Colour Inheritance in the Horse

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While the mode of inheritance of the different colours in horses has been explained by several workers, there is no general agreement as to difinition of certain colours, which can cause problems in interpretation. Our knowledge of the inheritance of coat colour has been largely derived not from planned experimentation but from the analysis of written stud books colour notation. But there is no general agreement as to what certain colours actually are. The coat colour in certain instances undergoes considerable modification with advancing age. Moreover, there is no common language in which different peoples can describe the same phenomena. It is very important to establish the accurate genotype for truthful registration.

Materials and Method

The coat colours of Thoroughbred yearlings foaled in 1966–1970 for further statistical analysis were recorded. And the coat colours of Hokkaido Native Ponies foaled during 10 years at the Livestock Farm of Hokkaido University were summarized.

Colours in horses exist in considerable variety and combinations. As a rule, however, the colours are readily recognizable. They are grouped according to international glossary.

Black : Where black pigment is general throughout the coat, limbs, mane, and tail, with no pattern factor present other than white markings.

Brown or Dark Bay : Where there is mixture of black and brown pigment in the coat, with black limbs, mane and tail (black points).

Bay : Bay varies considerably in shade from dull red approaching brown to a yellowish colour approaching chestnut, but it can be distinguished from the chestnut by the fact that the bay has a black mane and tail and almost invariably has black on the limbs and tips of the ears (black points).

Chestnut : This colour consists of yellow-coloured hair in different degree of intensity, which may be noted if thought desirable. Lighter coloured chestnuts may have flaxen manes and tails.

Gray : Where the body coat is a varying mosaic of black and white hairs, with the skin black. With increasing age the coat grows lighter in colour. As there are many variations

according to age and season, all of them should be described by the general term gray.

Roans : Roans are distinguished by the ground or body colours, all of which are permanent.

The next definitions are not fixed.

Buckskin or Dun : Yellow body, black points.

Isabel(las) : Yellow body, white mane and tail.

Results

Inheritance of A and B

The simplest explanation of the relationship of these colours is what suggested by WALTHER in 1912 and substantially adopted by various workers. Several of these workers drew for their conclusion upon the studies of CRAMPE (1887–1888), who had collected and analyzed a great deal of valuable data. Nearly for a century so far it has been supposed that chestnut is recessive or hypothetic to black, blown, bay and gray from the fact that chestnut should produce only chestnut and chestnut should be produced by all matings (chestnut rule) (Table 1).

For the purpose of confirming of this rule the auther analyzed the breeding records. Chestnut of all yearlings foaled durring five years are tabulated (Table 2). In this case these yearlings are not independent of each other because some of them are sibs. The frecuency of chestnut in each year is considerably constant. The auther adopted an approximate method of estimating based upon the mean frequency from the number of yearlings, assuming that chestnut may be controlled by a single recessive autosomal gene.

It must be tested whether the proportions of chestnut to the others from three kinds of genotypes agree with the expected value estimated by Mendel's law. So we first confirm whether the mating (Table 3) is randomly practiced as far as coat colour is cocerned. For this the author tested whether the proportions of these three kinds of mating types agree with those estimated on a hypotheses of random matings. The result of this test is indicated in Table 4. From this table it is concluded that the proportion of three genotypes in the three kinds of mating are in the equilibrium state, so the theoretical proportion of recessive offsprings from the two different types of mating may be calculated and compared with the observed values to test if the hypothesis for one pair of autosomal gene with recessive trait is true. In Table 5 the observed values are obtained in close agreement with those expected on the basis of SNYDER's ratio. From the mating of chestnut mares with the stallions whose genotypes are distinct by progeny test, it may be found that observed value closely agrees

with the expected one in segregation of B and b (Table 6).

Table 1. History of Research

	Chestnut	Bay	Brown	Black
Waither (1912)	m-B-	M-B-		M-bb
Wentworth (1913)	c(B,M)	CHB	CHBD	CH(D)
Winge (1920)	RRss	R-S-		rrS-
	rrss			
Adachi (1924)	A-bbCC	A-B-CC		aaB-CC
	aabbCC			
Wriedt (1925)	FFeegg	H		G
Munkel (1929)	aabbC-dd	aaB-C-dd		aaB-ccdd
	aabbccdd			A-B-ccdd
Crew & B.Smith (1930)	bbI-	B-Ii	B-Ii	B-ii
	bbii			
Gremmel (1939)	aaB-cc	aabbC-		A-B-C-
	A-B-cc	aaB-C-		
		A-bbC-		
		AAbbC-		
Castle (1940, '46)	A^bbCE	A^bBCD	AbCE	aBCE
	AbCE		$abCE^D$	$ABCE^D$
			A^bbCE^D	A^bBCE^D
			$AbCE^D$	
Simpson (1961)	A-bb	A-B-	A-bb	aaB-
	aabb			
Gones & Bogart (1973)	aabbddee	A-B-ddee	A^tA^tB-ddee	aaB-ddee
	aabbddEE	A-B-ddE-	A^taB-ddee	
	A-bbddee	aaB-ddE-		
	aabbddE-			
	A-bbddee			
	A-bbddE-			
	aabbDdee			

Table 2. Genotype Frequency and Gene Frequency of Chestnut

All Yearling	q^2	q
1966	0.306	0.553
1967	0.296	0.544
1968	0.308	0.555
1969	0.283	0.532
1970	0.299	0.547
Mean	0.298	0.546

Table 3. Inheritance of Coat Colour (Yearling in 1970)

	Chetnut	Dark Chestnut	Bay	Brown	Black	Total
Chestnut × Chestnut	83					83
Chestnut × Dark Chestnut	70	6				76
Dark Chestnut × Dark Chestnut	4	2				6
Chestnut × Bay	120	13	179	25	3	340
Chestnut × Brown	75	5	139	53	2	274
Chestnut × Black	5		5	5	4	19
Dark Chestnut × Bay	54	8	73	23	1	159
Dark Chestnut × Brown	14	5	36	29		84
Dark Chestnut × Black	1	2	1	3		7
Bay × Black	3	1	11	9	1	25
Bay × Brown	37	4	268	126	3	438
Bay × Bay	44	2	203	46		295
Brown × Black	1		3	13	3	20
Brown × Brown	3		39	100	4	146
Black × Black	1	1				2
Total	515	49	957	432	21	1,974

Table 4. Type of Mating

Type of Mating	Expected Frequency		Obs. Value	Freq.
Bay, Brown, Black × Bay, Brown, Black	$p^2(1+q)^2$	0.493	926	0.469
Bay, Brown, Black × Chestnut	$2pq^2(1+q)$	0.418	883	0.447
Chestnut × Chestnut	q^4	0.089	165	0.084

Table 5. Mating and Offspring in an Equilibrium Random-mating Population

Type of Mating	No. of Offspring		Expected Chestnut	Observed Chestnut	
			freq.	exp.	obs.
Bay, Brown, Black × Bay, Brown, Black	926	$\left(\frac{q}{1+q}\right)^2$	0.125	115.8	97
Bay, Brown, Black × Chestnut	883	$\frac{q}{1+q}$	0.353	311.7	302
Chestnut × Chestnut	165		100%		165

Table 6. Segregetion of B and b

Mating	n	Offspring						x^2
		XX		XY		YY		
		obs.	exp.	obs.	exp.	obs.	exp.	
BB × bb	124	—	—	124	124	—	—	
Bb × bb	283	—	—	123	141.5	160	141.5	4.84
bb × bb	165	—	—	—	—	165	165	

A, commonly called, is a pattern determiner. It is assumed that bay may be expressed by epistatic interaction between A and B. Black may be aaB–. Brown does not cover the same range as in common speech. It applies to horses that are black or nearly so, except for lighter areas around the muzzle and eyes and on the legs. In breedings, brown is a tricky and unpredictable colour. It is not always correctly distinguished from black, and true brown usually acts in breeding as if it were dark bay or dark chestnut. Most of the European Continental languages have no word for "Bay". In the translations that have been made for this account the word which, when translated into English, reads "Dark Brown". Those which, when translated, mean "Brown" have been designated "Bay", and those which give "Light Brown" in the translation are interpreted as "Light Bay".

Brown × brown gives a preponderance of brown (68.49%), the bay amounting to 26.71%. Bay × bay gives a preponderance of bay (68.81%), chestnut and brown amounting to about 15%. The genotype for brown is not fixed as yet. It may be assumed that very considerable errors depend on the difinition for brown. In my investigation, brown × brown can give bay. So brown belongs to A–B–.

Inheritance of G

Gray is epistatic to chestnut, black, brown and bay, thus gray × gray produces non-gray foal but a gray horse must have at least one gray parent (gray rule).

Inheritance of D and R (Table 7)

There is another determiner which comes in two forms, D and d. D tends to dilute or make paler the basis colour, d does not. The Table 3 suggests that isabella has the pattern determiners, aa, the chestnut determiners, bb, and also the partial dilution determiners, Dd, and buckskins have the A–B–Dd. The formulas – – – DD, with full dilution, produce creamello or what is called albino A. Apart from D, there is a theory that assumes the existence of gene c^{cr}, but in the theory there is no explanation for its allele c that should exist in it.

Roan acts like gray in breeding – Roan is dominant to non-roan. Homozygous roan may be lethal according to breeding record.

Non-Mendilean inheritance

About the coat colour in Thoroughbred, the appearance of white and roan in the world which is contradictory to the Mendel's law is tabulated in Table 8.

The cause of the production of these colours is not known so far and whether each colour comes of the same cause is not yet cleared up.

Roan in this case is not assumed to be what we call true roan. Colour genes are regarded to be difficult to mutate. But it may be supposed that there are uncommonly colour

Table 7. Inheritance of D and R

Parents		--bbddRr roaned Chestnut	aaB-ddrr Black	A-B-Ddrr Buckskin	--bbDdrr Isabella
--bbddrr	Chestnut			Chestnut, Isabella Buckskin	
--bbddR-	r. Chestnut Chestnut		Bay	Bay, r. Chestnut r. Black, Buckskin	Chestnut r. Chestnut Isabella
A-B-ddrr	Bay	Bay, r. Bay r. Chestnut		Bay Buckskin	
A-B-ddR-	r. Bay	Bay roaned Black		Bay roaned Bay	
A-B-ddrr	Brown				Buckskin
aaB-ddrr	Black	Bay			
aaB-ddR-	r. Black	r. Chestnut		Black r. Chestnut	
A-B-Ddrr	Buckskin	r. Black, r. Chestnut Buckskin, Bay, r. Bay		Black	
--bbDdrr	Isabella	Chestnut, Isabella r. Chestnut		Creamello	

Table 8. White and Roan in the Thoroughbred Contradictory to Mendel's law

Nation	Birth Year	Sex	Colour	Sire	Mare
U.S.A.	1896	Colt	White	Chestnut	Black
	1963	Colt	Roan	Chestnut	Chestnut
	1963	Filly	White	Chestnut	Dark Bay
	1970	Colt	Roan	Bay	White
	1972	Filly	White	Gray	White
	1975	Filly	White	Gray	White
	1977	Colt	White	Brown	Chestnut
German	1925	Filly	White	Dark Bay	Bay
Australia	1966	Filly	White	Gray	Bay
	1970	Colt	Bay or White	Brown	Bay
	1971	Colt	Chestnut or White	Brown	Bay
	1972	Colt	White	Chestnut	White
	1977	Filly	White	Gray	Bay
France	1963	Colt	White	Bay	Bay
	1974	Colt	White	White	Gray
	1975	Colt	White	White	Bay
Japan	1979	Colt	White	Dark Bay	Chestnut

genes which happen to mutate and some abnormality occurs in the enzyme production. The differences of their various phenotypes are caused by the modifier genes.

From the fact that both white and coloured horses are born in caes of either of their parents being white, it may be also supposed that one of homozygous recessive genes mutates to dominant (e.g. w to W), but it is impossible to theorize it because there are very few examples of such breeding.

Summary

There is no fully satisfactory classification of horse colours and no really sharp distinction between colours and patterns, but the names are fairly standardized. The genotype of these colours are as follows; Chestnut is – – bbdd. Bay may be reflected by epistatic effect of A and B. Black may be aaBBdd. Isabella may be – – bbDd and Buckskin is A–B–Dd and Creamello is – – – – DD. Gray factor G is eqistatic to all the other colour factors, Roan acts like gray. White and Roan which is contradictory to Mendel's law is described.

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馬の毛色遺伝

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馬の毛色の遺伝についての研究は極めて古いにもかかわらず，国により，人により命名に多少の違いがあることなどから今日でもなお論議が続いている。

血統書の記録の統計分析から，毛色の遺伝様式はメンデルの法則に従っていることが明確になった。従って色の濃淡を考慮しなければ，登録の際の親仔鑑別に応用することが出来る。なおメンデルの法則に矛盾する白毛色の出産例についても簡単に触れておいた。