Founder Effect: Assessment of Variation in Genetic Contributions among Founders

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Abstract We present a Monte Carlo method for determining the distribution of founders' genetic contributions to descendant cohorts. The simulation of genes through known pedigrees generates the probability distributions of contributed genes in recent cohorts of descendants, their means, and their variances. Genealogical data from three populations are analyzed: the Hutterite population of North America, the island population of Sottunga from the Åland archipelago, and the large Utah Mormon population. Two applications of the Monte Carlo method are presented. First we investigate the relative opportunity for founder effect in the three populations, which have dissimilar pedigree structures and dissimilar disease gene frequencies. Second, we measure the reproductive success of population founders in terms of the number of genes they contribute to a cohort some number of generations descendant and compare the effects of polygyny versus monogamy on reproductive success. The distribution of Hutterite founder contributions describes the context for a classic founder effect. Hutterite founders have a higher probability of leaving no genes in the population (72%) than Sottunga (48%) and Mormon (48%) founders. However, founder genes that survive among Hutterite descendants do so in larger numbers on average than founder genes in the other two populations. Greater variation among monogamous Hutterite founders compared with Mormon polygynous founders demonstrates that polygyny alone does not maximize the variance in reproductive success; other population characteristics are at least as important for determining variability among individuals in their genetic contributions to a gene pool. Our findings make it difficult to appreciate the reproductive advantage of polygyny in the Mormon population. Although the expected gene contributions and their variances were larger for polygynous founders compared with other Mormons, the main effect of polygyny

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was to increase the probability that *any* polygynist left a *few* genes among descendants. Furthermore, only 12% of the variation in the genetic contributions of Mormon founders is explained by their number of offspring. We conclude that shallow genealogical data (from one or a few generations) provide a poor measure of long-term reproductive success.

The variability among population founders in their gene contributions to a descendant cohort has important implications for determining the extent to which founder effect influences gene distributions in a population. In addition, population characteristics, such as mating patterns, can create variance structures in gene contributions with potentially important evolutionary significance.

Average genetic contributions have been assessed for several populations with known pedigrees (Cazes 1986; Roberts and Bear 1980), including one population treated further in this analysis (O'Brien et al. 1988a). However, no previous study of founder contributions has investigated the variability that underlies estimates of expected contributions [but see Thompson (1986) for an analytical solution for the variance of expected founder contributions].

We present a Monte Carlo method for determining the distribution of founders' genetic contributions to descendant cohorts. This method simulates the movement of genes through known pedigrees to generate the probability distributions of contributed genes in recent cohorts of descendants, their means, and their variances. The resulting distributions are empirically estimated; we make no assumptions about their approximation to a known distribution. The simulation considers a randomly chosen gene locus and accounts for overlapping paths of descent from a set of founders to all related descendants.

Two applications of the Monte Carlo method are presented. First, we investigate the opportunity for founder effect in three populations (North American Hutterites, the population of Sottunga, and Utah Mormons) with dissimilar pedigree structures and dissimilar disease gene frequencies. Comparisons among the three populations demonstrate the relative opportunity for founder effect to influence their disease gene distributions. In the second application of the method we measure the reproductive success of population founders in terms of the number of genes they contribute to a cohort some number of generations descendant. Comparisons among the three populations demonstrate the effects of variable characteristics, such as inbreeding and mating patterns, in particular, polygyny, on founder gene distributions.

Evaluation of Founder Effect

Many genetic diseases exhibit striking variation in prevalence from one population to another. Examples include cystic fibrosis, phenyl-

ketonuria, hemochromatosis, Tay Sachs disease, sickle cell disease, and thalassemia. Although explanatory mechanisms have been uncovered in a few cases (e.g., sickle cell disease and *falciparum* malaria among Africans), the causes of ethnic variation in genetic disease remain largely unknown.

Founder effect is a plausible explanation for elevated disease frequencies, particularly in small, isolated populations [see Diamond and Rotter (1987) for a brief review]. In a previous study we estimated the possible role of founder effect in generating high frequencies of von Willebrand disease and autosomal recessive tapetoretinal degeneration observed in the Åland Island parish of Sottunga (O'Brien et al. 1988a). Based only on estimates of expected genetic contributions of founders, we concluded that it is unlikely that the high prevalences of these diseases are due to an unusually large genetic contribution by any one (or a few) population founders. Now, with a method of assessing the variance structures underlying the expected contributions of founders, we can accurately estimate the probability with which a founder leaves n genes in a descendant cohort and provide confidence limits for these estimates.

Evaluation of Mating Structure and Reproductive Success

Although mating patterns and their evolutionary significance have long been of interest to anthropologists and evolutionary biologists, the particular importance of sex-biased multiple marriage patterns, such as polygyny, has come into focus over the past two decades (Salzano et al. 1967; Trivers and Willard 1973; Leuttnegger and Kelly 1977; Wade and Pruett-Jones 1990). It is now commonly held that disproportionate mating success among polygynous males (for example) should result in disproportionate genetic contributions to their gene pool (Neel and Salzano 1967). At the individual level this type of mating behavior provides a means of increasing one's reproductive success relative to others in the population. For this discussion the important evolutionary implications of sex-specific multiple mating patterns, and polygyny in particular, hinge on the assumption that variance in reproductive success among individuals at a point in time corresponds to variance in genetic contributions to a gene pool over time. Unfortunately, longer-term genetic consequences of polygyny have never been assessed for a human population because the necessary genealogical information is rarely available in populations where it is practiced. Usually the variance in male reproductive success is measured by the relative survivorship among offspring in one or a limited number of descending generations (Faux and Miller 1984;

Mealey 1985; Jorde and Durbize 1986; Boone 1988). In this study we directly measure the reproductive success of population founders in terms of the number of genes they contribute to a cohort several generations descendant.

Polygyny also has important evolutionary significance at the population or species level. To the extent that sex-biased variation is associated with phenotypic variation, the potential for selection to result in phenotypic differences between the sexes becomes effectively strong. Thus current thinking suggests that polygyny is a key behavioral attribute of the setting in which the evolution of sexual dimorphism in primates and other mammals took place (Kay et al. 1988; Beauchamp 1989; Krishtalka et al. 1990; Shapiro et al. 1991).

Materials and Methods

The Monte Carlo simulation was run in three populations with contrasting genealogical structures: North American Hutterites, the population of Sottunga, and Utah Mormons. The Hutterite population is a religious isolate that was established in the United States in 1875 by approximately 400 individuals. This group established three colonies in South Dakota. Because of a high fertility rate and continuous colony subdivision, more than 30,000 Hutterites currently live in over 300 colonies in the Dakotas, Montana, Alberta, and Saskatchewan. Each of the contemporary colonies ultimately descends from one of the three original settlements. The colony lineages that descend from those settlements form the largest subdivision of the population, known as the leut. In addition to forming geographic clusters, the three leute have developed distinguishing cultural characteristics, and interleut marriages occur rarely. Despite the essential importance of Hutterite population subdivision, the results of the analyses reported here include founders for the total population and descendants from all three leute.

Hutterite population growth over the last 125 years has been strictly internal. Therefore virtually all current members are descendants of the original founders, and a relatively high level of inbreeding has accrued in the population. Any randomly chosen pair of Hutterites is, on average, related more closely than second cousins (Mange 1964; Fujiwara et al. 1989). The Hutterite population is perhaps the best living example of a closed population forming a genetic isolate with genealogical data extending from the present to the founder group. Details of Hutterite population history, demography, genetic structure, and cultural characteristics can be found elsewhere (Eaton and Mayer 1953; Mange 1964; Steinberg et al. 1967; Martin 1970; Hostetler 1974; Morgan and Holmes 1982; Morgan 1983; O'Brien 1987).

There are no complete population surveys that provide specific incidences of genetic diseases among Hutterites. However, one study of Alberta's Hutterite population estimated a high incidence of cystic fibrosis: 1/313 births (Fujiwara et al. 1989). In addition, several rare or otherwise unknown autosomal recessive disorders occur in the population, including a recessive form of familial hypopituitarism (McArthur et al. 1985), Morquio syndrome (Lowry et el. 1985), a particular type of muscular dystrophy (Shokeir and Rozdilsky 1985), isolated juvenile cataracts (Shokeir and Lowry 1985), and a syndrome sharing characteristics with cerebro-oculo-facial-skeletal syndrome (Lowry et al. 1985).

The second population we studied is the island population of Sottunga, one of five Lutheran parishes located at the outer reaches of the Åland archipelago in the Baltic Sea. The population of Åland is Swedish in origin. Although the islands are known to have been inhabited much earlier, the founders of the contemporary population date to the end of the Great Northern War in 1721. During that war, the archipelago was temporarily depopulated, and at the end of the war approximately 5000 individuals inhabited the islands. Further details about Åland's population origins, settlement, and demographic history are given by Eriksson et al. (1980), Jorde et al. (1982), and Mielke et al. (1976, 1987). Although the population of Sottunga has always been small and the island has always been geographically isolated, immigration and emigration have limited the genetic isolation of the island, particularly since 1900.

Several previous studies have pointed out the high incidence of some rare genetic diseases in Åland, including autosomal recessive forms of tapetoretinal degeneration (Forsius et al. 1980) and the autosomal dominant von Willebrand disease. The latter disorder has an estimated incidence among European populations of 1/125, including all forms and degrees of severity (Sadler 1989), but it occurs in more than 10% of Sottunga's population (Lehmann et al. 1980).

The third population considered in this study is a sample from the large Mormon population of Utah. We chose as founders for this study individuals ancestral to the pioneer group who settled Utah beginning in 1847. These individuals are Northern European in origin, and the population has virtually no characteristics of a genetic isolate.

There are no rare genetic disorders known to occur with unusual frequencies among Utah Mormons. The prevalence of some disorders, such as cystic fibrosis, hemachromatosis, phenylketonuria, and neural tube defects do not diverge from estimates for other large Caucasian populations (Edwards et al. 1988; Jorde 1989).

Population Samples: Founders and Descendants. In this study the definition of a founder is any individual who appears in a genealogy, whose parents do not, and who has one or more offspring in the ge-

nealogy. Selecting founder groups for comparability among populations is more difficult than selecting contemporary descendant cohorts because founders are not arbitrarily designated; they are the minimum number of individuals who account for all the independent genomes in a population. In the Hutterite genealogy 185 individuals meet our founder definition, and *all* of them are included in the analyses that follow. (Genealogical data for this population predates the North American migration; therefore the number of founders is smaller than the 400 individuals who established the first Hutterite communities in North America.) Hutterite founders' years of birth range from 1712 to 1953, although only nine founders were born in the twentieth century.

Because of the large size of the Utah Population Database, Mormon founders are a *sample* of more than 300,000 individuals who meet our founder definition. Not only is this a large number of individuals, but they enter the genealogy continuously over time. To sample founders from this genealogy, we restricted their years of birth to the interval 1700–1847. Of the nearly 30,000 individuals who meet this additional criterion, we took a random sample of 2838 individuals. These founders, born in the early and pioneer periods, and their descendants constitute a genealogy representing the long-standing pioneer "stock" of the state.

Because the Sottunga genealogy is relatively small, *all* individuals who meet the definition of founder are included in the study. The birth years of the 225 Sottunga founders span the largest interval of the three populations, 1577–1943.

The genetic contributions of founders are assessed for specific descendant cohorts selected arbitrarily but for comparability among the three populations. For the Hutterite and Mormon populations descendants are individuals born in the interval 1925–1950. Because of Sottunga's smaller population size, the birth interval for Sottunga descendants was extended to those born between 1900 and 1950.

Table 1 summarizes the characteristics of the founder and descendant groups for each population. In Table 1 we also give values for two Mormon groups in addition to the "pioneers." For purposes of illustrating the effect of polygyny on founder contributions, a second Mormon sample was drawn from among the 30,000 pioneer founders in the genealogy. This sample consists of all the founders who practiced polygyny and their descendants. There are 1295 polygynous founders born between 1700 and 1847. The wives of polygynists, not all of whom meet the founder criterion, are evaluated as a group for comparison to the polygynists.

It should be noted that our sample of Mormon pioneer founders, 2838 individuals, includes both polygynous and monogamous founders. Polygynists constitute approximately 5% of this sample, which accu-

Table 1. Characteristics of the Genealogies

Characteristic	*Hutterites*	*Mormon Pioneers*	*Mormon Polygynists*	*Mormon Polygynists' Wives*	*Sottunga*
Number of founders	185	2,838	1,295	3,195	225
Range of birth years	1712–1953	1700–1847	1700–1847	1700–1847	1577–1943
Number of descendants	6,760	93,865	86,774	86,774	481
Range of birth years	1925–1950	1925–1950	1925–1950	1925–1950	1900–1950
Pedigree total	30,538	330,621	300,668	300,668	2,720
Average generation length (years)	29.2	29.1	27.6	27.6	32.8
Average F	0.03215	0.00010	0.00010	0.00010	0.00433

rately represents the proportion of polygynists among all 30,000 pioneer founders.

Table 1 shows that, although the founder groups for these populations are only roughly contemporary, the mean birth years of founders in each population are not far apart. These values range from 1820.5 among Hutterite founders to 1824.8 among Mormon polygynists. The mean birth year for descendants is more variable among the populations, ranging from 1924 in the Sottunga cohort to 1939.6 for Hutterites. Table 1 also reports the average generation length in each population. This value was calculated as the difference between mothers' birth years and the average birth year of their offspring.

The mean inbreeding coefficient F among members of the descendant cohorts in each population is also given in Table 1. The inbreeding coefficient describes the relatedness among descendants through descent from common ancestors. The level of inbreeding varies considerably among the populations, and, given the closed nature of the Hutterite pedigree compared with the other two populations, it is not surprising that the Hutterites have the highest value by a wide margin.

Simulation. A recursive algorithm was designed to generate the distributions of ancestor contributions, their means, and variances. To illustrate the algorithm in Figure 1, we select two individuals, **a** and **b**, from a descendant cohort and place them together in a simple pedigree. The algorithm begins by assigning two alleles to every founder in the pedigree (Figure 1A), then proceeds to identify the ancestors of descendant **a**. At the terminal ends of **a**'s pedigree, each founder has two genes to contribute, one of which is selected randomly to descend one generation. In the next generation one of two genes (from each parent) is again randomly assigned to descend a generation, and so on until individual **a** is reached and assigned one gene from each parent (Figure 1B). In this manner the two genes of all the founders to whom **a** is related are taken into consideration so that if **a** is related to four founders, having eight genes among them, the simulation establishes which two of the eight genes **a** will inherit.

Likewise, the ancestors of **b** are compiled and their genes randomly drawn to descend each generation until **b** is assigned two genes from among the eight genes of the four founders related to **b**. But note that within an iteration paths of descent are assigned randomly drawn alleles only once so that related descendants, such as **a** and **b**, are not given independent gene assignments through the shared portion of their pedigrees (Figure 1C). In one iteration all individuals of a cohort are assigned two genes in this fashion. One-thousand iterations of the simulation produce the values in Tables 3 and 4, and the distributions shown in Figures 2 and 3.

Results

Figure 2 plots the probability of a founder leaving n (where $n > 0$) gene copies in each of the three populations. The distributions are plotted on a logarithmic scale and show marked differences among the populations. The Hutterite distribution in particular has a distinct shape compared with the other two populations. These founders have a smaller probability of contributing few copies of a gene and a higher probability of contributing many gene copies compared with Mormon pioneer and Sottunga founders. The shapes of the distributions for the Mormon and Sottunga populations are similar, although Mormon founders have a slightly smaller probability of leaving few gene copies and a higher probability of leaving more gene copies.

Values describing these distributions are given in Table 2. First, we note that Hutterite founders have only a 28% chance on average of leaving any copies of a given gene in their descendant cohort, compared with a 52% chance for both Mormon pioneers and Sottunga founders. However, a gene that is successfully reproduced among Hutterite descendants occurs in larger copy number than in the Mormon and Sottunga descendant cohorts. This difference is reflected in both the mean expected contribution, which is the average of all founders' expected values (each for 1000 iterations), and the maximum number of gene copies left by founders. Hutterite founders have a much larger mean and maximum (35.6 and 1891, respectively) compared with Mormon pioneers (7.8 and 574) and Sottunga founders (2.1 and 93). This is notable given that the Hutterite founders have a much lower probability of leaving any copies of a given gene.

Accompanying the mean expected values in Table 2 are two standard deviations. The first, SD(b), pertains to the variation between founders in their expected contributions, and the second, SD(w), is the variation within founders (over 1000 iterations) in their expected contributions. Each standard deviation is accompanied by a coefficient of variation (CV), or simply the standard deviation to mean ratio. Again Hutterite founders have the highest values, demonstrating greater variability in their genetic contributions to descendants than founders in the other two populations.

Figure 3 shows the distributions of founder contributions for the Mormon pioneers, for male founders who practiced polygyny, and for the wives of polygynists. These three distributions are similar in shape and in the maximum number of gene copies left by a founder. However, the polygynists have a much higher expected value than the pioneer group as a whole (15.9 vs. 7.8). The difference in expected values is even greater when polygynists are compared with their wives (15.9 vs. 6.4). Furthermore, a polygynist founder has an 82% chance of making a contribution to descendants, compared with a 54% chance for their wives and a 52% chance for the pioneer group as a whole.

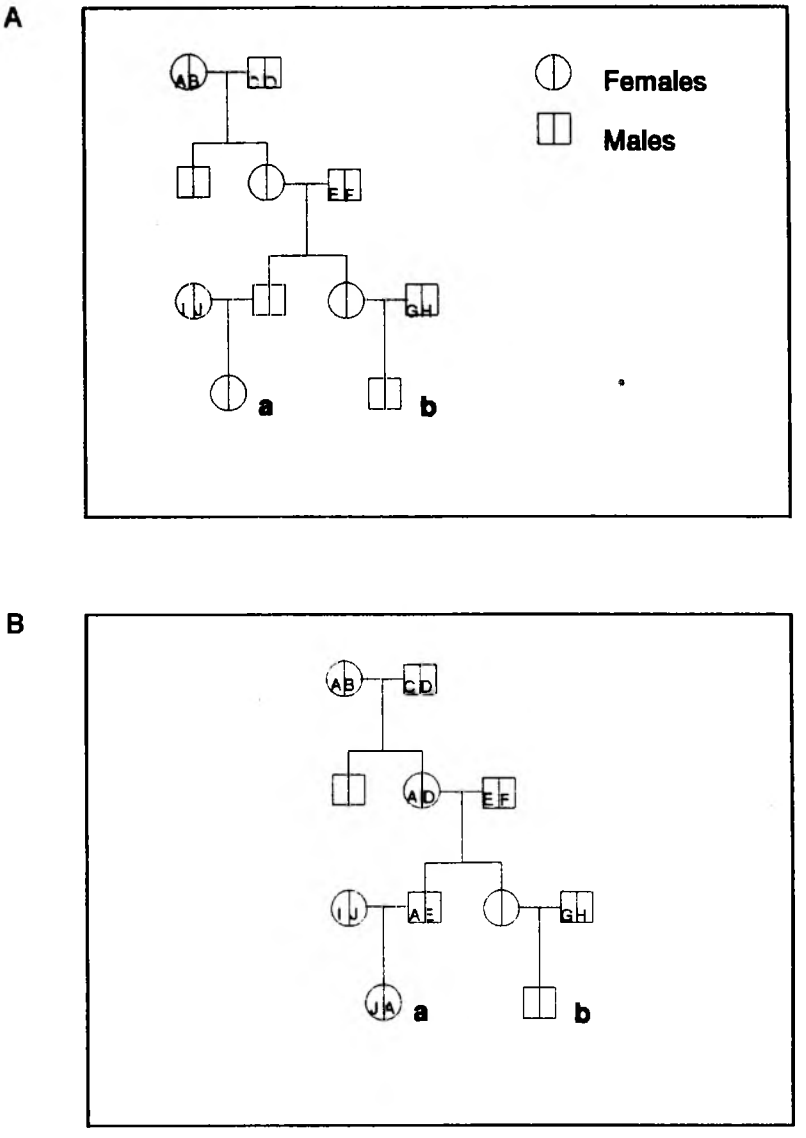

Figure 1. Recursive gene assignment algorithm. (A) All pedigree founders are assigned two alleles. (B) An allele is randomly drawn starting at the top of **a**'s pedigree, and at each descending generation until **a** is assigned one allele from each parent. (C) Alleles are randomly drawn from each of **b**'s ancestors at each descending generation until **b** is assigned one allele from each parent.

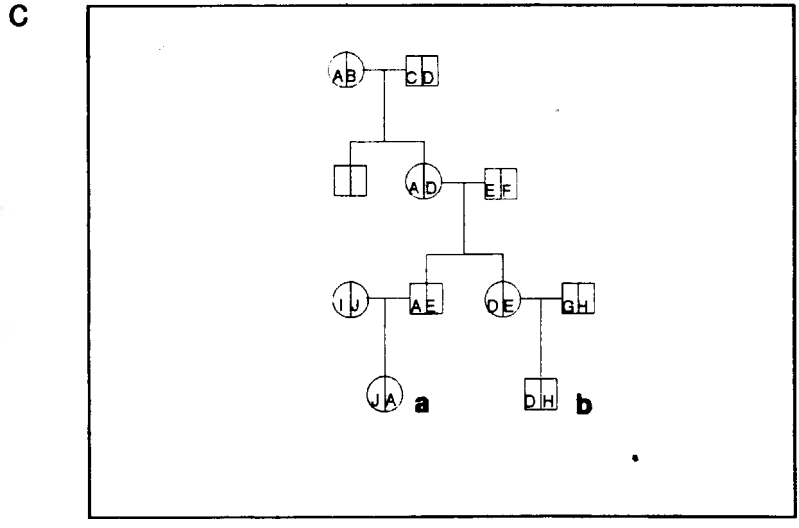

Figure 1. Continued.

Table 3 provides upper confidence limits for the number of copies of a founder gene present in each of the three descendant cohorts. The same confidence limit reaches a much higher number of gene copies for Hutterite founders because of the much longer tail on that distribution. In Table 3 we also give the gene frequencies (p) associated with the number of gene copies (N) at the cutoff points of the given confidence limits. At the 99.9% level, a Hutterite founder gene could occur with a frequency of 0.14, compared with 0.08 in Sottunga and 0.0018 among Mormon descendants. These values demonstrate the comparative opportunities for founder effect in the three populations. A Mormon founder has little chance of contributing a disproportionate number of gene copies to the descendant cohort. The fact that there are no known genetic diseases that occur with unusual frequency among Mormons is consistent with this result. Moderate founder effects could be expected in Sottunga, where a founder gene could affect 5–8% of the descendant population. The case of von Willebrand disease, which occurs among 10–20% of Sottunga's population, suggests that more than one founder introduced the gene into the population, a conclusion that was reached in a previous study of expected founder contributions in Sottunga (O'Brien et al. 1988a). Finally, there exists an opportunity for dramatic founder effects in the Hutterite population, and indeed there are a number of genetic disorders found among Hutterites that occur more rarely in other populations. Others have attributed the elevated incidence of cystic fibrosis among Hut-

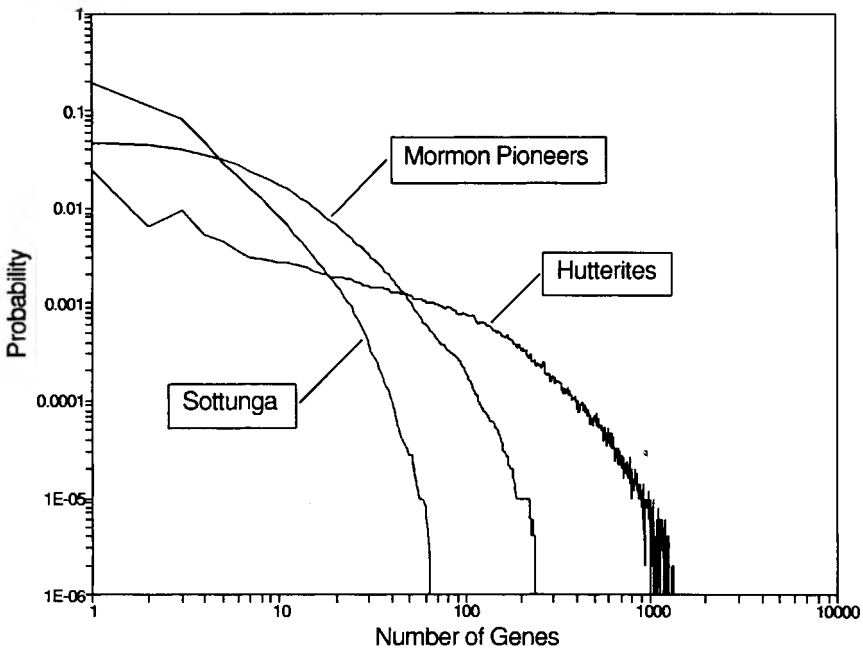

Figure 2. Distributions of founder gene contributions in three populations.

Table 2. Comparison of Expected Founder Contributions among Groups

	Hutterites	*Mormon Pioneers*	*Mormon Polygynists*	*Mormon Polygynists' Wives*	*Sottunga*
Mean	35.6	7.8	15.9	6.4	2.1
SD(b)	68.5	14.0	20.2	11.1	1.9
CV(b)	1.9	1.8	1.3	1.7	0.9
SD(w)	40.5	5.8	8.8	4.7	2.7
CV(w)	1.1	0.7	0.6	0.7	1.3
Maximum	1891	574	526	525	93
Probability > 0	0.28	0.52	0.82	0.54	0.52

The mean is the average number of gene copies among descendants (for all founders and 1000 iterations per founder). The maximum is the largest number of gene copies contributed by any founder.

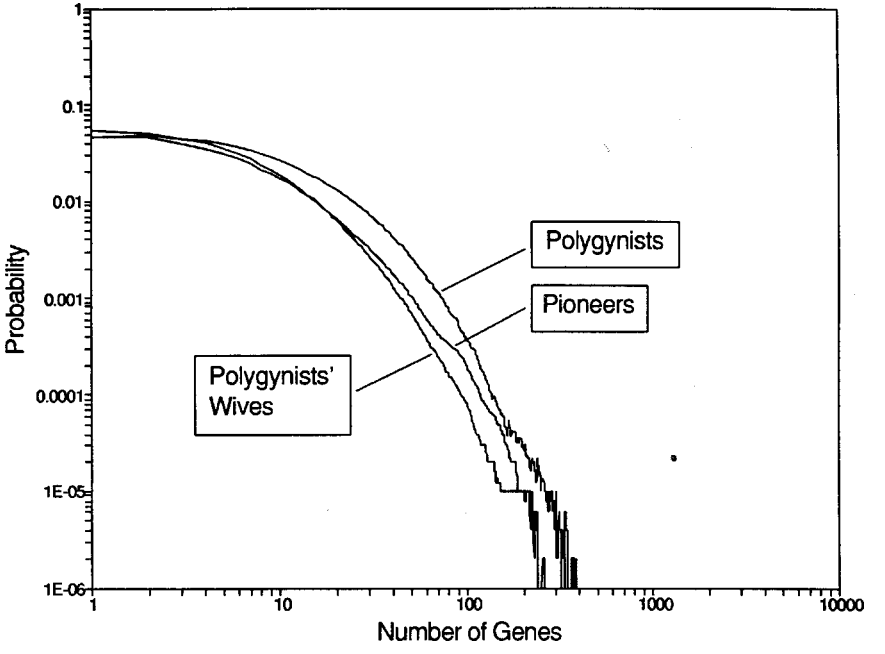

Figure 3. Distributions of founder gene contributions for three subgroups of founders in the Utah Mormon population.

terites to founder effect and drift (Fujiwara et al. 1989; Klinger et al. 1990).

Discussion

Two notable results derive from these distributions of founder contributions. First, the Hutterite distribution describes the basis for a classic founder effect. The closed nature of the Hutterite population, its small

Table 3. Confidence Limits for Founder Contributions

Confidence Level	*Hutterites*		*Mormon Pioneers*		*Sottunga*	
	N	*p*	*N*	*p*	*N*	*p*
90%	115	0.0170	25	0.0003	9	0.0187
95%	227	0.0336	39	0.0004	13	0.0270
99%	558	0.0825	88	0.0009	24	0.0499
99.9%	977	0.1445	170	0.0018	40	0.0832

number of founders entering the population during a restricted period of time, its rapid expansion, and its high inbreeding level produce the prime conditions under which any random allele can spread rapidly, given that it has a survivorship greater than 0.

The Mormon population shares the Hutterite characteristics of a small founder group relative to the number of descendants and a high population growth rate; furthermore, in this study founders were selected from a restricted time period. However, a substantial level of inbreeding has never developed because of a high migration rate in this population (Jorde 1989). Whereas the closed nature of the Hutterite population dictates that most marriages are consanguineous, this is not characteristic of Mormons, and the bottleneck effect of inbreeding (i.e., by reducing N_e) does not occur. Despite a larger probability of a Mormon founder making any genetic contribution to the descendant cohort, the expected and maximum contributions are smaller than for Hutterite founders.

In Sottunga, where migration has also had a prominent role in the island's demographic history, founder contributions describe a distribution similar in shape to the Mormon one. Here again, a significant reduction of N_e through inbreeding has not occurred. The small chance for founders to make disproportionate contributions to Sottunga's gene pool and the unusual frequencies of tapetoretinal and von Willebrand diseases have been previously discussed (O'Brien et al. 1988a,b). The incidence of these diseases in Åland suggests that multiple founders have introduced these genes into the population of Sottunga. It is also of concern that interisland migration and finite pedigree information have obscured pedigree links so that both the number of related individuals and the number of paths of relationship between individuals are undervalued.

The second point of particular interest pertains to the within- and between-population comparisons of the variance in genetic contributions among founders. Our comparison between the Hutterite and Mormon populations shows that polygyny alone does not cause greater variation among individuals in their genetic contributions compared with that found in some monogamous populations. The monogamous marriage pattern of Hutterite founders produced much greater consequences for the variance among founders in their gene contributions over many generations. Other factors, such as migration and inbreeding, have important effects on the variance among individuals in their genetic contributions to a population gene pool. Thompson and Neel (1978) have shown by simulation that population growth effects, particularly periodic events of rapid population increase, enhance founder effect in much the same fashion as it is manifest in the Hutterites: decreased survival probabilities of a gene together with increased expected numbers of a gene that survives.

Another view of the effects of population structure on the variance among founders in their genetic contributions is shown in Table 4, which

Table 4. Distribution of Founder Contributions by Pedigree Path Length for the Three Populations

	Hutterites		*Mormon Pioneers*		*Sottunga*		
Generation	*Paths*	*Net*	*Paths*	*Net*	*Paths*	*Net*	*P*
0	2	0.00030	0	0	0	0	1
1	22	0.00163	6	0.00032	262	0.27235	0.5
2	74	0.00274	624	0.01662	217	0.11279	0.25
3	765	0.01415	28,234	0.37599	488	0.12682	0.125
4	3,393	0.03137	73,709	0.49079	1,049	0.13630	0.0625
5	16,375	0.07570	37,513	0.12489	1,370	0.08901	0.03125
6	86,666	0.20032	4,255	0.00708	2,090	0.06789	0.015625
7	351,332	0.40603	481	0.0004	3,596	0.05841	0.007813
8	376,554	0.21759	258	0.00011	5,045	0.04097	0.003906
9	99,554	0.02876	94	2.0×10^{-5}	7,622	0.03095	0.001953
10	4,203	0.00061	6	6.2×10^{-7}	6,869	0.01395	0.000977
11	10	7.2×10^{-7}	0	0	3,004	0.00305	0.000488
12	0		0	0	555	0.00028	0.000244
13	0		0	0	116	2.9×10^{-5}	0.000122
14	0		0	0	12	1.5×10^{-6}	6.1×10^{-5}
Total paths	938,950		145,180		32,167		
Descendants	6,760		93,865		481		

Path length = number of generations of gene transmission from a founder to a descendant.
Net probability = probability of gene survivorship (P) times total number of paths of length x divided by the total number of descendants.

reports the total number of paths between founders and their descendants by path length, measured as the number of generations in the path, for each population. The probability of gene survivorship over a path of each length P is given; when P is multiplied by the number of paths at each generation length and divided by the total number of descendants, the net contribution of paths of varying lengths is obtained. These distributions highlight fundamental differences between the populations.

Among Hutterites the largest number of paths is eight generations deep, and paths of seven generations constitute the largest portion of the net contribution. Pedigree paths between founders and descendants in this population are generally old; the per-path probability of gene survivorship decreases with path length even as the number of paths increases. In Sottunga the largest number of paths occurs at an even greater number of generations. However, the greatest contributions to the net are from one generation because Sottunga's founders enter the population at all time periods and only a small proportion of the descendants' pedigree information is deep. The largest number of paths and the greatest contribution to the net are concordant at four generations for Mormon pioneer founders. The pedigree paths for this population sample are not particularly old, on the whole, and are more consistent in depth among founders because founders were sampled from a restricted time period.

The figures shown in Table 4 further depict the high rate of gene extinction among Hutterite founders given in Table 2. The distributions of founders and pedigree paths through time shown in Table 4 regulate the rate of gene survivorship in these population pedigrees. The relative antiquity of founders' genes in the Hutterite population gives any particular founder's gene a comparatively low probability of survivorship.

Equally interesting is the within-population comparison between the polygynous Mormons and their wives. As we would expect, polygynists have higher expected values and variances in their genetic contributions to the descendant cohort. Based on the shape of these distributions and given that they are truncated on the left at zero, the variances increase with larger mean values. Note, however, that the variance to mean ratio is smaller for the polygynists than for their wives and the pioneer group. A few factors contribute to these differences. The greater coefficient of variation for the pioneer group reflects the pooled nature of that sample (it includes polygynists and monogamists). The higher coefficient of variation among polygynists' wives is due in part to a slight decrease in fertility by wife order in this population (Bean and Mineau 1986). The smaller coefficient of variation among polygynists corresponds to a general shift to the right of their distribution because fewer of them make contributions of zero. It is also of interest that the maximum expected contribution of a polygynist is the same as for their wives, whereas a larger maximum contribution is reached by a monogamist from the pi-

oneer sample. The main effect of polygyny, compared with monogamy among the Mormon samples, is to increase the mean contribution considerably, less so the variance. For comparison with other populations in which polygyny is practiced, the mixed Mormon pioneer group gives more appropriate distribution parameters.

It is difficult to appreciate the reproductive advantage of polygyny at the individual level in the Mormon population. Although the expected contributions of Mormon polygynists are definitely higher than for their wives or the pioneer population as a whole, the main effect of polygyny among Mormon founders was to vastly increase the probability that any polygynist left a few genes among descendants. Despite larger variance estimates for polygynists compared with monogamists in "shallow" analyses of reproductive success, the correlation between the number of offspring of founders and their expected contributions in the descendant cohort is not strong (Pearson's $r = 0.35$). Again, although polygynous founders have more offspring on average ($n = 16.6$) than monogamists ($n = 7.7$) and make larger average contributions to the gene pool some number of generations later, only 12% of the variation in gene contributions is explained by their number of offspring. In terms of one's genes, therefore, number of offspring is a poor measure of long-term reproductive success.

What is perhaps not apparent from the Mormon example is the effect of polygyny in populations similar to those in which we spent most of our evolutionary history. It is probably reasonable to conjecture that certain structural or behavioral characteristics lacking in the Mormon population are as important as polygyny for establishing large variances among individuals in reproductive success. In populations such as Amazonian tribal groups, where there is both empirical and simulation evidence of founder effect (Neel 1973; Thompson and Neel 1978), population characteristics in conjunction with polygyny may cause large variances among males in reproductive success with long-term effects. However, further studies of the integrity of gene lineages through time and other population characteristics are needed to make meaningful conclusions about the effects of polygyny on the variance structures (among males or between the sexes) of those populations.

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