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Identity by Descent in Island-mainland Populations

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ABSTRACT

A new model is presented for the genetic structure among a collection of island populations, with fluctuating population sizes and continuous overlapping generations, using a stochastic birth, death and immigration (BDI) process. Immigrants enter each island from a large mainland population, with constant gene frequencies, according to a Poisson process. The average probability of identity by descent (IBD) for two haploid individuals randomly selected from an island population is $f_0 = (\phi f_1 + \lambda)/(\phi + \lambda)$, where f_1 is the probability of IBD for two randomly selected immigrants, λ is the birth-rate for each individual, and ϕ is the arrival rate of immigrants into each island. The value of f_0 is independent of the death process, time and N. The expected level of genetic differentiation among island populations is $F_{ST} = (1 - 1/n)\lambda/(\phi + \lambda)$, where n is the total number of islands receiving immigrants. Because f_0 and F_{ST} are independent of the death process, for a BDI model, the population genetic structure for several general demographic situations may be examined using our equations. These include stochastic exponential, or logistic (regulated by death rate) growth within islands, or a "source-sink" population structure. Because the expected values of both f_0 and F_{ST} are independent of time, these are achieved immediately, for a BDI model, with no need to assume the island populations are at genetic equilibrium.

MANY plant and animal populations in nature are highly fragmented (LARSON *et al.* 1984; LEBERG 1991; FRANCE *et al.* 1992). A common pattern of population subdivision involves one or more large "mainland" populations surrounded by numerous smaller "island" populations. HANSKI (1994) has termed such population complexes "island-mainland" metapopulations. The islands, in this case, may be patches of a critical habitat type, hosts for a parasite, or other disjunct resources, as well as actual geographical islands. Populations inhabiting islands tend to be small in size and are frequently isolated from other populations, exchanging only a limited number of migrants. Because small, semi-isolated populations are thought to play an important role in the evolution of new species and in the adaptation of populations to new environments (WRIGHT 1937), the genetic structure of populations occupying island habitats should be of special interest to evolutionary biologists.

The ecological and demographic features of island-mainland population complexes have been extensively studied (see MACARTHUR and WILSON 1969; reviewed by HANSKI 1994), but the genetic outcomes for a population structure of this form are less well understood. WRIGHT (1931) considered the genetic structure of a large collection of island populations of constant size N, with discrete nonoverlapping generations, and with a fraction m of the individuals on each island replaced by migrants from a source with constant gene frequencies in each generation. The theoretical properties of Wright's island model have been well studied and an approximate equilibrium genetic structure may be obtained by diffusion theory (see CROW and KIMURA 1970).

Wright's island model makes several quite restrictive assumptions about the demographic properties of island populations, which often may not be satisfied for species in nature. The model implicitly assumes that (1) the populations have discrete nonoverlapping generations, (2) individual populations do not fluctuate in size due to stochastic variation in the total number of progeny in each generation and (3) no chance fluctuations occur in the number of immigrants in each generation (migration is deterministic). The second assumption may be stated mathematically as

$$N = \sum_{i=1}^{N} X_i, \qquad (1)$$

where X_i is the number of offspring for the ith individual, N is as defined above, and the X_i are multinomial random variables with unit means. The assumption that population size is constant is necessary to obtain an approximate solution for the gene frequency distribution under a Fisher-Wright demographic model using diffusion theory (FELLER 1951). Assumption 3 may generally be relaxed with limited effect (NAGYLAKI 1979). Thus, Wright's island model does not allow for the chance variations in size, over time and space, that normally occur among populations due to sampling vari-

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ance in the total number of offspring in each generation, even if the demographic parameters are constant.

Much recent theory has focused on the effects of modifying particular assumptions of the standard Fisher-Wright (FISHER 1930; WRIGHT 1931) genetic model (which Wright's island model is based upon) to take into account a number of demographic influences including population size bottlenecks (NEI *et al.* 1975; GOODNIGHT 1987; WATTERSON 1989), temporal fluctuations in population size (WRIGHT 1931; WHITLOCK 1992), asymmetrical migration rates (BODMER and CAVALLI-SFORZA 1968), population age structure (CHARLESWORTH 1980) and population extinction and founding events (SELANDER 1975; SLATKIN 1977; MARUYAMA and KIMURA 1980; WADE and MCCAULEY 1988; EWENS 1989; WHITLOCK and MCCAULEY 1990; GILPIN 1991; LANDE 1992). As noted by MORAN (1962; p. 2), however, "the combined result (of two or more population features) need not be such that it can be easily guessed from the separate results."

It is important then to investigate the genetic outcomes for models that combine several demographic factors, in addition to evaluating their effects independently. One way in which the genetic effects of various demographic influences may be treated simultaneously in modeling island-mainland populations is to investigate the genetic properties of an alternative demographic model to Wright's. In this paper, we present a stochastic model of the genetic structure for a collection of populations occupying island habitats, with immigrants arriving from a large mainland population. The populations are assumed to be haploid with continuous overlapping generations. We use a birth, death and immigration (BDI) process to investigate the genetic structure of an island-mainland population complex of this form. To our knowledge, this is the first model of the genetic structure for a continuous generation species with population subdivision and migration. The results are presented in terms of the average probability of identity by descent (IBD; MALÉCOT 1948) for random pairs of alleles within, and among island populations. We contrast the expected level of genetic differentiation among populations, in terms of F_{ST} (WRIGHT 1951), under a continuous-generation BDI model, with predictions based on WRIGHT's (1931) discrete-generation island model.

ANALYTIC THEORY

Consider a collection of populations of a species, each inhabiting one of a large number of disjoint habitat patches. All patches are of equal quality so that the birth and death rates for the individuals in each patch are equal among patches. Individuals are haploid and reproduce by asexual binary fission. The number of individuals inhabiting each patch fluctuates over time due to mortality, reproduction and immigration from a large external source population. Each individual has a constant expected rate of reproduction λ, and a constant probability of death μ, so that the transition probabilities for a population of size N to size $N+1$ or $N-1$, due to a birth or a death, are linearly proportional to N.

Migrants from an external source population enter each habitat patch according to a Poisson process with time-homogeneous parameter ϕ. The expected number of immigrants per unit time ϕ is assumed to be independent of N, the local population size of any particular island. This model describes the dynamics of island populations, under a fairly general set of conditions, provided the mainland populations are large and relatively stable, and act as a continuous source of immigrants. This demographic model is the well-known linear BDI process and may be represented as a continuous-time ergodic Markov chain with time-homogeneous transition rates.

The linear BDI process: Consider a haploid population in which individuals give birth at a rate λ and die at a rate μ, and into which immigrants arrive at a rate ϕ. All three events are assumed to occur in a stochastic manner. During a small interval of time Δt, the probability of a single birth in a population of size N is

$$\lambda N \Delta t, \tag{2}$$

the probability of a single death is,

$$\mu N \Delta t, \tag{3}$$

and the probability of a single immigrant arrival is,

$$\phi \Delta t. \tag{4}$$

The probability of more than one event during an interval of length Δt is of order $o(\Delta t)$ and may be neglected. This is the classical formulation of the linear BDI process (reviewed in RENSHAW 1991; pp. 41–44).

KENDALL (1948, 1949) obtained a general solution for the probability generating function (p.g.f) of population size for a linear BDI process. We focus on the outcomes for the initial condition $N(0) = 0$. In this case, the p.g.f. of N (given that $\lambda \neq \mu$) is

$$\varphi[z] = \left(\frac{\lambda - \mu}{\lambda \exp[(\lambda - \mu)t] - \mu}\right)^{-\phi/\lambda} \times \left\{1 - z\frac{\lambda\,(\exp[\lambda - \mu)t - 1]}{\lambda \exp[(\lambda - \mu)t] - \mu}\right\}^{-\phi/\lambda}, \tag{5}$$

and for the case $\lambda = \mu$ is

$$\varphi[z] = (1 + \lambda t)^{-\phi/\lambda}\left\{1 - \frac{\lambda t z}{1 + \lambda t}\right\}^{-\phi/\lambda}. \tag{6}$$

If $\mu < \lambda$, the result is stochastic exponential population

growth on each island (with immigration) and a steady-state distribution of population sizes does not exist. The expectation of N is then a function of t and is given by

$$E[N|t] = \frac{\phi}{\lambda - \mu}\{\exp[(\lambda - \mu)t] - 1\}, \quad (7)$$

and the variance of N at time t is given by

$$\text{Var}[N|t] = \frac{\phi(\exp[(\lambda - \mu)t] - \mu)(\exp[(\lambda - \mu)t] - 1)}{(\mu - \lambda)^2}. \quad (8)$$

Thus, both the mean and the variance of N increase over time when the birth rate exceeds the death rate. If $\mu > \lambda$, a steady-state population size distribution is reached and the probability mass function for the distribution may be obtained from Kendall's solution by taking the limit of the p.g.f. as time approaches infinity. The steady-state population size is then observed to follow a negative binomial distribution

$$P[N] = \binom{\frac{\phi}{\lambda} + N - 1}{N}\left[1 - \frac{\lambda}{\mu}\right]^{\phi/\lambda}\left[\frac{\lambda}{\mu}\right]^{N}, \quad (9)$$

with expectation,

$$E[N] = \frac{\phi}{\mu - \lambda}, \quad (10)$$

and variance,

$$\text{Var}[N] = \frac{\phi\mu}{(\mu - \lambda)^2}, \quad (11)$$

This second case provides a model of a "source-sink" population structure in which island populations are maintained by immigration, which compensates for a net loss of individuals in the island populations due to mortality.

If $\mu = \lambda$, so that the death rate exactly balances the birth rate, the expectation of N is a linearly increasing function of t and is given by,

$$E[N|t] = \phi t, \quad (12)$$

and the variance is given by,

$$\text{Var}[N|t] = t(\phi + \lambda t). \quad (13)$$

In this case, the distribution of population sizes approaches a Poisson distribution as λ approaches zero. The above results show that the BDI process may produce a variety of population size distributions, and model a number of different ecological situations, depending on the values of the demographic parameters.

Identity by descent: For a haploid species, with overlapping generations in continuous time, consider a single genetic locus with selectively neutral alleles and a region composed of a large number of habitat patches whose population dynamics follow the BDI process outlined above. It is assumed, for simplicity, in our initial development of the model, that the probability of IBD among migrants is always zero. Each migrant into a population then represents a unique allele type, and two alleles may be IBD only in the case that one is descended from the other or both are descended from a common ancestor. This assumption may be relaxed to allow for any pattern of genetic structure in the mainland population without any difficulty and the general case is treated in the APPENDIX. Mutation is assumed to occur at a very low rate within island populations, by comparison with immigration, and to follow an infinite-allele model (KIMURA and CROW 1964) so that its effects are identical to those of immigration (with no IBD among immigrants), but orders of magnitude smaller and may be neglected.

We now consider the probability that two alleles randomly drawn from a single population are identical by descent (IBD; MALÉCOT 1948) and will denote this probability by f_0, following MARUYAMA (1970). For a moderately large number of islands (greater than ~10), this probability is equal to WRIGHT's (1951) measure of genetic differentiation F_{ST} (see discussion below). The probability that two random alleles from a single island population are IBD is given by

$$f_0^N = \sum_{i=1}^{k} \frac{n_i(n_i - 1)}{N(N - 1)}, \quad (14)$$

where n_i is the number of alleles of type i in the population, N is the total number of alleles (haploid individuals) in the island population and k is the number of unique allele types.

To determine f_0 for populations under this model, it is useful to first derive the size distribution of the families of unique allele types in the population at time t. We follow KARLIN and MACGREGOR (1967) and KENDALL (1975) in considering the random variables,

$$\xi_0(t), \xi_1(t), \ldots \xi_N(t), \quad (15)$$

where $\xi_i(t)$ is the number of families of unique allele types that contain i members at time t. Obviously it must be the case that

$$N(t) = \sum_{i=1}^{N} i\xi_i(t), \quad (16)$$

where $N(t)$ is the total number of alleles (haploid individuals) in the population at time t. In this analysis, we will be interested in the behavior of f_0^N, the conditional probability of IBD for two alleles drawn from an island population of size N. The expectation (E) for the conditional probability of IBD (f_0^N), given N, is related to the distribution of the $\xi_i(t)$ in the following way:

$$E[f_0^N] = \sum_{i=1}^{N} \frac{i(i - 1)}{N(N - 1)} E[\xi_i(t)|N]. \quad (17)$$

For our model, with time-homogeneous ϕ, TAVARÉ (1989) obtained a solution for the expectation of $\xi_i(t)$, conditional on N, if the time interval is chosen so that $\lambda = 1$. In this case, the model has only two parameters, μ and ϕ. The conditional distribution of the $\xi_i(t)$ (taken from TAVARÉ) is then

$$\mathrm{E}[\xi_i(t) \mid N] = \frac{\phi N! \phi_{(N-i)}}{i\phi_{(N)}(N-i)!}, \tag{18}$$

where $\phi_{(N)} = \phi(\phi + 1)\ldots(\phi + N - 1)$. Substituting equation (18) into equation (17) above, equation (17) reduces to

$$\mathrm{E}[f_0^N] = \frac{1}{\phi + 1}, \tag{19}$$

which is independent of N, t and μ. Equation (19) is also the unconditional expectation of f_0. Because λ and ϕ are both scaled by t, we may reparameterize (19) as a function of ϕ and λ to obtain, for general λ,

$$\mathrm{E}[f_0^N] = \frac{\lambda}{\lambda + \phi}. \tag{20}$$

Thus, the expected probability of IBD within an island population of size N depends only on the birth rate and the expected number of migrants if there is no IBD among migrants. If the probability of IBD among migrants, denoted by f_1, is greater than zero, a more general equation, for which the above result (20) is a limiting case, may be obtained by a direct inductive proof (see APPENDIX). The general form of the equation is

$$\mathrm{E}[f_0^N] = \frac{\phi f_1 + \lambda}{\phi + \lambda}, \tag{21}$$

which depends on the expected number of migrants and the birth rate, as well as f_1, the probability of IBD among migrants.

Genetic differentiation among populations: A useful measure of the degree of genetic differentiation among populations, originally proposed for a two-allele model by WRIGHT (1951), is the ratio of the observed variance in gene frequency among disjunct populations to that expected under panmixia. This is equivalent to the correlation between random alleles from the same population, relative to that between random alleles taken from the entire collection of populations. For an arbitrary number of alleles, NEI (1973) extended this measure by defining it in terms of the probabilities of identity by descent of alleles. His measure (taken from SLATKIN and BARTON 1989) may be represented as

$$F_{ST} = \frac{f_0 - \bar{f}}{1 - \bar{f}}, \tag{22}$$

where f_0 is as defined above, and $\bar{f}$ is the probability of IBD for two random alleles selected from, and averaged over, the entire collection of populations $(f_1\phi + \lambda)/(\phi + \lambda)$. For the BDI demographic model, f_0 is given by as shown above (equation 21). The value of $\bar{f}$ for a BDI process is

$$\bar{f} = \frac{n\phi f_1 + \lambda}{n\phi + \lambda}, \tag{23}$$

where n is the total number of islands receiving immigrants. This result follows from the observation that the collection of islands as a whole behaves as a single large island receiving an average of $n\phi$ immigrants in unit time. For a collection of n islands, with $f_1 < 1$, F_{ST} is then given by

$$F_{ST} = \left(1 - \frac{1}{n}\right)\frac{\lambda}{\phi + \lambda}. \tag{24}$$

As the number of islands n becomes large, it is clear that $1 - 1/n$ approaches one, so that F_{ST} approaches $\lambda/(\phi + \lambda)$. The average level of genetic differentiation among island populations is then independent of N, t, μ and f_1.

Indirect estimates of gene flow: In studying the genetic structure of subdivided populations in nature, empiricists have made extensive use of the approximate (diploid) equilibrium result for the average genetic differentiation, as measured by F_{ST} (WRIGHT 1951), under a discrete-generation island model,

$$F_{ST} = \frac{1}{4Nm + 1}, \tag{25}$$

where N is the population size and m is the fraction of individuals in each population replaced by migrants in each generation. This result has been used to estimate gene flow in terms of the composite parameter Nm (the number of migrants per generation) from genetic estimates of F_{ST} (LEWONTIN 1974; SLATKIN and BARTON 1989; reviewed by SLATKIN 1994) using the estimator,

$$Nm \cong \frac{1}{4}\left(\frac{1}{F_{ST}} - 1\right). \tag{26}$$

An estimator of the joint parameter ϕ/λ, using a genetic estimate of F_{ST}, may be derived for a BDI model of a haploid species with continuous overlapping generations, in a similar manner to obtain

$$\frac{\phi}{\lambda} \cong \frac{1}{F_{ST}}\left(1 - \frac{1}{n}\right) - 1. \tag{27}$$

If the birth rate λ is known, one can then estimate the number of migrants, per unit time, using the equation,

$$\hat{\phi} \cong \lambda\left(\frac{1}{F_{ST}}\left[1 - \frac{1}{n}\right] - 1\right). \tag{28}$$

For n greater than ~10, equation (28) is well approximated by

$$\hat{\phi} \cong \lambda\left(\frac{1}{F_{ST}} - 1\right). \quad (29)$$

This estimator is very similar in form to the one based on Wright's model, except that it is scaled by a factor λ, rather than the constant $\frac{1}{4}$. Both estimators require that the probability of IBD among migrants is constant.

Comparison with Wright's island model: At genetic equilibrium, the expected value of F_{ST} (for a haploid species) under WRIGHT's (1931) island model is approximately

$$F_{ST} \cong \frac{1}{2Nm + 1} \quad (30)$$

Because the BDI process involves continuous, overlapping generations, we shall first determine the equivalent of a generation for island populations regulated according to a BDI process and then equate this to a generation in Wright's model. Consider an island population that increases by a stochastic birth and immigration process with rates λ and ϕ, respectively. Initially the island population is of size zero, and it is allowed to increase to size N.

To compare our model with Wright's, we define a generation for the continuous-time BDI process to be an interval during which N individuals arise, by birth or immigration, followed by N deaths; each death selects at random from the individuals alive; the process so described is not a BDI process, but the average IBD remains $(\phi f_1 + \lambda)/(\phi + \lambda)$ (see APPENDIX). We then consider the average number of migrants that remain in the population following an interval with N arrivals and N deaths. The expected number of migrants after N arrivals is the sum of probabilities of a migrant arriving at population size $N + k$, where $0 \leq k \leq N - 1$; after N deaths, the expected number of migrants is reduced by half, and if we denote the remaining number of migrants by M, we obtain

$$E[M] = \frac{1}{2}\sum_{k=0}^{N-1} \frac{\phi}{(N + k)\lambda + \phi}, \quad (31)$$

which may be approximated using

$$E[M] = \frac{1}{2}\int_{\tau=0}^{\tau=N-1} \frac{\phi}{(N + \tau)\lambda + \phi}\, d\tau$$

$$= \frac{\phi}{2\lambda} \ln\left[\frac{2\lambda(N - 1) + \phi}{N\lambda + \phi}\right]. \quad (32)$$

If $N \gg \phi/\lambda$ and $N \gg 1$, then this is approximately

$$E[M] = \frac{\phi}{\lambda}\frac{\ln 2}{2}. \quad (33)$$

Substituting this value for Nm in Wright's model we have

$$F_{ST} = \frac{\lambda}{\phi \ln 2 + \lambda}. \quad (34)$$

For a moderately large number of islands developing under a BDI process (see above), the expected value of F_{ST} is simply $\lambda/(\phi + \lambda)$. Thus, by considering only the number of surviving migrants in each generation, and applying Wright's equation, we would underestimate the effect of migration on F_{ST} by a factor of $\log_e 2$. In Wright's discrete-generation island model, all the parents die; the offspring generation has greater IBD than the parents, on average. In the BDI model, some of the parents survive, and therefore the IBD is lower, on average. As a result, the estimated effect of immigration on IBD is smaller for Wright's model.

Relation between demographic structure and f_0: Because equation (21) for f_0, under a BDI demographic model, depends only on the ratio ϕ:λ and the constant f_1 and is independent of μ, N and t, it may be applied to a wider range of demographic structures than those considered in the original BDI model. Three conditions are required for equation (21) to be valid: (1) the relative rates of birth per individual and immigration remain in constant proportion ϕ:λ; (2) every individual in a population has an equal probability of dying and an equal probability of giving birth, whenever a birth or death occurs (*i.e.*, an individual's probability of dying or giving birth does not depend on features such as age or allele type) and (3) the probability of IBD among migrants (f_1) is constant. In ecological terms, the rate of immigration and the individual birth rate must each be independent of the local population density, or they must vary jointly with density in a constant ratio; births and deaths must occur at random and the mainland population must be large enough that the gene frequencies among migrants do not change during the time when the island populations are developing.

A range of demographic structures may be investigated within this framework: (1) if $\lambda > \mu$, the BDI process provides a model of exponentially growing populations (with immigration); (2) if $\lambda < \mu$, the BDI process provides a model of a "source-sink" population complex (VAN HORNE 1983; PULLIAM 1988), where the island habitats contain the "sink" populations and (3) if μ is an increasing function of N, the BDI process provides a stochastic model of the logistic growth of island populations, with density-dependent population regulation due to an increase in the individual death rate with increasing population size. In all three cases, the genetic result predicted by equation (21) remains correct.

A nonequilibrium theory of population genetic structure: The neutral theory of population genetic structure has been developed mostly based on the Fisher-

Wright model of population demographic structure (FISHER 1930; WRIGHT 1931) and is concerned with predicting the expected genetic properties of populations when a "balance" is reached between the forces of migration, mutation and genetic drift, *i.e.,* the point of genetic equilibrium. For an infinite-island model, the time required to approach halfway toward this equilibrium, from some initial nonequilibrium variance, is $\ln (1/2)/\ln [(1 - m)^2(1 - (1/2N))]$ (WHITLOCK 1992).

Because the expected genetic differentiation among populations, and the time required to reach genetic equilibrium are both functions of migration rate and population size, an important question arising in studies of populations with detectable differentiation is whether they have persisted long enough to have reached genetic equilibrium. An "equilibrium assumption" is particularly important when estimates of Nm are derived from genetic estimates of F_{ST}, as discussed above, using equation (26), which predicts the equilibrium value of F_{ST} (see *e.g.,* WHERHAHN 1987; WASER and ELLIOT 1991; reviewed by SLATKIN and BARTON 1989; SLATKIN 1994).

For a BDI process, populations of two or more individuals immediately achieve the value of f_0 and F_{ST} predicted by equations (21) and (24), respectively (on average). Thus, for an island-mainland population complex whose demographic structure can be approximated by a BDI process, there is no need to assume the system has persisted for any particular length of time (*i.e.,* no time is required to reach "equilibrium"). As long as the initial conditions hold (*i.e.,* the population has evolved by a BDI process since either its last extinction, or its origination), equations (21) and (24) may be applied. This interesting result suggests the possibility of a non-equilibrium theory of population genetic structure.

DISCUSSION

Rather than modifying existing models of demographic-genetic structure by manipulating particular assumptions, we have presented in this paper the genetic outcomes for a more general model of population structure with stochastic variation in size, duration and age among populations, using a BDI process. The BDI demographic model allows for a dynamic extinction process among populations, variation in individual population sizes, and a naturally arising age structure for individuals and populations. In particular, the model is more realistic for studying species with continuous overlapping generations than Wright's discrete-generation island model.

The effect on the genetic differentiation among islands of regular population extinctions, arising due to demographic stochasticity, may also be readily studied using the approach developed in this paper and will be examined in detail in a separate publication (B. RANNALA, unpublished observations). The model we have presented most accurately describes ecological "island-mainland" population complexes, with continuous overlapping generations, and allows us to determine the probability of IBD for random individuals within and among populations and the average genetic differentiation among island populations.

Few studies have examined the genetic structure of populations for demographic models differing from the one proposed by FISHER (1930) and WRIGHT (1931), despite the great ecological importance of alternative population demographic structures in nature (LANDE 1988). In a pioneering study, MORAN (1958) considered a population structure based on a birth-death process in which each event comprises a random individual giving birth and another random individual dying (excluding the individual just born). Moran's model thus retains the constant population size assumption invoked by FISHER and WRIGHT, while allowing for random births and deaths in continuous time, and the result is a population that behaves, genetically, as a Fisher-Wright population whose size is roughly halved (see discussion in GALE 1990). MORAN suggested that this reduction in effective population size, for his continuous-generation model, is due to an additional element of randomness caused by the process of choosing the survivors following each death.

Our analysis of the genetics of a BDI model suggests that population size no longer plays such an important role in population genetics theory if the assumptions of a constant population size and discrete nonoverlapping generations are relaxed. FELLER (1951) has suggested that the assumption of a constant population size, for the Fisher-Wright model, plays a critical role in the theory, and that dropping this assumption "will lead us to an entirely new theoretical model." Our findings lend support to his conjecture.

A number of important results are obtained by examining the average probability of IBD for a BDI process. The most significant finding is that the expected value of f_0 is a simple function of λ, ϕ, and f_1, the individual birth rate, the expected number of immigrants, and the probability of IBD among immigrants. The outcome is that population size has only an indirect effect (and that in special cases) on the value of f_0, and the death process has no effect, so long as individuals die at random.

The familiar biological dictum that "there can be exchange of only a few individuals per generation if the isolation is to have significant effects" (WRIGHT 1939) also no longer holds under a BDI model, because the effect of migration on F_{ST} depends on the birth rate as well as the number of immigrants [see equation (24)]. Because f_0 and F_{ST} are independent of the death process, equations (21) and (24) may be applied to a

broad range of demographic structures among island populations, including exponentially growing populations, source-sink population complexes and populations with density-dependent regulation due to an increased death rate. Finally, our equation for the average value of f_0 may be applied without making any assumptions regarding the age of the populations under consideration (*i.e.*, there is no need to assume "genetic equilibrium") so long as each population has been regulated by a BDI process, with constant f_1, since its inception or its last extinction.

The findings of this study suggest that further research should be focused on the genetics of demographic models other than the Fisher-Wright model. The need for more general demographic models in population genetics theory has long been recognized by a number of workers in probability theory (FELLER 1951; BARTLETT 1955; MORAN 1962), but the solutions for the genetic stucture of populations under more general stochastic demographic models have often been considered too difficult. Our findings suggest that some simple solutions exist, for more general models of demographic structure, at least for measures such as the probability of IBD of random alleles, and the genetic differentiation among populations as measured by F_{ST}.

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APPENDIX

Theorem: Consider a population of at least two individuals with population size determined by a birth, death and immigration (BDI) process with birth rate λ and immigration rate ϕ (it will be shown that the death rate μ is irrelevant and may be less than, equal to, or greater than λ). The probability that two immigrants are identical by descent (IBD) is given by f_1. The probability that two individuals drawn at random from the population are IBD, denoted by f_0, is given by

$$f_0 = \frac{\phi f_1 + \lambda}{\phi + \lambda}.$$

Proof: Consider first that the population is composed of only two individuals and that this state has been reached from an initial state of zero by the arrival of two individuals. The first individual is necessarily an immigrant, and the second may have arisen by a birth event or an immigration event with probabilities in the ratio $\lambda:\phi$; the probability of IBD equals one if the second individual is due to a birth, and f_1 if the individual is an immigrant, so the unconditional probability of IBD is

$$\frac{\phi f_1 + \lambda}{\phi + \lambda}.$$

Now consider a population composed of three individuals, with this state having been reached from an initial state of zero by the arrival of three individuals. A population of two individuals will increase to three individuals by a birth event with probability,

$$\frac{2\lambda}{\phi + 2\lambda},$$

or by an immigration event with probability,

$$\frac{\phi}{\phi + 2\lambda}.$$

If the increase is due to a birth, the probability of IBD equals

$$\frac{1}{3} + \frac{2}{3}\left(\frac{\phi f_1 + \lambda}{\phi + \lambda}\right).$$

This result follows from the observation that a random pair of individuals contains one of the following combinations: the new individual and its parent, with probability of IBD equal to 1; the new individual and the nonparent, with probability of IBD equal to $(\phi f_1 + \lambda)/(\phi + \lambda)$; or the two remaining individuals, with probability of IBD equal to $(\phi f_1 + \lambda)/(\phi + \lambda)$.If the increase is due to the arrival of an immigrant, the probability of IBD is

$$\frac{1}{3}\left(\frac{\phi f_1 + \lambda}{\phi + \lambda}\right) + \frac{2}{3} f_1.$$

This result follows from the observation that a random pair of individuals contains one of the following combinations: the new individual and one of the two remaining individuals, with probability of IBD equal to f_1; the two remaining individuals, with probability of IBD equal to $(\phi f_1 + \lambda)/(\phi + \lambda)$. The overall probability of IBD for two random individuals drawn from a population of three individuals is then

$$\frac{2\lambda}{\phi + 2\lambda}\left(\frac{1}{3} + \frac{2}{3}\left[\frac{\phi f_1 + \lambda}{\phi + \lambda}\right]\right) + \frac{\phi}{\phi + 2\lambda}\left(\frac{2}{3} f_1 + \frac{1}{3}\left[\frac{\phi f_1 + \lambda}{\phi + \lambda}\right]\right) = \frac{\phi f_1 + \lambda}{\phi + \lambda}.$$

In general, if a population has reached a size of $n + 1$ from n due to a single arrival, the probability that the arrival was a birth is

$$\frac{n\lambda}{\phi + n\lambda},$$

and the birth event results in a probability of IBD equal to

$$\frac{2}{n(n+1)} + \left(1 - \frac{2}{n(n+1)}\right)\left(\frac{\phi f_1 + \lambda}{\phi + \lambda}\right).$$

This result follows from by observing that a random pair of individuals comprises a new-born individual and its parent with probability $2/n(n+1)$, and the probability of IBD is then 1; or it is some other pair with probability $1-2/n(n+1)$ and the probability of IBD is then $(\phi f_1 + \lambda)/(\phi + \lambda)$ (since the new-born individual has the same probability of IBD, with any individual other than its parent, that its parent does). The probability that the arrival was an immigrant is given by

$$\frac{\phi}{\phi + n\lambda},$$

and the immigration event results in a probability of IBD equal to

$$\frac{2}{n+1} f_1 + \left(1 - \frac{2}{n+1}\right)\left(\frac{\phi f_1 + \lambda}{\phi + \lambda}\right).$$

The result follows by observing that the immigrant is among the pair of individuals selected with probability $2/(n+1)$, and the probability of IBD is then f_1; the immigrant is not among the pair of individuals selected with probability $1-2/(n+1)$, and the probability of IBD is then $(\phi f_1 + \lambda)/(\phi + \lambda)$. The unconditional probability of IBD in a population of size $n+1$, that has grown from a population of size n by a single arrival is then

$$\frac{n\lambda}{\phi + n\lambda}\left(\frac{2}{n(n+1)} + \left[1 - \frac{2}{n(n+1)}\right]\left[\frac{\phi f_1 + \lambda}{\phi + \lambda}\right]\right)$$

$$+ \frac{\phi}{\phi + n\lambda}\left(\frac{2}{n+1} f_1 + \left[1 - \frac{2}{n+1}\right]\left[\frac{\phi f_1 + \lambda}{\phi + \lambda}\right]\right)$$

$$= \frac{\phi f_1 + \lambda}{\phi + \lambda}.$$

Now consider a population of two individuals that results from three new arrivals (starting at zero) and a death. The death removes a random individual, and by symmetry the remaining pair of individuals must have the same probability of IBD as the two potential pairings eliminated by the death. A population of two individuals that is reached by three arrivals and a death therefore has a probability of IBD equal to $(\phi f_1 + \lambda)/(\phi + \lambda)$. In general, any population of size $n-1$ that is a result of n arrivals and a death will have a probability of IBD equal to $(\phi f_1 + \lambda)/(\phi + \lambda)$ by the same argument (*i.e.*, the death removes $n-1$ potential pairings, which have the same probability of IBD as any other $n-1$ pairs, and so the probability of IBD is unchanged).

Finally, any sequence of arrivals and deaths will leave the probability of IBD unchanged, and so the probability of IBD for any arbitrary population (even given the particular sequence of arrivals and deaths, though not the sequence of births and immigrations) is

$$\frac{\phi f_1 + \lambda}{\phi + \lambda}.$$