

ON THE "JAPANESE" RABBIT.

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INTRODUCTION.

SINCE 1917 I have been observing the behaviour of the so-called "Japanese" rabbit in crosses with various forms. Early in the present year (1924) I learned from Professor Castle that he also had been studying the heredity of the Japanese pattern during the past few years. As our experiments have led us independently to practically the same conclusion, I have adopted Professor Castle's suggestion that the two sets of records should appear in the same number of this *Journal*. Where references are made to Professor Castle's work in the following account they refer to the paper which immediately precedes the present one.

THE JAPANESE RABBIT.

Except that it certainly has nothing to do with Japan little seems to be known of the origin of the Japanese rabbit. According to A. Wulf¹ it originated in France in 1887, and was subsequently improved in England. I have, however, seen animals of this pattern, along with other domesticated rabbits, exposed for sale in butchers' shops near Genoa, and should not be surprised if it were found to be generally, though sparsely, distributed among the mongrel rabbit population of Europe.

The only notes relating to the genetics of the Japanese rabbit would appear to be those of Endre Pap², who gives data to shew that the pattern behaves as a simple recessive to full black. He also quotes Hagedoorn to the effect that the Japanese pattern is to be found in the blue and in the chocolate series as well as in the black. With this statement my own observations are in agreement, since both chocolate Japanese and blue Japanese have been produced in the course of my work. Pap also states that most Japanese rabbits shew some white Dutch markings³, thereby becoming tricolors, though there does not appear to be any linkage between the Dutch and the Japanese patterns. With this statement also my own work agrees. Tricolors appeared in F_2 from a cross between a

¹ *Album der Rasse-Kaninchenzucht*, Würzburg, n.d.

² *Zeit. f. ind. Abst. Vererb.* Vol. xxvi. 1921.

³ This of course is not true of the English breed.

Japanese and a "Spotted Dutch"¹ rabbit; nor did I observe any indication of linkage between the two patterns.

The Japanese rabbit exhibits very great variation in the amount of the dark marking, as well as in its distribution. The dark hairs may extend over the greater part of the body, though more diffused among the yellow in some regions than in others; or they may be represented by a few hairs only, so that the animal appears as a practically yellow rabbit. For the most part, however, the range of dark marking lies between these two extremes. A peculiar feature is the manner in which it tends to form transverse markings over the hinder part of the body. The ground colour of the belly is normally white, or nearly so; but it often appears greyish, owing to scattered dark hairs. In no region of the body are the dark hairs banded with yellow, even though the animal carries the agouti factor. Considerable variation in shade is to be found in the yellow ground colour of the coat, which may be anything between a clear creamy yellow, and a rich deep colour approaching that found in the so-called "New Zealand Red"². I have not made any attempt to analyse the variations observed.

There is one further point of interest in connection with the Japanese pattern. An animal may carry the agouti factor, or it may carry the tan factor, or it may carry neither of these: i.e. when crossed with normal black a Japanese may give agoutis, or black and tans, or blacks, according to its genetical constitution. I have, however, failed to find any point of visible difference between these various Japanese. The belly may be as light in an animal that carries neither agouti nor tan as in an animal that does carry one or other of these two factors. Nor do the "tan" points of an agouti or a tan rabbit (i.e. the yellow marks on the feet, ears, nose, and nape of neck) serve to distinguish Japanese which carry the agouti or tan factors from those which do not. They may be obscured, or partially so, by black hairs, equally in a Japanese that contains the agouti or tan factors, and in one that does not.

In one case however the appearance of the Japanese would seem to serve as a guide to its genetical constitution. For in a Japanese which throws tortoise, and at the same time lacks the agouti factor, the general colour is more sooty, with yellowish belly and darker points as in a tortoise.

¹ For an explanation of this term cf. *Journ. Genetics*, Vol. ix. p. 309.

² This statement is meant to include all of the Japanese I have bred, the majority of which have been animals extracted from various crosses. In the pure bred Japanese the yellow ground colour is more uniform.

EXPERIMENTAL DATA.

A. The original Japanese ♂ (*Q* 70)¹ was mated with a blue ♀ (*Q* 13) extracted from a Flemish-Polish cross, and known not to contain the factor which presents the appearance of agouti markings (= the D-factor of my earlier paper², and the dominant extension factor of Castle). She produced eleven full blacks in two litters. Three *F*₂ litters from such *F*₁ blacks resulted in six blacks, five blues, four normal Japanese, and one blue Japanese.

B. The same Japanese ♂ (*Q* 70) was also mated with a chocolate ♀ (*Q* 111) shewing the "Spotted Dutch" type of marking. The four *F*₁ animals were black. From them was bred an *F*₂ generation consisting of fourteen black, six chocolate, five normal (= black) Japanese, three chocolate Japanese. Two of the black Japanese were of the tricolor type alluded to above on p. 231.

These matings served to shew that the Japanese pattern behaves as a simple recessive to self-colour, and that the black of the normal Japanese may be replaced by blue or by chocolate.

C. An unlooked for result was obtained when two of the black *F*₁ animals from **A** were mated back to Japanese. By this time the original pair of purchased Japanese had been disposed of. But a litter of five Japanese had been bred from them, and it was with two of these that the two *F*₁ blacks were mated. The results were:

*F*₁ ♂ (*Q* 144) × ♀ Jap. (*Q* 130) gave 2 agoutis, 2 blacks, 1 Japanese.

*F*₁ ♀ (*Q* 147) × ♂ Jap. (*Q* 129) gave 1 agouti, 4 blacks, 8 Japanese.

Since the *F*₁ animals did not carry the agouti factor, it must have been brought in by the Japanese (*Q* 129 and *Q* 130), and they must have received it from their mother (*Q* 71); for their father (*Q* 70) had already been shewn not to contain it. This meant that the individuals in a strain of Japanese breeding true to the characters of the breed, might nevertheless differ from one another in the presence or absence of the agouti factor. The presence of the agouti factor does not bring about banding in the black hairs of the Japanese. As earlier work had proved the existence of a black which is dominant to agouti, it was natural to regard the black of the Japanese as of this nature.

There was, however, a difficulty. The heterozygote *ex* dominant black × agouti is not black, but agouti-black, i.e. predominantly black but with some agouti banding³. Hence one would have expected in

¹ Purchased from the well-known breeder, Mr C. J. Davies.

² *Journ. Genetics*, Vol. II, p. 227, 1912.

³ *Journ. Genetics*, Vol. II, p. 225, 1912, and Pl. XII, fig. 2.

the above experiment, not agoutis, but agouti-blacks. More recently, however, Onslow shewed that in some cases the heterozygous form between dominant black and agouti may be much nearer to agouti in appearance, taking the form of steel¹. This suggested that the Japanese might be homozygous for a dominant black of which the heterozygous state, on an agouti basis, was not far removed in appearance from a rather dark agouti.

At this stage the Japanese experiments were dropped for a year owing to lack of accommodation, and it was not until the autumn of 1920 that I was able to return to them. A fact which called for explanation in Exp. C was that although both agoutis and blacks appeared among the self-coloured rabbits, yet all of the nine Japanese bred had the normal black markings. The non-appearance of animals with the Japanese pattern, but with agouti-banded hairs in place of black ones, suggested that the pattern and the dominant black were in some way linked together, and the following experiments were made.

D. A cross was made between the Japanese and the black Flemish, a form of black recessive to agouti. Some of the F_1 animals were blacks and some were agoutis, the Japanese used being evidently heterozygous for agouti. Of the blacks 3 ♀♀ were mated to their brother, and the F_2 generation consisted of 38 blacks and 10 Japanese, evidently a simple Mendelian relation. The absence of a tortoise class, as in Exp. A above, suggested that the relation between normal black, Japanese, and tortoise might be that of a series of multiple allelomorphs.

The agouti F_1 animals (3 ♀♀ and 2 ♂♂) were also bred together, and in F_2 produced 19 agouti, 6 black, and 9 Japanese, a close approach to a 9 : 3 : 4 ratio. All of the Japanese had the normal black markings, and again there was an absence of yellow and of tortoise.

A fresh point was brought out by this experiment. One of the F_1 ♂♂ (S 27) shewed some dark hairs on the belly, while in the other (S 33) the left side of the head was much darker than the right, being in fact what might be described as dark steel. Some of the F_2 agoutis were also noticed as being unusually dark. These facts suggested that the agouti which carries Japanese may have something of the Japanese pattern superimposed, as it were, upon the normal agouti type, and this has been confirmed by later observations. Japanese markings on an agouti are most easily determined by inspection of the belly of the baby rabbit of 1-2 weeks. At this stage the hair is short, and the dark hairs,

¹ *Journ. Genetics*, Vol. XII. 1922. Mr. Onslow's results were known to me some time before he published them.

if present, are conspicuous. Later on when, as often happens, a darker underfluff appears, the Japanese markings tend to become lost unless they occur in large and well-marked patches. Elsewhere on the body the Japanese markings are rarely prominent; for being steel instead of full black, and generally diffuse, they grade into the rest of the coat. Moreover if the dark markings are scanty, as frequently happens in the Japanese, an agouti rabbit which bore them would not be distinguishable from an ordinary agouti. The densest black marks on an ordinary Japanese are those which may occur on the head, and it is on the head of the agouti which carries Japanese that one finds the most conspicuous Japanese markings, as in ♂ *S* 33 mentioned above.

E. Some results closely comparable with the above were obtained from the mating between a Japanese ♀ (*S* 4, known not to carry the agouti factor) and a homozygous black and tan ♂ for which I am indebted to my friend Mr T. H. Riches. The litter comprised seven black and tans, and these when bred together gave an F_2 generation consisting of 35 black and tan, 14 black, and 16 Japanese—obviously a 9 : 3 : 4 ratio. Two of the Japanese were subsequently tested and shewn to be heterozygous for the tan factor. It was found that some of the F_2 tans shewed irregular dark markings on the belly, while others were without such markings. Presumably the former belonged to the class of tan which carries Japanese.

The earlier experiments suggested that the factors for self-colour, Japanese, and dilute colour (yellow or tortoise) behaved as a series of multiple allelomorphs. For neither tortoise, nor yellow, nor tortoise tan appeared in the F_2 generation from crosses between Japanese with black, agouti, or black and tan respectively. Hence dilute × Japanese should give either dilute or Japanese in F_1 , and a 3 : 1 ratio of the two classes in F_2 .

F. Accordingly Japanese was mated with yellow, with the result that the seven F_1 animals obtained were all Japanese. All of these animals, viz. five ♀♀ and two ♂♂ were used in the production of the F_2 generation shewn in Table I.

It will be noticed that tortoise young as well as yellows were produced from ♀ *S* 41 × ♂ *S* 24. It was subsequently shewn by crossing with the black and tan ♂ (*S* 50) referred to above, as well as with a pure chocolate ♂ (*S* 81), that three of the ♀♀, viz. *S* 23, *S* 25, and *S* 46 were homozygous for the agouti factor, while the other two, viz. ♀ *S* 40 and ♀ *S* 41 were

TABLE I.

		Jap.	Yellow	Tortoise		Agouti	Tan	Black
♀ <i>S</i> 23	× ♂ <i>S</i> 24	31	18	—	× ♂ <i>S</i> 50	16	—	—
♀ <i>S</i> 25	× " "	25	6	—	× " "	10	—	—
♀ <i>S</i> 46	× " "	10	3	—	× " "	13	—	—
	× ♂ <i>S</i> 42	9	6	—				
♀ <i>S</i> 40	× " "	7	5	—	× " "	2	2	—
	× ♂ <i>S</i> 24	6	—	—	× ♂ <i>S</i> 81	2	—	5
♀ <i>S</i> 41	× " "	13	1	2	× " "	4	—	3
"	× ♂ <i>S</i> 42	4	3	—	× ♂ <i>S</i> 50	3	2	—
Total		105	42	2				

heterozygous (cf. Table I). Of the two ♂♂ one, *S* 24, was shewn to be heterozygous, for when mated with a chocolate ♀ (*S* 80) he gave four agoutis and three non-agoutis: the other, *S* 42, was not tested on this point.

The F_2 generation consisted of 149 animals, of which 105 were Japanese, and 44 yellows (including tortoise), expectation of course being 3:1. I am inclined to attribute the slight excess of yellows to the fact that the Japanese markings are sometimes so reduced that the animal may be mistaken for a yellow. This is supported by the fact that it is the earlier litters that are responsible for the excess of yellows. On dividing the F_2 population into two halves consisting of the earlier and the later litters respectively I find that the former contains 47 Japanese: 27 yellow, and the latter 58 Japanese: 17 yellow. At the time the earlier litters were recorded I had not appreciated the extreme reduction which the Japanese pattern might sometimes undergo, and it is not improbable that a few of the young recorded as yellows were genetically Japanese.

Of the agoutis produced by crossing ♀ *S* 23 and ♀ *S* 46 with the black and tan ♂ *S* 50, a buck and several does were mated together. Independent tests had shewn that some of these agouti ♀♀ were heterozygous for yellow, and some for Japanese (others remaining yet untested), while the buck carried Japanese. The matings might therefore be expected to give agoutis, tans, and Japanese only, in the ratio 9:3:4. The actual numbers, 46 agouti, 10 tans and 18 Japanese are not far removed from the expected ratio. Of both the tans and the agoutis some were normal, while others shewed Japanese markings on the belly. The proportions of the Japanese marked agoutis and tans would differ according as the does used carried Japanese or yellow. If they carried the former the Japanese marked agoutis and tans should be twice as numerous as the normal ones¹: if the latter, the normals should be twice

¹ Assuming the markings always to shew in animals carrying Japanese. In cases where the Japanese marking is much reduced these dark-coloured animals would almost certainly not shew it.

as numerous as the Japanese marked ones: This point cannot, however, be dealt with further, since the constitution of all of the nine does used has not yet been determined.

G. Lastly I may make mention of a cross between Japanese ♀ and tortoise ♂. The seven F_1 animals were from their appearance termed "Tort-Japs," for in general colour they were tortoise, though with some Japanese markings. In all of them however the markings were slight, in two cases being reduced to a few black hairs on the back. A small F_2 generation was bred and recorded as 9 Japanese, 3 yellows, and 11 tortoise. Some of the Japanese were recorded as normal, and others as "Tort-Japs." In almost all of them the markings were scanty, and I am inclined to consider that the three animals recorded as "yellow" were genetically Japanese, in which the black markings were almost absent. It is also possible that some of those recorded as tortoise may have been "Tort-Japs."

DISCUSSION OF DATA

The various experiments recorded above are clearly in accordance with the view that normal black, tortoise and Japanese are alternative in heredity. And since we know that D-black behaves as though it were alternative to normal black, we should naturally expect it to fall into the same series. This expectation has been translated into fulfilment by Professor Castle's work. We are dealing therefore with a series of four allelomorphs corresponding to the four alternative characters:

Dominant black	...	D
Japanese	d
Recessive black	...	E
Tortoise	e

And this would appear to be as far as purely Mendelian analysis can at present take us.

Yet, though we leave firm ground, a few speculations may not be out of place. We have seen that the black of the Japanese behaves as though it were of the nature of the D-black. May we not regard the Japanese as standing in something of the same relation to D-black as tortoise does to E-black¹? There is in either case a diminution of melanic pigment with a corresponding increase in yellow. In neither case is the

¹ The relation is unlikely to be the same. For if so E-black × Japanese should give rise to some tortoise animals in F_2 . If we take the view that we are dealing with an intensity-dilution pair common to both kinds of black we must make the further supposition that there is very close linkage between such a distributional pair and the two blacks, a supposition for which at present there is no experimental evidence.

dilution uniform all over the body. The black pigment in the tortoise is denser in certain regions, viz. nose, ears, feet, and tail; and in some tortoise it is far denser than in others. In the Japanese the areas of density are far less regular, though the black pigment tends to collect in certain regions of the body more than in others. When reduced in amount it tends to disappear, roughly, in those regions of the body where a Dutch marked rabbit is white¹. But although the melanic pigment tends to disappear it never does so completely, for even in the most yellow areas of a Japanese rabbit careful search will reveal the existence of occasional dark hairs. Melanic pigment is to be found all over the body of the Japanese, but, in its dilute form, the D-black pigment does not "spread" well, and so we obtain an apparently mosaic effect. The dilute E-black spreads more evenly, and though there is a greater density of black in the "points," as in a Himalayan, the darker areas grade uniformly into the lighter. But the light hairs, unlike those of the Japanese, contain some melanic pigment.

The apparent identity of Japanese black with D-black is brought out in an interesting way in the relation of them both to the agouti factor. In a Japanese containing the agouti factor (A) the black hairs, as we have seen, remain unbanded. And this is equally true whether the animal be homozygous or heterozygous for d. For the animal represented by the formula ddAA is visibly indistinguishable from that represented by deAA. Some years ago I drew attention to the fact that, where all carried the agouti factor, the homozygous dominant black was indistinguishable in appearance from the dominant black which carried yellow². Adopting our present set of symbols both DeAA and deAA rabbits are full blacks, without any trace of agouti banding. The agouti factor fails to lead to banding where the factor for dominant black, whether in the intense (D) or in the dilute (d) state, is on a basis of yellow, i.e. in the absence of the E factor. When however the E factor is present in addition to the factor for agouti, the black produced by the dominant black factor, whether in the intense or the dilute state, is subject to banding. The DEAA animal shews some agouti banding. The corresponding animal in the dilute form, the dEAA animal, is, visibly, a Japanese agouti. The yellow area of the Japanese becomes agouti, while the black areas become dark steel or agouti-black.

¹ I have occasionally bred Japanese which might not unfairly be described as irregularly Dutch marked, the white being replaced by yellow, though the dark areas were, of course not fully black.

² *Journ. Genetics*, Vol. v. 1915, p. 47.

If we regard Japanese as a dilute form of dominant black we must look upon yellow as a basis underlying these four forms of black, viz. D-black, d-black (= Japanese), E-black, and e-black (= tortoise). We do not at present know of a yellow without melanic pigment, and must consider the four members of the allelomorphic series under discussion as corresponding to four states of melanic pigmentation. Yellow must be supposed to underlie the two intenser forms of black as well as the two dilute ones. This view is in accordance with the result of crossing E-black with chinchilla, an agouti which lacks yellow. That such a cross gives normal agoutis supports the view that the E-black carries yellow. But here, and probably also in the D-black, the yellow is crowded out, as it were, by the great development of the melanic pigment.

However, we are still faced with the problem of framing some conception of the biochemical relation that obtains between our two forms of black—the D-black and the E-black. Either we must regard them as chemically distinct, or we must suppose that they are chemically similar, and that the differences in their genetical behaviour are due to some difference in the respective mediums in which they are produced. That the latter possibility is the less probable seems to be indicated by the existence of the Japanese-agouti, which is best interpreted by supposing that the E-black is uniformly distributed, while at the same time the D-black is distributed irregularly. The fact that this takes place in the same animal certainly suggests that we are concerned with two distinct pigments. And this is supported by the further fact that the "Tort-Jap" shews both the black patches of the Japanese and the dilute melanic pigmentation of the tortoise. The case would be an interesting one for biochemical investigation.

Note. Since the above account was written my friend, Mr J. B. S. Haldane, has kindly sent me the following data from experiments made by himself and L. K. Haldane. The Japanese used in this work was bred from my original stock.

1. From the cross Japanese \times yellow, or Japanese \times tortoiseshell, an F_2 generation was raised consisting of 66 Japanese and 21 yellow or tortoise.

2. F_1 ex Japanese \times tortoise, or F_1 ex Japanese \times yellow, mated back either to yellow or tortoise, gave 26 Japanese and 27 yellow or tortoise.

These results are closely in accordance with the simple Mendelian

relation between Japanese on the one hand, and yellow or tortoise on the other already suggested by Professor Castle and myself.

3. An F_2 Japanese buck from 1, with only a small patch of black on one cheek and on one flank, was mated with several yellow and tortoise does. He gave 8 yellow or tortoise and 11 Japanese, all of which latter were more heavily marked with black pigment than himself. The case is of interest in view of Professor Castle's statement (p. 228 above) that a rabbit, which is genetically a Japanese-yellow heterozygote, may be without the black markings characteristic of the Japanese.