

Letter to the Editor

A Note on the Change in Gene Frequency of a Selected Allele in Partial Full-Sib Mating Populations

Armando Caballero

Institute of Cell, Animal and Population Biology, University of Edinburgh, Edinburgh EH9 3JT, Scotland

Manuscript received March 19, 1995

Accepted for publication October 28, 1995

THE change in gene frequency of a selected allele in an infinite partially inbred population was derived by WRIGHT (1942). POLLAK (1995) recently argued that although WRIGHT's expression holds for the case of partial selfing, it does not hold for partial full-sib mating. I point out in this note, however, that the model of selection used by POLLAK is different to that which would apply for partial selfing. If the same model of selection as for partial selfing is assumed, WRIGHT's argument also holds for partial full-sib mating.

Assume a biallelic locus with genotypes *AA*, *Aa* and *aa*, genotypic frequencies $p^2 + pqF$, $2pq(1 - F)$ and $q^2 + pqF$, respectively, where *F* is the equilibrium inbreeding coefficient, and relative fitnesses $S = 1 + s$, $H = 1 + sh$ and 1, respectively. With this general model, the change in gene frequency of allele *A* after one generation of selection is approximately

$$\Delta p \approx pqs[F + h - Fh], \quad (1)$$

if *p* is small. Under partial selfing it can be assumed that selection applies as differential viabilities between zygote formation and adulthood. The surviving adults can then carry out selfing or random mating with a given proportion. Therefore, selection precedes mating, and the probability that an individual survives and mates is independent of whether it will produce selfed offspring or not. (Alternatively, if a model of fertility selection is considered, the fertility of an individual is assumed to be independent of its ability to produce selfed offspring).

If this model is generally assumed, it appears intuitive that the change in gene frequency from Equation 1 should hold for any type of partial inbreeding for the same equilibrium value of *F*. However, POLLAK (1995) found that Equation 1 fails to hold for partial full-sib mating, being

$$\Delta p \approx pqs(1 + m)[F + h - Fh], \quad (2)$$

where $m = 2F/(1 + F)$ is the correlation between the frequencies of alleles in the mates. Thus, he argued that because there is a correlation between the frequen-

cies of the mates, the change in gene frequency for partial full-sib mating has an additional term relative to that for partial selfing (Equation 1).

The computation of the frequency of full-sib mating pairs among surviving offspring made by POLLAK appears to entail formation of pair bonds before selection, so that the contribution of the mating pair depends on the product of the survival rates of the mates. For example, from his Table 1, he computed the frequency of full-sib mating pairs of type *AA* × *AA* obtained from the surviving offspring of the mating type *AA* × *AA* (with frequency X_1) in the previous generation as X_1S^2 . If selection precedes the formation of pairs, this frequency should be X_1S . Let us illustrate this with the following example. Imagine a population with 100% full-sib mating at the equilibrium state and, therefore, with $F = 1$ and genotypic frequencies p , 0 and $q = 1 - p$ for genotypes *AA*, *Aa* and *aa*, respectively, in a given generation. Thus, the frequency of allele *A* is *p* in that generation. Given that there is 100% full-sib mating, the only possible mating types, their frequencies and offspring are shown in the three first columns of the table below. The two last columns show the frequency of full-sib mating pairs in the surviving offspring and according to POLLAK's argument, respectively.

Mating type	Frequency	Offspring	Offspring pairs	Offspring pairs (POLLAK)
<i>AA</i> × <i>AA</i>	<i>p</i>	<i>S(AA)</i>	$\frac{pS}{pS + q} (AA \times AA)$	$\frac{pS^2}{pS^2 + q} (AA \times AA)$
<i>aa</i> × <i>aa</i>	<i>q</i>	<i>(aa)</i>	$\frac{q}{pS + q} (aa \times aa)$	$\frac{q}{pS^2 + q} (aa \times aa)$

Thus, if selection occurs among the offspring as differential viabilities from zygote to adult, and thereafter, the surviving adults mate (in this case always between full sibs); the change in gene frequency of allele *A* is $[pS/(pS + q)] - p \approx pqs$, in accordance with Equation 1. Under POLLAK's model, which seems to assume formation of pairs before selection, the change in gene frequency of allele *A* is $[pS^2/(pS^2 + q)] - p \approx 2pqs$, as obtained with Equation 2.

In general, the change in gene frequency in an infi-

Author e-mail: a.caballero@ed.ac.uk

nite partial full-sib mating population with the general model stated above can be computed as follows. Let $i, j = 1, \dots, 6$ denote each of the six possible mating types $AA \times AA, AA \times Aa, AA \times aa, Aa \times Aa, Aa \times aa$ and $aa \times aa$, respectively, with frequencies X_i in generation t . We compute first the probabilities of full-sib mating couples and later, those of random mating couples in generation $t + 1$. Thus, $Prob$ (full-sib mating type j in generation $t + 1$) = $\sum_{i=1}^6 [Prob$ (surviving offspring from the mating type i in generation t) $\times Prob$ (couple of type j from the surviving offspring of the mating type i in generation t)]. For example,

$$\begin{aligned} & Prob \text{ (full-sib mating type } AA \times AA \text{ in generation } t + 1) \\ &= \left(\frac{X_1 S}{T} \times 1 \right) + \left(\frac{X_2(S + H)}{2T} \times \frac{S^2}{(S + H)^2} \right) \\ &+ \left(\frac{X_4(S + 2H + 1)}{4T} \times \frac{S^2}{(S + 2H + 1)^2} \right) \\ &+ \text{ other terms being zero,} \end{aligned}$$

where $T = X_1 S + X_2(S + H)/2 + X_3 H + X_4(S + 2H + 1)/4 + X_5(H + 1)/2 + X_6$. If $s \ll 1$, the above probability can be approximated by $(X_1 S + X_2 S^2/4 + X_4 S^2/16)/T$, while with POLLAK's model the result would approximately be $(X_1 S^2 + X_2 S^2/4 + X_4 S^2/16)/T^2$. Analogously,

$$\begin{aligned} & Prob \text{ (full-sib mating type } AA \times Aa \text{ in generation } t + 1) \\ &= \left(\frac{X_2(S + H)}{2T} \times \frac{2SH}{(S + H)^2} \right) \\ &+ \left(\frac{X_4(S + 2H + 1)}{4T} \times \frac{4SH}{(S + 2H + 1)^2} \right) \end{aligned}$$

+ other terms being zero, or approximately $SH(X_2/2 + X_4/4)/T$ if $s \ll 1$, while POLLAK's result would approximately be $SH(X_2/2 + X_4/4)/T^2$. And analogously for the other mating types.

The probability of random mating couples in generation $t + 1$ is straightforwardly obtained from the genotypic frequencies in the surviving offspring. Thus, for example, the frequency of genotype AA in the surviving offspring is $S(X_1 + X_2/2 + X_4/4)/T$, and therefore, the frequency of random mating pairs $AA \times AA$ is that value squared. If a proportion β of the matings are between full sibs, and a proportion $1 - \beta$ are at random, the

above probabilities should be weighted by these factors. Using these relations in a recurrent way, the exact change in gene frequency per generation can be computed, and the results are consistent with Equation 1.

In summary, POLLAK's model for partial full-sib mating assumes formation of pairs before selection. This implies, in some way, a selection of couples rather than individuals, as previously suggested by CABALLERO and HILL (1992). A possible explanation of the model is that if one of the mates in a couple dies, the survivor does not mate. For randomly mated couples this does not have an effect on the change in gene frequency, as the correlation of gene frequencies between mates is zero. However, for full-sib couples this has an effect as there is an expected correlation between mates. In the partial selfing case there is no formation of couples and survival of individuals is assumed to be previous or, at least, independent of their ability to produce selfed offspring. If the same selection model is assumed for partial full-sib mating (mating after selection), the change in gene frequency has the same formulation as for partial selfing (Equation 1).

A similar reasoning to that used by POLLAK (1995) was also used in a previous paper by the same author [see Table 2 by POLLAK (1988)]. The implications of these papers would be important in terms of the fixation probability of genes because, for the same equilibrium inbreeding coefficient, fixation rates of mutant genes would be larger for partial full-sib mating than for partial selfing by a factor of $(1 + m)$. In the extreme case, with 100% full-sib matings ($F = m = 1$), the fixation probability of an additive mutant gene would be twice that obtained with 100% selfing.

I thank W. G. HILL for helpful comments on the manuscript, an anonymous referee for helping in the clarification of POLLAK's model and the Biotechnology and Biological Sciences Research Council for financial support.

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Communicating editor: B. S. WEIR