Genetic Patterns Suggest Exponential Population Growth in a Declining Species

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Recent theoretical studies have suggested that patterns of sequence divergence and relationships among alleles sampled from Populations are affected by population size and rates of growth. However, the degree of concordance between changes-to Populations and to the patterns of allelic relationships within populations is not well understood. Threshold effects, time lags, or the effects of earlier demographic events may all prevent recent changes in population size from being reflected in the current patterns of allelic relationships. This has implications for analysis of species subject to recent fluctuations in Population size. We have analyzed the patterns of sequence divergence and genealogy of mitochondrial DNA (mtDNA) alleles in the coconut crab, *Birgus latro,* using restriction enzyme analysis. Populations from the Pacific Ocean had mtDNAs with high diversity, a starlike phylogeny, and a Poisson distribution of sequence differences, i.e., the genetic signature of a rapidly expanding Population. Yet population size in the Pacific has decreased dramatically (by at least an order of magnitude) over at least the last 100 to 1,000 years. In contrast to Pacific Ocean Populations, the large protected Population on Christmas Island (Indian Ocean) had a strongly structured mtDNA phylogeny with a multimodal distribution of sequence differences, as expected from a stable population. The obvious discrepancy between genetic and census data for the Pacific population is consistent with the view that the pattern of allelic relationships that we infer to have resulted from a past period of population growth is robust to further changes in population size. Thus, if a species is not in genetic equilibrium due to past growth events, then the effects of more recent events may not be detectable.

Introduction

The ability to determine the relationships among mitochondrial DNA (mtDNA) alleles (Avise 1989) has heralded significant developments in population genetics theory that are yet to be fully explored with empirical data. Recent modeling of the effects of changes in population size on the pattern of genetic variation within a population (Slatkin and Hudson 1991; Rogers and Harpending 1992; Nee, Holmes, and Harvey 1995) has indicated that allelic relationships within populations are affected by demographic history. A population which is growing exponentially, or which has previously undergone rapid population growth, is expected to show two characteristic features. The first is a starlike phylogeny of alleles, which arises because there is much less stochastic elimination of lineages in a rapidly growing population (Avise, Neigel, and Arnold 1984). The second, related, feature is a Poisson frequency distribution of pairwise differences between alleles. This arises because most alleles are descended from one ancestral type. In contrast, a stable or declining population is expected to have a more strongly structured allelic phylogeny with a geometric distribution of allelic differences, although simulations indicate that other, multimodal, distributions are more likely (Rogers and Harpending 1992). A population that has experienced a reduction in size is expected to show a rapid increase in the proportion of alleles that are identical, or nearly so. This theory has recently been used to make inferences about historical changes in population size of humans, viruses, and other species (e.g., Harpending et al. 1993; Nee, Holmes, and Harvey 1995; Rogers 1995).

A number of questions still remain, however, before this theory can be confidently applied to real populations. First, there may be a threshold effect in the magnitude of change in population size (increase or decrease) before a change can be detected in the frequency distribution of pairwise differences between alleles (the mismatch distribution). Theoretical results (Rogers and Harpending 1992) indicate that even relatively small changes may be evident. However, simulations reveal that in stable and growing populations the estimators may have broad confidence intervals under certain circumstances (Rogers 1995). Simulations are yet to be conducted to determine how easily population reductions can be detected in real data sets.

Second, it is uncertain how long it takes .for the genetic structure of a population, specifically the pattern of allelic relationships, to respond to changes in population size. Rogers and Harpending (1992) found that the mismatch distribution may respond relatively quickly to an increase or decrease in population size, although the distribution may not reach equilibrium for thousands of generations. Analytical studies indicate that the mismatch distribution's approach to equilibrium is much faster after a population decline than after population growth (Rogers and Harpending 1992). However, the time scale used in these studies is an evolutionary one—that is, in units of hundreds or thousands of generations ($1/(2u)$, where u is the mutation rate). Whether responses can be detected within shorter, ecological, time scales remains to be seen.

Third, and perhaps most importantly, it is possible that past changes in population size may produce a ge-

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Key words: population growth, pairwise genetic differences, mismatch distribution, lineages through time, *Birgus latro.*

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Mol. Biol. Evol. 13(8):1106–1113. 1996
 ISSN: 0737-4038

netic pattern in the mismatch distribution that is robust to further changes in population size. In particular, Rogers (1996) has shown that, after an initial burst of growth, subsequent population changes may have little effect on the mismatch distribution. That is, the effects of recent demographic changes may be masked by the effects of earlier events.

With these unresolved questions in mind, it is important to examine this theoretical approach using data from species with a known (or partially known) demographic history. As part of an investigation into the population structure of the coconut crab, *Birgus latro, we* have analyzed the pattern of mtDNA diversity in this species. These crabs occur on isolated tropical islands throughout the Indo-Pacific. However, because of intense harvesting for food and destruction of habitat, populations on most Pacific islands have decreased greatly or disappeared entirely over many hundreds of years, resulting in a population decline in the Pacific of at least an order of magnitude (Brown and Fielder 1991). Here we examine what mtDNA diversity can reveal about population dynamics in this species.

Material and Methods

Individual coconut crabs were collected from eight locations covering much of their range; seven islands from the Pacific Ocean and one, Christmas Island, from the Indian Ocean. Collection locations and sample sizes are as follows: Christmas Island (28), Japan (19), Philippines (4), Papua New Guinea (15), Solomon Islands (35), Vanuatu (18), Niue (25), and Cook Islands (16).

All individuals were analyzed for restriction site variation in mtDNA (Lavery, Moritz, and Fielder 1996). Restriction fragment data from 160 individuals were obtained by analyzing purified mtDNA cut with five 4-bp recognizing restriction enzymes, end-labeled with ^{32}P and subjected to electrophoresis through agarose and polyacrylamide gels (Dowling, Moritz, and Palmer 1990). There were 189 restriction sites detected, of which 147 showed evidence of site gains or losses. There was no evidence of insertions or deletions. From the composite restriction profiles, 113 alleles were identified and sequence divergences between pairs of alleles were calculated using the site approach and the maximum-likelihood estimator of Nei and Tajima (1983). The neighbor-joining method (Saitou and Nei 1987) was used to construct a phylogenetic tree of the relationships among the 113 mtDNA alleles. Frequency distributions were made of the pairwise differences (number of site changes) between all individuals examined in the Indian Ocean and Pacific Ocean populations.

Explicit predictions for declining populations are few. Most of our statistical comparisons were therefore between expectations for expanding versus constant populations. The smooth, unimodal distributions that typically result from expanding populations can be readily distinguished from the ragged, multimodal distributions that result from long-term stationary populations by means of a simple measure of the raggedness of the distribution (Harpending et al. 1993). The measure of mean raggedness was made for the Pacific and Indian Ocean mismatch distributions. These values were tested for significance using the following procedure (carried out by a simulation program supplied by H. Harpending). Mismatch distributions were simulated for 1,000 samples of the size of the Pacific population (132) for each of two hypotheses: (1) constant population size (zero growth) and (2) 1,000-fold growth. Raggedness was calculated for each mismatch distribution, and the frequency distribution of raggedness was determined over all 1,000 simulated samples. The actual raggedness for the Pacific mismatch distribution was then compared with the range of raggedness values for each of the two hypotheses. Monte Carlo probability was calculated as the proportion of simulated values equal to or more extreme than the actual raggedness. A similar procedure was followed for the Christmas Island sample, except that the two hypotheses simulated here were (1) zero growth and (2) lo-fold growth.

Rogers and Harpending's (1992) model of rapid population growth is based on three parameters: $\theta_0 = 2N_0u$, $\theta_1 = 2N_1u$, and $\tau = 2ut$, where an initial population of effective size N_0 is assumed to grow (or shrink) rapidly to a new size of N_1 at a time t generations before the present. The mutation rate, u, is the per-generation probability that a mutation strikes a particular nucleotide in the region under study. This model was fitted to the mismatch distributions of the Indian Ocean and Pacific Ocean populations using the method of moments (Rogers 1995). Confidence intervals for the three parameters were found by using 1,000 simulated data sets to test the fit of each combination of a range of values of the three parameters, as described in Rogers (1995) and carried out using Rogers' program MISMATCH.

Methods of estimating population sizes based on the mismatch distribution have been criticized as being far less efficient than methods which use, as their raw information, the times between nodes (the coalescence events) in the genealogical tree of the sampled sequences (Felsenstein 1992). The phylogenetic tree structure of *B. latro* mtDNAs was taken into account by using the approach of Nee, Holmes, and Harvey (1995), which makes inferences based on plots of the number of lineages versus time, as implemented in the program ENDEPI (Rambaut and Harvey, personal communication). An exponentially growing population is expected to exhibit a graph of decreasing slope (i.e., convex) over time when the number of lineages is plotted logarithmically, and to show a linear relationship with time when the number of lineages is given an "epidemic" transformation (Nee, Holmes, and Harvey 1995). By contrast, a population of constant size is expected to exhibit a graph of increasing slope (i.e., concave) when the number of lineages is plotted logarithmically, and to show a linear relationship with time when an "endemic" transformation is applied. The significance of these graphical patterns was determined using the one-sample Kolmogorov-Smimov statistic, which compares observed and expected cumulative frequency distributions (Sokal and Rohlf 1995).

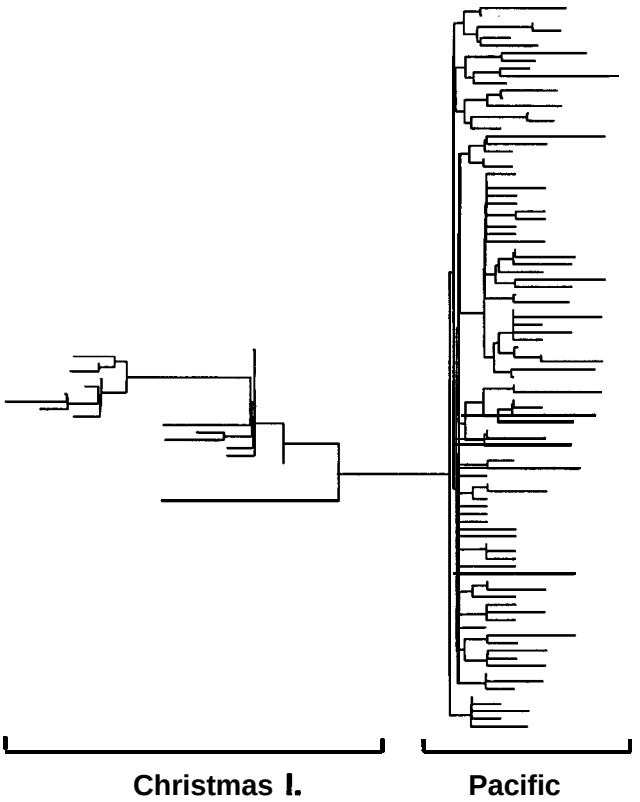

FIG. I.-Neighbor-joining tree showing relationships among the 113 *B. latro* mtDNA haplotypes sampled from Christmas Island in the Indian Ocean and various Pacific islands.

Results

Phylogenetic analysis of the mtDNA data revealed that B. *latro* populations from the Indian and Pacific Oceans comprise two genetically distinct groups (fig. 1), separated by the South-East Asian archipelago. There was no distinct genetic subdivision among Pacific populations, but rather a pattern of isolation by distance, characterized by relatively high gene flow. There is strong concordance in this pattern between both allozyme and mtDNA data (Lavery, Moritz, and Fielder 1995, 1996). The crabs from the Pacific Ocean islands had very high allelic diversity for mtDNA (0.98), with 96 distinct alleles among the 132 individuals examined. However, the nucleotide diversity is low (0.45%) because the levels of sequence divergence among alleles are very low; 85% of alleles are less than 0.7% divergent and maximum divergence is 1.2%. Accordingly, the phylogeny of the Pacific alleles (fig. 1) has little structure, resembling the "star" phylogeny expected from an expanding population. The mismatch distribution of mtDNAs sampled from the Pacific population is very close to Poisson (fig. 2A) with a very low proportion (1%) of identical alleles (zero sites different), again the pattern expected from an expanding population, and different from that expected for a declining population. The "raggedness" test of Harpending et al. (1993) confirms that the Pacific mismatch distribution is consistent with rapid growth (1,000-fold), but is significantly different ($P < 0.05$) from that expected from populations of stable size.

When the Pacific data are represented as a semilogarithmic "lineages-through-time" plot (Nee, Holmes, and Harvey 1995), the curve rises sharply and then becomes less steep toward the present (fig. 3*A*), as expected from an exponentially growing population. The curve deviated significantly ($P < 0.001$) from that of a linear relationship (fig. 3A). This pattern of apparent exponential (or greater) growth is further supported when, under the "epidemic" transformation (Nee, Holmes, and Harvey 1995), the transformed data are shown to be an approximately linear function of time for almost the entire length of the curve (fig. 3B). The sharp rise at the end of the curve implies that the growth may have been greater than exponential in this most recent period.

The Christmas Island population of *B. latro* exhibits a very different pattern of mtDNA diversity from that of the Pacific Ocean population. The allele phylogeny is much more structured (fig. 1) and allelic diversity is lower (0.91), but nucleotide diversity is higher (0.59%). This is because of the presence of a few relatively divergent but common alleles; there are two major clusters which have diverged by about 1%, and an additional single allele which was 1.3% divergent. The mismatch distribution (fig. 2B) is multimodal and has a substantial proportion (9%) of paired comparisons between identical alleles (zero sites different). This is very distinct from a Poisson distribution. These features are among the patterns that might be expected in a stable population (Slatkin and Hudson 1991; Rogers and Harpending 1992). Applying the "raggedness" test confirms that the Christmas Island distribution is consistent with stable population size, but is significantly different ($P < 0.05$) from that expected from rapid growth (lo-fold or greater).

When the Christmas Island data are represented as a semilogarithmic "lineages-through-time" plot (Nee, Holmes, and Harvey 1995), the curve steepens toward the present (fig. 4*A*), as expected from a population of near constant size. The curve deviated marginally ($P < 0.05$) from that of a linear relationship (fig. 4A). Under the "endemic" transformation (Nee, Holmes, and Harvey 1995), the data show a slight downward curvature (fig. 4*B*), suggesting that the Christmas Island population may have undergone some small linear rate of growth.

Rogers and Harpending (1992) have suggested a model of rapid population growth based on three parameters (θ_0, θ_1, and τ) as an alternative to the Poisson model. A 95% confidence region for these parameters was constructed by fitting this model to the *B. lutro* mtDNA data. While the confidence region for the Christmas Island data was broad (largely due to the relatively small sample size), that for the Pacific data was very narrow. The Pacific data gave the estimates $\theta_0 < 1.0$, $\theta_1 = 5$ 1.75, and $\tau = 4.09$, resulting in a distribution also very close to Poisson. The Pacific confidence region excludes the hypothesis of no growth and the hypothesis of lo-fold growth. The lower bound on the magnitude of the population expansion is somewhere between lo-fold and

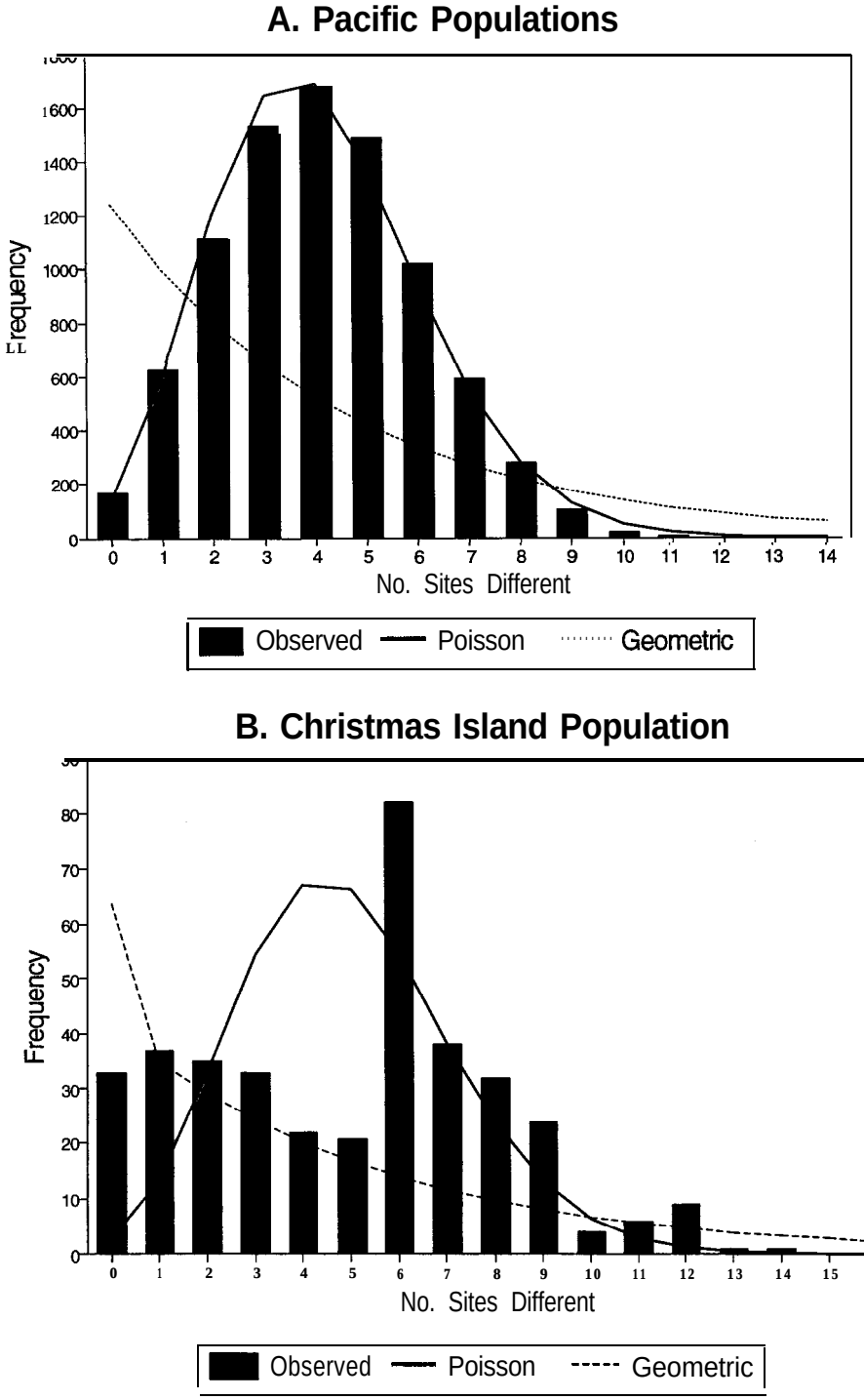

FIG. 2.-Frequency distributions of pairwise sequence differences between *B. latro* individuals. Also plotted are. the ideal distributions if the populations had undergone an exponential increase in size (Poisson distribution) or had maintained a stable population size (geometric distribution). A, Pacific populations. *B,* Christmas Island (Indian Ocean) population.

100-fold (no upper bound was determined). The initial population was likely to be small, as the 95% confidence region has $0.1 \leq \theta_0 \leq 1.0$. There was also a narrow bound on the time of the expansion, with $3 \leq \tau \leq 5$. Using the equations of Rogers and Harpending (1992), and assuming a standard whole mtDNA mutation rate of 10^{-8} per nucleotide per year (Moritz, Dowling, and Brown 1987), it was estimated that a population expansion began between 197,000 and 329,000 years ago, with an initial effective (female) population size for the Pacific Ocean *B. latro* of between 1,300 and 13,000 individuals. Although these exact values are sensitive to the assumed mutation rate, the estimated ratio of final to initial population size is independent of mutation rate. More recent and thorough examination (Rogers 1992, 1995) has shown that the estimators used above have

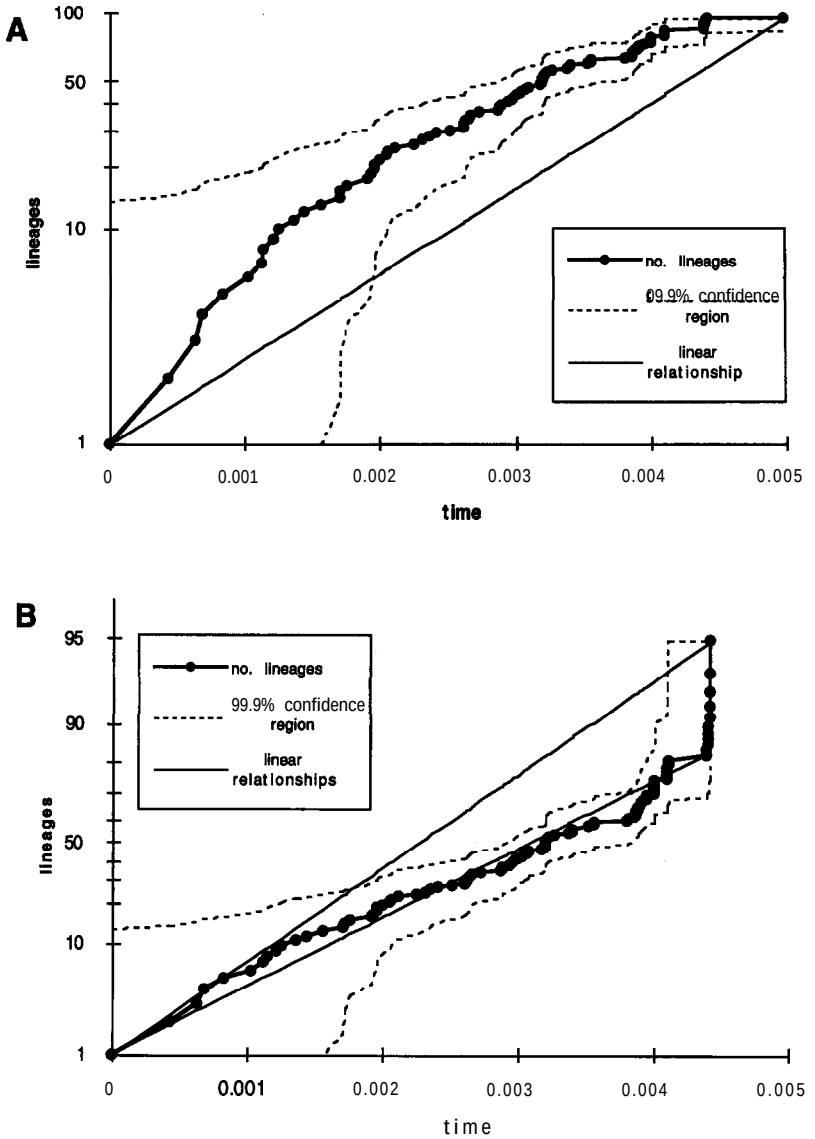

FIG. 3.—Plots of the number of lineages through time in the Pacific population of *B. latro*. A, Logarithmic transformation of the number of lineages. *B*, Epidemic transformation (Nee, Holmes, and Harvey 1995).

favorable statistical properties, and are relatively insensitive to violations of assumptions (including the model of sudden expansion, constant mutation rate across nucleotide sites, and no population subdivision).

Discussion

The combination of the high allelic diversity, the "star" phylogeny of alleles, the Poisson mismatch distribution, and the pattern of increasing lineages through time provides compelling evidence that *B. latro* have undergone exponential population growth on Pacific Ocean islands. An alternative explanation for this pattern of mtDNA variation is a selective sweep, i.e., the replacement of mtDNAs through the entire population with a phenotypically advantageous allele, followed by an accumulation of neutral variants (Maruyama and Birky 1991). However, the geographic pattern of *B. latro* mtDNA variation in the Indo-Pacific is highly concordant with that of five independent nuclear allozyme loci (Lavery, Moritz, and Felder 1995, 1996). Both data sets show that the Indian Ocean and Pacific Ocean populations are highly divergent, and that populations from different Pacific islands have diverged marginally in an isolation-by-distance fashion. It seems unlikely that either (1) selection has acted identically on the mtDNA locus and all allozyme loci to produce this geographic pattern or (2) selection has acted strongly enough on the mtDNA locus alone to produce a selective sweep, without at the same time altering the geographic pattern of variation compared to other independent genetic markers. However, it is conceivable that a mtDNA sweep occurred long enough ago that the geographic pattern of mtDNA variation may now be approaching a new equilibrium-one which reflects the same isolation-by-distance pattern seen in the allozyme variation.

The confidence region placed a lower bound on θ_0 of 0.1, indicating that the initial effective population size

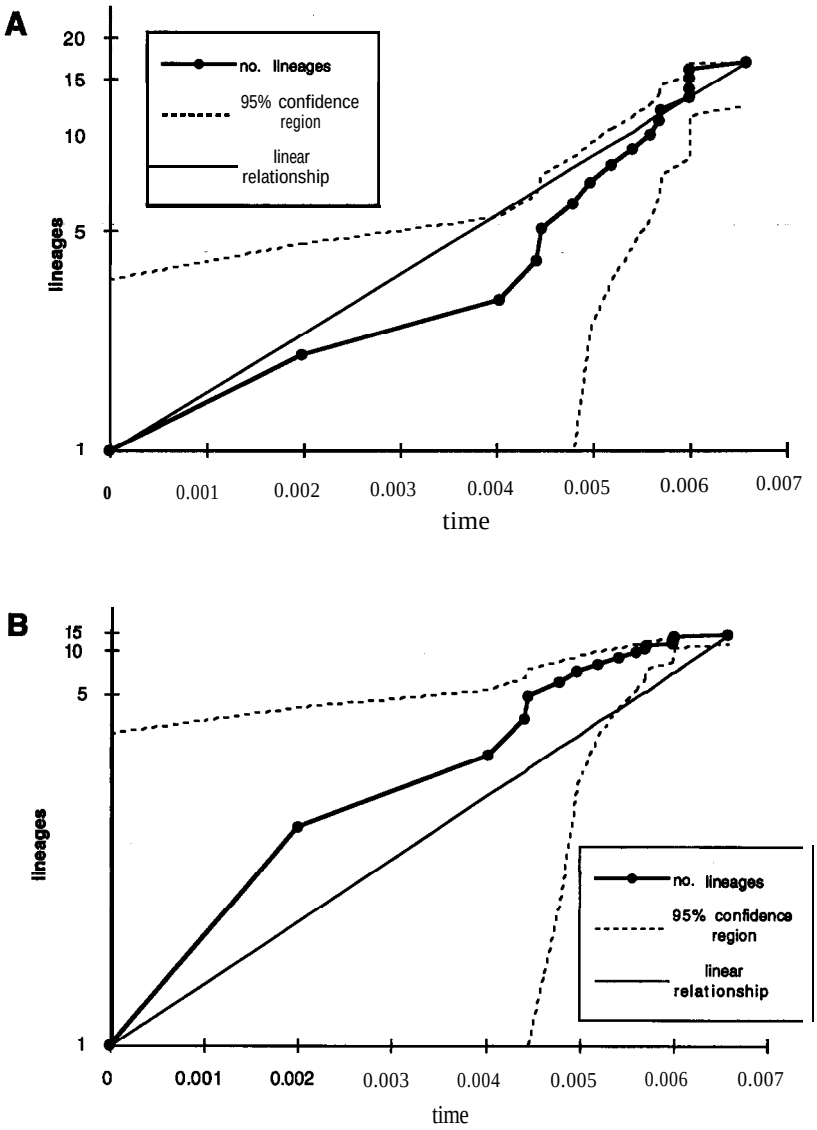

FIG. 4.-Plots of the number of lineages through time in the Christmas Island population of B. *latro*. *A*, Logarithmic transformation of the number of lineages. ***B***, Endemic transformation (Nee, Holmes, and Harvey 1995).

was not extremely small. If the Pacific mismatch distribution was produced by the selective sweep of a favorable mutation, then the initial population consisted of a single mutant mitochondrion. Thus, $\theta_0 = 2u$ under the selection hypothesis. Our lower bound on θ_0 of 0.1 appears to preclude a selective sweep unless the mutation rate was approximately 0.05, which is unrealistically large.

Marjoram and Donnelly (1994) have shown that an alternative pattern of growth (constant size followed by exponential growth), or the existence of population subdivision, may affect the mismatch distribution by making it more multimodal. The lack of any strong population subdivision in Pacific B. *latro,* and the strongly unimodal pattern in the Pacific mismatch distribution, suggest that their cautions regarding this type of analysis are not applicable to this study and that, if anything, our conclusions may be overly conservative.

On the available evidence, we cannot unequivocally reject the hypothesis of a selective sweep being the cause of the Pacific mismatch distribution. However, we consider population growth more likely and, thus, for the purposes of discussion, we will assume from this point that this is correct. Given that population growth is responsible, the Poisson pattern of differences among mtDNA alleles could result from exponential growth, from a single rapid burst of growth, or from continuous slower growth (Slatkin and Hudson 1991; Rogers and Harpending 1992). The lineages-through-time analysis suggests that the growth was (at least) exponential. The size of the actual increase in numbers appears to be substantial, with the effective population size rising by at least two to three orders of magnitude.

The large and rapid increase in ***B. latro*** population size in the Pacific inferred from the genetic patterns is in stark contrast with recorded recent trends for the spe-

cies. Numbers have rapidly declined on all but the most remote islands over at least the last 100 years and probably much longer, such that *B. latro* is now extinct in many areas. Many scientific reports have documented the decline or extinction of *Birgus latro* on islands throughout their range since European colonization (Wells, Pyle, and Collins 1983; Brown and Fielder 1991). Coconut crabs are highly desired as food, are easily captured, have very slow growth rates, and have very irregular recruitment, making them extremely vulnerable to overexploitation (Fletcher, Brown, and Fielder 1990). Thus, substantial population reductions are likely to have occurred in the Pacific not only since the arrival of Europeans (100 to 300 years ago), but ever since human colonization of the Pacific, up to 3,500 years ago (as has been clearly demonstrated for Pacific birds; Steadman 1995). This population crash in the Pacific is of at least an order of magnitude in size-a decline which should be detectable in the mismatch distribution (Rogers and Harpending 1992). In contrast, coconut crabs are still very abundant on Christmas Island. The island was uninhabited until about 100 years ago, the colonists had little desire for coconut crabs as food, and tbe species has been largely protected on the island for the last 2 decades.

We suggest that the obvious discrepancies between genetic and census data for the Pacific population may have a simple explanation. The genetic signal of growth appears to be a relict of a past period of demographic change, i.e., a large population increase in *B. latro* mtDNA during the Pleistocene. The more recent population decline may not be evident in the mismatch distribution due to one or both of the following factors: First, the population reduction may be too recent to be apparent in the genetic signature of the population. Second, and more likely, the genetic pattern that has resulted from past growth is robust to further changes in population size, which are known to have occurred. Population decrease following expansion has been modeled to some degree by Rogers (1996, fig. 3). His results suggest that, after rapid growth (theta growing from 1 to 500), subsequent periods of population decline (or growth) will have no great effect on the pattern resulting from the initial expansion, unless there is a major, prolonged bottleneck, or until equilibrium is once again approached.

A possible explanation for apparent differences in population history between the Pacific and Christmas Island populations is that population growth could (and did) occur in the Pacific, but was not possible on Christmas Island. Coconut crabs may have colonized the Pacific region from the Indian Ocean and rapidly expanded their range and population size during one or more periods of the Pleistocene when sea levels were lower. During these periods, the number and extent of emergent islands in the Pacific increased dramatically, providing substantially more habitat, and distances between adjacent islands were reduced, greatly facilitating colonization via pelagic larvae (Gibbons 1985; Lavery, Moritz, and Fielder 1995, 1996). It is this apparent historical population increase, rather than the recent precipitous decline, that is reflected in current patterns of mtDNA diversity within the Pacific region. In contrast, the number and extent of island masses in the Indian Ocean did not change dramatically during the Pleistocene. Christmas Island itself has remained largely unchanged in size for the last 20 million years (Gray 1981).

The results for the coconut crab have significant implications for the use of genetic data in examining recent population processes. Simulation studies (Slatkin and Hudson 199 1; Rogers and Harpending 1992) had already suggested that it was not possible to distinguish between past and continuing population growth from patterns of genetic diversity-we conclude that it may be similarly impossible to identify recent declines. Recent demographic events may not be discernible from analysis of mismatch distributions (or lineage-through-time plots) because their effects are masked by those of earlier events. It is likely that many species are not in equilibrium as a result of past demographic events and, if this is so, more recent events may not be detectable. This study has shown that the patterns of sequence divergence among alleles in a species may provide valuable insights into evolutionary history. However, the study has also demonstrated that these patterns have the potential to be highly misleading about recent demographic processes.

Acknowledgments

A. Rogers kindly fitted the coconut crab data to his model of population expansion and assisted in its interpretation. H. Harpending provided calculations of the raggedness statistics. J. Bull, A. Rogers, H. Harpending, and S. Easteal provided valuable comments on the manuscript. Assistance with sample collection was provided by (among others): C. Schiller and R. Fletcher (co-investigators); A. Carlot and W. Bakeo (Vanuatu); D. Phillips and I? Goh (Christmas Island); P. Nichols and S. Diake (Solomon Islands); S. Talagi, B. Punu, and T. Mautama (Niue); J. Dashwood, K. Passfield, and T. Rongo (Cook Islands); l? Bacolod (Philippines); A. Wafy (Papua New Guinea); and T. Hayashibara, N. Oshiro, and A. Ebisawa (Japan). Financial assistance was provided by the Australian Centre for International Agricultural Research, an Australian Postgraduate Research Award (to S.L.), the Linnean Society of New South Wales, the Australian Marine Sciences Association, and the University of Queensland.

LITERATURE CITED

AVISE, J. C. 1989. Gene trees and organismal histories. Evolution 43:1192–1208.

AVISE, J. C., J. E. NEIGEL, and J. ARNOLD. 1984. J. Mol. Evol. 20:99–105.

BROWN, I. W., and D. R. FIELDER. 1991. The Coconut Crab: aspects of *Birgus latro* biology and ecology in Vanuatu. Australian Centre for International Agricultural Research, Canberra.

DOWLING, T., C. MORITZ, and J. PALMER. 1990. Nucleic acids II: restriction site analysis. Pp. 250-317 *in* D. M. HILLIS

and C. MORITZ, eds. Molecular systematics. Sinauer, Sunderland, Mass.

FELSENSTEIN, J. 1992. Estimating effective population size from samples of sequences: a bootstrap Monte Carlo integration method. Genet. Res. Camb. **60**:209–220.

FLETCHER, W. J., I. W. BROWN, and D. R. FIELDER. 1990. Growth of the coconut crab ***Birgus latro*** in Vanuatu. J. Exp. Mar Biol. Ecol. **141**:63–78.

GIBBONS, J. R. 1985. The biogeography and evolution of Pacific island reptiles and amphibians. Pp. 125-142 ***in G.*** GRIGG, R. SHINE and H. EHMANN, eds. Biology of Australasian frogs and reptiles. Royal Zoological Society of New South Wales, New South Wales.

GRAY, H. 1981. Christmas Island naturally. *H*. Gray, Geraldton, Western Australia.

HARPENDING, H. C., S. T. SHERRY, A. R. ROGERS, and M. STONEKING. 1993. The genetic structure of ancient human populations. Curr. Anthropol. **34**:483–496.

LAVERY, S., C. MORITZ, and D. R. FIELDER. 1995. Changing patterns of population structure and gene flow at different spatial scales in ***Birgus latro*** the coconut crab. Heredity 74: 531-541.

———. 1996. Indo-Pacific population structure and evolutionary history of the coconut crab ***(Birgus latro).*** Mol. Ecol. (in press).

MARJORAM, P., and I? DONNELLY. 1994. Pairwise comparisons of mitochondrial DNA sequences in subdivided populations and implications for early human evolution. Genetics 136: 673-683.

MARUYAMA, T., and C. W. BIRKY. 1991. Effects of periodic selection on gene diversity in organelle genomes and other systems without recombination. Genetics **127**:449–45 1.

MORITZ, C., T. E. DOWLING, and W. M. BROWN. 1987. Evolution of animal mitochondrial DNA: relevance for population biology and systematics. Annu. Rev. Ecol. Syst. 18: 269-292.

NEE, S., E. C. HOLMES, and I? H. HARVEY. 1995. Inferring population history from molecular phylogenies. Philos. Trans. R. Soc. Lond. B **349**:25–31.

NEI, M., and F. TAJIMA. 1983. Maximum likelihood estimation of the number of nucleotide substitutions from restriction sites DNA. Genetics **105**:207–217.

ROGERS, A. R. 1992. Error introduced by the infinite-sites model. Mol. Biol. Evol. **9**:1181–1 184.

———. 1995. Genetic evidence for a Pleistocene population explosion. Evolution **49**:608–615.

———. 1996. Population structure and modem human origins. ***In*** DONNELLY and TAVARE, eds. Progress in population genetics and human evolution. Springer Verlag, New York (in press).

ROGERS, A. R., and H. HARPENDING. 1992. Population growth makes waves in the distribution of pairwise genetic differences. Mol. Biol. Evol. **9**:552–569.

SAITOU, N., and M. NEI. 1987. The neighbor-joining method: a new method for reconstructing phylogenetic trees. Mol. Biol. Evol. **4**:406–425.

SLATKIN, M., and R. R. HUDSON. 1991. Pairwise comparisons of mitochondrial DNA sequences in stable and exponentially growing populations. Genetics **129**:555–562.

SOKAL, R. R., and F. J. ROHLF. 1995. Biometry. Freeman and Co., New York.

STEADMAN, D. W. 1995. Prehistoric extinctions of Pacific island birds: biodiversity meets zooarchaeology. Science 267: 1123-I 130.

WELLS, S. M., R. M. PYLE, and N. M. COLLINS. 1983. Coconut or robber crab. Pp. 309-316 ***in S.*** M. WELLS, R. M. PYLE and N. M. COLLINS, eds. I.U.C.N. invertebrate red data book. I.U.C.N., Gland, Switzerland.

SIMON EASTEAL, reviewing editor

Accepted June 24, 1996