THE EFFECT OF MATING FREQUENCY ON PHENOTYPIC RATIOS IN SIBSHIPS WHEN ONLY ONE PARENT IS KNOWN

RICHARD HIGHTON

Department of Zoology, University of Maryland, College Park

Received May 16, 1966

IN human genetic studies and in organisms that can be bred in the laboratory, the phenotypes of both parents and their offspring are known and it is relatively easy to determine the mode of inheritance of single unit characters from phenotypic ratios of sibships. On the other hand, it is not possible to undertake laboratory breeding experiments with many kinds of animals and plants, although data on the phenotype of one parent, usually the mother, and its offspring are sometimes available. The interpretation of these data may be difficult because it is often not known how many times the known parent has mated (in the case of animals) or from how many other plants pollen has been derived (in the case of higher plants). It is the purpose of this paper to show the effects of mating behavior on the expected phenotypic frequencies in sibships for single gene traits with complete dominance.

A dominant parent mating at random will be expected to have $(1 + pq)/(1 + q)$ dominant offspring and $q^2/(1 + q)$ recessive offspring, while a recessive parent will be expected to produce p dominant and q recessive offspring, where p and q are the respective gene frequencies of the dominant and recessive genes (LI 1955: p. 17, Table 7). These formulae can be used to determine whether a given trait is dominant or recessive at certain gene frequencies (Figures 1, 2 in HIGHTON 1959).

The mating behavior will have a decided effect on the distribution of phenotypes in families with more than one offspring. Table 1 gives formulae for predicting the expected frequency of phenotypes in broods of dominant and recessive parents with two different mating behaviors, monogamy (all offspring in a brood full sibs) and polygamy (all offspring within a brood half sibs.) Figures 1 to 4 show the cumulative expected proportions of offspring of broods of size 8 as the gene frequencies vary from 0 to 1. Variances can be calculated by the "delta method" (LI 1955: pp. 15-16).

The frequency of phenotypically uniform broods from a recessive monogamous parent approaches p^2 (for all dominant broods) and q^2 (for all recessive broods) vary closely in broods of size 8 or more (see Figure 3). Therefore mixed broods have a frequency close to $2pq$ in larger broods, independent of the size of the brood. In broods from a polygamous recessive parent, the frequency of mixed broods rapidly approaches 1 at most gene frequencies, as pure broods become

TABLE 1

The formulae for obtaining the probabilities of phenotypic ratios of broods of size 2 or more from one known parent with different types of mating behavior

Phenotype of known parent	Type of brood	All full sibs	All half sibs
Dominant	All dominant	$\frac{p + 2p^2q + 4pq^2 (\frac{3}{4})^N + 2q^3(\frac{1}{2})^N}{1 + q}$	$\frac{p}{1 + q} + \frac{2q}{1 + q} \left(\frac{1 + p}{2}\right)^N$
	Mixed	$\frac{2q}{1 + q} \frac{N!}{D! R!} \{2pq (\frac{3}{4})^D (\frac{1}{4})^R + q^2(\frac{1}{2})^N\}$	$\frac{2q}{1 + q} \frac{N!}{D! R!} \left(\frac{1 + p}{2}\right)^D \left(\frac{q}{2}\right)^R$
	All recessive	$\frac{2q}{1 + q} \{2pq (\frac{1}{4})^N + q^2 (\frac{1}{2})^N\}$	$\frac{2q}{1 + q} \left(\frac{q}{2}\right)^N$
Recessive	All dominant	$p^2 + 2pq (\frac{1}{2})^N$	p^N
	Mixed	$\frac{N!}{D! R!} 2pq (\frac{1}{2})^N$	$\frac{N!}{D! R!} p^D q^R$
	All recessive	$q^2 + 2pq (\frac{1}{2})^N$	q^N

N is brood size, D and R are the number of dominants and recessives in the brood, and p and q are gene frequencies.

FIGURE 1.—The relation of gene frequency and the expected distribution of types of broods of size 8 from a monogamous dominant parent (all offspring full sibs).

FIGURE 2.—The relation of gene frequency and the expected distribution of types of broods of size 8 from a polygamous dominant parent (all offspring half sibs).

FIGURE 3.—The relation of gene frequency and the expected distribution of types of broods of size 8 from a monogamous recessive parent (all offspring full sibs).

very rare (Figure 4). The difference in the mating behavior has far less effect on the distribution of sibships of dominant parents (compare Figures 1 and 2).

There are, of course, other types of families that may occur when the mating behavior is not so strictly determined. With internal fertilization, a female may mate 2, 3 or more times before her eggs are fertilized, but not in such a way to insure that all the offspring in a brood are half sibs. When all eggs are fertilized at about the same time, it would be highly unlikely that they would be all half sibs, except in very small broods, but rather it would be expected that there would be various combinations of full sibs and half sibs.

The formula that may be used to calculate the probability of obtaining a particular number of groups of full and half sibs in a brood, knowing the number of times a female has mated and the size of the brood is

$$C \frac{N!}{f_1! f_2! f_3! \dots} \frac{1}{X^N}$$

where C is the number of combinations that this particular type of brood can be produced with the given number of matings, N is the number of offspring in the

FIGURE 4.—The relation of gene frequency and the expected distribution of types of broods of size 8 from a polygamous recessive parent (all offspring half sibs).

TABLE 2
Expected proportions of brood types in broods of 7 when a female mates a variable number of times

Type of brood	Number of matings							General formula
	1	2	3	4	5	6	7	
All full sibs	1	1	1	1	1	1	1	$\frac{1}{X^6}$
6 full sibs, 1 half sib	0	7	14	21	28	35	42	$\frac{7(X-1)}{X^6}$
5 full sibs, 2 half sibs	0	0	42	126	252	420	630	$\frac{21(X-1)(X-2)}{X^6}$
4 full sibs, 3 half sibs	0	0	0	210	840	2100	4200	$\frac{35(X-1)(X-2)(X-3)}{X^6}$
3 full sibs, 4 half sibs	0	0	0	0	840	4200	12600	$\frac{35(X-1)(X-2)(X-3)(X-4)}{X^6}$
2 full sibs, 5 half sibs	0	0	0	0	0	2520	15120	$\frac{21(X-1)(X-2)(X-3)(X-4)(X-5)}{X^6}$
5 full sibs, 2 full sibs	0	21	42	63	84	105	126	$\frac{21(X-1)}{X^6}$
4 full sibs, 3 full sibs	0	35	70	105	140	175	210	$\frac{35(X-1)}{X^6}$
3 full sibs, 3 full sibs, 1 half sib	0	0	140	420	840	1400	2100	$\frac{70(X-1)(X-2)}{X^6}$
4 full sibs, 2 full sibs, 1 half sib	0	0	210	630	1260	2100	3150	$\frac{105(X-1)(X-2)}{X^6}$
3 full sibs, 2 full sibs, 2 full sibs	0	0	210	630	1260	2100	3150	$\frac{105(X-1)(X-2)}{X^6}$
3 full sibs, 2 full sibs, 2 half sibs	0	0	0	1260	5040	12600	25200	$\frac{210(X-1)(X-2)(X-3)}{X^6}$
2 full sibs, 2 full sibs, 2 full sibs, 1 half sib	0	0	0	630	2520	6300	12600	$\frac{105(X-1)(X-2)(X-3)}{X^6}$
2 full sibs, 2 full sibs, 3 half sibs	0	0	0	0	2520	12600	37800	$\frac{105(X-1)(X-2)(X-3)(X-4)}{X^6}$
7 half sibs	0	0	0	0	0	0	720	$\frac{(X-1)(X-2)(X-3)(X-4)(X-5)(X-6)}{X^6}$
Total (X^6)	1	64	729	4096	15625	46656	117649	1

The denominator (X^6) is omitted from all probabilities in the table, only the numerator is shown. The denominator is given at the bottom of each column.

brood, $f_1, f_2, f_3, \dots$ are the number of full sibs in the first, second, third, $\dots$, sets of full sibs, and X is the number of times the known parent has mated.

As an example of the use of this formula, consider broods of size 7. There are 15 different possible types of broods as listed in Table 2. This table shows how the probability of occurrence of each of these broods varies with the number of matings, assuming that a sperm from each of the matings has an equal probability of fertilizing each egg. If this were not the case, as for example if sperm from the first mating had a higher probability of fertilizing more ova than those from later matings, then weighting would be necessary. If a female mates with five different males A, B, C, D, and E, then there are 60 different ways that a brood of 4 full sibs, 2 full sibs, and 1 half sib could be produced (offspring with male parents *AAAABBC*, *AAAABBD*, *AAAABBE*, *AAAACCB*, etc.). The probability of producing this type of brood is therefore

$$60 \cdot \frac{7!}{4! 2!} \cdot \frac{1}{5^7} = \frac{1260}{15625}$$

as in Table 2. Note that for all general formulae the numerator includes $(X-1)(X-2)(X-3) \dots (X-M+1)$ where M is the minimum number of unknown parents necessary to produce this type of brood.

Once the probability of each type of brood is obtained, then the frequencies of dominant and recessive offspring in broods of varying size from a female parent that has mated any number of times can be predicted. This is done by calculating the array of probabilities for the specific brood size as in each column of Table 2 and the expected proportions of each type (by multiplying the probabilities calculated from the appropriate formulae in Table 1 for each group of full sibs by that for the total number of half sibs). For example, in broods of 4 from a recessive female that has mated five times, the probability that all members of the brood are full sibs is $1/125$, $16/125$ that there are three full sibs and one half sib, etc. If there are all full sibs, then $\frac{1}{8} p (1+7p)$ will be expected to include four dominant offspring, $\frac{1}{2} pq$ will be expected to have three dominant (D) and one recessive (R) offspring, etc. The probability of getting 4 dominant, 3 dominant and 1 recessive, 2 dominant and 2 recessive, etc. offspring in a brood of four in which three are full sibs and one is a half sib can be obtained by multiplying the array of probabilities of getting a brood of three full sibs times the array of probabilities of a single half sib being dominant or recessive:

$$\begin{aligned} & [\frac{1}{4}p(1+3p) D^3 + \frac{3}{4}pq D^2R + \frac{3}{4}pq DR^2 + \frac{1}{4}q(1+3q)R^3] [p^D + q^R] = \\ & \frac{1}{4}p^2(1+3p) D^4 + \frac{1}{4}pq(1+6p) D^3R + \frac{3}{4}pq D^2R^2 + \frac{1}{4}pq(1+6q) DR^3 + \frac{1}{4}q^2 \\ & (1+3q)R^4 \end{aligned}$$

In this example, this type of brood is expected to occur $16/125$ of the time. The probabilities of getting each type of brood of four offspring from a recessive female that has mated five times are given in Table 3. Table 4 shows the effect of the number of matings on the various types of families where p is .1. Figure 5 shows the way number of matings affect brood structure in families of four from recessive mothers at all gene frequencies.

I wish to thank Drs. JOHN CRENSHAW, JAMES HUHEEY, C. C. LI, EDWARD KELLER, KEN-ICHI

TABLE 3
Expected types of broods of 4 from a recessive female that mates five times

Type of brood	Frequency	4 Dominant	3 Dominant 1 Recessive	2 Dominant 2 Recessive	1 Dominant 3 Recessive	4 Recessive
All full sibs	$\frac{1}{125}$	$\frac{1}{8} p(1+7p)$	$\frac{1}{2} pq$	$\frac{3}{4} pq$	$\frac{1}{2} pq$	$\frac{1}{8} q(1+7q)$
3 full sibs, 1 half sib	$\frac{16}{125}$	$\frac{1}{4} p^2(1+3p)$	$\frac{1}{4} pq(1+6p)$	$\frac{3}{4} pq$	$\frac{1}{4} pq(1+6q)$	$\frac{1}{4} q^2(1+3q)$
2 full sibs, 2 half sibs	$\frac{72}{125}$	$\frac{1}{2} p^3(1+p)$	$p^2q(1+2p)$	$\frac{1}{2} pq(1+6pq)$	$pq^2(1+2q)$	$\frac{1}{2} q^3(1+q)$
2 full sibs, 2 full sibs	$\frac{12}{125}$	$\frac{1}{4} p^2(1+p)^2$	$p^2q(1+p)$	$p^2q^2 + \frac{1}{2} pq(1+p)(1+q)$	$pq^2(1+q)$	$\frac{1}{4} q^2(1+q)^2$
All half sibs	$\frac{24}{125}$	p^4	$4p^3q$	$6p^2q^2$	$4pq^3$	q^4

TABLE 4
The effect of the number of matings on the frequency of various types of families of size 4 for recessive mothers in a population where p is .1

Number of matings	4 Dominant	3 Dominant 1 Recessive	2 Dominant 2 Recessive	1 Dominant 3 Recessive	4 Recessive
1 (All full sibs)	.0213	.0450	.0675	.0450	.8213
2	.0045	.0277	.0682	.1627	.7370
3	.0027	.0193	.0760	.1793	.7227
4	.0017	.0153	.0716	.2043	.7072
5	.0012	.0128	.0682	.2202	.6975
6	.0009	.0112	.0657	.2312	.6909
All half sibs	.0001	.0036	.0486	.2916	.6561

FIGURE 5.—The effect of the number of matings on the expected frequencies of broods of size 4 from a recessive parent plotted in the same manner as in Figures 1 to 4.

KOJIMA, JANE POTTER, and SEWALL WRIGHT for kindly reading the manuscript and offering many helpful suggestions, but any errors that may remain are mine. RUDOLPH DANSTEDT and ROBERT JAEGER generated some of the theoretical curves on a computer. The National Science Foundation (Grant GB-3235) provided financial support.

SUMMARY

Formulae are given for calculating the expected frequencies of dominants and recessives in broods when the phenotype of only one parent is known under different types of mating behavior varying from monogamy to complete polygamy. If large numbers of broods are available, these may be used to determine mating behavior in organisms where parent-offspring phenotypic data are available.

LITERATURE CITED

- HIGHTON, R., 1959 The inheritance of the color phases of *Plethodon cinereus*. *Copeia* **1**: 33-37.
 LI, C. C., 1955 *Population Genetics*. University of Chicago Press.