-distributions (Slatkin and Hudson 1991), based on the sampled mitochondrial control region sequences, were consistent with exponential expansions in most western North Atlantic fin whale populations, presumably because most sampled populations were founded after the Pleistocene glaciations (Bérubé et al. 1998). Hence, the absence of significant levels of genetic divergence at nuclear loci might not be due to low levels of current gene flow, but rather might be a result of recent divergence not yet evident in the nuclear genome due to its larger effective population size.

To distinguish between the two above hypotheses proposed by Bérubé et al. (1998), we employed a modification of the Nielsen and Wakeley (2001) approach to assess the relative effect of genetic divergence and migration in the evolutionary history of the fin whale populations off the Atlantic coast of Spain and in the Mediterranean Sea. In particular, we were interested in estimating the relative effect of migration. Would a model of ancestral divergence between the two populations with low subsequent migration rates better explain the observed data, or is it necessary to invoke current migration to explain the observed distribution of variation at the mitochondrial control region? Among the polymorphic nucleotide sites in the mitochondrial control regions sampled by Bérubé et al. (1998), there were nine apparent incidences of multiple mutations at the same site. Therefore, we modified the approach by Nielsen and Wakeley (2001) to accommodate a finite-site mutation model.

MATERIALS AND METHODS

Sequence Data

The data used in our estimations were nucleotide sequences collected from the variable 5′ end of the mitochondrial control region. In total, 111 mitochondrial control region sequences were collected from 39 individual fin whales sampled off Atlantic Spain and 72 individual fin whales sampled in

the Ligurian Sea, located in the western Mediterranean Sea. Experimental procedures and haplotype frequencies of each population are presented in Bérubé et al. (1998). The mitochondrial control region nucleotide sequence of each unique haplotype is available in GenBank (accession numbers AF119956–AF120006).

Data Analyses

To discriminate between the relative effects of divergence and migration, we employed the method developed by Nielsen and Wakeley (2001). In this method, a coalescence model is established with three parameters: θ, two times the effective female population size (N_f) times the mutation rate (μ); T, the divergence time between the two populations scaled by the population size; and M, the migration rate between the two populations, also scaled by the population size. We assumed the two populations diverged from each other at time T, before which they were a single panmictic population. In addition, we allowed migration of M individuals per generation between the populations in the time since divergence. Inferences regarding the parameters are based on the posterior distribution of the parameters, $p(T, M, \theta \mid \boldsymbol{x})$, where $\boldsymbol{x}$ is the DNA sequence data. To estimate this posterior distribution, it is necessary to make some assumptions regarding these parameters before the data is observed. The prior distributions describe this information, and for the purpose of this study we assumed that all possible values are equally likely, that is, a uniform distribution. However, to ensure that the posterior distribution is a proper probability distribution, it is necessary to set a maximum value for the different parameters. Here, we decided on two different sets of the maximum value of T and M at 10.0 and 50.0, respectively. Because of the assumption of uniform prior distributions, the posterior distributions are proportional to the likelihood function. The results can, therefore, be interpreted both in a Bayesian and in a classical likelihood framework.

To modify the method of Nielsen and Wakeley (2001) to include the possibility of multiple mutations in the same site, we used the HKY model (Hasegawa et al. 1985) instead of the infinite sites model. In the HKY model, it is assumed that DNA sequences evolve according to a continuous Markov chain model with rate matrix $\mathbf{Q} = \{q_{ij}\}$:

$$q_{ij} = \begin{cases} \mu\kappa\pi_j & \text{if transition} \\ \mu\pi_j & \text{if transversion,} \end{cases} \quad (1)$$

where κ is the transition/transversion rate ratio and π_j is the stationary frequency of nucleotide j. The π_j values $j \in \{A, C, T, G\}$, were estimated directly as the observed nucleotide frequencies data. In the following, we assumed uniform (0, 10, or 50, see above) prior distributions for both θ and κ, where

$$\theta = 2N_f \sum_{i \in (A,C,T,G)} \pi_i \sum_{j \in (A,C,T,G)} q_{ij}. \quad (2)$$

Calculations of the likelihood, conditional on the genealogy, can easily be performed for this model using the Felsenstein (1981) algorithm.

The Markov chain was simulated for 5.5×10^6 cycles, and the results for the first 5×10^5 cycles were discarded as burn-in time. For the remaining 5×10^6 cycles, values of M, θ, and T were sampled after each cycle of the chain. Further details regarding the methods are presented in Nielsen and Wakeley (2001). To assess the effect of estimating θ, M, and T under the HKY mutation model, we also estimated the same parameters assuming an infinite-site mutation model. To conduct the estimation under an infinite-site mutation model, all sites incompatible with an infinite site mutation model were removed. Nucleotide sites that were in conflict with an infinite site mutation model were identified as pairs of variable nucleotide sites were all four possible haplotypes were present. Those sites that were in conflict with most other sites in this manner were removed until there were no conflicting sites.

Prior to both estimations, we estimated Tajima's D (Tajima 1989) for each population samples and associated P-values assuming a neutral model with no population structure using the program DnaSP (ver. 3.51, Rozas and Rozas 1999). An alternate estimate of the number of female migrants per generation was obtained from the degree of divergence estimated as Wright's F_{ST} from the mitochondrial sequence data. The effective number of female migrants per generation is given by

$$\hat{F} = \frac{1}{1 + 2N_f m}, \quad (3)$$

where m denotes the migration rate (Wright 1969).

A similar estimate of the total number of migrants (i.e., Nm) was obtained from the microsatellite loci analyzed by Bérubé et al. (1998) using the private allele method by Barton and Slatkin (1986) as implemented in GenePop (ver. 3.3, Raymond and Rousset 1995).

Identifying the Most Likely Mutation Model

We employed the default hierarchical likelihood ratio test implemented in ModelTest (Posada and Crandall 1998) in conjunction with PAUP (Swofford 2003) to estimate which of the 52 possible mutation models characterized in ModelTest's modelblock3 module.

Results

Deviations from Expectations under Neutrality

For neither population sample did we detect any significant deviation from neutrality using Tajima's D as test statistic. Tajima's D was estimated at 0.34816 and 0.29577 for the Atlantic Spain and Ligurian Sea samples, respectively. In neither case did the observed estimate differ significantly ($P > 0.10$) from the expectation under neutrality. This observation agrees with the shape of mismatch distributions (Slatkin and Hudson 1991) presented by Bérubé and coworkers in their original study (Bérubé et al. 1998). Because Tajima's D is influenced both by demographic factors, such as population subdivision and changes in population size (e.g., Simonsen et al. 1995), and by selection, it is possible that the lack of significance could be due to a cancellation of effects.

Estimation Assuming a HKY Mutation Model

The results of our estimations (θ, M, and T) are presented in terms of the posterior distribution for θ, M, and T in Figure

1. Because we employed uniform priors, these distributions are also proportional to the marginal likelihood functions for each parameter. The posterior distribution for θ (assuming a HKY mutation model) is symmetric with most probability mass surrounding θ = 4.0, corresponding to the integrated maximum-likelihood estimate (Fig. 1A). The integrated likelihood function is found by integrating out all other parameters and is, under a uniform prior, given by the marginal posterior distribution of θ. The posterior distribution for *T* is almost uniform, except that very little probability mass is located in the region close to where $T = 0$ (Fig. 1B). This result implies that all values of *T* are compatible with the data, except very small values. In other words, there seems to be no evidence for a recent divergence between the two populations. We did not observe any significant change of the posterior distributions when increasing the maximum value of *M* and *T* from 10.0 to 50.0.

Recent estimates of abundance for the Atlantic Spain and Mediterranean populations are 4466 and 3583 individuals, respectively (Sanpera and Jover 1989; Forcada et al. 1996). Age at sexual maturation in North Atlantic fin whale females has been estimated at 7.7 years (Aguilar et al. 1988). In a homogeneously structured population with a 1:1 sex ratio and subject to a natural mortality rate of 0.04, a commonly accepted value for fin whales (Anonymous 1992), about 68% of females would be sexually mature. Taking these values into account, it is reasonable to consider that the effective population size, assuming low variance in offspring number, is on the order of 1200–1500 individual females. If we assume an average generation time of approximately six years, the divergence time between the populations must be at least 600 years, but could be orders of magnitude larger. The posterior distributions for *T* and for the other parameters are not quite smooth because these were obtained by sampling from a Markov chain.

The most interesting results are obtained by inspection of the posterior distribution for *M*. The distribution has a maximum at $M = 2$, suggesting that on average two individuals (females) are exchanged between the two populations in each generation. In addition, very small or very large values of *M* can easily be rejected. A 95% highest posterior density credible interval (a type of Bayesian confidence interval), is given by (0.54, 6.9). In other words, our estimation suggest that at least one migrant is exchanged between the two populations every second generation.

An appropriate test for testing the hypothesis of $M = 0$ is to compare the likelihood value at $M = 0$ to the likelihood value obtain at the maximum-likelihood estimate of *M*. If the log likelihood ratio is sufficiently large, we can reject the hypothesis of $M = 0$. When the likelihood ratio is large, it can be difficult to estimate accurately using Markov chain Monte Carlo simulations. However, the likelihood ratio in this case is larger than seven. Based on the simulations presented in Nielsen and Wakeley (2001), this corresponds to a *P*-value of <0.01. Clearly, there is strong evidence in the data against a model of no migration, and we can thus conclude that recurrent migration between the two populations must be a common feature of their evolutionary past.

Alternate Estimates of Migration Rate

The observed degree of divergence at the mitochondrial control regions was estimated at $F_{ST} = 0.097$ (Bérubé et al. 1998), which translates into a migration rate of 4.7 females per generation (Wright 1969). The estimate of migration based upon the data obtained from Mendelian-inherited microsatellite by Bérubé et al. (1998), could not be estimated from Wright's F_{ST}, which was negative (i.e., $Nm \sim \infty$). However, using the rare allele method (Barton and Slatkin 1986) yielded an estimate of 4.9 migrants per generation. It is not surprising that the classical F_{ST} based estimate and the estimate based on rare alleles yield higher rates of migration than the likelihood method, because the latter method incorporates the possibility of recent shared ancestry whereas the former methods do not.

Estimation Assuming an Infinite Site Mutation Model

Of the 19 segregating sites among the total dataset, nine were removed for the data to be compatible with an infinite-site mutation model. We recognize that the set of polymorphic sites removed is one of several possible combinations. Therefore, our assessment does not constitute an exhaustive exploration of the relative effects of employing different mutation models in this kind of estimation.

The posterior distributions estimated under an infinite site mutation model differ substantially (almost nonoverlapping) with respect to θ and *M* (Fig. 1A, B). The maximum of the posterior distributions for all three parameters are much better defined than was the case for the posterior distributions obtained assuming a HKY mutation model (Fig. 1). Contrary to the estimation conducted under an HKY mutation model, the posterior distributions estimated assuming an infinite site mutation model point to near-zero migration and divergence time approximately three times that estimated under a HKY mutation model.

Identifying the Most Likely Mutation Model

We employed PAUP (Swofford 2003) and ModelTest (Posada and Crandall 1998) to estimate which of the mutation models implemented in ModelTest best fits the observed data. The mutation model that yielded the best fit with the observed data was that developed by Tamura and Nei (1993) assuming some invariable sites (proportion estimated at 0.72), unequal base frequencies, and unequal transition rates among bases as well as a substantial degree of heterogeneity in substitution rate among the variable sites (shape parameter of the Γ distribution, α, was estimated at 0.31).

DISCUSSION

The objective of this study was to use nucleotide sequence data collected from the mitochondrial control region in two adjacent populations of fin whales to assess if the observed genetic divergence is due to low current gene flow or recent divergence followed by no gene flow. The results from our estimations strongly support the hypothesis of recurrent gene flow over zero gene flow and recent divergence. Using the method presented here we obtained an estimate of $M = 2$,, which is similar but slightly lower than the estimates derived

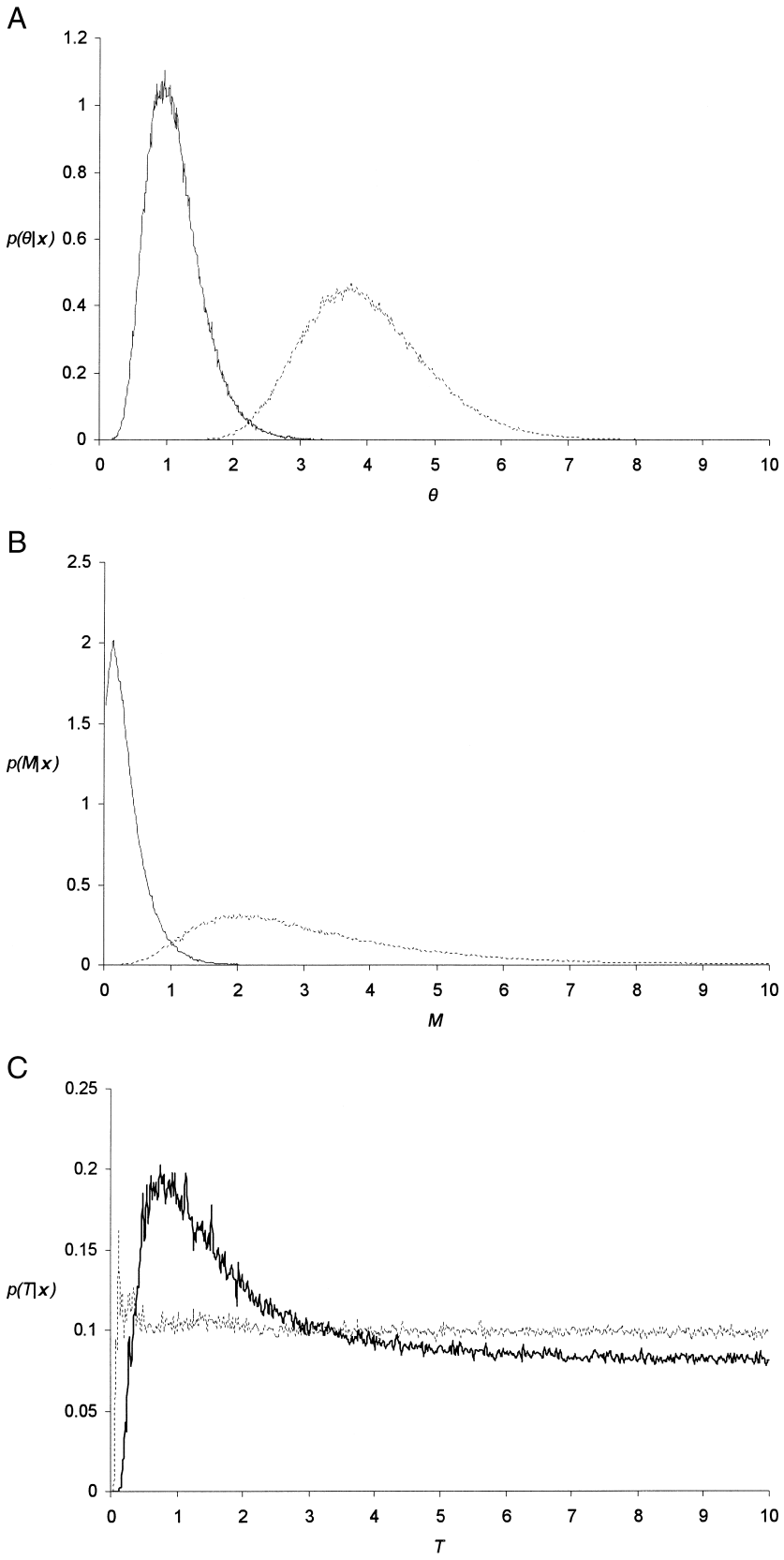

FIG. 1. The posterior distribution of θ, *M*, and *T* under an infinite site and HKY model. The posterior distribution of θ (**A**), *M* (**B**), and *T* (**C**). To generate the distribution, a uniform prior (0, 10) was assumed for θ and κ, and a uniform prior on (0, 10) was assumed for *T* and *M*; a Markov chain was simulated for 5.5×10^6 generations, where the first 5×10^5 generations were used as burn-in time. The posterior density was estimated from the Markov chain Monte Carlo output using a histogram estimator with 500 bins. Black line denotes the distributions obtained assuming an infinite-site mutation model, and the gray broken line the distributions obtained assuming a HKY mutation model.

from F_{ST} and even that derived from the frequency of rare alleles at Mendelian-inherited loci. An estimate of migration based on the estimate of divergence time, *T*, was poorly resolved, only allowing us to conclude that the two populations likely diverged more than 0.6 times $2N_f$ (where N_f is the effective population size of females) generations ago, but with no resolution as to the upper boundary of *T*.

Bérubé et al. (1998) recently presented similar data from another semiclosed water body, the Sea of Cortez (Baja California). Their results showed a very high degree of genetic divergence at the mitochondrial control regions as well as at 18 nuclear microsatellite loci. The estimated degree of genetic divergence was comparable to that observed among different oceanic cetacean populations ($F_{ST} \approx 0.3$), indicating a very high degree of reproductive isolation. The results presented here suggest that no generalizations can be made with respect to the degree of genetic isolation of fin whale populations inhabiting semiclosed waters, such as the Mediterranean Sea and Sea of Cortez.

The objective of our study was to determine the reason for the observed discrepancy in the degree of genetic divergence estimated at the mitochondrial control region and nuclear microsatellite loci between the Atlantic Spain and Mediterranean fin whales reported by Bérubé et al. (1998). One hypothesis was that the two populations diverged recently (i.e., population have not yet achieved an equilibrium in terms of divergence and migration), which could explain why a lesser degree of genetic divergence was observed at nuclear loci given the larger effective population size of this genome. The results of the estimation conducted here reject this hypothesis and suggests that a model of recurrent gene flow is more likely given the mitochondrial sequence data available. A higher degree of genetic divergence at maternally inherited loci, such as mitochondrial DNA, compared to Mendelian-inherited markers such as microsatellite loci, would be indicative of a large contribution to gene flow by males relative to females (e.g., Karl et al. 1992; Palumbi and Baker 1994). Such male-mediated gene flow is possible in two ways. The first would be that fin whales observed in the Mediterranean Sea represent a summer feeding population that breeds elsewhere during the winter as part of an eastern North Atlantic fin whale population, as is observed in North Atlantic humpback whales (Palsbøll et al. 1995). However, the paucity of fin whale sightings and strandings in the Strait of Gibraltar and neighboring waters (Beaubrun 1995; Beaubrun and Rousel 2000; Fernández-Casado et al. 2000), together with the existence of a fin whale wintering ground between Italy and the Mediterranean coasts of northern Africa (Marini et al. 1995), seems inconsistent with the notion that Mediterranean Sea fin whales, which are estimated to number about 3500 individuals (Forcada et al. 1996), migrate to and from the North Atlantic during the autumn and spring, respectively. Another possibility is occasional gene flow with a bias toward male-mediated gene flow between the current populations off Atlantic Spain and in the Mediterranean Sea. Certainly the effective number of female migrants per generation estimated here ($M = 2$) is sufficiently low to be compatible with the aforementioned paucity of fin whale sightings in the Strait of Gibraltar. However, the estimates of *M* obtained in this study and by Bérubé et al. (1998) are all evolutionary measures and hence most likely reflect the degree of exchange prior to the intensive whaling in the Gibraltar Strait conducted in the early 20th century. During the 1920s, one land factory and two floating factories took in this area 4149 fin whales in only six years of activity. The density of whales was initially extremely high; in 1923, oil production per catcher boat was one of the highest values ever recorded for a whaling operation, and whales were caught all year-round. Such level of removals was unsustainable and the operation abruptly collapsed as annual catches plummeted. A residual whale fishery, catching only few dozen whales per season, was again attempted in 1948, but it was finally abandoned in 1955 because of lack of whales to harvest (Sanpera and Aguilar 1992).

The local population around the Gibraltar Straits appears not to have recovered since (Clapham et al. 1999). The possible effect on gene flow between the eastern North Atlantic and Mediterranean Sea fin whale populations due to this whaling operation is too recent to have a measurable effect on the parameters estimated in this study and might well have resulted in recent reproductive isolation, not detectable by evolutionarily based genetic approaches.

Estimation under Different Mutation Models

We conducted our estimations under two different mutation models: the HKY and the infinite-site mutation model. The latter model is more easily implemented in these kinds of estimations, and thus estimations under a HKY mutation model (or other finite-site mutation models) are typically lacking. However, our results clearly show that one can arrive at radically different conclusions if applying the wrong mutation model during estimation. For the data to be compatible with an infinite-site mutation model, we had to remove nine of a total of 19 segregating sites. The subsequently lower diversity yielded an estimate of θ (the maximum of the posterior distribution) four times lower than that obtained under a HKY mutation model. Eliminating sites to make the data fit the infinite sites model is likely to preferentially remove mutations on long lineages of the genealogy, which are more likely to have experienced multiple mutations. The long lineages near the root of the genealogy are also the lineages that are most likely to have experienced migration between the two populations. The effect will be that the data becomes more compatible with more recent divergence times and less compatible with a model that includes high rates of migration. This may explain the observation that after removal of nine incompatible sites in our dataset, the posterior distributions assuming an infinite sites model suggest that there has been little migration between the populations.

Finally, the proportion of shared alleles is a reflection of the time of divergence. A bias in the removal of sites toward migrant alleles will thus bias the estimate of divergence time upward, as was indeed the case in our study. In conclusion, our estimations showed that (in this instance) employing an erroneous mutation model in the estimation of θ, *M*, and *T* will yield substantially different point estimates as well as an artificially high confidence in those estimates (evident by a more narrowly defined maximum in the posterior distribution).

Although a finite mutation model, such as that employed in this study, is more realistic for a rapidly evolving locus, such as the animal mitochondrial control region, the assumption of an equal substitution rate at all sites is clearly incorrect. Our analyses revealed a severe skew in mutation rates, suggesting that most sites evolve slowly if at all, and a few at very high rates. Therefore, an obvious extension of this work is to use estimation methods that permit implementing the appropriate evolutionary model, for example, unequal mutation rates among sites. The relevant parameters (e.g., α the shape parameter of the Γ distribution) can be estimated from the collected sequence data using routines implemented in commonly used software packages, such as ModelTest (Posada and Crandall 1998).

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