THE FREQUENCY AND HERITABILITY OF MUZZLE COLOR AND SEVERAL COAT AND SKIN COLOR CHARACTERISTICS IN MILKING SHORTHORN CATTLE

by

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INTRODUCTION

The color of the skin on the hairless area between the nostrils of the bovine -- referred to here as the muzzle -- has been observed for many years. Because this area is so easily observed it can be assumed that muzzle color may have served as an aid in selection of the foundation animals for various breeds. Indications of this use in selection are still present today in the color requirements for registration. Animals are not excluded from registry by an objectionable muzzle color, but at least two dairy breeds indicate a preferred color in their scorecard.

In the Guernsey and Milking Shorthorn breeds, muzzle color influences the desirability of animals. Therefore, as would be expected, their value may be reduced in the sales ring if they have a dark muzzle. Discrimination against black muzzle color in prospective herd sires is particularly severe. From the standpoint of sales value, then, muzzle color is an economically important trait in at least two breeds and may be given some consideration in selection in other breeds.

This study was undertaken to determine the frequency of black muzzles, the variability of their expression, and the possible correlation existing between muzzle color and other visible characteristics in the Milking Shorthorn breed of cattle. Estimates of heritability of muzzle color were studied as well as the frequency of various coat colors, color pattern, and markings.

REVIEW OF LITERATURE

The muzzle has received only limited study by research workers in the past. Most work has been either in the field of histology of the muzzle or on the inheritance of the color of the muzzle.

In the early 1900's after the rediscovery of Mendel's Laws, any easily observed trait that showed a degree of variation was destined to be studied. This was true in the case of the bovine muzzle. There is no general agreement as to the exact mode of inheritance in the early work; however, the more recent work would indicate that it may be quite complex.

Histology

According to Mackie and Nisbet (1959) the muzzle is the only hairless part of the integument. It consists of the central portion of the upper lip and the extension of this upwards between the nostrils. The surface of the muzzle is divided by furrows which give it a very characteristic structure. They reported the epidermis, which is 1-1.5 mm. thick, is divided into four layers: the stratum germinativum, or the deep layer; the stratum mucosum; the stratum granulosum; and the stratum corneum, or the tough surface layer. Their histological examination of the pigmented muzzle shows numerous melanin granules, mainly in the stratum germinativum; this agrees with the reports of Billingham and Medawar (1948), Medawar (1953) and Maximow and Bloom (1957, p. 329).

Barnicot and Birbeck (1958) stated that integumentary melanin is produced only by melanocytes. These workers as well as Fitzpatrick and others (1958) and Medawar (1953) describe melanocytes as cells consisting of a perikaryon and branches from it containing myriads of pigmented cytoplasmic granules. It is generally agreed that the branches, or dendrites, which radiate in all directions from the perikaryon lie between the dermis and epidermis and send secondary branches into the basal layer of the epidermis.

DuShane (1948) observed that the dendrites of the melanocyte actually enter the epidermal cells and that there is a passage of melanin granules into them. Barnicot and Birbeck (1958), and Medawar (1953) agree that there is a transfer of melanin granules; however, Medawar stated each dendrite ends in a flattened swelling upon the epidermal cell but does not enter it. He said the transfer may be passive inoculation or active ingestion. At any rate, there is a transfer of melanin.

Narrison (1948) reported it was experimentally shown in 1943 that melanocytes in the amphibia arise from the neural crest and later this was shown to be true in higher animals. He further stated that melanocytes are guided from the neural crest to their final location by the surrounding tissue but the tendency for them to distribute themselves in some pattern is genetically controlled.

Medawar (1953) reported that melanocytes are reproductively self-sufficient. They are perpetuated by division of cells in the epidermis itself and there is no evidence that they are maintained by immigration from the dermis. He also stated there is no reason to believe this division can occur only in immature cells not yet producing pigment. Before an old melanocyte is shed, it first discharges its melanin granules and loses its ability to synthesize more melanin. It is then pushed out and sloughed off just as the other epidermal cells. Chase (1958), however, has a different view on the source of new melanocytes. He stated that stem cells may be in the dermis and become melanocytes after old ones are expended, and that melanocytes undergo mitosis before melanin is formed in the cell.

According to Medawar (1953), the pigmentation of the hair and epidermis is due to two anatomically independent systems. The loss of melanocytes from the hair follicle is permanent, but such a loss from the epidermis is replaced. Although the melanocytes of both systems are embryologically alike, their activity may be different, as in the case of black hair from white skin in the human. He also reported that many color differences in a single animal are of a pure contingent origin: for example, body temperature variation in the body parts of the Himalayan rabbit and hormones in the male as it reaches puberty. The differences in pigmentation among the variously colored areas of a spotted animal are due to differences in melanocyte activity, and this is perpetuated in cellular heredity. This difference is not due to differences in the structure, density, or distribution of melanocytes.

Inheritance of Muzzle Color

In comparison to the more important economic traits in cattle, muzzle color has received little attention in the past. The work that has been reported shows little agreement on the exact mode of inheritance.

Gowen (1918) was the first to report any work on muzzle color inheritance. From his results of mating beef and dairy breeds, he observed that animals with dark muzzles always produced dark muzzled offspring. This led him to report that the pigmented condition is dominant to the unpigmented.

Pitt (1920) studied muzzle color inheritance in her father's herd of Hereford cattle. From the mating of a dark muzzled bull with two clear muzzled cows, four dark muzzled progeny resulted. A bull from this mating was then mated with clear muzzled cows, resulting in a 50-50 ratio in the offspring. Her conclusion was that the dark muzzle is inherited as a simple dominant.

In the Stjernsund breed of Sweden, Funkquist (1920) postulated that muzzle color is controlled by two genes and a clear muzzle is due to a third gene, epistatic to the two others.

Ibsen (1933) reported a complete study of color inheritance in cattle. He stated that the B gene is responsible for black muzzle color in the Holstein and Ayrshire breeds. A clear muzzle in these breeds is due to the action of the white spotting gene s or its modifier lw. He stated in the Guernsey and Shorthorn breeds the B loci are homozygous recessive; therefore, the muzzle should be clear. To explain the dark muzzles in these breeds, Ibsen postulated the presence of a Ps gene, responsible for pigmented skin spotting. These dark spots can appear anywhere but are most noticeable on the hairless or short-haired areas. Under this theory it would be possible to have a carrier of the Ps gene with a clear muzzle but pigmented spots elsewhere on the body. Mating two such individuals could even produce a dark muzzled offspring.

Bogart and Ibsen (1937) studied the skin of the muzzle microscopically and found all cells contained black pigment, regardless of the coat color of the individual. This was true even in albinos. This discovery led them to revise Ibsen's color formulas to make all breeds homozygous dominant for the B gene and include an E gene which must be present for the expression of the black color. They also concluded that the Ps gene was a modifier of the B locus.

Wriedt (as reported by Gowen (1926)) found from his data on English Red Polled cattle that clear muzzles were dominant to dark muzzles in Red Polled cattle.

In more recent work on crossing dairy and beef cattle, Cole and Johansson (1948) concluded that there is presumably no specific gene for muzzle color, but that the color depends on the intensity of pigmentation and the distribution of white spotting on the animal. They also stated that white on the muzzle bears the same relation to the general level of pigmentation as do the white star and inguinal spot and a correlation of white on all these areas is to be expected.

It is interesting to note that the theory advanced by Ibsen (1933) and revised by Bogart and Ibsen (1937), although inadequately supported by simultaneously published evidence, can be used to explain the results of most of the early work. When Gowen (1918) reported getting all dark muzzles from dark muzzled parents it can be assumed that he was dealing with individuals described by Ibsen as PsPs or BBEE with the modified S̲ gene.

In Miss Pitts' (1920) work with Hereford cattle, the dark muzzled bull could have been of the PsPs genotype, and the cows, psps, making the progeny, Psps. One of these male offspring when mated to clear muzzled cows would give half clear muzzles and half dark muzzles. Her conclusion of dominant inheritance could be checked by mating several clear muzzled animals resulting from the mating of a dark muzzled and a clear muzzled parent and observing the ratio.

Even the three factor theory suggested by Funkquist (1920) can be explained by Ibsen's conclusion. Several matings of like to like could be used to test Funkquist's theory.

Inheritance of Coat Color

The exact mode of inheritance of Shorthorn coat color has been the subject of much study. The early workers described it as a single factor trait with the roan colored individuals as heterozygotes. Wright (1917) discussed the work done prior to that time and concluded the single factor theory best fitted the facts.

Duck (1923), after a study of early Shorthorn herd books, reported that Shorthorn color inheritance was controlled by two genes, R and E. He said red was the real color, white was the absence of color, roan was not a separate color but a blending of red and white due to the dominant E gene, and red and white marks was a dilution of red in the absence of the dominant E gene. Red animals could have three genotypes, RRee, RREe and RREE. White animals could have three genotypes, rree, rrEe, and rrEE. Roan animals could have two genotypes, RrEE or RrEe and red and white marked animals would all be Rree. Table 1 gives the frequency of each color type as reported by Duck (1923).

Table 1. Frequency of Shorthorn color types.

	1900	1914	1921
	%	%	%
Red	49.4	62.9	49.6
RWM	27.5	13.9	11.1
Roan	20.3	21.1	35.3
White	2.8	2.1	4.0

It is interesting to note the reduction in the number of red and white marked animals and the increase in the number of roan animals.

Ibsen (1933) postulated the existence of an incompletely dominant gene N which causes hair of any color to become devoid of pigment and therefore white. This theory explains the origin of blue roan color resulting from Shorthorn-Angus crosses. He further suggests the presence of a roan modifier gene Rm which changes roan color to red. He felt this was necessary to explain the exceptions which arise from the use of a single factor theory. However, most exceptions can be explained as errors in classification. This is especially true with 90 per cent white animals classified as roan and 90 per cent white animals classified as white with red points. Ibsen also stated that no animal seems to carry the S gene for self color, but a large majority of the nn individuals show very little white spotting, indicating a large number of Lwlw genotypes.

Roberts (1937) studied Shorthorn color inheritance in one herd and reported the results of all types of matings agree with the theoretical expectations on the basis of a single factor. It must be assumed that this is the result of work with one herd and does not include results from a breeding test with a solid color black breed.

It would appear then the theory that Ibsen (1933) postulated offers the best explanation for the inheritance of Shorthorn color.

Treece and Gilmore (1956) have data that show a very highly significant association between the head pattern and the amount of body pigment in the Holstein breed. A solid head pattern meant the animal had an average of 90 per cent of its body pigmented. Animals with a shield pattern were 80 per cent pigmented while those with a blaze were 40 per cent pigmented. They also reported a highly significant difference of 5.86 percentage units more pigment on the females than on the males. Treece and others (1958) also reported a significant difference of 6.84 percentage units in favor of the females in the population they studied. They suggested the sex difference could be due to a gene on the Y chromosome which reduces the amount of pigment in the male.

Briquet and Lush (1947) reported the heritability of white spotting is very high, probably more than 90 per cent. Therefore, mass selection is the most effective method of changing the color of a herd. This is shown quite clearly in the data reported by Duck (1923) where the percentage of red and white marked animals dropped 16.4 units in just four years time.

A heritability as high as that reported by Briquet and Lush (1947) brings up the question of how this ties in with the LwLw theory postulated by Ibsen (1933). Results of mating predominantly pigmented individuals with nearly white individuals seems to indicate a many-factor additive inheritance scheme rather than a single factor theory.

EXPERIMENTAL PROCEDURE

A check sheet was developed and used to record observations made on each individual studied. The check sheet and its explanation are a part of the Appendix.

During the months of July and August, 1959, 27 Kansas Milking Shorthorn herds were visited and 759 animals observed. These herds were chosen because they each included a sizeable number of animals and could be easily visited. In addition to the Kansas cattle, observations were made on 160 Milking Shorthorns on exhibit at the 1959 Illinois State Fair. Of the 919 total animals in the study, 553 were placed in a random sample population because they came from herds in which every animal was observed. They should thus be representative of registered Kansas Milking Shorthorn cattle. The remaining 366 animals were designated as a selected population because they came from herds where only a selected part of the herd could be observed, because of weather conditions or time restrictions. The selected population, of course, includes the cattle observed at the Illinois State Fair because they represent only part of several herds.

The data were prepared for machine tabulation and the frequency of occurrence of each trait was obtained. Heritabilities and phenotypic correlations were determined. The analysis of the data was carried out according to procedures outlined by Snedecor (1956).

RESULTS

Frequency of Various Types of Pigmentation on Several Body Areas

Muzzle Pigmentation. A comparison of the various types of muzzle pigmentation for each coat color classification appears in Table 2.

A greater percentage of the white animals had some pigmentation on their muzzle than animals of any other coat color. The greatest percentage of clear muzzles was found in the red color group.

Of the 8.3 per cent of the random population with spotted muzzles, 84.8 per cent had black spots and 15.2 per cent had red spots. There were 71.7 per cent of the animals with small spots and 28.3 per cent with large spots. An equal number of animals had a few spots, some spots and many spots on their muzzles.

Of the 7.7 per cent of the selected population with spotted muzzles, 96.4 per cent had black spots and 3.6 per cent had red spots. There were 67.9 per cent of the animals with small spots and 32.1 per cent with large spots. Of these, 46.4 per cent had a few spots, 32.2 per cent had many spots and 21.4 per cent had some spots.

Table 2. Proportion of animals in each coat color group showing various types of muzzle pigmentation.

Coat Color	Muzzle Color			
	Clear	Black	Smutty	Spotted
	%	%	%	%
Random Population				
Red	85.83	0.79	7.87	5.51
Red, White Marks	80.32	1.06	10.64	7.98
White	58.60	3.45	24.15	13.80
Roan	73.12	0.96	16.31	9.61
Total	77.72	1.09	12.86	8.33
Selected Population				
Red	74.22	2.06	16.50	7.22
Red, White Marks	68.42	0.88	21.05	9.45
White	43.75	0.00	50.00	6.25
Roan	70.50	5.03	18.00	6.47
Total	69.65	2.73	19.94	7.65

Effect of Sex. The frequency of pigmented muzzles found in animals two months or less of age from the random population was determined for each sex. It was decided that animals in this age group would not be affected much by selection and therefore any deviation from the expected one to one ratio could be considered a result of a sex difference in the expression of pigmented muzzles. When the data from the random population were tested for an association between sex and muzzle pigmentation, it was found that muzzle color is probably independent of sex in this population ($X^2 = .17$, df $= 1$, $.75 > P > .50$).

Effect of Age. Conversation with breeders of Milking Shorthorn cattle indicated a belief that pigmentation of the muzzle was affected by age. It was decided to test the data for an association between age of the animal and the pigmentation of the muzzle. It was found that muzzle color is probably independent of age in the female random population studied ($X^2 = 6.34$, df = 6, $.50 > P > .25$).

Effect of Coat Color. It was observed that animals of certain color groups seemed to have pigmented muzzles more frequently than others. A test for an association between coat color and muzzle pigmentation was made. It was found that muzzle color is probably not independent of coat color in the population studied ($X^2 = 15.86$, df = 5, $.010 > P > .005$). The animals in the white coat color group had the highest percentage of dark muzzles, followed by the roan animals. To make certain that the association between muzzle color and coat color was real and not just a measure of an age and color relationship, a test for independence was made between each coat color group and age. In each group, coat color was found to be independent of age. Apparently then, the association between coat color and muzzle color is real.

Eyelid Pigmentation. Cole and Johansson's (1948) work indicated that muzzle pigmentation may be a result of the total body pigmentation. With this in mind it was observed that the area at the corner of the eye -- referred to here as the eyelid -- often exhibits pigment spots or freckles. The proportion of animals from each population having pigmented eyelids can be found in Table 3.

Here again breeders mentioned an age difference in the expression of the pigmented condition. At least in the females of the random population, there

Table 3. Proportion of animals showing various types of pigmentation of the eyelid area.

	Eyelid Color				
	Clear	Black	Smutty	Red Spots	Black Spots
	%	%	%	%	%
Random Population					
Males	98.44	0.00	0.00	1.56	0.00
Females	87.34	0.21	0.42	12.03	0.00
Total Population	88.17	0.18	0.37	10.78	0.00
Selected Population					
Males	95.00	0.00	0.00	5.00	0.00
Females	75.95	1.27	0.63	18.99	3.16
Total Population	79.80	1.01	0.51	16.16	2.52

seemed to be an association between age and eyelid pigmentation ($X^2 = 64.06$, $df = 11$, $P < .005$). As the age of the animal increases, the more likely it is to have pigmented eyelids.

Of the 10.9 per cent of the animals from the random population with pigment spots on the eyelid, all had red spots. The spots were small on 98.3 per cent and large on only 1.7 per cent of the animals. Forty-nine per cent of those with spots had a few spots, 39 per cent had some, and 12 per cent had many spots. In the selected population, 13.9 per cent of the animals had pigment spots on the eyelid. Of these, all were red; 97.7 per cent were small and 2.3 per cent were large. The degrees of spotting were much like the random population: 56.8 per cent few, 27.3 per cent some, and 15.9 per cent many.

Mouth Pigmentation. The skin on the outside of the lower lip is very similar to that of the muzzle and sometimes has the same type of pigmentation. The proportion of animals from each population with pigmented mouths is shown in Table 4.

Table 4. Proportion of animals showing various types of pigmentation of the mouth.

	Mouth Color				
	Clear	Black	Smutty	Red Spots	Black Spots
	%	%	%	%	%
Random Population					
Males	95.83	0.00	4.17	0.00	0.00
Females	93.75	0.89	4.76	0.00	0.60
Total Population	94.01	0.78	4.69	0.00	0.52
Selected Population					
Males	83.33	12.50	4.17	0.00	0.00
Females	80.55	9.26	8.33	0.93	0.93
Total Population	81.05	9.85	7.58	0.76	0.76

It is interesting to note that a greater percentage of the mouths than muzzles were observed to be clear.

Only 0.52 per cent of the random population had spots on the mouth and all of these were large black spots. Fifty per cent of the animals had few spots and 50 per cent had some spots. In the selected population, 1.1 per cent of the animals had spots on the mouth. Of these, one third were red and two thirds were black. All the animals had large spots; 33.3 per cent had few spots and 66.7 per cent had many spots.

In the female random population there was no indication that age had any association with pigment on the mouth ($X^2 = 9.38$, df $= 10$, $.50 > P > .25$). This of course agrees with the results of a similar test between age and muzzle color.

Teat Pigmentation. It was observed that some animals had dark spots on the teats and this seemed to be especially noticeable in older cows. The proportions of animals having pigment on the teats are shown in Table 5.

Table 5. Proportion of animals showing various types of pigmentation on the teats.

	Teat Color				
	Clear	Black	Smutty	Red Spots	Black Spots
	%	%	%	%	%
Random Population					
Females	97.67	0.26	0.26	0.00	1.81
Selected Population					
Females	95.90	0.00	0.82	0.00	3.28

In the random population, there probably is a relationship between age of the animal and pigmentation of the teats ($X^2 = 9.79$, df $= 4$, $.050 > P > .025$). As an animal ages the more likely she is to have pigment on her teats.

Of the 1.8 per cent of the random population with spots on the teats, all had black spots: 85.7 per cent were small and 14.3 per cent were large. The amount of spotting was different than that reported for other areas; 28.6 per cent had few spots, 14.3 per cent had some spots and 57.1 per cent had many spots on the teats. In the selected population the number with spots was 1.7 per cent and they all had black spots. Seventy-five per cent of the animals had small spots and 25 per cent had large ones. Fifty per cent of the animals had few spots; 25 per cent some; and 25 per cent many spots on the teats.

Udder or Scrotum Pigmentation. Pigmentation of the udder and of the scrotum were also observed. In the random population, 99.2 per cent of the animals had a clear udder or scrotum. The one individual observed to have pigment on the udder had many, large black spots. The selected population was 100 per cent clear on the udder or scrotum.

Vulva Pigmentation. The vulva is another area where the hair is thin and pigment spots can be observed. The proportions of animals having pigment on the vulva are shown in Table 6.

Table 6. Proportion of animals showing various types of pigmentation on the vulva.

	Vulva Color				
	Clear	Black	Smutty	Red Spots	Black Spots
	%	%	%	%	%
Random Population					
Females	97.81	0.00	0.24	1.95	0.00
Selected Population					
Females	99.16	0.00	0.00	0.84	0.00

Of the 1.9 per cent of the random population having pigment spots on the vulva, all had red spots; 25 per cent had small spots and 75 per cent had large spots. Few spots were found on 37.5 per cent of the animals; 25 per cent had some spots and 37.5 per cent had many spots. Only 0.84 per cent of the selected population had pigment spots on the vulva and they were all small red spots. Fifty per cent of the animals had few spots and 50 per cent had some spots.

Anus Pigmentation. The proportions of animals having pigment on the anus are shown in Table 7.

Table 7. Proportion of animals showing various types of pigmentation on the anus.

	Anus Color				
	Clear	Black	Smutty	Red Spots	Black Spots
	%	%	%	%	%
Random Population					
Males	100.0	0.00	0.00	0.00	0.00
Females	98.05	0.00	0.24	1.71	0.00
Total Population	98.23	0.00	0.22	1.55	0.00
Selected Population					
Males	100.0	0.00	0.00	0.00	0.00
Females	99.22	0.00	0.00	0.78	0.00
Total Population	99.34	0.00	0.00	0.66	0.00

Of the 1.5 per cent of the random population with anal spots, all were red. Small spots were found on 42.9 per cent of the animals and 57.1 per cent had large spots. Few spots accounted for 42.9 per cent; 28.6 per cent had some spots and 28.6 per cent had many anal spots. Only 0.64 per cent of the selected population had spots on the anus and all were red. Fifty per cent were large and 50 per cent were small while 50 per cent of the animals had few spots and 50 per cent had some.

Escutcheon Pigmentation. Only two animals were observed to have any pigment on the escutcheon area. One had some small black spots and the other one had smutty pigmentation over the entire area. In other words, 99.5 per cent of the random population and 100.0 per cent of the selected population were observed as clear in this area.

Frequency of Various Color Characteristics

Coat Color. Milking Shorthorn cattle may have a variety of different coat colors. Those most frequently referred to are red, white, and roan. For the purposes of this study, coat color was classified into six groups. Table 8 shows the proportion from each population in each group.

Table 8. Proportion of animals in each coat color group.

	Coat Color					
	Red	Red, White Marks	Solid White	White, Red Points	Even Roan	Broken Roan
	%	%	%	%	%	%
Random Population	23.18	33.94	0.91	4.38	6.57	31.02
Selected Population	26.58	30.96	0.82	3.56	6.03	32.05
Total	24.54	32.75	0.86	4.05	6.36	31.44

In addition to the proportion of animals in each group, the red, red and white marked, and roan groups were further grouped according to the per cent of red hair on the body. Tables 1 through 3 in the Appendix give this information.

Neck Color Patterns. The animals in the two roan coat color groups were observed to have a variety of different color patterns on the neck. The proportions of animals with neck color patterns can be found in Table 9.

The animals from each population found in each neck color group were further classified according to the amount of red hair on the body. This information can be found in Tables 4 and 5 in the Appendix.

Table 9. Proportion of animals with various neck color patterns.

	Neck Color Patterns		
	Red	Light Roan	Dark Roan
	%	%	%
Random Population			
Roan Animals	36.75	35.54	27.71
Selected Population			
Roan Animals	41.88	27.35	30.77
Total Population	38.87	32.27	29.08

Leg Color Patterns. Milking Shorthorn cattle have many variations in the color markings on the legs. In this study the proportion of each type found in each coat color group was recorded. This information can be found in Table 10.

Table 10. Proportion of animals of the total population in each coat color group having various leg color markings.

	Leg Color Markings				
Coat Color	Solid Red	Partly Red	Spotted Red	White Stocking	Red Stocking
	%	%	%	%	%
Red					
Forelegs	99.78	0.00	0.22	0.00	0.00
Hindlegs	95.30	0.45	4.25	0.00	0.00
Red, White Marks					
Forelegs	76.68	3.86	18.29	1.17	0.00
Hindlegs	45.30	14.43	35.74	4.53	0.00
Even Roan					
Forelegs	72.81	7.02	18.42	1.75	0.00
Hindlegs	45.61	25.44	27.19	1.75	0.00
Broken Roan					
Forelegs	40.79	18.41	35.92	4.51	0.36
Hindlegs	10.65	55.62	25.36	8.33	0.00

Head Markings. Most of the head markings in Milking Shorthorn cattle consist of white spots which vary in size from a small dot to a large shield. Other individuals of the breed have solid red heads. Table 11 gives the proportions of animals with various head markings.

Table 11. Proportion of animals in the total population in each coat color group with various head markings.

Coat Color	Head Markings: No Marking	Dot	Shield	Other
	%	%	%	%
Red	100.00	0.00	0.00	0.00
Red, White Marks	15.77	15.44	68.46	.34
Even Roan	51.72	6.90	41.38	0.00
Broken Roan	15.30	5.34	79.36	0.00
Total	39.60	7.59	52.69	.12

It can be seen in Table 11 that a large percentage of the even roan animals have no head markings. Also of interest is the close similarity of percentages between the broken roan and the red and white marked groups.

Belly Markings. In this study the animals in each coat color group were further grouped according to the location of the white on their belly. The proportions of animals having white markings in various locations can be found in Table 12.

Switch Color. The color of the switch varies within each coat color group. In this study the proportion of animals in each group with various colored tail switches are shown in Table 13.

Table 12. Proportion of animals in the total population in each coat color group having white belly markings in various locations.

Location of Belly Markings	Coat Color: Red	Red, White Marks	Even Roan	Broken Roan	Total
	%	%	%	%	%
Entirely White	3.27	41.98	76.60	98.58	53.11
Anterior	64.02	39.59	19.15	0.71	31.58
Middle	3.74	1.71	0.00	0.00	1.55
Posterior	0.93	0.34	0.00	0.00	.36
Anterior and Middle	8.88	14.68	2.13	0.71	7.78
Anterior and Posterior	0.00	0.34	0.00	0.00	.12
Middle and Posterior	0.00	0.00	0.00	0.00	0.00
Entirely Red	19.16	1.37	2.13	0.00	5.50

Table 13. Proportion of animals in the total population in each coat color group having various colored tail switches.

Coat Color	Tail Switch Color: Mixed	White	Red
	%	%	%
Red	86.49	4.05	9.46
Red, White Marks	65.07	31.85	3.08
Even Roan	54.39	45.61	0.00
Broken Roan	22.58	76.70	0.72
Total	56.00	40.24	3.76

Heritability of Various Traits Studied

Muzzle Pigmentation. A study of the literature indicated that pigment on the muzzle is expressed as an all-or-none trait. Animals in the random populations were rated as clear or pigmented and an analysis of variance performed (Table 14).

Table 14. Analysis of variance for muzzle pigmentation.

Source of Variation	Degrees of Freedom	Mean Square	F	Expected Mean Square
Among sire groups	124	0.2536	1.92**	$\sigma^2 + 1.92\ \sigma^2_B + 4.35\ \sigma^2_A$
Among dam groups within sire	363	0.1505	1.14	$\sigma^2 + 0.86\ \sigma^2_B$
Within dam groups	63	0.1323		σ^2

** $P < .01$

This analysis indicated a difference ($P < .01$) among sire groups in the frequency of pigmented muzzles. There were no pronounced differences ($.25 > P > .20$) among dam families within sires in the frequency of pigmented muzzles.

The heritability of muzzle pigmentation was estimated from the paternal half-sib, maternal half-sib and mid-parent correlations in this analysis. The estimates were 0.57, 0.47, and 0.52, respectively.

The estimates are rather uniform and any existing variation can be explained by sampling errors. It is interesting to note that the estimate computed from the maternal half-sib correlation is not large enough to indicate any variance due to dominance.

Eyelid Pigmentation. Eyelid pigment is also thought to be an all-or-none trait. The animals from the random population were rated as clear or pigmented and an analysis of variance performed (Table 15).

Table 15. Analysis of variance for eyelid pigmentation.

Source of Variation	Degrees of Freedom	Mean Square	F	Expected Mean Square
Among sire groups	124	0.1850	4.512**	$\sigma^2 + 1.92\ \sigma^2_B + 4.24\ \sigma^2_A$
Among dam groups within sire	351	0.0815	1.988**	$\sigma^2 + 0.85\ \sigma^2_B$
Within dam groups	61	0.0410		σ^2

** $P < .01$

The analysis indicated a difference ($P < .01$) among sire groups and among dam families within sires in the frequency of pigmented eyelids.

The heritability of eyelid pigmentation was estimated from the paternal half-sib, maternal half-sib and mid-parent correlations in this analysis. The estimates were 0.49, 1.99 and 1.19, respectively. The last two estimates may be considered to be one. These estimates are biased by the effects of age on the pigmentation of the eyelids, as previously noted.

Head Markings. The animals from the random population, excluding the ones with white heads and white heads with red points, were rated in a graded series giving shield the value of zero, dot the value of one and solid red head the value of two. An analysis of variance was performed on these data (Table 16).

This analysis indicated a difference ($.05 > P > .01$) among sire groups in the frequency of the different head patterns. The dam families within sires did not contribute to the variance since all the variation was accounted for within the dam groups.

Table 16. Analysis of variance of head markings.

Source of Variation	Degrees of Freedom	Mean Square	F	Expected Mean Square
Among sire groups	121	1.2919	1.678*	$\sigma^2 + 1.94\,\sigma^2_B + 4.27\,\sigma^2_A$
Among dam groups within sires	341	.7516	.977 NS	$\sigma^2 + 0.82\,\sigma^2_B$
Within dam groups	55	.7697		σ^2

* $P < .05$

The heritability of head markings was estimated from the paternal half-sib correlation in this analysis. The estimate was 0.56.

Correlation of Various Traits Studied

The phenotypic correlation between pigmented muzzle and pigmented eyelid was computed to be 0.22, which is significantly different from zero ($P < .001$).

Cole and Johansson (1948) stated that a correlation could be expected between head marking and muzzle color. The phenotypic correlation between these two characteristics was computed from the data from the random population. Since the head patterns were graded from zero to two with the shield assigned the value of zero the correlation was -0.10. This value is significantly different from zero ($.05 > P > .01$).

DISCUSSION

There were no differences in muzzle pigmentation associated with sex or age differences. The popular belief among breeders that muzzle color changes with age might be explained by the fact that as the animal ages the skin of the muzzle becomes thicker. This could cause the pigment present to appear to be less intense.

The percentage of animals with dark muzzles varied with the color of the body hair coat. In the random population, white animals made up 5.3 per cent of the total population, but contained 9.8 per cent of all the pigmented muzzles. The roan animals made up 37.6 per cent of the population and contained 45.5 per cent of the pigmented muzzles. However, the red animals made up 57.1 per cent of the population but accounted for only 44.7 per cent of the pigmented muzzles. This would suggest an association between the degree of roaning and muzzle pigmentation. There is apparently a dosage effect in which the NN genotype results in the greatest percentage of pigmented muzzles followed by the Nn genotype. The association could involve at least two different genetic happenings. Linkage could be involved, or the <u>N</u> gene could have a pleiotropic effect on muzzle color.

There was a correlation of 0.22 between eyelid pigmentation and muzzle pigmentation. This means that an animal with pigmented eyelids is more likely to have a dark muzzle than one with clear eyelids. This correlation would have only limited use in selection because most selection of breeding animals is made before the eyelid pigment develops and because the correlation is so small as to be almost ineffective.

The correlation between muzzle pigmentation and solid, dot and shield head markings is -0.10. As the amount of white in the head marking increases, the less likely the animal is to have a dark muzzle. This is in agreement with work reported by Cole and Johansson (1948) in which they reported that a correlation should exist between the amount of white on the head and muzzle color. Selection for increased amounts of white in the shield or dot of the head marking could possibly decrease the percentage of pigmented muzzles.

Much of the early work on the inheritance of muzzle color suggested that dominance was involved (Gowen 1918, 1926; Pitt 1920; Funkquist 1920). The heritability estimates for muzzle pigmentation in this study indicated that dominance was not involved. The estimate calculated from the maternal half-sib correlation contains all of the dominance variance and therefore if dominance were important, it should be the largest estimate. However, in this study the paternal half-sib estimate was the largest. The inheritance of muzzle pigmentation then seems to be due to additive gene action with a strong non-genetic effect of unknown origin accounting for part of the variance. The mid-parent estimate of 0.52 for the heritability of muzzle pigmentation would indicate that selection against dark muzzles should be successful. In fact, progress should be about equal to that possible with butter fat test and 50 per cent greater than that for milk production.

Eyelid pigmentation increased with age. The older an animal is the more likely it is to have pigmented eyelids. In fact, 60 per cent of the animals more than 10 years of age in this study had pigmented eyelids. Nearly all of the animals with pigmented eyelids had spots that were small and very dark red or nearly brown. Since they are more common in older animals, the melanocytes in the eyelid area might have become more active because of continued exposure to the rays of the sun. The heritability estimates for eyelid pigmentation in this study are quite divergent. This can be explained by the fact that the effect of age was not accounted for, thus creating biases in the various components.

Teat pigmentation changed with age. As a cow grows older, the more likely she is to have pigmented teats. This is in agreement with the observation of Clapp (1938) in the Holstein Friesian breed. He stated that the pigmented areas which often exist on the teats of that breed increase in size with increased age of the cow. In this study nearly 20 per cent of the cows more than 10 years of age had some pigment on the teats. Again this increased occurrence of pigmented teats among older cows could possibly be explained by the increased activity of the melanocytes in the area due to continued exposure to the rays of the sun.

Such a limited number of animals had pigment on the udder, scrotum, vulva and anus that no attempt was made to correlate the pigment found in these areas with that on the muzzle.

The percentage of the various coat color groups found in this study differ somewhat from those reported by Duck (1923) (Tables 1 and 8). He reported a greater number of red animals than were found in this study. However, in the time since he reported his work, there has been increased emphasis placed on roan animals, which could account for the difference in the results of the two studies.

An attempt was made to use the data on coat color in this study to test the N gene theory for roaning postulated by Ibsen (1933). The red and the red and white marked animals were assumed to be of the nn genotype. The even roan and the broken roan animals were assumed to be of the Nn genotype. The solid white animals and the white animals with red points were considered to have the NN genotype. The gene frequencies of N and n were computed and the genotypic frequencies determined. The results of the gene frequency test based on the equilibrium proportions very closely approximated the actual percentages found in the population which suggested that the coat color percentages in the population could be explained by the N gene theory.

The same approach was also used in testing the Lw gene theory. However, no combination of phenotypes could be arranged that would give the equilibrium proportions. This brings out the point mentioned previously regarding the inheritance of white spotting. Briquet and Lush (1947) estimated the heritability of white spotting to be in excess of 90 per cent. A heritability this high suggests that if the Lw gene actually exists, it must be incompletely penetrant. Its effect should be easily tested. There should be little or no overlap in phenotypes and the observed and expected proportions should correspond closely.

Head markings offer an example of the similarity between the red and the even roan animals (Table 11). The same is true with the red and white marked animals and the broken roan animals. This suggests that even roan is a red or nearly red animal with the incompletely dominant roaning gene N. Of course, then, broken roan would be the result of the N gene acting upon a red and white marked animal.

Of the animals in the red coat color group, 80.8 per cent had some form of white marking on the belly. Ibsen (1933) reported that no Shorthorn animal carried the S gene for self color. The 19.2 per cent of the animals in this study observed to be totally red, except possibly for some white hairs in the switch, would seem to contradict this report. These animals presumably are of the ss genotype with some of the many modifiers of this locus permitting the total red conditions.

SUMMARY AND CONCLUSIONS

The frequency and heritability of dark muzzle color as well as of other characteristics were studied. Dark muzzles are considered undesirable. This study was made to help clarify existing theories on the subject.

Data collected on 919 Milking Shorthorns furnished evidence concerning age effects, sex effects and coat color inheritance. The data were grouped into a random and a selected population depending upon the circumstances under which the data were obtained.

There were no age nor sex differences in muzzle pigmentation. There was an association between the degree of roaning and muzzle pigmentation, with the N gene having a dosage effect on muzzle pigmentation. The mid-parent estimate of muzzle pigmentation heritability was 0.52. Examination of the heritability estimates for muzzle pigmentation suggested that dominance is not important and that the inheritance of muzzle pigmentation is due largely to additive gene action.

There was an association between age and eyelid pigmentation, older animals being more likely to have pigmented eyelids than young animals. The correlation between eyelid pigmentation and muzzle pigmentation was 0.22. Heritability estimates for eyelid pigmentation were computed, but biases due to the age effect obviates the usefulness of the estimate.

A correlation of -0.10 was found between muzzle pigmentation and the amount of white in the head marking. The heritability of head markings was estimated at 0.56 by the paternal half-sib correlation.

Age and pigmentation of the teats seemed to be associated, for older cows have the greatest percentage. About 20 per cent of the cows more than 10 years of age had some pigment on the teats.

The random population studied was composed of 23.2 per cent red animals, 33.9 per cent red and white marked animals, 5.3 per cent white animals and 37.6 per cent roan animals. These percentages suggested that in this population coat color inheritance could be explained by the N gene theory. An attempt to fit this population to the Lw gene theory was unsuccessful.

The percentage of head markings and belly markings suggested a genetic similarity between the red coat color and the even roan coat color. The same similarity was found between the red and white marked animals and the broken roan animals. The roans were the result of the action of the N gene on the red coat color.

Muzzle pigmentation was shown to be largely due to additive gene action. Therefore, in the selection of Milking Shorthorn cattle for breeding purposes, preference should be given to those animals which have a clear muzzle. The size of the heritability estimate suggests that selection progress can be made. The rate of improvement will be about as rapid as that for butterfat test and 50 per cent more rapid than for milk production.

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APPENDIX

Table 1. Proportion of even roan animals having various percentages of red hair on their body.

Per cent of red on body	Population		
	Random	Selected	Total
	%	%	%
0-24	0.00	0.00	0.00
25-49	8.33	18.18	12.07
50-59	5.56	9.09	6.90
60-69	5.56	4.55	5.17
70-79	5.56	0.00	3.45
80-84	0.00	9.09	3.45
85-89	13.89	0.00	8.62
90-94	33.33	45.56	37.93
95-99	27.78	13.64	22.41

Table 2. Proportion of broken roan animals having various percentages of red hair on their body.

Per cent of red on body	Population		
	Random	Selected	Total
	%	%	%
0-24	5.88	5.98	5.92
25-49	12.94	7.69	10.80
50-59	5.29	2.56	4.18
60-69	7.65	12.82	9.76
70-79	13.53	22.22	17.07
80-84	8.82	15.39	11.50
85-89	25.29	19.66	23.00
90-94	17.06	11.97	14.29
95-99	4.71	1.71	3.48

Table 3. Proportion of the red white marked animals having various percentages of red hair on their body.

Per cent of red on body	Population: Random	Population: Selected	Population: Total
	%	%	%
0-24	0.00	0.00	0.00
25-49	0.00	0.00	0.00
50-59	0.00	0.00	0.00
60-69	1.08	0.00	0.67
70-79	0.54	0.89	0.67
80-84	2.15	0.00	1.34
85-89	3.76	0.89	2.68
90-94	10.22	14.16	15.28
95-99	82.26	84.07	82.94

Table 4. Proportion of even roan animals with various percentages of red hair on their body in each neck color group.

Per cent of red on body	Neck Color Pattern		
	Red	Light roan	Dark roan
	%	%	%
0-24	0.00	0.00	0.00
25-49	0.00	7.69	0.00
50-59	0.00	7.69	0.00
60-69	0.00	0.00	7.69
70-79	0.00	3.85	3.85
80-84	0.00	0.00	0.00
85-89	3.85	0.00	11.54
90-94	7.69	3.85	19.23
95-99	23.08	0.00	0.00
Total	34.62	23.08	42.30

Table 5. Proportion of broken roan animals with various percentages of red hair on their body in each neck color group.

Per cent of red on body	Neck Color Pattern		
	Red	Light roan	Dark roan
	%	%	%
0-24	0.00	5.00	2.14
25-49	0.71	7.14	7.14
50-59	0.00	4.29	2.14
60-69	0.00	0.71	5.00
70-79	5.71	0.71	8.57
80-84	5.71	4.29	0.00
85-89	14.29	7.14	0.00
90-94	8.57	5.71	0.00
95-99	2.14	2.86	0.00
Total	37.14	37.86	25.00

CHECK SHEET

Name | No. | Tatoo | Birth Date | Sex

Sire | Dam | Maternal Grand Sire

Pigment	Black	Clear	Smutty	Color	Size	Spotted %	Location	Remark
Muzzle								
Eyelid								
Eye								
Mouth								
Teats								
Udder or Scrotum								
Vulva								
Anus								
Escutcheon								
Ears								
Hooves								

			White		Roan		
Coat Color	Red	RWM	Solid	Red Points	Even	Broken	Neck
Body							
% Red							

Legs	Solid Red	Partly Red	Spotted Red	White Stocking	Red Stocking	Spotted Red Stock.	Distal Spots
R fore							
L fore							
R rear							
L rear							

Head	
Belly	
Switch	

Explanation of Check Sheet

The following pedigree information was obtained: name or number, sex, birth date, sire, dam, and maternal grand sire.

In the section marked pigment, the following information was checked for each area listed:

(1) Black - solid black pigment in the area.

(2) Clear - uniformly clear or buff colored area.

(3) Smutty - solid pigmentation intermediate in intensity between black and clear.

This classification was further marked according to the exact location of the pigment in the case of the muzzle.

(a) E - entire muzzle.

(b) M - middle of the muzzle.

(c) S - upper one half of the muzzle.

(d) I - lower one half of the muzzle.

(e) R - right one half of the muzzle.

(f) L - left one half of the muzzle.

(4) Spotted - distinctly outlined spots rather than general smuttiness.

This classification was further divided according to this breakdown.

(a) color - red or black.

(b) size - small if less than one fourth inch or large if more than one fourth inch.

(c) amount - few, some or many.

(d) location - same classification as in (3) above.

In the section marked coat color the following classification was checked depending on the color of the animal:

(1) Red - Solid red except for underline and tail switch.

(2) Red and White marked - Solid red except for underline, tail switch, and marks on head, legs or body.

(3) White - (a) solid white.
(b) white with red point on ears and nose.

(4) Roan - Intermingling of red and white hairs.
(a) Even - roan evenly distributed over body.
(b) Broken - mixtures of white and roan areas.

The neck of the roan individuals was classified as red, light roan or dark roan.

The per cent of red seen in a side view including head and tail but excluding underline was recorded.

In the section marked legs the appropriate classification was checked depending on the marking of each leg.

(1) Solid red - leg encircled with red from hoof to hock.

(2) Partly red - leg red from hoof to hock but not completely encircled.

(3) Spotted red - leg red from hoof to hock except for a few white spots near hoof.

(4) White stocking - leg white from hoof to near hock and encircled by red above.

(5) Red stocking - leg red from hoof to near hock and encircled by white above.

(6) Spotted red stocking - same as (5) except for red spots above the hoof.

(7) Distal spots - leg white with red spots near hoof.

In the section marked head the pattern of color on the face was checked according to this classification:

(1) None - no white mark on face.

(2) Dot - a small white spot on face.

(3) Shield - a large white spot on face.

(4) Other - any other face marking such as a brockle face or mottled face.

In the section marked belly the location of the white on the underline was checked according to this classification:

(1) Entire - an entirely white underline.

(2) Anterior - a white area between front legs.

(3) Middle - a white area around navel.

(4) Posterior - a white area between the hind legs but not on the udder or scrotum.

(5) Any combination of white areas such as Anterior-Middle were also checked.

(6) None - an entirely red underline.

In the section marked switch the color of the switch on the tail was checked according to this classification:

(1) Mixed - red and white hairs in switch.

(2) White - entirely white switch.

(3) Red - entirely red switch.

THE FREQUENCY AND HERITABILITY OF
MUZZLE COLOR AND SEVERAL COAT AND SKIN COLOR CHARACTERISTICS
IN MILKING SHORTHORN CATTLE

by

RAY RONALD SCHOOLEY

B. S., Kansas State University, 1958

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Pigmented muzzles are known to be objectionable in at least two breeds. Hence, dark muzzled animals sell at a reduced price when sold for breeding purposes. With this reduced value for such animals, the need for information concerning the inheritance of the trait can be readily seen.

This study was undertaken to determine the frequency and heritability of pigmented muzzles, the variability of their expression and the possible correlations existing between muzzle color and other visible characteristics in the Milking Shorthorn breed of cattle. Observations were made on 919 animals from 27 Kansas herds and from animals on exhibit at the 1959 Illinois State Fair. Of these, 553 were considered a random sample of the breed and the remaining 366 were considered to represent a selected population.

Sex and age as studied in the random population were not associated with the pigmentation of the muzzle but age was associated with eyelid and teat pigmentation. The amount of pigment on the eyelid and teats increased with increased age.

There was an association between the degree of roaning and muzzle pigmentation with the N gene having a dosage effect on muzzle pigmentation. There was a phenotypic correlation of -0.10 between muzzle pigmentation and the amount of white in the dot or shield of the head marking. The phenotypic correlation between muzzle pigmentation and eyelid pigment was 0.22.

The heritability of muzzle pigmentation as estimated by the mid-parent correlation was 0.52. Contrary to the existing literature, the inheritance of muzzle pigmentation was found to be due largely to additive gene action rather than dominance.

Estimates of heritability of eyelid pigmentation were made but biases due to the age effect made the estimate of little value.

The heritability of head markings was estimated from the paternal half-sib correlation which was 0.56.

The percentages of the various coat color groups found in this study fitted the single factor, incompletely dominant, theory of the roaning gene N. An attempt to fit this population to the Lw gene theory of white spotting inheritance was unsuccessful.

The evidence from this study suggested that red or nearly red animals and even roan animals may be genetically alike except for the roaning gene N. Likewise, the red and white marked animals and the broken roan animals may be alike except for the N gene.