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Probabilities of Concordance of Twins With Respect to Genetic Markers
A General Formulation

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The formulas needed in the determination of monozygosity in twin pairs using genetic markers are derived and presented. A general formula for the calculation of concordance probabilities independent of gene frequencies and allele number is derived, enabling either manual computation or computer programming for any Mendelian markers usable in twin zygosity diagnosis.

Key words: Twin zygosity diagnosis, Genetic markers, Concordance probabilities, Computer programming

INTRODUCTION

Twins have been much studied in the attempt to determine the relative importance of environmental and genetic effects on many human attributes. In twin studies there is an obvious need to differentiate accurately between monozygotic (MZ) and dizygotic twins (DZ).

When the individuals of a twin pair differ with respect to a mendelian trait, the pair is classified DZ. On the other hand, a pair without such a difference is MZ with only a certain probability. The availability of an increasing number of blood markers has made twin zygosity diagnosis by blood markers a method of first choice. Formulas for the calculation of the probability of monozygosity and other closely related quantities have been developed by, inter alia, Smith and Penrose [5], Sutton et al [6], Gaines and Elston [2], Selvin [4], and Lykken [3].

Smith and Penrose [5] presented the basic formulas for the system of one dominant and one recessive allele, though tabulated results are given for some other types of systems. Selvin [4] described a more general method for the calculation of the concordance probability by phenotypes of a DZ twin pair. He presented formulas expressing some of the conditional probabilities shown in Tables I–IV, in the Appendix. These formulas, however, are not sufficient for all systems, eg, the Rh system. Wyslouchowa and Orczykowska-Świat-

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kowska [7] have presented the formulas for frequencies of different combinations of genotypes of sibs, which were also applied to the Rh system.

The basic formulas derived in this paper are not dependent on the markers used or on the gene frequencies of the population to be studied. The tables of Smith and Penrose [5], used by many investigators, are based on English gene frequencies. Gene frequencies vary, however, in different populations, resulting in different concordance probabilities, and thus the use of Smith and Penrose's tables in other populations can produce inaccuracies in classification probabilities. As universally applicable formulas and algorithms have not been available, some authors have resorted to simplifications based on two allelic cases.

Sutton et al [6] derived and presented some of the formulas needed for the calculation of probabilities of misclassification and a posteriori probabilities. Gaines and Elston [2] present some of the general principles for constructing an algorithm for calculating the ratio of the probability of dizygosity to the probability of monozygosity for cases with more than two alleles at a single locus, after presenting detailed formulas for two-allele cases. In this paper completely general formulae for the calculation of this ratio are derived and presented in a form that makes possible computer programming. In addition tables of formulae are also presented should manual calculation be more convenient in special cases. Both sets of formulae are presented and derived in a totally general form.

GENERAL FORMULATION

Probability of Concordance of a Dizygotic Twin Pair for One Multiallelic Locus

In the following we will consider a random mating population operating under the Hardy-Weinberg law [1, pp 45–59]. Let us consider a set of blood markers M $\{M_i\}_{i=1}^{k}$ and let $A = \{A_i\}_{i=1}^{n}$ be a set of *alleles* of an arbitrary blood marker M belonging to the set M. The combinations (A_{i1}, A_{i2}), $A_{i1}, A_{i2} \in A$ form all possible *genotypes* associated with the marker in question. Because the order of alleles in the pair (A_{i1}, A_{i2}) is irrelevant, the number of possible genotypes of the marker M is $g = n(n + 1)/2$. For brevity we denote the genotypes with $A_{i1}A_{i2}$. All the possible *parental mating types* associated with the marker M are then formed by combining the couples A_iA_j in all possible ways. We denote them with $A_{i1}A_{i2} \times A_{i3}A_{i4}$, where A_{i1}, A_{i2}, A_{i3}, and A_{i4} are any elements of the set A. The number of all possible parental mating types of the marker M is $g(g + 1)/2$. The frequencies of the alleles A_i, $i = 1, \ldots, n$ in each blood marker, are denoted by $p_i = P(A_i)$, $i = 1, \ldots, n$, where $\sum_{i=1}^{n} p_i = 1$. Assuming that random union of gametes follows from random mating, the genotype frequencies can be computed from the expansion of:

$$(p_1 + \ldots + p_n)^2 \tag{1}$$

Homozygote genotypes A_iA_i are then found by frequency p_i^2 and correspondingly the frequency of *heterozygote* genotypes A_iA_j is $2p_ip_j$.

Since these events are independent of each other, the probability of the mating $A_{i1}A_{i2} \times A_{i3}A_{i4}$ is obtained as a product of the frequencies p_{i1}, p_{i2}, p_{i3}, and p_{i4} of the alleles A_{i1}, A_{i2}, A_{i3}, and A_{i4}, taking into account the number of combinations of allele pairs

(parental genotypes) for the alleles under consideration. Thus we obtain the following formula for the probability of the mating $A_{i1}A_{i2} \times A_{i3}A_{i4}$:

$$P(A_{i1}A_{i2} \times A_{i3}A_{i4}) = C(i1,i2,i3,i4) \cdot p_{i1}p_{i2}p_{i3}p_{i4}(1 + \delta^*_{i1,i2})(1 + \delta^*_{i3,i4}), \tag{2}$$

where

$$C(i1,i2,i3,i4) = 1 + (\delta^*_{i1,i3} + \delta^*_{i2,i4} - \delta^*_{i1,i3}\delta^*_{i2,i4}) \cdot (\delta^*_{i1,i4} + \delta^*_{i2,i3} - \delta^*_{i1,i4}\delta^*_{i2,i3}) \tag{3}$$

and

$$\delta^*_{ir,is} = \begin{cases} 0, \text{ if } ir = is, \\ 1, \text{ if } ir \neq is, \end{cases} \tag{4}$$

that is, $\delta^*_{ir,is} = 1 - \delta_{ir,is}$, where $\delta_{ir,is}$ is Kronecker's delta. The value of the coefficient C(i1,i2,i3,i4) is 2 when the genotypes of the mating pairs are different; otherwise its value is 1.

In order to compute the probability of the combination of the genotypes $A_{j1}A_{j2}$ and $A_{j3}A_{j4}$ for the sib pair in the specified mating type $A_{i1}A_{i2} \times A_{i3}A_{i4}$, we must take into account the relations between pairs $A_{j1}A_{j2}$ and $A_{j3}A_{j4}$ and the relations of both of these pairs to the mating type in question.

The relations between pairs $A_{j1}A_{j2}$ and $A_{j3}A_{j4}$ can be taken into account using a coefficient C(j1,j2,j3,j4) as in Equation (2). The relations between both of the pairs, $A_{j1}A_{j2}$, A_{j3},A_{j4}, and the mating type, $A_{i1}A_{i2} \times A_{i3}A_{i4}$, are derived from the fact that from this parental type only *four* kinds of genotype combinations are possible for children: $A_{i1}A_{i3}$, $A_{i1}A_{i4}$, $A_{i2}A_{i3}$, and $A_{i2}A_{i4}$, one gene being inherited from the mother and one from the father. Each of these combinations is assumed to be equiprobable.

The relations can be expressed in the form of logical expressions for the indexes of alleles. As an example, we take the relations for $A_{j1}A_{j2}$:

$$((i1 = j1) \wedge (i3 = j2)) \vee ((i1 = j2) \wedge (i3 = j1))$$
$$((i1 = j1) \wedge (i4 = j2)) \vee ((i1 = j2) \wedge (i4 = j1))$$
$$((i2 = j1) \wedge (i3 = j2)) \vee ((i2 = j2) \wedge (i3 = j1))$$
$$((i2 = j1) \wedge (i4 = j2)) \vee ((i2 = j2) \wedge (i4 = j1))$$

When all of these expressions are false, the corresponding probability is zero. Thus the parental type $A_{i1}A_{i2} \times A_{i3}A_{i4}$ is impossible for the genotype combination $A_{j1}A_{j2}$. The probability increases from zero to one by increments of 1/4 when any of the expressions becomes true. The corresponding relations for the other pair $A_{j3}A_{j4}$ are obtained by substituting j1 and j2 by j3 and j4. These logical expressions can be transformed into the form of probabilities with aid of Kronecker delta symbols $\delta_{ir,is}$ defined above.

So we obtain the following formula for the probability of the pair $A_{j1}A_{j2} \cap A_{j3}A_{j4}$ in the mating $m' = A_{i1}A_{i2} \times A_{i3}A_{i4}$:

$$P(A_{j1}A_{j2} \cap A_{j3}A_{j4} \mid m') = C(j1,j2,j3,j4) \cdot \sum_{i=i1,i2} \sum_{k=i3,i4} (\delta_{i,j1}\delta_{k,j2} + \delta_{i,j2}\delta_{k,j1} - \delta_{i,j1}\delta_{k,j2}\delta_{i,j2}\delta_{k,j1})/4 \cdot \sum_{i=i1,i2} \sum_{k=i3,i4} (\delta_{i,j3}\delta_{k,j4} + \delta_{i,j4}\delta_{k,j3} - \delta_{i,j3}\delta_{k,j4}\delta_{i,j4}\delta_{k,j3})/4 \quad (5)$$

where

$$C(j1,j2,j3,j4) = 1 + (\delta^*_{j1,j3} + \delta^*_{j2,j4} - \delta^*_{j1,j3}\delta^*_{j2,j4}) \cdot (\delta^*_{j1,j4} + \delta^*_{j2,j3} - \delta^*_{j1,j4}\delta^*_{j2,j3})$$

The conditional probability for a given parental mating type is then obtained as a product of the probability of the mating, given by Equation (2), and the probability of the combination of genotypes, Equation (5), of the sib pair (DZ twin pair):

$$P_m(A_{j1}A_{j2} \cap A_{j3}A_{j4}; DZ) = P(m') \cdot P(A_{j1}A_{j2} \cap A_{j3}A_{j4} \mid m') \quad (6)$$

The total conditional probability in a given blood system is the sum of the conditional probabilities, Equation (6), of all possible parental mating types:

$$P(A_{j1}A_{j2} \cap A_{j3}A_{j4}; DZ) = \sum_{m=1}^{g(g+1)/2} P_m(A_{j1}A_{j2} \cap A_{j3}A_{j4}; DZ) \quad (7)$$

The above formulas can be used in the construction of an algorithm, taking into account all possible parental mating types for any number of alleles at a locus. Thus, a generally applicable computer program can be prepared.

Computation of Probability of Concordance of DZ Pairs, for Known Genetic Markers

The computation of the probability of concordance can alternatively be done by applying knowledge of the genetic properties of the markers to be used. At any one time a maximum of four different alleles can form the genotype combinations of the sib pair. As the intrapair permutation of alleles and interpair permutation of genotypes does not affect the genotypes, the greatest number of types of allelic combinations that can be formed is seven.

In Tables I–VII of the Appendix the formulas for the conditional probabilities are derived for the seven different combinations of genotypes of sib pairs. For known genetic markers, the parental mating types are known. Therefore, a limited number of combinations of the equations from those given in the tables below suffice for the calculation of concordance probability. Formulas in Tables I–V are used when considering the concordance probabilities of phenotypes in the blood markers of sib pairs. Formulas in Tables VI and VII cannot be used, as concordance between the phenotypes of the sib pairs is never found.

Computation of Phenotype Concordance Probabilities and Discriminating Powers

Concordance of genetic markers is determined by concordance of phenotypes. Thus, the correspondence of genotypes and phenotypes must be known, as two or more genotypes

may be expressed as the same phenotype. This is determined by the *laws of inheritance.* For each marker the laws of inheritance may be expressed in the form of symmetrical (n × n) matrix H(i,j), where each row represents the first allele and each column the second allele. Let $S = \{1,2, \ldots, q\}$ be the set of indexes of all possible phenotypes of the marker M. With aid of the matrix H its genotype index pair (i,j) can be transformed into the corresponding phenotype index s by defining:

$$h_{i,j} = s; s \in S, i, j = 1, \ldots, n \tag{8}$$

Let us denote the phenotype of the genotype A_iA_j with $\bar{A}_s = \overline{A_iA_j}$. Let $A_{j1}A_{j2}$ and $A_{j3}A_{j4}$ be the genotypes of DZ twins. If

$$h_{j1,j2} = h_{j3,j4} = s, s \in S \tag{9}$$

the pairs are phenotypically identical. When relation (9) is true the DZ twins are said to be *concordant* with respect to the marker M. The conditional probability associated with this event will be called *concordance probability* and is denoted by $P(\bar{A}_s \cap \bar{A}_s; DZ)$.

When calculating the probability of concordance there are two situations: a) parental phenotypes are known; b) parental phenotypes are unknown. The situation in which the parental phenotypes are known will be discussed briefly before presentation of the situation where parental phenotypes are unknown.

Parental phenotypes known. The calculation is very simple if the parental genotypes can be derived for the markers used, ie, each phenotype $\bar{A}_s$, $s \in S$ has one and only one corresponding genotype A_iA_j. In this case the probability of the genotype of the sib pair for a specific parental mating type $A_{i1}A_{i2} \times A_{i3}A_{i4}$ is used. These probabilities are given by Equation (5) and expressed in column 3 of Tables I–V.

When there are two or more genotypes corresponding to a given parental phenotype, the probability of the genotype combination of the sib pair for the parental mating has to be weighted by the relative frequencies of all the genotypes that produce the measured phenotype. As weights we must use the probability of the mating (column 2 in Tables I–V) of each parental genotypic mating type expressed by Equation (2). The weights have to be standardized to sum to unity.

Parental phenotypes unknown. When the parental phenotypes are unknown the probability of concordance of a DZ twin pair is calculated assuming panmixia and using the population gene frequencies of the markers. The calculation of the probability of concordance needs knowledge of the alleles of the system, the laws of inheritance, and the phenotypes that the alleles can form. This calculation is performed according to the principles described below.

For each phenotype $\bar{A}_s$, $s \in S$, all possible genotypes A_iA_j, $i, j \in I_1 = \{1, \ldots, n\}$, that fulfil the condition

$$\bar{A}_i\bar{A}_j = \bar{A}_s \tag{10}$$

are formed. Let us denote the number of these genotypes by q_s. As mentioned before, intrapair permutations of alleles and interpair permutation of genotypes are irrelevant in this context. Therefore, the number of genotype combinations for the phenotype $\bar{A}_s$ becomes $q_s(q_s + 1)/2$.

Let us denote the set of index pairs (i, j)of all genotypes that fulfil the condition (10) with $G_s = \{(i,j)\}$. Let $A_{j1}A_{j2}$ and $A_{j3}A_{j4}$ be any two of these and denote the set of genotype pair indexes with $C_s = \{(j1,j2), (j3,j4)\}$. For each of these combinations we compute the probability:

$$P(A_{j1}A_{j2} \cap A_{j3}A_{j4}; DZ) \tag{11}$$

selecting the appropriate formula from Tables I–V or using the general algorithm based on Equations (2) and (5).

As each combination of phenotypically concordant pairs of genotypes is independent, the probability of concordance for the DZ pair with respect to the specific phenotype $\bar{A}_s$ is obtained by summing over the set C_s the probabilities (11) to obtain:

$$P(\bar{A}_s \cap \bar{A}_s; DZ) = \sum_{C_s} P(A_{j1}A_{j2} \cap A_{j3}A_{j4}; DZ),\ s \in S \tag{12}$$

Finally, we obtain the total concordance probability for a DZ pair with respect to the marker M:

$$P_M(\text{Conc}; DZ) = \sum_{s=1}^{q} \sum_{C_s} P(A_{j1}A_{j2} \cap A_{j3}A_{j4}) \tag{13}$$

The discriminating power of the marker system M is defined as

$$Q_M = 1 - P_M(\text{Conc}; DZ) \tag{14}$$

The computation of the relative chances of dizygosity and the probabilities of misclassification then follows general Bayesian principles as presented by, for example, Sutton et al [6].

CONCLUDING REMARKS

Mathematical formulas expressing concordance probabilities with respect to blood markers were presented in this paper. The basic formulas are applicable to any Mendelian marker, whose laws of inheritance are known. It was assumed that these markers obey the Hardy-Weinberg law and that the markers are sex-independent, ie, markers with loci on sex chromosomes are excluded. Based on these, a completely general algorithm can be constructed that is applicable to any mendelian marker satisfying the assumptions made.

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APPENDIX

Derivation of Formulas for Computation of Concordance Probability of DZ Pairs for All Different Allelic Combinations

TABLE 1. Derivation of Formula for Probability $P(A_iA_i \cap A_iA_j; DZ)$ Where A_i Is Any Allele Belonging to the Set A and K is Collective Symbol for All Other Alleles

Parental mating type	Probability of mating	Probability of $A_iA_j \cap A_iA_j$ pair in the mating	$P_m(A_iA_i \cap A_iA_j; DZ)$
(1) $A_iA_i \times A_iA_j$	p_i^4	1	p_i^4
(2) $A_iA_j \times A_iK$	$4p_i^3(1-p_j)$	$\frac{1}{2}\cdot\frac{1}{2}=\frac{1}{4}$	$p_i^3(1-p_i)$
(3) $A_iK \times A_iK$	$4p_i^2(1-p_i)^2$	$\frac{1}{4}\cdot\frac{1}{4}=\frac{1}{16}$	$\frac{1}{4}p_i^2(1-p_i)^2$

$$P(A_iA_i \cap A_jA_i; DZ) = \sum_{m=1}^{3} P_m(\cdot) = \tfrac{1}{4}p_i^2(1+p_i)^2$$

TABLE 2. Derivation of Formula for Probability $P(A_iA_i \cap A_iA_j; DZ)$ Where $A_i, A_j \in A$; K' Is Collective Symbol for All Other Alleles of the Set A Than A_i and A_j

Parental mating type	Parental mating type	Probability of $A_iA_i \cap A_iA_j$ pair in the mating	$P_m(A_iA_i \cap A_iA_j; DZ)$
(1) $A_iA_i \times A_iA_j$	$4p_i^3p_j$	$2\cdot\frac{1}{2}\cdot\frac{1}{2}=\frac{1}{2}$	$2p_i^3p_j$
(2) $A_iA_j \times A_iA_j$	$4p_i^2p_j^2$	$2\cdot\frac{1}{4}\cdot\frac{1}{2}=\frac{1}{4}$	$p_i^2p_j^2$
(3) $A_iK' \times A_iA_j$	$8p_i^2p_j(1-p_i-p_j)$	$2\cdot\frac{1}{4}\cdot\frac{1}{4}=\frac{1}{8}$	$p_i^2p_j(1-p_i-p_j)$

$$P(A_iA_i \cap A_iA_j; DZ) = \sum_{m=1}^{3} P_m(\cdot) = p_i^2p_j(1+p_i)$$

TABLE 3. Derivation of Formula for Probability $P(A_iA_j \cap A_iA_j; DZ)$

Parental mating type	Probability of mating	Probability of $A_iA_j \cap A_iA_j$ pair in the mating	$P_m(A_iA_j \cap A_iA_j; DZ)$
(1) $A_iA_i \times A_iA_j$	$4p_i^3p_j$	$\frac{1}{2}\cdot\frac{1}{2}=\frac{1}{4}$	$p_i^3p_j$
(2) $A_iA_i \times A_jA_j$	$2p_i^2p_j^2$	1	$2p_i^2p_j^2$
(3) $A_iA_j \times A_iA_j$	$4p_i^2p_j^2$	$\frac{1}{2}\cdot\frac{1}{2}=\frac{1}{4}$	$p_i^2p_j^2$
(4) $A_iA_j \times A_jA_j$	$4p_ip_j^3$	$\frac{1}{2}\cdot\frac{1}{2}=\frac{1}{4}$	$p_ip_j^3$
(5) $A_iA_i \times A_jK'$	$4p_i^2p_j(1-p_i-p_j)$	$\frac{1}{2}\cdot\frac{1}{2}=\frac{1}{4}$	$p_i^2p_j(1-p_i-p_j)$
(6) $A_jA_j \times A_iK'$	$4p_ip_j^2(1-p_i-p_j)$	$\frac{1}{2}\cdot\frac{1}{2}=\frac{1}{4}$	$p_ip_j^2(1-p_i-p_j)$
(7) $A_iA_j \times A_iK'$	$8p_i^2p_j(1-p_i-p_j)$	$\frac{1}{4}\cdot\frac{1}{4}=\frac{1}{16}$	$\frac{1}{2}p_i^2p_j(1-p_i-p_j)$
(8) $A_iA_j \times A_jK'$	$8p_ip_j^2(1-p_i-p_j)$	$\frac{1}{4}\cdot\frac{1}{4}=\frac{1}{16}$	$\frac{1}{2}p_ip_j^2(1-p_i-p_j)$
(9) $A_iK' \times A_jK'$	$8p_ip_j(1-p_i-p_j)^2$	$\frac{1}{4}\cdot\frac{1}{4}=\frac{1}{16}$	$\frac{1}{2}p_ip_j(1-p_i-p_j)^2$

$$P(A_iA_j \cap A_iA_j; DZ) = \sum_{m=1}^{9} P_m(\cdot) = \tfrac{1}{2}p_ip_j(1+p_i+p_j+2p_ip_j)$$

TABLE 4. Derivation of Formula for Probability $P(A_iA_j \cap A_iA_k; DZ)$

Parental mating type	Probability of mating	Probability of $A_iA_j \cap A_iA_k$ pair in the mating	$P_m(A_iA_j \cap A_iA_k; DZ)$
(1) $A_iA_i \times A_jA_k$	$4p_i^2p_jp_k$	$2 \cdot \frac{1}{2} \cdot \frac{1}{2} = \frac{1}{2}$	$2p_i^2p_jp_k$
(2) $A_iK \times A_jA_k$	$8p_ip_jp_k(1 - p_i)$	$2 \cdot \frac{1}{4} \cdot \frac{1}{4} = \frac{1}{8}$	$p_ip_jp_k(1 - p_i)$
(3) $A_iA_j \times A_iA_k$	$8p_i^2p_jp_k$	$2 \cdot \frac{1}{4} \cdot \frac{1}{4} = \frac{1}{8}$	$p_i^2p_ip_k$

$$P(A_iA_j \cap A_iA_k; DZ) = \sum_{m=1}^{3} P_m(\cdot) = p_ip_jp_k(1 + 2p_i)$$

TABLE 5. Derivation of Formula for Probability $P(A_iA_j \cap A_kA_l; DZ)$

Parental mating type	Probability of mating	Probability of $A_iA_j \cap A_kA_l$ pair in the mating	$P_m(A_iA_j \cap A_kA_l; DZ)$
(1) $A_iA_k \times A_jA_l$	$8p_ip_jp_kp_l$	$2 \cdot \frac{1}{4} \cdot \frac{1}{4} = \frac{1}{8}$	$p_ip_jp_kp_l$
(2) $A_iA_l \times A_jA_k$	$8p_ip_jp_kp_l$	$2 \cdot \frac{1}{4} \cdot \frac{1}{4} = \frac{1}{8}$	$p_ip_jp_kp_l$

$$P(A_iA_j \cap A_kA_l; DZ) = \sum_{m=1}^{2} P_m(\cdot) = 2p_ip_jp_kp_l$$

TABLE 6. Derivation of Formula for Probability $P(A_iA_i \cap A_jA_k; DZ)$

Parental mating type	Probability of mating	Probability of $A_iA_i \cap A_jA_k$ in the mating	$P(A_iA_i \cap A_jA_k; DZ)$
$A_iA_j \times A_iA_k$	$8p_i^2p_jp_k$	$2 \cdot \frac{1}{4} \cdot \frac{1}{4} = \frac{1}{8}$	$p_i^2p_jp_k$

TABLE 7. Derivation of Formula for Probability $P(A_iA_i \cap A_jA_j; DZ)$

Parental mating type	Probability of mating	Probability of $A_iA_i \cap A_jA_j$ in the mating	$P(A_iA_i \cap A_jA_j; DZ)$
$A_iA_i \times A_jA_j$	$4p_i^2p_j^2$	$2 \cdot \frac{1}{4} \cdot \frac{1}{4} = \frac{1}{8}$	$\frac{1}{2}p_i^2p_j^2$

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