

## 150. Probability-theoretic Investigations on Inheritance.

### V<sub>1</sub>. Brethren Combinations.

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#### 1. Brethren combination.

In order to discuss the problem presented at the end of the preceding chapter,<sup>1)</sup> we go back, in principle, more further and consider a combination of two children having a mother in common. We shall namely attempt to eliminate the dependence on mother's type from the probabilities, treated in § 5 of IV, depending on a type of mother. After elimination, the combination probabilities of her two children will be obtained under the assumption that they have generally a mother in common. According to § 3 and § 5 of IV, we distinguish two cases where a father is and is not common, respectively.

We begin with the problem in which a father is also common. We denote, in general, by

$$(1.1) \quad \sigma(hk, fg)$$

the probability of combination consisting of brethren with types  $A_{hk}$  and  $A_{fg}$ , the order being taken into account, who belong to the same family. From definition, we get immediately the relation

$$(1.2) \quad \sigma(hk, fg) = \sum_{i \leq j} \pi(ij; hk, fg).$$

The symmetry relation (3.8) of IV yields the corresponding one stating that

$$(1.3) \quad \sigma(hk, fg) = \sigma(fg, hk).$$

By means of the results in § 3 of IV, we can calculate the probabilities of brethren combinations, based on (1.2). Although, if we made use of  $\pi'$ 's contained in (3.24) of IV instead of  $\pi$ 's, we could calculate those for mixed case which would be denoted by

$$(1.4) \quad \sigma'(hk, fg),$$

we shall now, for the sake of brevity, restrict ourselves to the pure case (1.1).

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1) Y. Komatu, Probability-theoretic investigations on inheritance, I. Distribution of genes; II. Cross-breeding phenomena; III. Further discussions on cross-breeding; IV. Mother-child combinations. Proc. Japan Acad., **27** (1951), 371-377; 378-383, 384-387; 459-465, 466-471, 472-477, 478-483; 587-592, 593-597, 598-603, 605-610, 611-614, 615-620. These papers will be referred to as I; II; III; IV, respectively.

We first consider a first child of a homozygote  $A_{ii}$ . Then, its mother must have the gene  $A_i$  at least one, and hence

$$(1.5) \quad \begin{aligned} \sigma(ii, ii) &= \pi(ii; ii, ii) + \sum_{j \neq i} \pi(ij; ii, ii) \\ &= \frac{1}{2}p_i^3(1+p_i) + \sum_{j \neq i} \frac{1}{4}p_i^2p_j(1+p_i) = \frac{1}{4}p_i^2(1+p_i)^2, \end{aligned}$$

$$(1.6) \quad \begin{aligned} \sigma(ii, ij) &= \pi(ii; ii, ij) + \pi(ij; ii, ij) + \sum_{h \neq i, j} \pi(ih; ii, ij) \\ &= \frac{1}{2}p_i^3p_j + \frac{1}{4}p_i^2p_j(1+p_i+p_j) + \sum_{h \neq i, j} \frac{1}{4}p_i^2p_hp_j \\ &= \frac{1}{2}p_i^2p_j(1+p_i) \quad (j \neq i), \end{aligned}$$

$$(1.7) \quad \sigma(ii, jj) = \pi(ij; ii, jj) = \frac{1}{4}p_i^2p_j^2 \quad (j \neq i),$$

$$(1.8) \quad \begin{aligned} \sigma(ii, jh) &= \pi(ij; ii, jh) + \pi(ih; ii, jh) \\ &= \frac{1}{4}p_i^2p_jp_h + \frac{1}{4}p_i^2p_hp_j = \frac{1}{2}p_i^2p_jp_h \quad (j, h \neq i; j \neq h). \end{aligned}$$

The cases where the second child is of a homozygote can immediately be obtained in view of the symmetry relation (1.3).

There remain merely cases where the brethren are both of heterozygotes. If the types of brethren are identical,  $A_{ij}(i \neq j)$  say, then their mother must have at least one of the genes  $A_i$  and  $A_j$ . Hence, we get

$$(1.9) \quad \begin{aligned} \sigma(ij, ij) &= \pi(ii; ij, ij) + \pi(jj; ij, ij) + \pi(ij; ij, ij) \\ &\quad + \sum_{k \neq i, j} (\pi(ik; ij, ij) + \pi(jk; ij, ij)) = \frac{1}{2}p_i^2p_j(1+p_j) \\ &\quad + \frac{1}{2}p_j^2p_i(1+p_i) + \frac{1}{4}p_i p_j (p_i + p_j) (1 + p_i + p_j) \\ &\quad + \sum_{k \neq i, j} (\frac{1}{4}p_i p_k p_j (1 + p_j) + \frac{1}{4}p_j p_k p_i (1 + p_i)) \\ &= \frac{1}{2}p_i p_j (1 + p_i + p_j + 2p_i p_j) \quad (i \neq j), \end{aligned}$$

and similarly

$$(1.10) \quad \begin{aligned} \sigma(ij, ih) &= \pi(ii; ij, ih) + \pi(ij; ij, ih) + \pi(ih; ij, ih) \\ &\quad + \pi(jh; ij, ih) + \sum_{k \neq i, j, h} \pi(ik; ij, ih) = \frac{1}{2}p_i^2p_jp_h \\ &\quad + \frac{1}{4}p_i p_j p_h (p_i + p_j) + \frac{1}{4}p_i p_h p_j (p_i + p_h) \\ &\quad + \frac{1}{4}p_j p_h p_i (1 + p_i) + \sum_{k \neq i, j, h} \frac{1}{4}p_i p_k p_j p_h = \frac{1}{2}p_i p_j p_h (1 + 2p_i) \\ &\quad (j, h \neq i; j \neq h); \end{aligned}$$

and for any quadruple  $i, j, h, k$  different each other we obtain

$$(1.11) \quad \begin{aligned} \sigma(ij, hk) &= \pi(ih; ij, hk) + \pi(ik; ij, hk) + \pi(jh; ij, hk) \\ &\quad + \pi(jk; ij, hk) = \frac{1}{4}p_i p_h p_j p_k + \frac{1}{4}p_i p_k p_j p_h + \frac{1}{4}p_j p_h p_i p_k \\ &\quad + \frac{1}{4}p_j p_k p_i p_h = p_i p_j p_h p_k. \end{aligned}$$

All the possible cases have thus been worked out. Summing up, we can construct the following table; the suffices  $i, j, h, k$  are supposed to be different each other.

2nd child		$A_{ii}$	$A_{jj}$	$A_{ij}$	$A_{4n}$	$A_{jn}$	$A_{nn}$	$A_{nk}$
1st child	$A_{ii}$	$\frac{1}{2} p_i^2(1+p_i)^2$	$\frac{1}{2} p_i^2 p_j^2$	$\frac{1}{2} p_i^2 p_j(1+p_i)$	$\frac{1}{2} p_i^2 p_n(1+p_i)$	$\frac{1}{2} p_i^2 p_j p_n$	$\frac{1}{2} p_i^2 p_n^2$	$\frac{1}{2} p_i^2 p_n p_k$
	$A_{jj}$	$\frac{1}{2} p_i^2 p_j^2$	$\frac{1}{2} p_j^2(1+p_j)^2$	$\frac{1}{2} p_i p_j^2(1+p_j)$	$\frac{1}{2} p_i p_j^2 p_n$	$\frac{1}{2} p_j^2 p_n(1+p_j)$	$\frac{1}{2} p_j^2 p_n^2$	$\frac{1}{2} p_j^2 p_n p_k$
	$A_{ij}$	$\frac{1}{2} p_i^2 p_j(1+p_i)$	$\frac{1}{2} p_i p_j^2(1+p_j)$	$\left\{ \frac{1}{2} p_i p_j(1+p_i) \right. \\ \left. + p_j + 2p_i p_j \right\}$	$\frac{1}{2} p_i p_j p_n(1+2p_i)$	$\frac{1}{2} p_i p_j p_n(1+2p_j)$	$\frac{1}{2} p_i p_j p_n^2$	$p_i p_j p_n p_k$
	$A_{4n}$	$\frac{1}{2} p_i^2 p_n(1+p_i)$	$\frac{1}{2} p_i p_j^2 p_n$	$\frac{1}{2} p_i p_j p_n(1+2p_i)$	$\left\{ \frac{1}{2} p_i p_n(1+p_i) \right. \\ \left. + p_n + 2p_i p_n \right\}$	$\frac{1}{2} p_i p_j p_n(1+2p_n)$	$\frac{1}{2} p_i p_n^2(1+p_n)$	$\frac{1}{2} p_i p_n p_n p_k(1+2p_n)$
	$A_{jn}$	$\frac{1}{2} p_i^2 p_j p_n$	$\frac{1}{2} p_j^2 p_n(1+p_j)$	$\frac{1}{2} p_i p_j p_n(1+2p_j)$	$\frac{1}{2} p_i p_j p_n(1+2p_n)$	$\left\{ \frac{1}{2} p_j p_n(1+p_j) \right. \\ \left. + p_n + 2p_j p_n \right\}$	$\frac{1}{2} p_j p_n^2(1+p_n)$	$\frac{1}{2} p_j p_n p_n p_k(1+2p_n)$
	$A_{nn}$	$\frac{1}{2} p_i^2 p_n^2$	$\frac{1}{2} p_i p_j p_n^2$	$\frac{1}{2} p_i p_j p_n^2(1+p_n)$	$\frac{1}{2} p_i p_j p_n^2(1+p_n)$	$\frac{1}{2} p_j p_n^2(1+p_n)$	$\frac{1}{2} p_n^2(1+p_n)^2$	$\frac{1}{2} p_n^2 p_k(1+p_n)$
	$A_{nk}$	$\frac{1}{2} p_i^2 p_n p_k$	$\frac{1}{2} p_j^2 p_n p_k$	$p_i p_j p_n p_k$	$\frac{1}{2} p_i p_j p_n p_k(1+2p_n)$	$\frac{1}{2} p_j p_n p_k(1+2p_n)$	$\frac{1}{2} p_n^2 p_k(1+p_n)$	$\left\{ \frac{1}{2} p_n p_k(1+p_n) \right. \\ \left. + p_k + 2p_n p_k \right\}$

The following identities are obvious :

$$(1.12) \quad \sum_{h \leq k} \sigma(ji, hk) = \bar{A}_{ij} \quad \text{and} \quad \sum_{i \leq k} \sigma(ij, hk) = \bar{A}_{hk}.$$

The passage to the results on phenotypes can be done by a usual procedure. But, in each concrete case, they may be derived rather simply by means of the corresponding mother-children combination.

## 2. Brethren combination with different fathers.

We next turn our attention to the problem in which two children have a mother alone in common. Although we could, corresponding to (5.6) of IV, discuss also the mixed case, we shall here restrict ourselves to the case of (5.9) of IV. We now denote by

$$(2.1) \quad \sigma_0(hk, fg)$$

the probability of combination consisting of brethren with types  $A_{hk}$  and  $A_{fg}$ , the order being taken into account, whose fathers are not in common. We then get, corresponding to (1.2), the relation

$$(2.2) \quad \sigma_0(hk, fg) = \sum_{i \leq j} \pi_0(ij; hk, fg).$$

The symmetry relation corresponding to (1.3) is immediate, namely

$$(2.3) \quad \sigma_0(hk, fg) = \sigma_0(fg, hk).$$

The value of each  $\sigma_0(hk, fg)$  can be calculated in quite a similar manner as that of  $\sigma(hk, fg)$ . We have only to make use of  $\pi_0$ 's instead of  $\pi$ 's in the latter case. We obtain the following results :

$$(2.4) \quad \begin{aligned} \sigma_0(i\dot{i}, i\dot{i}) &= \pi_0(i\dot{i}; i\dot{i}, i\dot{i}) + \sum_{j \neq i} \pi_0(ij; i\dot{i}, i\dot{i}) \\ &= p_i^4 + \sum_{j \neq i} \frac{1}{2} p_i^3 p_j = \frac{1}{2} p_i^3 (1 + p_i), \end{aligned}$$

$$(2.5) \quad \begin{aligned} \sigma_0(i\dot{i}, i\dot{j}) &= p_i^3 p_j + \frac{1}{2} p_i^2 p_j (p_i + p_j) + \sum_{h \neq i, j} \frac{1}{2} p_i^2 p_h p_j \\ &= \frac{1}{2} p_i^2 p_j (1 + 2p_i), \end{aligned} \quad (j \neq i),$$

$$(2.6) \quad \sigma_0(i\dot{i}, j\dot{j}) = \frac{1}{2} p_i^2 p_j^2 \quad (j \neq i),$$

$$(2.7) \quad \sigma_0(i\dot{i}, j\dot{h}) = \frac{1}{2} p_i^2 p_j p_h + \frac{1}{2} p_i^2 p_h p_j = p_i^2 p_j p_h \quad (j, h \neq i, j \neq h);$$

$$(2.8) \quad \begin{aligned} \sigma_0(i\dot{j}, i\dot{j}) &= p_i^2 p_j^2 + p_i^2 p_j^2 + \frac{1}{2} p_i p_j (p_i + p_j)^2 \\ &\quad + \sum_{k \neq i, j} (\frac{1}{2} p_i p_k p_j^2 + \frac{1}{2} p_j p_k p_i^2) \end{aligned}$$

$$= \frac{1}{2} p_i p_j (p_i + p_j + 4p_i p_j) \quad (i \neq j),$$

$$(2.9) \quad \begin{aligned} \sigma_0(i\dot{j}, i\dot{h}) &= p_i^2 p_j p_h + \frac{1}{2} p_i p_j p_h (p_i + p_j) + \frac{1}{2} p_i p_h p_j (p_i + p_h) \\ &\quad + \frac{1}{2} p_j p_h p_i^2 + \sum_{k \neq i, j, h} \frac{1}{2} p_i p_k p_j p_h \end{aligned}$$

$$= \frac{1}{2} p_i p_j p_h (1 + 4p_i) \quad (j, h \neq i; j \neq h),$$

$$(2.10) \quad \begin{aligned} \sigma_0(i\dot{j}, h\dot{k}) &= \frac{1}{2} p_i p_h p_j p_k + \frac{1}{2} p_i p_k p_j p_h + \frac{1}{2} p_j p_h p_i p_k \\ &\quad + \frac{1}{2} p_j p_k p_i p_h = 2p_i p_j p_h p_k; \end{aligned}$$

in the last relation it being supposed that the suffices  $i, j, h, k$  are different each other. Under the same supposition, the following table can be constructed.

2nd child 1st child	$A_{ii}$	$A_{jj}$	$A_{ij}$	$A_{in}$	$A_{jn}$	$A_{nn}$	$A_{nk}$
$A_{ii}$	$\frac{1}{2} p_i^2(1+p_i)$	$\frac{1}{2} p_i^2 p_j^2$	$\frac{1}{2} p_i^2 p_j(1+2p_i)$	$\frac{1}{2} p_i^2 p_n(1+2p_i)$	$p_i^2 p_j p_n$	$\frac{1}{2} p_i^2 p_n^2$	$p_i^2 p_n p_k$
$A_{jj}$	$\frac{1}{2} p_i^2 p_j^2$	$\frac{1}{2} p_j^3(1+p_j)$	$\frac{1}{2} p_i p_j^2(1+2p_j)$	$p_i p_j^2 p_n$	$\frac{1}{2} p_i^2 p_n(1+2p_j)$	$\frac{1}{2} p_j^2 p_n^2$	$p_j^2 p_n p_k$
$A_{ij}$	$\frac{1}{2} p_i^2 p_j(1+2p_i)$	$\frac{1}{2} p_i p_j^3(1+2p_j)$	$\left\{ \begin{array}{l} \frac{1}{2} p_i p_j(p_i+p_j) \\ + 4p_i p_j \end{array} \right.$	$\frac{1}{2} p_i p_j p_n(1+4p_i)$	$\frac{1}{2} p_i p_j p_n(1+4p_j)$	$p_i p_j p_n^2$	$2p_i p_j p_n p_k$
$A_{in}$	$\frac{1}{2} p_i^2 p_n(1+2p_i)$	$p_i p_j^2 p_n$	$\frac{1}{2} p_i p_j p_n(1+4p_i)$	$\left\{ \begin{array}{l} \frac{1}{2} p_i p_n(p_i+p_n) \\ + 4p_i p_n \end{array} \right.$	$\frac{1}{2} p_i p_j p_n(1+4p_n)$	$\frac{1}{2} p_i p_n^2(1+2p_n)$	$\frac{1}{2} p_i p_n p_k(1+4p_n)$
$A_{jn}$	$p_i^2 p_j p_n$	$\frac{1}{2} p_j^2 p_n(1+2p_j)$	$\frac{1}{2} p_i p_j p_n(1+4p_j)$	$\frac{1}{2} p_i p_j p_n(1+4p_n)$	$\left\{ \begin{array}{l} \frac{1}{2} p_j p_n(p_j+p_n) \\ + 4p_j p_n \end{array} \right.$	$\frac{1}{2} p_j p_n^2(1+2p_n)$	$\frac{1}{2} p_j p_n p_k(1+4p_n)$
$A_{nn}$	$\frac{1}{2} p_i^2 p_n^2$	$\frac{1}{2} p_j^2 p_n^2$	$p_i p_j p_n^2$	$\frac{1}{2} p_i p_n^2(1+2p_n)$	$\frac{1}{2} p_j p_n^2(1+2p_n)$	$\frac{1}{2} p_n^3(1+p_n)$	$\frac{1}{2} p_n^2 p_k(1+2p_n)$
$A_{nk}$	$p_i^2 p_n p_k$	$p_j^2 p_n p_k$	$2p_i p_j p_n p_k$	$\frac{1}{2} p_i p_n p_k(1+4p_n)$	$\frac{1}{2} p_j p_n p_k(1+4p_n)$	$\frac{1}{2} p_n^2 p_k(1+2p_n)$	$\left\{ \begin{array}{l} \frac{1}{2} p_n p_k(p_n+p_k) \\ + 4p_n p_k \end{array} \right.$

-To be continued-