Major aspects of Appaloosa horse coat color genetics
by Sandra Sowerwine Montgomery

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE in Animal Science
Montana State University
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Abstract:
In a study of records and questionnaires concerning 211 Appaloosa stallions and their progeny, of which 5903 were registered, 52 full blanket stallions produced 20% more registered get and 18% more appaloosa get per mare bred than did the average of the 55 half blanket, 35 leopard, 34 spotted blanket and 35 roan leopard stallions, which are ranked in order of production. Approximately 90% of the appaloosa get of leopard and full blanket stallions were born colored vs 57% of the roan leopard get. All comparisons of the percent production of different patterns by the 5 sire classes were significant. Full blanket stallions produced the most white and leopards produced the most spots. Full blankets, half blankets and leopards were produced only by appaloosa parents. Most parents of leopards had over-all patterns. "Whitened" mares out-produced "non-whitened" mares. Appaloosa mares produced some solid white blanket offspring; solid mares produced very few, but more white mottled and speckled get. No specific patterns were highly heritable. White & spots, white mottled and "All other" patterns were produced in a 2:1:1 ratio. Though evidence of sex-linkage and influence was encountered, the data were insufficient for conclusions. A proposed model of appaloosa genetics includes 7 gene pairs. Three white-spotting genes may be lethal when homozygous. Solid white blankets are produced by the homozygous Ap gene. Leopards result from a homozygous extension (EaP) gene. Spotted blankets are the result of synergism between white-spotting genes, often supplemented by recessive dark-spotting genes (ss). A recessive (ww) gene pair allows white expression. The appaloosa roan gene is sex influenced and not lethal when homozygous. The Ap gene is necessary for expression of appaloosa pattern.

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Date May 24, 1974

MAJOR ASPECTS OF APPALOOSA HORSE COAT COLOR GENETICS

by

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A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree

of

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TABLE OF CONTENTS

	Page
VITA.	ii
ACKNOWLEDGEMENTS.	iii
INDEX TO TABLES	v
ABSTRACT.	vii
INTRODUCTION.	1
REVIEW OF LITERATURE.	2
Modes and Locations of Gene Action	2
Synergistic and Pleiotropic Effects.	5
Genetics of Basic Coat Color in Horses	5
Genetics of Appaloosa and Other Spotted Phenotypes	13
EXPERIMENTAL CONDITIONS	15
EXPERIMENTAL PROCEDURES	20
RESULTS AND DISCUSSION.	25
Percent Appaloosa Production of the Five Sire Classes. . .	25
Patterns Produced by the Five Sire Classes	32
Parentage of the Five Sire Types	36
Influence of Dams on Progeny of Full Blanket Sires	37
Influence of Dams on Progeny of Five Sire Classes.	45
Evidence of Sex-Influence and Linkage in Appaloosa Inheritance	48
SUMMARY AND CONCLUSIONS	53
GENETIC HYPOTHESIS.	56
LITERATURE CITED.	60

INDEX TO TABLES

TABLE		Page
1	Production of 5 Sire Classes. (From Breeding Reports)	26
2	Production of 5 Sire Classes. (Information from Breeders)	27
3	Comparisons of Full Blanket vs All Other Patterns	28
4	Percentages of Appaloosa-Born and Solid-Born Appaloosa Offspring Produced by 5 Sire Classes	31
5	Percentages of Different Patterns Produced by 5 Sire Classes	34
6	A Comparison of Information on 5 Leopard Sires.	35
7	Parentage of the Five Stallion Classes.	38
8	Percent Registered Get Produced by 3 Classes of Mares	40
9	Percentages of Different Patterns Produced by 3 Mare Classes	41
10	Percentages of Different Patterns Produced by 5 Classes of Appaloosa Mares and Full Blanket Stallions.	43
11	Percentages of Different Patterns Produced by "Whitened" and "Non-Whitened" Appaloosa Mares and Full Blanket Stallions	44
12	Percentages of Registered Foals Produced by 5 Classes of Stallions and "Non-Whitened" or "Whitened" Mares	46
13	Percentages of Different Patterns Produced by 5 Classes of Sires and Registered Solid Dams	47

INDEX TO TABLES (Continued)

TABLE		Page
14	Roan and Solid Progeny from 9 Types of Matings Between 3 Classes.	49
15	Roan and Solid Offspring from 4 Types of Matings.	51
16	A Proposed Model of Appaloosa Pattern Inheritance	58
17	Some Genotypes and Resulting Phenotypes	59

ABSTRACT

In a study of records and questionnaires concerning 211 Appaloosa stallions and their progeny, of which 5903 were registered, 52 full blanket stallions produced 20% more registered get and 18% more appaloosa get per mare bred than did the average of the 55 half blanket, 35 leopard, 34 spotted blanket and 35 roan leopard stallions, which are ranked in order of production. Approximately 90% of the appaloosa get of leopard and full blanket stallions were born colored vs 57% of the roan leopard get. All comparisons of the percent production of different patterns by the 5 sire classes were significant. Full blanket stallions produced the most white and leopards produced the most spots. Full blankets, half blankets and leopards were produced only by appaloosa parents. Most parents of leopards had over-all patterns. "Whitened" mares out-produced "non-whitened" mares. Appaloosa mares produced some solid white blanket offspring; solid mares produced very few, but more white mottled and speckled get. No specific patterns were highly heritable. White & spots, white mottled and "All other" patterns were produced in a 2:1:1 ratio. Though evidence of sex-linkage and influence was encountered, the data were insufficient for conclusions. A proposed model of appaloosa genetics includes 7 gene pairs. Three white-spotting genes may be lethal when homozygous. Solid white blankets are produced by the homozygous Ap gene. Leopards result from a homozygous extension (E^{ap}) gene. Spotted blankets are the result of synergism between white-spotting genes, often supplemented by recessive dark-spotting genes (ss). A recessive (ww) gene pair allows white expression. The appaloosa roan gene is sex influenced and not lethal when homozygous. The Ap gene is necessary for expression of appaloosa pattern.

INTRODUCTION

As the value of the Appaloosa horse increases it becomes an economic necessity for the serious breeder to produce as much color contrast in his horses as possible. A solid-colored foal from highly-valued breeding stock is a sizeable economic loss. Unfortunately, a large number of these financial disappointments are born every year to loud-colored parents.

Understanding the genetics of appaloosa coat colors would enable breeders to avoid most such solid-colored foals. Though considerable time has been spent determining the genetics of the basic colors of horses, the appaloosa patterns have been neglected, mainly because of their complexity. Realizing their problem, the members of the Appaloosa Horse Club funded a study, conducted by Robert W. Miller, Associate Professor of Animal Science at Montana State University, to shed light on the genetics of appaloosa coat color. In the course of his research Mr. Miller found that a small group of fourteen stallions with solid white blankets produced a higher percentage (20% more) of appaloosa colored foals than any other class of sire. The present inquiry was then conceived to determine whether the same results would appear in a study concentrating on a large number of these solid white blanketed sires. The results of this study should add to present knowledge of appaloosa coat pattern genetics.

REVIEW OF THE LITERATURE

Modes and Locations of Gene Action

Our comprehension of the genetics of appaloosa patterns depends on an understanding of the basic mechanisms of pigment development, migration and distribution. A general summary of this process and its variations is given by Jones (1971).

The melanoblasts originate in the neural crest and migrate to the dermal-epidermal junction during early embryonic life, where they proliferate and spread through mitotic division. From there they migrate into the hair follicles or remain at the junction of dermis and epidermis. After maturation into dendritic melanocytes, melanin granules (yellow phaemelanin and black eumelanin) are produced and injected into the hair follicles (to become integrated in the hair cells) or into the epidermal cells.

This process of evenly distributed pigmentation can be altered or interrupted by several different mechanisms at five locations: at the neural crest, in the migrating melanoblast, in the peripheral melanocyte, during melanin synthesis and within the hair itself.

One example of a white spotting gene acting on the neural crest is the Rump-white (Rw) gene in the mouse. When heterozygous the gene causes a white rump, but when homozygous it is lethal due to neurological abnormalities. It is believed that the dominant spotting gene Tobiano (S, or T) in horses also acts at the neural crest, but without causing neurological dysfunction.

When a gene exerts its effect on the migrating melanoblasts, certain areas of the body will lack melanocytes and remain white. The belted gene is an example of entire clones of melanoblasts that are inhibited from migration. The target area will have sharp outlines, but may contain dark spots where melanoblasts may have migrated in from the adjacent areas.

There is evidence that a gene (W) in the mouse, which causes a solid white body in the presence of sufficient modifiers, exerts its action by inhibiting mitosis in the migrating melanoblasts. This inhibition also affects the germ cells, causing sterility. Selection against the modifiers reduces the white area. Here the edges of the white area are less distinct, resembling the appaloosa blanket.

Other genes suspected of interfering with mitosis in the migrating melanocytes are the Silver (Sl) locus in the mouse, causing phenotypes ranging from varnished roan to full white, the Roan (Rn) locus in the horse, and the recessive Flexedtail (f) gene in the mouse, which produces a kinked tail and increased white spotting.

An example of gene action at the hair itself is the Blotchy (blo) gene in the mouse, where abnormal hair cells restrict the entry of melanin granules. It is also surmised that abnormal dendrites of the melanocytes can restrict the movement of melanin into the recipient cells or cause abnormalities in location or clumping within the cell. The Dilution (D) gene in mice and horses is an example, where the

melanin granules are clumped on one side of the hair cells because of misshapen melanocytes.

Most color gene action occurs within the functioning melanocyte, including some types of melanin inhibition. In a review by Miller (1969) the role of tyrosinase in the conversion of tyrosine to melanin was discussed and the work cited (Koller, 1930) where tyrosinase was found lacking in recessive white rabbit skin, but present with a tyrosinase inhibitor in dominant white rabbit skin. Tyrosinase was present in all colored rabbit skin.

Albinism is also caused by an inhibition of melanin formation wherein the pigmentation process stops at the premelanosome stage and melanin is never deposited in the granules. This recessive of the Color (C) gene occurs in several classes of mammals but is not known to exist in horses.

Another possible instance of this type of gene action is the Gray (G) gene in the horse. The foal is born pigmented but whitens progressively as each hair coat sheds. This phenomenon has no histological explanation to date.

Two genes appear to alter the cellular environment of the melanocyte, causing a switch from normal melanin production to a reddish form of phaemelanin. These are the Pattern (A) gene and the Extension (E) gene.

Among some spotted animals darker spots appear where there is a difference in local hair type. Apparently the cellular environment leads to differences in melanocyte structure and function.

A final mode of gene action is illustrated by the (B) gene, which causes the protein framework of the melanosome to accept deposits of either eumelanin or phaemelanin, but not of both.

Synergistic and Pleiotropic Effects

One known synergistic effect involving two color genes has been observed in the mouse between alleles of the (W) and (Sl) loci (Jones, 1971). Heterozygous (W) and (Sl) together produce a totally white mouse, which neither gene in a heterozygous condition would do alone.

Pleiotropic effects are abundant among the color genes. They range from lethals when homozygous, such as the Rump-white (Rw) gene in the mouse and the Roan (R) and White (W) genes in horses, to harmless oddities such as the Flexed (f) gene in mice (Jones, 1971).

There is a strong possibility that some of the "appaloosa characteristics" may be due to pleiotropic effects of color genes. These "characteristics" include mottled skin, horizontally striped hooves, unpigmented sclera, sparse mane and tail, and occasionally a kinked tail.

Genetics of Basic Coat Color in Horses

In a major early effort to determine the genetics of coat color in horses Anderson (1914) tabulated the results of over 26,550 matings from

the contemporary studbooks. He initially pointed out that the various registers contained about a 2% error in the tabulation of color. Anderson found bay dominant to black, chestnut recessive to all, while gray, roan and dun were epistatic to the basic colors. He did not consider brown a true color, but thought browns were either dark bays or light blacks.

Castle (1940), with a solid background in laboratory animal genetics entered the field of horse genetics with a proposal that the following four major genes determine basic horse coat colors:

A, the pattern gene, has 3 alleles: A = wild type dun,
A^b = bay pattern, a = no pattern.

B, the pigment gene, has 2 alleles: B = black pigment,
b = brown pigment.

C, the color gene, might have albino alleles, but none are known in horses.

E, the extension gene, has 2 alleles: E = black hairs interspersed through the body color,
E^D = dominant black, which obscures the wild type or bay pattern.

Additionally, gray (G) produces white hairs in the basic colored coat, but only after the juvenile coat is shed; while roan (Ro) produces white hairs in the juvenile coat. Various mutant white spotting genes occur in horses, both dominant and recessive.

Professor Castle published several more papers during the next twenty-odd years, adding to and amending his original views.

Castle (1946) reviewed the work of Salisbury and Britton (1941) where the Palomino was shown to be a heterozygote for a dominant dilution gene (D) and homozygous for the brown gene (bb). A homozygous dilution (DD) would produce a "pseudo-albino" or "cremello" while a non-dilute (dd) would produce a chestnut.

Another type of "albino" discussed was the dominant white (W) which produces white horses with pigmented eyes. This gene is epistatic to all others, and apparently is lethal in the homozygous dominant form (WW).

Castle questioned whether dilution (D) and dominant white (W) might be alleles at the same locus, proposing test crosses to determine this hypothesis.

Castle (1948) presented a comparative study of horse and other mammalian color genetics. He compared genes A, B and C to their corresponding loci in other mammals and proposed a recessive gene (f) for flaxen mane and tail. This gene would reduce black-brown pigmentation without affecting the yellow-red pigmentation over the body. The dilution gene (D) would reduce all types of pigmentation, evident in the "albino" (DD). He also proposed a dominant mutation from A to A' which would produce a dominant black similar to other animals.

Domanski and Prowochenski (1948) held the view that duns and palominos are homozygous for the dilution gene (DD) and that this gene acts only in the presence of bay. Possibly these authors were working with the silver dapple (S) gene, which produces a dilute chestnut when present in heterozygous or homozygous form.

Castle and King (1951) after classifying over 100 matings restated that palomino and buckskin horses are heterozygous for the (D) gene. Palominos are homozygous for brown pigment (bb), but must also have the (A) pattern gene. A "crypto-palomino" (genotype = aa bb Dd) would appear a uniform dilute chestnut. Buckskins have a black pigment (B) gene, and must also carry an (A) pattern gene. A "crypto-buckskin" (genotype = aa B-Dd) would appear as a dilute black, hardly discernible from a true black.

While reviewing A los Colores del Caballo (Ordriozola, 1951), Castle (1951a) took exception to Ordriozola's view that another allele (a^t) at the pattern (A) locus is necessary to explain "brown" coat color. He held that browns are really blacks, bays or chestnuts. He also questioned two other views held by Odriozola: that all horse color differences are due to quantitative differences in eumelanin; and that dilution (D) is actually an albinotic allele of the color (C) gene, thus renamed (c^{cr}).

Castle then suggested that the extension (E) gene has a third allele, recessive (e) which causes a restriction of black-brown pigmentation to the eyes and extremities.

Odriozola maintained that the essential differences between gray and roan are the time of the first appearance of white hairs, the distribution of white hair and the progressiveness of the whitening.

Castle (1951b) discussed the dominant black (E^D) allele in other mammals and reasoned that the same allele in horses would explain the occasional bay foal produced by supposedly recessive black parents. He also proposed that "brown" horses might be heterozygous for the E^D allele, while non-fading jet-black horses would be homozygous (E^DE^D). Castle also rescinded his earlier view (1947) that dominant black might arise from mutation at the A locus, stating that bay offspring could never then result from a recessive black x a dominant black mating, as they occasionally do.

In an extensive paper Castle (1954) correlated horse coat color genetics with the genetics of more intensively studied laboratory animals. He reiterated the view that the genes A, B, C, D and E determine basic horse colors as they do in other mammals. He brought up the possibility that the gene Silver dapple (S) in ponies might be allelomorphic to Dilution (D) in horses. (S) reduces the intensity of black-brown pigment much more energetically than does (D).

Castle also brought up the question of the homozygous Roan (RR) genotype. Since no roan stallion has sired exclusively roan offspring it appears that RR may be lethal as is the WW genotype.

Castle and Singleton (1960) upheld Odriozola (1951) in his view that a fourth allele (a^t) of the A locus would produce the color commonly called "brown". This phenotype is nearly black, but shows tan color at the muzzle, eyes, flank and underline, much as the black and tan (a^t) rabbit. The a^t allele would be intermediate between A and a. In combination with the E alleles the phenotypic color would range from near-bay to black.

In a summary of palomino horse genetics Castle and Singleton (1961) suggested a reason for the palomino white mane and tail as opposed to the buckskin black. Since the only genopytic difference is in the b versus B alleles, diluted brown (bD) must be optically inconspicuous, while diluted black (BD) is not. In this paper, as well as a later one (Castle, 1961), the genotype of the claybank or red dun was proposed as a^t-bb Dd (E-or ee).

Singleton and Bond (1966) offered more evidence that the A allele is necessary for expression of the dilution gene, here called C^{cr}, an allele of C. They claimed no dilution of an aa or a^t-genotype will occur. They remain uncertain as to an explanation of the genotype of the claybank dun.

Lasley (1969) proposes that the A allele allows the mane and tail to be a different color than the body. The B gene causes black mane and tail, while the bb genotype causes flaxen mane and tail.

Smith (1969) stated that there is no linkage between any two known color genes.

Jones (1971) stated that recessive ee can cause bay in the absence of A, also lighten the AB bay to a yellow bay. He felt that there might be two recessive genes that cause flaxen mane and tail. He also proposed that claybank dun is caused by a dilution of chestnut or sorrel with dark red mane and tail, while grulla would be a dilute black.

Following is a summary of basic color genes in horses according to Castle:

A locus - Pattern gene - 4 alleles:

A^{+}-wild type pattern-sooty bay with "zebra" markings

A-bay pattern-red body with dark extremities

a^{t}-brown pattern-black and tan, "zebra" markings

a-no pattern-uniform color

B locus - Pigment gene - 2 alleles:

B-black pigment

b-brown pigment

C locus - Color gene - no known alleles

D locus - Dilution gene - 2 alleles:

D - dilution-incompletely dominant

D locus (continued)

d-"normal" non-diluted color

E locus - Extension gene - 3 alleles:

E^D-dominant extension-extends excess dark pigment throughout the coat, masking any pattern

E-extension-allows black or brown pigment to extend normally throughout the coat

e-restriction-restricts dark pigment to the eyes and extremities

G locus - Gray gene - 2 alleles:

G-gray-juvenile coat is colored, white hair appears when this coat is shed, whitening is progressive with age

g-non-gray

R locus - Roan gene - 2 alleles:

R-roan-foal is born with white hairs interspersed with basic body color hairs. Not as progressive as gray, horse doesn't become white. In homozygous form, RR may be lethal.

r-non-roan

S locus - Silver dapple - 2 alleles (?)

S-silver dapple-dilutes black (BE) to a color resembling dappled chestnut with white mane and tail, and dilutes black (Bee) to sorrel, no dapples, with white mane and tail. The homozygote is only slightly lighter in shade. May be an allele of the D locus.

s-"normal" non-diluted color

W locus - White - 2 alleles:

W-dominant white-epistatic to all other colors. Apparently lethal in homozygous form.

w-non-white.

Genetics of Appaloosa and Other Spotted Phenotypes

One of the earlier studies of spotted phenotypes in horses was conducted by Klemola (1933) on piebald (tobiano) and overo horses.

The dominant piebald pattern generally entails white on the neck, shoulders, back and croup. Head and eye color is generally normal and the legs are white. White areas have distinct margins.

The recessive overo pattern, which Klemola called splashed white, causes white on the underside of the body and much white on the head. Wall eye is very prevalent in this type. Klemola claimed that wall eye is always present, but can also be present in solid colored horses.

These two forms of white spotting are fully developed at birth and the patterns never change. Klemola also stated that white on the legs and face are recessive in nature.

Castle (1954), calling the piebald gene (P), felt that a horse homozygous for P would be whiter than a heterozygote, thus considered less attractive and used less for breeding purposes. Most piebalds of his knowledge produced about 50% spotted foals.

Lasley (1969) felt that the appaloosa blanket pattern, which he called (W^1) would be generally dominant to the leopard pattern (W^2), but not completely.

Hare (1969) described the leopard as a horse born white with spots, a pattern which doesn't change during the life of the horse. This pattern is not the same as that of a horse born dark, later roaning out

to become light with spots. Leopard breeding is necessary to produce leopards. Hare also feels that the leopard is a different strain of spotted horse than the western appaloosa, even possessing differently textured hair.

Wagner (1969) concurs with Hare on the description of a leopard, and proposes that the roaned out spotted horse never loses all of the pigment on its body. He states that leopards are commonly considered superior as color sires. They also produce more leopard offspring than other patterns will.

The gray (G) gene causes a rapid loss of hair color in appaloosas, but the skin remains pigmented.

The roaning (R) gene, however, never permanently lightens the frontal bones of the face, the ears, hocks, knees, point of hip, or mane, tail and cannons if dark to start with. This gene allows the skin and hair to lose pigment and regain it. Not only the coat pattern can change, but also the type of pigment exhibited.

Jones (1971) believes there are two types of appaloosa genes -- those that cause a loss of color over local areas (ranging from small spots to large white areas), and those which cause an increase of pigmentation in small local areas.

He proposes three major genes that cause the appaloosa blanket patterns:

W^{ap} causes a white spotted blanket

Sl^{ap} causes a frosty white blanket

Rn^{ap} causes a roaning over the hips

He feels that modifying genes cause the variations observed. Many modifiers are probably indicated by bald face, stocking legs, mottled skin, striped hooves, and white sclera. Two minor genes are also mentioned--blotch (blo) which causes a blotched roan appearance, and flexed tail (f) which causes a white rump and flexed tail when homozygous.

When either W^{ap} or Sl^{ap} are homozygous and a large number of modifiers are present, leopard pattern might result. Leopard pattern might also appear when both W^{ap} and Sl^{ap} are heterzygous. Rn^{ap} doesn't produce leopard by itself. Jones feels that homozygous W^{ap}, without modifiers, probably produces the prototype appaloosa blanket with spots.

Carr (1972) defined few-spotted leopards as white horses with dark leg patches and ears, dark hair in fore and rear flanks, and roan under the neck. These dark areas generally roan. A few spots may be present on the neck and hips. It was his belief that few-spotted leopards produce a very high percentage of appaloosa foals, approaching 100% for mares and 90% for studs. About 75% of the foals from few-spot dams and 40% from few-spot sires are born leopard. One few-spot sire was cited that produced 53 appaloosa foals out of 57 total foals, with 19 leopards and 21 blanketed offspring. Apparently few-spotted leopard sires are

uncommon, probably partly because they are not as attractive as horses with more contrast in their patterns.

Miller (1969) reported on two extensive studies of appaloosa horse coat colors. The first study included 9,955 horses. Several sex-influenced differences were found. Males exhibited more white, more spots and more blanket fringe roaning. Females had more solid white blankets, more speckled patterns, more roan blankets, and were more likely to be roans. This study showed that non-spotted parents can produce spots and that non-blanketed parents can produce blanketed offspring.

The second study included 5,721 horses of which 165 were sires, 3,158 were mares, and 2,398 were the progeny of the foregoing. Appaloosa mares produced significantly more appaloosa foals than did solid mares (78.5% of all foals born versus 64.2%). However, when the sires had solid white blankets, spots only, or were mottled, this difference was lessened. These classes of sires were small. Fourteen sires with solid white blankets produced 20% more appaloosa foals of those born than did sires with blanket and spots. This difference was highly significant.

Other points include:

1. Spots may be self-colored or darker, but never lighter than the basic body color.
2. The appaloosa horse always displays the minor "appaloosa characteristics" in skin, eye and hooves.

3. The Gray (G) gene causes early graying in appaloosas.

4. The Roan (R) gene acts differently in appaloosas than it does in other horses. Roan horses may be born solid-colored, but roan in a year or two. It may be dominant in females, but incompletely dominant in males, where it may be expressed as blanket fringe roaning.

Miller proposed the following scheme for appaloosa color genetics:

(Ap) = appaloosa expression gene, must be present for any appaloosa pattern to be expressed.

A series of quantitative modifying genes to control white, with a possible pair of recessive (ww) genes necessary for the expression of white.

A series of similar genes to control spotting, again recessive (ss).

A sex influence where perhaps the male heterozygote displays a pattern while the female heterozygote does not.

Some sample genotypes might be:

Ap-ww ss - blanket and spots

Ap-ww Ss - blanket, no spots

Ap-Ww ss - spots, no blanket

Ap-Ww Ss - solid, no pattern

Any of these genotypes could produce a spotted blanket pattern in their offspring.

EXPERIMENTAL CONDITIONS

Since the horse is a large, expensive animal with a generation interval of several years, a direct experimental study including hundreds is essentially impossible. In a study of the present type, personal observation of each horse would be the second best alternative. Unfortunately, this would entail extensive travel throughout the United States, which is also economically impossible. The data available within the realm of possibility are the records kept by the Appaloosa Horse Club in Moscow, Idaho.

An individual file is kept on every animal registered with the Appaloosa Horse Club. This file includes:

A picture of the horse, taken at the time of registration. Under the old foundation registry, a second picture of the adult horse when and if a foundation registration was applied for.

A word description of color and pattern of the horse.

Stallion breeding reports (which include the registration number of any registered get resulting from each breeding.)

Copies of any correspondence with owners, breeders, etc. pertaining to said horse.

Transfer reports (which include owner names and addresses).

A notification of lease when applicable.

A card file is also kept with the production records of all sires and dams.

The stud books of the association give a word description of every registered horse. However, these word descriptions tend to be very general and rather inaccurate. An accurate description stating "white with spots" may describe a horse with a frosted, mottled or solid blanket with two, fifty or more spots. As an example of inaccurate descriptions, a sample of 15 horses described as "white over loin and hips" included 4 with spotted blankets, 3 with white mottling, 5 with roaned hips, and only 3 with solid white blankets. No mention is made in these descriptions of overall roaning, white speckles, dark specks or other characteristic appaloosa patterns. Horses displaying these patterns are described by color and facial or leg markings only.

Another limiting factor of the data is the fact that a very large percentage of appaloosa foals from the recorded matings are never registered, while there is no record at all of solid foals born from these matings. Information from stallion owners partially fills the void, but also tends to be vague and inaccurate. All in all, there is a very high percentage of error inherent in the data.

EXPERIMENTAL PROCEDURES

The primary purpose of this study was to determine whether solid white blanket sires produce more appaloosa foals than do sires of other patterns. Secondarily, the purpose was also to determine as much about appaloosa genetics as possible.

With these aims in view, data was collected at the Appaloosa Horse Club in Moscow, Idaho on 107 white blanketed stallions and 104 stallions displaying white and spots. The white and spots stallions were of three types: 35 were leopard pattern, 35 were roan leopards, and 34 had white blankets containing large spots. The leopard and roan leopard patterns were chosen partly for their reputations for producing high percentages of appaloosa progeny, and partly because there were very few represented in the Miller (1969) study. The blanket with spots pattern was used since this is considered the prototype of the Appaloosa breed, and a highly desirable pattern.

It became evident very early that there are two types of solid white blankets, so the white blanket stallions were classified as to type. A description of the patterns follows:

Fifty-two stallions displayed a large, deep, solid-white blanket over at least the hips and loins, generally over the body, and occasionally past the withers. This blanket encircles the body and hindquarters and reaches usually to the hocks, excluding roan patches at

the flanks, both fore and rear. For classification purposes, this pattern is termed "full blanket."

Fifty-five stallions displayed a large but shallow solid-white blanket over at least the hips and loins, often over the body. This blanket reaches no further down than the stifle and approximately three-fourths of the way down the ribs. For the study this pattern is termed "half blanket."

The leopard stallions were born white with spots over the entire body and head. Often the head and neck had dark patches that whitened later.

The roan leopard stallions, however, are not true leopards. These horses were born dark, often with spotted blankets. With age they roaned out to a white or near white with spots over the body and hips, and occasionally over the neck. Their heads are not spotted.

The blanket with spots stallions displayed large blankets over hips and loins, often extending to the withers. The spots within the blankets were very large, what are often termed "apple" spots. No horses with smaller spots were used. These horses will be known in this study as "spotted blanket."

The selection criteria for individual stallions was pattern and a record of having bred 12 or more mares in the years between 1962 to 1969. The selection method was to randomly pick individual files from those of all horses born before 1960. Large packets were pulled,

checked for appropriate pattern, then checked for breeding records.

Data collected on each stallion selected included: color, pattern, extent of pattern, whether he roaned with age, and any other differences in juvenile and aged pictures (when available). The registration numbers of his sire and dam were taken, or their color, pattern and breeding if not registered Appaloosas.

From the breeding reports were listed all mares bred and the registration numbers of any progeny from each mating. The mares were classified in four groups: appaloosas, solid mares with known appaloosa breeding, solid grade mares, and solid registered mares (of other breeds). The color and pattern of these mares was recorded when stated.

Owner names and addresses were taken from transfer reports and correspondence.

Where the registration numbers of the sires and dams were given, color, pattern, and the extent of the pattern was taken from their respective individual files.

Time was not available for checking the individual files of the 5,903 registered offspring, so the remaining data (at great sacrifice of accuracy) were taken from the stud books. The main data available here were word descriptions of color, pattern, and extent of pattern. The color of unregistered dams was also occasionally stated.

The stud book data were not collected on all registered progeny, but only on those produced by 21-23 of the more heavily bred stallions

of each class. Therefore, this part of the study was based on 110 stallions and their 3,550 registered offspring.

Questionnaires were sent to most of the owners and lessees, past and present, of the 211 stallions. These questionnaires stated the purpose of the study and asked for the following information about each stallion:

Number of foals born between 1963 and 1970,

Number of registerable appaloosas,

Number of foals actually registered,

Of the appaloosa foals, how many were born colored and how many were born solid,

How many of each pattern were there? (Nine patterns and an "any other" category were listed.)

Of the 281 questionnaires mailed, 84 replies were received and useable data were obtained on 39 stallions.

The comparisons made between the five types of stallions included:

Percentages of appaloosa offspring produced,

Percentages of the different patterns produced,

Percentages of foals born appaloosa, or born solid and became appaloosa,

Differences in parentage of the five types.

Comparisons among the mares bred included:

Appaloosa versus solid mares,

Roan versus non-roan mares, and

A comparison among appaloosa mares.

Several more comparisons were made, some of which were suggested by the data (which is not generally recommended, but in this case, justified in additional information).

The Chi-square (X^2) test criterion was used for all the comparisons made in this study. Its use is valid for enumeration data of this type (Steel and Torrie, 1960), and it allows individual comparisons between the different classes of stallions and mares. It also offers simplicity of computation, analysis and interpretation.

RESULTS AND DISCUSSION

Percent Appaloosa Production of the Five Sire Classes

This study included a total of 211 stallions which were bred to 16,017 mares to produce 5,903 registered offspring, for an average production of 36.9% registered get per mare bred.

The first comparison made in the study was to determine whether full blanket stallions and half blanket stallions were actually different classes. The percentage of registered offspring per mare bred (taken from the breeding reports) was the criterion used. The difference was very highly significant ($P < .005$), thus the two classes were considered separately throughout the study.

Table 1 shows the production records of the 5 classes of sires as taken from the breeding reports, also the results of the X^2 comparisons made between these classes.

The same comparisons were made using the data furnished by the owners of 39 of the stallions. These stallions were bred to 2,712 mares producing a total foal crop of 2,066, of which 1,760 were born or became appaloosa. The average production was 64.9% appaloosa per mare bred. Table 2 shows these production records, also the results of the X^2 comparisons between the classes.

In table 3 the full blanket stallions were compared to all others, and results from the Miller study (1969) were borrowed for comparison. Though the classes in the present study were much more specific than

those of the Miller inquiry, the results and scope of the differences are remarkably similar.

TABLE 1. PRODUCTION OF 5 SIRE CLASSES (From Breeding Reports)

No. Sires	Sire Class	No. Mares Bred	Av.No. Mares Bred	Range	No. Reg. Get	Av. Reg. Get/ Sire	% Reg. Get/ Mare Bred
52	Full blanket	4,494	86	15-322	2,316	45	51.5
55	Half blanket	2,942	53	13-138	1,085	20	36.9
35	Leopard	2,941	84	13-200	996	28	33.9
34	Spotted blanket	3,360	99	14-423	956	28	28.5
35	Roan leopard	2,280	65	18-183	550	16	24.1
211	All patterns	16,017	76		5,903	28	36.9

X^2 Comparisons

	X^2	ns	*	**	***
Full blanket vs half blanket	152.9631				X
Half blanket vs leopard	6.3145		X		
Leopard vs spotted blanket	21.504				X
Spotted blanket vs roan leopard	12.979				X

(ns, not significant; *, P-.05; **, P-.01; ***, P-.005)

TABLE 2. PRODUCTION OF 5 SIRE CLASSES (Information from Breeders)

No. Sires	Sire Class	No. Mares Bred	Av. No. Mares Bred	Range	No. Born	No. App.	% App. of Total Foals	% App./ Mare Bred	% Reg. Get/ Mare Bred
9	Full blanket	867	96	24-322	718	671	93.5	77.4	44.9
11	Half blanket	487	49	6-109	387	339	87.6	69.6	40.3
5	Spotted blanket	496	99	30-217	368	300	81.5	60.5	28.1
6	Leopard	480	80	35-178	336	262	78.0	54.6	35.3
8	Roan leopard	382	48	12-101	257	188	73.2	49.2	23.4
39	All patterns	2,712	69		2,066	1,760	85.2	64.9	35.5

X^2 Comparisons (% App. of Total Foals)	X^2	ns	*	**	***
Full blanket vs half blanket	13.063				X
Half blanket vs spotted blanket	4.090		X		
Spotted blanket vs leopard	1.095	X			
Leopard vs roan leopard	2.089	X			
Spotted blanket vs roan leopard	6.143		X		

TABLE 3. COMPARISONS OF FULL BLANKET vs ALL OTHER PATTERNS

Information Source	Criterion	Full Blanket %	All Others %	Differences
Breeding Reports	% Reg/ Mare Bred	51.5	31.1	20.4
Individual Breeders	% App/ Mare Bred	77.4	59.4	18.0
	% App of Total Foals	93.5	80.8	12.7
Miller Study (1969)		White only	White & Spots	
	% App/ Mare Bred	73.2	51.1	22.1
	% App of Total Foals	87.3	67.6	19.7

Confidence Limits: 16.5%, 24.3% (Full Blanket vs All Others)

As can be seen in table 1, the solid white blanket stallions produced more registered offspring than the other classes of stallions. In addition, the full blanket stallions far exceeded the half blanket stallions in production.

As a percentage of the production of full blanket stallions, those of the other classes produced as follows:

half blanket	72%
leopard	66%
spotted blanket	55%
roan leopard	47%

All the differences were very highly significant except for the comparison between half blankets and leopards, which was significant

at the .05 level.

Half blanket and roan leopard stallions were bred less heavily than the other stallion classes. This might possibly be because their patterns are considered less desirable by breeders than the other patterns. The spotted blanket stallions were bred the most extensively, which is undoubtedly due to their attractive pattern.

Since such a small number of breeders responded with useable information, the data in table 2 have limited usefulness. They do indicate, however, that nearly half the appaloosas produced are never registered. They also indicate that the appaloosa production of full blanket sires might approach 100% of all foals. Some of the breeders stated that their full blanket stallions produced approximately 80% appaloosa-born foals with the remaining 20% developing some pattern within two years.

Again, as a percentage of full blanket stallions, the production of the other classes was as follows:

	% App. of Total Foals	% App/ Mare Bred
Half blanket	94%	90%
Spotted blanket	87%	79%
Leopard	83%	71%
Roan Leopard	78%	54%

The differences here weren't as large as they were in the over-all study, but the comparison between full blanket and half blanket stallions was still very highly significant. The difference between half blanket

and spotted blanket was significant at the .05 level, as was the difference between spotted blanket and roan leopard. The comparisons of spotted blanket versus leopards and leopards versus roan leopards were not significant. The reversal in position between leopards and spotted blankets is of interest. The explanation is possibly that these extremely small classes are not representative of the larger samples taken in the over-all study (as represented by the percent registered get per mare bred). At any rate, since the difference is not significant, these results don't invalidate those of the over-all study.

A high rate of uncontrolled bias is inherent in data of this type. While one breeder may be reluctant to admit that his stallion doesn't produce 100% appaloosa foals, another breeder may lose track of his solid-born foals at weaning, before they develop a pattern. With such small samples, either occurrence will drastically influence the results.

It is also pertinent that as the percentage of appaloosa foals declines, the apparent reproductive rate also drops. From the data in table 2 the full blanket stallions produced an 83% foal crop, while the roan leopards produced one of only 67%. This trend was noted in the Miller (1969) study when registered dams were compared to unregistered. It is doubtful that the reproductive rate is really lower, but only that the breeders' concern declines. It's a matter of speculation whether the percentage of appaloosas produced would rise or fall if the true numbers were known with certainty.

A slight trend of the same type appears in table 3. It is also relevant that the confidence limits of the true difference between full blanket stallions and all other classes, computed on the data from the breeding reports, doesn't even include the figure obtained from the individual breeder data. This verifies the non-reliability of these data. The Miller (1969) study, however, showed a difference well within the confidence interval and in close agreement with the breeding report data.

The breeders provided the only available data on the number of appaloosas that were born colored and the number that were born solid but became appaloosa before maturity. These data, on 1,760 appaloosas sired by the 5 classes of stallions, are presented in table 4.

Table 4. PERCENTAGES OF APPALOOSA-BORN AND SOLID-BORN APPALOOSA OFFSPRING PRODUCED BY 5 SIRE CLASSES

Sire Class	No. App. Born	Born App.	Born Solid	% Born App.	% Born Solid	% Total Foals Born App.
Leopard	262	237	25	90%	10%	71%
Full blanket	671	582	89	87%	13%	81%
Half blanket	339	262	76	78%	22%	68%
Spotted blanket	300	222	78	74%	26%	60%
Roan leopard	188	108	80	57%	43%	42%

$X^2 = 104.2^{***}$

Obviously there are distinct differences between the sire classes for this trait. The changes are due mainly to roaning, but white spots, white speckles and dark spots often appear after the juvenile coat is shed. The few foals by leopard sires that changed had appaloosa dams, which suggests that leopards may not carry the genes which bring about a color or pattern change. When foals by full blanket sires changed, they tended to develop white speckles. However, the solid-born foals by the other 3 sire classes tended to roan, especially those by roan leopards.

Patterns Produced by the Five Sire Classes

This portion of the study is based on information from the stud books and from the individual breeders. In both cases a word description of pattern was the only information available. The data from both sources are presented in table 5.

Separate chi-square tests were run for each pattern from each data source. Nearly all of the comparisons proved significant or highly significant, even those on the limited information from the individual breeders.

It may be noted that there is no leopard class in the stud book information. This is because in the stud book leopards are often described as "bay (etc.), white and spots over body and hips," which is identical to the description of a spotted blanket horse. In actuality, the horse may have bay patches only on neck and legs, being white with spots from nose to tail.

It may also be noted in the information from the breeders that the leopard classes are rather large. No distinction is necessarily made between leopards and roan leopards; therefore, they, and perhaps some (extensive) spotted blanket horses, are all lumped together in one class.

The "other" class in table 5 includes horses displaying over-all roaning, white speckles, dark specks and similar appaloosa patterns. These patterns are not described in the stud book, so no enumeration of the different classes was possible.

The white and spots class includes spotted blankets, some roan leopards, and some white mottled with dark spots patterns. The white blanket class contains solid white blankets, white mottled blankets and some roaned blankets. The roan blanket class includes solid roan blankets, roan blankets containing white or dark spots, and possibly some roan leopards. The white mottled class contain white spotted patterns of all kinds. The dark spots class includes roan leopards and solid colors displaying only dark spots. This class would probably be larger if the horses were all described at maturity.

Table 5. PERCENTAGES OF DIFFERENT PATTERNS PRODUCED BY 5 SIRE CLASSES

Data Source	No. Sires	Sire Class	No. App. Foals	% White & Spots	% White Blanket	% Roan Blanket	% White Mottled	% Dark Spots	% Leopards	% Other	% Any White	% Any Spots	% All Other
Stud Book	22	full	1,064	49.4	16.0	6.6	16.7	3.4	--	7.9	82.1	54.3	13.0
Breeders	5	blanket	241	46.1	7.4	8.3	10.8	--	14.1	13.3	78.4	60.2	21.6
Stud Book	22	half	626	44.9	15.0	6.2	18.5	3.7	--	11.7	78.4	50.0	16.5
Breeders	8	blanket	301	37.5	18.3	7.3	14.3	1.3	1.7	19.4	72.3	41.1	26.1
Stud Book	21	leopard	733	51.2	10.1	5.3	8.6	8.3	--	16.5	69.9	61.4	19.7
Breeders	5		137	34.3	11.5	2.9	11.0	.7	31.4	10.2	86.1	65.4	13.7
Stud Book	23	spotted	698	44.4	9.6	6.2	17.5	4.2	--	18.2	71.5	50.6	22.4
Breeders	6	blanket	300	36.6	16.7	11.7	9.7	4.7	10.3	10.3	73.3	51.6	22.0
Stud Book	22	roan	429	43.8	9.1	11.7	14.9	7.9	--	12.6	67.8	52.2	23.8
Breeders	8	leopard	93	31.2	5.4	14.0	9.7	5.4	7.5	26.8	53.8	44.1	40.8
Significance of differences				* / *	*** / ***	* / *	*** / ns	*** / **	-- / ***	*** / ***			
Stud Book	110	All	3,550								75.1	54.6	17.6
Breeders	32	Sires	1,072								74.0	51.5	23.7
Significance of differences											ns	ns	***

As can be seen at the bottom of table 5, the pattern displayed by a horse does not seem to determine whether or not it will be registered except in the case where it displays neither white nor spots. Therefore, the observed difference in information from the two data sources is probably due mainly to classification differences, not any real difference in siring ability within sire classes.

According to the stud book, full blanket, then half blanket stallions sired the most white-containing patterns, while leopards sired the most spotted offspring. The individual breeder data show leopards siring a very high percentage of white-containing patterns. However, it is probable that the large leopard progeny class, which is included in the "any white" class, contains a sizeable proportion of roan leopards. This presumption is based on the following:

The individual breeder data are based on five leopard stallions and their 137 appaloosa progeny. These same five sires, according to the stud book, produced 129 registered offspring, giving an excellent comparison which is presented in table 6.

Table 6. A COMPARISON OF INFORMATION ON 5 LEOPARD SIRES

Data Source	No. App. Foals	% White & Spots	% White Blanket	% Roan Blanket	% White Mottled	% Dark Spots	% Leopard	% Other	% Any White	% Any Spots	% All Other
Stud Book	129	51.2	10.1	4.7	6.2	7.8	--	20.2	68.2	58.9	24.0
Breeders	137	34.3	11.5	2.9	11.0	.7	31.4	10.2	86.1	65.4	13.7

The stud book information on these five stallions is very similar to the data on the total twenty-two stallions. Here again, classification methods have caused the apparent differences. In this study the information on larger numbers must be relied on more heavily, but the limited data from the individual breeders provide a very interesting supplement.

Parentage of the Five Sire Types

Theoretically, a study of the parentage of the 5 sire types should yield nearly as much useful information as a study of their progeny. In this case, pictures of the registered parents were available for classification, so the information gathered is much more precise. Unfortunately, 74 of the 422 parents (17.5%) of the 211 stallions were unknown, which lessens the usefulness of the data. However, there were large differences between the five classes concerning the number of unknown parents, so even this lack of information has some application.

In the data presented in table 7, the white and spots category includes spotted blankets and white mottled with spots (which was less than 2% in all classes). The roan blanket class contains roan blankets with or without spots. The dark spots group includes roan leopards and solid-colors containing spots. The speckled class includes both white and dark speckles. The solid group contains registered horses of five other breeds plus solid horses of unknown breeding.

Several pertinent items appeared in these data that are not presented in table 7. One such item: two of the spotted blanket stallions were apparently produced by registered AQHA parents. However, these quarter horses were mainly of unknown breeding and it must be presumed that there was some appaloosa ancestry behind them or an error in recorded parentage.

Another interesting sidelight is that 40% of the parents of the leopard stallions exhibited over-all patterns (nose to tail), while a maximum of 10% of the parents of the other stallion classes did. Of the leopard stallions 71.4% had one parent with over-all pattern. In fact, only 14.3% had two known parents without over-all patterns.

Of the leopards, 77% had one leopard parent, but none had two leopard parents.

Of the 104 leopard, spotted blanket and roan leopard stallions, none had both parents exhibiting the same pattern. However, out of 55 half blanket stallions, one set of parents was white with spots, one set had roan blankets, and one set was roan with dark specks. Of the 52 full blanket stallions, two pairs of parents exhibited full blankets, while three pairs had spotted blankets.

White and spots was the most common pattern among sires, except for the leopard class, where there were more leopard sires. Leopard sires were also common in the spotted blanket and full blanket classes. Solid sires were common in the spotted blanket and roan leopard classes. Dark

Table 7. PARENTAGE OF THE FIVE STALLION CLASSES

Stallion Class		% White & Spots	% Full Blanket	% Half Blanket	% Roan Blanket	% Dark Spots	% White Mottled	% Leopard	% Speckled	% Solid	% Unknown	(Of those known) % With White	(Of those known) % With Spots
52 Full Blanket	Sires	63	13	2	2	2	2	10	6	0	0	66	57
	Dams	19	13	0	17	8	6	4	27	0	6	68	58
	All	41	13	1	9.5	5	4	7	16.5	0	3		
55 Half Blanket	Sires	51	5	4	7	5	7	7	5	2	5	53	49
	Dams	7	2	2	20	13	15	5	20	2	15	59	56
	All	29	3.5	3	13.5	9	11	6.5	12.5	2	10		
35 Leopard	Sires	14	6	0	3	9	0	57	3	0	9	47	54
	Dams	3	6	0	6	17	3	6	20	0	40	62	72
	All	8.5	6	0	4.5	13	1.5	31.5	11.5	0	24.5		
34 Spotted Blanket	Sires	29	0	0	0	9	3	15	0	21	24	32	36
	Dams	6	6	0	12	6	6	0	9	12	44	49	56
	All	17.5	3	0	6	7.5	4.5	7.5	4.5	16.5	34		
35 Roan Leopard	Sires	26	3	0	9	17	3	3	0	11	29	24	41
	Dams	6	0	0	9	23	9	0	11	14	29	34	58
	All	16	1.5	0	9	20	6	1.5	5.5	12.5	29		

spots were common only in sires of roan leopards, while full blanket sires were common only in the full blanket class.

Speckled was the most common pattern among dams, except in the spotted blanket and roan leopard classes. Spots were the most common pattern for dams of roan leopards and common in the half blanket and leopard classes, while solid dams were most common in the spotted blanket class and were common in the roan leopard class. Roan blankets were common among dams of the blanketed classes. Full blanket and white and spots patterns were common only in the dams of full blanket stallions.

The size of the unknown parent groups ranges from 3% in the full blanket class to 34% in the spotted blanket class.

An important class in table 7 is the percent of solid parents for each stallion class. There are no solid parents in the full blanket and leopard classes, and only two quarter horse parents in the half blanket class. This contrasts with sizeable numbers of solid parents in the spotted blanket and roan leopard classes.

Of the known parents, those of full blanket stallions exhibited the most white, and those of leopards had the most spots.

Influence of Dams on Progeny Of Full Blanket Sires

Since the sire is only half of the genetic picture, a detailed study of a portion of the mares bred to full blanket stallions was deemed necessary. The breeding reports of full blanket stallions were selected for this portion of the study on the following criteria:

The color and pattern of the majority of the mares bred must be listed;

The proportion of registered get must be near 51.5%--the average of the entire class;

The majority of the registered get must have registration numbers between 30,000 and 140,000 (these were the stud books available) so that word descriptions of the progeny would be available.

Eight full blanket stallions were selected which had produced 454 registered offspring from 868 matings for an average production of 52.3% (near the average of 51.5%).

The mares were originally divided into four classes: appaloosas, solid mares with known appaloosa breeding, solid mares of unknown breeding, and registered solid mares of the other breeds. The class containing solid mares with known appaloosa breeding was so small (2 mares, 5 offspring) that it was consolidated into the class of solid mares of unknown breeding, which undoubtedly contained many similar mares.

Table 8 gives the percentage of registered offspring produced by the three classes of mares.

Table 8. PERCENT REGISTERED GET PRODUCED BY 3 CLASSES OF MARES

Mares:	Appa-loosa	Grade Solid	Reg. Solid	Total	All Solid	X^2
No. Bred	356	367	145	868	512	App. x Grade ***
No. Reg. Get	207	156	91	454	247	Grade x Reg. ***
% Reg. Get	58.15	42.51	62.76	52.30	48.24	App. x Reg. ns

Surprisingly, registered solid mares out-produced appaloosa mares but the difference was not significant. However, these two groups out-produced grade solid mares by 20% and 16% respectively, and the difference was very highly significant. In the Miller(1969) study, appaloosa mares out-did solid mares when bred to white only stallions, but the difference was not significant.

It is doubtful that registered solid mares would actually produce 20% more appaloosa offspring than would grade solid mares. Rather, it is more probable that the investment in registered mares makes registration of the resulting progeny more likely.

Table 9 shows the patterns produced by the three classes of mares when bred to full blanket stallions. The class breakdowns are the same as those of previous tables except that the "unknown" class contains horses with registration numbers above 140,000 whose word descriptions were not available.

Table 9. PERCENTAGES OF DIFFERENT PATTERNS PRODUCED BY 3 MARE CLASSES

Mare Class	No. App. Foals	% White & Spots	% White Blanket	% White Mottled	% Roan Blanket	% Dark Spots	% All Other	% Unknown	% With White	% With Spots
Appaloosa	207	43	24	12	6	2	5	8	79	46
Grade Solid	156	47	0	19	12	5	11	5	67	53
Reg. Solid	91	52	3	22	3	0	15	4	77	55
X^2 (all mares)		ns	***	ns	*	*	**	ns	*	ns
X^2 (App. vs Reg. Solid)		ns	***	*	*	ns	***	ns		

The largest differences between appaloosa and solid dams were in the white blanket and "all other" (speckled, over-all roaning, etc.) classes. The apparent difference in white and spots was not significant, while it was barely significant for the white mottled class. The other significant differences appear to be between the two classes of solid dams, so are probably due to small numbers or registration preferences.

A discussion of the white blanket class now seems in order. Of the 247 appaloosa offspring out of solid mares, only 3 displayed a solid white blanket. The three dams were registered quarter horse mares, 2 sorrels and 1 bay. One mare was appendix registered and the other two had unregistered roan dams. It is possible that these mares might have actually been appaloosas (re. the 2 pairs of quarter horses that produced the spotted blanket stallions). There is also the possibility that offspring of registered quarter mares were deemed more marketable than those of grade appaloosa mares.

In the latter part of this study, all evidence has pointed to the proposition that solid white blankets of both types are produced only by appaloosa parents (see the "% Solid" class of table 7). The 2 quarter horses of 110 from that portion of the study, and the 3 quarter horses of 247 from this portion have apparently produced solid white blanket progeny at an approximate rate of 1.5%, which is well within the limits of registration errors. This figure is also undoubtedly within the percentage of quarter horses exhibiting minor appaloosa

patterns. It is therefore proposed that if these horses did indeed produce solid white blanket progeny, they were almost certainly appaloosas.

Appaloosa mares bred to the 8 full blanket stallions were classified according to pattern to determine how highly heritable the dam's pattern might be. Only 169 mares were used for this portion because data on the patterns of the remainder were not available. The mares were divided into 5 pattern classes: white & spots, white blanket, white mottled, dark spots, and an "other" category which includes roan blankets, speckles, flakes and specks. Table 10 shows the types of offspring produced by these mares and the full blanket stallions.

Table 10. PERCENTAGES OF DIFFERENT PATTERNS PRODUCED BY 5 CLASSES OF APPALOOSA MARES AND FULL BLANKET STALLIONS

No. Mares	Pattern Class	% White & Spots	% White Blanket	% White Mottled	% Roan Blanket	% Dark Spots	% All Other	% With White	% With Spots
24	White & Spots	42	33	21	0	4	0	96	46
25	White Blanket	44	32	20	0	0	4	96	44
20	White Mottled	45	35	10	0	0	10	90	45
28	Dark Spots	43	32	4	7	7	7	79	53
72	All Other	44	19	14	17	1	4	78	47
169	Total	44	27	14	8	2	5	85	47
X^2		ns	ns	ns	*	ns	ns	ns	ns

As can be seen in table 10, the percentage of roan blankets in the progeny was the only significant difference observed. Interestingly, the 69 mares with white areas produced no roan blankets, while the 100 mares without white areas produced 24. In fact, if the mares had been grouped into only these 2 classes, white areas vs none, most of the differences would have been significant. The percentages in the white & spots class are remarkably similar. It must be stressed that the numbers in these classes are very small so the validity of this particular portion of the study may be questionable.

These mares were then grouped according to basic body color--whether they were "non-whitened" (bay, sorrel, dun, etc.) or "whitened" (white, grey or roan). The percentages of the 6 patterns in the progeny are presented in Table 11.

Table 11. PERCENTAGES OF DIFFERENT PATTERNS PRODUCED BY "WHITENED" AND "NON-WHITENED" APPALOOSA MARES AND FULL BLANKET STALLIONS

No. Mares	Mare Class	% White & Spots	% White Blanket	% White Mottled	% Roan Blanket	% Dark Spots	% All Other	% With White	% With Spots
106	Non-whitened	43	28	18	6	2	3	90	45
64	Whitened	44	25	6	11	3	11	75	52
X^2		ns	ns	*	ns	ns	*	*	ns

The "non-whitened" appaloosa mares produced more white; specifically, more progeny in the white mottled class and less in the "other" class. Otherwise, differences were not significant. Again the white and spots class was very similar. The dark spots class is also very similar, but very small, probably because of the prepotent white of the sires.

From the data in tables 10 and 11, it appears that when bred to full blanket sires, appaloosa mares do not tend to reproduce their own patterns. Whether or not they do when bred to other types of sires awaits further study. However, as seen earlier among sires, those mares with white areas tend to produce a greater number of progeny with white, and those with spots tend to produce more spots.

Influence of Dams on Progeny of Five Sire Classes

Along the same line, it is of interest to determine whether there is a difference in over-all appaloosa production by "non-whitened" or "whitened" mares. Consequently, 10 sires from each of the 5 stallion classes were selected and the percentage of appaloosa progeny were recorded for "non-whitened" or "whitened" mares. Stallions selected had produced meaningful numbers of registered get from mares whose basic body color was known. Consequently, these sires had out-produced the averages of their respective classes by large margins. Mares were both appaloosa and non-appaloosa. The "whitened" class again contained white, grey and roan mares. This data is presented in table 12.

Table 12. PERCENTAGES OF REGISTERED FOALS PRODUCED BY 5 CLASSES OF STALLIONS AND "NON-WHITENED" OR "WHITENED" MARES

Sire Class	% Reg.	Whitened Mares Total Bred	Whitened Mares Total Reg.	Whitened Mares % Reg.	Non-whitened Mares Total Bred	Non-whitened Mares Total Reg.	Non-whitened Mares % Reg.	X^2
Full Blanket	58	242	145	60	677	387	57	ns
Half Blanket	50	161	88	55	335	158	47	ns
Leopard	47	353	190	54	623	272	44	***
Spotted Blanket	34	285	108	38	737	244	33	ns
Roan Leopard	33	220	86	39	397	117	29	*
All Sires	45			49			43	***

On the whole, "whitened" mares out-produced "non-whitened" mares consistently, averaging a difference of 6%, which was very highly significant. Within classes, however, only with leopard or roan leopard sires were the differences significant. Despite the obvious trend, a larger study would have to be undertaken to determine if the rest of the differences are real.

The following portion of the study was for the purpose of determining the patterns carried by the 5 sire types. Using the same 50 selected sires of the 5 classes, data on the patterns of the progeny of all registered solid mares (of other breeds) are presented in table 13. The dams should have no appaloosa breeding, but since they are mainly

quarter horses, a few might do so. Information on total white and total spots from table 5 (over all mares bred to 110 stallions) was added as a comparison.

Table 13. PERCENTAGES OF DIFFERENT PATTERNS PRODUCED BY 5 CLASSES OF SIRES AND REGISTERED SOLID DAMS

Sire Class	No. App. Foals	% White & Spots	% White Mottled	% Roan Blanket	% Dark Spots	% All Other	From Table 5 % With White	From Table 5 % With Spots
Full blanket	266	55	27	7	2	9	81	57	82	54
Half blanket	67	46	31	4	6	12	78	54	78	50
Leopard	77	57	10	6	8	19	68	66	70	61
Spotted blanket	145	46	19	5	6	24	66	53	72	51
Roan leopard	79	41	22	5	10	23	62	54	68	52
All Sires	634	50	23	6	5	16	74	56	75	55
X^2		***	*	ns	*	***	ns	ns	ns	ns

The roan blanket class alone was without significant differences between sire classes, excepting the total white and total spots groupings.

Apparently the differences between the registered solid mares and all mares are not very large when total white or spots are considered.

The largest difference between the 2 groups was 6%, which would not be significant with classes of this size.

It might be noted that there were no white blanket progeny listed. Approximately 1% of the progeny were white blanket, but were considered white mottled in this portion because of the likelihood of errors in mare descriptions. There was a similar percentage of leopards born, but the same error is assumed, and these are listed in the dark spots class.

The sire's pattern does not appear to be highly heritable, but the tendency to produce certain types of patterns apparently is. Although there weren't significant differences between sires in total white or spots production, there appear to be consistent tendencies for white blanket stallions to produce more white and for leopard stallions to produce more spots.

As a group, all sires tended to produce white & spots, white mottled, and all other offspring in a 2:1:1 ratio. The "all other" group here includes mostly roaned or speckled patterns. The leopards produced more white & spots and less white mottled, while the spotted blanket and roan leopard sires produced less white and more roan or speckles.

Evidence of Sex-Influence and Linkage in Appaloosa Inheritance

Little reliable data were collected on this aspect of appaloosa genetics, but presentation of the evidence available might prove useful at a later date.

The parents of the 128 white blanket and spotted blanket stallions were classified as to whether they were basically solid (S), ie, non-whitened, white (W) or roan (R). Then the stallions were classified either solid or roan. The results of each type of mating and the production of each class are presented in table 14. (S x R) = solid stallion, roan mare.

Table 14. ROAN AND SOLID PROGENY FROM 9 TYPES OF MATINGS BETWEEN 3 CLASSES

Matings	SxS	SxR	SxW	RxS	RxR	RxW	WxS	WxR	WxW	Total No.
No. Solid	21	28	5	14	18	3	2	8	0	99
No. Roan	3	9	5	0	8	2	0	1	1	29
Total	24	37	10	14	26	5	2	9	1	128

Parentage:	Stallions			Mares		
	Solid	Roan	White	Solid	Roan	White
No. Solid (%)	54 (76)	35 (78)	10 (77)	37 (92)	54 (75)	8 (50)
No. Roan (%)	17 (24)	10 (22)	2 (23)	3 (08)	18 (25)	8 (50)
Total	71	45	12	40	72	16

% Roan Parents = 57%
% Roan Progeny = 23%

There is a great discrepancy shown between the percentage of roan parents and the percentage of roan offspring. There is also very little "fit" between the observed frequencies of roan offspring and the expected frequencies. R x R matings should produce 2 or 3 roans to 1 solid

(depending on whether or not homozygous roan is lethal), S x S matings should yield all solid progeny, and S x R matings should give a 1:1 ratio.

There are several possible reasons for the discrepancies found here. One or several might explain the unusual results of table 14:

1. Description errors--S x S should yield only solids, yet 3 such matings produced roans. Since theoretically impossible, these exceptions are assumed due to errors.
2. Immature descriptions--some of these horses were described when foals. As mature horses, more might have been roans.
3. Mistaken color identity--there is a strong possibility that some of the white mares may be roans while white-speckled parents may be listed erroneously as roan.
4. Sex-linkage--since these progeny are exclusively male, they would inherit the color of their dams if sex-linkage were present. Though this tendency shows in the data, agreement is far from complete.
5. Sex-influence--possibly males don't express roaning as completely as do females. Miller (1969) found a tendency toward fringe blanket roaning in stallions and body roaning in mares. Since there was no classification for fringe roaning in this study, this line of reasoning can't be pursued.

Without further information, it is possible that all of these factors are present in these data to some extent.

Data on roaning were also collected on the 8 full blanket stallions used earlier, and their 414 registered offspring. Mares and progeny listed as white or grey were considered roans, since none were leopard. Three stallions and 109 mares were roan. Chi-square tests were done to determine the goodness of fit to the usual ratios of roan to solid. The results are presented in table 15.

Table 15. ROAN AND SOLID (NON-ROAN) OFFSPRING FROM 4 TYPES OF MATINGS

(No.) Matings:	(48) RxR	(139) RxS	(61) SxR	(166) SxS
Roan Offspring	24	19	16	15
Solid Offspring	24	120	45	151
Usual Ratio:	3:1 or 2:1	1:1	1:1	0:1
X^2	*** *	***	***	ns

Hypothesis: RxS = SxR. $X^2 = 4.63*$

Several causative factors may again be involved in the above results. Certainly error is a factor, since 15 roans were produced by solid parents. Neither roan sires nor dams produced the expected proportion of roans, so juvenile descriptions probably play a causative role. Roan mares produced significantly more roan offspring than did roan stallions, which indicates sex-linked inheritance. There is no

evidence of sex-influence, since the roan male:roan female ratio is not abnormal.

Evidence of other types of sex-influenced gene action was given by individual breeders. One owner of a half blanket stallion stated that all male get (24) were born appaloosa, but only 1 female was out of 30 born. Seven more females became appaloosa later. Another owner of a half blanket stallion reported that from a foal crop of 96, all 23 solid females colored, but none of the 6 solid males did. Again, more males than females were born appaloosa. A spotted blanket stallion, when bred to appaloosa mares, produced all appaloosa males and all solid females. The females roaned out later. A leopard stallion owner stated that foals born appaloosa averaged 2 males to 1 female.

SUMMARY AND CONCLUSIONS

According to the stud book data, full blanket stallions produced 20% more registered offspring per mare bred than the average of the half blanket, leopard, spotted blanket, and roan leopard stallions (51.5 vs 31.1%). Confidence limits for the true difference in production were 16.5% and 24.3%. The individual breeder data gave a difference of 18% in appaloosa production per mare bred (77.4 vs 59.4%). Ranked in order of production, full blanket stallions produced 51.5%, half blanket - 36.9%, leopard - 33.9%, spotted blanket - 28.5%, and roan leopard - 24.1% registered get per mare bred. All differences were significant. According to some breeders, full blanket stallions might approach 100% appaloosa production, with around 80% of the foals born appaloosa and the rest developing some pattern in their first few years. There were significant differences in the percentages of total foals born appaloosa, which ranged from 81% from full blanket sires to 42% from roan leopard sires.

Basically roan mares significantly out-produced basically solid (non-whitened) mares (by 6%), especially when bred to leopard or roan leopard stallions (10% more). When bred to full blanket stallions, registered mares of other breeds (solid) out-produced appaloosa mares, but not significantly so (63 vs 58%). Both of these groups produced more registered get than did solid grade mares (43%). The difference was very highly significant, but probably not a "real" one.

Full blanket stallions sired the most offspring with white, while leopards sired the most offspring with spots. These two types sired the highest percentages of white and spots patterns, 49.4 and 51.2% respectively. The genetic differences of the sires were reflected in the patterns of their progeny - all pattern percentages were significantly different. The types of patterns produced by half blanket and spotted blanket stallions were very similar.

When bred to registered solid mares, full blanket stallions still produced the most white and leopards again produced the most spots. All pattern comparisons were again significant except in the % roan blanket class.

The patterns displayed by appaloosa mares when bred to full blanket stallions caused no significant differences in the types of patterns displayed by their progeny except in the roan blanket class. Mares with white produced no roan blankets, while other appaloosa mares did. All types of appaloosa mares produced from 42 - 45% white and spots. Basically roan or non-roan appaloosa mares produced similar patterns, except that basically non-roan mares tended to produce more white.

The pattern types produced by registered solid dams bred to the five classes of stallions were similar to those produced by all mares, except that registered solid dams produced more white & spots and white mottled progeny, less solid white blanket offspring.

From the foregoing it appears that specific patterns are not highly heritable, but only a tendency toward white or spots.

The full blanket, half blanket and leopard stallions were produced by appaloosa parents. However, one fourth of the parents of the leopards were unknown. About half of the parents of spotted blanket and roan leopard stallions were appaloosa. The remainder were either solid or unknown. White and spots was the major pattern among sires of all classes except leopards, where leopards were more common. White speckled was the major pattern among dams of classes except spotted blanket, where solid dams were most common. The parents of leopards tended to have all-over patterns.

According to breeders, more males are born appaloosa and more females roan out before maturity. Much evidence of sex linkage or influence in roaning was encountered, but the data are biased by juvenile descriptions and other error sources, which makes any hypothesis questionable at the present.

Genetic Hypotheses

In light of the present research, as well as those studies preceding it, some tentative genetic hyptheses are now proposed.

A dominant color gene (Ap) is undoubtedly necessary for expression of appaloosa color patterns and even for expression of the minor appaloosa characteristics such as striped hooves, white sclera, and mottled skin. The (Ap) gene allows the expression of dark spots and white areas when heterozygous, but inhibits dark spotting within the white areas over the body and hips when homozygous.

An extension gene (E^{ap}) causes the extension of white through the coat in the presence of genes that prevent pigment formation. When heterozygous over-all white mottling or speckles may occur. When homozygous a white phenotype is expressed.

A pair of recessive (ww) genes are possibly necessary before any white can be expressed in the phenotype. A mutant (W) gene possibly restores normal pigment formation.

It is proposed that there are 3 major pigment-preventing genes active in appaloosa pattern formation. These genes may be termed mottled (M), blanket (B) and silver (Sl). At least one of these genes must be present, along with the (Ap) and (ww) genes, in order for white areas to be present in the coat. The (M) gene probably causes minor white spotting in the sacral area in its heterozygous form. The (B) gene probably causes more extensive white mottling over the sacral area

when heterozygous. The (Sl) gene causes a frosty blanket in the heterozygous state. Any 2 or all 3 of these genes can act synergistically to produce spotted blankets of varying sizes.

After examination of the pattern ratios (basically 1:2:1 in appaloosa progeny), it is proposed that these 3 genes are possibly lethal in the homozygous state. This type of lethal would express itself mainly as a "missed" breeding, much as it does in white (WW) and roan (RR) horses.

In addition to the spotted blanket (where the pigment cells are "clumped" within areas otherwise devoid of pigment), dark spots may also be caused by a spotting gene (ss) which is probably recessive in nature.

The roan (R^{ap}) gene in appaloosas is probably not lethal when homozygous. Though probably located at the same locus as the (R) gene, it appears to be a separate allele. In the homozygous form it may possibly cause the varnished roan and other nearly-white phenotypes. In heterozygous form it may or may not be expressed in the juvenile.

There are undoubtedly several more modifying genes that cause minor variations in pattern in conjunction with the major genes discussed.

Though the actions of most of the genes discussed are obviously sex-influenced, insufficient evidence is available for any proposed explanation at present.

Several of the proposed genotypes and the resulting phenotypes follow in tables 16 and 17.

Table 16. A PROPOSED MODEL OF APPALOOSA PATTERN INHERITANCE

Proposed Allele	Resulting Phenotypes		
	Homozygous recessive	Heterozygous	Homozygous dominant
Ap(Appal.)	(apap)no appaloosa characteristics	(Apap)allows appaloosa patterns	(ApAp)allows white areas, inhibits all spots over sacral area
W(White)	(ww)allows white expression	(Ww)no white expressed	(WW)no white expressed
S(Spots)	(ss)causes dark spots	(Ss)causes no spots	(SS)causes no spots
M(Mottled)	(mm)no white area	(Mm)minor white spotting	(MM)possibly lethal?
B(Blanket)	(bb)no white area	(Bb)white mottling	(BB)possibly lethal?
Sl(Silver)	(slsl)no white area	(Slsl)roan blanket	(SlSl)possibly lethal?
R^{ap}(Roan)	($r^{ap}r^{ap}$)solid color	($R^{ap}r^{ap}$)variations of progressive roaning	($R^{ap}R^{ap}$)varnish roan or nearly white
E^{ap}(Extension	($e^{ap}e^{ap}$)no extension of white	($E^{ap}e^{ap}$)extended white mottling or speckles	($E^{ap}E^{ap}$)extended white (leopard,white)

Table 17. SOME GENOTYPES AND RESULTING PHENOTYPES

Genotype	Phenotype
(all have ww ss $e^{ap}e^{ap}$)	
ApAp Mm Bb Sls1	full blanket
ApAp Mm Bb sls1 (or B S1, or M S1)	half blanket
Apap Mm Bb Sls1	spotted blanket, large spots
Apap Mm Bb sls1 (or B S1, or M S1)	spotted blanket, large spots
Apap Mm bb sls1	white spots over hips
Apap mm Bb sls1	white mottled over hips
Apap mm bb Sls1	spotted roan blanket
(all have ww ss $E^{ap}e^{ap}$)	
ApAp Mm Bb Sls1	full blanket, white flakes over body
Apap Mm Bb Sls1	spotted blanket, white flakes over body
Apap mm bb Sls1	white speckles and dark spots over body
(all have ww ss $E^{ap}E^{ap}$)	
ApAp Mm Bb Sls1	white over entire body, spots over body except sacral area
Apap Mm Bb Sls1	white and spots over entire body (leopard)
(with Ww Ss)	
Apap Mm Bb Sls1 $E^{ap}e^{ap}$ (or any other genotype)	minor appaloosa characteristics, no pattern
Apap $R^{ap}R^{ap}$(any M,B,S1)Ww ss E^{ap}	roan leopard
Apap $R^{ap}R^{ap}$ mm bb sls1 ww ss $E^{ap}E^{ap}$	roan leopard

LITERATURE CITED

Anderson, W.S. 1914. The inheritance of coat color in horses. Bull.#180. Ken. Agr. Exp. Sta.

Carr, Gene. 1972. "Few-spotted" leopards - a possible key to high color production. App. News 6:18.

Castle, W.E. 1940. The genetics of coat color in horses. Jour. Hered. 31:127.

Castle, W.E. 1946. Genetics of the palomino horse. Jour. Hered. 37:35.

Castle, W.E. 1948. ABC of color inheritance in horses. Genet. 33:22.

Castle, W.E. 1951a. Genetics of the color varieties of horses. Jour. Hered. 42:297.

Castle, W.E. 1951b. Dominant and recessive black in mammals. Jour. Hered. 42:48.

Castle, W.E. 1954. Coat color inheritance in horses and in other mammals. Genet. 39:35.

Castle, W.E. 1961. Genetics of the claybank dun horse. Jour. Hered. 52:121.

Castle, W.E. and King, F.L. 1951. New evidence on the genetics of the palomino horse. Jour. Hered. 42:61.

Castle, W.E. and Singleton, W.R. 1960. Genetics of the "brown" horse. Jour. Hered. 51:127.

Castle, W.E. and Singleton, W.R. 1961. The palomino horse. Genet. 46:1143.

Domanski, A.J. and Prawochenski, R.T. 1948. Dun coat color in horses, Jour. Hered. 39:367.

Hare, M.P. 1969. Accent on spots. App. News 6:34.

Jones, W.E. 1971. Genetics of the Horse. Edwards Bros. Inc. Ann Arbor.

Klemola, V. 1933. The "pied" and "splashed white" patterns in horses and ponies. Jour. Hered. 24:65.

Lasley, J.F. 1969. Coat color inheritance in horses. Q.H. Jour. 6:39.

Miller, R.W. 1969. Appaloosa Coat Color Inheritance. App. Horse Club, Inc. Moscow.

Singleton, W.R. and Bond, Q.C. 1966. A allele necessary for dilute coat color in horses. Jour. Hered. 57:75.

Smith, A.T. 1969. Morgan coat color genetics. The Morgan Horse 8:14.

Stell, R.G.D. and Torrie, J.H. 1960. Principles and Procedures of Statistics. McGraw-Hill. New York.

Wagner, P. 1969. Appaloosa gene expression. App. News 10:30.

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