COEFFICIENTS OF INBREEDING AND RELATIONSHIP

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IN the breeding of domestic animals consanguineous matings are frequently made. Occasionally matings are made between very close relatives—sire and daughter, brother and sister, etc.—but as a rule such close inbreeding is avoided and there is instead an attempt to concentrate the blood of some noteworthy individual by what is known as line breeding. No regular system of mating such as might be followed with laboratory animals is practicable as a rule.

The importance of having a coefficient by means of which the degree of inbreeding may be expressed has been brought out by Pearl[1] in a number of papers published between 1913 and 1917. His coefficient is based on the smaller number of ancestors in each generation back of an inbred individual, as compared with the maximum possible number. A separate coefficient is obtained for each generation by the formula

$$Z_n = 100\ (1 - \frac{q_{n+1}}{p_{n+1}}) = 100\ (1 - \frac{q_{n+1}}{2^{n+1}})$$

where $q_{n+1}/2^{n+1}$ is the ratio of actual to maximum possible ancestors in the $n + 1$st generation. By finding the ratio of a summation of these coefficients to a similar summation for the maximum possible inbreeding in higher animals, *viz.*, brother-sister mating, he obtains a single coefficient for the whole pedigree.

This coefficient has the defect, as Pearl himself pointed

[1] AMERICAN NATURALIST, 1917, 51: 545–559; 51: 636–639.

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out, that it may come out the same for systems of breeding which we know are radically different as far as the effects of inbreeding are concerned. For example, in the continuous mating of double first cousins, an individual has two parents, four grandparents, four great grandparents and four in every generation, back to the beginning of the system. Exactly the same is true of an individual produced by crossing different lines, in each of which brother-sister mating has been followed. Yet in the first the individual will be homozygous in all factors if the system has been in progress sufficiently long; in the second he will be heterozygous in a maximum number of respects.

In order to overcome this objection Pearl has devised a partial inbreeding index which is intended to express the percentage of the inbreeding which is due to relationship between the sire and dam, inbreeding being measured as above described. A coefficient of relationship is used in this connection. These coefficients have been discussed by Ellinger[2] who suggests certain alterations and extensions by means of which the total inbreeding coefficient, a total relationship coefficient and a total relationship-inbreeding index for a given pedigree can be compared on the same scale.

An inbreeding coefficient to be of most value should measure as directly as possible the effects to be expected on the average from the system of mating in the given pedigree.

There are two classes of effects which are ascribed to inbreeding: First, a decline in all elements of vigor, as weight, fertility, vitality, etc., and second, an increase in uniformity within the inbred stock, correlated with which is an increase in prepotency in outside crosses. Both of these kinds of effects have ample experimental support as average (not necessarily unavoidable) consequences of inbreeding. The best explanation of the decrease in vigor is dependent on the view that Mendelian

[2] AMERICAN NATURALIST, 1920, 54: 540–545.

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factors unfavorable to vigor in any respect are more frequently recessive than dominant, a situation which is the logical consequence of the two propositions that mutations are more likely to injure than improve the complex adjustments within an organism and that injurious dominant mutations will be relatively promptly weeded out, leaving the recessive ones to accumulate, especially if they happen to be linked with favorable dominant factors. On this view it may readily be shown that the decrease in vigor on starting inbreeding in a previously random-bred stock should be directly proportional to the increase in the percentage of homozygosis. Numerous experiments with plants and lower animals are in harmony with this view. Extensive experiments with guinea-pigs conducted by the Bureau of Animal Industry are in close quantitative agreement. As for the other effects of inbreeding, fixation of characters and increased prepotency, these are of course in direct proportion to the percentage of homozygosis. Thus, if we can calculate the percentage of homozygosis which would follow on the average from a given system of mating, we can at once form the most natural coefficient of inbreeding. The writer[3] has recently pointed out a method of calculating this percentage of homozygosis which is applicable to the irregular systems of mating found in actual pedigrees as well as to regular systems. This method, it may be said, gives results widely different from Pearl's coefficient, in many cases even as regards the relative degree of inbreeding of two animals.

Taking the typical case in which there are an equal number of dominant and recessive genes (A and a) in the population, the random-bred stock will be composed of 25 per cent. AA, 50 per cent. Aa and 25 per cent. aa. Close inbreeding will tend to convert the proportions to 50 per cent. AA, 50 per cent. aa, a change from 50 per cent. homozygosis to 100 per cent. homozygosis. For a natural coefficient of inbreeding, we want a scale which

[3] *Genetics*, 1921, 6: 111–178.

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runs from 0 to 1, while the percentage of homozygosis is running from 50 per cent. to 100 per cent. The formula $2h-1$, where h is the proportion of complete homozygosis, gives the required value. This can also be written $1-2p$ where p is the proportion of heterozygosis. In the above-mentioned paper it was shown that the coefficient of correlation between uniting egg and sperm is expressed by this same formula, $f = 1-2p$. We can thus obtain the coefficient of inbreeding f_b for a given individual B, by the use of the methods there outlined.

The symbol r_{bc}, for the coefficient of the correlation between B and C, may be used as a coefficient of relationship. It has the value 0 in the case of two random individuals, .50 for brothers in a random stock and approaches 1.00 for individuals belonging to a closely inbred subline of the general population.

In the general case in which dominants and recessives are not equally numerous, the composition of the random-bred stock is of the form $x^2\ AA,\ 2xy\ Aa,\ y^2\ aa$. The percentage of homozygosis is here greater than 50 per cent. The rate of increase, however, under a given system of mating, is always exactly proportional to that in the case of equality. The coefficient is thus of general application.

If an individual is inbred, his sire and dam are connected in the pedigree by lines of descent from a common ancestor or ancestors. The coefficient of inbreeding is obtained by a summation of coefficients for every line by which the parents are connected, each line tracing back from the sire to a common ancestor and thence forward to the dam, and passing through no individual more than once. The same ancestor may of course be involved in more than one line.

The path coefficient, for the path, sire (S) to offspring (O), is given by the formula $p_{o.s} = \frac{1}{2}\sqrt{(1+f_s)/(1+f_o)}$, where f_s and f_o are the coefficients of inbreeding for sire

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and offspring, respectively. The coefficient for the path, dam to offspring, is similar.

In the case of sire's sire (G) and individual, we have $p_{o.g} = p_{o.s}\ p_{s.g} = \frac{1}{4}\sqrt{(1+f_g)/(1+f_o)}$, and for any ancestor ($A$) we have for the coefficient pertaining to a given line of descent $p_{o.a} = (\frac{1}{2})^n\sqrt{(1+f_a)/(1+f_o)}$, where n is the number of generations between them in this line.

The correlation between two individuals (r_{bc}) is obtained by a summation of the coefficients for all connecting paths.

Thus

$$r_{bc} = \Sigma p_{ba}p_{ca} = \Sigma\left(\frac{1}{2}\right)^{n+n'}\frac{1+b_a}{\sqrt{(1+b_b)(1+b_c)}},$$

where n and n' are the number of generations in the paths from A to B and from A to C, respectively.

The formula for the correlation between uniting gametes, which is also the required coefficient of inbreeding, is

$$f_o = \tfrac{1}{2}r_{sd}\sqrt{(1+f_s)(1+f_d)},$$

where r_{sd} is the correlation between sire and dam and f_s and f_d are coefficients of inbreeding of sire and dam. Substituting the value of r_{sd} we obtain

$$f_o = \Sigma\,(\tfrac{1}{2})^{n+n'+1}(1+f_a).$$

If the ancestor (A) is not inbred, the component for the given path is simply $(\frac{1}{2})^{n+n'+1}$ where n and n' are the number of generations from sire and dam respectively to the ancestor in question. If the common ancestor is inbred himself, his coefficient of inbreeding (f_a) must be worked out from his pedigree.

This formula gives the departure from the amount of homozygosis under random mating toward complete homozygosis. The percentage of homozygosis (assuming 50 per cent. under random mating) is $\frac{1}{2}(1+f_o) \times 100$.

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By this means the inbreeding in an actual pedigree, however irregular the system of mating, can be compared accurately with that under any regular system of mating.

As an illustration, take the pedigree of Roan Gauntlet, a famous Shorthorn sire, bred by Amos Cruickshank. This bull traces back in every line to a mating of Champion of England with a daughter or granddaughter of Lord Raglan. For the present purpose we will assume that these bulls were not at all inbred themselves and not related to each other. Since the sire traces twice to Champion of England and twice to Lord Raglan and the dam once to each bull, there are in all four lines by which the sire and dam are connected.

Individual	Common Ancestors of Sire and Dam	f_a	n	n'	$(\frac{1}{2})^{n+n'+1} \times (1 + b_a)$
Roan Gauntlet 45,276 (35,284)	Champion of England (17,526)	0	2	1	.062500
			2		.062500
	Lord Raglan (13,244)	0	3	3	.007812
			3		.007813
					.140625

The coefficient of inbreeding comes out 14.1 per cent., a rather low figure when compared to such systems as brother-sister mating (one generation 25 per cent., two generations 37.5 per cent., three generations 50 per cent., ten generations 88.6 per cent.) or parent-offspring mating, (one generation 25 per cent., two generations 37.5 per cent., three generations 43.8 per cent., approaching 50 per cent. as a limit).

As an example of closer inbreeding, take the pedigree of Charles Collings' bull, Comet. The sire was the bull Favorite and the dam was from a mating of Favorite with his own dam. As Favorite was himself inbred to some extent, it is necessary to calculate first his own coefficient of inbreeding.

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Individual	Common Ancestors of Sire and Dam	f_a	n	n'	$(\frac{1}{2})^{n+n'+1} \times (1 + f_a)$
Favorite (252)	Foljambe (263).....	0	1	1	.1250
	Favorite (cow).....	0	2	1	.0625
					.1875
Comet (115)	Favorite (252).....	.1875	0	1	.2969
	Phœnix.....	0	1	1	.1250
	Foljambe.....	0	2	2	.0312
	Favorite (cow).....	0	3	2	.0156
					.4687

In the case of Comet, Foljambe and Favorite (cow) each appears twice in the pedigree of the sire and three times in the pedigree of the dam. However, only those pedigree paths which connect sire and dam and which do not pass through the same animal twice are counted. The listing of Favorite (252) and Phœnix as common ancestors eliminates all but one path in each case as regards Foljambe and Favorite cow. The remaining paths are those due to the common descent of Bolingbroke, the sire's sire and Phœnix as the dam's dam from the above two animals.

By tracing the pedigrees back to the beginning of the herd book, the coefficients of inbreeding are slightly increased. This meant going back to the seventh generation for one common ancestor of the sire and dam of Favorite. The coefficient in the case of Favorite becomes .192 instead of .188 and that of Comet .471 instead of .469. Remote common ancestors in general have little effect on the coefficient. It will be noticed that Comet has a degree of inbreeding almost equal to three generations of brother-sister mating or an indefinite amount of sire-daughter mating where the sire is not himself inbred.

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