128. Probability-theoretic Investigations on Inheritance. IV₁. Mother-Child Combinations.[1]

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1. Mother-child combination.

If the types of an inherited character of both parents are known, the probability of each possible type of a child produced from the mating can immediately be obtained. In fact, in case of a character consisting of m genes A_i $(i = 1, \ldots, m)$ with respective distributions p_i, the table in § 3 of I serves this purpose; probability of producing each type, divided by the corresponding probability of mating, represents just the required probability. When phenotypes, instead of genotypes, are in question, it is only necessary to bring together the concerning probabilities.

Now, a question arises how becomes the probability of each possible type of a child produced from a mating, if we know the type of only one of its parents. Since, in general, any Mendelian dominant cannot appear in the type of a child unless presents in the type of at least one of its parents, it is possible to prove non-paternity in a certain proportion of the cases in which the putative father is not the true father; any inherited character may be and have practically been applied to such cases of bastardization from medico-legal standpoint. The treatment of the last problem, which will be discussed in a later chapter, is based upon probabilities of the so-called *mother-child combination*. From the probability-theoretic view-point, whether we say father-child combination or mother-child combination, it is a matter of indifference, while we now use the latter terminology customarily.

In a concrete case of ABO human blood type, the probabilities of mother-child combinations have already been derived by Schiff[2]. The classical result on mother-child combination due to Schiff is listed in the following table.

1) Y. Komatu, Probability-theoretic investigations on inheritance. I. Distribution of genes; II. Cross-breeding phenomena; III. Further discussions on cross-breeding. Proc. Japan Acad., **27** (1951), 371–377; 378–383, 384–487; 459–465,. 466–471, 472–477, 478–483. These papers will be referred to as I; II; III; respectively

2) Cf. F. Schiff, Technik der Blutgruppenuntersuchung. (Berlin, 1932), S. 8; A. S. Wiener, Blood groups and blood transfusion. 2nd ed. (Springfield and Baltimore, 1939), p. 133; etc.

Type of mother	Frequency of each type of mother	Frequency of each type of child			
		O	A	B	AB
O	r^2	r^3	pr^2	qr^2	0
A	$p(p+2r)$	pr^2	$p(p^2+3pr+r^2)$	pqr	$pq(p+r)$
B	$q(q+2r)$	qr^2	pqr	$q(q^2+3qr+r^2)$	$pq(q+r)$
AB	$2pq$	0	$pq(p+r)$	$pq(q+r)$	$pq(p+q)$
	1	r^2	$p(p+2r)$	$q(q+2r)$	$2pq$

It will be very remarkable in the table that there exists a symmetry with respect to the principal diagonal. Namely, the probability of any pair in the table is equal to that of the pair obtained by interchanging the mother and the child in the original pair.

The above table concerns phenotypes. Similar table on genotypes can rather previously be obtained. However, we shall proceed, more generally, to build up the corresponding table concerning the inherited character which consists, as before, of m genes A_i ($i = 1$, ..., m) with distribution-probability $\{p_i\}$; the distribution is here also supposed to be in an equilibrium state.

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

(1.1) $\qquad\qquad \pi(ij; hk) \qquad\qquad (i, j, h, k = 1,\ldots, m)$

the probability of appearing of a combination of a mother with A_{ij} and her child with A_{hk}. Based on a principle of Mendelian inheritance, $\pi(ij; hk)$ is equal to zero, provided

(1.2) $\qquad\qquad (i-h)(i-k)(j-h)(j-k) \neq 0$,

i.e., unless at least one of h and k coincides with i or j. Evidently, the quantity $\pi(ij; hk)$ is symmetric with respect to i and j and to h and k; namely, there exist identical relations

(1.3) $\qquad \pi(ij; hk) = \pi(ji; hk) = \pi(ij; kh) = \pi(ji; kh)$

for any i, j, h, k. Consequently, it is unnecessary to distinguish four quantities contained in (1.3) each other. We may regard that such notations represent the unique object, without causing any confusion. Hence, we now make an *agreement* that the sum of four quantities (1.3), eventually two or one if one or two homozygotes are related, will anew be represented by any one of them, unless the contrary is explicitly stated. Correspondingly, it would suffice essentially to introduce the notations such as

$\qquad\qquad \pi(ij; hk) \qquad\quad (i, j, h, k = 1,\ldots, m; i \leqq j; h \leqq k)$,

whose total number is evidently equal to

(1.4) $\qquad\qquad (\tfrac{1}{2}m(m+1))^2 = \tfrac{1}{4}m^2(m+1)^2$.

On the other hand, for each of m homozygotes A_{ij} ($i = j$) there

exist $m(m-1)/2$ possible pairs of h, k $(h \leq k)$ satisfying (1.2), and for each of $m(m-1)/2$ heterozygotes A_{ij} $(i < j)$ there exist $(m-2)(m-1)/2$ possible pairs of analogous h, k. Hence, among all the quantities, the quantities whose number is equal to

(1 5) $$m\tfrac{1}{2}(m-1)m + \tfrac{1}{2}m(m-1)\tfrac{1}{2}(m-2)(m-1)$$
$$= \tfrac{1}{4}m(m-1)(m^2-m+3) ,$$

vanish always in view of (1.2). There remain thus

(1.6) $\tfrac{1}{4}m^2(m+1)^2 - \tfrac{1}{4}m(m-1)(m^2-m+3) = \tfrac{1}{2}m(2m^2-m+1)$

quantities not identically vanishing. Moreover, as we shall see later in (1.21), that the quantities (1.1) possess a symmetry property with respect to pairs i, j and h, k, *the quantities $\pi(ij\,; hk)$ essentially distinct from each other and also from zero amount thus to*

(1.7) $\tfrac{1}{2}(\tfrac{1}{2}m(2m^2-m+1) + \tfrac{1}{2}m(m+1)) = \tfrac{1}{2}m(m^2+1)$.

In order to construct a table on mother-child combination, we first consider a mother with a homozygote A_{ii}. Possible type of a child produced from this mother is one of those m kinds containing the gene A_i at least one, namely A_{ii}, A_{ij} $(j \neq i)$. The genotypes of a father who can produce a child[3] A_{ii} with this mother must be one of those m kinds represented by A_{ii}, A_{ik} $(k \neq i)$. Probability of the event that the mating $A_{ii} \times A_{ii}$ or $A_{ik} \times A_{ii}$ occurs and then produces a child A_{ii} is equal to

(1.8) $\qquad p_i^4, \qquad p_i^3 p_k \quad (k \neq i)$

respectively. It will be noticed that, in the present case, the order of members in the mating $A_{ik} \times A_{ii}$ being taken into account, a half of the corresponding value $2\,p_i^3 p_k$ listed in the table in §3 of I must be used. Thus, summing up all the values in (1.8), we obtain

(1.9) $\qquad \pi(ii\,;\, ii) = p_i^4 + p_i^3 \sum_{k \neq i} p_k = p_i^4 + p_i^3 (1-p_i) = p_i^3$.

The genotype of a father who can produce a child A_{ij} $(j \neq i)$ with the mother A_{ii} must be one of those m kinds represented by A_{ij}, A_{hj} $(h \neq i)$. Probability of the event that the mating $A_{ij} \times A_{ii}$ or $A_{hj} \times A_{ii}$ $(h \neq i)$ occurs and then produces a child A_{ij} is equal to

(1.10) $\qquad p_i^3 p_j, \qquad p_i^2 p_h p_j \quad (h \neq i)$

respectively; the case $h = j$ being, of course, contained. Thus, similarly as before, by summing up all the values in (1.10),

(1.11) $$\pi(ii\,;\, ij) = p_i^3 p_j + p_i^2 p_j \sum_{h \neq i} p_h$$
$$= p_i^3 p_j + p_i^2 p_j (1-p_i) = p_i^2 p_j \quad (j \neq i) .$$

By comparing (1.11) with (1.9), we know that the result (1.11) remains valid even for $j = i$. As already noticed, we finally have

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3) An individual possessing a type A will, in the following lines, briefly be expressed as an individual A.

(1.12) $\pi(ii ; hk) = 0$ $(h, k \neq i)$.

We next consider a mother with a heterozygote $A_{ij} (i \neq j)$. Possible type of a child produced from this mother is one of those $2m-1$ kinds containing at least either of the gene A_i or A_j, namely

(1.13) A_{ii} , A_{jj} , A_{ij} , $A_{ik} (k \neq i, j)$, $A_{hj} (h \neq i, j)$.

The genotype of a father who can produce a child A_{ii} with the mother A_{ij} must be one of those m kinds containing the gene A_i at least one ; namely A_{ii} , A_{ij} , $A_{ik} (k \neq i, j)$. Hence, we get, as before,

(1.14) $\pi(ij ; ii) = p_i^3 p_j + p_i^2 p_j^2 + p_i^2 p_j \sum_{k \neq i, j} p_k = p_i^2 p_j$.

For A_{jj} in (1.13), we get, based upon an obvious symmetry property, immediately from (1.14),

(1.15) $\pi(ij ; jj) = p_i p_j^2$.

For A_{ij} in (1.13), possible matings being $2m-1$ kinds $A_{ij} \times A_{ij}$, $A_{ik} \times A_{ij} (k \neq j)$, $A_{hj} \times A_{ij} (h \neq i)$, we get

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

(1.16) $$= 2p_i^2 p_j^2 + p_i^2 p_j (1-p_j) + p_i p_j^2 (1-p_i)$$

$$= p_i p_j (p_i + p_j)   (i \neq j) .$$

For $A_{ik} (k \neq i, j)$, possible matings being m kinds $A_{hk} \times A_{ij}$, we obtain

(1.17) $\pi(ij ; ik) = p_i p_j p_k \sum_h p_h = p_i p_j p_k$ $(k \neq i, j ; i \neq j)$.

Finally, by making use of (1.3), we get further from (1.17)

(1.18) $\pi(ij ; hj) = p_i p_j p_h$ $(h \neq i, j ; i \neq j)$.

Evidently, we have

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

Thus, the above obtained results will be put together in the following table. As already noticed, instead of writing the probability $\pi(ii ; ii)$ separately from $\pi(ii ; ij)$ with $j \neq i$, the former may be written together within $\pi(ii ; ij)$ by taking away the restriction $j \neq i$. Since a child A_{jj}, combined with a mother A_{ij}, is characterized only by possessing just one gene A_j in common, this combination may, in view of symmetry relation (1.3), be represented by that of a child A_{ii} with a mother A_{ij}. Similary, $\pi(ij ; hj)$ may be represented by $\pi(ij ; ik)$. Further, $\pi(ij ; ii)$ may be represented by $\pi(ij ; ik)$ $(k \neq j)$. Based on such reasons, nothing is essentially lost, if the parts with asterisk would be all erased out.

Type of mother	Frequency of each type of mother	Frequency of each type of child		
		A_{ii}*	A_{ij} $(j \neq i)$*	A_{hk} $(h, k \neq i)$
A_{ii}	p_i^2	p_i^3*	$p_i^2 p_j$	0

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

For each type of mother, the total sum of the probabilities of combined children is. of course, equal to the frequency of the type of the mother ; namely,

$$\pi(ii\,;\,ii) + \sum_{j \neq i} \pi(ii\,;\,ij) = p_i^3 + p_i^2 \sum_{j \neq i} p_j = p_i^2 \,,$$

$$(1.20) \quad \pi(ij\,;\,ii) + \pi(ij\,;\,jj) + \pi(ij\,;\,ij) + \sum_{k \neq i, j} \pi(ij\,;\,ik) + \sum_{h \neq i, j} \pi(ij\,;\,hj)$$

$$= p_i^2 p_j + p_i p_j^2 + p_i p_j\,(p_i + p_j) + p_i p_j \sum_{k \neq i, j} p_k + p_i p_j \sum_{h \neq i, j} p_h = 2p_i p_j$$

$$(i \neq j)\,.$$

As shows the table, it is noteworthy that the symmetry, previously observed on the table for *ABO* blood type, is not accidental, but essential. Namely, the *symmetry relation*

$$(1.21) \qquad\qquad \pi(ij\,;\,hk) = \pi(hk\,;\,ij)$$

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

The above table concerns genotypes. The similar table concerning phenotypes will then easily be obtained according to respective inheritance law. If the gene A_i is dominant against none of the remaining genes, the phenotype A_i consisting of a unique genotype A_{ii}, it is only necessary to replace A_{ii} by A_i. If each of both genes A_i and A_j is dominant against none of the remaining genes, it suffices to replace A_{ii}, A_{ij}, A_{jj} by the corresponding phenotypes A_i, $A_i A_j$, A_j.

The cases where dominance relations are really existent come into question. If the gene $A_i \equiv A_{i_1}$ is dominant against and only against the genes A_{i_a} $(2 \leq a \leq \alpha)$, the phenotype A_i consists of α genotypes

$$(1.22 \qquad\qquad A_{i_1 i_a} \equiv A_{i_1} A_{i_a} \qquad (a = 1, \ldots, \alpha)\,,$$

and similarly, if the gene $A_j \equiv A_{j_1}$ is dominant against and only against the genes A_{j_b} $(2 \leq b \leq \beta)$, the phenotype A_j consists of β genotypes

$$(1.23) \qquad\qquad A_{j_1 j_b} \equiv A_{j_1} A_{j_b} \qquad (b = 1, \ldots, \beta)\,.$$

Consequently, the probability of combination between a mother with phenotype A_i and a child with phenotype A_j is then given by the sum of $\alpha\beta$ pairs composed of (1.22) and (1.23). Namely, denoting by $\mathit{\Pi}(A_i\,;\,A_j)$ or more briefly by

$$(1.24) \qquad\qquad \mathit{\Pi}(i\,;\,j)$$

the probability in consideration, we obtain

(1.25) $$\Pi(i ; j) = \sum_{a=1}^{\alpha} \sum_{b=1}^{\beta} \pi(i_1 i_a ; j_1 j_b) .$$

It is a matter of course that the symmetry relation (1.21) on genotypes is succeeded also by the corresponding one on phenotypes; namely, the symmetry relation is valid for every pair i, j.

In conclusion, it may be noticed that the probability of mother-child combination allows of an another interpretation. The quantity $\pi(ij ; hk)$, introduced in (1.1), being the probability of appearing of the combination of a mother A_{ij} and its child A_{hk}, the ratio defined by

(1.27) $$\frac{\pi(ij ; hk)}{\bar{A}_{ij}} = \begin{cases} \pi(ii ; hk)/p_i^2 & (j = i) , \\ \pi(ij ; hk)/2p_i p_j & (j \neq i) \end{cases}$$

represents the probability of a child A_{hk} produced from the fixed type A_{ij} of a mother. On the other hand, we now consider an analogous ratio defined by

(1.28) $$\frac{\pi(ij ; hk)}{\bar{A}_{hk}} = \begin{cases} \pi(ij ; hh)/p_h^2 & (k = h) , \\ \pi(ij ; hk)/2p_h p_k & (k \neq h) . \end{cases}$$

It will be regarded as *the probability of the event that, for the fixed type A_{hk} of a child, its mother is of the type A_{ij}.* Such an event belongs to a category of the concept of the so-called *probability of causes,* and the above stated fact may really be illustrated by means of the well-known *Bayes' theorem.*

In fact, we consider a fixed type A_{hk} of a child. The possible types of its mother are those possessing at least one of the genes common to the child. As probability a priori of the type A_{ij} of a mother, we may take its frequency A_{ij} in the general distribution. Since, in general, for a fixed type A_{ij} of a mother, a child A_{hk} is produced with a probability (1.27), the probability a posteriori of the event that, knowing the type A_{hk} of a child, its mother is of the type A_{ij}, is given by the Bayes' formula:

(1.29) $$\bar{A}_{ij} \frac{\pi(ij ; hk)}{\bar{A}_{ij}} \bigg/ \sum \bar{A}_{\xi\eta} \frac{\pi(\xi\eta ; hk)}{\bar{A}_{\xi\eta}} = \pi(ij ; hk)/\sum \pi(\xi\eta ; hk) ,$$

the smmation being extended over all possible pairs of (ξ, η), i.e., over pairs (ξ, η) with $\xi \leq \eta$ possessing at least one suffix common to h or k. But if there exists no common suffix between (ξ, η) and (h, k), then the quantity $\pi(\xi\eta ; hk)$ vanishes. Hence, the summation may extend over all possible pairs (ξ, η) with $\xi, \eta = 1, \ldots, m$; $\xi \leq \eta$, and thus the sum $\sum \pi(\xi\eta ; hk)$ is evidently equal to $\bar{A}_{hk}$. Consequently, we see that the ratio (1.28) represents just the probability a posteriori given in (1.29).

The same remains valid also on phenotypes.