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THE FERTILITY OF HYBRIDS IN A MAMMALIAN SPECIES-CROSS

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Sterility is a common phenomenon in the hybrids obtained by mating members of distantly related groups or types, both in animals and in plants. In fact, there is a tacit understanding among the taxonomists that members of the same species produce fertile offspring when mated inter se; but a successful cross between members of different species or genera may result in sterility of one or both sexes among the hybrids. In case both sexes are sterile, a further genetic study becomes impossible. When one sex alone among the hybrids is sterile, that sex is usually the male; and since the females are fertile, it becomes possible to study the inheritance of characters and fertility of offspring by crossing these female hybrids back to the males of either parent species.

Among mammals, at least, work on inheritance and fertility in species crosses is in its inception. Various compilers, such as Rörig and Przibram, have given lists of mammalian species crosses, with brief mention of the partial or complete dominance of one parent, and the fertility of the hybrids, when known. Grateful as we are for the facts that are thus accumulated, we must, nevertheless, admit their general inadequacy; for most mammalian species crosses were made by those who were merely interested in sheer possibility of the cross. Those breeders who are interested in the economic mammals have been the most fortunate, because most attention has been directed to their study. The consensus of opinion is that the time-honored cross between horse and ass results in sterile male mules but that the female mule is occasionally fertile with either the horse or ass (Waldow von Wahl, 1907). The zebroid (zebra × horse) is supposedly sterile in both sexes (Ewart, 1899; Iwanoff, 1911). The same is true of the zebrule (zebra × ass). When the cow and bison are crossed, they produce fertile female catteloes, but sterile males (Boyd, 1908; Iwanoff, 1911).

The offspring of the fertile female mule have merely been mentioned, but further reports regarding their fertility and other characters are lacking. The female hybrids between the cow and bison have been crossed back to males of both parent stocks, thus producing one-quarter bison, or three-quarters bison. The one-quarter bison females are fertile, as may be expected. The three-quarters bison female have not been fully tested, but are possibly also fertile. The one-quarter bison males are not always fertile, for Boyd reports the appearance of but one out of four tested males. Iwanoff reports a fertile three-quarters bison male; and supposes, on purely theoretical grounds, that a mating of such a fertile male with a quarter-bison female would result in fertile one-half bison of both sexes.

Material.—It has been the good fortune of the writer to work with the progeny of a mammalian species cross which in many respects is comparable to the horse-ass cross and bison-cow cross. It is my purpose to report briefly on the fertility of these offspring. The parent species were the wild Brazilian cavy (Cavia rufescens) and the domesticated guinea-pig (Cavia porcellus). The two forms differ consistently and clearly in color, texture of hair, size, shape of skulls and skull sutures, tooth formation, and the like. There is no doubt but that the two parent stocks are separate species; for, even if the evidence of the systematist were really arbitrary, such evidence must obtain more weight when one considers that the male hybrids are completely sterile.

The original crosses between these two species were the result of mating the wild males to the tame females. The reciprocal cross was not attempted, for, it was feared that the smaller wild female would succumb in pregnancy when mated to the much larger sized tame male. The wild males were wholly fertile, with tame females, although matings were secured only with much difficulty. The tame females bore their hybrid young in due time and with the usual guinea-pig average per litter. Now since the average number per litter in the tame guinea-pig is much larger than in the wild, and since a tame female gives this larger average, even when impregnated by a wild male, we have every reason to believe that such wild males are wholly fertile with tame females and the abundant number of spermatozoa insures complete fertilization. Having obtained these one-half wild hybrids, the females were mated back to the wild males and the tame guinea-pig males, producing three-quarters wild, and one-quarter wild respectively. The matings to the wild males were not very successful and only one three-quarters wild male was reared

to maturity. He was sterile. The matings to the tame males were wholly successful, and produced 83 one-quarter wild. Pursuing the same method of mating the hybrid females of one generation back to the tame guinea-pig males, there were produced a regular series of more dilute wild-blooded generations ranging from $\frac{1}{4}$ wild to the $\frac{1}{512}$ wild. In all, over 1700 hybrids of various blood dilutions have thus been produced. The fertility of about 400 male hybrids has been tested. All female hybrids are fertile.

Problems.—The wild males were wholly fertile in captivity, hence captivity itself may be eliminated as a factor causing the sterility of their less wild hybrid sons. The problem immediately suggested itself: how great must be the blood dilution, or for how many generations must the hybrid females be crossed back to the guinea-pig in order to eventually produce fertile male hybrids? When fertile male hybrids were produced, would all their offspring be fertile in both sexes, if such males were mated to their hybrid sisters or guinea-pig females?

Method.—To judge an animal's fertility, the breeding test is hardly sufficient. It is well known that a male may be potentially fertile, and yet fail to show it because of some physiological state, such as the emaciation of sickness or the sluggishness of obesity. Furthermore the number of males to be tested increased so rapidly that facilities were lacking to breed all of them. Hence, another test was devised. By making a small incision in the scrotum and puncturing the epididymis at one or several points, and placing the liquid contents in a normal salt solution at bodily temperature, with the aid of a microscope a complete index of the male's fertility was obtained.

Results.—Now, whereas any male always gave the same microscopic test during his adult life, there was a great difference between individual hybrids. Some males might not possess any sperm at all; but in their place were found a few or many incompletely matured spermatogonia. Other males might possess a few non-motile or motile spermatozoa in addition. Still others might have an abundance of motile spermatozoa, just as any normal male. All grades and combinations were found; but the last class alone could be successfully mated to females. Fully 200 offspring from such males have been born.

The results of the experiments on the male hybrids up through the sixth generation are given in the table presented. The one-half wild hybrid males had no spermatozoa. The succeeding generations

of less intense wild males present a consistent series, in which a continually increasing percentage of males show spermatozoa. Of the 21 males tested in the sixth generation, or the $\frac{1}{64}$ wild, all had spermatozoa. But the mere presence of sperm does not produce fertile males. In order that fertilization of the egg shall take place, the sperm must be motile to reach and penetrate the egg. Many males with immotile sperm were mated to females, but invariably gave the same result: no progeny.

When we consider those males which had any motile spermatozoa whatsoever, we find the same sort of a series. The $\frac{1}{2}$ wild hybrid males had no sperm and naturally would have none which were motile. The $\frac{1}{4}$ wild males likewise had no *motile* sperm, although we saw in the previous column that 25 per cent showed sperm. The $\frac{1}{8}$ wild males were the first which showed motile sperm, and were likewise the first to be successfully mated with females. The per-

Table of fertility of hybrid males.

Class of hybrids.	Total number tested.	per cent with any sperm.	per cent with any motile sperm.	per cent readily fertile.
$\frac{1}{2}$ wild	6	0	0	0
$\frac{1}{4}$ wild	22	25.0	0	0
$\frac{1}{8}$ wild	71	47.8	17.3	9.8
$\frac{1}{16}$ wild	94	71.1	46.6	35.5
$\frac{1}{32}$ wild	89	88.7	62.9	60.7
$\frac{1}{64}$ wild	21	100.0	66.7	66.7

centage of males with motile sperm increased rapidly in each succeeding generation until finally the $\frac{1}{64}$ wild showed 66.7 per cent with motile sperm. So far as I have been able to test, it would seem that any male with motile spermatozoa is fertile; but in those cases in which immatured spermatogonia or non-motile spermatozoa greatly outnumber the motile spermatozoa, the chances that such will reach and penetrate an egg are small. An intimate study of the motility of sperm and the possibilities of obtaining offspring from male hybrids, has led me to believe that any male with an abundance of motile sperm is readily fertile. Abundance of motile sperm means at least one-half motile. The last column gives the percentages of male hybrids in each generation, which are readily fertile and which can successfully impregnate females. This last category shows the same sort of increase that the others show. It is therefore clear that fertile male hybrids may be produced in constantly increasing numbers in the offspring of a cross which originally gave only sterile males and fertile

females. In the original cross, elements are introduced or formed which prevent the full maturation of the male reproductive cells, but the female reproductive cells seem unaffected. These disturbing elements may be eliminated by continually crossing the female hybrids back to normal tame males, thus producing fertile male hybrids.

Offspring of fertile male hybrids.—It is not out of place to mention the fertility of the sons of the fertile male hybrids. The male hybrids with an abundance of motile spermatozoa could be successfully mated to female hybrids, and to tame female guinea-pigs.

When a fertile male hybrid was mated to a female hybrid their male offspring were not necessarily fertile. We hardly expected they would be, for the female might transmit the disturbing elements in this cross just as much as when mated to a tame guinea-pig. About forty male hybrids from this sort of a cross have been tested, and they give all grades between absolute sterility and fertility.

When, on the other hand, a fertile male hybrid was mated to the guinea-pig female, all the male offspring have been fertile. This is the expected outcome, for the fertile male hybrid may be regarded as a sort of recessive, in which the disturbing elements introduced in the original cross have been eliminated; and when he is mated to the female guinea-pig, no such elements are again introduced. About thirty male hybrids from this class of crosses have been tested and all found to be wholly fertile.

Practical application.—If the cattaloes, mules, and other mammalian hybrids are at all comparable to the hybrids in these experiments, then fertile races of such hybrids may be produced in the same manner. As a simple illustration, I may say that all the color, coat, size, and anatomical characters known in guinea-pigs, have been transferred to these hybrids. Any combination of these characters may be united with fertility. It is conceivable that desired characters in hybrids between other mammalian species may be combined with fertility of both sexes, in the same manner.

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