

131. *Probability-theoretic Investigations on Inheritance.*

IV₄. *Mother-Child Combinations.*

(Further Continuation.)

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4. *Mother-children combination concerning families with several children.*

We have discussed, in the preceding section, the probabilities of mother-children combinations concerning families with two children. The results can be further generalized to several children case. We now consider the set of a mother and her n children produced from a common father, n being arbitrary but fixed.

Consider again an inherited character consisting of m genes A_i ($i = 1, \dots, m$) with distribution-probability $\{p_i\}$, the distribution being here also supposed to be in an equilibrium state. In general, the number of permutations, admitting the repetition, of selecting any n types of children without kinship is equal to

$$(4.1) \quad 2^{-n} m^n (m+1)^n.$$

But, if the children are restricted such that they have a common mother, then the corresponding number becomes

$$(4.2) \quad m^n \quad \text{or} \quad (2m-1)^n$$

according to the mother of a homozygote or of a heterozygote, respectively. If they are further restricted such as to have a father also in common, then number of possible permutations reduces to a very small one. In fact, corresponding to that in §3 of IV, we get the following table.

| Mating | $A_{ii} \times A_{ii}$ | $A_{ii} \times A_{ik}$ | $A_{ii} \times A_{ih}$ | $A_{ii} \times A_{hk}$ | $A_{ij} \times A_{ij}$ | $A_{ij} \times A_{ik}$ | $A_{ij} \times A_{hk}$ |
|-------------|------------------------|------------------------|------------------------|------------------------|------------------------|------------------------|------------------------|
| Permutation | 1 | 2^n | 1 | 2^n | 3^n | 4^n | 4^n |

Making use of a table on one-child case written in §3 of IV, we can easily construct the corresponding table on n -children case.

We denote by $\pi(A_{ij}; A_{h_1 k_1}, \dots, A_{h_n k_n})$ or briefly by

$$(4.3) \quad \pi(ij; h_1 k_1, \dots, h_n k_n) \quad (i, j, h_\nu, k_\nu = 1, \dots, m; \nu = 1, \dots, n)$$

the probability of appearing of a combination of a mother A_{ij} and her n children among which ν th child is of type $A_{h_\nu k_\nu}$ for $\nu = 1, \dots, n$. This quantity is, as before, equal to zero provided either of n relations holds :

$$(4.4) \quad (i-h_\nu)(i-k_\nu)(j-h_\nu)(j-k_\nu) \neq 0 \quad (\nu = 1, \dots, n).$$

In general, the different types of children belonging to the same family are at most 4; moreover, if the mother is of a homozygote, they reduce to at most two. Symmetry relations

$$(4.5) \quad \begin{aligned} \pi(ij; \dots, h_\nu k_\nu, \dots) &= \pi(ji; \dots, h_\nu k_\nu, \dots) = \pi(\hat{i}j; \dots, k_\nu h_\nu, \dots) \\ &= \pi(j\hat{i}; \dots, k_\nu h_\nu, \dots) \end{aligned} \quad (\nu=1, \dots, n)$$

result immediately from the definition. Thus, we can make again an *agreement* corresponding to that immediately subsequent to (3.3) of IV. Symmetry relations

$$(4.6) \quad \pi(ij; \dots, h_\mu^{\hat{\mu}} k_\mu, \dots, h_\nu^{\hat{\nu}} k_\nu, \dots) = \pi(ij; \dots, h_\nu^{\hat{\nu}} k_\nu, \dots, h_\mu^{\hat{\mu}} k_\mu, \dots) \\ (\mu, \nu = 1, \dots, n)$$

corresponding to (3.4) of IV, are also obvious.

Now, a mother of homozygote A_{ii} can produce children of at most two types among m possible types containing the gene A_i . There are m cases where n children are together of the same type. All the cases where $n-\nu$ ($0 < \nu < n$) children are of the same type each other and the remaining ν are of the same type each other but different from the former $n-\nu$, amount to

$$\binom{m}{2} \binom{n}{\nu} = \frac{m(m-1)}{2} \frac{n!}{\nu! (n-\nu)!}.$$

On the other hand, there exist m possible types of mother with homozygote. Hence, the whole number of non-vanishing combination-probabilities, containing homozygotic mothers, is equal to

$$(4.7) \quad m \left(m + \binom{m}{2} \sum_{\nu=1}^{n-1} \binom{n}{\nu} \right) = m^2(1 + (2^{n-1} - 1)(m-1)).$$

Next, a mother of heterozygote A_{ij} ($i \neq j$) can produce children of at most four types among $2m-1$ possible types containing at least one of A_i and A_j . There are $2m-1$ cases where n children are together of the same type. The cases where $n-\nu$ ($0 < \nu < n$) are of the same type each other and the remaining ν are of the same type each other but different from the former $n-\nu$, amount to

$$\binom{2m-1}{2} \frac{n!}{\nu! (n-\nu)!}.$$

The cases where n children are divided into three classes of different types consisting of $n-\mu-\nu$, μ , ν ($0 < \mu, \nu; \mu+\nu < n$) children amount to

$$\binom{2m-1}{3} \frac{n!}{\mu! \nu! (n-\mu-\nu)!}$$

and those where n children are divided into four classes of different types consisting of $n-\lambda-\mu-\nu$, λ , μ , ν ($0 < \lambda, \mu, \nu; \lambda+\mu+\nu < n$) children, to

$$\binom{2m-1}{4} \frac{n!}{\lambda! \mu! \nu! (n-\lambda-\mu-\nu)!}$$

In view of the identities

$$\sum_{\substack{0 \leq \mu, \nu \\ \mu + \nu < n}} \frac{n!}{\mu! \nu! (n-\mu-\nu)!} = \sum_{\substack{0 \leq \mu, \nu \\ \mu + \nu \leq n}} \frac{n!}{\mu! \nu! (n-\mu-\nu)!} - \sum_{\nu=0}^n \frac{n!}{\nu! (n-\nu)!} - 2 \sum_{\nu=1}^{n-1} \frac{n!}{\nu! (n-\nu)!} - 1$$

$$= (1+1+1)^n - (1+1)^n - 2(2^n - 2) - 1 = 3(3^{n-1} - 2^n + 1)$$

and

$$\sum_{\substack{0 \leq \lambda, \mu, \nu \\ \lambda + \mu + \nu < n}} \frac{n!}{\lambda! \mu! \nu! (n-\lambda-\mu-\nu)!} = \sum_{\substack{0 \leq \lambda, \mu, \nu \\ \lambda + \mu + \nu \leq n}} \frac{n!}{\lambda! \mu! \nu! (n-\lambda-\mu-\nu)!} - \sum_{\substack{0 \leq \mu, \nu \\ \mu + \nu \leq n}} \frac{n!}{\mu! \nu! (n-\mu-\nu)!}$$

$$- 3 \sum_{\substack{0 \leq \mu, \nu \\ \mu + \nu < n}} \frac{n!}{\mu! \nu! (n-\mu-\nu)!} - 3 \sum_{\nu=1}^{n-1} \frac{n!}{\nu! (n-\nu)!} - 1$$

$$= (1+1+1+1)^n - (1+1+1)^n - 3 \times 3(3^{n-1} - 2^n + 1) - 3 \times 2(2^{n-1} - 1) - 1 = 4(4^{n-1} - 3^n + 3 \cdot 2^{n-1} - 1),$$

we see that the number of non-vanishing combination-probabilities, containing heterozygotic mothers, is equal to

$$(4.8) \quad \binom{m}{2} \left(2m-1 + \binom{2m-1}{2} \sum_{\nu=1}^{n-1} \frac{n!}{\nu! (n-\nu)!} + \binom{2m-1}{3} \sum_{\substack{0 \leq \mu, \nu \\ \mu + \nu < n}} \frac{n!}{\mu! \nu! (n-\mu-\nu)!} \right.$$

$$\left. + \binom{2m-1}{4} \sum_{\substack{0 \leq \lambda, \mu, \nu \\ \lambda + \mu + \nu < n}} \frac{n!}{\lambda! \mu! \nu! (n-\lambda-\mu-\nu)!} \right) = \frac{1}{6} m(m-1)(2m-1)$$

$$\times (3 + 6(2^{n-1} - 1)(m-1) + 3(3^{n-1} - 2^n + 1)(m-1)(2m-3)$$

$$+ 2(4^{n-1} - 3^n + 3 \cdot 2^{n-1} - 1)(m-1)(2m-3)(m-2)).$$

Thus, the total number of non-vanishing combination-probabilities reduces to the sum of (4.7) and (4.8), namely

$$(4.9) \quad m^2(2^{n-1}(m-1) - (m-2)) + \frac{1}{6}m(m-1)(2m-1)(2 \cdot 4^{n-1}(m-1)$$

$$\times (2m-3)(m-2) - 3^n(m-1)(2m-3)(2m-5) + 3 \cdot 2^n(m-1)$$

$$\times (m-2)(2m-5) - (m-2)(2m-3)(2m-5)).$$

The result for $n = 2$ is a special case contained in (4.9).

If we remember the symmetry relations (4.6), the number of non-vanishing combination-probabilities essentially different each other will be extremely less than (4.9). Indeed, in the case of homozygotic mothers, such a number is at most

$$(4.10) \quad m \left(m + \binom{m}{2} \right) = \frac{1}{2}m^2(m+1).$$

In case of heterozygotic mothers, three cases are distinguished according to $n = 2, n = 3, n \geq 4$, and such a number is at most

$$\binom{m}{2} \left(2m-1 + \binom{2m-1}{2} \right) = \frac{1}{2}m^2(m-1)(2m-1) \quad (n = 2),$$

$$\binom{m}{2} \left(2m-1 + \binom{2m-1}{2} + \binom{2m-1}{3} \right)$$

$$(4.11) \quad = \frac{1}{6}m(m-1)(2m-1)(2m^2 - 2m + 3) \quad (n = 3),$$

$$\begin{aligned} & \binom{m}{2} \left(2m-1 + \binom{2m-1}{2} + \binom{2m-1}{3} + \binom{2m-1}{4} \right) \\ &= \frac{1}{12} m^2 (m-1) (2m-1) (2m^2 - 5m + 9) \quad (n \geq 4). \end{aligned}$$

Hence, the total number of non-vanishing combination-probabilities essentially different each other is, as the sum of (4.10) and (4.11), given by

$$\begin{aligned} & m^2(m^2 - m + 1) && (n = 2), \\ (4.12) \quad & \frac{1}{2} m^2(m+1) + \frac{1}{6} m(m-1)(2m-1)(2m^2 - 2m + 3) && (n = 3), \\ & \frac{1}{2} m^2(m+1) + \frac{1}{12} m^2(m-1)(2m-1)(2m^2 - 5m + 9) && (n \geq 4). \end{aligned}$$

The result for $n = 2$ contained in (4.12) is nothing but the one already stated. It may be especially noticed that the number is independent of n provided $n \geq 4$. For instance, if m is equal to 2, 3, 4 or 10, then the numbers in (4.12) become 13, 93, 418 or 52705 for $n = 3$, and 13, 108, 628 or 227125 for $n \geq 4$, respectively.

We now enter into our main discourse. The order of n children being indifferent, as remarked in (4.6), we denote briefly by

$$(4.13) \quad \pi(ij; h_1 k_1^{n_1}, h_2 k_2^{n_2}, \dots, h_\alpha k_\alpha^{n_\alpha}) \quad \left(\sum_{v=1}^{\alpha} n_v = n \right)$$

the probability of the combination composed of a mother of A_{ij} and the 1st to n_1 th children of $A_{h_1 k_1}$, the (n_1+1) th to (n_1+n_2) th children of $A_{h_2 k_2}$, ..., the $(n_1+\dots+n_{\alpha-1}+1)$ th to $(n_1+\dots+n_{\alpha-1}+n_\alpha) = n$ th children of $A_{h_\alpha k_\alpha}$, where α is a number such as $1 \leq \alpha \leq 4$. By permutating the order of children, there will appear $n! / \prod_{v=1}^{\alpha} n_v!$ probabilities which have the same value.

We first consider a mother of homozygote A_{ii} . Possible type of a father who can produce a child A_{ii} with this mother are A_{ii} , A_{ih} ($h \neq i$). If the type of father is A_{ii} , then that of a child is always A_{ii} , while if the type of father is A_{ih} , then a child A_{ii} is produced in probability $1/2$. Thus we get, as in (3.10) of IV,

$$(4.14) \quad \pi(ii; ii^n) = 1p_i^i + 2^{-n} 2p_i^2 \sum_{h \neq i} p_h = 2^{-n+1} p_i^2 (1 + (2^{n-1} - 1)p_i).$$

The type of a father who can produce at least two children A_{ii} and A_{ih} ($h \neq i$) with a mother A_{ii} must be A_{ih} , whence it follows

$$(4.15) \quad \pi(ii; ii^{n-\nu}, ih^\nu) = 2^{-n} 2p_i^2 p_h = 2^{-n+1} p_i^2 p_h \quad (h \neq i; 0 < \nu < n).$$

Possible types of a father who can produce a child A_{ih} ($h \neq i$) are A_{ih} , A_{hh} and A_{hk} ($k \neq i, h$), and hence we get

$$\begin{aligned} (4.16) \quad & \pi(ii; ih^n) = 2^{-n} 2p_i^2 p_h + 1p_i^2 p_h^2 + 2^{-n} 2p_i^2 p_h \sum_{k \neq i, h} p_k \\ &= 2^{-n+1} p_i^2 p_h (1 + (2^{n-1} - 1)p_h) \quad (h \neq i). \end{aligned}$$

Since the only possible type of a father who can produce at least two children A_{ih} ($h \neq i$) and A_{ik} ($k \neq i, h$) is A_{hk} , we obtain

$$(4.17) \quad \pi(ii; ih^{n-\nu}, ik^\nu) = 2^{-n} 2p_i^2 p_h p_k = 2^{-n+1} p_i^2 p_h p_k \\ (h, k \neq i; h \neq k; 0 < \nu < n).$$

The last result remains valid, as seen from (4.15), if only one of h or k coincides with i . Thus, the case of a homozygotic mother has been worked out essentially.

We next consider a mother of heterozygote A_{ij} ($i \neq j$). In case where n children are together of the same homozygote, we get

$$(4.18) \quad \pi(ij; ii^n) = 2^{-n} 2p_i^2 p_j + 4^{-n} 4p_i^2 p_j^2 + 4^{-n} 4p_i^2 p_j \sum_{h \neq i, j} p_h \\ = 4^{-n+1} p_i^2 p_j (1 + (2^{n-1} - 1)p_i),$$

$$(4.19) \quad \pi(ij; jj^n) = 4^{-n+1} p_i p_j^2 (1 + (2^{n-1} - 1)p_j).$$

In case where n children are together of the same heterozygote, we get

$$(4.20) \quad \pi(ij; ij^n) = 2^{-n} 2p_i^2 p_j + 2^{-n} 2p_i p_j^2 + 2^{-n} 4p_i^2 p_j^2 + 4^{-n} 4p_i^2 p_j \sum_{h \neq i, j} p_h \\ + 4^{-n} 4p_i p_j^2 \sum_{h \neq i, j} p_h = 4^{-n+1} p_i p_j (p_i + p_j) (1 + (2^{n-1} - 1)(p_i + p_j)),$$

$$(4.21) \quad \pi(ij; ih^n) = 4^{-n} 4p_i^2 p_j p_h + 4^{-n} 4p_i p_j^2 p_h + 2^{-n} p_i p_j p_h^2 \\ + 4^{-n} 4p_i p_j p_h \sum_{k \neq i, j, h} p_k = 4^{-n+1} p_i p_j p_h (1 + (2^{n-1} - 1)p_h) \quad (h \neq i, j),$$

$$(4.22) \quad \pi(ij; jh^n) = 4^{-n+1} p_i p_j p_h (1 + (2^{n-1} - 1)p_h) \quad (h \neq i, j).$$

Only possible type of a father who can produce at least two children A_{ii} and A_{ij} is A_{ij} , whence it follows

$$(4.23) \quad \pi(ij; ii^{n-\nu}, jj^\nu) = 4^{-n} 4p_i^2 p_j^2 = 4^{-n+1} p_i^2 p_j^2 \quad (0 < \nu < n).$$

Possible types of a father who can produce at least two children A_{ii} and A_{ij} are A_{ii} , A_{ij} , A_{ih} ($h \neq i, j$), and hence we obtain

$$(4.24) \quad \pi(ij; ii^{n-\nu}, ij^\nu) = 2^{-n} 2p_i^2 p_j + 4^{-n+\nu} 2^{-\nu} 4p_i^2 p_j^2 + 4^{-n} 4p_i^2 p_j \sum_{h \neq i, j} p_h \\ = 4^{-n+1} p_i^2 p_j (1 + (2^{n-1} - 1)p_i + (2^\nu - 1)p_j) \quad (0 < \nu < n),$$

and similarly

$$(4.25) \quad \pi(ij; jj^{n-\nu}, ij^\nu) = 4^{-n+1} p_i p_j^2 (1 + (2^\nu - 1)p_i + (2^{n-1} - 1)p_j) \\ (0 < \nu < n).$$

The last two results remain valid, as seen from (4.18) and (4.19), also for $\nu = 0$.

In similar manners, we get in turn the following results:

$$(4.26) \quad \pi(ij; ih^n) = 4^{-n} 4p_i^2 p_j p_h + 4^{-n} 4p_i p_j^2 p_h + 2^{-n} 2p_i p_j p_h^2 \\ + 4^{-n} 4p_i p_j p_h \sum_{k \neq i, j, h} p_k = 4^{-n+1} p_i p_j p_h (1 + (2^{n-1} - 1)p_h) \quad (h \neq i, j; 0 < \nu < n),$$

$$(4.27) \quad \pi(ij; ii^{n-\mu-\nu}, ih^\mu, jh^\nu) = 4^{-n} 4p_i^2 p_j p_h = 4^{-n+1} p_i^2 p_j p_h \quad (h \neq i, j; 0 < \mu + \nu < n),$$

$$(4.28) \quad \pi(ij; jj^{n-\mu-\nu}, ih^\mu, jh^\nu) = 4^{-n+1} p_i p_j^2 p_h \quad (h \neq i, j; 0 < \mu + \nu < n),$$

$$(4.29) \quad \pi(ij; ij^{n-\mu-\nu}, ih^\mu, jh^\nu) = 4^{-n} 4p_i^2 p_j p_h + 4^{-n} 4p_i p_j^2 p_h \\ = 4^{-n+1} p_i p_j p_h (p_i + p_j) \quad (h \neq i, j; 0 < \mu + \nu < n),$$

$$(4.30) \quad \pi(ij; ii^{n-\mu-\nu}, jj^\mu, ij^\nu) = 4^{-n+\mu+\nu} 4^{-\mu} 2^{-\nu} 4p_i^2 p_j^2 = 2^{-2n+\nu+2} p_i^2 p_j^2 \\ (0 < \mu \leq \mu + \nu < n),$$

$$(4.31) \quad \pi(ij; ii^{n-\lambda-\mu-\nu}, ij^\lambda, ih^\mu, jh^\nu) = 4^{-n} 4 p_i^2 p_j p_h = 4^{-n+1} p_i^2 p_j p_h \\ (h \neq i, j; 0 < \mu + \nu \leq \lambda + \mu + \nu < n),$$

$$(4.32) \quad \pi(ij; jj^{n-\lambda-\mu-\nu}, ij^\lambda, ih^\mu, jh^\nu) = 4^{-n+1} p_i p_j^2 p_h \\ (h \neq i, j; 0 < \mu + \nu \leq \lambda + \mu + \nu < n),$$

$$(4.33) \quad \pi(ij; ih^{n-\lambda-\mu-\nu}, ik^\lambda, jh^\mu, jk^\nu) = 4^{-n} 4 p_i p_j p_h p_k = 4^{-n+1} p_i p_j p_h p_k \\ (h, k \neq i, j; h \neq k; 0 < \lambda + \nu < n).$$

Thus, the case of a heterozygotic mother has also been worked out essentially.

It will be noticed that, for instance, the result (4.23) is contained in (4.30), as a special case $\nu = 0$. Moreover, in (4.31) to (4.33) the case $0 < \lambda, \mu, \nu < n$ does not really appear for $n < 4$.

The passage to the corresponding results on phenotypes in which recessive genes are interested can be done by means of the usual procedure. Finally, we notice that the mixed mother-child combinations could also be discussed; the fundamental interrelations analogous to (3.29) of IV being then of importance.

— To be continued —