CHAPTER IX

THE EFFECTS OF INBREEDING

WHAT is the probable source of the evil effects which have been frequently observed to follow inbreeding?

By inbreeding we mean the mating of closely related individuals. As there are different degrees of relationship between individuals, so there are different degrees of inbreeding. The closest possible inbreeding occurs among plants in what we call self-pollination, in which the egg-cells of the plant are fertilized by pollen-cells produced by the same individual. A similar phenomenon occurs among some of the lower animals, notably among parasites. But in all the higher animals, including the domesticated ones, such a thing is impossible because of the separateness of the sexes. For here no individual produces *both* eggs and sperm. The nearest possible approach to self-pollination is in such cases the mating of brother with sister, or of parent with child. But this is less close inbreeding than occurs in self-pollination, for the individuals mated are not in this case *identical* zygotes, though they may be *similar* ones.

It has long been known that in many plants self-pollination is habitual and is attended by no recognizable ill-effects. This fortunate circumstance allowed Mendel to make his remarkable discovery by studies of garden-peas, in which the flower is regularly self-fertilized, and never opens at all unless made to do so by some outside agency. Self-pollination is also the rule in wheat, oats, and the majority of the other cereal crops, the most important economically of cultivated plants. Crossing can in such plants be brought about only by a difficult technical process, so habitual is self-pollination. And crossing, too, in such plants is of no particular benefit, unless by it one desires to secure new combinations of unit-characters.

In maize, or Indian corn, however, among the cereals, the case is quite different. Here enforced self-pollination results in small unproductive plants, lacking in vigor. But racial vigor is fully restored by a cross between two depauperate unproductive individuals obtained by self-fertilization, as has recently been shown by Shull. This result is entirely in harmony with those obtained by Darwin, who showed by long-continued and elaborate experiments that while some plants do not habitually cross and are not even benefited by crossing, yet in many other plants crossing results in more vigorous and more productive offspring; that *further, the advantage of crossing in such cases* has resulted in the evolution in many plants of floral structures, which insure crossing through the agency of insects or of the wind.

In animals the facts as regards close fertilization are similar to those just described for plants. Some animals seem to be indifferent to close breeding, others will not tolerate it. Some hermaphroditic animals (those which produce both eggs and sperm) are regularly self-fertilized. Such is the case, for example, with many parasitic flat-worms. In other cases self-fertilization is disadvantageous. One such case I was able to point out some fifteen years ago, in the case of a sea-squirt or tunicate, Ciona. The same individual of Ciona produces and discharges simultaneously both eggs and sperm, yet the eggs are rarely self-fertilized, for if self-fertilization is enforced by isolation of an individual, or if self-fertilization is brought about artificially by removing the eggs and sperm from the body of the parent and mixing them in sea-water, very few of the eggs develop, — less than 10 %. But if the eggs of one individual be mingled with the sperm of any other individual whatever, practically all of the eggs are fertilized and develop.

In the great majority of animals, as in many plants, self-fertilization is rendered wholly impossible by separation of the sexes. The same individual does not produce *both* eggs and sperm, but only one sort of sexual product. But among sexually separate animals the same degree of inbreeding varies in its effects. The closest degree, mating of brother with sister, has in some cases no observable ill-effects. Thus, in the case of a small fly, Drosophila, my pupils and I bred brother with sister for fifty-nine generations in succession without obtaining a diminution in either the vigor or the fecundity of the race, which could with certainty be attributed to that cause. A slight diminution was observed in some cases, but this was wholly obviated when parents were chosen from the more vigorous broods in each generation. Nevertheless crossing of two inbred strains of Drosophila, both of which were doing well under inbreeding, produced offspring superior in productiveness to either inbred strain. Even in this case, therefore, though inbreeding is tolerated, cross-breeding has advantages.

In the case of many domesticated animals, it is the opinion of experienced breeders, supported by such scientific observations as we possess, that decidedly bad effects follow continuous inbreeding. Bos ('94) practiced continuous inbreeding with a family of rats for six years. No ill-effects were observed during the first half of the experiment, but after that a rapid decline occurred in the vigor and fertility of the race. The average-sized litter in the first half of the experiment was about 7.5, but in the last year of the experiment it had fallen to 3.2, and many pairs were found to be completely sterile. Diminution in size also attended the inbreeding, at the end amounting in the case of males to between 8 and 20 %.

Experiments made by Weismann confirm those of Bos as regards the falling off in fertility due to inbreeding. For eight years Weismann bred a colony of mice started from nine individuals, — six females and three males. The experiment covered 29 generations. In the first 10 generations the average number of young to a litter was 6.1; in the next 10 generations, it was 5.6; and in the last 9 generations, it had fallen to 4.2. But sweeping generalizations cannot be drawn from these cases. Each species of animal must probably be tested for itself before we shall know what the exact effects of inbreeding are in that case. In guinea-pigs, a polydactylous race built up by the closest inbreeding out of individuals all descended from one and the same individual has now been in existence for ten years. It consists of one of the largest and most vigorous strains of guinea-pigs that I have ever seen, and has shown no indications of diminished fertility.

In the production of pure breeds of sheep, cattle, hogs, and horses inbreeding has frequently been practiced extensively, and where in such cases selection has been made of the more vigorous offspring as parents, it is doubtful whether any diminution in size, vigor, or fertility has resulted. Nevertheless it very frequently happens that when two pure breeds are *crossed*, the offspring surpass either pure race in size and vigor. This is the reason for much cross-breeding in economic practice, the object of which is not the production of a new breed, but the production for the market of an animal maturing quickly or of superior size and vigor. The inbreeding practiced in forming a pure breed has not of necessity *diminished* vigor, but a cross does temporarily (that is in the F_1 generation) *increase* vigor above the normal. Now why should inbreeding unattended by selection decrease vigor, and cross-breeding increase it? We know that inbreeding tends to the production of homozygous conditions, whereas cross-breeding tends to produce heterozygous conditions. Under self-pollination for 1 generation following a cross, *half* the offspring become homozygous; after 2 generations, ¾ of the offspring are homozygous; after 3 generations ⅞ are homozygous, and so on. So if the closest inbreeding is practiced there is a speedy return to homozygous, pure racial conditions. We know further that in some cases at least heterozygotes are more vigorous than homozygotes. The heterozygous yellow mouse is a vigorous lively animal; the homozygous yellow mouse is so feeble that it perishes as soon as produced, never attaining maturity. Cross-breeding has, then, the same advantage over close-breeding *that fertilization has over parthenogenesis.* It brings together differentiated gametes, which, reacting on each other, produce greater metabolic activity.

Inbreeding, also, by its tendency to secure homozygous combinations, tends to bring to the surface latent or hidden recessive characters. If these are in nature defects or weaknesses of the organism, such as albinism and feeble-mindedness in man, then inbreeding is distinctly bad. Existing legislation against the marriage of near-of-kin is, therefore, on the whole, biologically justified. On the other hand, continual crossing only tends to *hide* inherent defects, not to exterminate them; and inbreeding only tends to bring them to the surface, not to *create* them. We may not, therefore, lightly ascribe to inbreeding or intermarriage the *creation* of bad racial traits, but only their manifestation. Further, any racial stock which maintains a high standard of excellence under inbreeding is certainly one of great vigor, and free from inherent defects.

The animal breeder is therefore amply justified in doing what human society at present is probably not warranted in doing, — viz. in practicing close inbreeding in building up families of superior excellence and then keeping these pure, while using them in crosses with other stocks. For an animal of such a superior race should have only vigorous, strong offspring if mated with a healthy individual of any family whatever, within the same species. For this reason the production of "thoroughbred" animals and their use in crosses is both scientifically correct and commercially remunerative.

BIBLIOGRAPHY

Bos, Ritzema.
1894. "Untersuchungen ueber die Folgen der Zucht in engster Blutverwandtschaft." *Biol. Centrbl.*, 14, pp. 75–81.

Castle, W. E., Carpenter, F. W., Clark, A. H., Mast, S. O., and Barrows, W. M.
"The Effects of Inbreeding, Cross-breeding and Selection upon the Fertility and Variability of *Drosophila.*" *Proc. Amer. Acad. Arts and Sci.*, 41, pp. 731–786.

Guaita, G. von.
1898. "Versuche mit Kreuzungen von verschiedenen Rassen des Hausmaus." *Ber. naturf. Gesellsch. zu Freiburg*, 10, pp. 317–332. [Contains observations of Weismann.]