Genetic Drift and Gene Flow in Post-Famine Ireland

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Abstract This study examines the genetic impact of the Great Famine (1846–1851) on the regional genetic structure of Ireland. The Great Famine resulted in a rapid decrease in population size throughout Ireland in a short period of time, increasing the possibility of genetic drift. Our study is based on migration and anthropometric data collected originally in the 1930s from 7211 adult Irish males. These data were subdivided into three time periods defined by year of birth: 1861–1880, 1881–1900, and 1901–1920. Within each time period the data were further subdivided into six geographic regions of Ireland. Estimates of Wright's F_{ST} were calculated from parent-offspring migration data and from 17 anthropometric variables (10 head measures, 7 body measures). Over time, the average population size decreased, but average rates of migration increased. The estimates of F_{ST} at equilibrium from migration matrix analysis suggest that the net effect of these opposite effects is a reduction in among-group variation. Closer examination shows that within each time period the rate of convergence to equilibrium is slow, meaning that the expected levels of genetic homogeneity revealed from migration matrix analysis are not likely to be seen over short intervals of time. Estimates of F_{ST} from anthropometric data show either relatively little change in microdifferentiation or some increase, depending on which variables are analyzed. Investigation of a simple model of demographic and genetic change shows that, given the demographic changes in post-Famine Ireland, F_{ST} could in theory increase, decrease, or remain the same over short intervals of time. Overall, the Great Famine appears to have had minimal impact on the genetic structure of Ireland on a *regional* level. Comparison with studies focusing on *local* genetic structure shows the opposite. It appears that the level of genetic impact depends strongly on the level of analysis; local populations are affected to a greater extent by demographic shifts than regional populations. We also provide formulas for the standard errors of F_{ST} from metric traits and related statistics.

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The Great Famine of 1846–1851 was a recent and dramatic event in the demographic history of Ireland (here, the term "Ireland" refers to the entire island, currently made up of two nations—the Republic of Ireland and Northern Ireland). Before the potato was introduced as a crop in the early 1700s, the hilly landscape and large amount of bog in Ireland had limited agricultural output. Because the potato is relatively nutritious and can be grown in a variety of conditions, its introduction allowed the carrying capacity of the population to increase. In particular, fathers were more easily able to subdivide their land, thus allowing more than one son to inherit some portion of the family farm. Because landholding was often a prerequisite for marriage, this change led to an increased frequency of marriage. In addition, there is evidence suggesting a decrease in the average age of marriage (Kennedy 1973).

The net result of these changes and others was an increase in the birth rate and a rapid increase in population size (Connell 1950; Brody 1973). As shown in Figure 1, the total population size of Ireland increased from slightly over 2 million in the late 1600s to over 8 million by 1841 (Vaughan and Fitzpatrick 1978). The Great Famine was a five-year period of continual potato blight, leading to a shortage of food compounded by the need to pay rent to English landholders. An estimated 1 million people died during this time and an additional 1.3 million emigrated (Bittles and Smith 1994). The economic and health problems continued for many years, particularly in the western part of Ireland. The social consequences were a return to patterns of single-son inheritance, a decrease in the rate of marriage, an increase in the age at marriage, and an increase in emigration rates (Kennedy 1973). The demographic data show that the overall population of Ireland continued to decrease well into the twentieth century (see Figure 1).

An obvious genetic consequence of population reduction is an increase in the rate of random genetic drift. For example, Bittles et al. (1986) suggested that the high frequency of certain recessive disorders in parts of Ireland might be due to increased genetic drift after the Great Famine. Despite the potential genetic consequences of the Great Famine, few studies in Irish human biology have specifically addressed this issue, other than as one of many potential historical factors affecting human variation. What is clearly needed is a diachronic approach, where changes in the degree and pattern of biological variation can be assessed over time, focusing on the potential genetic impact of the Great Famine. Most studies of Irish population biology, however, look at genetic variation at a single point in time [e.g., Hooton et al. (1955), Sunderland et al. (1973), Tills (1977), Tills et al. (1977), Greally and Roberts (1991), and Relethford and Crawford (1995)].

One notable exception is the continuing historical demographic study of the Ards Peninsula in Northern Ireland. These studies have examined post-Famine demographic changes in local populations, including using surnames to estimate patterns of genetic variation (Bittles et al. 1986; Smith et al. 1990;

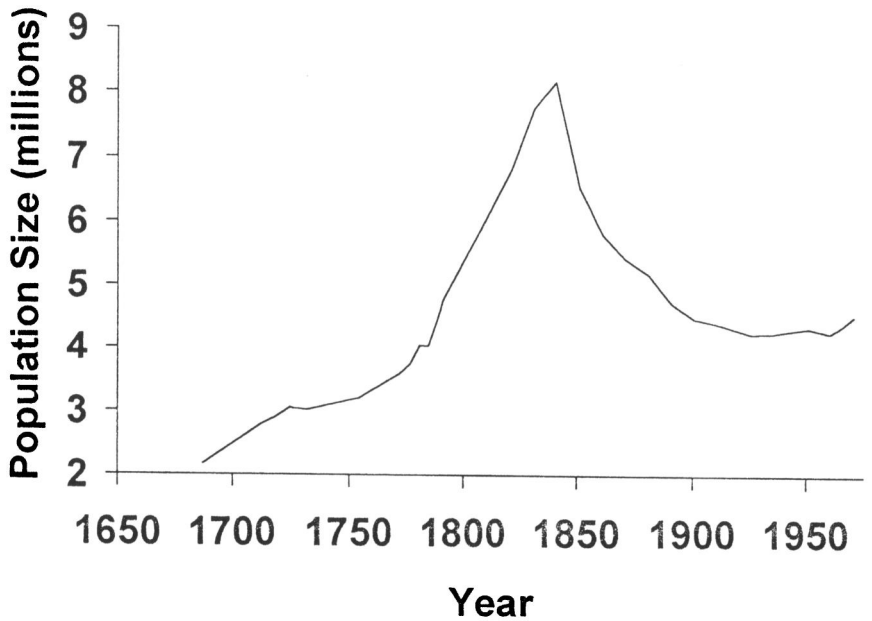

Figure 1. Population size of Ireland from 1687 to 1971. Source of data: Vaughan and Fitzpatrick (1978).

Bittles and Smith 1991, 1994). The key importance of these studies is a research design specifically geared to looking at the potential genetic impact of the Great Famine.

The purpose of the present study is somewhat related, although from a different perspective. By using several generations of migration and anthropometric data, we focus on the potential genetic impact of the Great Famine on *regional* rather than *local* patterns of human variation. Previous research using these data has shown that biological variation in Ireland is best explained by the interaction of several past events in population history. Given the rapid demographic change accompanying the Great Famine, what impact do such changes have on changing the picture of genetic variation in Ireland? The question of potential genetic impact resulting from genetic drift is compounded by the potential for related changes in migration patterns. Rapid changes in population size might have an impact on rates of gene flow, which in turn might enhance or counter the effects of genetic drift. There is some evidence from several human populations of an inverse relationship between population size and gene flow. For example, Brennan and Relethford (1982) demonstrated an increase in off-island emigration accompanying population

decline on Sanday Island in the Orkney Islands. Several studies have shown higher exogamy rates in smaller populations when compared with medium-sized populations [e.g., Relethford (1986) and Relethford and Mielke (1994)]. These relationships may reflect a lack of suitable mates within small populations, thus necessitating exogamous marriage. We might therefore expect an increase in gene flow in Ireland at the same time that population size declines. If so, then the two trends might counter one another. Other possibilities include an increase *or* decrease in the level of microdifferentiation, depending on the proportional changes in both gene flow and genetic drift. In reality, the situation is apt to be more complex, because the level of microdifferentiation depends not only on population size and migration rates but also on past levels of microdifferentiation (Relethford 1991a).

Our specific study addresses the impact of post-Famine demographic changes by looking at changes in estimates of migration rates and genetic structure obtained from a large cross-sectional study conducted in the 1930s. The sample consists of parent-offspring migration data and anthropometric measures for 7211 adult males from 31 of the 32 Irish counties. This sample is divided into six regions and three time periods, thus allowing analysis of spatial and temporal trends in population structure. Temporal changes in microdifferentiation are assessed using estimates of Wright's F_{ST} and are related to known patterns of demographic change. Two specific questions are addressed: (1) How does migration change over time in post-Famine Ireland? and (2) how do changes in population size and migration interact and affect the level of genetic variation among populations? Unlike the Ards Peninsula study, our focus is on countrywide variation.

Materials

The data used in this study were originally collected between 1934 and 1936 as part of an anthropological study of Ireland conducted by Harvard University. Anthropometric and demographic data were collected from almost 9000 adult males by C. Wesley Dupertuis and from almost 2000 adult females by Helen Dawson. This survey resulted in two publications focusing on "racial" variation (Hooton 1940; Hooton et al. 1955) and one publication on age-related variation (Hooton and Dupertuis 1951). Much of the original data have since been recoded in computer format, as described by Relethford and Crawford (1995).

Data were available for 8385 males. We restricted analysis to those males that had complete demographic and anthropometric data and who were born in Ireland. We further restricted our analysis to those individuals between 15 and 74 years of age; this provides us with information on subjects born roughly between 1861 and 1920. Complete data were available for 7211 adult males. For each individual data were available for age, counties of birth and

Table 1. Sample Sizes by Geographic Region and Time Period

	Time Period (Year of Birth)			
Geographic Region	*1861–1880*	*1881–1900*	*1901–1920*	*Total*
Southwest	365	714	943	2022
West	161	346	582	1089
Midlands	98	301	710	1109
North	151	410	624	1185
East	129	282	398	809
South	178	348	471	997
Total	1082	2401	3728	7211

residence, birth counties of both parents, and 17 anthropometric measurements (weight, stature, acromion height, biacromial breadth, chest depth, chest breadth, sitting height, head circumference, head length, head breadth, head height, minimum frontal diameter, bizygomatic breadth, bigonial breadth, upper facial height, nose height, and nose breadth).

To assess temporal trends in genetic structure, we subdivided the total sample into three samples based on approximate year of birth, obtained by subtracting age from the midpoint of data collection (1935). Three 20-year subsamples were used; this number was determined by consideration of sample sizes: 1861–1880, 1881–1900, and 1901–1920. The use of temporal subsets of cross-sectional data is widely known, but seldom have human biologists had samples large enough for useful subdivision. Jorde, Workman et al.'s (1982) study of genetic markers and migration in the Åland Islands is a notable exception.

The total sample was also divided into six geographic regions. These regions were chosen on the basis of geographic proximity, considerations of sample size, and our previous analysis based on these data (Relethford and Crawford 1995), which looked at genetic structure among 31 of the 32 Irish counties (the remaining county was not considered because of small sample size).

Sample sizes by geographic region and time period are reported in Table 1. Many individual sample sizes are large and the lowest ($n = 98$) is reasonably close to our initial desire for minimum subsamples of at least 100. Sample sizes are largest in the most recent time period, reflecting the greater number of young adults sampled by Dupertuis. To remove potential confounding effects of age-related variation, we regressed each anthropometric variable on age and age^2 and then used the residuals as age-corrected data. The age correction was done separately within each of the three time periods so that temporal changes in genetic structure would not be removed by age adjustment.

Methods

The level of genetic microdifferentiation was assessed from both migration and anthropometric data using R matrix estimation. An R matrix is a matrix of standardized variances and covariances of populations around the contemporary values of allele frequencies. In genetic terms the elements r_{ij} of the R matrix are computed for each allele:

$$r_{ij} = \frac{(p_i - \bar{p})(p_j - \bar{p})}{\bar{p}(1 - \bar{p})}, \tag{1}$$

where p_i and p_j are the allele frequencies in populations i and j, respectively, and $\bar{p}$ is the weighted mean allele frequency over all populations in the analysis (the weighting is done using population sizes, not sample sizes) (Harpending and Jenkins 1973). The elements of this matrix are then averaged over all alleles. The R matrix provides information on relationships among populations defined relative to the contemporary array of allele frequencies (the values of $\bar{p}$). The R matrix has a number of useful properties for studying genetic structure. The average weighted element of the R matrix ($w_i w_j r_{ij}$) is equal to 0, and pairs of populations with positive r_{ij} values are more closely related than on average. Likewise, pairs of populations with negative r_{ij} values are less closely related than on average. In addition, the weighted average diagonal of the R matrix provides a familiar and useful index of genetic microdifferentiation—F_{ST}. That is,

$$F_{ST} = \sum_{i=1}^{g} w_i r_{ii}, \tag{2}$$

where g is the number of populations and w_i is the relative *population* size of population i. This estimate of Wright's F_{ST} is defined relative to the contemporary array of allele frequencies, not to the (unknown) founding array. As used here (or in any analysis based on contemporary allele frequencies), F_{ST} is a *reduced* variance measure (Rogers and Harpending 1986; Wood 1986). Although originally applied to data from genetic markers, R matrices have recently been estimated from a variety of data. We use these newer methods to estimate F_{ST} from migration matrices and anthropometrics.

Migration Matrix Analysis. Migration matrix analysis allows prediction of an R matrix and F_{ST} at an equilibrium between the forces of gene flow and genetic drift. We use Rogers and Harpending's (1986) method of R matrix estimation, which is based on the migration matrix among populations (M), the effective sizes of each population (N_e), and an estimate of external gene flow (s). For each time period the elements of the migration matrix m_{ij} indicate the number of subjects born in region j whose parents were born in region i. Effective population sizes for each of the six regions for each time period

were taken provisionally as one-third the census population size (Jorde 1980). We examine potential problems with this crude estimate later. Census population sizes were obtained from Vaughan and Fitzpatrick (1978) for the midpoint of each time period (the 1871 census for the period 1861–1880, the 1891 census for the period 1881–1900, and the 1911 census for the period 1901–1920). The rate of external gene flow was estimated as the proportion of parents born outside Ireland.

Rogers and Harpending (1986) showed that different results are obtained depending on whether newborns or adults are considered. Because the anthropometric data are assigned to regions based on the county of birth, we use Rogers and Harpending's statistics for *newborns.*

Following Rogers and Harpending (1986), we computed F_{ST} from parent-offspring migration data using three different methods, referred to as the unrestricted, symmetric, and approximate solutions. The unrestricted method uses the exact migration matrix, assuming that any asymmetry in migrant exchange does not affect the relative size of populations. The symmetric solution, most often used, takes an average number of migrants between populations i and j and between populations j and i. Rather than use a simple average, we used the more appropriate maximum-likelihood estimate suggested by Rogers and Harpending (1986). Finally, we also used Rogers and Harpending's island model approximation for newborn F_{ST}, which is

$$F_{ST} = \frac{1 + 2m_e}{1 + 4N_e m_e} \tag{3}$$

(the corresponding formula for adult F_{ST} has a 1 in the numerator). Here, m_e is Rogers and Harpending's effective migration rate and N_e is the reduced variance effective population size, computed as

$$N_e = \frac{\bar{n}g}{g - 1}, \tag{4}$$

where $\bar{n}$ is the average effective population size over g populations.

In addition to estimates of R and F_{ST}, Rogers and Harpending's (1986) method provides other useful parameters of genetic structure. One is the effective migration rate, defined as

$$m_e = \left(\frac{g - 1}{2}\right) \sum_{i=2}^{g} \left[\frac{1}{1 - (1 - s)^2 \lambda_i^2}\right], \tag{5}$$

where s is the rate of external gene flow and λ_i is the ith eigenvalue of the migration matrix. This is a useful estimate of the effect of migration on F_{ST} that can be compared across samples and does not confound the effects of mobility and population size. Another useful parameter is the half-life till convergence, computed as

$$h = \frac{\ln(0.5)}{2(1 - s)\lambda_2}. \quad (6)$$

It would take h generations to reach 50% of the equilibrium value of F_{ST}, $2h$ generations to reach 75% of equilibrium, and so on. This parameter is also useful as an index of how rapidly genetic structure will change in situations of demographic change (Relethford 1991a).

Anthropometric Analysis. For each time period we estimate R and F_{ST} from anthropometric data using the methods outlined by Williams-Blangero and Blangero (1989) and Relethford and Blangero (1990). These methods are based on an equal and additive effects model of quantitative genetics and provide a multivariate estimate of R based on population means and the pooled within-group additive genotypic covariance matrix. Because we have no estimates of heritability or the genotypic covariance matrix, we substitute the phenotypic covariance matrix. As shown by Williams-Blangero and Blangero (1989), this substitution provides an estimate of the *minimum* F_{ST} and is a useful comparative measure. We make one additional correction, first suggested by Relethford (1991b): a correction for sampling error to F_{ST}. We do this by subtracting the quantity $1/2n_i$ from the r_{ii} values, where n_i is the sample size of group i. Derivation of this bias correction term is provided in the appendix. The unbiased minimum F_{ST} is then computed using Eq. (2) with the adjusted r_{ii} values. Standard errors were derived using a formula derived in the appendix. All analyses were performed using head measures and body measures separately in addition to the full set of variables.

Results

Migration Matrix Analysis. The symmetric migration rate matrices are reported in Table 2, and summary results are given in Table 3. The average effective population size decreased over time, dropping 16% from the first time period (1861–1880) to the second (1881–1900) and dropping an additional 10% from the second time period to the third (1901–1920). The rate of external gene flow s increases slightly from the first time period ($s = 0.0055$) to the second ($s = 0.0079$), but this change is not significant (test of proportions: $Z = 1.083$, $p = 0.279$). The rate of external gene flow is the same in the second and third time periods.

Table 3 also reports the total endemicity rate for all three time periods, which is the proportion of individuals born in the same region as a parent. This rate decreases significantly from the first to second time period ($Z = 2.601$, $p = 0.009$) and from the second to third time period ($Z = 5.952$, $p < 0.001$). This decrease indicates increased migration among regions *within* Ireland. These changes in among-region migration over time are also shown

Table 2. Parent-Offspring Migration Matrices for Each Time Period Using Symmetric Migration Numbers[a]

Birth Region of Parents	*Birth Region of Offspring*					
	Southwest	*West*	*Midlands*	*North*	*East*	*South*
1861–1880						
Southwest	0.9721	0.0134	0.0000	0.0000	0.0066	0.0247
West	0.0078	0.9788	0.0000	0.0010	0.0026	0.0015
Midlands	0.0000	0.0000	0.9652	0.0029	0.0067	0.0045
North	0.0000	0.0022	0.0108	0.9917	0.0066	0.0000
East	0.0060	0.0041	0.0168	0.0045	0.9712	0.0097
South	0.0142	0.0015	0.0072	0.0000	0.0062	0.9596
Effective population size	351,154	203,327	126,388	467,704	316,513	201,691
1881–1900						
Southwest	0.9700	0.0111	0.0036	0.0004	0.0104	0.0226
West	0.0066	0.9696	0.0118	0.0017	0.0025	0.0053
Midlands	0.0013	0.0069	0.9474	0.0006	0.0089	0.0073
North	0.0005	0.0038	0.0024	0.9843	0.0162	0.0039
East	0.0094	0.0038	0.0232	0.0113	0.9432	0.0313
South	0.0123	0.0048	0.0114	0.0016	0.0188	0.9297
Effective population size	300,321	177,253	103,590	388,580	271,356	163,049
1901–1920						
Southwest	0.9603	0.0166	0.0078	0.0019	0.0110	0.0268
West	0.0094	0.9447	0.0156	0.0018	0.0086	0.0113
Midlands	0.0025	0.0090	0.9024	0.0023	0.0127	0.0161
North	0.0025	0.0041	0.0091	0.9710	0.0285	0.0021
East	0.0111	0.0151	0.0391	0.0221	0.9138	0.0481
South	0.0142	0.0106	0.0261	0.0009	0.0254	0.8955
Effective population size	266,365	151,149	87,115	344,040	267,109	140,941

a. Each matrix is column stochastic; that is, each column of each matrix sums to 1. Symmetric migrant numbers were derived from the observed migration matrix using Rogers and Harpending's (1986) maximum-likelihood estimate.

by an increase in Rogers and Harpending's effective migration rate over time, from 0.029 to 0.047 to 0.070.

Rates of s and m_e are low compared with other populations studied by Rogers and Harpending (1986), who found a range in m_e of 0.10–0.33 for 13 samples of human populations. However, it must be kept in mind that the present study focuses on larger geographic regions and is expected to show higher endemicity rates and lower effective migration rates.

Table 3 reports F_{ST} for all three time periods based on the unrestricted, symmetric, and approximate solutions. There is only a small difference between these estimates for the first time period and no difference for the second or third time periods. Even though the chi-square log-likelihood tests of sym-

Table 3. Results of Migration Matrix Analysis

	Time Period		
Estimate	*1861–1880*	*1881–1900*	*1901–1920*
Average effective population size (N_e)[a]	333,355	280,830	251,344
Rate of external migration (s)	0.0055	0.0079	0.0079
Average endemicity (p_{ij})[b]	0.9730	0.9605	0.9354
Effective migration rate (m_e)	0.0288	0.0465	0.0700
Equilibrium half-life (h) in generations	25	13	9
Equilibrium F_{ST} (newborns)			
Unrestricted solution	0.000030	0.000021	0.000016
Symmetric solution	0.000027	0.000021	0.000016
Approximate solution	0.000028	0.000021	0.000016

a. Rogers and Harpending's (1986) reduced variance effective population size.
b. Computed from the observed migration matrix before symmetric estimation.

metry suggested by Rogers and Harpending (1986) were all significant ($p < 0.05$), there is no impact on the F_{ST} values. For all practical purposes, the migration structure of Ireland for all three time periods can be represented by symmetric migration.

The equilibrium F_{ST} values (reflecting differentiation among newborns) are low in all three time periods and clearly decrease over time. These F_{ST} values are quite low compared with many anthropological studies (Jorde 1980), reflecting the larger geographic units of analysis used in the present study, which results in estimates of F_{ST} based on large effective sizes and low rates of gene flow. The effect of the size of the unit of analysis is well known (Harpending 1974; Fix 1979) and can be seen clearly in the low estimates of F_{ST} from migration matrices for large geographic subdivisions, such as those used in studies of Iceland (Jorde, Eriksson et al. 1982) and the Utah Mormons (Jorde 1982).

The equilibrium half-life h decreases from a high of 25 generations in the first time period to a low of 9 generations in the third time period. Even the lowest value is greater than that observed in most human populations studied to date (Rogers and Harpending 1986). The high half-life estimates reflect relatively low levels of migration, again because of the larger geographic units considered in the present study.

Anthropometric Analysis. The unbiased minimum F_{ST} values from anthropometrics and their standard errors are reported in Table 4 for all measures, for head measures, and for body measures. All F_{ST} values are significantly different from 0, indicating significant among-group variation. There is some tendency for the F_{ST} values estimated from head measures to be greater than those estimated from body measures. The F_{ST} values estimated

Table 4. Unbiased Minimum F_{ST} Estimates Based on Anthropometrics (Standard Errors in Parentheses)

Anthropometric Measures Used	*Time Period*		
	1861–1880	*1881–1900*	*1901–1920*
All	0.0049 (0.0010)	0.0054 (0.0006)	0.0065 (0.0005)
Head	0.0050 (0.0013)	0.0065 (0.0008)	0.0087 (0.0007)
Body	0.0047 (0.0014)	0.0045 (0.0009)	0.0045 (0.0006)

from all anthropometric measures and those estimated from head measures show a clear increase over time, particularly for the head measures. The F_{ST} values estimated from body measures remain relatively constant over time. A Z test was used to compare F_{ST} estimates in adjacent time periods by using the pooled standard error. When considering all anthropometric measures, there is no significant change in F_{ST} from the first to the second time period or from the second to the third time period. The same results also apply to the F_{ST} values estimated from body measures. For the head measures the increase in F_{ST} from the first to the second time period is not significant ($Z = 0.983, p = 0.326$), but it is significant between the second and third time periods ($Z = 2.070, p = 0.038$).

The minimum F_{ST} estimates from anthropometrics are much greater than those estimated from migration matrix analysis. A difference between observed values (based on biological data) and predicted values (based on migration data) of F_{ST} has been found in other studies [e.g., Jorde, Eriksson et al. (1982), Jorde, Workman et al. (1982), and Roberts (1982)] and most likely reflects several factors. First, migration matrix estimates assume no prior genetic relationship among populations; that is, they do not include past history that clearly affects levels of microdifferentiation. Second, estimates of effective population size are likely to be overstated because of the lack of information regarding variation in fertility and others factors that further reduce a population's effective size. Third, migration matrix estimates are based on the assumption of equilibrium, which may not be appropriate. Where equilibrium has not been reached, such as the present study where there is a long half-life to convergence, observed and predicted estimates of F_{ST} are unlikely to be of the same magnitude. Rogers and Harpending (1986) found the best agreement between estimates of F_{ST} from genetic and migration data when convergence to equilibrium was rapid. This is clearly not the case for the present study, as shown by the high half-life values in Table 3.

Discussion

Our analyses show that any interpretation of post–Great Famine genetic structure must take into account the opposite trends in population size and

migration. Overall population size continued to decline following the Great Famine. Relethford (1991a) showed that an increase in population size could result in an increase in F_{ST}, a decrease in F_{ST} or no change at all. On the other hand, a decrease in population size will always lead to an increase in F_{ST} under certain assumptions. Relethford's (1991a) model is not useful in the present study, however, because it assumes that migration rates remain constant over time. For post-Famine Ireland migration has *increased* over time. The increase in Rogers and Harpending's (1986) effective migration rate has been shown to be due to a decrease in endemicity within Ireland, not to any changes in external migration.

The reason for this increase in migration is not clear from the type of data we have. There is precedent from several demographic studies to suggest that a reduction in population size results in greater exogamy, presumably because of the need to look further for available mates [e.g., Brennan and Relethford (1982) and Relethford and Mielke (1994)]. In any case, our main objective here is to deal with the observed reality of an increase in migration rates and their effect on genetic structure. Although a decrease in population size is expected to lead to an increase in F_{ST}, an increase in migration is expected to have the opposite effect: F_{ST} should decline. Obviously, the net effect of these opposite forces will determine the actual direction of change (if any) in F_{ST}.

Simple inspection of the rate of change in key parameters suggests that F_{ST} should have decreased in post-Famine Ireland. Although the effective population size decreased 25% from the first to the third time period, the effective migration rate (m_e) increased 143%. If we consider the product of effective population size and effective migration rate as a first approximation to the expected level of microdifferentiation, this value increases 83% from the first to the third time period. Given that this product is inversely related to the expected level of microdifferentiation, this change suggests a reduction in among-group variation. Analysis of the expected F_{ST} from Rogers and Harpending's migration matrix model allows us to be more precise and to consider the interaction between local population sizes, the migration matrix, and external migration. As shown in Table 3, the expected F_{ST} values from migration decrease over time: a 41% decline from the first to the third time period.

Overall, it would seem that the expected impact of post-Famine population decrease on regional genetic structure was countered by a corresponding increase in migration (which may be related in some manner to the changes in population size). The F_{ST} estimates from anthropometric data, however, suggest the opposite; depending on the specific measurements used, the estimated minimum F_{ST} remains constant or increases. For head measures F_{ST} increases 74% from the first to the third time period. To complicate matters further, the estimates of F_{ST} from migration and from anthropometrics are different by several orders of magnitude. However, such differences are

not unexpected, given our inability to estimate precisely all the known demographic and cultural factors that would lead to smaller estimates of effective size and the fact that estimates of F_{ST} from metric data are affected by the previous genetic structure of the country.

Although one interpretation is that the migration data and/or the anthropometric data are biased in some manner, we suggest instead that these differences are a reflection of exactly what is being estimated. Estimation of F_{ST} from migration data makes the critical assumption that the population is at equilibrium. This is a dangerous assumption in terms of the population history of Ireland—even our data from only three "generations" show major demographic shifts over time. Consideration of the population history of Ireland (Connell 1950; Kennedy 1973) suggests further that there was probably no time in Ireland's recent past when the equilibrium assumption could be defended for more than a short period of time.

Violation of the assumption of demographic equilibrium is not necessarily a problem. Given an appropriate genetic structure (high migration rates in particular), equilibrium might be reached in a short period of time. Rogers and Harpending (1986) and Relethford (1991a) identified several human populations that showed a rapid convergence to equilibrium, such as the Makiritare Indians, Bougainville islanders, and the Gainj of Papua New Guinea. The best clue to the rate of convergence is Rogers and Harpending's (1986) half-life estimate. As shown in Table 3, the equilibrium half-life has declined over time in post-Famine Ireland (resulting from increased migration). Even so, the migration pattern in the third time period suggests 9 generations to reach 50% of equilibrium. This means that 75% of the equilibrium F_{ST} would be reached in $2h = 18$ generations and that 82.5% of the equilibrium F_{ST} would be reached in $3h = 27$ generations. It would therefore take considerable time for regional variation in Ireland to reach equilibrium. In other words, it would take a long time for the observed migration patterns to erase previous patterns of genetic structure and population history. The anthropometric estimates of F_{ST} refer to an *observed* pattern of genetic structure, not a *predicted* equilibrium state. The two estimates, observed and expected, will agree with one another only when convergence to equilibrium is rapid, which is not the case for post-Famine Ireland.

A more appropriate question is whether the observed changes in F_{ST} estimated from anthropometrics are consistent with the observed changes in population size and migration in a *single* generation, rather than comparison at equilibrium. One way of answering this would be to take the minimum R matrix from anthropometrics at a given generation and subject it to one generation of migration and drift to determine the minimum R matrix (and F_{ST}) in the next generation. Unfortunately, this method would require greater specificity in estimation of effective population size. We are unable to quantify the many factors that could influence effective population size in Ireland, such as the high rate of celibacy (Kennedy 1973), variance in fertility, and, perhaps

most important, the problem of using regional agglomerations of local populations (Chakraborty et al. 1988). We suspect that our use of the traditional estimator of one-third total population size is a gross overestimate, but we do not know the specific degree of overestimation.

Some insight *can* be obtained if we simplify such an analysis and make only the assumption that the estimated equilibrium F_{ST} values from migration analysis are *proportional* to the true values, that is, that the observed rate of change in these estimates is the same as the true values, regardless of the specific true values of F_{ST}. To provide some insight into possible dynamics, we use a modification of the models outlined by Relethford (1991a). The expected value of F_{ST} in generation $t + 1$ ($F_{ST(t+1)}$) can be expressed as

$$F_{ST(t+1)} = a(1 - b) + bF_{ST(t)}, \tag{7}$$

where $F_{ST(t)}$ is the value of F_{ST} in generation t, a is the expected equilibrium value of F_{ST} given current migration rates and population size, and b estimates the rate of change in F_{ST} over time, defined as

$$b = (1 - s)^2\lambda_2^2, \tag{8}$$

where s is the rate of external migration and λ_2 is the second eigenvalue of the migration matrix (Relethford 1991a). Given these equations, we can then ask what effect a single generation of demographic change could have on the expected change in F_{ST} from generation t to generation $t + 1$. Demographic change will result in a new equilibrium value of F_{ST}. Because a represents the old equilibrium (before change), let a' represent the new equilibrium, defined as $a' = ca$. Here, c represents the proportional change in a' relative to a. Let b' represent the new value of b. F_{ST} in generation $t + 1$ can now be written

$$F_{ST(t+1)} = ca(1 - b') + b'F_{ST(t)}. \tag{9}$$

We are now in a position to consider under what conditions the value of F_{ST} can change from generation t to generation $t + 1$. F_{ST} will increase when $F_{ST(t+1)} \geq F_{ST(t)}$. That is,

$$ca(1 - b') + b'F_{ST(t)} \geq F_{ST(t)}, \tag{10}$$

giving

$$c \geq \frac{F_{ST(t)}}{a}. \tag{11}$$

If we have estimates of $F_{ST(t)}$ and a, we can derive c and compare it to the ratio of estimated values of F_{ST} in two adjacent generations. The problem here is that $F_{ST(t)}$ depends on a precise estimate of effective population size and on knowing the number of generations that have elapsed since initial founding of populations. However, as suggested by Relethford (1991a), we

can look at the extreme values by considering the minimum and maximum values of $F_{ST(t)}$ given demographic structure before change. The minimum value of $F_{ST(t)}$ is obtained by setting the initial value of F_{ST} equal to 0 and substituting into Eq. (7). This gives $a(1 - b)$, which when substituted into Eq. (11), gives

$$c \geq 1 - b. \tag{12}$$

The maximum possible value of $F_{ST(t)}$ is equal to a by definition, which, when substituted into Eq. (11), gives $c \geq 1$.

Following the logic set forth by Relethford (1991a), we can therefore state that:

If $c > 1$, then F_{ST} will always increase.
If $c < 1 - b$, then F_{ST} will always decrease.
If $1 - b \leq c \leq 1$, then F_{ST} could increase, decrease, or stay the same.

The boundary conditions of $c \leq 1$ and $c \geq 1 - b$ show the range of demographic change within which F_{ST} could change in either direction or not at all, depending on the specific value of F_{ST} before the change.

The advantage of this formulation is that we can look at some general predictions without having to know specifically the true values of F_{ST}; instead, we need only an estimate of b (easier to obtain than effective population size) and of the ratio of equilibrium values of F_{ST} between two generations. Again, we do make the assumption that our estimates of equilibrium F_{ST} from migration are *proportional* to the true values, even if we do not know the true values.

For illustration, we compare the first and second time periods. From the migration matrix analysis we take b from the second time period ($= 0.949$). Our limits of c are therefore 0.051 and 1.0. If the observed ratio c is less than 0.051, then F_{ST} will show a decrease from the first to the second time period. If the observed ratio c is greater than 1, then F_{ST} will show an increase from the first to the second time period. The observed ratio c is taken as the ratio of estimated equilibrium F_{ST} values from Table 3, which is $c = 0.000021/0.000027 = 0.78$. This value falls within the given limits of c and therefore suggests that F_{ST} could increase, decrease, or stay the same. The results in Table 4 suggest stability in F_{ST} from metrics, which is consistent with our demographic predictions. When we compare the second and the third time periods, we get $b = 0.925$ and limits of c of 0.075 and 1.0. The observed value of c is $0.000016/0.000021 = 0.76$. Again, this means that we could expect an increase in F_{ST}, a decrease in F_{ST}, or no change at all. The observed change in metrics (Table 4) is consistent with this prediction.

We have made a number of simplifying assumptions and do not have standard errors for any of these estimates. We have also used our time periods (each covering 20 years) as crude generations (for sample size considera-

tions), and evidence suggests that generation length was longer in post-Famine Ireland (Kennedy 1973). The purpose of the exercise, however, was not to provide exact predictions but to illustrate the *possible* range of changes in genetic microdifferentiation expected under a simple model of demographic change. For the type of demographic changes estimated from our migration matrix analysis, *any* observed pattern of changes in F_{ST} from metrics could be defended. The point here is that the difference in patterns of change in migration and metrics is not inconceivable. However, if we had observed a reduction in F_{ST}, we could also claim a good fit.

These results show that under certain situations of demographic change we could expect *any* pattern of change in F_{ST} estimated from biological data. This points out a weakness in traditional assessments of F_{ST}. Many studies look at changes in F_{ST} over time as indexes of underlying demographic change. If, for example, one sees an increase in F_{ST} over time, one is tempted to suggest a reduction in population size and/or a reduction in migration rates. Likewise, if one sees a reduction in F_{ST} over time, one might suggest an increase in population size and/or migration rate. As we have shown here, this type of interpretation is not the only possibility or even the most likely possibility. Different patterns in migration and biological data can be totally consistent with expected models.

What *can* we say about changes in microdifferentiation in post-Famine Ireland? The migration matrix analyses show clearly that migration rates increased as population size decreased. Ultimately, these changes would result in a decrease in F_{ST}. However, the rate of convergence is slow, and any short-term change in F_{ST} is possible under such conditions. The actual observed changes in F_{ST} estimated from anthropometrics are minor and are significant only for head measures between the second and third time periods. These results suggest that the rapid changes accompanying the Great Famine have had *minimal* impact on the level of microdifferentiation. The anthropometric data appear to reflect earlier patterns of population variation, a finding consistent with our other study in which we found strong reflections of early Irish history and little indication of post-Famine disruptions (Relethford and Crawford 1995).

Studies of genetic structure often suggest that demographic change erases previous history. Although we do not deny this possibility, we do note that our studies to date on the regional patterns of variation in Ireland do not fit this model. There appears to be a much longer time required to erase previous history. Judging from the high equilibrium half-lives in Table 3, we suggest that such a process could take considerable time in Ireland unless there is an acceleration of demographic change.

The lack of any major genetic impact suggested by this study and our previous research (Relethford and Crawford 1995) does not agree with the few other studies of post-Famine Ireland. Studies of *local* genetic structure in Northern Ireland have suggested significant demographic and genetic im-

pact of the Great Famine (Bittles et al. 1986; Smith et al. 1990; Bittles and Smith 1991, 1994). These findings are not necessarily inconsistent with our findings. We expect that demographic change will have a greater genetic impact on local populations as opposed to the regional populations used in our analyses. Demographic change might erase population history on a local level in a short period of time but could take a considerably longer time to have an impact on a regional level, because interpopulational migration is lower and population sizes are larger. We suggest that the focus of studies of genetic variation depends very much on the level of analysis. Studies of local populations often reveal short-term changes in demographic and genetic structure, whereas studies at a regional or continental level will most probably reflect long-term patterns corresponding to major events in population history. At a global level we see this even more clearly, with information on continental variation being used successfully to infer the history of modern human origins [e.g., Cavalli-Sforza et al. (1994)].

Appendix

In this appendix we provide the derivation of the standard errors of the minimum R matrix and minimum F_{ST} and the correction for sampling bias of the diagonals of the minimum R matrix. Standard errors and bias correction are also given for the genetic distances (d^2) derived from the minimum R matrix.

For metric traits the minimum R matrix for g groups based on t traits is a function of the codivergence matrix C, which has elements

$$\begin{aligned} c_{ij} &= (x_i - \mu)' P^{-1} (x_j - \mu)(1/2t) \\ &= \Delta_i' P \Delta_j (1/2t), \end{aligned} \tag{A.1}$$

where x_i and x_j are the mean vectors for groups i and j, μ is the vector of total means over all groups, P is the pooled within-group phenotypic covariance matrix, and the prime indicates transposition. Δ_i and Δ_j are the deviations of group means from the total means. Both P and the total means are computed by weighting by relative population size (w_i) (Relethford and Blangero 1990). [Note that Relethford and Blangero (1990) used a different definition of C, including the term $(1/2t)$ in their later equations. This appendix uses the definition in Eq. (A.1) throughout.] The minimum R matrix is then defined as

$$R = C(1 - F_{ST}). \tag{A.2}$$

Error Covariance Matrix of *C*. To derive standard errors for elements of the R matrix and for F_{ST}, we need to first derive the error covariance matrix of C. The variance of c_{ii} can be written

$$\text{var}(c_{ii}) = \left(\frac{\partial c_{ii}}{\partial x_i'}\right)\text{var}(\Delta_i)\left(\frac{\partial c_{ij}}{\partial x_i'}\right)'. \tag{A.3}$$

Because the partial derivative is

$$\frac{\partial c_{ii}}{\partial x_i'} = (1/t)\Delta_i' P^{-1}, \tag{A.4}$$

we obtain

$$\text{var}(c_{ii}) = (1/t^2)\Delta_i' P^{-1}\Sigma_i P^{-1}\Delta_i, \tag{A.5}$$

where $\Sigma_i = \text{var}(\Delta_i) = \text{var}(x_i)$.

The variance for the off-diagonal elements of C are derived in a similar manner. Because $\text{cov}(x_i, x_j) = 0$, we obtain

$$\text{var}(c_{ij}) = \left(\frac{\partial c_{ij}}{\partial x_i'}\right)\text{var}(\Delta_i)\left(\frac{\partial c_{ij}}{\partial x_i'}\right)' + \left(\frac{\partial c_{ij}}{\partial x_j'}\right)\text{var}(\Delta_j)\left(\frac{\partial c_{ij}}{\partial x_j'}\right)'. \tag{A.6}$$

Solving the partial derivatives

$$\frac{\partial c_{ij}}{\partial x_i'} = (1/2t)\Delta_j' P^{-1}, \tag{A.7a}$$

$$\frac{\partial c_{ij}}{\partial x_j'} = (1/2t)\Delta_i' P^{-1} \tag{A.7b}$$

gives

$$\text{var}(c_{ij}) = (1/4t^2)(\Delta_j' P^{-1}\Sigma_i P^{-1}\Delta_j + \Delta_i' P^{-1}\Sigma_i P^{-1}\Delta_i). \tag{A.8}$$

Similarly, the covariance of off-diagonal and diagonal elements can be derived as

$$\text{cov}(c_{ij}, c_{ii}) = (1/2t^2)(\Delta_i' P^{-1}\Sigma_i P^{-1}\Delta_j). \tag{A.9}$$

If we assume multivariate normality such that $x_i \sim \text{MVN}[\mu, P(1/n_i)]$ for all i, then

$$\Sigma_i = \text{var}(\Delta_i) = (1/n_i)P, \tag{A.10a}$$

$$\Sigma_j = \text{var}(\Delta_j) = (1/n_j)P, \tag{A.10b}$$

where n_i and n_j are the sample sizes of groups i and j, respectively. Substituting these values and Eq. (A.1) into Eqs. (A.5), (A.8), and (A.9) gives

$$\text{var}(c_{ii}) = \frac{2c_{ii}}{n_i t}, \tag{A.11}$$

$$\text{var}(c_{ij}) = (1/2t)\left[\frac{c_{jj}}{n_i} + \frac{c_{ii}}{n_j}\right], \tag{A.12}$$

$$\text{cov}(c_{ij}, c_{ii}) = \frac{c_{ij}}{n_i t}, \tag{A.13a}$$

$$\text{cov}(c_{ij}, c_{jj}) = \frac{c_{ij}}{n_j t}. \tag{A.13b}$$

Standard Errors of the *R* Matrix. Noting the relationship between the C and R matrices [Eq. (A.2)], consider from the Taylor series that

$$\text{var}(r_{ii}) = \left(\frac{\partial r_{ii}}{\partial c_{ii}}\right)^2 \text{var}(c_{ii}), \tag{A.14a}$$

$$\text{var}(r_{ij}) = \left(\frac{\partial r_{ij}}{\partial c_{ij}}\right)^2 \text{var}(c_{ij}). \tag{A.14b}$$

Solving for the partial derivatives of Eq. (A.2) gives

$$\frac{\partial r_{ii}}{\partial c_{ii}} = \frac{\partial r_{ij}}{\partial c_{ij}} = 1 - F_{ST}. \tag{A.15}$$

Solving Eqs. (A.14) gives the variances of the elements of the R matrix:

$$\text{var}(r_{ii}) = \frac{2r_{ii}(1 - F_{ST})}{n_i t}, \tag{A.16a}$$

$$\text{var}(r_{ij}) = \frac{(1 - F_{ST})}{2t}\left(\frac{r_{ij}}{n_i} + \frac{r_{ii}}{n_j}\right). \tag{A.16b}$$

The standard errors of r_{ii} and r_{ij} are simply the square roots of these values.

Standard Error of F_{ST}. Let c_0 be the weighted sum of the diagonal elements of the C matrix ($= \Sigma\, w_i c_{ii}$), which is related to F_{ST} by

$$F_{ST} = c_0/(1 + c_0). \tag{A.17}$$

The variance of c_0 is

$$\text{var}(c_0) = \sum w_i^2 \,\text{var}(c_{ii}) = (2/t) \sum \frac{w_i^2 c_{ii}}{n_i}. \tag{A.18}$$

The variance of F_{ST} can then be written

$$\text{var}(F_{ST}) = \left(\frac{\partial F_{ST}}{\partial c_0}\right)^2 \text{var}(c_0). \tag{A.19}$$

Solving for the partial derivative of Eq. (A.17) gives

$$\frac{\partial F_{ST}}{\partial c_0} = 1/(1 + c_0)^2, \tag{A.20}$$

which, when substituted into Eq. (A.19), gives

$$\text{var}(F_{ST}) = [1/(1 + c_0)^4](2/t)\left(\sum \frac{w_i^2 c_{ii}}{n_i}\right). \tag{A.21}$$

In terms of the R matrix, the variance of F_{ST} becomes

$$\text{var}(F_{ST}) = (2/t)(1 - F_{ST})^3\left(\sum \frac{w_i^2 r_{ii}}{n_i}\right). \tag{A.22}$$

The square root of Eq. (A.22) is the standard error of F_{ST}.

Bias Correction. The diagonal elements of C and R are subject to sampling bias, which is particularly noticeable with small sample sizes. The expectation of the diagonal elements of C is

$$E(c_{ii}) = E[(\Delta_i' P^{-1} \Delta_i)(1/2t)], \tag{A.23}$$

which can be written

$$E(c_{ii}) = (1/2t)\text{tr}(P^{-1}\Sigma_i) + (1/2t)(\mu_i' P^{-1} \mu_i), \tag{A.24}$$

where $\text{tr}(\cdot)$ denotes the matrix trace. The expected bias of c_{ii} is the first term in Eq. (A.24); that is,

$$\text{Bias}(c_{ii}) = (1/2t)\text{tr}(P^{-1}\Sigma_i). \tag{A.25}$$

Assuming normality of Δ, the trace is equal to t/n_i and the bias of c_{ii} is equal to $1/2n_i$, which is also equal to the bias of r_{ii}.

Therefore, to correct for sampling bias, the term $1/2n_i$ must be subtracted from the ith diagonal of the R matrix for all values of i. In some situations, primarily with small sample sizes and/or low values of r_{ii}, the bias-corrected estimate may be negative. In such cases the r_{ii} value should be set equal to 0. After these adjustments, the bias-corrected estimate of F_{ST} is obtained as the weighted sum of the bias-corrected diagonals of the R matrix.

Genetic Distances and the *R* Matrix. Although not used specifically in the analyses in this study, a common use of R matrices is to convert them into genetic distance matrices. This conversion is familiar and straightforward:

$$d_{ij}^2 = r_{ii} + r_{jj} - 2r_{ij} \tag{A.26}$$

(Harpending and Jenkins 1973; Williams-Blangero and Blangero 1989). Distances can also be written in terms of the C matrix:

$$\begin{aligned} d_{ij}^2(c) &= c_{ii} + c_{jj} - 2c_{ij} \\ &= (1 - F_{ST})d_{ij}^2. \end{aligned} \tag{A.27}$$

The variance of this distance is

$$\text{var}[d_{ij}^2(c)] = \text{var}(c_{ii}) + \text{var}(c_{jj}) + 4\,\text{var}(c_{ij}) + 2\,\text{cov}(c_{ii}, c_{jj}) - 4\,\text{cov}(c_{ii}, c_{ij}) - 4\,\text{cov}(c_{jj}, c_{ij}). \quad \text{(A.28)}$$

Noting that $\text{cov}(c_{ii}, c_{jj}) = 0$ and substituting the terms from Eqs. (A.11) through (A.13) gives

$$\text{var}[d_{ij}^2(c)] = \frac{2d_{ij}^2(c)}{t}\left(\frac{1}{n_i} + \frac{1}{n_j}\right). \quad \text{(A.29)}$$

Converting to the distance matrix based on the R matrix gives the variance of the distance matrix defined by Eq. (A.26):

$$\text{var}(d_{ij}^2) = \frac{2(1 - F_{ST})d_{ij}^2}{t}\left(\frac{1}{n_i} + \frac{1}{n_j}\right). \quad \text{(A.30)}$$

The distance defined in Eq. (A.26) can also be corrected for sampling bias. Simply substitute the bias-corrected r_{ii} and r_{jj} values into Eq. (A.26) to obtain a bias-corrected distance. If the resultant distance is negative, then truncate to 0.

Heritabilities. All the computations shown here use the pooled within-group phenotypic covariance matrix P. As such, all the R statistics are *minimum* estimates obtained for complete heritability, but they still provide useful and meaningful comparative statistics (Williams-Blangero and Blangero 1989). Information on heritability can be added, however, by substituting the pooled within-group additive genetic covariance matrix G_w for P throughout. Relethford and Blangero (1990) provide additional information on methods of estimating G_w where suitable data are available.

Computer Program. A computer program is available on request from J.H. Relethford that performs all the computations described here as well as the Relethford-Blangero analysis of within-group variances (Relethford and Blangero 1990) and Relethford's (1996) method for controlling for genetic drift. The program runs on the Windows 3.x and Windows95 operating systems. Please send a formatted 3.5 inch diskette and a disk mailer to J.H. Relethford if you wish a copy of this program.

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