

## **Phylogeography of Archaeological Populations: A Case Study from Rapa Nui (Easter Island)**

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Reconstructing the history and geography of human populations is a worthy goal. The empirical distribution of people and their artifacts provides the basic data to generate historical explanations about not only population-level phenomena but also the individual behaviors of which they are composed. Evolutionary models that specify the underlying processes that create and sort variation structure the way we collect historical information. From these models, testable predictions are generated that measure the fit of the model to our observations. These have the potential of identifying significant large-scale historical events such as colonization, migration, interaction, and competition.

Evolutionary models that explain the empirical distribution of genetic structure over geographic space are well suited to bridge general evolutionary models with anthropological theory. This is largely a result of well-developed theory and attendant methods that explain empirical molecular variation developed by population genetics and evolutionary systematics over the past fifty years (Felsenstein 2004). These methods have been greatly enhanced by focused attention on the problem of explaining variation over nonlinear, heterogeneous geographic space (Avice 2000; Epperson 2003).

Understanding the distribution of genetic variation over geographic space, however, is not sufficient to explain the creation and maintenance of that variation. The latter require models that specify the empirical outcomes of evolutionary change across ecologically and demographically heterogeneous landscapes. The goal of this class of models is to separate genetic patterning based on ancestry from that relating to subsequent interpopulation gene flow

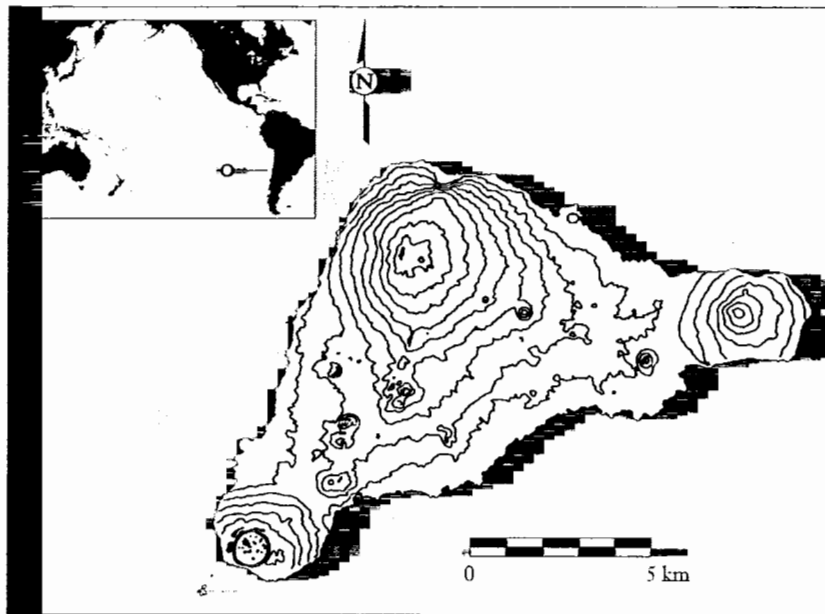
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(Templeton 1998). Teasing apart these components of molecular variation represents a major challenge for population genetics and evolutionary systematics.

In cases where the current geographic distribution is a small, discontinuous subset of a population's former range, analysis of modern genetic variability tends to fail to characterize historical population dynamics adequately (Pääbo 2000). Reconstruction of the evolutionary history of extinct or prehistoric populations using archaeological samples allows us to directly measure the effect of ecological and environmental variability on the molecular composition of a group of organisms under a variety of demographic scenarios. Well-studied archaeological populations offer the opportunity to test the utility of molecular approaches to reconstructing population structure and history.

The exploration of the social structure and spatial organization of the prehistoric inhabitants of Rapa Nui (Easter Island) (figure 9.1) is an example of how molecular studies can be integrated with detailed archaeological approaches and fine-scale geographic mapping. It is a story of changing social structure, influenced by dramatic long-term isolation and ecological deterio-

**Figure 9.1**  
**Map of Rapa Nui (Easter Island), with 100-Meter Contour Intervals Displayed**



Over 3,700 kilometers west of Chile, of which it is a province, Rapa Nui is 2,250 kilometers southeast of the nearest inhabitable island, Pitcairn. For this reason, Rapa Nui is generally considered the most isolated continuously inhabited island on Earth (Bahn and Flenley 1992). (Figure courtesy B. L. Shepardson.)

ration. The historical processes responsible for the development of Rapa Nui populations are examples of extremes. After A.D. 400, a small colonizing population, perhaps as few as 100 individuals, made landfall on arguably the most isolated place on Earth. For over 1,300 years, these Polynesian voyagers evolved an elaborate, isolated local culture on only 172 square kilometers of land, with a population that may have reached as high as 10,000 individuals.

The population developed a tradition of monumental architecture and social competition of phenomenal proportions. These activities, so apparently successful for most of the culture's history, ended abruptly soon after European contact in A.D. 1722, when the island population collapsed through the combined effects of European slavery, land annexation, and introduced disease (McCall 1994). By 1877, population declined to around 100 individuals, all of whom were virtually imprisoned in the island's only urban center in the late nineteenth century. The processes responsible for the history of Rapa Nui were extreme. With such dramatic changes to the population, it is clear that an ahistorical description of human variation over geographic space can never explain or fully capture the details of the "esoteric efflorescence" (Sahlins 1955) of human culture on Rapa Nui.

The history of the island demands close attention to model construction. The conceptual framework with the greatest power to resolve the evolutionary history of situations such as Rapa Nui requires the integration of fine-scale geographic history with phylogenetic reconstructions of human lineages and a model that incorporates neutral genetic drift. Archaeological information about population growth and demographic structure allows us to generate hypotheses about the geographic structure of populations. Analyses on these sources of data can provide independent tests of hypotheses generated from phylogenetic models that predict spatial structure, but the burden of the method rests on the analysis of genetic variation.

It is only through studies of gene flow that the history of biological populations can be revealed. Granted, the number of variables involved in genetic models of population history (e.g., rates of gene flow, effective population size and demographic trajectory, geographic subdivision, coalescence times, and gene genealogies) is large and may be difficult to estimate in ancient populations. To complicate matters further, the situation on Rapa Nui adds necessary constraints to the development of the model, given that Polynesian populations flourished on the island for a relatively short period and were likely initially very small. Thus, the study of Rapa Nui requires a carefully constructed model that is tuned for the special case that the island's history represents. Specifically, we require a model that (1) is robust for small sample sizes from populations of shallow generational depth, with unknown but presumably high gene flow, and (2) is capable of estimating phylogeny and structure where drift, rather than mutation, is the primary mechanism for geographical subdivision and phylogenesis (Nielsen et al. 1998).

In this chapter, I discuss the scope of molecular-history studies that are focused on explaining cases such as Rapa Nui. Using these studies as a guideline, I frame several testable hypotheses that concentrate on the analysis of skeletal data that was generated by previous research. My goal is to make the results of these independent analyses comparable. The project advocated here uses previously studied skeletal populations. In addition, I make use of recent comparative data assembled from spatial analysis of archaeological features of habitation and monumental constructions. These archaeological remains are believed to represent population segmentation and temporally variable social organization—and by extension, genetic relatedness.

### Rapa Nui Prehistory

The standard interpretation of the archaeological record of Rapa Nui holds that prehistoric populations consisted of a series of geographically distinct social groups (McCall 1979; McCoy 1976; Routledge 1919; Stevenson 1984, 2002). The artifactual record of Rapa Nui has generally been held up as a clear-cut case of population differentiation and social competition in a restricted environment (Bahn and Flenley 1992; Flenley and Bahn 2002; Stevenson 2002). Three main sources of information have traditionally been marshaled to explain the apparently high degree of social competition, monumental construction, and overall “esoteric efflorescence” (Sahlins 1955) on Rapa Nui. These are ethnographic evidence, biological studies, and archaeological remains.

#### *Ethnographic Evidence*

Ethnographic accounts of indigenous Rapa Nui culture have been used to reconstruct the prehistoric and protohistoric social hierarchical and kinship system. The accounts are based on interviews with individuals from remnant populations and date to the late nineteenth and early twentieth centuries, several hundred years after the events being recorded (Lavachery 1936; Métraux 1940; Routledge 1919; Thompson 1889).

The accounts indicate that Rapa Nui was divided among various lineages. Called *kainga*, these geographically localized areas were held by descent groups (*mata*) that were defined as affiliations of extended and nuclear families. The *mata* and *kainga* were roughly equivalent spatially. The term *mata* denotes a type of relatedness usually expressed by the anthropological term “clan,” and *kainga* are the geographic and possibly administrative areas occupied by clan-related individuals. Each *kainga* was anchored to a broad coastal territory, extending inland in pie-slice configuration. The *kainga* arrangement provided each *mata* a range of island environments for marine exploitation, inland and upland agriculture, and related subsistence activities (e.g., Stevenson et al. 2002). This coastal-inland arrangement of descent-based geography has

been reported elsewhere in Polynesia (Handy and Pukui 1972) and has been employed in some general models of the evolution of agricultural systems and political hierarchy (e.g., Ladefoged and Graves 2000; Ladefoged et al. 1996). As I show below, the ethnographic accounts and various land-division schemes proposed for Rapa Nui, while not appropriate as explanations of social differentiation in themselves, can be used to generate some basic molecular spatial hypotheses.

#### *Biological Evidence*

Gill (1986, 1990; Chapman and Gill 1997; Gill et al. 1997) used a variety of methods to examine Rapa Nui skeletal variation. Stefan (1999, 2000), Zimple and Gill (1986), Chapman (1993, 1997) and others have used skeletal remains to examine intransland population structure based on models of ethnohistoric social divisions. Stefan (1999, 2000), in his studies of minimum genetic distance and its contribution to phenotypic variability (Williams-Blangero and Blangero 1989), found evidence of greater between-group homogeneity within the male skeletal sample. This pattern appears to indicate higher islandwide mobility of males compared to females. However, his studies reveal no large-scale regional or lineage-based pattern of inbreeding. Stefan (1999: 416) concluded that, contrary to the story provided by ethnographic accounts, "differentiation of those tribes did not occur through the actions of cultural and genetic isolation."

Other studies do not agree with this conclusion. Some genetic isolation caused by group structure has been suggested based on studies of multiple individual burials in coastal caves (Shaw 2000). These studies suggest that there is evidence of small pockets of relative genetic isolation within segments of some subpopulations (Zimple and Gill 1986). The argument is based on the occurrence of three rare discrete traits of the postcranial skeleton. These are traits that achieve higher than expected frequency in discrete geographical locations (Gill and Owsley 1993; Shaw 2000; Stefan 1999). Other reports (e.g., Zimple and Gill 1986) have offered similar evidence for variable gene-flow schemes. These are based primarily on the appearance and frequency of rare discrete traits as well as on other heritable phenotypic markers.

#### *Archaeological Evidence*

Previous research into the development of lineages has focused on spatially patterned monumental architecture and the occurrence of discrete residences and subsistence features hypothesized to be associated with them (McCoy 1976; Stevenson 1984, 1986, 2002). In an extension of the ethnographic accounts and observations of historic settlement patterns for Rapa Nui (Lavachery 1936; Métraux 1940; Routledge 1919; Thompson 1889), several

authors (McCall 1979; McCoy 1976; Stevenson 1984; Stevenson et al. 2002) have proposed a settlement-subsistence model in which habitations were clustered in a narrow margin along the coast, allowing access to both marine resources and inland farming areas. Habitation-site density decreases markedly beyond 1,000–1,500 meters inland from the coast, implying that in the absence of controlling topographic or hydrographic variability, settlement pattern is influenced by access to marine resources and in relation to the large ceremonial platforms (ahu). Temporally, the model suggests that the record was initially patterned by dispersed residences that were representative of local lineage autonomy and that coalesced in the middle period into increasingly nucleated, more densely clustered habitations. This accretion of small, widely distributed settlements is argued to represent the incorporation of autonomous local lineages into multiple lineage clusters.

In his analysis of obsidian-hydration dates for areas previously surveyed by McCoy (1976), Stevenson (1984) concluded that by the sixteenth century all previously independent lineages on the southern coast of Rapa Nui were incorporated into four politically autonomous multilineage descent groups, which persisted until the eighteenth century. The latter part of prehistory on Rapa Nui is roughly correlated with evidence of environmental deterioration and the beginnings of population-level resource and subsistence stress. The commonsense explanation for the development of multilineage political associations is that resource stress caused by high populations and the demands of monumental-stature construction and movement resulted in the need for greater cooperation among previously autonomous lineages. This arrangement lasted until the early eighteenth century, when multiple lineage centers were abandoned and the southern-coast populations reverted to the autonomous lineage-based configuration of two centuries earlier (Stevenson 1984). Coincident with the increase in settlement density and lineage fission-fusion was human-induced ecological deterioration and resource stress.

The central theme of these descriptions of late Rapa Nui prehistory is a common archaeological story, and its main tenets have been invoked to explain the Maya “collapse” (Santley et al. 1986) and the Anasazi “abandonment” of the American Southwest (Fish et al. 1994). After A.D. 1400, rapidly growing Rapa Nui populations were nucleating into high-density coastal centers characterized by elite residences and elaborate ceremonial architecture (Stevenson 2002). By around A.D. 1500, the coastal centers consisted of many intermixed, previously autonomous lineages. As population pressure and resource exploitation began to affect these large regional centers after A.D. 1550–1600, factionalism and warfare increased, and the politically unified regional centers dissociated along lineage lines, re-aggregating as dispersed, more evenly distributed low-density coastal and inland communities. By the time of European contact in A.D. 1722, Rapa Nui was still a viable island society, albeit at far lower population than its high in the sixteenth century. However, the construc-

tion of monumental statues and large ceremonial buildings—the central focus of outside interest in Rapa Nui for almost 300 years—had ceased (Kirch 1984).

#### Analytical Methods

A geographic model of population divergence and phylogenetic relatedness employing a molecular analysis of Rapa Nui skeletal material can provide basic means for testing hypotheses of spatial segmentation of social groups through time. The model should include factors for small initial populations, rapid population growth, and selective pressures of ecological deterioration. Molecular approaches are an excellent means for building these kinds of models. Molecular data are sensitive to small, isolated populations with limited mobility because social or competitive barriers to migration and interaction can be measured with fidelity that archaeological and biological approaches are unable to replicate.

Depending on the approach used, empirical variation can be viewed as (1) the result of demographic and biological processes leading to broad patterns of geographic differentiation within and between populations or (2) the result of a genealogical process, whereby discrete allelic states define probable ancestor-descendant relationships. The former model employs pairwise measures of frequency distributions of alleles across space to estimate the amount of gene flow or interaction occurring within and between subpopulations (Wright's [1931, 1943] *F*-statistics). Pairwise measures generate a coefficient of similarity between any two individuals or groups. The coefficient of similarity combines information about the evolutionary history between groups plus ongoing gene flow via migration. Teasing apart the relative contributions of each process becomes a difficult proposition but one that is informed by spatial arrangement or other historical information.

The latter model uses an explicitly phylogenetic, or coalescent, approach that postdicts the pattern of the merging of sampled lineages backward in time (Jobling et al. 2004). Moving backward, each generation subsumes individuals possessing shared derived traits, such as novel genetic mutations, until all the individuals in the sample are joined to a common ancestor. The pattern of ancestral-state coalescence is the evolutionary description of the sampled population. Ongoing gene flow complicates the construction of gene genealogies under the coalescent method, but the genealogical history across different genes can give clues to the amount of ongoing gene flow (Barton and Wilson 1995). Ultimately, coalescent models are more robust to sampling effects than *F*-statistics, given that the resulting coalescent tree describes the genealogical relationship of only those individuals sampled in that generation. In contrast, measures of allelic diversity based on *F*-statistics are useful indicators of population structure and estimators of gene flow (Neigel 2002), especially when migration and drift, rather than mutation, are the primary forces for population differentiation.

To construct a model of genetic divergence and hierarchical population segmentation over time, we need to create expectations for detectable differences in molecular heterozygosity (i.e., patterns of different alleles at a given locus in regard to a given character) between subpopulations as a result of nonrandom migration and genetic drift. If many populations are compared in a matrix of pairwise genetic distance, and if mutation and selection pressure are low, this statistic reflects the amount of subpopulation differentiation resulting from restricted gene flow, provided that genetic drift is constant for all populations (Hutchison and Templeton 1999).

Population size in prehistoric and protohistoric Rapa Nui has been notoriously difficult to quantify for three reasons. First, the superposition of temporally unrelated archaeological features makes ground-based estimates of total population problematic (but see Stevenson 1984). Second, the loss of nearly the entire population from slave raids in the 1860s, as well as from introduced European diseases, creates a temporal, spatial, and cultural discontinuity. Third, a lack of good chronological dating of stone-lined chamber and cave bundle burials seriously limits paleodemographic reconstruction to estimate population sizes and demographic pressure across any temporal interval.

Population genetics tells us that the single most important parameter necessary when calculating loss of genetic diversity in small, isolated populations is the "effective population size," which is the sample of the population at large that typically participates in the founding of the next generation. Even within large, randomly mating populations, rarely is the effective population size the same as the total number of individuals. Reductions in absolute mating efficiency occur because of demographic differences in fertility between mating pairs or the unequal distribution of males and females.

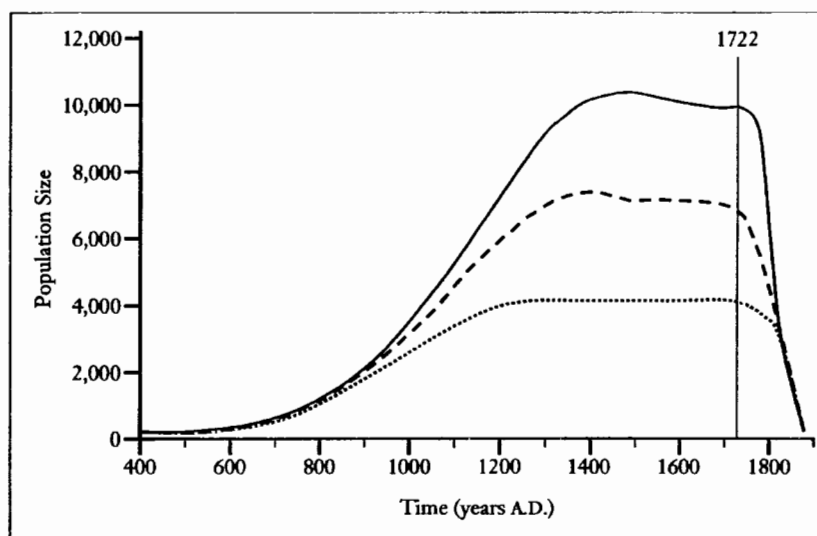
A demographic model of population growth is needed to estimate the effective population size in Rapa Nui from initial colonization through the nineteenth century. In circumscribed geographic ranges, models that incorporate growth-rate reductions from resource stress are better predictors of population size through time. Density-dependent demographic models predict that populations that approach the environmental carrying capacity of the landscape they exploit will suffer population growth-rate declines from reduced fertility in stressful environments (Alstad 2001; MacIntyre 1999).

A density-dependent model of prehistoric population growth (figure 9.2) provides estimates of both intrinsic growth rate and total population through time and better approximates living systems in finite environments. Density-dependent growth models assume overall population size will affect the per-capita growth rate of the population as a negative linear effect that increases as the population approaches the carrying capacity of the environment (Alstad 2001). At colonization, small initial populations are significantly below carrying capacity, and the intrinsic population growth rate is near maximum. As the population nears carrying capacity, the negative effect on the growth rate

results in reduction of intrinsic growth rate toward zero and eventually a stable equilibrium where the population size equals carrying capacity.

Numerous authors have speculated on both the time and size of initial colonization of Rapa Nui (Finney 1993; Irwin 1992; Kirch 1984). Some estimates favor a small founding population (40-150 individuals) and a settlement date as early as A.D. 400 (Heyerdahl and Ferdon 1961; but see Martinsson-Wallin and Crockford [2001] and Spriggs and Anderson [1993] for recent reassessments of the Rapa Nui radiocarbon chronology). The size of the prehistoric maximum population on Rapa Nui is an equally contentious issue. Most authors agree with the paleoenvironmental evidence that forest decline and population stress occurred by A.D. 1550 and that after that date the population leveled off and then began a slow decline toward a census

**Figure 9.2**  
Density-Dependent Population-Growth Curves for Rapa Nui



In this simulation, intrinsic growth rate is set to 0.006, corresponding to roughly 12 percent population growth per generation (20 years). This growth rate, while generally in agreement with other estimates, is not crucial to total-population estimates, other than as a device for building population at a specific level at a certain time. Although low by comparison to modern developing nations, which often serve as analogues to prehistoric colonizing populations, this growth rate fits the expectation of a population maximum in the sixteenth century. Included in this graph is the hypothetical rapid population decline after about A.D. 1750, which corresponds roughly to 10–15 percent population loss per generation. This decline reflects the combined effects of environmental deterioration, social instability, and introduced disease (syphilis, smallpox, and tuberculosis) subsequent to European contact in 1722 up to the census figure of 3000 in 1862. By 1880, only 111 native Rapa Nui remained.

population of 3,000 individuals in 1862. This is the year before the arrival of Peruvian slave traders, who exploited the local population for off-island mining concerns, reducing the total population to 111 people by 1877.

Estimates of population reached during the hypothesized prehistoric high in the sixteenth century range between 4,000 and 10,000 individuals, with most estimates between 6,000 and 8,000 (Bahn and Flenley 1992). Simulating population growth from a colonizing population size of 100 at an early date of A.D. 400 (Irwin 1992), and setting the intrinsic growth rate so that maximum population is reached by A.D. 1550, creates the population estimates shown in figure 9.2.

I expect the effective population size for the estimates of diversity loss to be some small fraction of the total potential breeding population (ca. 10,000 high census population) over the time period of interest. If we presume that the skeletal population represents a late-period population (A.D. 1500–1750), the effective population size over the 67.5 generations between A.D. 400 and A.D. 1750 is only 699 individuals. If the founding population that landed on Rapa Nui ca. A.D. 400 consisted of perfectly heterozygous ( $H_o = 0.5$ ) individuals, the expected heterozygosity is 0.476, meaning that less than a 0.03 reduction in genetic diversity is predicted over the 67.5 generations of continuous occupation.

If, however, we divide the island-wide effective population equally among the eleven ethnographically reported prehistoric tribal divisions shortly after contact, the expected tribe-level heterozygosity drops to 0.293. Table 9.1 demonstrates the expected reductions in heterozygosity under different levels

**Table 9.1**  
Expected Heterozygosity Reduction Based on Estimates of Effective Population Size for Rapa Nui

Island effective population size ( $N_e$ ) <sup>a</sup>	Heterozygosity reduction ( $H_{exp}$ ) <sup>b</sup>		Hypothesized social division <sup>c</sup>
699	0.48	(0.02)	None (island-wide interaction)
350	0.45	(0.05)	Moiety (subdivided population)
64	0.29	(0.21)	Tribal/Corporate (eleven separate political entities)
32	0.17	(0.33)	Lineage-Based (two lineages/factions per tribe)

<sup>a</sup> Based on density-dependent growth rate and maximum census population of 10,000 individuals.

<sup>b</sup> Calculated reduction from initial heterozygosity of 0.5.

<sup>c</sup> Reported by Routledge (1919)

of population subdivision. Based on the assumptions of the model of random genetic drift, we might expect slightly greater losses in heterozygosity in our Rapa Nui population if nonrandom mating and fluctuating size within subpopulations occurred.

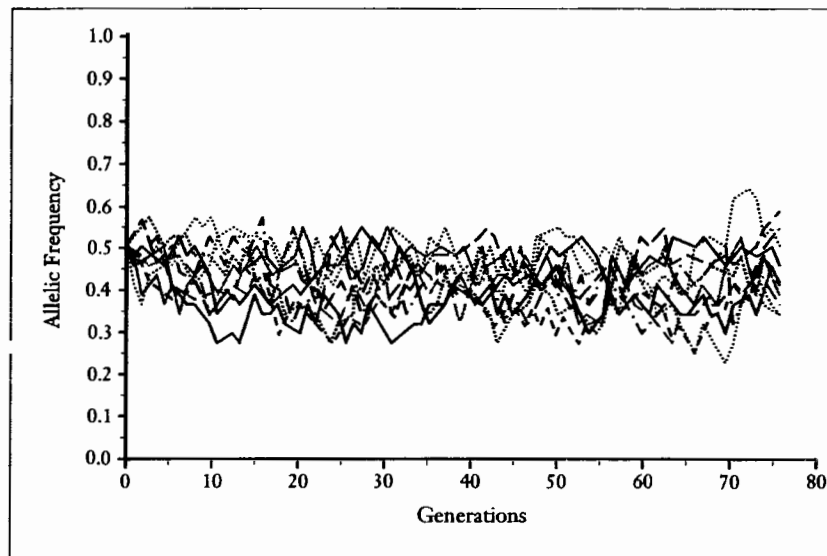
I hypothesize that the hierarchical population structure took the form of individual spatially defined lineages at the lowest level of inclusiveness and encompassed the entire island at its highest level. In between, the corporate descent unit described by Stevenson (1984, 2002) groups individual lineages, which are in turn nested into the ethnohistoric tribal boundaries (Routledge 1919) and moieties described by various authors (McCall 1984; Métraux 1940; Routledge 1919). Framing testable hypotheses for geographic genetic structure inevitably relies on ethnographic and archaeological social divisions. There exist few if any geographic barriers to gene flow by migration, and the island's small size precludes genetic models of isolation by distance (e.g., Malécot 1950; Wright 1943), unless mobility can be shown to be strongly and negatively correlated with population density. Nonetheless, geographically patterned population structure may emerge under several anthropological scenarios, including lineage-based marriage restrictions and social competition between descent groups (Métraux 1940).

Figure 9.3 provides a simple example of the effect of migration rate on the expected allelic frequencies in a hypothetical example of a developing population. Each simulation represents a subpopulation composed of ten demes, or subpopulations, each containing 100 individuals. Each deme interacts with the others, based on a migration rate of 0.15 per generation, averaged over all other demes. This migration rate corresponds to the exchange of fifteen individuals from each deme of 100 individuals in each generation. A migration rate of 0.15 per generation is considered relatively endogamous in human tribal populations (Birdsell 1973) and produces an average decrease in subpopulation heterozygosity from 0.5 to 0.479, reaching a semistable equilibrium after ten generations. If this simplistic model proves a robust approximation of the demographic history on Rapa Nui, random migration will mitigate genetic differentiation between subpopulations, and it might be difficult to discern subpopulation structure. We might also suppose that on Rapa Nui migration by mate exchange might have been significantly higher than modeled here. Routledge (1919: 221) noted that "in remembered times there were no group restrictions on marriage, which took place indiscriminately between members of the same or different clans."

#### Nonrandom Gene Flow

The notion that the population structure for Rapa Nui prior to the nineteenth century was hierarchically organized by lineage, and by extension, the family, offers hope that we can model these processes of genetic divergence within an anthropological framework integrated with genetic theory for small,

**Figure 9.3**  
**Allelic-Frequency Changes Over Time as a Response to Random Genetic Drift and Gene Flow**



Simulation shows the rate and trajectory of heterozygosity change for a sample of 10 demes of 100 individuals, exchanging migrants at a rate of 0.15, or 15 individuals per generation. Initial frequency of alleles is 0.5 for all demes. This corresponds to a homogeneous colonizing population.

interacting populations. The simple model presented here assumes there are no spatial barriers to migration and that all migrant exchange per generation is random with respect to the target deme and the allelic frequency of each migrant. But humans, as with other social mammals, tend to migrate nonrandomly across space in related groups (Fix 1978), which might bias the sex ratio of migrants based on rules of kinship and resource partitioning (Flinn and Low 1986). Also, competition may generate barriers to migration along the boundaries or within existing subpopulations (Read and LeBlanc 2003), either through patch depletion or social competition from mating control (Flinn and Low 1986). To understand the specific lineage histories and evolution of genetic divergence in Rapa Nui, tests of population structure must be sensitive to nonrandom gene flow in any form predicted from prior anthropological or archaeological observations.

Models of kin-structured migration posit that the migration of related individuals has a positive effect on the maintenance of heterozygosity, especially measures of between-group to within-group variance, and may partially offset the homogenizing effect of random migration (Rogers 1987). Migration is

expected to maintain heterozygosity in randomly interacting populations, reducing the visibility of population substructure. Kin-structured migration can generate the opposite effect, maintaining population substructure and creating visible effects over time and distance (Fix 1999). Included within this general class of nonrandom migration is the anthropological notion that in Rapa Nui, some groups or demes practiced marriage-exchange alliances (*tumus*), which structured mate exchange between specific tribes (Métraux 1940).

Also of interest for Rapa Nui is nonrandom gene flow through what Neel (1967) called the "lineal effect," which is the result of kin-based fission of local co-resident populations that produces new, kin-structured population migrations. Stevenson (1984, 1986) suggests that this kind of process explains late prehistoric populations based on his study of southern-coast settlement patterns after A.D. 1400. Neel and Salzano (1967) demonstrated that such fission and fusion processes could generate significant amounts of localized heterogeneity, a kind of kin-structured founder effect (Fix 1999).

Sex-biased gene flow, in the form of spatially structured male-female craniometric variation (Stefan 1999), may also have conferred localized heterogeneity. Analysis of sex-biased migration, especially for reconstruction of historical process in contrast to population structure (Templeton 1998; Templeton et al. 1995), will rely on sex-specific alleles (mtDNA, Y chromosome) and their relationship to dual-inheritance genetic variation (nuclear polymorphism). For Rapa Nui, the low mtDNA variation in eastern Polynesia (Murray-McIntosh et al. 1998) and the hypothesized small colonizing population may preclude resolving sex-biased migration as a historical process in the archaeological population.

Viewed in this way, analysis of subpopulation differentiation in Rapa Nui under nonrandom migration holds promise for testing previous observations of spatially clustered phenotypic traits. Gene flow via nonrandom migration may tend to maintain heterozygosity differentially with respect to random migration under various ideal models (Kimura and Weiss 1964; Malécot 1950; Wright 1943, 1951). If migration is viewed as a stochastic process under the ideal models, then nonrandom migration can be viewed as an augmentation (Fix 1999).

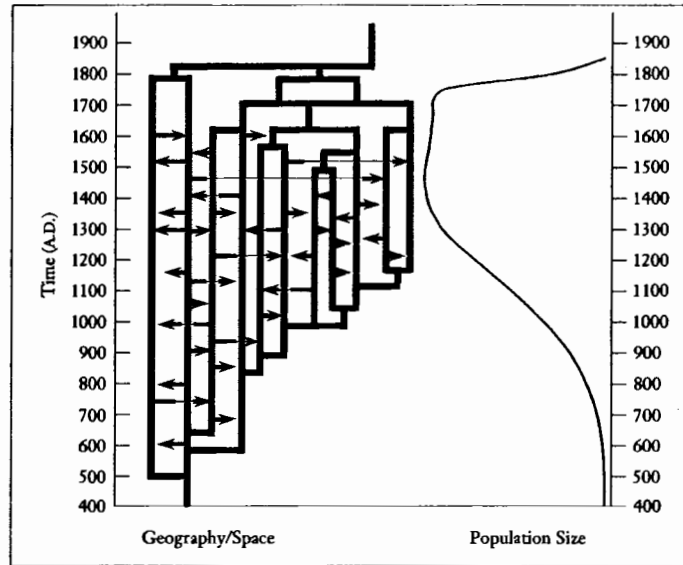
If prehistoric Rapa Nui is characterized by lineal fission and establishment of new coastal settlements during the period of rapid population growth (figure 9.4), then the effects of kin-structured migration will generate a spatial pattern of discrete pockets of low genetic variation and the appearance of greater isolation between geographically proximate subpopulations. Skeletal material in the caves on Rapa Nui's southern coast, although probably later than the period of rapid population expansion, suggests that long-term habitation by localized and isolated populations was occurring (Shaw 1996, 2000).

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### Conclusion

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**Figure 9.4**  
**Example of Demographic Structuring and Its Effect on Lineage Evolution**



As Rapa Nui population growth accelerated after about A.D. 800, new lineages emerged, with subpopulations expanding into and colonizing new coastal areas (fission). After A.D. 1500, environmental deterioration coupled with social instability resulted in the fusion of previously independent lineages. The phylogeographic-branching pattern shown here represents averages of multiple lineages in regional descent groups.

Analysis of prehistoric molecular variation over geographic space creates independent historical explanations that can be compared to archaeological or other spatial-temporal data. Critical to these explanations is the ability to discern spatial variation at scales pertinent to the demographic structure of the target population. Different classes of DNA polymorphism are capable of resolving population structure at multiple scales, depending on the evolutionary history of the organism. In order to generate meaningful explanations for hierarchical structure, defined subpopulations must show a reduction in the average proportion of population heterozygosity relative to the expected proportion of heterozygous genotypes in a randomly mating population (Hartl and Clark 1997).

Partial barriers to gene flow, in the form of geographic or social boundaries to migration or isolation by distance in a continuous population, can generate measurable discontinuous as well as clinal distributions of heterozygosity reduction, given sufficient time and effective population size. Whereas the reduction of heterozygosity through genetic drift within and between small populations is more rapid relative to larger populations, similarly small amounts

of random gene flow from migration are required to obliterate the observation of hierarchical structure and subpopulation divergence (Crow and Kimura 1970).

Although it probably is true that estimating phylogenetic structure, especially in small, interacting populations, is better approximated by models that specify an explicit model of evolution (Nielsen et al. 1998; Templeton 1998), estimators of differentiation based on Wright's  $F$ -statistics will continue to serve a valuable role (Neigel 2002). The relationship between  $F$ -statistics and anthropologically important parameters such as population size and rate of migration between demes overcomes some of the loss of relevant data imposed by averaging allelic frequencies into genetic distances.

The question being asked here is not focused on genetic drift or heterozygosity reduction but on the amount of gene flow and heterozygosity maintenance that can be predicted from patterned variation in the interaction of genetic drift and gene flow. Genetic drift is a stochastic process, ratcheting variability out of populations in unpredictable ways. Modifications to the process of genetic drift, such as mutation, migration, and selection, provide data to generate explanations for the differential persistence of variation in a study population. Rapa Nui is an excellent laboratory in which to test our ability to resolve differences in human association through time and to identify and explain these differences under variable life-history strategies.

Here the goal is almost the opposite of standard phylogenetic analysis. Rather than elucidating structure through the identification of ancestral states and then explaining the differences according to bifurcating nodes, studies such as the one discussed here attempt to identify historically significant amounts of gene flow that enhance relatedness among otherwise geographically separate, bifurcating populations. Mitigation of genetic drift through population interaction, especially if the interaction is not purely negatively correlated with geographic distance (Wright 1943), has important implications that must be understood.





# **Part 4**

## **Culture**



