THE ENGLISH RABBIT AND THE QUESTION OF MENDELIAN UNIT-CHARACTER CONSTANCY

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Whatever the theoretical importance of Mendel's law, its practical utility depends largely upon the purity of the gametes. If Mendelian unit-characters can through hybridization be recombined in desirable ways *without essential modification* during the process, Mendel's law is evidently a distinct acquisition to the practical breeder. Nevertheless if crossing is likely to produce considerable changes in the characters which it is desired to combine in a new race, it is evident that Mendelian crosses must be used judiciously and with caution by the practical breeder.

Considerations such as these have led W. E. Castle for several years to concentrate his studies of genetic problems upon the question of gametic purity. As a crucial experiment he conceived the plan of deriving an entire race of animals, not from a single *pair* of ancestors, but from a single gamete, so far as concerns a particular unit-character. It was thought that in a race so derived, if the principle of gametic purity holds, there should be no variation whatever in the particular unit-character concerned.

Color patterns of mammals seemed especially well adapted for such studies, since they are early differentiated and clearly Mendelize in crosses. The so-called 'English' piebald rabbit presents an especially fine example of such a color pattern. The figures give a good idea of this striking pattern in which white and colored areas are interspersed much as in the 'coach-dog.' It would be a distinct gain to breeders if they could reduce the variation in details of the English pattern so that 'prizewinners' could be bred without the production of so many 'wasters,' which depart in essential points from the standard pattern adopted for the breed. This was an additional reason for undertaking work with the English rabbit.

The first standard-bred English rabbits which Castle had under observation, when mated *inter se*, produced young of three sorts. About half the young were fairly good 'standard' English extensively marked with colored spots (see fig. 3). About one-fourth were much whiter than the standard demands, their spots being fewer and smaller (see fig. 1). And the remaining fourth were without spots, that is were

self colored. This last class was found to be recessive and not to produce English offspring, if mated *inter se*.

The *whiter-than-standard* English proved to be homozygous for the pattern, the 'standard' English being heterozygous and breeding like their parents.

From these observations it was clear (1) that the English pattern is a Mendelian dominant and (2) that the breeding of English rabbits resembles that of blue Andalusian fowls. For the standard bred animal is a heterozygote in the production of which there is bound to be a constant production of 'wasters' unless either the standard is changed or the homozygote can be changed to conform with the standard, producing an animal with more color. In the latter case homozygotes could be bred with each other and wasters eliminated. The question whether the pattern can be changed becomes therefore one of practical as well as theoretical interest.

In making crosses of English with other breeds of rabbits, there was found to be considerable variation among the heterozygous English produced, some being much whiter than others; i.e., having less extensive colored spots. Plus (dark) and minus (light) selections were made to see to what extent the pattern was capable of modification. These selection experiments are still in progress but will be reported upon at another time.

The single-gamete experiment, with which this report will deal, was placed in the hands of P. B. Hadley, who has carried it out at the Rhode Island Agricultural Experiment Station.

As foundation stock for the experiment a single *heterozygous* English rabbit of standard character (grade 2, fig. 5) was selected. To mate with him, it was desired to obtain a distinct breed of rabbits, free from the English pattern, and as pure (uniform) in all respects as possible. For this purpose the 'Belgian hare' was chosen. A buck and two does obtained from G. W. Felton, Cliftondale, Mass., were found to breed very true. From them was bred a stock of does very uniform in character, twelve of which, together with one of the parents (2A) were mated with the selected English buck which we may henceforth call by his record number ♂21A. The young thus produced will be called 'Series I' offspring. About half of them were self (non-English), the remainder (187 in number) were English.* The latter, although all

* The total number of young obtained from ♂ 21A, when mated with Belgian hare does has been to the time of writing 436. The English young now number 210, the non-English (self) number 226. For Series II matings presently to be described the corresponding numbers of young are: English 219, non-English 196, total 415. For Series I and II combined the numbers are : English 429, non-English 422, total 851. This is unmistakably a 1 : 1 Mendelian ratio.

undoubtedly heterozygous, varied in whiteness from grade 1 to grade 4, figures 1 to 4, the *modal* or commonest condition being about the same as that of the father (grade 2). The distribution of the young in relation to our grades is shown in the Table. Statistical treatment of the table gives the *average grade* of the young as 2.43, that is some-

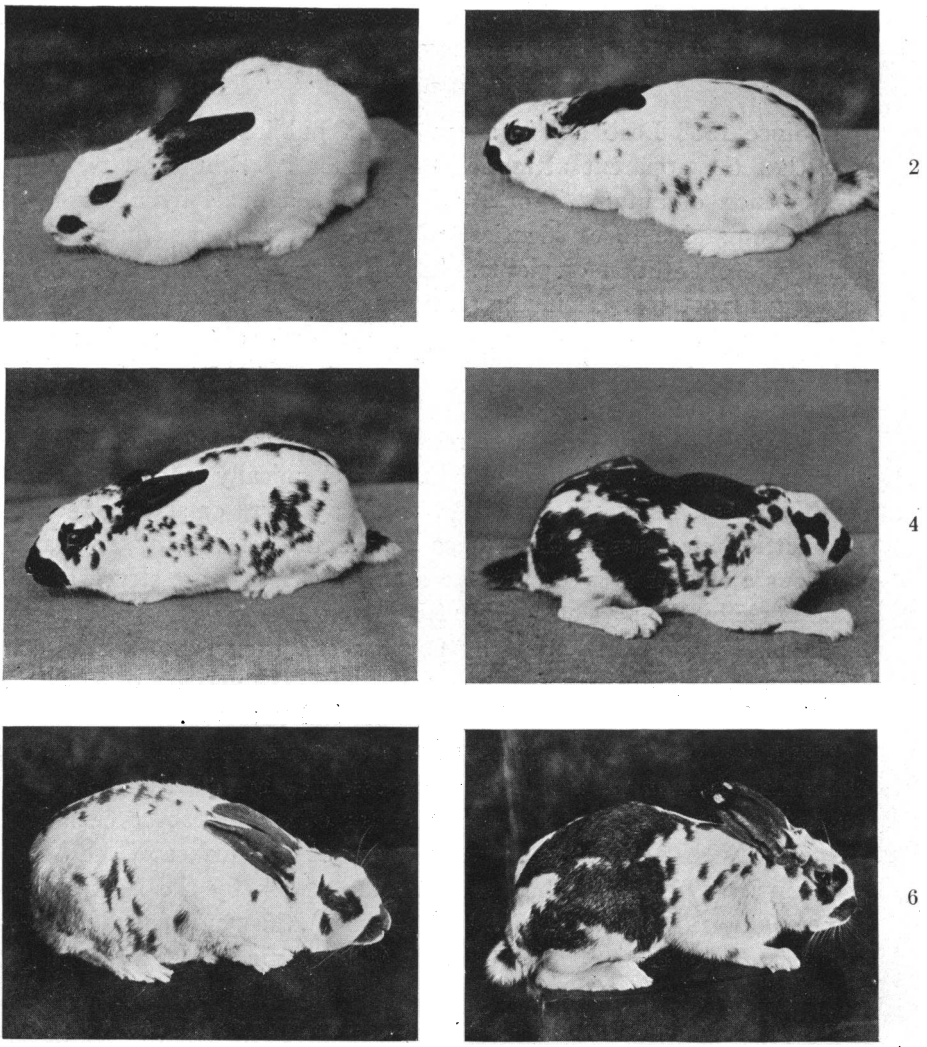
TABLE SHOWING THE DISTRIBUTION OF GRADES OF OFFSPRING IN THE FIRST AND SECOND SERIES OF MATINGS FOR EACH INDIVIDUAL MOTHER

MOTHER	SERIES	GRADES OF YOUNG													TOTALS		AVERAGE
		1.00	1.25	1.50	1.75	2.00	2.25	2.50	2.75	3.00	3.25	3.50	3.75	4.00	Ser. I	Ser. II	
16A	I					1	2	2							5		2.30
	II					3	1	1	2	1	7	3	3			21	3.08
16B	I		1		1	3	1	1	1	2			1		11		2.39
	II			1	1	2	1		1	2	1	3				12	2.67
16D	I					2	5			1	2	3	1		14		2.79
	II								3	1	6		2			12	3.19
16E	I			2		5		2	1	1			1		12		2.29
	II										1	3	1			5	3.50
16F	I	1				2	1	5	3	2		3			17		2.62
	II				1	2	1	3	3			1				11	2.48
16G	I		1	2		2	3	1	2	3	1				15		2.35
	II						1	2	2	3	1	2	1	1		13	3.06
16H	I			1		3	3	1	2	2	2	1	2	1	18		2.76
	II					3		2	1	1	8	2	2	1		20	3.06
17E	I		1	1	3	4	3	3	1	1	2	2			21		2.36
	II					1	2	5	5	3	4	4	2	1		27	2.97
17G	I			1	9	6	3	3	2	1	2	1	1		29		2.27
	II		1	1		1	1	1	1	1	1	1				9	2.44
18D	I		1			3	3	3		1	2	2			15		2.53
	II					2	1	2	3	1	2	5				16	2.91
18F	I				3	1						1			5		2.15
	II				1	1	2		4	2	1	1	2	2		16	2.97
18H	I			1	1		3	1	1	3					10		2.43
	II				1		3	3	4	2	3		1	2		19	2.87
2A	I		1	2	1	1	4	2	3	1					15		2.22
	II				1	2				1	2	2				8	2.78
Totals	I	1	5	10	18	33	31	24	16	18	11	13	6	1	187		2.43
	II		1	2	5	17	13	19	29	18	37	27	14	7		189	2.92

what *darker* than the father. Inspection of the table shows that more than half of the young are darker than the father, which supports in a general way the statistical average grade. If we consider separately the average grade of the young produced by each mother, we find that it ranges from 2.15 in the case of ♀18F, which had 5 English young, to 2.79 in the case of ♀16D which had 14 English young. The average number of young to a mother is 14.4.

After this series of matings had been completed, a second series was begun in which the same 13 females were mated with one of the darkest bucks produced in the Series I matings (a son of ♀16 E). The selected buck was ♂40A (fig. 6) grade 3.75, considerably darker than his father (fig. 5). This series of matings produced 189 English young, together with a like number of self (non-English) young. The grade distribution of the English young is shown in Table 1, Series II. All of the 13, mothers except one (♀16F) produced darker offspring in the Series II than in the Series I matings. The lowest average grade was shown by the young of ♀17G, viz. 2.44. For Series I matings, the lowest average was 2.15. The highest average grade in the Series II matings was given by the young of ♀16E, viz. 3.50. For Series I matings, the highest average was 2.78. Consequently both maximum and minimum averages were higher in the Series II than in the Series I matings. The grand average of all the 189 Series II offspring was 2.92, as compared with 2.43, the average grade of the Series I young. The modal grade of the Series II young is 3.25. The modal grade for Series I was 2.00. Since the mothers were identical in both series, the difference in the young can be attributed only to the difference in the fathers. The male used in the Series II matings differed genetically as well as somatically from his father who sired the Series I young. Not only was he darker, but he also produced darker English young. Yet the father contained only a single dose (one gamete) of English pattern and the son derived his English pattern exclusively from this same source. Hence the English unit-character had changed quantitatively in transmission from father to son. This seems to us conclusive evidence against the idea of unit-character constancy, or "gametic purity." If unit-characters are not constant, selection reacquires much of the importance which it was regarded as possessing in Darwin's scheme of evolution, an importance which many have recently denied to it.

The question whether an imaginary 'unit-factor' for English pattern has or has not changed in correlation with the visibly changed English unit-character is not here discussed. We recognize that it has an academic interest, which however scarcely affects the practical question whether the visible Mendelizing characters of animals are subject to change through crossing or through selection or both.



FIGS. 1-4, PHOTOGRAPHS OF FOUR ENGLISH RABBITS FORMING A GRADED SERIES IN AMOUNT OF COLORED FUR.

These were adopted as our standard Grades 1-4, in terms of which all the rabbits described in these experiments have been classified.

FIG. 5, RABBIT ♂21A, FATHER OF THE SERIES I YOUNG.

FIG. 6, RABBIT ♂40A, FATHER OF THE SERIES II YOUNG.