

CONTRIBUTIONS TO THE GENETICS OF THE DOMESTIC RABBIT

W. E. CASTLE AND PAUL B. SAWIN



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I

ENGLISH AND DUTCH SPOTTING AND THE
GENETICS OF THE HOTOT RABBIT

By W. E. CASTLE
Bussey Institution, Harvard University

With six plates

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ENGLISH AND DUTCH SPOTTING AND THE GENETICS OF THE HOTOT RABBIT

In previous publications I have shown that English and Dutch patterns of white spotting are inherited as unifactorial Mendelian characters, the former behaving as a dominant, the latter as a recessive in crosses with unspotted (self) individuals. Each of the characters acts as an inhibitor of pigment production in particular regions of the coat and its action is stronger, that is larger white areas are produced, when its gene is homozygous (represented doubly) than when it is heterozygous (represented singly) in the zygote. But Dutch expresses itself very little in heterozygotes and so may properly be classed as recessive, although the difference between dominant and recessive characters in general is to be regarded as one of degree of expression rather than of kind. Both English and Dutch vary in expression through genetic agencies other than their heterozygous or homozygous state. In the case of English and to some extent also in the case of Dutch, such variation can be accounted for as due to modifying factors, which apart from the spotting gene itself would perhaps not produce a spotted coat.

ENGLISH

Plate 3 shows the ordinary range of variation of the English pattern. Figures 1 and 2 show its appearance in homozygotes, figures 3 to 6 in heterozygotes, as seen in "checkered giants." Special modifying genes are probably responsible for the more massed, fused and extended state of the typical spots, seen in figures 7 to 10. Other special modifiers are probably responsible for the pattern of very numerous and separate small spots found in the exhibition type of English seen in Plate 4, figure 1.

The English gene has its fullest expression in numerous distinct, colored spots on a white background in heterozygotes. The spots are carefully listed in the standards of fanciers. In homozygotes the size of these spots is diminished and many of them disappear altogether. Compare for example figure 1 with figure 2 of Plate 4, or figures 1 and 2 of Plate 3 with figures 3 to 6 of the same plate. The maximum of distinct, colored spots, which is desired by the fancier but is found only in heterozygotes, may be listed as follows.

A butterfly-shaped spot bestrides the nose. So characteristic is this marking in carefully bred strains of exhibition English or in Checkered Giants that such strains are frequently referred to as "butterflies." Not all individuals heterozygous for the English gene show this marking and it was not formerly insisted on as a feature of prize-winning animals. But absence of the butterfly on the nose is probably not due to a modification

of the English gene itself or to a different allelomorph of it, but rather to some modifying factor. Dutch can function as such a modifier, as I shall show, and very probably did so function in the less improved strains of English having a white nose. Inspection of Plate 1 will show that the first manifestation of a gene for Dutch is a white nose, a white fore-foot or a star in the forehead. A gamete carrying a low grade of Dutch (Plate 1, figs. 1-3) uniting with a gamete carrying the English gene will often produce an English individual with a white nose, as I have observed in crossing a small race of rabbits with Checkered Giants.

A circle of colored fur surrounds the eye, and there is a smaller distinct spot below it. The ears are colored but not uniformly. The pigmentation shows a tendency to break up into smaller spots, especially along its margins. A *spinal stripe* begins on the neck and continues with occasional interruptions out on to the dorsal surface of the tail.

Spots on either side of the spinal stripe are found chiefly on the middle of the back where they are largest and most numerous and extend farthest down the sides, but show a tendency to run together into a continuous dorsal blanket. Such fusion is not desired by the fancier who aims to secure by selection an open "herring-bone" pattern.

Lateral spots beginning on the shoulder continue backward and downward along the sides below the "herring-bone" and form the "chain." A *spot is found near the middle of each leg* (at morphological wrist and ankle). On the under side of the body, there is a colored spot at each teat and an imperfectly expressed *mid-ventral line*, counterpart of the mid-dorsal or spinal stripe. The *scrotum* or other *external genitalia* may be mottled.

A homozygous condition of the English gene causes many of these spots to disappear, or reduces the size of those which remain. This is better understood if we think of the English gene as causing the white areas rather than the colored spots. It produces the inhibition of pigment formation, of which the colored spots are mere residua, unaffected areas. Naturally, two doses of the English gene accentuate the inhibition and so diminish the unaffected areas.

Other inhibitors of pigmentation, genetically distinct from the English gene are the genes for Dutch marking and for Vienna White. When either of these is associated with the English gene in a zygote, they have a combined action to whiten the coat, that is the colored spots are diminished in number and size. Doubtless other genes also modify the expression of the English gene, as in the type of modification seen in figures 7 to 10 of Plate 3, though apart from the English gene they have no observable effect, but such genes have not as yet been individually identified.

DUTCH

The only known allelomorph of the English gene is non-English. The case of Dutch is more complicated. The entire range of variation of the Dutch pattern is shown in Plate 1. The prize-winning type of the fancier shown

in figure 8 is not ordinarily true breeding, but produces three types of Dutch marked animals in a 1:2:1 ratio. Two of these types (the less numerous ones) are true breeding (homozygous). I have called them Dark-Dutch and White-Dutch respectively (see Plate 2, figs. 2 and 3). Fancier's Dutch (Plate 2, fig. 1) is a heterozygote between these two and so not true breeding, in which it resembles the well-known blue Andalusian fowl. White-Dutch (Plate 1, figs. 9-17) differs from Dark-Dutch in the following respects: (1) White-Dutch usually has a wider white belt, (2) the area posterior to the belt is broken up into a number of small spots, and (3) the anterior surface of the iris is unpigmented, producing a blue or "wall" eye. I regard these two types as allelomorphs of the same gene and in support of this view have presented evidence that both show linkage with the same gene, angora. This, however, would not prove beyond question that they are allelomorphs, but only that their genes lie in the same chromosome, and Punnett and Nachtsheim question the allelomorph interpretation. But so many cases of multiple allelomorphism have now been established beyond question both for the rabbit and for other animals, that the allelomorph interpretation has much in its favor. At one time I described a third Dutch allelomorph "tan" Dutch combining some of the features of the other two, but it is possible that I was mistaken in this and that I was really dealing with a modified White-Dutch type, since it had wall eyes in some cases. Its pigmentation was in general more extensive than that of typical White-Dutch and it lacked the interrupted spotting posterior to the belt, but both of these differences may have been due to genetic modifiers. As the race is no longer extant, it is impossible to determine the matter by new experiments. The two types, White and Dark, are readily obtained at any time by inbreeding ordinary standard exhibition Dutch, and I am strongly of the opinion that they are allelomorphs. Occasionally, however, one finds a standard Dutch individual which is not a heterozygote of the two types but produces a uniform progeny when mated with a homozygous individual (White-Dutch, Dark-Dutch, or self). Hurst has described and figured such animals and I have recently obtained one from a fancier. They are in my experience, as in that of Hurst, rare as compared with the ordinary heterozygous type. They are probably modified Dark-Dutch, an explanation which I hope shortly to test by new experiments.

The genes for White-Dutch and for English, though producing very different phenotypes, are closely linked with each other, as I was able to show in 1926. They lie in the same linkage system as angora with which they show about 13 or 14 per cent of crossingover. In a cross of English with White-Dutch, F_1 animals are produced which are unmistakably English in pattern but have the typical English spots reduced in number and extent (see figs. 2 and 3, Plate 7, Castle 1926). The colored spots which persist are those of the eye and ear, usually also a spot or two representing remnants of the spinal stripe or of the chain of side spots. The eyes are full colored (brown) as in ordinary English individuals. The White-Dutch

pattern, recessive in the F_1 animals, has a whitening influence on the coat about equal to that of a second dose of the English gene, though it specifically eliminates all nose markings, which may persist, much reduced in extent, in homozygous English.

COMBINED ENGLISH AND DUTCH

A back-cross of such F_1 animals with homozygous White-Dutch produces as a rule equal numbers of (1) English individuals like F_1 in appearance and genetic constitution and (2) of homozygous White-Dutch. The latter have blue (wall) eyes, the former brown eyes. From such a back-cross was reported in 1926 only one individual in 730 which was not clearly of one class or the other. This individual was apparently English but different from the other English segregates in that (1) its colored spots were limited to the eye and a part only of each ear, (2) its eyes were blue, not brown, and (3) its coat was angora, not short. The reduced English spotting and the blue eye indicated a homozygous condition of the Dutch gene. But pigmentation at the base of the tail which is invariably present in even the whitest ordinary White-Dutch was in this animal entirely wanting, evidence that the English gene was present and inhibiting it. This interpretation was supported by the fact that the individual was long haired. For in the original cross an angora Dutch was mated with a short-haired English, and the back cross was made to angora Dutch. Hence the peculiar individual was apparently homozygous for the linked genes White-Dutch and angora, and at the same time heterozygous for English. The combination could have arisen only by the union of a gamete carrying Dutch and angora (furnished by the Dutch angora parent) with a similar gamete (furnished by the F_1 parent) to which had been added by a crossover the English gene. Hereafter in this paper this individual will be referred to as the crossover individual.

Concerning him I said in 1926 "Mated with homozygous White-Dutch females, he has produced four litters of young, part of which are ordinary White-Dutch and others very light English like himself, with no body spots whatever and very restricted head spots (eye and ear)." In the following pages I propose to give a fuller account of these and other progeny of the crossover individual.

The crossover male was mated with a considerable number of homozygous White-Dutch females including his own mother, and by them produced 148 young of which 71 resembled himself, showing the presence of an English gene in addition to a homozygous condition as regards White-Dutch. The other 77 young were ordinary White-Dutch individuals of grades ranging from 8 to 16 (table 1 and Plate 1). The 71 young which contained an English gene linked with one of the White-Dutch genes fall into four groups which will be indicated by the four grades (supplementary to those figured in Plate 3) 1, $\frac{1}{2}$, $\frac{1}{4}$ and 0. Grade 1 is used to indicate an animal which

TABLE 1—Classification of the young sired by the original crossover English-Dutch male, 6559.

Mothers	Grade of English young						Grade of Dutch young										Total
	4	3	2	1	$\frac{1}{2}$	$\frac{1}{4}$	0	0	1-2	3-4	5-6	7-8	9-10	11-12	13-14	15-16	
White-Dutch (grades 12-17)	11	43	11	6	71	1	6	23	35	12	77
English Daughters (grades $\frac{1}{4}$ -1)	13*	14	12	1	40	2	6	6	2	16
Self or Dark Dutch (grade 0-2)	3	5	6	1	..	17	..	16	7	5	18

*Eight of these had only one eye spot; one had a small back spot.

has eye-spots and also a small pigmented area on one or both ears; grade $\frac{1}{2}$ indicates that the individual has eye-spots only; grade $\frac{1}{4}$ signifies that the individual has a pigmented spot surrounding one eye only; and grade 0 indicates that the animal has no pigmented fur, though the eyes as in all the other groups are colored. The frequencies of these classes were 11, 43, 11 and 6 respectively (table 1). More than half the individuals (43) have both eyes surrounded with pigmented spots but are elsewhere white. This may be regarded as the modal phenotype of this genetic combination. The corresponding modal phenotype among the 77 White-Dutch young born in the same litters and presumably having a like combination of modifying factors lies within the range of grades 11 to 14, Plate 1 (58 individuals). The only genetic difference between the two types is that one contains an English gene in addition to the genetic complex of homozygous White-Dutch, whereas the other does not. When the English gene is absent, there is always a pigmented area of varying size at the base of the tail and on the rump; when the English gene is present this area is wanting, and the only pigmented fur is found in the eye spots or less often on the ears.

The crossover male was also mated with several of his crossover (English) daughters of grades $\frac{1}{4}$, $\frac{1}{2}$ or 1, producing 40 English-Dutch (crossover) young and 16 White-Dutch young, a fair approximation to the expected 3:1 ratio. The Dutch young were of grades 9 to 16, with a majority (12) in the middle groups (grades 11 to 14) as in the back-cross population, indicating a similar assortment of modifying factors. The English (crossover) young are of the same four types as in the back-cross group with frequencies of 13, 14, 12 and 1, respectively. The modal group is again that with a pair of eye-spots and no other pigmentation (grade $\frac{1}{2}$).

The crossover male was also mated with a few unspotted (self) females or such as were near self, being Dark-Dutch of grades 1 or 2 (table 1). In such matings he produced 18 young unspotted or low grade Dutch (grades 0-4), and 16 unmistakably English young of grades 1 to 4. All except one of the 16 English young had colored spots additional to eye spots, either ear spots, a partial back stripe, or side spots, or a combination of some or all of these. The one doubtful case is that of a yellow individual which died young. Although he was recorded as having only one pigmented eye spot, it is quite possible that inspection at a later age would have revealed pigmented areas on ears or body also. These matings show that with only one White-Dutch gene present, the one borne in the crossover gamete, a typical English pattern may be developed, whereas a homozygous state of White-Dutch associated with an English gene reduced the pigmentation to eye spots or at most to small additional ear spots. The same complex of factors which increases the pigmentation in the English group of young to grade 4 English, apparently increases the pigmentation in the Dutch group to grade 0 (self), i.e., completely obliterates Dutch markings.

Certain of the crossover young sired by the original crossover male were mated inter se or with typical White-Dutch animals. The young produced by these matings are classified in table 2. The young derived from matings

with White-Dutch fall into two classes as did the young produced in similar matings by the original crossover male. The crossover (English) young number 55 distributed in the four grades 1, $\frac{1}{2}$, $\frac{1}{4}$, and 0, with frequencies of 2, 21, 16, and 16, respectively. The modal group is again grade $\frac{1}{2}$ with eye spots only. The Dutch young range in grade from 10 to 15, but number 27 only. The reason why the Dutch young are in this group of matings less numerous than 50 per cent, as in the similar matings of the original crossover male, is that certain of the parents were homozygous for the crossover combination, English-Dutch, and so produced only crossover young.

TABLE 2—Later descendants of the crossover English-Dutch male, 6559.

Parents	Grade of English young					Dutch young (grades 10-15)
	1	$\frac{1}{2}$	$\frac{1}{4}$	0	Total	
English (0- $\frac{1}{4}$) x White-Dutch	2	21	16	16	55	27
English (0-1) bred inter se	8	77	75	85*	245	28

*One with a small tail spot.

In the matings inter se of crossover (English-Dutch) individuals of grades 0-1 (table 2), there were also produced less than 25 per cent of Dutch young for the reason just stated, that some individuals were crossover homozygotes. The English-Dutch young produced by such matings numbered 245, with a great majority of them having only eye-spots or no colored fur at all. One individual which had no spots on the head had a small spot on the tail. Most of them had blue (wall) eyes like the original crossover male and White-Dutch individuals in general. No particular record was made of this feature until a comparative study came to be made of the Hotot rabbit. Then it was found that an occasional individual among them had brown eyes, or eyes partly brown (mosaic). This may be explained as due to the evenly balanced but opposite tendencies of the linked genes English and Dutch. Typical English individuals, whether homozygous or heterozygous, are brown-eyed; White-Dutch homozygotes are blue-eyed. In crossover individuals the homozygous state of the Dutch gene usually produces blue eyes, but the tendency of the English gene to produce a brown eye may counteract the influence of the Dutch gene partially or wholly, so as to produce mosaic or wholly brown eyes.

It may be observed in table 2 that the modal class of crossover young produced in the inter se matings is the grade 0 group. Parents of that group were given preference in the matings made in the later generations. This perhaps explains why that group came to predominate, through the segregation of a particular set of modifying factors.

THE HOTOT RABBIT

Blanc de Hôtot¹, Plate 6, figure 1, is the name of a breed of large-sized white rabbits kept in France and distinguished by a peculiar and striking color pattern. The animals are entirely white except for a circle of colored

¹ Hereafter in this paper for simplicity Hotot.

fur surrounding each eye. The eyes themselves are colored. In the two animals which I have seen the eyes were brown, as in ordinary self-colored rabbits. Whether there is any variation in the eye color within the breed, I have had no opportunity to observe.

When I first learned of the existence of this breed of rabbits I was struck by its close resemblance to the modal class of my English-Dutch crossover race, having eye spots only, and I sought an opportunity to compare the two races genetically. Only recently have I been able to do so. Through the kindness of Dr. Wade Wright of the Metropolitan Life Insurance Co. of New York who imported some Hotot rabbits from France and gave them to Dr. Wade Brown of The Rockefeller Institute, I received two male individuals in 1930. My hearty thanks are due to both these gentlemen for generously providing me with experimental material which I had sought in vain elsewhere in America. From one of the animals which I thus obtained (Plate 6, fig. 1) numerous offspring have been secured in crosses presently to be described and these throw light on the genetic constitution of the breed. When Hotot is crossed with self-colored rabbits, offspring are produced which have the characteristic markings of English rabbits, colored areas additional to the eye spots being produced regularly on the ears, and in a spinal stripe, less often also on the sides, tail and nose (see Plate 6, fig. 2). This result supports Nachtsheim's opinion that Hotot is in some way derived from the English mutation.

When the Hotot male is mated to his English marked F_1 daughters from the cross with self does, two classes of young are produced in equal numbers. One class is typical Hotot in character with a spot surrounding one or both eyes but with no other spots. The other class consists of English marked animals like their F_1 mothers and presumably like them heterozygous. These bear, in addition to eye spots, ear-spots and usually also back spots, side spots or nose spots, or a combination of all of them. It is evident from this result that the Hotot character segregates as a unit, but varies in expression as does the English-Dutch unit of two closely linked genes, since the eye spot may be present on one side only, or on neither side (grade 0).

An F_2 generation from Hotot crossed with self consists of three types in approximately a 1:2:1 ratio. These are respectively, selfs, English of about grade 2 (like the F_1 parents) and extracted Hotot. The first and last mentioned groups are obviously homozygotes, the middle group heterozygous.

In three such F_2 litters there were recorded 5 self individuals, 9 English of grades $1\frac{1}{2}$ or 2, that is with spots additional to eye spots, and 8 with eye spots or no spots at all.

The last group included one individual with two eye spots, 2 individuals with one eye spot each, and 5 individuals with no eye spots (grade 0). It is important to note that certain of the extracted homozygous Hotot individuals had mosaic eyes similar to those found in the English-Dutch race.

My own "crossover" race, which resembles Hotot, also produces English marked young in crosses with self (see Plate 5, fig. 3). Its genetic constitution is known to be a synthesis of English with the particular type of

Dutch which I have designated White-Dutch, and for this reason I have suggested elsewhere (Castle 1930) that Hotot may have resulted from a similar synthesis. This suggestion is strongly supported by the experimental evidence which I shall presently summarize.

The chief difference between the Hotot male which was used in my experiments and my synthetic English-Dutch race consists in the eye color. The Hotot male has a brown eye, my English-Dutch rabbits usually have a blue eye (Plate 4, fig. 3), but I find among them, on making a careful inspection of my stock, one which has brown eyes (Plate 5, fig. 2), one which has the right eye chiefly brown (mosaic) and the left eye blue. Compare Plate 6, figures 3 and 4. It is accordingly possible for the English-Dutch phenotype to be brown-eyed partly or wholly, though in my experience it is usually blue. Brown eye, with the anterior wall of the iris pigmented, is characteristic of English; blue eye with the anterior wall of the iris unpigmented is characteristic of White-Dutch. In Hotot and my English-Dutch race the two tendencies seem to be pretty evenly balanced, with brown eye predominating in the former, blue eye in the latter.

In crosses of the two races with each other, the balanced state is expressed still more strongly. The Hotot male (a homozygote as regards Hotot pattern) having brown eyes has been mated both with English-Dutch having blue eyes and with pure White-Dutch having blue eyes. The results are similar in both cases. Combining them, we have in a total of 27 young, 12 which are blue-eyed, 6 which have one eye blue, the other mosaic, 3 which have both eyes mosaic, and 3 which have one eye blue, the other brown. Three young died before their eye character had been determined.

As to eye-spots in this group of young, 14 individuals have the spot of colored fur round each eye, 10 have one eye spot only, 3 have none. No other spots than eye-spots are developed in any of the young. In other words the phenotype common to both parent races is present in the great majority of their offspring, and none deviate from it in the sense of adding spots characteristic of English unassociated with Dutch (ear spots), or of Dutch unassociated with English (rump or tail spots).

The evidence that Hotot and my synthetic English-Dutch race are of like genetic constitution may then be summarized thus:

1. The two are similar in appearance (phenotypically).
2. They reproduce the common phenotype when mated with each other.
3. Both produce similarly marked English young, which are brown eyed, when mated with an unspotted (self) race.
4. Both show simple segregation of the typical condition when a back-cross is made of the English marked F_1 animals with the parent type, and the type segregates vary in a similar way.
5. Both produce similarly marked Hotot type young when mated with White-Dutch. These young have eye spots only, or rarely no spots at all in the fur, and their eyes are either blue or mosaic, or at most they have only one eye brown.

6. An F_2 from Hotot mated with self produces extracted Hotot animals, some with and others without eye spots, also some with mosaic, others with uniformly pigmented eyes, a parallel variation to that found in the English-Dutch race.

There is accordingly every reason to think that the Hotot rabbit arose, as the synthetic English-Dutch race is known to have arisen, by a crossover between the closely linked genes English and White-Dutch in an individual heterozygous for both.

POSTSCRIPT

It might be well to consider the bearing of these observations upon the conception of "step allelomorphism" presented by Agol ('31). He holds that genes are not discontinuous units composing chromosomes, but that "the entire chromosome is continuous" and "one gene passes directly into another," the component genes or portions of the chromosome being themselves composite. Complete allelomorphism is found only when exactly corresponding parts of a pair of chromosomes are considered, these parts having equivalent somatic effects. In the example which he elaborates, a gene scute is considered to be completely allelomorphic to another gene scute only when it affects exactly the same quota of bristles on the body of *Drosophila*. But if it affects only a part of these bristles, it is only partially allelomorphic and must be given a different designation as scute¹, scute², etc. Multiple allelomorphs on this view are portions of homologous chromosomes coming opposite each other in synapsis *in part* but overlapping so that one includes portions not included in the other.

The concept seems to be based on a comparison of somatic effects, it being assumed that identical somatic effects are due to identical genetic agencies. This is demonstrably not true. White fur in rabbits may result from a variety of genetic agencies, lying in different linkage systems (chromosomes), and so not allelomorphic on any conception of allelomorphism yet formulated.

Genes of the rabbit which produce white fur are (1) the gene for albinism, *c*, which is located in the same chromosome with genes *b* (brown) and *y* (yellow fat), (2) the genes for White Dutch and for English which are located in the same chromosome with *l* (angora), (3) the gene for Vienna White which lies in a third chromosome. On Agol's conception, English and Dutch might be considered step allelomorphs, since they have physiological effects which are similar in certain parts of the coat, and are demonstrably located in the same chromosome at loci not far apart.

But Vienna White has local somatic effects (especially in heterozygotes) which closely resemble those of White Dutch. The resemblance is much closer than that between English and Dutch. Yet the gene for Vienna White is not borne in the same chromosome as White Dutch, English and Angora, and so can not be considered an allelomorph of White Dutch on the conception of allelomorphism formulated either by Agol or by Morgan.

Our present knowledge agrees better with the conception of a gene as an organic compound of definite and stable constitution found ordinarily only at a particular locus of a particular chromosome. Allelomorphs of the same gene differing in their somatic effects doubtless differ in their constitution, perhaps analogous with the differences in chemical isomers.

It is quite conceivable that by translocation, true allelomorphs might come to lie in non-homologous chromosomes, in which case they might no longer be recognizable as allelomorphs, but would function as duplicate genes. Such cases are probably rare and have been demonstrated thus far only in the case of plants in which polyploidy is common.

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