

backward. The present famous animal is traced through his sire to a grandsire and through it to a great grandsire, all of which were outstanding individuals of their breed. Looking back to what happened, we sometimes see an unbroken succession of outstanding merit. If we could turn the pedigree around and look forward from the first famous animal in the line, we might see what really happened. The outstanding individual which was the first in this blood-line was used in one of the leading herds of the breed. He had many sons and daughters; and, as far as the breeder could pick them out, only the best of his sons were saved for tentative use in leading herds, where they were mated to better-than-average females. That son whose offspring proved him to be the best became the leading sire of his generation and his supposedly best sons were eagerly sought and in turn were tried out in the leading herds of their time. This may have lasted several generations, or at least as long as even one outstanding son of the outstanding sire in each generation could be found. In a breed where one herd or a small group of herds which get their sires from each other maintain a leading position over many years, it sometimes happens that from grandsire to sire and to son there was an unbroken succession of outstanding breed leaders. This will become familiar to everyone who studies pedigrees of that breed, and people will soon be referring to this as a "very valuable blood-line." Really what happened in such cases was nothing more fundamental than an intense selection among the sons in each generation.

Because of its vagueness, blood-line is in bad repute as a scientific word. Its claim to retention in the animal breeder's vocabulary is that it is widely used now and that everyone understands—at least in a general way—what is meant by it. The relationship coefficient and inbreeding coefficient are not yet widely used and understood. They would often require a long translation or explanation. There is no way to make blood-line quantitative, but it is often useful where only a qualitative meaning is necessary.

It is more nearly correct biologically to think of the individual as one knot in an enormous network of descent, rather than as belonging to some blood-line. The network is irregular in practically all respects except that each individual has two and only two parents. Figure 44 shows a network which corresponds in a small way¹ to the irregular and interlocking lines of descent which constitute the pedigree structure of a breed. Each small circle represents an individual, and the short straight lines connect parent and offspring. Each individual's ancestry widens out rapidly until, not many generations into the past, its pedi-

¹ Except that the figure shows more inbreeding and hence more separation into distinct families than is usual.

gree includes nearly the same animals as the pedigrees of its contemporaries do, but with some ancestors repeated rarely and others repeated many times. Some individuals leave many sons and daughters, others few, and still others leave none. The breed is continuous in time and

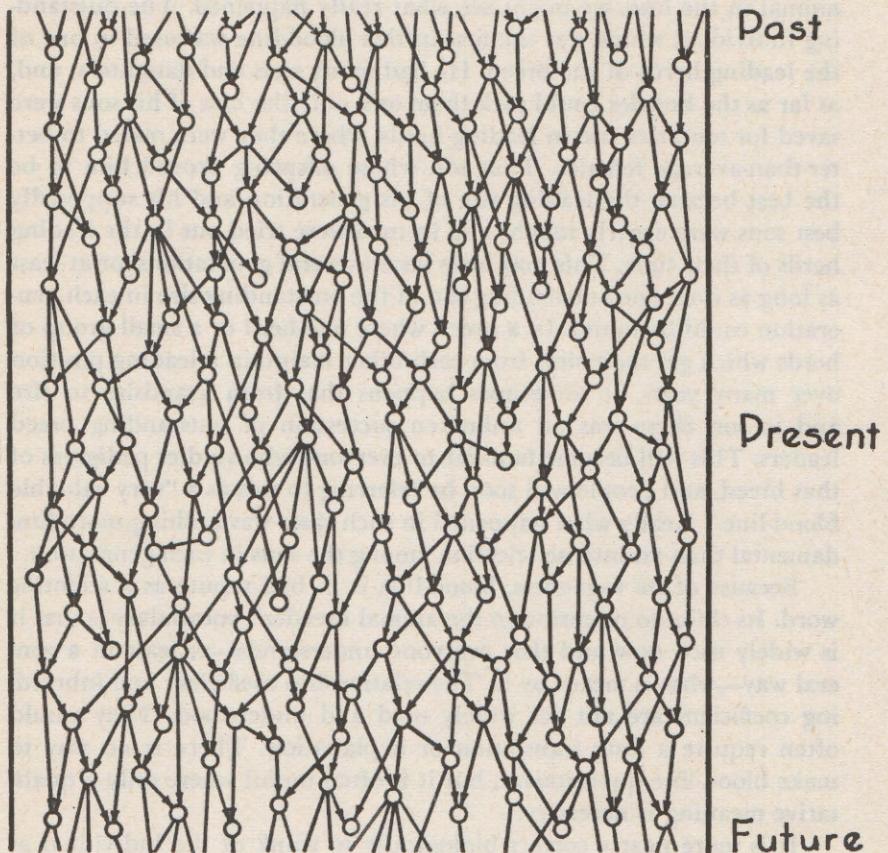


FIG. 44. The pedigree of a population, showing that it is a network of descent and is not composed of "blood lines" which are separate.

space and changes but slowly. The individuals are discontinuous, and each is different from all the others. Each individual is related to all the others but in widely varying degrees. One blood-line can no more be lifted out by itself than one strand of a fishing net could be picked up without picking up all the others. Those nearest would be affected soonest and most strongly. The fishing net, however, is much more regular than the pedigree structure of a breed.

SUMMARY

"Blood-line" is an elastic term used sometimes as synonymous with family, sometimes as a substitute for relationship, and sometimes to describe vaguely a breeding system.

Because of its vagueness, blood-line is in bad repute as a scientific term. But, because it is so widely understood by breeders, blood-line will sometimes be found useful in conveying a general qualitative idea about breeding topics where the speaker does not wish to call attention to the quantitative aspect of that idea.

REFERENCES

- Malin, D. F. 1923. *The evolution of breeds*. Des Moines: Wallace Publishing Company. This book contains abundant references to blood and the word "strain," or family. These show how one can speak more definitely on the subject and yet avoid the use of "blood-line."
- Whitney, Leon F. 1933. *The basis of breeding*. New Haven: E. C. Fowler. (Presents many arguments against any use at all of "blood" to mean inheritance.)

CHAPTER 26

Outbreeding Systems

Outbreeding is the general scientific term for mating animals distinctly less closely related to each other than the average of the population concerned. Its general effects are the opposite of those of inbreeding. Outbreeding increases the heterozygosity of the individual and increases the uniformity of the breed when it is first practiced, although in a generation or two it comes to a limit in these respects. Continued outbreeding merely serves to hold this individual heterozygosity and breed uniformity. Any families which may have started to separate from the rest of the breed are blended again toward the breed average by crossing them with each other.

The practical usefulness of outbreeding rests on the general fact that favorable effects of genes are apt to be dominant over the unfavorable ones. Therefore, outbreeding increases the average individual merit of the animals but lowers the breeding values of the best among them. It increases at first the uniformity of the breed, but hampers further progress in breed improvement. This superiority of the outbred animals over the average of their parents in individual merit is so general a phenomenon in many kinds of plants and animals that it has been called "hybrid vigor" or "heterosis." It is not often extreme unless the parents are from different inbred lines or have in some other way been made distinctly different from each other in the genes they carry. The maximum practical usefulness of outbreeding systems is in the production of market animals or purebred animals which are to be shown to advertise the herd but which are not intended for breeding use.

CROSSBREEDING

Crossbreeding is the mating of two animals which are both purebred but belong to different breeds. The mating of a purebred sire of one breed to high grade females of another is often included under the term crossbreeding.

Crossbreeding is often practiced in producing swine, sometimes in producing poultry, and in some regions is extensively practiced by

sheepmen. Thus, in the northwestern range states many sheepmen plan to keep one-quarter to one-half Merino or Rambouillet blood in the ewes but use mutton rams on these ewes to produce market lambs. Crossbreeding is rarer with cattle and horses; but there are certain well-established practices of it, such as the production of blue-gray cattle for feeding by crossing Angus and white Shorthorns, or the practice of certain ranches—e.g., the SMS ranch near Stamford, Texas—in maintaining an undercurrent of Shorthorn blood but of using bulls in the ratio of 90 Herefords to 10 Shorthorns. Crossbreeding among cattle is also practiced on a commercial basis along the Gulf coast, where many cattlemen try to keep a quarter to a half Brahman blood in the cow herd, but for siring the market steers and heifers use bulls from the beef breeds which originated in Europe.

There have been many crossbreeding experiments with sheep, but most of those have been planned to find what kind of ram is most profitable for use upon range-bred ewes carrying a considerable amount of Merino or Rambouillet blood. There have been several crossbreeding experiments with swine to find how much general advantage there might be in such crossing. The few crossbreeding experiments which have been conducted with cattle have been directed mainly toward a genetic analysis of the difference between breeds rather than toward finding whether crossbreeding is a commercially successful practice.

Crossbreeding, like any other form of outbreeding, tends to lower the breeding value of the individual by making it more heterozygous and by making selection among the crossbred individuals less effective. Like other forms of outbreeding it promotes individual merit because of general dominance of genes favorable to size, vigor, fertility, etc.

When the crossbreds are used for breeding purposes, their offspring are more variable than the crossbreds were and generally average somewhat lower in individual merit. If both parents are crossbreds, the offspring usually average below their purebred grandparents in individual merit. Often the distribution of the offspring of crossbreds is distinctly skewed, there being few which exceed the average of the crossbreds and many which fall below it—some of them far below.¹ But if

¹ Besides the general dominance of favorable effects, it is probable that much of this asymmetry in the distribution of the offspring of crossbreds is caused by gene interactions such as those studied by Rasmusson (1933, *Hereditas*, 18:245–61). In more general terms it can be pictured as shown in Figures 20 and 21. The pure breeds crossed will usually have been in different peaks, each more desirable than the adjacent genotypes. A general tendency to dominance of the favorable effects of genes may keep the crossbreds high in individual merit. But when the crossbreds reproduce, many of their offspring will fail to get some of the genes vital for the successful functioning of the complete sets of genes which came to the crossbreds from each of their purebred parents. Many of the offspring of the crossbreds will, therefore, fall into some of the intervening valleys of low merit.

one is to make full use of the heterosis of the crossbred females, it may be necessary to use them for breeding. For example, in swine the number of pigs farrowed and weaned and their weight at birth and probably also at weaning are perhaps more dependent on the dam's characteristics as a mother and nurse than on the genes which the pigs themselves have, although the latter certainly play a part. It will be necessary to use the crossbred females for breeding if this part of their heterosis is to be used. Similar consideration would apply to egg production in poultry and milk production in dairy cows. Some swine producers attempt to solve this by keeping the crossbred gilts for breeding purposes and breeding them to a purebred boar of a third breed. If all three breeds nick well with each other in crosses, the pigs from such a "triple cross" should show many of the advantages of the original crossbreds besides permitting their dams to show the effects of heterosis on their fecundity and nursing ability. The triple-cross pigs are usually more variable, since their crossbred dams transmit various combinations of genes to them. The breeds can be chosen so that the triple-cross pigs will be as uniform in color as the first-cross pigs. This is done by choosing for the third cross a boar of a breed which has a conspicuous and dominant color, such as solid white. This practice might theoretically be continued to a fourth or even a fifth cross with only a little loss of heterosis in the dams, but it becomes increasingly difficult to find more breeds which are distinct from those already used and yet which nick well with all of them. Actually this practice is rarely carried past the triple-cross.

"Criss-crossing" is another method proposed² for utilizing heterosis in the dams but not incurring the full decline in average individual merit which usually occurs when crossbreds are mated together. The plan is to use purebred sires all the time but to alternate breeds. Thus, sows produced by crossing breeds *A* and *B* would be mated back to *A*. Their daughters (carrying 75 per cent of *A* blood) would be mated to a *B* boar. The gilts thus produced (carrying 37½ per cent of *A* blood) would then be mated to an *A* boar. If this were practiced regularly, it would approach the condition in which each crop of pigs had 1/3 of its inheritance from one breed and 2/3 from the other, but all the sires used would be purebreds. The Minnesota Station reports good results from this system, as far as it was carried in six years of experimenting. Some practical difficulties with overlapping of generations are to be expected in herds where only one boar is kept and is used both on gilts and on older sows. This would not occur where all the sows are the same age. Figure 45 shows examples of how pedigrees would appear after several generations of regular criss-crossing or three-breed crossing.

² 1935, Minnesota Agr. Exp. Sta., Bul. 320.

Whether crossbreeding is a sound commercial policy depends on the balance between the extra size, vigor, fertility, etc., which is usually gained by crossbreeding and the extra cost of replacement which is incurred when the crossbred parents are replaced. Heterosis does not occur uniformly in all crosses. That is, not all breeds nor all animals within the same breed "nick" equally well. The heterosis from crossing breeds of farm animals is not apt to be larger than around 2 to 8 per

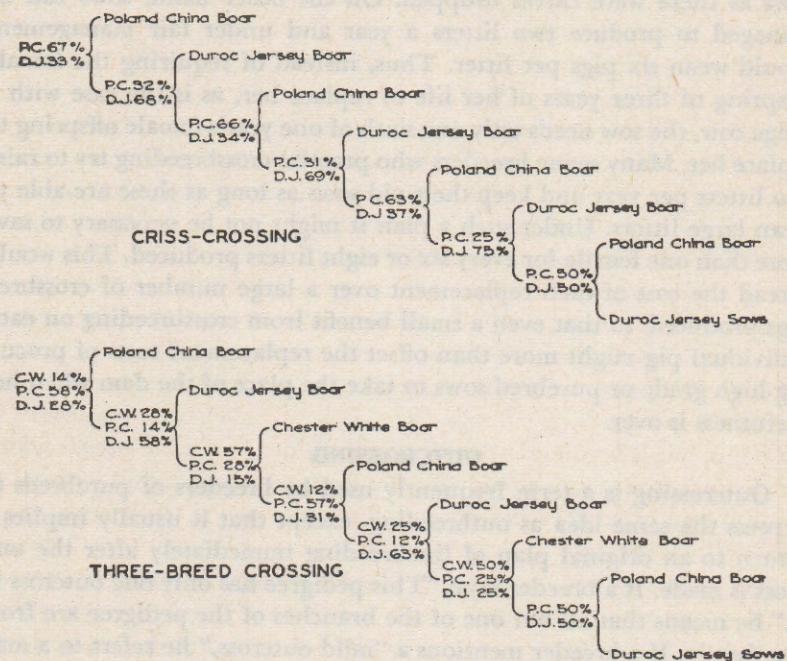


FIG. 45. Illustrative pedigrees of "criss-crossed" and "three-breed crossed" pigs.

cent increase over the average of the parental breeds for such things as size, growth rates, fertility, or other complex physiological traits. It is generally largest for vitality as measured by percentage raised of those born. There is nothing in animal breeding to correspond to the very large amount of heterosis which the corn breeders often find when they cross two inbred lines. Presumably the underlying principles are the same, but nothing corresponding closely to the inbred lines of corn exists in the breeds of farm animals.

Crossbreeding is most likely to be profitable where fertility is highest and the percentage of replacements necessary to keep up the female herd is lowest. For example, with cattle under most range conditions 70 calves weaned per 100 cows per year is considered a good calf crop. With

half the calves being females, a herd would need to be kept three years in order to produce enough females to replace the original cows even if all heifer calves which lived to weaning time were used without selection. If the average cow only stays in the herd about six to eight years, nearly half of all her daughters will be needed to maintain the number. If crossbreeding were practiced and all calves were sold for beef, this would necessitate an annual replacement of about one-fourth as many cows as there were calves dropped. On the other hand, sows can be managed to produce two litters a year and under fair management should wean six pigs per litter. Thus, instead of requiring the female offspring of three years of her life to replace her, as is the case with a range cow, the sow needs only one-sixth of one year's female offspring to replace her. Many swine breeders who practice crossbreeding try to raise two litters per year and keep their old sows as long as these are able to wean large litters. Under such a plan it might not be necessary to save more than one female for every six or eight litters produced. This would spread the cost of each replacement over a large number of crossbred pigs produced, so that even a small benefit from crossbreeding on each individual pig might more than offset the replacement costs of procuring high grade or purebred sows to take the place of the dam when her usefulness is over.

OUTCROSSING

Outcrossing is a term frequently used by breeders of purebreds to express the same idea as outbreeding, except that it usually implies a return to an original plan of linebreeding immediately after the outcross is made. If a breeder says: "This pedigree has only one outcross in it," he means that all but one of the branches of the pedigree are from one family. If a breeder mentions a "mild outcross," he refers to a mating with an animal which is not quite of the family he is breeding but which is related to it. A man after having practiced linebreeding for a time may say that he needs an outcross. In this case he means that he needs to mate his stock to animals from some other line; but the usual implication is that, after one generation of outbreeding, he will return to using animals of his original family, attempting by selection to hold the good traits introduced by the outcross, while by linebreeding to his chosen family again he tries to recapture and hold all the good traits he already had in that family. The corn breeders call this kind of a process "convergent improvement" when used on their more intensely inbred material.

Outcrossing is a minor part but eventually a necessary part of most linebreeding programs. Any linebreeding which is carried far is apt to fix some undesired traits so that mild outcrossing may be necessary to

remedy them. If the outcross is a success, the breeder is sometimes so carried away by enthusiasm for it that he gives up his plan of returning to his original family and decides to mate the outcrossed animals together. To do this is the same in principle, although less extreme in degree, as attempting to fix desired crossbred traits by breeding crossbred females to crossbred males.

BACKCROSSING

Backcrossing is the mating of a crossbred animal back to one of the pure parent races which were crossed to produce it. It is a term commonly used in genetic studies but not widely used by breeders. In genetic analyses, particularly where one of the parents possesses all or most of the recessive traits, the backcross permits a surer analysis of the genetic situation than an F_2 generation does. General experience with backcrosses in practical animal breeding has not been quite as satisfactory as experience with crossbreds. The backcrosses retain some of the heterosis in many cases, but rarely as much as the first crosses or the triple crosses.

TOPCROSSING

Topcross usually refers to the last sire in a pedigree. When a breeder mentions a "Scotch-topped" Shorthorn, he means a purebred Shorthorn whose dam belongs to a family not originating in Scotland but whose sire and perhaps maternal grandsire were "straight Scotch." When a breeder says that "this animal has four topcrosses of Scotch blood," he means that it is by a Scotch sire, that its dam is by a Scotch sire, that its maternal grandam is by a Scotch sire and that the dam of the maternal grandam is by a Scotch sire. Presumably the pedigree farther back in the maternal line is not Scotch.

Top crossing is the same in principle as grading, except that topcrossing is usually applied to different families within a pure breed, whereas grading is applied to the continued use of sires of one pure breed starting with foundation females which were of another breed or of no particular breed at all.

In plant breeding topcrossing is sometimes used to mean the production of seed by putting pollen from an inbred sire on plants from a good commercial variety.

GRADING

When the pure breeds were new and relatively scarce in this country, grading common or mongrel stock up to the purebred level by the continued use of sires of a pure breed was the quickest way available for improving commercial herds. Many of the experiment stations conducted experiments or demonstrations in the results of such grading.

Generally the first cross showed a marked improvement over the original stock. The further improvement made by each successive cross was progressively less. Grading can rapidly bring the stock near the level of the pure breed which is being used for the grading. Grading will remain the most important form of breeding for the commercial market as long as the merit of the pure breeds is distinctly above that of the commercial herds, and unless heterosis itself is so important that wider outbreeding plans, such as criss-crossing, are more profitable than continued grading to one pure breed. The fact that in so many grading experiments the major improvement has come in the first cross seems to indicate that some of the improvement in the first cross was from heterosis. No doubt the original mongrels in such experiments had at least a few desirable genes which should have been kept if there had been any way to select them and keep them while letting the rest of the genes from the mongrels be bred out by the continued grading.

SPECIES HYBRIDS

The mule is the only commercially important species hybrid in North American animal husbandry. Male mules are always sterile as far as is yet known. A few well-authenticated cases of fertile mare mules have been reported,³ but these have been so rare that they have had no commercial importance. These fertile mare mules might possibly be the means of transferring some characteristics from the ass species to the horse species or the reverse. Because mules are sterile the problems of mule breeding are only those of choosing the most suitable kinds or breeds of mares and of jacks for crossing. The reciprocal cross, called a "hinny," has been made many times, but is generally regarded as inferior to the mule as a work animal.

Crosses between zebu cattle and cattle breeds of European origin are of considerable economic importance in the Gulf coast region of the United States and in nearly all the tropical regions of the world. Some would regard these as species crosses, but the majority opinion is that zebras and the cattle of European origin are not distinct species. Intermediate types exist in the regions between their native lands, as in southeastern Europe, Asia Minor, southern Siberia, and the northeastern regions of Africa.

Crosses between European cattle and the American bison have been made. Some would regard this as a generic cross. The males are sterile, but many of the females are fertile. By backcrossing these females to cattle and to bison, attempts to form a new breed, the "cattalo," have been made on a fairly large scale, but commercial success was not achieved.

³ For two examples, see *Jour. of Heredity* 19:412-16, 1928.

Other species crosses which involve farm animals but have hardly passed the stage of zoological curiosities or menagerie specimens include: horse and zebra, European cattle and yak, American bison and yak, American bison and European bison or wisent, yak and zebu, mouflon and domesticated sheep, bactrian and dromedary camels, chicken and guinea hen, pheasant and hen, and peacock and hen. Hybrids between yaks and other cattle are economically important in some parts of China. Crosses between sheep and goats may start to develop, but the embryos die and are resorbed or aborted long before the normal gestation period is completed. A similar fate happens to the embryos from crosses of chickens and turkeys.

Species hybrids do not seem to offer as much opportunity for economic improvement in animal breeding as they do in plant breeding.

SUMMARY

Outbreeding generally leads to individual excellence but low breeding worth.

Outbreeding systems hamper progress in further improvement of a breed because they destroy families by constantly crossing together any which start to develop. They thus make the breed temporarily more uniform than if outbreeding were not practiced.

Crossbreeding is a special form of outbreeding where the parents belong to different breeds. It generally results in increased size, vitality and fertility; but the amount of this increase is variable in different crosses. The economy of crossbreeding depends upon whether the increase in these things is more than enough to balance the possible confusion and increase in cost of replacements under a crossbreeding system.

Crossbreeding is more apt to be profitable where fertility is highest and females can be kept for the longest period of time and where the cost of their replacement is lowest. Mainly for these reasons crossbreeding is practiced most widely with swine and poultry and next with sheep.

Outcrossing usually applies only to matings within a pure breed. It may mean the same thing as outbreeding but usually implies also an intention to return to the original family or strain after making the one outbreeding mating.

Backcrossing is mating a crossbred animal back to the same kind of animal as one or the other of its parents.

Topcross refers to the sire, maternal grandsire, and sires of the other females in the purely maternal line. Generally it is used only within pure breeds.

Grading is the continued use generation after generation of males

of one pure breed on an original foundation of another breed or of no particular breed. Grading is the most economical way of lifting the commercial stock rapidly toward the level of the purebreds.

REFERENCES

For recent reports on experiments with crossbreeding, see the following bulletins from agricultural experiment stations: Arkansas 411, California 598, Iowa 380, Minnesota 320, Mississippi 347, Nevada 153, Pennsylvania 279, and Wyoming 210. See also articles in *Journal of Animal Science* 1:213-20, and *Scientific Agriculture* 16:322-36 and 19:177-98. Also see mimeographed leaflet BDIM-Inf. 30, May 1946, from the USDA.

Mating Like to Like

Although many writings on animal breeding stress the importance of mating like to like, it is usually *selection* which is being discussed. The familiar recommendation to "breed the best to the best" usually implies that the worst (and the mediocre as far as numbers will permit) are to be discarded. That would be selection, whereas mating like to like would require also the mating of the worst to the worst and the mediocre to the mediocre—at least among those selected to be parents.

Actually some selection is always practiced; that is, the different types are not permitted to reproduce at equal rates. The nearest actual approach to mating like to like without selection occurs in breeds where there is a marked disagreement about the ideal type, some breeders working toward one goal and some toward another. So far as concerns those traits on which there is disagreement, these cases show some approach to the mating of like to like in the breed as a whole, although in each individual herd the practice is merely selection. There is a little of this at all times in all breeds because some breeders emphasize certain characteristics more and other characteristics less than other breeders do. Also a breeder who uses more than one sire at a time might, if he chooses, mate the best sire to the best females, the second best sire to the second best group of females, etc., until finally the poorest sire among those he uses will be left for mating to the poorest bunch of females which he keeps. This would be mating like to like within the selected group. By contrast he might try to balance the groups of females so that the mates of each sire would be about equal to the mates of every other sire in average merit. This he might well do if his primary object was an accurate progeny test of the sires. Or he might mate the best male to the poorest group of females he kept, the second best male to the next to the poorest group of females, etc. That would be mating unlikes within the group selected to be parents. That is the subject of the next chapter. "Best" and "worst" might describe net merit or, for one characteristic at a time, we could be more specific by using such terms as: largest or smallest, coarsest or most refined, most active or most sluggish, darkest or lightest, etc.

These illustrations will show how any given intensity of selection may be accompanied by any intensity of mating like to like, ranging from almost perfect positive through random mating to almost perfect negative. To see clearly what additional would be accomplished by superposing a system of mating like to like on a certain intensity of selection, which would be practiced anyhow, it is simplest to consider how mating like individuals together, regardless of pedigree, would change a population not under selection.

The fundamental difference in principle between inbreeding and mating like individuals together regardless of pedigree is that inbreeding is the mating of individuals which are apt to have *the same genes*, while assortive mating is the mating of individuals which tend to have *similar characteristics*, irrespective of their relationship. Characteristics are only partly caused by the genes, and it often happens that characteristics which appear to be the same are caused by very different combinations of genes. To the extent that variations in characteristics are caused by environment or by epistatic deviations or by dominance deviations, the mating of like individuals may cause only a slight tendency for mates to be alike in the genes they have. That can be expressed quantitatively as follows for purely assortive mating. If m is the correlation between the net hereditary values of mates, t the correlation between the visible or measurable characteristics of mates, and h the correlation between the characteristic and the net hereditary value of the same individual, then under purely assortive mating $m = h^2t$ and m cannot exceed h^2 , even if the breeder has succeeded in getting the mates to be perfectly alike (except for sex) in all characteristics he can see or measure. On the other hand, under purely inbreeding systems $t = h^2m$ and t cannot exceed h^2 . As a numerical example consider a moderately heritable characteristic for which $h^2 = .2$. Under purely phenotypic assortive mating m could not exceed .2 even if t were made perfect. In actual practice it would be less. By contrast in the first generation of full brother-sister inbreeding m would be .5 and t would be only .1. The actual consequences of phenotypic assortive mating depend largely on what size of m really is achieved. Hence they are very slight for characteristics moderate or low in heritability.

The example shown in Table 19 deals with variation in only one characteristic. The practical breeder must nearly always consider many traits. He will be using only one or at most a few sires but will have several females, no two of which are alike, to mate to each sire. Many of the animals he might choose to mate together are alike in some characteristics, moderately unlike in others, and perhaps extreme opposites in still others. If he considers many characteristics, it will be impos-

sible for him to achieve in all respects a high degree of resemblance between mates. This is in addition to the general situation, discussed in the preceding paragraph, that under assortive mating, likeness in net hereditary values will be less than outward likeness. In actual practice assortive mating can rarely cause m to have high values for any characteristic other than net merit.

ONE PAIR OF GENES

If only one pair of genes is involved and if there is no dominance or other reason for mistaking hereditary values—i.e., if h and t of the next to the last paragraph each equal 1.0—the results are the same as in self-fertilization. If dominance is complete but there is no other complication, the change is in the same direction and the final result is the same but progress is slower. If the attempt to mate like to like is not quite perfectly successful—i.e., if t is less than 1.0 or if anything other than dominance makes h less than 1.0—the population will come to equilibrium while a few heterozygotes still remain.

TWO PAIRS OF GENES—SIMPLEST CASE

If this mating of like to like is for a characteristic influenced by two pairs of genes, lacking dominance and with equal effects, then we have the situation shown in Table 19 which starts with a random breeding

TABLE 19
PROPORTIONS OF EACH PHENOTYPE UNDER A PERFECTLY ACCURATE SYSTEM OF MATING
LIKE TO LIKE, q_A AND q_B REMAINING AT .5

Genotypes	aabb	aaBb Aabb	aaBB AAbb AaBb	AaBB AABb	AABB
Phenotypes	No Plus Genes	1 Plus Gene	2 Plus Genes	3 Plus Genes	4 Plus Genes
Generation:					
Start.....	6.2%	25.0%	37.5%	25.0%	6.2%
1.....	13.6%	20.8%	31.2%	20.8%	13.6%
2.....	19.3%	16.5%	28.4%	16.5%	19.3%
3.....	23.9%	13.8%	24.6%	13.8%	23.9%
.....
∞.....	50.0%	0.0%	0.0%	0.0%	50.0%

population in which the two pairs of genes are independent and the two alleles of each pair are equally abundant, that is, in which $q_A = q_B = .5$.

The result is a decrease in the proportion of the intermediate

phenotypes and a corresponding increase in the two extreme phenotypes. If the mating of like to like is perfect and is carried on forever, it approaches as a limit the condition in which all of the genotypes have disappeared except the two homozygous extreme ones. If the mates are not exactly alike phenotypically, as, for example, if an occasional mistake is made in classifying an individual, progress will be slower, and the ultimate goal will be an equilibrium which falls short of complete fixation of the two extreme phenotypes.

This system of breeding tends to fix the extreme types, provided those are both outwardly and genetically extreme; but, in contrast to inbreeding, it cannot fix intermediate types. The likeness between parent and offspring and the likeness between full brothers increases very rapidly, although that may not be clear from this example. The variability of the population is greatly increased, since the population tends to become concentrated at the two extremes.

MANY PAIRS OF GENES

Many more than two pairs of genes may affect the characteristic, and the effects of the different pairs of genes will rarely be equal. The more genes there are, the slower is the rate of increase in homozygosis. The likeness of parent and offspring or of full brothers also increases at a slower rate when n is large, although these likenesses are not nearly as much affected by changes in gene number as is the rate of increase in homozygosis.

GENERAL RESULTS OF MATING LIKE TO LIKE

Very little genuine fixation of type is ever accomplished by this system of breeding because increase in homozygosis is dependent upon the number of genes being very small and upon the breeder's not being deceived by dominance, environmental effects, or epistasis. Figure 46 shows what happens to homozygosis as a result of mating like to like. Here n is the number of gene pairs involved, while m is the correlation between the net hereditary values of mates. Both m and n set limits on the amount of homozygosis which may finally be attained, and n has a tremendous influence on the rate at which it is attained. Only with very high values of m and very low values of n can such a breeding system alter homozygosis much. The values of m cannot often be high in actual practice, and n will probably be large for all characteristics of much economic importance.¹

¹ The fraction of the heterozygosis of a random breeding population which will still remain when assortive mating has done all it can is $\frac{2n(1-m)}{2n(1-m)+m}$. Since m cannot exceed 1.0 (it must usually be much smaller) and n can be large, this fraction will rarely be much less than unity. *Genetics*, 6:153.

Mating like to like increases the resemblance of parent and offspring very much, each individual resembling its sire not only because it received half its inheritance from him but also because it received half its inheritance from its dam who resembled the sire more than if mating had been random. That is, the dam was chosen to have many genes

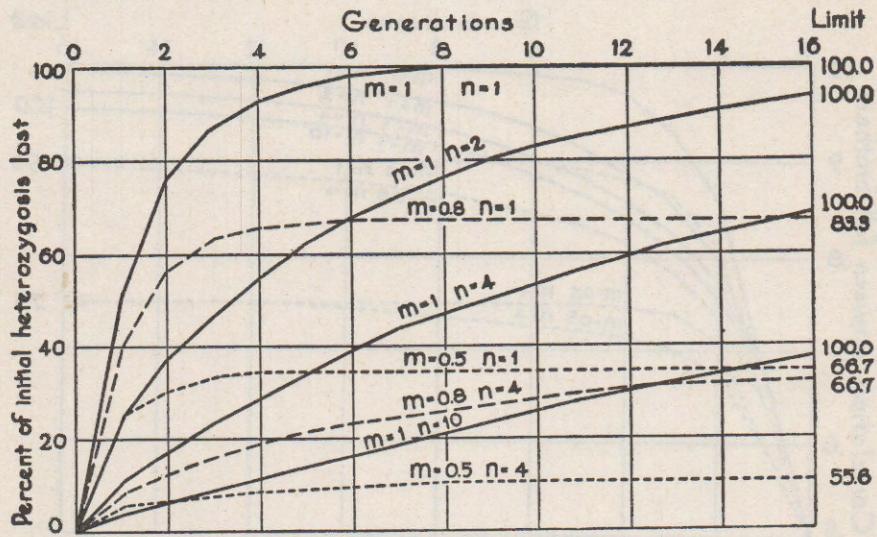


FIG. 46. The percentage of initial heterozygosity which is lost by continued assortative mating of various intensities, m , and with n pairs of equal genes involved. (After Wright in *Genetics*, 6:175.)

which produce the same kinds of effects as the sire's genes do, although they may not be genes from the same allelic series. The limit which the parent-offspring correlation approaches is determined by m , large n merely making the approach to that limit a little slower. The parent-offspring correlation goes far toward its limit in the first two generations in which mating like to like is practiced.

Figure 47 shows what happens to the correlation between full brothers under purely assortive mating in the extremely simple case of no dominance, no epistasis, and no environmental variations which are incorrectly discounted. The limits are determined by m and the only effect of large n is to make progress a little slower. This system of breeding has considerable effect, even when m is small and n is large. The existence of dominance and epistasis and environmental effects has the effect of making m lower than it need be otherwise. Environmental effects might increase the correlations if these effects tended to be the same for brothers.

A high degree of resemblance between parent and offspring and a

high degree of resemblance between full brothers seem to indicate that the breeder is gaining control over his material, but that is partly contradicted by the fact that there is little increase in real homozygosis. This has long been recognized in a general way by breeders in the confidence they have in the mating of like to like as a means of getting the

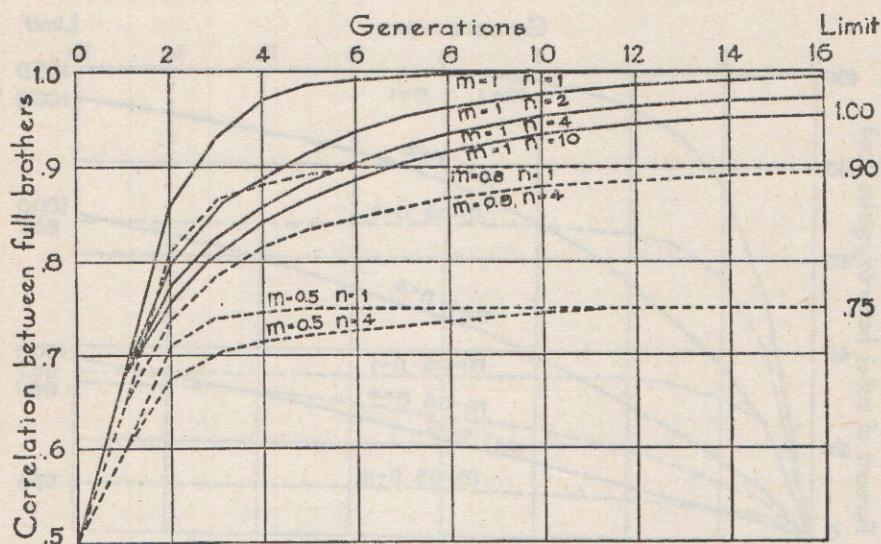


FIG. 47. The correlations between brothers in successive generations under different degrees, m , of assortive mating and with n pairs of genes involved. (After Wright in *Genetics*, 6:170.)

kind of herd they want, but again and again the more experienced among them express the idea that inbreeding is really necessary if type is to be "fixed."

Mating like to like is one of the most powerful tools which breeders have for creating extreme diversity in a population. Inbreeding tends to fix intermediate families as well as extreme ones and thereby tends to double the additive genetic variance of the population. But mating like to like tends to scatter the population toward the two opposite extremes of each characteristic for which it is practiced. For example, assortive mating for stature within most local races of man is enough to make the standard deviation about 20 or 25 per cent larger than it would be if mating were entirely random with respect to stature. If the characteristic is highly enough hereditary that m in assortive mating can rise above .5, mating like to like can make the standard deviation in an unselected population larger than the most extreme inbreeding can.²

² *Genetics*, 6:154.

In each individual herd the mating of like to like will usually be accompanied by selection which will discard one or the other extreme. If all breeders select toward the same ideal, this will not change the variability of the whole breed any more than selection changes the variability within a single herd. But if the breeders disagree markedly about the ideal and some of them discard animals which other breeders think are very desirable, this process can easily produce a lack of uniformity, in the breed as a whole, so pronounced that everyone familiar with the breed will be aware of it. Examples which have shown some tendency in that direction are: "Island type" and "American type" in Jerseys; "hot bloods" and "big types" in Poland-Chinas. Even when all breeders work toward the same ideals, a little of this herd heterogeneity within a breed will arise because some breeders will try harder than others or will be financially able to outbid others for the animals thought best. Such inequality of striving toward the same ideal produces to a very mild degree something of the same results as a divergence of ideals.

The changes brought about by purely assortive mating are temporary. If there has been no accompanying selection, the population returns far toward its initial condition in the very first generation after random mating is resumed. In actual practice there will, of course, have been some selection; and that is apt to have changed gene frequency enough that the population will never return exactly to its initial condition.

SUMMARY

Mating like to like has almost no effect on homozygosity except in very simple and rare genetic circumstances.

Mating like to like immediately increases the resemblance between parent and offspring and between full brothers.

Mating like to like comes near to the full limit of its effects within a very few generations after it is begun.

Mating like to like tends to scatter a population toward the two extremes with respect to each character for which such mating is practiced. It, therefore, greatly increases the variability of the population if both extremes are kept and heritability is high.

In actual practice mating like to like is always accompanied by selection.

The effects of mating like to like disappear almost at once when random mating is resumed, except as the accompanying selection may have made some permanent changes in gene frequency.

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CHAPTER 28

Mating Unlike Individuals

The mating of unlike individuals (negative assortive mating on the basis of somatic resemblance) is most commonly practiced either to mark time while the breeder is deciding what his goal is to be or, where the ideal is an intermediate, to correct defects by mating each animal to one which is equally extreme but in the opposite direction. This is sometimes called *compensatory* mating.

Everyone does some of this from time to time, at least for minor traits. There are no absolutely perfect animals. A breeder usually realizes that his females are good in some respects but below his standard in others. Under such circumstances he is almost certain to seek for his next sire one which is particularly strong where his females are weak. Since he cannot find a sire which is absolutely perfect in all respects, he will accept one which is a little below his standard in characteristics for which the females are unusually good. In the breeding of Rambouillet or Merino sheep, it is common practice for breeders to seek "light C" rams to mate to their "heavy B" ewes and "heavy B" rams to use on their "light C" ewes. Many are confident that this type of mating is more apt to produce a high percentage of lambs which are on the borderline of being the desired heavy C's or light B's than would be produced from parents both of which were the desired type. Another prominent example of mating unlikes is in the breeding of dual-purpose cattle, where there is considerable mating of those which vary most toward the extreme dairy type with others which vary most toward the extreme beef type.

CONSEQUENCES

The consequences of mating unlikes are the reverse of those mating like to like. Heterozygosity is increased only a very little. The maximum effect of mating unlikes, even if continued indefinitely, would be

to make the heterozygosity $\frac{2n(1-m)}{2n(1-m)+m}$ of what it would be under random mating, m being negative. In the impossibly extreme case when

$m = -1.0$, that would increase the heterozygosity by only $\frac{1}{4n-1}$ of what it would be under random mating. That would increase heterozygosity by one-third if only one pair of genes were involved, by one-seventh if there were two pairs, only by one-eleventh if there were three, etc. If the value of m is nearer zero, the power of this breeding system to affect heterozygosity will be still further reduced. When m is as near zero as -2 , the increase in heterozygosity cannot exceed one-eleventh of the original amount even when n is 1 and cannot exceed one-forty-seventh if n is 4. Since m must usually be low and n may well be large, it is obvious that average homozygosity is scarcely affected at all.

The mating of unlikes together makes the correlation between parent and offspring distinctly lower, since the two parents are quite different from each other and the effects of the genes which an offspring inherits from one tend to be canceled by the effects of the genes it inherits from the other. Likewise, this system of mating tends to lower the correlation between brothers, although not as much as the correlation between parent and offspring is lowered.

Mating unlikes together tends to make the whole population uniform since an extreme individual in one direction tends to be mated with one which is extreme in the other. The offspring of each mating thereby usually average nearer the population average than they would if mating were random. If mating were random, there would be some matings where both parents happened to be extreme in the same direction. This reduction in variability nearly reaches its limit within the first and second generations after the mating of unlikes begins. In the very first generation produced by mating unlike individuals, the vari-

ance becomes $\frac{2+m}{2}$ times what it was under random mating. Of course m is negative, but it has to be small unless heritability is high. The maximum effect on the variability of a whole population occurs when n is large and m is strongly negative. That maximum effect is to halve the variance when $m = -1.0$ and n is very large. If $m = -4$, the maximum effect is to reduce the variance two-sevenths when n is very large and one-sixth when n is only 1. The original variability will reappear almost at once when the mating of unlikes is abandoned.

A system of mating unlikes is most useful when the desired type is an intermediate. Under such conditions the maximum proportion of desired individuals among the offspring can be obtained by mating males which are of the desired type to females which are also of the desired type and mating any breeding animals which deviate from the ideal in one direction to those which deviate equally far in the other direction.

Mating unlikes together is extensively practiced commercially to correct defects. This is a sound practice wherever there are enough females undesirably extreme in one direction to justify the keeping of a male equally extreme in the other direction.

SUMMARY

Mating unlikes together in the absence of selection leads to:

1. A more uniform population than under random mating, with a larger percentage of intermediate offspring and fewer extremes in either direction. This increased uniformity reaches nearly its full extent in the first generation after the mating of unlikes is begun. If the mating of unlikes ceases, the population returns almost at once to its original variability under random mating.
2. Only a slight increase in heterozygosity under the very simplest genetic situations and practically no change in heterozygosity under the situations apt to be encountered.
3. A distinctly lower resemblance between parent and offspring and a somewhat lower resemblance between other relatives than under random mating.

Mating unlikes is useful in holding the population together as a more uniform group until the average type or some other intermediate type can be fixed by close inbreeding.

Mating unlikes is useful in correcting defects wherever the ideal is intermediate and some animals are too extreme in one direction while others are too extreme in the other direction.

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CHAPTER 29

The Relative Importance of Sire and Dam

In general, sire and dam are equally important in inheritance. There are three exceptions which are sometimes of practical importance. The first is that a sire can have many more offspring in a single season.¹ Therefore, the sire is much more important than any one dam in determining the inheritance of the next generation in the herd, although not more important in determining the inheritance of any one animal. This is the basis for the common statement that "The sire is half the herd."² The second exception is sex-linked inheritance. The general rule in sex-linked inheritance is that sons are more like their dams, and daughters are more like their sires than in ordinary inheritance. The third exception is the one already discussed in Chapter 14 that where the merits of the two parents are not equally well known, less attention should be paid to the less well known one in estimating the merits or breeding value of their offspring.

HIGHER FERTILITY OF THE SIRE

When a breeder with a one-sire herd buys a sire, he is buying half the inheritance of many offspring. When he buys a dam he is buying half the inheritance of her sons and daughters only. Therefore, he can afford to spend more money to procure a desirable sire than to procure an equally desirable female.

Every individual has as many female as male ancestors. Because of the larger number of offspring per male used for breeding than per female, it is the usual rule that a breed is influenced more by some of its males than by any equal number of females. However, about half of what the male transmits came to him from his dam. It occasionally

¹ Monogamous species, such as pigeons, doves, and some foxes, are exceptions to this. Among them the sire generally leaves about the same number of offspring as the dam.

² This statement is an exaggeration in the many cases where a sire is kept in service for less than the average length of a generation. For example, in small dairy herds, one sire is rarely used much more than two years; but the average productive life of the cows is more nearly four years. Rarely are more than half the cows in a herd daughters of one bull. Only half of their genes come from him; hence one sire rarely furnishes more than a fourth of the genes of the whole herd, although he does furnish half of the genes of his own offspring.

happens that a female will exert more influence on a breed than any contemporary male. A notable case is that of the Holstein-Friesian cow, De Kol 2nd, whose relationship to the whole breed (about 10 per cent) is more than that of any other cow or bull. She is almost a great grandam of the whole breed today.³ Naturally she could not exert this much influence by having an enormous number of calves, although she did live at least 16 years and produced 14 calves. She exerted her remarkable influence on the breed through the fact that she had five different sons which were quite prominent sires of the breed in their time and saw extended service in leading herds. At least four other sons and one daughter also left registered descendants. This is an exceptional case, yet it illustrates how a female may exert a tremendous influence on a breed if several of her sons are saved for extensive use. There is some reason for thinking that more improvement in the dairy breeds can be accomplished by the careful selection of cows which are to be the dams of sires and therefore the grandams of the next generation than can be done directly by selecting among the bulls. However, the exact balance of the quantitative relations involved here is not yet clear.

SEX-LINKED INHERITANCE

In all farm animals except poultry, so far as is yet known, the male has an *X* and a *Y* chromosome and the female has two *X* chromosomes. In poultry this situation is reversed. The discussion which follows may be applied to poultry by substituting the other sex.

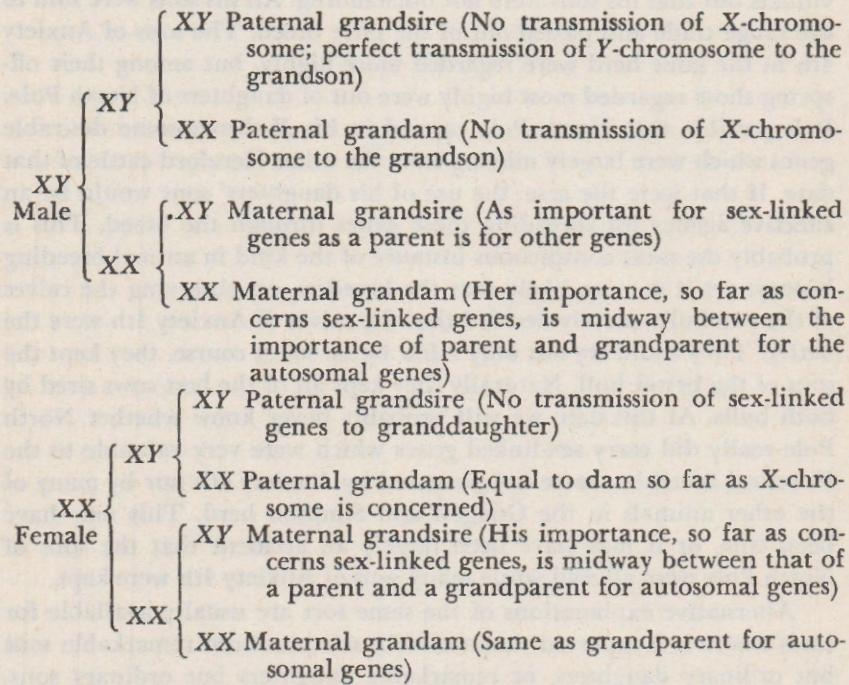
Genes carried by the *Y* chromosomes would, of course, be transmitted from sire to son in unbroken lines if there were no crossing over between *X* and *Y*. It would not be easy to distinguish the effects of such genes from secondary sexual characteristics. It is unlikely that the *Y* chromosomes can often, if ever, be entirely empty, or they would have been lost long ago without harm to the species. Yet genetic research has found only a few genes on *Y* chromosomes.

In some species of fish, in man, and perhaps in most mammals, some parts of the *X* chromosomes are homologous with parts of the *Y* chromosomes and these can cross over. Genes carried in these regions show "partial sex-linkage." Their behavior is intermediate between that of autosomal genes and that of the completely sex-linked genes which are carried on the nonhomologous parts of the *X* chromosome. The latter are meant when sex-linkage is discussed in the following pages. Examples of partially sex-linked genes in man are those for retinitis pigmentosa and those for *total* color blindness. The genes for the ordinary red-green color blindness are completely sex-linked.

The genes carried on the *X* chromosomes are those responsible for

³ *Jour. of Heredity*, 27:61-72.

sex-linked traits. The male receives all of his sex-linked genes from his dam; and, so far as those genes are concerned, he is no relative at all of his sire. The female receives half of her sex-linked genes from her dam and half from her sire just as with her other genes. But her sire can only transmit one kind of X chromosome to her, whereas the dam can transmit either one of the pair she has. So far as daughters are concerned, this amounts to the same thing as if the sires were completely homozygous for their sex-linked genes, whereas the dams are as heterozygous for sex-linked genes as they are for other genes. Consequently, paternal half sisters will receive from their sire identical sex-linked genes; but maternal half sisters need not be any more like each other in sex-linked genes than they are in other genes. The following pedigree diagrams of the X and Y chromosome situation for males and for females show what happens when this is extended to the grandparental generation. The notes show the part which each grandparent plays in the sex-linked inheritance of the grandson or granddaughter.



If it is assumed, on the basis of chromosome number, that about 5 per cent of the genes are sex-linked, then the expected statistical effects of sex-linkage are those shown in the last two columns of Table 20. The existence of sex-linkage will have so small an effect that for most charac-

teristics it would be difficult to prove that there is any sex-linkage. Differences in the correlations observed between various kinds of relatives have sometimes been interpreted as indicating sex-linkage, but it is rarely possible to be sure that such differences were not caused by (1) sampling errors, (2) greater similarity of environment for some kinds of relatives or (3) differences in the selection which had been practiced for various kinds of relatives. It is to be expected that there will be some sex-linkage in the inheritance of most characteristics which are affected by many genes but that only rarely will a large fraction of the genes be sex-linked. In such rare cases the corrections will more nearly approach those in columns 1 and 2 of Table 20. The main point which Table 20 demonstrates is that only rarely will sex-linkage alter resemblances noticeably.

In breed lore there are many cases where a sire was noted for his daughters but not for his sons, or vice versa. In Hereford history it is said that the daughters of North Pole were exceptionally good individuals but that his sons were not outstanding. All his sons were sold to the range trade and passed out of the pure breed. The sons of Anxiety 4th in the same herd were regarded more highly, but among their offspring those regarded most highly were out of daughters of North Pole. It is possible that North Pole carried in his X-chromosome desirable genes which were largely missing from the other Hereford cattle of that date. If that were the case, the use of his daughters' sons would be an effective agency for spreading those genes through the breed. This is probably the most conspicuous instance of the kind in animal breeding history; yet it is more likely that the breeders, on observing the calves of the two bulls, merely decided that the calves of Anxiety 4th were the better. They could try out only a few bulls; so, of course, they kept the sons of the better bull. Naturally they kept all of the best cows sired by both bulls. At this date we will probably never know whether North Pole really did carry sex-linked genes which were very valuable to the Hereford breed but were not possessed by Anxiety 4th nor by many of the other animals in the Gudgell and Simpson herd. This may have been true, or it may have been largely an accident that the sons of North Pole were all sold while many sons of Anxiety 4th were kept.

Alternative explanations of the same sort are usually available for cases where it is reported that a certain sire produced remarkable sons but ordinary daughters, or remarkable daughters but ordinary sons. Sex-linkage is a possible explanation in such cases, but it is probable that the major factor has usually been the selection which the breeder practiced and whether he was at that time selling many males to head other herds or was selling only females.

TABLE 20
EXPECTED EFFECTS OF SEX-LINKAGE ON CORRELATIONS* BETWEEN MALES OR FEMALES
AND VARIOUS OF THEIR RELATIVES

	All Genes Sex-linked		Male or Female	5% of Genes Sex-linked	
	Male	Female		Male	Female
<i>Ancestors</i>					
Sire.....	.00	.71	.50	.487	.512
Dam.....	.71	.50	.50	.512	.500
Paternal grandsire.....	.00	.00	.25	.244	.244
Paternal grandam.....	.00	.50	.25	.244	.268
Maternal grandsire.....	.50	.35	.25	.268	.256
Maternal grandam.....	.35	.25	.25	.256	.250
<i>Collateral relatives</i>					
Full brother.....	.50	.35	.50	.500	.494
Full sister.....	.35	.75	.50	.494	.515
Paternal half brother.....	.00	.00	.25	.244	.244
Paternal half sister.....	.00	.50	.25	.244	.268
Maternal half brother.....	.50	.35	.25	.268	.256
Maternal half sister.....	.35	.25	.25	.256	.250
<i>Half first cousin (female)</i>					
Through paternal grandsire.....	.00	.00	.062	.061	.061
Through paternal grandam.....	.00	.25	.062	.061	.083
Through maternal grandsire.....	.18	.125	.062	.073	.067
Through maternal grandam.....	.09	.062	.062	.064	.062

* For traits entirely determined by heredity, without dominance or epistasis and in a population breeding at random.

SUMMARY

Because the sire can have so many more offspring per year than the dam, he is a more important individual than any one female so far as the whole herd is concerned, although not more important so far as concerns any one offspring.

This makes it possible to cull prospective sires more closely than prospective dams and profitable to pay more for an unusually good sire than for an equally good dam.

Every individual has the same number of female and male ancestors. A female who has more than two sons which are widely used may exert more influence on a breed than any one of her sons. This has actually happened at times, although most animals which have influenced a breed much have been males.

Sex-linked inheritance has the effect of making daughters resemble their sires, and sons resemble their dams, more closely than if there were no sex-linkage. This is not often important.

Most cases reported from animal breeding history where a certain

sire produced good daughters but ordinary sons, or the reverse, are probably to be explained as incidental results of the sales or culling policy in that herd. Sex-linkage may have played a part in some of these cases.

Sometimes one side of the pedigree will seem to be more important than the other merely because more is known about it, and therefore more use can be made of it for prediction.

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