COMPONENTS OF VARIATION UNDER SIB-MATING

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I. INTRODUCTION

MATHER (1949*a* and *b*) has described how the heritable portion of continuous variation in certain experimental populations may be partitioned into two components, D and H , the former depending upon differences in phenotype between homozygotes, and the latter upon departures in phenotype of heterozygotes from the average expression of corresponding homozygotes. Bateman and Mather (1951) considered the case of selfing after an initial cross of two inbred lines and obtained (as powers of $\frac{1}{2}$) the general formulæ for the coefficients of D and H in the different measures of variation in each generation. Nelder (1952) has described a general method of obtaining these coefficients for various systems of inbreeding and of obtaining the forms of D and H when linkage causes these to vary from generation to generation.

We have used Nelder's method to obtain the coefficients of D and H under sib-mating after an initial cross of two inbred lines. These coefficients are, of course, essential for the analysis of inbreeding experiments using sib-mating, whether as in animals as the closest possible system of inbreeding, or in plants as a system intermediate between selfing and random mating.

2. COMPONENTS OF VARIATION

Consider two alleles, A and a , of one gene, and the possible genotypes AA , aa , Aa . The possible mating pairs are given on the left of table 1, and their proportions in a population form a 6-vector which under sib-mating changes according to the transformation matrix,

$AA \times AA$	1	.	$\frac{1}{4}$	.	$\frac{1}{16}$	.
$aa \times aa$	.	1	.	$\frac{1}{4}$	$\frac{1}{16}$	.
$AA \times Aa$	.	.	$\frac{1}{2}$	.	$\frac{1}{4}$	.
$aa \times Aa$	.	.	.	$\frac{1}{2}$	$\frac{1}{4}$	.
$Aa \times Aa$	.	.	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	1
$AA \times aa$	.	.	.	.	$\frac{1}{8}$	.

Denote by S_0 the generation in which the homozygotes AA and aa are crossed, and by S_l the l th generation of subsequent sib-mating. The first two generations S_1 and S_2 coincide of course with the F_1 and F_2 of a selfing series. The proportions of mating pairs in S_l may be

obtained from the latent roots and vectors of the above matrix and are given in table 1.

TABLE 1

$AA \times AA$	$\frac{1}{5}$	$\frac{5}{2} - 4g(l+4) + 4^{-l}$
$aa \times aa$		$\frac{5}{2} - 4g(l+4) + 4^{-l}$
$AA \times Aa$		$g(l) - 4^{-l+1}$
$aa \times Aa$		$g(l) - 4^{-l+1}$
$Aa \times Aa$		$g(l-1) + 4^{-l+1}$
$AA \times aa$		$\frac{1}{2}g(l-2) + 2 \cdot 4^{-l}$

where $g(l) = 2^{-l+1}(2f(l+1) - f(l))$ and $f(l)$ is the Fibonacci series 0, 1, 1, 2, 3, 5, 8, 13, ... with $f(0) = 0, f(1) = 1, f(l+2) = f(l+1) + f(l)$ and $f(-l) = (-1)^{l-1}f(l)$.

Following Nelder, we say that plants of generation S_k , which have a common ancestral pair in $S_l (l < k)$ but not in S_{l+1} , form an l -group. We define V_{lSk} as that item in the heritable variance of generation S_k which is given by the variance of the means of $(k-l+1)$ -groups taken round the means of the $(k-l)$ -groups and averaged over the latter. Hence V_{lSk} can be expressed as the difference of the total variance of $(k-l+1)$ -group means and $(k-l)$ -group means in S_k . We compute the variance of $(k-l)$ -group means using the mean of S_{k-l} as variate while the frequencies are those of S_l .

Let d , $-d$ and h be the deviations of the phenotypes of AA , aa and Aa respectively from the mean phenotype of AA and aa . Then the contributions of the various mating pairs to the mean of S_{k-l} are given in table 2.

TABLE 2

d
$-d$
$\frac{1}{2}d + 2^{-k+l-1}f(k-l+2)h$
$-\frac{1}{2}d + 2^{-k+l-1}f(k-l+2)h$
$2^{-k+l}f(k-l+1)h$
$2^{-k+l+1}f(k-l)h$

Writing D for d^2 and H for h^2 we find after some reduction that

$$V_{lSk} = 2^{-l-1}f(l)D + 2^{-2k+1}\{4(-)^{k-l} + 2^l(-)^{k-l}(3f(l-2) - f(l-1)) \\ + 2^{l-1}(27f(2k-l-2) - 4f(2k-l-1) \\ - f(2k-2l-3) - 8f(2k-2l-2) \\ + (-2)^{l-1}(f(2k-3l-5) + 8f(2k-3l-4)))\}H/25.$$

We must make one correction. Table 2 is incorrect for $k-l = 1$, since in this case it gives the mean of each mating pair, while for $V_{(k-1)Sk}$ we want the variance of individuals and not of pairs about their family means. It happens, as we might therefore expect, that the above formula for V_{lSk} must be doubled when $l = k-1$. Tables 3 and 4 contain the coefficients of D and H in V_{lSk} up to $k = 10$.

The formula for the coefficient of H is cumbersome, but we need only use it to calculate the nine results for $l = 1, 2, 3$ and $k-l = 1, 2, 3$.

Denote the coefficient of $2^{-2k+1} H$ in V_{lsk} by $h(l, k)$. These are the figures in the main body of table 4 (but multiplied by 2 in the leading diagonal). Then

$$h(l, k+3) = 2h(l, k+2) + 2h(l, k+1) - h(l, k)$$

and

$$h(l+3, k+3) = 3h(l+2, k+2) + 2h(l+1, k+1) - 4h(l, k).$$

These enable the remainder of the table to be constructed by extension along the rows and diagonals. As examples of the use of the tables we note that

$$V_{2S4} = \frac{1}{8}D + \frac{5}{128}H \quad (\text{directly from tables 3 and 4})$$

and

$$V_{4S11} = \frac{3}{32}D + \frac{6411}{2097152}H \quad (\text{by extension from table 4 since } 6411 = 2 \times 2450 + 2 \times 935 - 359 \text{ and } 2097152 = 4 \times 524288).$$

For several genes segregating independently, D and H become Σd^2 and Σh^2 . With linkage the forms of D and H change from

TABLE 3

$l \backslash k$	2	3	4	5	6	7	8	9	10	divisors
1	2	1	1	1	1	1	1	1	1	4
2		2	1	1	1	1	1	1	1	8
3			4	2	2	2	2	2	2	16
4				6	3	3	3	3	3	32
5					10	5	5	5	5	64
6						16	8	8	8	128
7							26	13	13	256
8								42	21	512
9									68	1024

TABLE 4

$l \backslash k$	2	3	4	5	6	7	8	9	10
1	2	2	3	9	22	59	153	402	1051
2		6	5	12	31	81	212	555	1453
3			22	19	42	111	287	754	1971
4				70	59	138	359	935	2450
5					230	195	450	1175	3055
6						742	627	1458	3799
7							2406	2035	4722
8								7782	6579
9									25190
divisors	8	32	128	512	2048	8192	32768	131072	524288

generation to generation, but in all cases the coefficients of D and H in V_{lSk} remain unaltered.

It should be noted that a law of conservation of heritable variation holds (Mather, 1949*b*). The grand mean of S_k is $2^{-k+1}f(k)h$. The square of the coefficient of h plus the sum of the coefficients of D and H , for given k , is always unity.

3. COVARIANCES

Let $W_{lS(k-1)k}$ be the covariance between $(k-l)$ -group means in S_k and S_{k-1} . Instead of using the squares of terms in table 2 with the frequencies of table 1 we construct an auxiliary table from table 2 by replacing k by $k-1$ and then use the products of corresponding terms from table 2 and the auxiliary table with the frequencies of table 1. Hence

$$\begin{aligned} W_{lS(k-1)k} = & 2^{-l-1}f(l)D + 2^{-2k+2}\{2(-)^{k-l-1} \\ & + 2^{l-1}(-)^{k-l}(f(l-1)-3f(l-2)) \\ & + 2^{l-1}(27f(k-l-3)-4f(2k-l-2)) \\ & - f(2k-2l-4)-8f(2k-2l-3) \\ & + (-2)^{l-1}(f(2k-3l-6)+8f(2k-3l-5))\}H/25. \end{aligned}$$

The coefficients of D are independent of k and are the same as for V_{lSk} . Table 5 contains the coefficients of H . Once the first nine terms have been evaluated the table may be extended using the same relations as for the variance table. Since $k-l > 1$ a correction like that in the previous section is not needed.

Examples $W_{lS23} = \frac{1}{4}D$ (Tables 3 and 5.)

$$W_{4S67} = \frac{3}{32}D + \frac{81}{4096}H \quad (\text{Tables 3 and 5.})$$

Covariances between means m generations apart may be denoted by $W_{lS(k-m)k}$. The coefficients of D are the same as before, and

TABLE 5

$l \backslash k$	3	4	5	6	7	8	9	10
1	0	2	5	14	36	95	248	650
2		2	7	19	50	131	343	898
3			6	25	67	178	465	1219
4				22	81	219	578	1513
5					70	265	715	1890
6						230	857	2315
7							742	2777
8								2406
divisors	16	64	256	1024	4096	16384	65536	262144

the coefficients of H may be obtained simply from tables 4 and 5 as follows. Let $h(l, k, m)$ be the coefficient of $2^{-2k+m+1}H$ in $W_{IS(k-m)k}$. Then $h(l, k, m+2) = -h(l, k, m+1) + h(l, k, m)$. This means for example that the main body of the $W_{IS(k-2)k}$ table is the difference of the main bodies of tables 4 and 5, and the divisors in the $W_{IS(k-2)k}$ table are half those in table 5.

Examples $V_{3S7} = \frac{2}{16}D + \frac{111}{8192}H$ (Tables 3 and 4.)

$$W_{3S87} = \frac{2}{16}D + \frac{67}{4096}H \quad (\text{Tables 3 and 5.})$$

$$W_{3S57} = \frac{2}{16}D + \frac{44}{2048}H \quad (\text{since } 44 = 111 - 67).$$

$$W_{3S47} = \frac{2}{16}D + \frac{23}{1024}H \quad (\text{since } 23 = 67 - 44).$$

4. SUMMARY

The coefficients of D and H in the different measures of continuous variation are obtained for the generations of a population started by a cross between true breeding lines and maintained by continued sib-mating. The coefficients are set out for generations up to S_{10} in tables, 3, 4 and 5.

5. REFERENCES

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