



The Hardy-Weinberg principle

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Abstract

Hardy-Weinberg genotypic proportions can be maintained in a population under non-random mating. A compact formula gives the proportions of mating pair types. These are illustrated by some simple examples.

Key words: Hardy-Weinberg equilibrium, non-random mating.

Received: March 11, 2005; Accepted: May 5, 2005.

Consider a population with respect to a single locus having alleles a and A with respective frequencies q and p . Denote frequencies of genotypes aa , aA and AA by f_0 , f_1 and f_2 . Denote the 3×3 matrix of mating-pair frequencies by $[f_{ij}]$, $i = 0, 1, 2; j = 0, 1, 2$. Suppose the population has attained Hardy-Weinberg (H-W) proportions $f_0 = q^2$, $f_1 = 2pq$, $f_2 = p^2$.

Then H-W proportions are maintained if the elements of $[f_{ij}]$ are given by

$$f_{ij} = f_i f_j (1 + v e_i e_j), \quad (1)$$

where $e_0 = -p/q$, $e_1 = 1$ and $e_2 = -q/p$.

Random mating is defined by matrix (1) with $v = 0$, i.e. $f_{ij} = f_i f_j$.

Under the stated conditions, the sum of elements in the first (zero) row of $[f_{ij}]$ is $f_0 = q^2$. This sum is also the frequency of type aa in the offspring, as can be seen by summing the appropriately weighted terms of $[f_{ij}]$, noting that $f_{11} = 4f_{02}$.

The applicable interval of v , as a function of q , is governed by the need for the f_{ij} to be non-negative. Without loss of generality, consider q in the range $0 < q \leq 1/2$. Then the interval containing permissible values of v is $(-q^2/p^2, q/p)$. At the lower limit, reading from left to right and from top to bottom row, the elements of $[f_{ij}]$ are 0 , $2q^3$, $q^2(p - q)$, $2q^3$, $4q^2(p - q)$, $2q(p^3 + q^3)$, $q^2(p - q)$, $2q(p^3 + q^3)$, $(p - q)(p^2 + q^2)$. For the upper limit, the values are q^3 , 0 , pq^2 , 0 , $4pq^2$, $2pq(p - q)$, pq^2 , $2pq(p - q)$, $p(p^3 + q^3)$. Thus it can be seen that the mating scheme defined by (1) gives a wide spectrum of

non-random mating which maintains H-W proportions, i.e. the "Hardy-Weinberg Principle" is more general than is usually envisaged.

Stark (1980) gives a more general mating scheme which subsumes (1). Li (1988) showed that random mating is a sufficient condition, not a necessary one, for the attainment of the Hardy Weinberg proportions, but here we provide for the first time a truly generalized mathematical argumentation to prove the fact. Stark (1977 a,b) give a more detailed description of the underlying mating model and several diagrams which illustrate the ranges of applicability of formula (1).

References

- Li CC (1988) Pseudo-random mating populations. In celebration of the 80th anniversary of the Hardy-Weinberg law. *Genetics* 119:731-737.
- Stark AE (1977a) Models of correlation between mates and relatives and some applications. Unpublished Ph.D. Thesis, School of Community Medicine, The University of New South Wales, Kensington, Australia.
- Stark AE (1977b) Dwa uogólnienia prawa Hardy'ego-Weinberga w genetyce populacji (The Hardy-Weinberg Law of Population Genetics and two Generalizations). *Matematyka Stosowana IX*:123-137.
- Stark AE (1980) Inbreeding systems: Classification by a canonical form. *J Math Biol* 10:305.

Editor: Fábio de Melo Sene