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The Probability of Exclusion of Ancestries Based on Genetic Observations

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SUMMARY

One can extend exclusion of ancestry beyond paternity: for example, to grandparents or other types of ancestors. Naturally, the probability of successful exclusion is smaller for more remote ancestors. The case that we have especially considered is that of exclusion on the basis of grandparents, of which there have been recent applications.

A method of calculating the average probability of exclusion, P, in such situations is developed and applied to different genetic systems including DNA polymorphisms available today. As usual, multiallelic genes like HLA are by far the most informative, but a substantial number of other genes should also be tested to reach a reasonable probability of exclusion. The effect of inbreeding on P is demonstrated to be negligible.

INTRODUCTION

The forensic problem of exclusion of paternity has been partly solved through the understanding of the inheritance of blood genetic markers. Numerous critical reviews can be consulted on this subject [1–3]. Appropriate procedures for calculating the probability of exclusion of a particular father's phenotype given any set of proved or alleged familial information is now available [4–8]. To do this, it is usual to estimate the proportion of males in the population who are excluded by phenotypes of a mother-child pair. This proportion, called average probability of exclusion of paternity when the mother-child pair is also taken at random in the population, gives an indication of the efficiency of a particular genetic system in detecting false paternity in a given population.

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The reliability of the diagnosis of paternity is improved by using many genetic systems, particularly multiallelic systems. Among them, HLA has been until recently the most informative, and the calculation of the average probability of exclusion of paternity has been described with [9] or without [10] the restrictive hypothesis of no blank alleles.

However, the average probability of exclusion of paternity does not cover all possible situations that can occur, especially the case of joint exclusion of the child by the father AND the mother, briefly described by Cotterman [11] for one-locus and two codominant alleles, the case of exclusion by grandparents that must be considered when parental information is lacking, or even the case of exclusion by more remote ancestors.

Here, we present a simple method to evaluate the average probability of exclusion (P) in such situations. We discuss the effects of the number of loci, the frequencies of alleles, nonrandom mating, and small populations.

METHOD

Let us define $p(c_i)$ as the probability of the ith phenotype among the n_c possible phenotypes of the child, or as the probability of the ith phenotypes of a child-parent pair, where the parent is known with certainty; $p(a_j)$ as the probability of the jth phenotype among n_a possible combinations of phenotypes of putative ancestries. Then, the average probability of exclusion, P, is defined as follows:

$$P = \sum_{i}^{n_c} \sum_{j}^{n_a} \delta p(c_i) p(a_j) \quad ,$$

where the summations are over all n_a and n_c. δ is a parameter that is equal to zero if the probability of c_i given a_i is different from zero, $p(c_i|a_j) \neq 0$, and equal to one otherwise.

For the case of exclusion of paternity, a_j is then a jth father's phenotype, F_j, and c_i is the ith combination of mother-child's phenotype, MC_i, so that:

$$P = \sum_{i}^{MC} \sum_{j}^{F} \delta p(F_j) p(MC_i) \quad ,$$

which is identical to a formula proposed by Chakravarti and Li [10].

We present here a general calculation of P that can be easily applied to different types of exclusion of a child from putatives ancestries as follows: (1) both parents: $P(1,1)$; (2) one parent in one lineage and both grandparents in the other lineage: $P(1,2)$; (3) no parent in one lineage and one in the other lineage: $P(0,1)$; (4) four grandparents: $P(2,2)$; (5) no parent in one lineage and both grandparents in the other: $P(0,2)$.

If only one grandparent is known in each lineage, the probability of exclusion is obviously equal to zero: information on at least all alleles in one lineage is

necessary to obtain a P different from zero. Information on a sib of a parent instead of information on the parent, for instance, is irrelevant to the problem. If both grandparents are known in one lineage but only one is known in the other, we have a situation identical to (5).

Considering a multiallelic system at one locus with n codominant alleles A_1, A_2, . . . , A_n with frequencies p_1, p_2, . . . , p_n, respectively, we have

$$\sum_{i=1}^{n} p_i = 1 \ .$$

If there is a blank allele A_0 with frequency p_0 that is recessive to other codominant alleles, we have

$$\sum_{i=1}^{n-1} p_i + p_0 = 1 \ .$$

Now we suppose m ancestries in the maternal lineage and f ancestries in the paternal lineage. Both m and f can take the values 1, 2, 4, . . . corresponding to one parent, two grandparents, four great-grandparents, . . . , respectively. The situation where f or m is equal to zero will be discussed later.

Table 1 shows the different combinations of phenotypes, their probabilities, and the child's phenotypes that are expected to be excluded. Even when using a computer, it was not realistic to consider all combinations of the child's

TABLE 1

PROBABILITY OF EXCLUSION OF ANCESTRIES GIVEN THE CHILD'S PHENOTYPE

		$1 - (1 - p_i)^{2m}$			$(1 - p_i)^{2m}$			
			$z^m - y^m$			y^m	$(1 - p_i - p_j)^{2m}$	
		A_i	A_iA_j	A_iA_x	A_j	A_jA_x	A_x	A_0
$1 - (1 - p_i)^{2f}$	A_i	0110	0001	0111	0000	1001	0110	0110
	$z^f - y^f$ A_iA_j	0001	0001	0011	0001	1101	0101	0111
	$z^f - y^f$ A_iA_x	0111	0011	0111	0011	1011	0111	0111
$(1 - p_i)^{2f}$	A_j	0000	0001	0011	1100	1101	1100	1100
	y^f A_jA_x	1001	1101	1011	1101	1101	1101	1101
	$(1 - p_i - p_j)^{2f}$ A_x	0110	0101	0111	1100	1101	1110	1110
	$(1 - p_i - p_j)^{2f}$ A_0	0110	0101	0111	1100	1101	1110	1110
	1 Σ	0000	0001	0011	0000	1001	0100	0100

NOTE: With $y = 1 - d\,\Sigma p_i^2 - (1 - d)p_i^2 - 2p_i(1 - p_i) - 2p_0(1 - p_i - p_j)$ and $z = 1 - \Sigma p_i^2 - 2p_0(1 - p_0)$. $P(m,f)$ is obtained by multiplying the probability of the row (m or maternal lineage), the probability of the column (paternal lineage), multiplying by 1 or 0 depending on the child's phenotype where the four digits represent the coefficients pertaining to A_i, A_iA_j, A_j, A_0, as given in every cell of the matrix, and finally summing over all cells. A_x is an allele that is not A_i, A_j, or A_0. The 1 value is used when the combination of ancestries' phenotypes excludes the child's phenotype.

phenotypes, which increase far more quickly than the number of alleles n, and then to check the occurrence of exclusion for every combination. It was sufficient to estimate only the combinations where $\delta = 1$ or $p(c_i|a_j) = 0$, and to examine successively such situations for each of the three possible child's phenotypes: A_i, A_0, A_iA_j.

The Child's Phenotype is A_i

The probability of a child A_i is

$$p(c = A_i) = p_i^2 + 2p_ip_0 \ . \tag{1}$$

The exclusion occurs when (1) both paternal and maternal ancestries do not have any alleles A_i, event of probability:

$$s_{i1} = (1 - p_i)^{2(m+f)} \tag{2}$$

and (2) one of the ancestries in one line (say the mother's) has one or two alleles A_i with the probability $1 - (1 - p_i)^{2m}$; then exclusion occurs only if all the ancestries in the paternal lineage are heterozygotes without A_i or A_0, with probability equal to

$$y_i^f = \left[\sum_{i \neq j} \sum_{k \neq i \neq j} (p_j p_k)\right]^f \tag{3}$$

The term y_i can be rearranged or written in a different way as follows: $y_i = 1 - \Sigma_i p_i^2 - 2p_i(1 - p_i) - 2p_0(1 - p_i - p_0)$, where $\Sigma_i p_i^2$ is the probability of being homozygous for any allele, $2p_i(1 - p_i)$ is the probability of being heterozygous for A_i, and $2p_0(1 - p_i - p_0)$ is that of being heterozygous for A_0 but not A_i. Notice that y_i is reduced to $y_i = 1 - p_i^2 - 2p_i(1 - p_i)$ when there are no blank alleles. Indeed, in this case, exclusion can also occur when the paternal ancestries are homozygous, except homozygote A_iA_i. Therefore, y_i can be rewritten in the synthetic form:

$$y_i = 1 - d\Sigma p_i^2 - (1 - d)p_i^2 - 2p_i(1 - p_i) - 2p_0(1 - p_i - p_0) \ , \tag{4}$$

where $d = 0$ if there is no blank allele and $d = 1$ otherwise. Finally, we have in this second situation:

$$s_{i2} = y_i^f \cdot [1 - (1 - p_i)^{2m}] + y_i^m \cdot [1 - (1 - p_i)^{2f}] \ , \tag{5}$$

and the probability of exclusion given that the child is A_i is

$$p(\mathrm{E}|c = A_i) = s_{i1} + s_{i2} \ . \tag{6}$$

The Child's Phenotype is A_0

The probability that a child is A_0 is

$$p(c = A_0) = p_0^2 \ . \tag{7}$$

Such a child is excluded when all m (or f) parents in one lineage OR the $m + f$ parents in both lineages are heterozygotes without any alleles A_0. If

$$z = 1 - \Sigma p_i^2 - 2p_0(1 - p_0) \tag{8}$$

is the probability of being heterozygous without A_0, then

$$P(\mathrm{E}|c = A_0) = z^m + z^f - z^{m+f} \ . \tag{9}$$

Of course, in the case of no blank alleles, this probability is not calculated.

The Child's Phenotype is $\mathrm{A_iA_j}$

The probability of a child A_iA_j is

$$p(c = A_iA_j) = 2p_ip_j \ . \tag{10}$$

The exclusion occurs in three different situations: (1) when both paternal and maternal ancestries do not have either A_i or A_j, event of probability:

$$s_{ij1} = (1 - p_i - p_j)^{2(m+f)} = p_x^{2(m+f)} \ , \tag{11}$$

with $p_x = 1 - p_i - p_j$; (2) when one line (say the mother's) does not have either alleles A_i or A_j, with a probability p_x^{2m}, and the other line (father's) has A_i or A_j, with a probability $(1 - p_x^{2f})$, so that:

$$s_{ij2} = p_x^m(1 - p_x^{2f}) + p_x^f(1 - p_x^{2m}) \ ; \tag{12}$$

and (3) when both lines have A_i but not A_j or the converse, with a probability:

$$s_{ij3} = [p_i^2 + 2p_i(1 - p_i - p_j)]^{m+f} + [p_j^2 + 2p_j(1 - p_i - p_j)]^{m+f} \ ,$$

or

$$s_{ij3} = [(1 - p_i)^2 - p_x^2]^{m+f} + [(1 - p_j)^2 - p_x^2]^{m+f} \ . \tag{13}$$

Therefore,

$$P(\mathrm{E}|c = A_iA_j) = s_{ij1} + s_{ij2} + s_{ij3} \ , \tag{14}$$

this probability being unchanged in the absence of blank alleles.

Finally, the average probability of exclusion $P(m,f)$, using equations (1)–(14), is

$$P(m,f) = \sum_i p(c = A_i) \cdot P(\mathrm{E}|c = A_i) + \sum_i \sum_{j \neq i} p(c = A_iA_j) \cdot P(\mathrm{E}|c = A_iA_j) + p(c = A_0) \cdot P(\mathrm{E}|c = A_0) \quad . \tag{15}$$

This formula is valid only if m or f is different from zero. Otherwise, $P(0,f)$ or $P(m, 0)$ can be easily found from table 1 (see the last row) and is defined as follows: (1) when no blank allele is known—

$$P(0,f) = p_i^2(1 - p_i)^{2f} + p_ip_jp_x^{2f} \tag{16}$$

(same formula for $P(m,0)$ with m instead of f) and (2) when a blank allele is known:

$$P(0,f) = p_i^2 \cdot y_i^f + p_ip_jp_x^{2f} + p_0^2 \cdot z^f \quad , \tag{17}$$

(same formula for $P(m,0)$ with m instead of f), with z and y_i as defined previously and with $d = 1$. If $n = 2$, $p_x = (1 - p_i - p_j) = 0$ and the second term in the right part of equations (16) and (17) vanishes, and $y_i = 0$ if $n = 2$ or 3 and $z = 0$ if $n = 2$.

EFFECTS OF INBREEDING

Equation (15) assumes random mating and a large population at equilibrium, but these assumptions can easily be relaxed to a certain extent by rewriting the probability of A_iA_i and that of A_iA_j as $(1 - x)p_i^2 + xp_i$ and $2(1 - x)p_ip_j$, respectively, and putting them into equations (15). The parameter x is both the average coefficient of consanguinity α_g $(0 < \alpha_g < 1)$ as well as the coefficient of deviation from random mating δ $[-p_i/(1 - p_i) < \delta < 1]$, p_i being the smallest allele frequency, on the basis of the definitions and restrictions developed by Jacquard [12]. For instance, if we assume a constant value of α_g through 3 generations and a panmictic proportion of genotypes in the initial population, then P increases weakly with α_g (or with δ if $\delta > 0$) for a given set of allele frequencies (table 2).

Two simple examples illustrate this conclusion. When the exclusion of the child occurs only by means of the mother's genotype at a locus with two codominant alleles A_1 and A_2 with frequencies p and q, we find $P(0,1) = p(\mathrm{M} = A_1A_1) \cdot p(c = A_2A_2) + p(\mathrm{M} = A_2A_2) \cdot p(c = A_1A_1) = 2[(1 - x)p^2 + xp][(1 - x)q^2 + xq]$, which increases with x. For the case of the ABO system, exclusion of type $P(0,1)$ occurs only through the combination of a child heterozygous AB and a homozygous mother O (or inversely) so that, p, q, and r

TABLE 2

EFFECT OF THE AVERAGE COEFFICIENT OF CONSANGUINITY α_g ON THE AVERAGE PROBABILITY OF EXCLUSION $P(m,f)$; EXAMPLE OF 10 EQUALLY FREQUENT ALLELES AND NO BLANK ALLELE

α_g	$P(1,1)$	$P(1,2)$	$P(2,2)$	$P(0,1)$	$P(0,2)$
0	.932	.811	.676	.657	.434
.005	.932	.812	.678	.659	.436
.05	.937	.824	.697	.672	.455
.5	.970	.920	.856	.794	.635

being the frequencies of the alleles A, B, and O: $P(0, 1) = 4(1 - x)pq[(1 - x)r^2 + xr]$, which is also greater than $4pqr^2$ when $x > 0$.

Salmon and Brocteur suggested [13] that the probability of exclusion of a putative father is reduced in an isolate since the real father has a nontrivial genetic relationship to him. However, as they pointed out elsewhere [4], the probability of exclusion of an individual taken at random in the population depends on his genetic relationship to the real father and to the mother. This probability is higher when the individual is not the real father but is related to the mother (her father or her brother), and the probability of exclusion of the individual is lower when the real father is related to the mother. As these two situations occur simultaneously in a small population, their joint effects compensate each other, and, thus, P is expected to display only a slight variation with α_g, as is effectively observed (table 2), even if α_g is high. This variation comes from the increase caused by inbreeding of the ratio homozygotes/heterozygotes and its influence on P. However, this increase is not always observed in a really small population: the frequency of consanguineous matings can be less than expected because of incest prohibition.

DISCUSSION

A major concern underlying this work refers to the cases of children who have been abducted and adopted, their parents having disappeared or been killed for political reasons (for example, in Argentina between 1975 and 1983). The question is then to test whether a specific child is biologically related to a known set of grandparents who want to recognize him as their relative.

Before solving this problem of inclusion of grandpaternity, it is of interest to specify the chance of excluding a set of grandparents, or even remote ancestors, given a child's phenotype. The average probability of exclusion P provides us with such information.

As could be expected, the more remote the ancestries, the smaller is P (table 3), with the general following relationship: $P(1,1) < P(1,2) < P(2,2) <$ or $> P(0,1) < P(0,2)$, where the sequence can be modified depending on the number of alleles and their frequencies.

Notice that P is higher when both mother and father can be excluded [P(MF|C)] than when only the father can be excluded given that the mother-child couple is certain [P(F|MC)]. This has been previously proved for the case

TABLE 3

VARIATION OF THE AVERAGE PROBABILITY OF EXCLUSION $P(m,f)$ ACCORDING TO THE NO. ALLELES n, THE PRESENCE OF A BLANK ALLELE ($d = 1$) OR NOT ($d = 0$), THE AVAILABLE INFORMATION ON REMOTE ANCESTORS (m AND f, RESPECTIVELY, ON MATERNAL AND PATERNAL LINEAGES)

		$P(1,1)$	$P(1,2)$	$P(2,2)$	$P(0,1)$	$P(0,2)$
$n = 3$	$d = 0$	.5185	.3155	.1515	.2222	.0741
	$d = 1$	.2716	.1311	.0477	.0494	.0082
$n = 10$	$d = 0$	.9318	.8110	.6760	.6570	.4343
	$d = 1$	.9121	.7943	.6524	.5184	.3283
$n = 20$	$d = 0$	.9815	.9385	.8861	.8146	.6640
	$d = 1$	.9785	.9360	.8818	.7310	.5906

NOTE: Alleles are assumed to be equiprobable.

of two codominant alleles [11]: $P(\text{MF}|\text{C}) = pq(1 - pq) + pq(1 - 4pq + 6p^2q^2)$ and $P(\text{F}|\text{MC}) = pq(1 - pq)$. For instance, P is .834 instead of .750 for one locus with 10 equiprobable codominant alleles.

The average probability of exclusion P has been calculated from the frequencies of the Italian population [14] in $k = 18$ different systems and has been cumulated over all systems in a general P by: $P_T = 1 - \Pi_{i=1}^{k}(1 - P_i)$, using either only *HLA-B* or both *HLA-A* and *HLA-B*, which are assumed to be independent. P has been also calculated from the frequencies of 22 DNA polymorphic systems (one per chromosome), using the frequencies reported at the Human Gene Mapping 7 Workshop [15] (table 4).

As the maximum value of P occurs with equal probability and frequency of alleles [9], we observe the important decrease of P in real situations that reflects the variability of allele frequencies within the genetic system. For instance, $P(1,1)$ is .841 in the Italian population for *HLA-A*, but is .912 for 10 alleles of $p = .10$.

TABLE 4

OVERALL AVERAGE PROBABILITY OF EXCLUSION $P(m,f)$

	$P(1,1)$	$P(1,2)$	$P(2,2)$	$P(0,1)$	$P(0,2)$
(1)*	.9996	.9918	.9552	.8994	.6173
	.9999	.9973	.9770	.9422	.7061
(2)	.9998	.9929	.9156	.9351	.5842
(3)	.9999999	.99994	.9962	.9935	.8409

NOTE: The overall average probability of exclusion $P(m,f)$ was estimated by using (1) 18 different genetic systems calculated from frequencies observed in the Italian population [14]: ABO, Rh, MNSs, K, Fy, Hp, Gc, Gm, Km, AcP, PGM1, AK, ADA, GPT, ESD, GLO1, HLA-A, and HLA-B; (2) 22 DNA polymorphic systems (one per chromosome) and calculated from frequencies related elsewhere [15]: AT3, P0MC, D3S2, ALB, D5S4, D6S2, COLIA2, MOS, ASS, D10S1, HBB, D12S3(B), D13S2(A), D14S1, D15S1, D16S1, GH1, D18S3(B), C3(A), D20S4, D21S11(1), and IGLC; and (3) overall average probability using both (1) and (2).

* Without HLA-A.

As underlined by Chakravarti and Li [10], the effect of the blank allele decreases when the number of codominant alleles increases. However, the discrepancy between presence and absence of blank is more important when information is lacking in one parental lineage. Moreover, the effect of the blank allele depends on its frequency, p_0. For example, $P(1,1) = .834$ when $p_0 = .10$ with 10 equiprobable alleles but falls to .626 when $p_0 = .40$, other codominant alleles being equally frequent.

When information on the mother and the father is lacking, it is still possible to exclude the grandparents given the phenotype of the child with the relatively high average probability $P(2,2) > .95$. A probability of .95 means that from 100 random associations of a child and four putative grandparents, the grandparents will be excluded as the real grandparents of the child in 95 cases on average. This probability can be easily increased by increasing the number of loci and/or alleles. Using mtDNA markers that are transmitted through the maternal line, $P = \Sigma_i p_i(1 - p_i)$, which is higher than the expected value given by any $P(0,2)$. However, this information is only available in the specific case of known maternal grandmother.

The probability of exclusion is an index providing information on the usefulness of a specific set of loci to perform diagnosis of grandparentage and on the efficiency of such a diagnostic criterion as a function of the number and the remoteness of ancestors in both maternal and paternal lineages. Thus, the estimation of the probability of grandpaternity, as an extension of the probability of paternity [16], can be sufficiently powerful to attribute grandparents to a child in particular cases [17, 18].

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THE NATIONAL INSTITUTE OF GENERAL MEDICAL SCIENCES HUMAN GENETIC MUTANT CELL REPOSITORY HEMOGLOBINOPATHY CELL COLLECTION. The National Institute of General Medical Sciences (NIGMS) Human Genetic Mutant Cell Repository would like to inform investigators interested in studying the various hemoglobinopathies and thalassemias that the Repository now has available for distribution a number of cell cultures useful for investigations in these research areas. A fairly extensive collection of lymphoblast cultures containing characterized β-thalassemia mutations has been accumulated with the expert guidance of Dr. Haig Kazazian of the Johns Hopkins Medical School. Cultures are available with characterized mutations that account for more than 95% of the β-thalassemia alleles in the Mediterranean basin population. In addition, there are cultures from two Chinese individuals with mutations that probably account for 80%–85% of the β-thalassemia alleles in South China. These cultures should be useful to investigators interested in: (1) improving oligonucleotide hybridization techniques of specific mutations in genomic DNA; (2) improving prenatal diagnostic techniques; and (3) developing newer technologies to detect known single base changes in DNA fragments. The hemoglobinopathy cell collection also includes cultures from individuals with sickle-cell anemia and characterized DNA polymorphisms, along with others with important deletions in the α- or β-globin gene cluster. A moderate fee is charged for the cell cultures. A catalog summarizing information on cultures in this collection and on cultures representing other genetic diseases stored in the Repository, as well as details of procedures for submitting and obtaining cell cultures, may be obtained by contacting: Dr. Arthur E. Greene, The Human Genetic Mutant Cell Repository, Institute for Medical Research, Copewood and Davis Streets, Camden, NJ 08103. Telephone: (609)966-7377. Cable address: INMEDRES.