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THEORETICAL AND APPLIED GENETICS

A Note on the Island Model with Sex Dependent Migration

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Summary. A theoretical calculation is presented which extends Wright's island model of drift and migration to differential migration between the two sexes. In this circumstance, local demes no longer have Hardy-Weinberg frequencies. There may be local heterozygote excess or deficiency depending, respectively, on whether migration occurs before or after mating. The magnitude of the local departure from Hardy-Weinberg is directly proportional to the difference between the migration parameters of the two sexes. These results could have important implications for studies where genetic markers are used for inferring population structure. An example from a study of Marmot colonies is cited.

Key words: Sex dependent migration – Genetic drift – Island model – Heterozygote excess – Population structure

1 Introduction

Swartz and Armitage (1980) report data from marmot colonies where there is a considerable difference between the two sexes migrating into the colonies. These authors also report fixation indices, F, resulting from allozyme studies. Negative values were obtained which indicated heterozygote excess. There is a possibility of a direct connection between the heterozygote excess and the sex dependent migration. This is because the latter could bring about local differences in gene frequency between the two sexes, which, in turn, upon random mating would produce the well known result of heterozygote excess as compared to Hardy-Weinberg expectation.

Because the dispersal behavior of males and females must be different in many organisms, the possibility of the creation of heterozygote excess for this reason alone seems worthy of theoretical study. In this note I present the theoretical results of one way to model such a system, which is simply the extending of Wright's classic island model to migration to two variations in which the migration parameters are sex dependent.

The results of the calculations to be presented are analogous to the heterozygote excess due to sex differences in finite populations as reviewed and developed by A.D.H. Brown (1979, pp. 16-17). In this latter case, however, the allele frequency differences between the sexes arise from the stochastic effects of finite population size; whereas, in the case which I shall consider, the effect is due to differential migration between the sexes.

I wish to state at the outset, that the theory to be developed is an idealized representation of nature, so that the results will not be directly applicable to experimental data. As with many such models the object is simply to alert the experimentalist to some new kinds of genotypic patterns which he might expect to encounter in the field.

The classic island model, when applied to migration, assumes a collection of demes of size N each which receives immigrants from a pool to which all demes contribute. The i^{th} deme has allele frequency p_i and receives immigrants carrying allele frequency $\overline{p}$ which is $E(p_i)$ over all demes.

I shall start by first recapitulating Wright's construction of the island model. This will provide a basis for comparing both the analytical procedures, and also the results obtained when this model is extended in two different ways.

2 Review of Wright's Island Model with Migration

Following Wright (1969, Chap. 12), the demes are composed of immature individuals with variance of allele frequency among demes of σ_t^2. Unmated individuals enter deme i such that (1-M) of the deme are natives and M are immigrants. There is then random mating within the

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deme. After immigration, the allele frequency $\widetilde{p}_i$ in the ith deme among mated individuals is

$$\widetilde{p}_i = (1 - M)\, p_i + M\overline{p} \tag{1}$$

The variance among demes has been reduced to σ^2_{tm}

$$\sigma^2_{tm} = (1 - M)^2\, \sigma^2_t \tag{2}$$

Also, the progeny from random mating in the ith deme are

$$\begin{aligned} f(A_1A_1) &\equiv \widetilde{P}_i = \widetilde{p}^2_i = p^2_i - 2M\,(p^2_i - p_i\overline{p}) + \\ &\quad M^2\,(p_i - \overline{p})^2, && \text{(3A)} \\ f(A_1A_2) &\equiv \widetilde{H}_i = 2\widetilde{p}_i\widetilde{q}_i = 2p_iq_i - \\ &\quad \overline{2M}\,(2p_iq_i - p_i\overline{q} - q_i\overline{p}) + 2M^2(q_i - \overline{q})\,(p_i - \overline{p}), && \text{(3B)} \\ \text{and } f(A_1A_2) &\equiv \widetilde{Q}_i = \widetilde{q}^2_i = q^2_i - 2M\,(q^2_i - q_i\overline{q}) + \\ &\quad + M^2\,(q_i - \overline{q})^2. && \text{(3C)} \end{aligned}$$

The global genotype frequencies over all demes can be obtained from taking expectations of each genotype over demes, which are

$$\begin{aligned} E(\widetilde{P}_i) &\equiv \overline{P} = \overline{p}^2 + \sigma^2_t\,(1 - M)^2, && \text{(4A)} \\ E(\widetilde{H}_i) &\equiv \overline{H} = 2\overline{pq} - 2\sigma^2_t\,(1 - M)^2, && \text{(4B)} \\ \text{and } E(\widetilde{Q}) &\equiv \overline{Q} = \overline{q}^2 + \sigma^2_t\,(1 - M)^2. && \text{(4C)} \end{aligned}$$

The deme genotypes (3) and global genotypes (4), thus, would represent large numbers of young individuals resulting from the deterministic effect of migration, and prior to the stochastic effects due to random drift which occur before the next generation is produced. The genotype frequencies of this specific stage of the life cycle will be the object of study in the models to be presented later.

Nevertheless, we now proceed to complete the life cycle in order to show how a steady state of demic diversity, or equilibrium variance, is obtained.

New variance is generated because a finite number of individuals, N, in each deme are chosen to found the next generation. Following Wright (1969, p. 292), this new variance over demes can be obtained by a calculation analogous to a one way ANOVA where demes represent 'treatments.' 1, 2, 3 ... k demes. Thus,

$$\begin{aligned} \sigma^2_{t+1} &= E(\sigma^2_{wi}) + \sigma^2_A. \\ \text{where } E(\sigma^2_{wi}) &= \text{expected variance within demes} && (5) \\ \sigma^2_A &= \text{variance among demes} \end{aligned}$$

The variance of gene frequencies in a sample of N individuals from deme i is $\widetilde{p}_i\widetilde{q}_i/2N$. So,

$$\begin{aligned} E(\sigma^2_{wi}) &= E(\widetilde{p}_i\widetilde{q}_i/2N), \\ \text{and } E(\sigma^2_{wi}) &= \frac{1}{2N}\,\{\overline{pq} - \sigma^2_A\}. && (6) \end{aligned}$$

The variance among demes, σ^2_A, is given by (2). Substituting (6) and (2) into (5) yields σ^2_{t+1}.

$$\begin{aligned} \sigma^2_{t+1} &= \frac{1}{2N}\,\{\overline{pq} - \sigma^2_t\,(1 - M)^2\} + \sigma^2_t\,(1 - M)^2, && (7) \\ \text{or } \sigma^2_{t+1} &= \frac{pq}{2N} + \sigma^2_t\,(1 - M)^2\,(1 - \frac{1}{2N}). \end{aligned}$$

At equilibrium $\sigma^2_{t+1} = \sigma^2_t \equiv \hat{\sigma}^2$. Solving for $\hat{\sigma}^2$ yields:

$$\hat{\sigma}^2 = \frac{\overline{pq}}{2N\,(2M - M^2) + (1 - M)^2} \tag{8A}$$

for small M this reduces to

$$\hat{\sigma}^2 = \frac{\overline{pq}}{4NM + 1}. \tag{8B}$$

These well known results are recapitulated here because analogous methodology will be used in developing the sex dependent migration models to follow, and also, as already stated, comparisons of the results of these models will be made with the deterministic stage represented by genotypic frequencies (3) and (4).

It is important to note that this model assumes that the immigrants and natives do not mate until after the immigration process, resulting in the offspring in each deme being Hardy-Weinberg frequencies for alleles $\widetilde{p}_i$, $\widetilde{q}_i$.

In what follows, two models will be developed where the amount of migration is sex dependent. One will entail immigration of unmated females and will be termed the 'Marmot model', because according to Swartz and Armitage the immigrant females are virgin. The other model will be termed the 'Pollen-Seed model.' In the latter model seeds carry fertilized zygotes, which is equivalent to migration of fertilized females. The pollen produced by plants is equivalent to sperm carrying males in animals.

A good example of the 'Pollen-Seed' model in animals is the wasp *Polistes apaches*. According to Professor R.M. Metcalf, Department of Zoology at the University of California, Davis, many female wasps return to build nests in the same locality in which they were born, but in the meantime they have mated with males drawn from a much larger area. (Because the males are haploid they are precise analogoues of pollen grains.) In this case a deme might represent the eaves of several houses on a street in the sprawling suburbia surrounding the city of Davis, California.

3 The Marmot Model

Let m and n denote the male and female migration parameters, respectively. After migration into deme i the male and female allele frequencies $\tilde{p}_{i♂}$ and $\tilde{p}_{i♀}$ will be as follows:

$$\tilde{p}_{i♂} = (1 - m)p_i + m\bar{p}, \tag{9}$$

and $$\tilde{p}_{i♀} = (1 - n)p_i + n\bar{p}. \tag{10}$$

The genotypic frequencies resulting from random union of these gametes in deme i are,

$$A_1 A_1 \quad \tilde{P}_i = \tilde{p}_i^2 - \frac{1}{4}(m - n)^2 (\bar{p} - p_i)^2, \tag{11A}$$

$$A_1 A_2 \quad \tilde{H}_i = 2\tilde{p}_i\tilde{q}_i + \frac{1}{2}(m - n)^2 (\bar{p} - p_i)^2, \tag{11B}$$

$$A_2^2 A_2 \quad \tilde{Q}_i = \tilde{q}_i^2 - \frac{1}{4}(m - n)^2 (\bar{p} - p_i)^2, \tag{11C}$$

where $\tilde{p}_i = \dfrac{\tilde{p}_{t♀} + \tilde{p}_{i♂}}{2}$ or from (9), (10),

$$\tilde{p}_i = p_i + \frac{(m + n)}{2} (\bar{p} - p_i). \tag{12}$$

The global genotype frequencies are

$$\bar{P} = E(\tilde{P}_i) = \bar{p}^2 + \sigma_t^2 (1 - m)(1 - n), \tag{13A}$$

$$\bar{H} = E(\tilde{H}_i) = 2\overline{pq} - 2\sigma_t^2 (1 - m)(1 - n), \tag{13B}$$

and $$\bar{P} = E(\tilde{P}_i) = \bar{q}^2 + \sigma_t^2 (1 - m)(1 - n). \tag{13C}$$

Equations (11) and (13) carry the important information, but before further examination, we first complete the cycle by calculating σ_{t+1}^2.

The one way ANOVA procedure will be employed. Equation (11) can be used to calculate the expected within-deme variance $E(\sigma_{wi}^2)$. However, the procedure has the complication that the genotypic frequencies, $\tilde{P}_i$, $\tilde{H}_i$, $\tilde{Q}_i$ are not in Hardy-Weinberg frequencies; that is, the pairing of alleles A_1, A_2 in zygotes is not independent. The allele frequency $\tilde{p}_i$ is, by definition, the following function of $(\tilde{P}_i, \tilde{H}_i)$

$$\tilde{p}_i = \tilde{P}_i + \frac{1}{2}\tilde{H}_i$$

Sampling N individuals from a trinomial distribution with probabilities $\tilde{P}_i$, $\tilde{H}_i$, $\tilde{Q}$, the 'within deme' variance works out to be,

$$\sigma_{wi}^2 = \frac{\tilde{P}_i (1 - \tilde{P}_i) + \frac{1}{4}\tilde{H}_i (1 - \tilde{H}_i) - \tilde{P}_i\tilde{H}_i}{N}$$

This variance can be expressed in a more convenient way by changing the variables, $(\tilde{P}_i, \tilde{H}_i, \tilde{Q}_i)$ to two independent variables, the allele frequency $\tilde{p}_i$ and the deviation of the homozygotes from Hardy-Weinberg frequencies, d_i in the following way:

$$\tilde{P}_i = \tilde{p}_i^2 + d_i$$
$$\tilde{H}_i = 2\tilde{p}_i\tilde{q}_i - 2d_i$$
$$\tilde{Q}_i = \tilde{q}_i^2 + d_i$$

After this transformation, it can be shown that

$$\sigma_{wi}^2 = \frac{\tilde{p}_i\tilde{q}_i + d_i}{2N} \tag{14}$$

This result is quite general for non-Hardy-Weinberg genotypic frequencies. Another useful form of it can be obtained by substituting $d_i = F_i\tilde{p}q_i$

$$\sigma_{wi}^2 = \frac{\tilde{p}_i\tilde{q}_i (1 + F_i)}{2N} \tag{15}$$

For the present purposes Eq. (14) will be used and inspection of (11) shows that, in this case,

$$d_i = -\frac{1}{4}(m - n)^2 (\bar{p} - p_i)^2.$$

Substituting this into (14) and taking expectations yields the following,

$$E(\sigma_{wi}^2) = \frac{\overline{pq} - \sigma_A^2 - \frac{1}{4}(m - n)^2 \sigma_t^2}{2N}$$

Where σ_A^2 is the variance among demes after migration. Proceeding as non page 3, (Eq. (5)),

$$\sigma_{t+1}^2 \quad \frac{\overline{pq} - \sigma_A^2 - \frac{1}{4}(m - n)^2 \sigma_t^2}{2N} + \sigma_A^2$$

The variance among demes after migration can be obtained from (12).

$$\sigma_A^2 = (1 - \frac{m + n}{2})^2 \sigma_t^2.$$

Which gives the recursion for the variance as follows,

$$\sigma_{t+1}^2 = \frac{\overline{pq}}{2N} + \sigma_t^2 \left[(1 - \frac{m + n}{2})^2 - \frac{\left(1 - \frac{m + n}{2}\right)^2 + \frac{1}{4}(m - n)^2}{2N}\right]. \tag{16}$$

At equilibrium, $\sigma_{t+1}^2 = \sigma_t^2 = \hat{\sigma}^2$, which is the following:

$$\hat{\sigma}^2 = \frac{\overline{pq}}{2N\left(m + n - \frac{(m + n)^2}{4}\right) + \left(1 - \frac{m + n^2}{2}\right) + \frac{1}{4}(m - n)^2}. \tag{17}$$

For small m, n this becomes,

$$\hat{\sigma}^2 = \frac{\overline{pq}}{2N(m+n)+1}. \tag{18}$$

and if m = n = M, the result is the same as the classical result, Eq. (8B).

We now return to the new features which appear with sex dependent migration. These are revealed by the genotypic frequencies for demes, Eq. (11), and for the whole population, Eq. (13).

The genotypic frequencies in demes show the anticipated excess of heterozygotes as compared to Hardy-Weinberg expectations. Specifically, d_i, the deviation of the homozygotes from Hardy-Weinberg expectations, is

$$d_i = -\frac{1}{4}(m-n)^2 (\bar{p} - p_i)^2. \tag{19}$$

Let this deviation for the average deme be $\bar{d}$, defined ($E(d_i)$), then

$$\bar{d} = -\frac{1}{4}(m-n)^2 \sigma^2. \tag{20}$$

(Because we assume that some kind of equilibrium situation prevails, the 't' is dropped from σ_t^2.)

This would give an average excess of heterozygotes of $1/2\,(m\text{-}n)^2\,\sigma^2$.

In the case of the global genotypic frequencies, Eq. (13), we let D be the homozygote departure from Hardy-Weinberg expectation.

$$D = \sigma^2 (1-m)(1-n). \tag{21}$$

Since $D \geqslant 0$, the local heterozygote excess can never extend to the global level, at least in the Island model.

Equation (21) shows that if one or both sexes have a very high immigration rate (m in the case of Swartz and Armitage's marmots was m = .95), the excess homozygotes are reduced, and approach Hardy-Weinberg frequencies, as m (or n) $\rightarrow$ 1. In this extreme case, then, there would be no global evidence for subdivision, but local excess of heterozygotes would be found, providing local demes could be identified as such. However, the magnitude of this excess is not very great, as Eq. (20) shows. On the other hand, holding (m + n) constant, then as m $\rightarrow$ n the global excess of homozygotes rises to a maximum.

$$D = \sigma^2 (1-M)^2, \text{ where } m = n = M,$$

Thus, when m = n = M, both the genotypic distribution and the variance, (18), reduce, as they should, to the sex independent case discussed in the beginning.

Before proceeding to the 'Pollen-Seed' island model, a digression seems appropriate which illustrates the outcome of a model which is more closely analogous to the study of Swartz and Armitage. As in their study, most field studies will usually encompass some subset of demes which receive migrants from unknown sources, outside the study area. Letting p* denote the gene frequency carried by migrants, some of whom are alien to the study area, then the $\bar{d}$, for the average local deme, becomes,

$$\bar{d} = -\frac{(m-n)^2}{4}\left(\sigma^2 + (\bar{p} - p^*)^2\right), \tag{22}$$

and D for the whole study area will be,

$$D = \sigma^2 (1-m)(1-n) - \frac{(m+n)^2}{4}(\bar{p} - p^*)^2 \tag{23}$$

The local d is enhanced, and also the possibility now arises for a net excess of heterozygotes over the whole study area, since, D, can now be less than zero. Of course, with migration being the only deterministic effect in this idealized model, this is not an equilibrium situation. The whole study area $\bar{p}$ would eventually move to the alien gene frequency. We now turn to the Pollen-Seed version of the island model.

4 Pollen-Seed Model

In this model both sexes are allowed to migrate differentially as in the Marmot model. In this case, however, the males migrate first and engage in mating with local unmated females, and after this the mated females migrate. As I mentioned earlier, this scheme of sequential migration events is equivalent to the migration of pollen at the time when plants are flowering, and then, at a later time, the migration of the seeds which result from the pollination. After the male migration into a local deme i, the male and female allele frequencies will be as follows:

$$\hat{p}_{i♂} = (1-m)\,p_i + m\bar{p},$$

and $\hat{p}_{i♀} = p_i$.

The resulting gene frequency among the diploid immigrants is $(p_{i♂} + p_{i♀})\,\frac{1}{2}$ or,

$$\hat{p}_i = p_i + \frac{m}{2}(\bar{p} - p_i). \tag{24}$$

The local homozygote frequency is $p_{i♀}p_{i♂}$,

$$P_i = (1-m)\,p_i^2 + m\bar{p}p_i. \tag{25}$$

The global genotypic frequencies of seeds $\bar{P}$, $\bar{H}$, $\bar{Q}$ can be obtained from $E(P_i)$, and are as follows:

$$\bar{P} = \bar{p}^2 + \sigma^2 (1-m), \tag{26A}$$

$$\bar{H} = 2\overline{pq} - 2\sigma^2 (1-m), \tag{26B}$$

and $\bar{Q} = \bar{q}^2 + \sigma^2 (1-m)$. (26C)

These are the same as in the Marmot Model when n = 0 in that model. For the second migration event, seeds are drawn from the above genotypes and returned to deme i such that (1-n) are natives and n are immigrants. The new local gene frequency, denoted by $\tilde{p}_i$ is given by,

$$\tilde{p}_i = (1 - n)\,\hat{p}_i + n\bar{p}, \tag{27A}$$

or, substituting (24) for $\hat{p}_i$,

$$\tilde{p}_i = p_i\,(1 - n)\,(1 - \frac{m}{2}) + \bar{p}((1 - n)\frac{m}{2} + n). \tag{27B}$$

The new local homozygote frequency, $\tilde{P}_i$ will be,

$$\tilde{P}_i = (1 - n)\,P_i + n\bar{P}. \tag{28A}$$

Substituting (25) for P_i and (26A) for $\bar{P}$, gives,

$$\tilde{P}_i = (1 - n)\,(1 - m)\,p_i^2 + (1 - n)\,m\bar{p}p_i + n\bar{p}^2 + \sigma^2\,n(1 - m). \tag{29B}$$

The local deviation from Hardy-Weinberg frequenties, d_i, is

$$d_i = \tilde{P}_i - \tilde{p}_i^2,$$

and the average deviation $\bar{d}$ is $E(d_i)$ or

$$\bar{d} = E(\tilde{P}_i) - E(\tilde{p}_i^2). \tag{30A}$$

Substituting (27B) for $\tilde{p}_i$ and (29B) for $\tilde{P}_i$, and taking expectations results in the following,

$$\bar{d} = \sigma^2\,((2n - n^2)\,(1 - \frac{1}{2}m)^2 - \frac{m^2}{4}). \tag{30B}$$

Before examining (30B), it should first be noted that the global genotypic frequencies have not changed; that is, $E(\tilde{P}_i) = \bar{P}$, so that the global genotypic frequencies are still given by (26). The equilibrium variance was calculated using the same procedures as before. If migration rates are small enough so that second and higher order terms in m and n can be dropped the result is:

$$\hat{\sigma}^2 \simeq \frac{\overline{pq}}{2N\,(2n + m) + 1 + m} \tag{31A}$$

$$\text{or } \hat{\sigma}^2 \simeq \frac{\overline{pq}}{4Nn + 2Nm + 1} \tag{31B}$$

This result shows that with respect to the equilibrium variance the Pollen-Seed model receives more migrant genes into the local deme than in the Marmot model. Equating m = 0 in the above, results in the equilibrium variance having the same form as Eq. (18) in the Marmot or the classic model, Eq. (8B). This is because the immigration of virgin females and males in the Marmot model introduces the same number of genes as the immigration of diploid mated females or seeds in the Pollen-Seed model without any immigration of males or pollen at the earlier time in the life cycle when the plants or female animals are flowering.

If both kinds of migration occur and are of equal magnitude, m = n = M, then

$$\hat{\sigma}^2 = \frac{\overline{pq}}{6NM + 1}. \tag{28C}$$

Thus, neither the Marmot model nor the Pollen-Seed model differ greatly from the basic sex independent model in their effects on the variance, $\hat{\sigma}^2$, compare Eqs. (8B), (18) and (31B).

We now return to Eq. (30B) which gives the local deviation from Hardy-Weinberg frequencies, and which reveals the important difference between the Marmot model (Eq. 20) and the Pollen-Seed model.

If there is no seed migration, n = 0, then the Pollen-Seed model is identical to the Marmot model for the case where migration is restricted to males only; i.e., there is a deficiency of homozygotes, $\bar{d} = -\sigma^2\frac{m^2}{4}$. If there is no pollen migration, m = 0, then there is a local excess of homozygotes. This is to be expected, since the migration of diploid zygotes will produce a simple local Wahlund effect due to mechanical mixing.

This effect due to migration of seeds tends to dominate the counter effect due to the migration of gametes in the form of pollen (males). This can be shown by dividing the n, m parameter space by the function n = f(m) obtain-

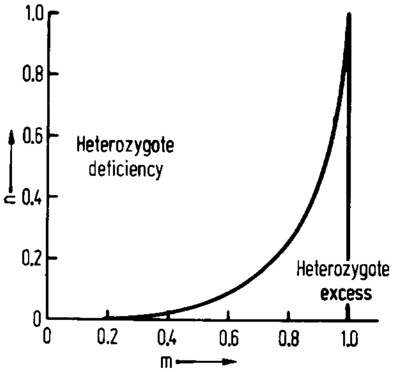

Fig. 1. n ≡ seed migration and m ≡ pollen migration. The function shown is

$$n = 1 - \sqrt{\frac{1 - m}{(1 - \frac{1}{2}m)^2}}$$

Combinations of n, m above the line produce average local deficiency of heterozygotes, while combinations below the line produce average local excess of heterozygotes ed when the local effects of the two kinds of migration just cancel rendering the $\bar{d}$ of Eq. (30B) equal to zero.

The resulting function is

$$n = 1 - \sqrt{\frac{1 - m}{(1 - \frac{1}{2}m)^2}} .$$

Figure 1 shows this curve. Quite clearly, for the Pollen-Seed model, any heterozygote excess due to sex dependent migration could only appear in species where there is substantial migration which is essentially restricted to the pollen (males).

Conclusions

As I stated in the introduction, the Island model with migration, including the extensions developed here to sex dependent migration, is not the kind of model which is ready-made for testing against field data. This is so for several reasons.

As discussed briefly on page 8, most field studies will deal with only some kind of subset of demes, and usually will have to accommodate in some way the immigration of aliens. Also, it would seem that stepping stone migration might be a better representation of migration patterns. Stepping stone migration permits more differentiation among demes than indicated by the Island model equilibrium variances derived in this article; however, perhaps the main results reported here would also apply to a stepping stone model, although with lesser magnitude. Finally, patchiness in fitness might add to, and enhance dispersive effects of random drift. In this case there is no way, at present, to predict genotypic frequencies; so that a drift-migration model merely identifies the effects due to that component alone. Therefore, the purpose of this note is simply to employ a theoretical metaphor which might influence the approaches of experimentalists who are attempting to deduce population structure through the use of genetic markers. This metaphor has four features which may serve this purpose: First, the metaphor shows that there are at least two different kinds of migration with rather different consequences (Marmot model vs. Pollen-Seed model). The particular kind of migration involved in the organism being studied can often be identified, and even some notion of the relevant parameter values (m, n) estimated from direct biological observation rather than only by inference from genetic studies. Second, the metaphor shows that there is a very realistic mechanism for obtaining heterozygote excess without overdominant selection. However, the magnitude of this excess is not very large. Third, the Pollen-Seed metaphor shows that a population could exhibit near Hardy-Weinberg frequencies at both levels (local and global) and still have a differentiated demic substructure. Fourth, the Pollen-Seed metaphor shows that, in a certain sense, seed migration is 'more important' than pollen migration.

Most of these conclusions entail no surprises, in the sense that they are intuitively evident. For example, the second item, above, states that sex dependent migration will tend to generate heterozygote excess; this 'obvious' result nevertheless has some value because intuitive guesses about population dynamics can sometimes be wrong. For example, I anticipated that for extreme migration differences between the sexes, there might be a global excess of heterozygotes which, for the Island model at least, is not the case. Other results, as for example item four, concerning the relative importance of the two kinds of migration, brings out a relationship which was not anticipated. Thus, I feel I have gained some new insights concerning the effects of migration on population structure as a result of this mathematical exercise. It is hoped that this note will serve the same function for others.

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