GENETICS OF THE JAPANESE RABBIT.

By W. E. CASTLE.
Bussey Institution, Harvard University.

The so-called "Japanese rabbit" is a variety of the domestic European rabbit which has a yellow coat mottled with black. There is no more reason to suppose that it originated in Japan than there is to suppose that the Himalayan rabbit originated in the Himalayan mountains, or the Abyssinian cavy in Abyssinia. It is one of those outlandish names so commonly employed by breeders of pet-stock to obscure the origin of a novelty and throw competitors off the trail of duplicating its production. I have inquired of several Japanese scientists as to their acquaintance with the variety but all have disclaimed any knowledge of it.

The variety was apparently unknown in England in 1889 when K. W. Knight edited a revised and enlarged edition of *The Book of the Rabbit*. Had its existence been known at that time, the fact would doubtless have been mentioned.

In Rayson's *Rabbits for Prizes and Profit* (undated edition, probably issued about 1900), the variety is figured and described and its introduction to the notice of English fanciers is dated back to 1893, "when a short notice of it was published in a fancy paper." C. H. Lane in *Rabbits, Cats, and Cavies*, London, 1903, mentions the same date, probably taken from the same source. In Rayson's book we read "In the summer of 1895 the writer paid a special visit to the Jardin d'Acclimatation, in Paris, with the object of acquiring the best possible specimens of the breed, the French Zoo being the only place where they could then be obtained." This statement would lead one to believe that the variety probably originated in France within the last half-century and was first introduced into England about 1895.

The brindled or mottled coat, the distinguishing character of this variety, is similar in appearance to the tiger markings of Great Dane dogs and Boston bull terriers, to the brindled coat of the tortoise-shell guinea-pig, and the occasional brindling of cattle. It is inherited also in similar fashion. It is a simple Mendelian unit-character, an allelomorph of yellow and of black respectively, dominant over the former, recessive to the latter. This is exactly parallel with the condition in

guinea-pigs first clearly worked out by Ibsen, in which tortoise-shell is dominant over yellow and recessive to black.

The peculiarity of the case of the Japanese rabbit lies in its relation to the agouti or gray factor.

In guinea-pigs it is difficult or quite impossible by inspection to distinguish a yellow individual which possesses the agouti factor from one which does not possess it. But in black pigmented individuals the agouti is readily distinguished from the non-agouti by the banding of the hairs, the agouti individual having hairs tipped with black, below which comes a band of yellow, and then the basal part of the hair is of dull black. In the non-agouti individual, no yellow band is present, so the hair is black throughout its length.

In rabbits the agouti and non-agouti yellows are different in appearance, the latter being "sooty" even on the belly and under surface of the tail, which are clear white in an agouti yellow rabbit. The same difference is recognizable in the *yellow areas* of Japanese rabbits which *do* possess the agouti factor, as compared with those which do not. The former have white bellies, the latter do not. But in the *black patches* of their coats, agouti and non-agouti Japanese rabbits look alike. In neither sort is the black hair banded with yellow, though the yellow areas of the coat usually indicate clearly whether the agouti pattern is present or not. In doubtful cases demonstrative evidence may be obtained by mating the Japanese rabbit with an ordinary black one. If the Japanese parent carries the agouti factor, gray young will be produced; if not, black young. From these facts it is clear that the agouti factor has no effect on the *black* hairs of a Japanese rabbit, though it does on the yellow hairs. How are we to account for this?

Punnett was the first to show that there are two different kinds of black rabbits, dominant and recessive blacks[1]. In the former the agouti factor produces a scarcely perceptible ticking of the hair, or no ticking at all, whereas in ordinary (recessive) black rabbits presence of the agouti factor turns the coat into an ordinary gray (agouti). Yellow behaves as the allelomorph of either kind of black, and they as allelomorphs of each other. Yellow will always show the presence of the agouti factor by the white ventral surface and the absence of sootiness from the fur. Recessive black will also show the presence of the agouti factor by the yellow banding of the fur making the coat gray and the ventral surface whitish as in yellow agouti rabbits.

[1] Mr Feldman has recently shown that in *Mus rattus* also there occur both a dominant black and a recessive black variety.

If we could produce a rabbit part of whose coat was yellow, the other part being recessive black, and if we should then bring into it the agouti factor, the coat would become *gray*-and-yellow, with a white belly. Now in the Japanese rabbit, the black never becomes gray through the action of the agouti factor; it remains unticked black, *even on the belly*. This shows that the black of the Japanese rabbit is *dominant* black, and this in turn throws an interesting side-light on the origin of mottled animals and plants. The mottled condition is transmitted in a single gene and is in reality a mosaic of what are ordinarily distinct and alternative genetic states. The mottled guinea-pig is produced by a gene which is a mosaic of yellow and of recessive black (which the agouti factor will convert into gray). In the guinea-pig no other kind of black is known. But in the rabbit we have both dominant and recessive black. The agouti factor will change the latter to gray but not the former. The Japanese rabbit has arisen as a mosaic of yellow and dominant black, probably through incomplete separation of the two at the reduction division in a heterozygote between the two.

What about the commonly assumed simple and changeless character of genes? We may, if we choose, avoid the difficulty, as others have done, by calling this mosaic a "mutation."

THE EVIDENCE.

In May 1920 I obtained from a dealer two New Zealand Red does which had been bred to a Japanese buck. The New Zealand Red is a large variety of rabbit with an intense reddish-yellow coat, showing the presence of the agouti factor by the white belly and tail. Early in June the does gave birth to good sized litters, one consisting of six, the other of nine young, all with the characteristic Japanese mottling of black and yellow. The sire of these fifteen young was clearly homozygous for the Japanese pattern which he transmitted to all of the young. The Japanese character was also clearly dominant in every case over the self yellow condition of the mothers. One of the mothers was subsequently mated to self yellow bucks producing in each case only self yellow young. Hence the Japanese character of the two litters mentioned was clearly not derived from the mother, a homozygous yellow, but from the Japanese father.

Accordingly it was to be expected that the young would be heterozygous for the Japanese character, since they inherited the character from one parent only. Such proved indeed to be the case. An F_2 generation, obtained by mating the Japanese young one with another, contained

11 Japanese and 7 yellow young, the most probable expectation being 13·5 Japanese to 4·5 yellow. Also when F_1 Japanese individuals were mated with yellows, there were produced 117 Japanese and 128 yellow young. Evidently this is a 1 : 1 ratio. The slight excess of yellow young may have been due to a failure to classify as Japanese certain of the young which had very few black hairs in their coats and which may erroneously have been recorded as yellow or, as we shall see, it may be that a few of the Japanese young really did not have *any* black hairs in their coats. In no case did one of the Japanese young of either the F_2 or the back-cross generation bear gray hairs. The hairs that contained black pigment were invariably black throughout their length.

When an F_1 individual, heterozygous for the agouti factor as well as for Japanese, was mated with non-agouti yellow individuals, there were obtained both agouti and non-agouti yellows, and also agouti and non-agouti Japanese. At first it was found difficult to recognize the non-agouti Japanese, but after two individuals had been proved to be non-agouti by breeding tests in which they were mated to non-agouti yellows and produced only non-agouti yellow and Japanese young, no further difficulty was encountered. The under-surface of the tail, the belly, and the area around the eye are the best criteria, when they happen to be free from the Japanese mottling. In some of the most recently recorded litters, six non-agouti Japanese young were noted along with eight agouti Japanese young, the expected 1 : 1 ratio.

An F_1 Japanese female was mated with a non-agouti black male heterozygous for yellow, producing three Japanese, one yellow and two black young, the expectation being 1 Japanese : 1 yellow : 2 black or gray. Another F_1 Japanese female was mated with a blue angora male (with dominant extension factor) producing six black or steel gray young. One of these showed a lighter patch on one shoulder and was suspected accordingly of being heterozygous for the Japanese factor. When mated with yellow males she has produced 19 black young, 14 Japanese, and 4 yellow. The production of yellow young in this mating is contrary to expectation, since only black young and Japanese young should result, and these in equal proportions, if black, Japanese, and yellow are triple allelomorphs. Doubt might exist whether the yellow young are genetically as well as somatically yellow, for two of the Japanese young were at first recorded as yellow and so would have remained in the record had it not been discovered a few days later that each bore a few black hairs in its tail. Subsequent breeding tests made with these two animals proved them to be genetically Japanese-yellow heterozygotes. Three of

those recorded as yellow were destroyed before it was realized that the existence of such a class of young in this mating was problematical. The fourth individual, though it appears to be yellow, no black hairs having been detected anywhere on its body even after repeated careful inspections, is now adult and has been mated to a yellow female unrelated to the Japanese race, and has produced in two litters totalling 15 young, 5 clearly Japanese, the others being yellow. It is obvious therefore that this yellow animal is genetically a heterozygous Japanese. It seems probable therefore that such also were the other yellow young produced by this mother. She evidently is a heterozygote between black and Japanese and produces only two kinds of gametes, black and Japanese. In other words Japanese is a third allelomorph of black and of yellow, precisely like tortoise-shell in guinea-pigs. Since there are in rabbits two kinds of black, a dominant and a recessive kind, Japanese is really a *fourth* allelomorph of the extension factor. In order of dominance the four are E' (dominant black); E (ordinary recessive black); e^J, Japanese; and e, yellow.