

129. *Probability-theoretic Investigations on Inheritance.*IV<sub>2</sub>. *Mother-Child Combinations.*

(Continuation.)

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2. *Mixed mother-child combination.*

We have considered in the previous section a unique population in which an inherited character is distributed in an equilibrium state. In the present section we shall consider two populations  $X$  and  $X'$  each of which has an equilibrium distribution with respect to the inherited character. Every mating between  $X$  and  $X'$  will produce a half-breed. Thus, a problem arises, to determine the corresponding probabilities of mother-child combinations for such a cross-breeding case.

Let now the distributions of genes in  $X$  and  $X'$  be denoted by  $\{p_i\}$  and  $\{p'_i\}$ , respectively. To fix an idea, we suppose that in any mating its mother and father are chosen from  $X$  and  $X'$ , respectively. Then, the table, corresponding to that for pure breeding given in §3 of I, becomes as follows in the next page, the convention that the suffices  $i, j, h, k$  are different each other is here also made.

In the present case, the order of members in each mating must be taken into account. Accordingly, except  $\frac{1}{2}m(m+1)$  kinds of matings between the coinciding types, each of remaining matings in the previous table must be divided into two. Thus, the total number of combinations is, as inserted in the table, equal to

$$(2.1) \quad 2 \frac{1}{8}m(m+1)(m^2 + m + 2) - \frac{1}{2}m(m+1) = \frac{1}{4}m^2(m+1)^2;$$

this number is nothing but the square of that of possible genotypes of the inherited character under consideration.

We now denote by  $\pi'(A_{ij}; A_{hk})$  or briefly by

$$(2.2) \quad \pi'(ij; hk) \quad (i, j, h, k = 1, \dots, m)$$

the probability of appearing of a combination of a mother  $A_{ij}$  with her child  $A_{hk}$ . Again  $\pi'(ij; hk)$  is equal to zero provided (1.2) holds. The symmetry relations corresponding to (1.3) remain here also valid; namely,

$$(2.3) \quad \pi'(ij; hk) = \pi'(ji; hk) = \pi'(ij; kh) = \pi'(ji; kh)$$

Mating		Number of mating	Probability of mating	Probability of producing each type of child									
Mother	Father			$A_{ii}$	$A_{ij}$	$A_{ih}$	$A_{ik}$	$A_{jj}$	$A_{jh}$	$A_{jk}$			
$A_{ii}$	$A_{ii}$	$m$	$p_i^2 p_i'^2$	—	—	—	—	—	—	—	—	—	—
$A_{ii}$	$A_{ik}$	$m(m-1)$	$2p_i^2 p_i' p_k'$	—	—	—	$p_i^2 p_i' p_k'$	—	—	—	—	—	—
$A_{ik}$	$A_{ii}$	$m(m-1)$	$2p_i p_i p_k'^2$	—	—	—	$p_i p_i p_k'^2$	—	—	—	—	—	—
$A_{ii}$	$A_{hh}$	$m(m-1)$	$p_i^2 p_h'^2$	—	$p_i^2 p_h'^2$	—	—	—	—	—	—	—	—
$A_{ii}$	$A_{hk}$	$\frac{1}{2}m(m-1)(m-2)$	$2p_i^2 p_h' p_k'$	—	$p_i^2 p_h' p_k'$	—	$p_i^2 p_h' p_k'$	—	—	—	—	—	—
$A_{hk}$	$A_{ii}$	$\frac{1}{2}m(m-1)(m-2)$	$2p_i p_i p_k'^2$	—	$p_i p_i p_k'^2$	—	$p_i p_i p_k'^2$	—	—	—	—	—	—
$A_{ij}$	$A_{ij}$	$\frac{1}{2}m(m-1)$	$4p_i p_i p_i' p_j'$	$2p_i p_i p_i' p_j'$	—	—	—	$2p_i p_i p_i' p_j'$	—	$p_i p_i p_i' p_j'$	—	—	—
$A_{ik}$	$A_{ij}$	$m(m-1)(m-2)$	$4p_i p_i p_i' p_k'$	$p_i p_i p_i' p_k'$	—	—	$p_i p_i p_i' p_k'$	—	—	—	$p_i p_i p_i' p_k'$	—	$p_i p_i p_i' p_k'$
$A_{ij}$	$A_{hk}$	$\frac{1}{4}m(m-1)(m-2)(m-3)$	$4p_i p_i p_h' p_k'$	—	$p_i p_i p_h' p_k'$	—	$p_i p_i p_h' p_k'$	—	—	—	$p_i p_i p_h' p_k'$	—	$p_i p_i p_h' p_k'$
		$\frac{1}{4}m^2(m+1)^2$	1										

for any quadruple  $i, j, h, k$ . Therefore, we now again make a similar *agreement* as before, that the sum of quantities, identical based on (2.3), will anew be represented by any one of them. Hence, as before, it suffices essentially to introduce the notations such as

$$\pi'(ij; hk) \quad (i, j, h, k = 1, \dots, m; i \leq j; h \leq k),$$

whose total number is again equal to (1.4). Since, among them the quantities, being existent (1.5) in number, also vanish always, the number of remaining non-vanishing quantities is again equal to (1.6). But, in the present case,  $\pi'(ij; hk)$  and  $\pi'(hk; ij)$  will differ in general, and hence the reduction of (1.6) to (1.7) may not immediately be performed. It will, however, be seen later in (2.17) that, in spite of such asymmetry, a modified reduction will be possible.

The arguments for calculating each of the probabilities (2.2) is quite similar to that performed for the previous case treated in §1. Following the previous processes, we obtain the corresponding results in order. Thus, we get

$$(2.4) \quad \pi'(ii; ii) = p_i^2 p_i'^2 + p_i^2 p_i' \sum_{k \neq i} p_k' = p_i^2 p_i';$$

$$(2.5) \quad \pi'(ii; ij) = p_i^2 p_j' p_j' + p_i^2 p_j' \sum_{h \neq i} p_h' = p_i^2 p_j' \quad (j \neq i);$$

$$(2.6) \quad \pi'(ii; hk) = 0 \quad (h, k \neq i);$$

$$(2.7) \quad \pi'(ij; ii) = p_i p_j p_j'^2 + p_i p_j p_i' p_j' + p_i p_j p_i' \sum_{k \neq i, j} p_k' = p_i p_j p_i';$$

$$(2.8) \quad \pi'(ij; jj) = p_i p_j p_j';$$

$$(2.9) \quad \pi'(ij; ij) = 2p_i p_j p_i' p_j' + p_i p_j p_j' \sum_{k \neq j} p_k' + p_i p_j p_i' \sum_{h \neq i} p_h' = p_i p_j (p_i' + p_j') \quad (i \neq j);$$

$$(2.10) \quad \pi'(ij; ik) = p_i p_j p_k' \sum_h p_h' = p_i p_j p_k' \quad (k \neq i, j);$$

$$(2.11) \quad \pi'(ij; hj) = p_i p_j p_k' \quad (h \neq i, j);$$

$$(2.12) \quad \pi'(ij; hk) = 0 \quad (h, k \neq i, j).$$

The results are put together in the following table, asterisk notation having the same meaning as in the previous table of §1.

Type of mother	Frequency of each type of mother	Frequency of each type of child		
		$A_{ii}^*$	$A_{ij}^*$ ( $j \neq i$ ) <sup>*</sup>	$A_{hk}^*$ ( $h, k \neq i$ )
$A_{ii}$	$p_i^2$	$p_i^2 p_i'^*$	$p_i^2 p_j'$	0

Type of mother	Frequency of each type of mother	Frequency of each type of child					
		$A_{ii}^*$	$A_{jj}^*$	$A_{ij}$	$A_{ik}^*$ ( $k \neq i, j$ )	$A_{hj}^*$ ( $h \neq i, j$ ) <sup>*</sup>	$A_{hk}^*$ ( $h, k \neq i, j$ )
$A_{ij}$ ( $i \neq j$ )	$2p_i p_j$	$p_i p_j p_i'$	$p_i p_j p_j'^*$	$p_i p_j (p_i' + p_j')$	$p_i p_j p_k'$	$p_i p_j p_h'^*$	0

Here also hold the identical relations

$$\begin{aligned}
 & \pi'(i\bar{i}; i\bar{i}) + \sum_{j \neq i} \pi'(i\bar{i}; i\bar{j}) = p_i^2 p_j' + p_i^2 \sum_{j \neq i} p_j' = p_i^2, \\
 (2.13) \quad & \pi'(i\bar{j}; i\bar{i}) + \pi'(i\bar{j}; j\bar{j}) + \pi'(i\bar{j}; i\bar{j}) + \sum_{k \neq i, j} \pi'(i\bar{j}; i\bar{k}) + \sum_{h \neq i, j} \pi'(i\bar{j}; h\bar{j}) \\
 & = p_i p_j p_i' + p_i p_j p_j' + p_i p_j (p_i' + p_j') + p_i p_j \sum_{k \neq i, j} p_k' + p_i p_j \sum_{h \neq i, j} p_h' = 2p_i p_j (i \neq j).
 \end{aligned}$$

Now, the above result shows that the quantity

$$(2.14) \quad \pi'(i\bar{j}; h\bar{k}) / p_i p_j$$

is linear and homogeneous with respect to  $p_h'$  and  $p_k'$  whose coefficients are either 1 or 0. Moreover, comparing the above table with the previous one, we see that the quantity (2.14) has the same value as what is obtained from  $\pi(i\bar{j}; h\bar{k}) / p_i p_j$  by substituting  $p_h', p_k'$  instead of  $p_h, p_k$  respectively; namely, the relations

$$(2.15) \quad \pi'(i\bar{j}; h\bar{k}) / p_i p_j = [\pi(i\bar{j}; h\bar{k}) / p_i p_j]^{(p_h, p_j, p_h, p_k) - (p_h', p_j', p_h', p_k')}$$

hold identically, whence it follows

$$(2.16) \quad \pi'(i\bar{j}; h\bar{k}) \frac{p_i' p_j'}{p_i p_j} = [\pi(i\bar{j}; h\bar{k})]^{(p_h, p_j, p_h, p_k) - (p_i', p_j', p_h', p_k')}$$

Remembering the pure-symmetry relation (1.21) on the quantities  $\pi$ 's, we thus conclude that a quasi-symmetry relation

$$(2.17) \quad \pi'(i\bar{j}; h\bar{k}) \frac{p_i' p_j'}{p_i p_j} = \pi'(h\bar{k}; i\bar{j}) \frac{p_h' p_k'}{p_h p_k}$$

is valid identically for every quadruple  $i, j, h, k$ .

Based upon this quasi-symmetry relation, we immediately obtain the value of  $\pi'(h\bar{k}; i\bar{j})$  provided that of  $\pi'(i\bar{j}; h\bar{k})$  is known. Hence, also in this case, if we know the non-vanishing quantities, being existent (1.7) in number, which lie on and at one side of the principal diagonal, then we can calculate those at another side of it being existent  $\frac{1}{2} m^2(m-1)$  in number, and hence build up the whole table of mixed mother-child combination.

Now, the result on mixed mother-child combination may be regarded as a generalization of that on pure one. In fact, the latter is a special case of the former where the distribution  $\{p_i'\}$  coincides with  $\{p_i\}$ . But, conversely, as seen from the relations (2.16), the former is quite easily obtainable, as soon as the latter is known.

The passage from genotypes to phenotypes can be done in quite a similar manner as in §1. Indeed, under the same assumption as that on (1.22) and (1.23), the probability corresponding to (1.25) is given by

$$(2.18) \quad II'(i; j) \equiv II'(A_i; A_j) = \sum_{\alpha=1}^a \sum_{\beta=1}^b \pi'(i_\alpha i_\alpha; j_\beta j_\beta).$$

Finally, corresponding to (1.28), the ratio defined by

$$(2.19) \quad \frac{\pi'(ij; hk)}{A_{hk}} = \begin{cases} \pi'(ij; hh) / p_h p'_h & (k = h), \\ \pi'(ij; hk) / 2(p_h p'_k + p_k p'_h) & (k \neq h). \end{cases}$$

represents the probability a posteriori of the event that, for a fixed type  $A_{hk}$  of a child, its mother is of the type  $A_{ij}$ ; here the value of  $A_{hk}$  being determined according to the general formula on mixed distribution, already stated in (1.7) of III. The result on phenotypes, corresponding to (2.19), is also obtained; namely, the ratio defined by

$$(2.20) \quad \frac{II'(i; j)}{A_j} = II'(i; j) / \left( p_{j_1} p'_{j_1} + \sum_{\beta=2}^b (p_{j_\beta} p'_{j_\beta} + p_{j_\beta} p'_{j_1}) \right)$$

represents the probability a posteriori of the event that, for a fixed type  $A_j \equiv A_{j_1}$  of a child, its mother is of the type  $A_i \equiv A_{i_1}$ .

—To be continued—