FURTHER EXPERIMENTS ON THE INHERITANCE OF COAT COLOUR IN MICE.

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In Report IV of the Evolution Committee of the Royal Society, I published a preliminary account of the results of my breeding experiments to determine the inheritance of coat colour in mice. I now propose to complete that account by giving the results of my investigations into the genetic behaviour of pink-eyed mice with coloured coats and also of yellow mice.

I propose to begin with an account of the pink-eyed mice with coloured coats, but at the same time to leave the question of the behaviour of pink-eyed mice with yellow coats until I deal with dark-eyed yellow mice, and to confine myself at first to pink-eyed mice of any coat colour except yellow.

The albinos have been dealt with in Report IV. The pink-eyed mice with coloured coats as stated in Report IV have only apparently unpigmented eyes. Examination of sections of the eyes microscopically reveals the presence of pigment both in the retina and iris. The amount of pigment present is however so little, that it is extremely difficult to say of what colour it is.

There is a correlated absence of pigment in the hairs of these mice, so that they are much paler in colour than any of the corresponding varieties of dark-eyed mice. But this absence of pigment in the eyes and hair of the pink-eyed mice has a genetic significance different from that of the dilution of coat colour in the dark-eyed mice. For in the case of the dark-eyed mice, the absence of a factor which effects the dense deposition of pigment in the hairs gives rise to what are known as the dilute forms, and for each coloured type there is a dilute variety. The pale colours of the pink-eyed mice are not due to the same cause, and cannot be explained in the same way. For pink-eyed mice behave genetically like the concentrated and diluted varieties of dark-eyed mice and carry the conditions of concentration and dilution just as they do, and in their colourings the effects of these are shown. The paleness of colour therefore which accompanies the pink eye must be due to some other cause. This statement however applies only to those mice in which yellow pigment is absent. For it is possible to produce pink-eyed yellow mice with hair as deeply pigmented as that of dark-eyed yellow mice. These will be dealt with later on. Also in the case of the pink-eyed agouti mice, while the black and chocolate pigments are there in very much diminished quantities the yellow banding may be as deeply coloured as in the hair of the ordinary agouti. It is possible to arrange the pink-eyed mice in classes corresponding to those which have been distinguished among the dark-eyed mice.

Pink-eyed mice which behave genetically like black mice are of a pale greyish colour and were named lilacs by Mr Darbishire(6) who was the first to breed them and kindly gave me two living specimens.

In order to distinguish them from other lilac mice, on account of their colour, I have called them "blue lilacs." They breed perfectly true mated *inter se*. Mated with chocolate mice, they never throw any other colour but black in F_1.

In the F_2 generation from this mating two new varieties appear which I have named "chocolate-lilac" and "champagne" ("*café au lait*" of Cuénot) respectively.

The chocolate-lilacs vary very much in appearance in depth of colouring, but the colour is always browner than that of the blue lilac more resembling that of the silver fawn. For this reason I called them chocolate-lilacs, and I thought at first they were a chocolate variety of the pink-eyed mouse. But when mated with chocolate mice they throw a mixture of blacks and chocolates.

Chocolate-lilacs mated together throw blue lilacs, chocolate-lilacs and champagnes.

The champagne mice, mated with chocolates, throw only chocolates and are I believe the pink-eyed variety of chocolate. Mated *inter se*, they breed perfectly true, I therefore regard the blue lilacs as the homozygous pink-eyed variety of the dark-eyed black mouse, the chocolate-lilac mouse as the heterozygous variety of dark-eyed black (throwing chocolate) and the champagne as the homozygous chocolate pink-eyed form.

When the various forms are mated with the dilute forms of dark-eyed mice, blues or silver fawns, then in the F_2 generation pink-eyed mice without the factor for concentration are produced. These when mated with blues or silver fawns throw only the dilute varieties, whereas pink-eyed mice descended from unions between pink-eyed mice and dark-eyed mice of the concentrated form only throw concentrated forms when mated with the dilute varieties. There is a great deal of variation in the depth of colour of the pink-eyed mice and I think that the presence or absence of the factor for concentration accounts for this. Unfortunately I did not recognize this fact early enough in my experiments to be able to give numbers in support of this view. In the case of the champagne mice, however, a different variety which I called "silver champagne," arose and always appeared in the F_2 generation from a mating between champagne and silver fawn. These silver champagnes mated with dilute forms always gave dilute forms.

When the chocolate lilac mouse is mated with the ordinary wild colour or golden agouti mouse, the F_1 is always golden agouti. All possible forms should appear in F_2. Black, chocolate, golden agouti, cinnamon agouti, blue lilac, chocolate lilac, champagne, pink-eyed golden agouti, pink-eyed cinnamon agouti.

The pink-eyed agoutis, golden and cinnamon, are very much alike in appearance. In fact at first and for some time I took the pink-eyed cinnamon agouti to be a pale or dilute form of the pink-eyed golden agouti, and owing to the small amount of pigment present, I thought that the pink-eyed golden agouti must be the cinnamon variety. However, the genetic behaviour of the two forms when mated with chocolate showed their differences.

The pink-eyed golden agouti gives only golden agouti when mated with chocolate and the pink-eyed cinnamon agouti gives only cinnamon agoutis as a result of mating with chocolate.

The small amount of pigment present makes the microscopical determination very difficult.

Pink-eyed coloured mice are recessive to dark-eyed mice and when mated *inter se* never throw the dark-eyed form.

Taking all the results irrespective of colour and classifying only according to eye-colour, then as a result of mating pink-eyed mice with dark-eyed mice in F_2 I obtained

875	dark eye, *DE*,	303	pink eye, *PE*,	observed
883·5	„	294·5	„	calculated.

From matings between heterozygous *DE* with *PE*

105 *DE*,	113 *PE*,	observed
109	109	calculated.

In the case of the first mating I made between blue mice and blue lilac the numbers yielded in the F_2 generation are peculiar.

Instead of a ratio of 9 : 3 : 4 as I expected, I got 27 blacks, 17 blues and 18 blue lilacs.

The F_1 mice were black and therefore the blue lilacs were carrying the determiner for concentration.

The formula for the blue lilacs may be represented as *eDB*, where *e* is the absence of dark eye, *D* the factor for concentration, *B* the factor for blackness.

The blue mouse can be represented as *EdB*, where *E* is the presence of dark eye, *d* is the absence of concentration.

The figures given above may possibly be an indication of spurious allelomorphism between the factor for dark eye and the concentration factor.

The F_2 mating would then be $EdeD \times EdeD$. The results would then be a ratio of 2 black to 1 blue to 1 blue lilac, giving calculated results of 31 black to 15·5 blue to 15·5 blue lilac.

I was unable to repeat the combination owing to either the blues used being heterozygous in chocolate or the blue lilacs heterozygous in concentration.

If this interpretation be correct, then all the blacks should be heterozygous and all the blues homozygous. Unfortunately I only mated a few of the offspring. 6 blues only were mated and 3 of these died without young, the remaining 3 were homozygous; 5 blacks were mated, 3 died without young, one had only 4 young and these were all black, and the fifth was heterozygous.

The results of mating chocolate-lilac mice with dark-eyed varieties may give rise to various heterozygous forms.

Thus the F_2 generation of a mating between chocolate-lilac and blue (giving black F_1) was

19 black, 2 blue, 5 blue lilac, 6 chocolate-lilac.

If the mating was $EeDdBb \times EeDdBB$, the calculated numbers would be 18 black, 6 blue, 4 blue lilac and 4 chocolate-lilac.

From a mating of chocolate-lilac and black heterozygous in blue giving black F_1, I got

10 black, 4 blue, 6 blue lilac and 2 chocolate-lilac.

If the mating were as above between $EeDdBb \times EeDdBB$, there should be 12·3 black, 4·3 blue, 2·7 blue lilac and 2·7 chocolate-lilac.

Blue lilac × *chocolate*, $eeDDBB \times EEDDbb$ gives black F_1.

		Black	Chocolate	Blue lilac	Chocolate-lilac	Champagne
F_2.	Observed ...	21	6	0	4	6
	Calculated ...	20·7	6·9	2·3	4·6	2·3

Here no blue lilacs were obtained but an excess of champagnes.

Blue lilac × *chocolate*, $eeDdBB \times EEDdbb$ gives blues and blacks.

		Black	Blue	Chocolate	Silver fawn	Blue lilac	Chocolate-lilac	Champagne
F_2.	Observed	4	3	0	0	1	1	0

Chocolate-lilac × *chocolate*, $eBeb \times EbEb$ gives blacks and chocolates F_1.

F_2 from blacks	Black	Chocolate	Blue lilac	Chocolate-lilac	Champagne
Observed ...	16	7	0	3	0
Calculated ...	14·4	4·8	1·6	3·2	1·6
From black and chocolate					
Observed ...	8	16	0	0	5
Calculated ...	10·8	10·8	0	3·6	3·6
From chocolate × chocolate					
Observed ...	—	38	—	—	16
Calculated ...	—	40·5	—	—	13·5

Blue lilac × *silver fawn*, $eeddBB \times EEddbb$ giving blue F_1.

		Blue	Silver fawn	Blue lilac	Chocolate-lilac	Champagne
F_2.	Observed ..	43	19	3	10	3
	Calculated ...	43·9	14·6	4·9	9·7	4·9

Chocolate-lilac × *silver fawn*, $eeddBb \times EEddbb$ giving blue F_1.

		Blue	Silver fawn	Blue lilac	Chocolate-lilac	Champagne
F_2.	Observed ...	16	13	6	0	2
	Calculated ...	20·7	6·9	2·3	4·6	2·3

The champagnes in these last two cases were silver champagnes.

Silver fawn × *champagne* giving chocolate F_1,

$$EeDdbb \times EeDdbb.$$

		Chocolate	Silver fawn	Champagne
F_2.	Observed ...	5	2	5
	Calculated ...	6·75	2·25	3

These champagnes should have been of two sorts, champagne and silver champagne.

Silver fawn × champagne giving silver fawn F_1,

$Eeddbb \times Eeddbb$.

		Silver fawn	Silver champagne
F_2.	Observed ...	11	2
	Calculated ...	9·75	3·25

Chocolate heterozygous in pink-eye × chocolate-lilac,

$Eebb \times eeBb$.

	Black	Chocolate	Chocolate-lilac	Champagne
Observed ...	2	3	2	3
Calculated ...	2·5	2·5	2·5	2·5

Blue × champagne giving black F_1,

$EeDdBb \times EeDdBb$.

		Black	Blue	Chocolate	Silver fawn	Blue lilac	Chocolate-lilac	Champagne
F_2.	Observed	4	0	2	1	0	1	1
	Calculated	3·5	1·17	1·17	·4	·5	1	·5

Blue × champagne giving blue and black F_1,

$EeddBb \times EeDdBb$.

		Black	Blue	Chocolate	Silver fawn	Blue lilac	Chocolate-lilac	Champagne
F_2.	Observed	8	10	3	4	4	2	2
	Calculated	9	9	3	3	2	4	2

Blue carrying chocolate × champagne giving blue and chocolate,

$EeddBb \times EeDdbb$.

	Black	Blue	Chocolate	Silver fawn	Chocolate-lilac	Champagne
Observed ...	2	3	4	1	1	0
Calculated ...	2·1	2·1	2·1	2·1	1·3	1·3

Blue heterozygous in pink-eye and chocolate × champagne,

$EeddBb \times eeDdbb$.

	Black	Blue	Chocolate	Silver fawn	Chocolate-lilac	Champagne
Observed ...	3	0	5	3	1	1
Calculated ...	1·6	1·6	1·6	1·6	3·2	3·2

Blues carrying pink-eye mated together,

$EeddBB \times EeddBB$.

	Blue	Blue lilac
Observed ...	19	6
Calculated ...	18·75	6·25

Golden agouti × *chocolate-lilac* gives golden agouti F_1,

$GgBbEe \times GgBbEe$.

	Golden agouti	Cinnamon agouti	Black	Chocolate	Pink-eyed agouti	Pink-eyed cinnamon agouti	Blue lilac	Chocolate-lilac	Champagne
F_2. Observed	83	8	31	2	26	7	0	11	4
Calculated	72·9	24·3	24·3	8·1	24·3	8·1	2·7	5·4	2·7

Golden agouti × *pink-eyed agouti* gives golden agouti F_1.

	Golden agouti	Pink-eyed agouti
F_2. Observed ...	32	17
Calculated ...	36·75	12·25

Cinnamon agouti mated with chocolate-lilac giving cinnamon agouti F_1.

	Cinnamon agouti	Chocolate	Pink-eyed Cinnamon agouti	Champagne
F_2. Observed ...	14	4	3	1
Calculated ...	12·3	4·1	4·1	1·4

Agouti heterozygous in pink-eyed agouti × *pink-eyed agouti.*

	Agouti	Pink-eyed agouti
Observed ...	11	8
Calculated ...	9·5	9·5

Agouti heterozygous in pink-eye and chocolate × *pink-eyed agouti heterozygous in chocolate.*

	Agouti	Cinnamon agouti	Black	Chocolate	Pink-eyed agouti	Pink-eyed cinnamon agouti	Blue lilac	Chocolate-lilac	Champagne
Observed	7	0	2	1	10	0	0	1	0
Calculated	5·85	1·95	1·95	·65	5·85	1·95	·65	1·3	·65

Agouti heterozygous in pink-eye and chocolate × *black ditto.*

	Agouti	Cinnamon agouti	Black	Chocolate	Pink-eyed agouti	Pink-eyed cinnamon agouti	Blue lilac	Chocolate-lilac	Champagne
Observed	6	1	10	3	0	6	0	2	4
Calculated	9	3	9	3	3	1	1	2	1

Pink-eyed agouti × *pink-eyed agouti.* From this mating I obtained

Pink-eyed agouti	Pink-eyed cinnamon agouti	Chocolate-lilac
37	4	8

There were no blue lilacs and no champagnes. The explanation of this may be that the pink-eyed agoutis were not all carrying the same characters.

Another case I cannot explain is the following:

An albino heterozygous in E was mated with a yellow carrying agouti. From the agoutis F_1 of this union I obtained

17 agouti, 5 black, 1 chocolate-lilac, 1 champagne and 8 albinos.

There were no chocolates, no cinnamon agoutis, no pink-eyed agoutis of either sort, and no blue lilacs.

I have tried other matings of various sorts but the numbers yielded are too small to be worth quoting.

Yellow Mice.

The genetic behaviour of yellow mice differs in various particulars from that of other mice; and there is at present no very satisfactory explanation possible to account for this.

Hagedoorn(1) is the only one among many breeders of yellow mice whose experiences are not in accordance with my own. But from his account of his experiments, it is clear that he was using a different type of yellow mouse from that employed by the rest of us.

The type, which I and other breeders have used, must be regarded as a heterozygous dominant. For it never breeds true, no homozygous form has yet been obtained; and when mated with mice of other colours than yellow, some of the offspring are always yellow. Hagedoorn's mouse was a recessive and did breed true. His experiments are of interest as showing that another type of yellow mouse exists, but his results need not be considered further here.

I made 185 matings in all between yellows bred in every kind of way, but every one of these yellows proved to be heterozygous.

As a result of 127 matings between yellows I obtained 448 yellows and 232 other colours. I purposely excluded from the list all matings from which sables and albinos were obtained, so as to count only the pure yellow forms. Albinos can carry the yellow determiner, and the sable mouse, which is perhaps only a variant of the yellow, presents so many peculiarities as I shall show later on that for the present purpose I preferred to exclude it.

As a result of 104 matings between yellows and other colours I have obtained 297 yellows and 336 other colours.

The problem created by the absence of pure yellows has been discussed by Cuénot(2), Castle(5), Wilson, Morgan and others. There are two possibilities: (1) that in fertilization the zygotes, yellow × yellow, are never formed; (2) that these zygotes are formed but perish. If they are not formed we should expect the ratio of yellow to non-yellow to approximate in F_2 to 3 : 1, because the number of spermatozoa is indefinitely large; if on the other hand such zygotes are formed and perish, the F_2 ratio should be 2 : 1.

The F_2 numbers obtained are as follows:

	Yellow	Non-yellow
Cuénot (2)	263	100
Castle (5)	800	435
My own	448	232
	1511	767
Expectation at 2 : 1	*1518·6*	*759·3*
Expectation at 3 : 1	*1708·5*	*569·5*

From these figures there can I think be no longer any serious doubt that the pure yellow zygotes are actually formed in fertilization, but that for some unknown cause they are unable to develop. The case becomes therefore exactly comparable with that observed by Baur (7) for the *varietates aureae*, which form albino embryos incapable of existence.

It has been argued that if this representation is correct the average numbers per litter should be less for the mating yellow × yellow than for yellow mated with some other colour, and Cuénot and Castle record a difference of this kind, giving the following averages:

	Yellow × Yellow	Yellow × Non-yellow
Cuénot	3·38	3·74
Castle	4·71	5·57

From my experience I incline to doubt whether much importance can be attached to differences of this order.

The following averages have been compiled from an ample series, 75 litters being the lowest included.

yellow × yellow	3·90	young
yellow × other colour	3·97	"
black × black	4·60	"
black × other colour (not yellow)	3·99	"
chocolate × chocolate	3·96	"
chocolate × other colour (not yellow)	3·93	"
agouti × agouti	3·47	"
agouti × other colour (not yellow)	3·32	"
albinos × other colour (not yellow)	4·27	"

I have not mated albinos together often enough to make it worth while to compare the results of mating albino × albino with the other figures.

Only mice which lived long enough to have their colours determined are included in these averages, but Castle's figures evidently are based on the numbers actually born. It is clear nevertheless that large differences exist where no special disturbance, analogous to that we are considering, is to be suspected, and I doubt whether the observations can be used either for or against the conclusion that the ratio of yellow to non-yellow in F_2 is 2 : 1.

The non-viability of pure yellows raises an important physiological question, but we have no indication as to what may be its cause. It should be remembered that the mortality may, for aught we yet know, occur at any age between fertilization and maturity.

In the report to the Evolution Committee (3), I have already stated, that the pigments of the eye of the yellow mouse may be black or chocolate but never yellow. If the yellow mouse throws chocolate young but never black the eye will be found to be pigmented with chocolate, often chocolate pigment will also be found in the hairs of this animal.

A yellow mouse which throws black young will have black pigment in the eyes and some black pigment will always be found in the hair. I have never found black pigment in the hair of a mouse with chocolate only in the eyes.

I have examined several hundred yellow mice and never found an exception to this statement.

The hair and the eyes are a key to the genetic behaviour, or one may equally well say the genetic behaviour is the key to the pigments of the hair and eyes of the yellow mouse. Both black and chocolate pigments will be found in the eyes of the yellow mouse with agouti determiner.

Yellow mice are subject to an abnormal development of fat in their tissues. All the fat depôts become loaded to an extraordinary degree. This development of fat renders them unable to breed. It is a well-known fact to the breeders of Fancy mice.

The question of dilution is also a difficulty in yellow mice. Yellow mice vary very much in their colouring. Some are very deep yellow, some much paler, some are deeply coloured dorsally and very light underneath, pale almost to whiteness. I do not mean piebald, but the colour fades off gradually to a very pale cream. The result is that it is very difficult and often impossible to decide whether a mouse belongs to the dilute variety or not. Of course many mice are so pale all over, one would not hesitate to class them as dilute yellows, that is creams. But there is a very large section whose classification can only be determined by their genetic behaviour. To illustrate the difficulty I will mention the case of two mice which I bred together and classed as creams and they threw chocolates. If they had been real creams they should have thrown silver fawns. Another cream mouse which I had grew a chocolate streak, late in life, down its back, a reversal of the ordinary procedure.

When yellows are bred with pink-eyed mice, pink-eyed yellows will appear in F_2 as deeply coloured as the original yellow mouse which was grand-parent. As stated before the yellow bar of the pink-eyed agouti mouse is so deeply coloured and so bright that the inexperienced observer would put them in the yellow class. I believe that the so-called pink-eyed yellow mice of Plate's (4) classification must be really pink-eyed agoutis, either golden or cinnamon.

The pink-eyed yellow mice when produced behave exactly like the dark-eyed yellows. I have never succeeded in obtaining a homozygous pink-eyed yellow and when mated together they do not throw 3 yellows to 1 other colour; mated with any other colour they always throw some yellows. The dark eye is dominant to the pink eye, but the yellow colour behaves independently of the eye colour when pink-eyed yellow is mated with dark-eyed any other colour.

Pink-eyed yellows mated together throw pink-eyed yellows, blue lilacs, chocolate-lilacs and champagnes according to their genetic constitution.

From the matings of pink-eyed yellows I have obtained the following results,

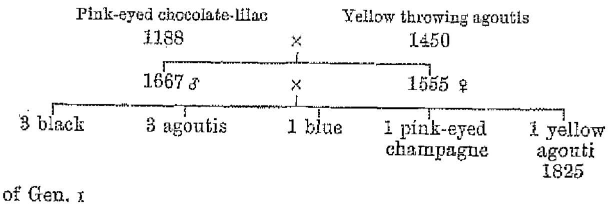
17 matings $PEY \times PEY$ gave 57 PEY, 45 PE other colour.

19 matings $PEY \times PE$ other colour gave 32 PEY, 33 PE other colour.

Before proceeding to give the tables of the results of the various matings I have carried out, I must now refer to two cases in which I obtained yellow mice by breeding together other varieties than yellow. In each case the mice had pink-eyed ancestry.

Case I. This mouse was not strictly speaking a yellow mouse. I could not class it as an agouti simply or as a sable. It was very yellow in colour, with the agouti barring on the dorsal surface and a yellow belly. It resembled a very yellow agouti with a yellow belly.

Its ancestry is shown by the following scheme:



Both 1667 ♂ and 1555 ♀ were agoutis and not to be distinguished in any way externally from any ordinary agouti.

I mated the yellow agouti mouse (1825 ♂) with 6 does, but unfortunately the matings were not all successful. With a chocolate ♀ there were 20 young (not one of which was agouti), 1 yellow, 4 blacks, 7 sables, 1 chocolate yellow belly, 3 chocolates, 3 albinos, 1 chocolate-lilac.

Mated with a yellow mouse carrying chocolate he gave 2 yellows, 2 sables, 3 blacks and 1 chocolate.

I tried him four times with agouti mice but in each case there was no result. I had hoped by such matings to obtain agoutis which would throw yellows or sables.

None of the offspring mated together produced any agoutis.

Case II. A champagne ♀ was mated with an agouti ♂. In the first generation there were

1 agouti, 4 cinnamon agouti, 1 chocolate.

The agouti which was a ♂ was mated with the only ♀ a cinnamon agouti, and there resulted

1 sooty yellow, 2 silver cinnamon agouti and 1 black.

Unfortunately death carried off the yellow before she could be mated. Subsequent litters of the parents did not contain any yellows.

In the subjoined tables the calculations are made on a 2 to 1 basis instead of the ordinary 3 to 1, adopting the conclusion indicated above.

TABLE OF RESULTS.

Dark-eyed Yellows.

Yellows carrying chocolate mated together :

Yellow	Chocolate	
136	68	observed
136	68	calculated

Yellows carrying chocolate × chocolate :

Yellow	Chocolate	
66	46	observed
56	56	calculated

Yellows carrying black and chocolate mated together :

Yellow	Black	Chocolate	
65	35	9	observed
72	27	9	calculated

Yellows carrying black and chocolate × chocolate :

Yellow	Black	Chocolate	
23	11	9	observed
21·4	10·7	10·7	calculated

Yellows carrying black × chocolate :

Yellow	Black	
6	18	observed
12	12	calculated

Yellows carrying black and chocolate × black heterozygous in chocolate :

Yellow	Black	Chocolate	
25	17	18	observed
30	15	15	calculated

Yellows carrying black × black :

Yellow	Black	
29	24	observed
26·5	26·5	calculated

Yellows heterozygous in black, chocolate and albino mated together :

Yellow	Black	Chocolate	Albino	
59	27	5	30	observed
45·3	34	11·3	30·4	calculated

Albinos heterozygous in yellow and chocolate × chocolate heterozygous in albino :

Yellow	Chocolate	Albino	
12	5	7	observed
8	4	12	calculated

In the following tables the yellows are not separated into yellows and creams on account of the difficulty stated above of distinguishing between them.

Yellows heterozygous in chocolate and silver fawn mated together :

Yellow and Cream	Chocolate	Silver fawn	
5	7	5	observed
11·2	4·2	1·4	calculated

Yellows heterozygous in chocolate and silver fawn × silver fawn :

Yellow and Cream	Chocolate	Silver fawn	
33	11	13	observed
29·0	14·5	14·5	calculated

Yellows heterozygous in chocolate and silver fawn × chocolate heterozygous in silver fawn:

Yellow	Chocolate	Silver fawn	
13	10	9	observed
16	12	4	calculated

Yellow heterozygous in black and albino × albino heterozygous in yellow and black :

Yellow	Black	Albino	
5	2	7	observed
4·6	2·3	6·9	calculated

Yellow × Agouti gives Yellow and Agouti.

F_1 yellow × F_1 yellow :

Yellow	Agouti	
60	32	observed
61·2	30·6	calculated

F_1 yellow × F_1 agouti :

Yellow	Agouti	
38	32	observed
35	35	calculated

Yellow heterozygous in agouti × chocolate :

Yellow	Agouti	
19	19	observed
19	19	calculated

Yellow heterozygous in agouti × black :

Yellow	Agouti	
11	18	observed
14·5	14·5	calculated

Yellow × Chocolate-Lilac gives Yellow and Black.

F_1 yellow × F_1 yellow:

Dark-eyed yellow	Black	Chocolate	Pink-eyed yellow	Blue lilac	Chocolate-lilac	Champagne	
46	12	3	24	0	1	9	observed
48	18	6	16	2	4	2	calculated

Here there was an excess of champagnes, no blue lilacs and only one chocolate-lilac.

F_1 yellow × F_1 black :

Dark-eyed yellow	Black	Chocolate	Pink-eyed yellow	Blue lilac	Chocolate-lilac	Champagne	
26	20	2	11	0	15	3	observed
28·8	21·6	7·2	9·6	2·4	4·8	2·4	calculated

Here there was an excess of chocolate-lilacs, no blue lilacs.

Dark-eyed yellow heterozygous in pink-eye × pink-eyed yellow :

Dark-eyed yellow	Black	Chocolate	Pink-eyed yellow	Blue lilac	Chocolate-lilac	Champagne	
34	5	5	27	0	2	7	observed
26·4	9·9	3·3	26·4	3·3	6·6	3·3	calculated

Yellow × Pink-eyed Agouti gives Yellows.

$F_1 \times F_1$:

Dark-eyed yellow	Agouti	Pink-eyed yellow	Pink-eyed agouti	
25	17	11	5	observed
28·8	14·4	9·6	4·8	calculated

Dark-eyed yellow heterozygous in chocolate and pink-eye:

Dark-eyed yellow	Chocolate	Pink-eyed yellow	Champagne	
11	9	1	1	observed
9·6	4·8	4·8	2·4	calculated

Dark-eyed yellow heterozygous in chocolate and pink-eye × chocolate heterozygous in pink-eye:

Dark-eyed yellow	Chocolate	Pink-eyed yellow	Champagne	
8	7	1	6	observed
8·4	8·4	2·8	2·8	calculated

Yellow heterozygous in pink-eye × blue lilac:

Dark-eyed yellow	Black	Chocolate	Pink-eyed yellow	Blue lilac	Chocolate-lilac	Champagne	
2	0	2	2	1	2	0	observed

Yellow heterozygous in pink-eye × chocolate-lilac:

Dark-eyed yellow	Black	Chocolate	Pink-eyed yellow	Blue lilac	Chocolate-lilac	Champagne	
4	2	4	2	0	0	2	observed

Yellow heterozygous in pink-eye and chocolate × champagne:

Dark-eyed yellow	Chocolate	Pink-eyed yellow	Champagne	
1	4	3	9	observed

Here there is an excess of pink-eye.

Pink-eyed yellow × pink-eyed yellow heterozygous in black and chocolate:

Pink-eyed yellow	Blue lilac	Chocolate-lilac	Champagne	
25	3	15	1	observed
28 8	3·6	7·2	3·6	calculated

Here there is an excess of chocolate-lilac possibly due to the fact that some of the yellows were heterozygous in blue lilac only and others in chocolate only, and those mated together would give chocolate lilacs only, no blues and no champagnes.

Pink-eyed yellow × pink-eyed yellow heterozygous in chocolate only:

Pink-eyed yellow	Champagne	
18	12	observed
20	10	calculated

Pink-eyed yellow × pink-eyed agouti:

Pink-eyed yellow	Pink-eyed agouti	
15	7	observed
11	11	calculated

Pink-eyed yellow heterozygous in pink-eyed agouti:

Pink-eyed yellow	Pink-eyed agouti	
12	8	observed
13·2	6·6	calculated

Pink-eyed yellow × chocolate-lilac:

Pink-eyed yellow	Blue lilac	Chocolate-lilac	Champagne	
8	2	8	3	observed
10·4	2·6	5·2	2·6	calculated

Pink-eyed yellow × champagne:

Pink-eyed yellow	Chocolate-lilac	Champagne	
7	4	7	observed
9·0	4·5	4·5	calculated

Sable Mice.

Among the yellow mice I used for my experiments were some individuals, which produced sables when mated with blacks or chocolates. As these appeared very early in my experiments, I at first concluded that sables would always result from such matings. Subsequent investigation however showed that the power to produce sables was limited only to certain mice and that it was a hereditary quality. At present I am unable to offer a scheme which correctly represents the relation of sables to the other colours.

Sable mice are well known to the Fancy. They differ from yellow mice in having a dark black or brown streak down the middle dorsal region while the rest of the mouse is yellow. The streak may be very narrow, when the mouse is said to be a light sable, or very broad when the mouse is a dark sable. As a general rule, the hairs in this dark streak show an agouti pattern, being black or chocolate barred with yellow. But this does not mean that the mouse is carrying agouti determiner. But it is possible to produce sables in which the barring of the dorsal hairs is absent, and at various times I have had black, blue, chocolate and silver fawn mice which differ only from the ordinary forms by having yellow bellies, and which from their genetic behaviour must be classed with the sables. They always moulted subsequently into ordinary sables.

The appearance of the sable mouse varies very much according to age. During the first few months the marking is very definite, but as age comes on the sable appearance is lost, so that a mouse, which was a very good specimen at three months may be hardly distinguishable from an ordinary yellow mouse at 18 months old. The amount of yellow in its colouring increases with the successive moults.

Sables are not to be confused with *sooty* yellow mice, which result from mating ordinary yellows with blacks or chocolates. The sooty yellow is a dirty colour all over and never shows a definite pattern.

I have never bred a homozygous sable mouse. Bred together, sables may throw sables, yellows, blacks, chocolates, and also agouti, if they are carrying the agouti determiner.

Yellows carrying the sable determiner mated together will throw sables, and sables mated together may throw yellows. By mating together yellows carrying sable I have obtained

111 yellows, 38 sables, and 69 other coloured mice.

By mating yellows carrying sable with other coloured mice, not yellows, I have obtained

78 yellows, 55 sables, and 80 other coloured mice.

Mating together sables, I have obtained

161 sables, 43 yellows, and 142 other coloured mice.

Mating sables with other colours, not yellow, I have obtained

93 sables, 90 yellows, and 174 other coloured mice.

Examination of the records suggests, that there is more than one sort of sable mouse, and that it is possible to produce sables which never throw yellows at all.

Thus I had as a result of 5 matings between blue sables, 29 blue sables, and 23 blue mice, and no yellows at all.

4 matings between blue sables and dark sables gave

16 sables and 8 other colours (no yellows).

7 matings between blue sables and blue gave

20 blue sables and 19 blues.

On examination of the results produced by mating sables together, I find that the matings in which yellows were produced, the offspring consist of 62 sables, 43 yellows and 64 other colours, while the offspring of the matings in which no yellows were produced, consist of 99 sables and 78 other colours, suggesting a 9 to 7 ratio.

The matings of sable × other colour show that the families in which yellow appeared consisted of

48 sables, 90 yellows, and 107 other colours,

in the remaining families there were 45 sables and 67 other colours.

Matings between sables and yellows without the sable determiner give

23 yellows and 18 other coloured mice, no sables.

Matings between yellows carrying sables with sables give

14 yellows, 28 sables and 17 other coloured mice.

These results suggest that sable is recessive to yellow. But at the same time it seems extraordinary that some of the sables should be able in their turn to throw yellows, and at present no adequate explanation is forthcoming. The fact that there is probably more than one kind of sable may supply the basis for explanation, but the question ought to be more fully worked out.

Sables, like yellow mice, show a tendency to become abnormally fat.

Besides obtaining ordinary sable mice, another form appeared unexpectedly in my experiments. These I called reversed sables, because in them the agouti pattern was reversed. The base of the hairs was yellow and the barring was black or chocolate.

This marking was only apparent in the young mouse; after about 6 months these mice moulted completely yellow, but it was a very conspicuous feature in early life.

I twice obtained mice which were agouti all over with the pattern reversed. They behaved exactly like sables and never threw any agouti young.

Matings between sables in which the reversed sables appeared gave

49 sables, 21 reversed sables, 19 yellows, 41 other colours.

Matings between sables and other colours, not yellow, in which reversed sables appeared,

12 sables, 12 reversed sables, 9 yellows, and 29 other colours.

The reversed sables are recessive to the other sable, mated together they produced reversed sables and other colours but never ordinary sables, and mated with ordinary sables did not produce reversed sables.

Sables which could throw reversed sables when mated with reversed sables, gave

10 sables, 8 reversed sables, 5 yellows, and 18 other coloured mice.

Owing to the great variation which obtains amongst sables, it has not been possible to classify them very satisfactorily.

Matings between dark sables (broad dorsal streak) × light sables (narrow dorsal streak) gave

8 dark sables, 3 light sables, 10 other colour.

Dark sable by yellow gave

10 dark sable, 5 light sable, 8 yellow, 8 other colour.

Sable × agouti gave

7 sable, 7 yellow, 17 agouti.

Sable × heterozygous agouti gave

29 sable, 26 yellow, 15 agouti, 23 black, 4 chocolate.

F_1 sables from sable × agouti gave

17 sable, 8 yellow, 5 agouti, 4 black, 2 chocolate.

Yellow carrying sable × yellow carrying agouti

6 sable, 14 yellow, 7 agouti.

Agouti Mice.

I have made some further matings between agoutis on account of the suggestion made by Cuénot (2) that a chocolate mouse was to be regarded as the dilute form of black. He made this suggestion in order to account for the results of breeding agouti by chocolate.

I therefore mated agouti with blue (dilute black).

F_1 was all agouti.

F_2 gave 30 ag., 13 dil. ag., 10 black, 4 blue,
32 10·7 10·7 3·6 calculated.

These dilute agoutis are well known to the Fancy as Silver Brown, though a better name would be silver agouti. According to Cuénot the cinnamon agouti would be the dilute form, and not the silver browns.

If cinnamon agouti is mated with silver fawn (dilute chocolate) the F_1 is cinnamon agouti.

F_2 39 c. ag., 10 dil. c. ag., 9 choco., 4 silver fawn,
34·8, 11·6, 11·6, 3·9 calculated,

so that in both cases of golden agouti and cinnamon agouti it is possible to produce a diluted form.

Other matings are: agouti × silver brown gives agouti F_1:

	Agouti	Silver brown	
F_2	45	16	observed
	45·75	15·25	calculated

Silver cinnamon × silver fawn gives silver cinnamon:

	Silver cinnamon agouti	Silver fawn	
F_2	25	10	observed
	26·25	8·75	calculated

Agouti × cinnamon agouti gives agouti F_1:

	Agouti	Cinnamon agouti	
F_2	9	4	observed
	9·75	3·25	calculated

This evidence is perfectly consistent with the scheme which I previously published(3) expressing the relations of black, chocolate, blue, silver fawn, to each other, and shows conclusively that Cuénot's representation of chocolate as a dilution form of black is incorrect.

Finally I wish to record the result of mating agoutis together heterozygous in black. The results should yield a ratio of 3 to 1, but my numbers are not in accordance with this ratio.

I obtained 76 agouti, 37 blacks.

The agoutis which result from mating agouti with black are much darker than the ordinary agouti and very often there is a markedly dark streak down the middle of the back.

The expenses of these experiments were partially defrayed by a grant from the Royal Society.

REFERENCES.

(1) HAGEDOORN, *Archiv Entwickelungsmechanik*, Vol. XXVIII. 1909.

(2) CUÉNOT, *Arch. de Zool. Exp. et Gén.* Vols. I. II. III. VI.

(3) DURHAM, Report IV. *Evolution Committee Royal Society.*

(4) PLATE, *Festschrift zum 60 Geburtstage Richard Hertwig*, Bd. II. 191.

(5) CASTLE, *Science*, N. S., Vol. XXXII. 1910.

(6) DARBISHIRE, *Biometrika*, Vol. II. 1903.

(7) BAUR, *Ber. Deutsch. Bot. Ges.* XXV. 1907.