Inheritance of the White and Pied Plumage Color Patterns in the Indian Peafowl (*Pavo cristatus*)

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The pied, dark pied, white, and blue white-flight plumage color phenotypes are described, and their relationships to each other explained. Crosses among and between these phenotypes and the wild-type blue indicate that a single autosomal locus is responsible for all of these phenotypes. The white mutant allele (*W*) when homozygous produces an all-white plumage. This allele is shown to be a weak incomplete dominant with about 60% penetrance when heterozygous with the wild-type allele (w^+), and this combination produces the blue white-flight phenotype. The pied phenotype does not breed true but produces whites, pieds, and dark pieds in a 1:2:1 ratio. Dark pieds breed true with about 79% penetrance, and when bred to whites produce all pieds. Thus, pieds are heterozygous for two mutant alleles (W/w^{wd}). In this three-allelic series, the white allele (*W*) is the most dominant and the dark pied allele (w^{wd}) the most recessive ($W > w^+ > w^{wd}$).

The Indian Peafowl (*Pavo cristatus*), a truly regal bird native to India and Ceylon, has been domesticated by man for a considerable length of time, as is indicated by early biblical references (I Kings 10:22 and II Chronicles 9:21). The peafowl is still a popular domesticated bird, in part due to several feather color mutations that have appeared and been maintained over the years. Even though some of these color variants have been popular for well over 100 years, only recently have any of them been studied extensively to determine their genetic basis.

A companion article to this report (Somes and Burger 1991) described the genetic basis of the blue and the black-shouldered plumage color phenotypes, as well as two more recent plumage color mutant phenotypes, the cameo and oaten. In this article we cover the inherited basis of the popular white and pied phenotypes and two lesser known phenotypes, blue white-flight (wf) and dark pied. The white and pied peafowl colors have been around for quite some time and were probably the first and second color mutant types in the peafowl. Darwin in 1868 mentioned a report by Dixon dated 1850 in which he spoke of a large flock of blue, white, and pied peafowl. Thus, they were common 140 years ago and probably for some time prior to that.

Comments in the lay literature concerning the inheritance of the white and pied phenotypes are quite confusing and, in some cases, actually contradictory. White is described by some as an incomplete dominant and by others as an incomplete recessive. Pieds are said by some to breed true, while others say that they do not. When whites are bred to blues, some say the offspring are pieds. Others say the offspring are a phenotype known as blue white-flights, which is generally a blue wild-type bird with some white primary flight feathers, a phenotype distinctively different from the pied phenotype. The data reported here, which has only been briefly mentioned elsewhere (Somes and Burger 1990), clear up this confusion and show how these various conclusions could easily have developed.

Materials and Methods

Descriptions

Blue. Blue is the genetic wild type for the *cristatus* peafowl species, whereas all other phenotypes are caused by mutant genes. Blue chicks are pale buffy brown with a dark brown nape and hind neck, and a deep rufous back. The sexes are very difficult to determine at this age, but female chicks tend to have darker tan tips on their secondaries than do male chicks whose secondaries are more of a cream color. As adults, peacocks have a bright glossy metallic blue head, and the upper neck and upper breast are silky blue with green and

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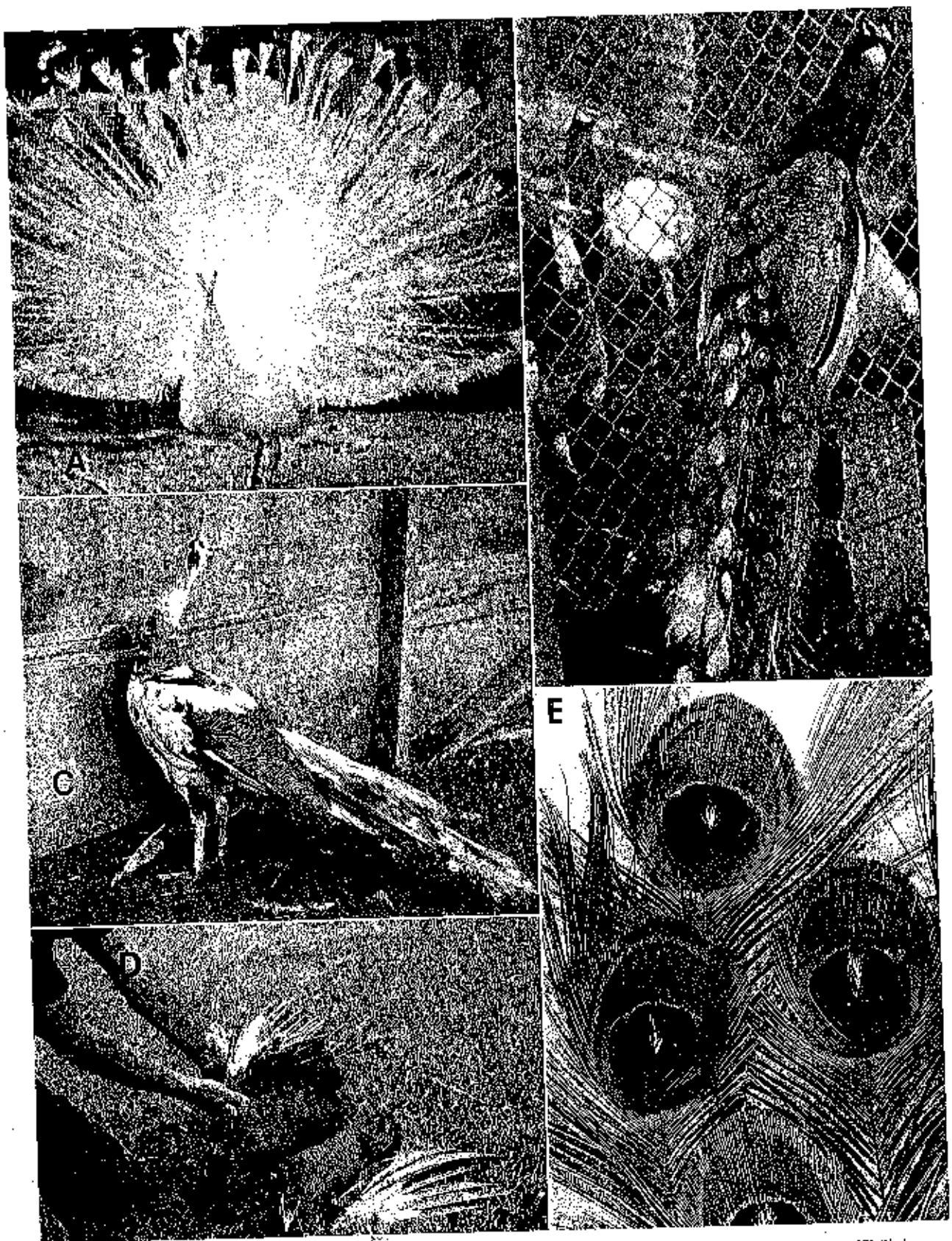

Figure 1. Peafowl color phenotypes: (**A**) White peacock, W/W; (B) Pied peacock with a limited amount of white showing, W/w^{wh}; (C) Pied peacock with a large amount of white showing, W/w^{wh}; (D) Dark pied peacock with white flights and coverts, w^{wh}/w^{wh}; (E) White centers on the train "eyes" of a dark pied peacock, w^{wh}/w^{wh}.

purplish shades. The lower breast, flank, and abdomen are black and dark glossy green, while thighs are pale buff. The back at the base of the neck is golden changing to metallic light green with each feather having a brown v-shaped patch narrowly edged with black. Shoulders, lesser wing coverts, and tertiaries are buffish-white and irregularly mottled and barred with black. Outer wing coverts and secondaries are blue-black, while the primaries are cinnamon. The train runs from coppery-bronze through gold to a dark green. The "eyes" of the train consist of a deep blue patch bordered by first a brilliant blue and then a coppery-brown ring. These rings are, in turn, encircled by a narrow ring of golden-green and, lastly, a lilac ring.

Blue peahens are much less colorful. The head and upper neck are chestnut-brown, while the lower neck, upper back, and upper breast are glossy metallic green. The lower breast is dark brown, while the abdomen is pale buff and the thighs and back are earthy brown. Shoulders, wing coverts, and secondaries are also earthy brown with paler brown markings. Primaries and rectrices are blackish brown.

White. White chicks are a cream-yellow color. As adults the white peafowl of both sexes are totally white (Figure 1A) and their eyes are blue, whereas the wild-type eye color is dark brown/black. The "eye" rings on the male's tail train, although totally white, can be discerned due to the normal feather structure differences associated with the feather eye area.

Pied. Pied chicks are the same color as blue chicks with cream-yellow splashes of varying sizes on the down feathers. Adult pieds are of the blue coloration except that they have splashes of white feathers in those areas where they show cream-yellow down as chicks. The white splashed areas can vary from small limited areas (Figure 1B) to extensive areas of the bird's surface (Figure 1C).

Dark pied. The dark pied chick may show a variety of phenotypes. A few chicks are similar to the blue chick in color, but the majority of them have some white showing, either as white coverts or white flights, or both, or a white "chuck" under the chin in addition to white coverts and flights. The adult dark pied phenotype is basically the same as the blue with a very limited amount of white showing. The primaries, coverts, and a few surrounding wing feathers are generally white (Figure 1D). Some males have a small white spot in the center of some of the train eyes (Figure 1F), and a few might also have a small spot on the breast.

Blue white-flight. The blue white-flight chick cannot be distinguished from either the blue or dark pied chick as the wf chick is capable of expressing the same five phenotypes as described for the dark pied chick. The adults of this phenotype appear as blues with pigment missing only from the flights or coverts or both.

Matings

The data presented in this paper were collected from within the peafowl collection of one of the authors (R.E.B.) over the time span of 1977 to 1991 and represent 91 individual matings. For the most part these matings were not set up to answer specific genetic questions; but, because of the extensive numbers and kinds of matings made and the detailed records kept, an analysis of the data does, in fact, answer genetic questions about these mutant color traits.

Chicks were classified for color phenotype at time of hatch, and these classifications were verified at an older age when the birds had grown their feathers. All birds were classified into one of four phenotypes—blue, white, pied, and wf. The wf classification included all of the four variants described under the dark pied phenotype above.

Results

White and Blue Crosses

Thirty of the matings involved the white and blue wild-type phenotypes in five typical genetic crosses. These data are presented in Table 1. White peafowl were shown to breed true, thus indicating that this phenotype was homozygous. When white birds were reciprocally bred to the wild-type blue, two-thirds of the F_1's were wf, and one-third were blue with no differences seen between reciprocal matings. These data were significantly different from the expectation of all F_1's being of the same phenotype and, thus, they indicated that the all-white phenotype was caused by homozygosity of an incompletely dominant gene with incomplete penetrance. The F_2 generation and one of the backcrosses were also complicated by this reduction in penetrance, and so these data were also significantly different from data expected if only wf was the F_1 type. In the lower half of Table 1 these same data have been modified by grouping together the wf and blue phenotypes, realizing that some of the blues are wild type while others are really the F_1 type. This modification eliminated errors in classification due to the reduced penetrance. When the wf and blue phenotypes are combined in this way, there are no significant differences in the data of any of these crosses. The data are thus consistent with *W* being an incomplete dominant. It was also noted that no pied individuals appeared from any of these crosses.

Pied and Blue Crosses

Fourteen individual matings were made involving the pied and blue wild-type phenotypes in four crosses. These data are presented in Table 2. The pied × pied matings produced four phenotypes. This showed that the pied phenotype was genetically heterozygous producing white, pied, blue, and what at first appeared to be wf. With four phenotypes resulting from this cross, these results were significantly different from the 1:2:1 ratio that would be expected from a heterozygous mating such as this. When these wf types from the pied × pied matings were interbred (cross no. 2), the results indicated that they were homozygous for their genotype, but with a slight reduction in penetrance. Because these wf-like birds bred true, they were obviously different from the white × blue F_1 wf, and so these new wf-like types were named "dark pied." When pied peafowl were mated to wild-type blue peafowl and to dark pied peafowl, the expected 1:1 ratios were obtained. Because penetrance was not complete for the dark pied phenotype, with most appearing similar to wf but a few as blue, the wf and blue phenotypes were combined and reanalyzed. This resulted in removal of significant differences from all of the crosses. These modified data are presented in the lower half of Table 2. These data showed that the dark pied phenotype resulted from homozygosity of a single gene (w^{pd}) that was allelic to *W* and recessive to it. When these two alleles were in the genotype together, the resulting plumage phenotype was the pied pattern.

White and Pied Crosses

The remaining 47 individual matings, consisting of five crosses, further verified the allelism between the genes responsible for the white and the dark pied phenotypes. These additional data are presented in Table 3. The data from the last cross in the table also showed that the wild-type allele w^+ was dominant to w^{pd}, thus indicating

Table 1. Crosses between white and blue peafowl

Cross	No. of matings	No. of progeny phenotypes: White	Pied	Wf[a]	Blue	Total	Ratio	χ^2	P
white × white (W/W) (W/W)	11	52	—	—	—	52	all	0.00	1.00
white × blue (W/W) (w^1/w^+)	5	—	—	20	10	30	all	—	<.01[b]
F_1 (wf) × F_1 (wf) (W/w^+) (W/w^1)	5	9	—	10	19	38	1:2:1	13.79	<.01[b]
white × F_1 (wf) (W/W) (W/w^+)	5	16	—	11	9	36	1:1	—	<.01[b]
blue × F_1 (wf) (w^1/w^+) (W/w^+)	4	—	—	5	9	14	1:1	1.14	>.25
Data modified for reduced penetrance[c]									
white × white (W/W) (W/W)	11	52	—		—	52	all	0.00	1.00
white × blue (W/W) (w^1/w^+)	5	—	—		30	30	all	0.00	1.00
F_1 (wf) × F_1 (wf) (W/w^1) (W/w^+)	5	9	—		29	38	1:3	0.04	>.75
white × F_1 (wf) (W/W) (W/w^+)	5	16	—		20	36	1:1	0.44	0.50
blue × F_1 (wf) (w^1/w^+) (W/w^+)	4	—	—		14	14	all	0.00	1.00

[a] Wf — blue white-flights.
[b] Significant difference.
[c] Wf and blue phenotypes combined.

that these three alleles had the following relationship to each other: $W > w^+ > w^{me}$. These data are also presented in the modified form (wf and blue phenotypes combined) at the bottom of this table, with the modification eliminating the significance in the segregation that was present in cross no. 4.

Discussion

Our previous article (Somes and Burger 1991), the first scientific paper ever on the inheritance of peafowl plumage colors, dealt with what were probably the third and fourth plumage color mutations in this species. Although the peafowl has been domesticated for quite some time, its number of mutant color genes is quite limited, and studies prior to that paper and this one were nonexistent. The previous reported two color patterns (Somes and Burger 1991) were each unique in that one (cameo) was inherited as a sex-linked recessive which reduced the otherwise exquisitely colored peafowl to a tan coloration. The other (black-shouldered), an autosomal recessive, exhibited extreme sexual dimorphism in the adult plumage. In the present study involving two mutants of long standing (white and pied), the inheritance and phenotypes are again unique. These two phenotypes result from two mutant alleles at the same locus. It would be impossible at this late date to know which of these alleles mutated first. When both mutated alleles were present and they combined, the result was the pied pattern. The beauty of the pied pattern

Table 2. Crosses between pied and blue peafowl

Cross	No. of matings	No. of progeny phenotypes: White	Pied	Wf[a]	Blue	Total	Ratio	χ^2	P
pied × pied (W/w^{me}) (W/w^{me})	6	14	24	4	5	47	1:2:1	—	<.01[b]
dk pied × dk pied (w^{me}/w^{me}) (w^{me}/w^{me})	5	—	—	12	1	13	all	—	<.01[b]
pied × blue (W/w^{me}) (w^1/w^+)	2	—	—	3	7	10	1:1	1.60	>.10
pied × dk pied (W/w^{me}) (w^{me}/w^{me})	2	—	10	7	—	17	1:1	0.53	>.25
Data modified for reduced penetrance[c]									
pied × pied (W/w^{me}) (W/w^{me})	6	14	24		9	47	1:2:1	1.09	>.50
dk pied × dk pied (w^{me}/w^{me}) (w^{me}/w^{me})	5	—	—		13	13	all	0.00	1.00
pied × blue (W/w^{me}) (w^1/w^+)	2	—	—		10	10	all	0.00	1.00
pied × dk pied (W/w^{me}) (w^{me}/w^{me})	2	—	10		7	17	1:1	0.53	>.25

[a] Wf — blue white-flights.
[b] Significant difference.
[c] Wf and blue phenotypes combined.

Table 3. Crosses between pied and white peafowl

Cross	No. of matings	No. of progeny phenotypes					Ratio	χ^2	P
		White	Pied	Wf[a]	Blue	Total			
white × pied (W/W) (W/w^{pd})	30	88	79	—	—	167	1:1	0.48	>.25
white × dk pied (W/W) (w^{pd}/w^{pd})	5	—	30	—	—	30	all	0.00	1.00
pied × F_1 wf (W/w^{pd}) (W/w^+)	3	2	7	8	5	22	1:3:1:1	3.82	>.25
white × F_1 dk pd (W/W) (w^{pd}/w^+)	2		3	2	5	10	1:1	- -	<.01[b]
F_1 wf × F_1 dk pd (W/w^+) (w^{pd}/w^+)	7	—	13	13	38	64	1:1:2	2.25	>.25
Data modified for reduced penetrance[c]									
white × pied (W/W) (W/w^{pd})	30	88	79		—	167	1:1	0.48	>.25
white × dk pied (W/W) (w^{pd}/w^{pd})	5		30		—	30	all	0.00	1.00
pied × F_1 wf (W/w^{pd}) (W/w^+)	3	2	7		13	22	1:3:2	3.00	>.10
white × F_1 dk pd (W/W) (w^{pd}/w^+)	2	—	3		7	10	1:1	1.60	>.10
F_1 wf × F_1 dk pd (W/w^+) (w^{pd}/w^+)	7	—	13		51	64	1:3	0.75	>.25

[a] Wf = blue white-flights; dk pd = dark pied.
[b] Significant difference
[c] Wf and blue phenotypes combined.

would then have ensured the conservation of the w^{pd} allele. The w^{pd} allele by itself produces what would probably have been considered an unattractive blue pattern and, thus, by itself would not have led to its conservation.

Figure 2 graphically shows the interaction of the three alleles at this locus, which results in six genotypes. These genotypes are shown in Table 4 with their corresponding phenotypes. The wild-type allele w^+ allows for full pigmentation, while each of the mutant alleles allows for increasing amounts of pigment inhibition. Pigment inhibition in each case is of the spotting type; thus, this is not a case of dilution. The w^{pd} allele's influence by itself is quite limited, whereas the W allele on the other hand can influence rather large areas. The weak influence of the w^{pd} allele when homozygous has only a slight effect on most individuals (dark pied) and a penetrance that averages about 79%. When this allele is heterozygous with the wild-type allele (w^{pd}/w^+), it is completely recessive. The W allele, on the other hand, has a much stronger pigment inhibition effect; when homozygous, it exhibits complete penetrance and produces an all-white bird. However, its effects are around the threshold of response when it is heterozygous with w^+. Background genes must be involved such that only about 60% of individuals heterozygous for W and w^+ show a slight pigment reduction (the blue white-flight phenotype). When both of these mutant alleles are combined in the same individual (W/w^{pd}), their additive effects result in the pied pattern. Here, also, the pied pattern can vary considerably depending on background genes.

Because of reduced penetrance in several genotype combinations (W/w^+ and w^{pd}/w^{pd}) it was not always possible to distinguish between the w^+/w^+, w^{pd}/w^+, W/w^+, and w^{pd}/w^{pd} genotypes when more than one of these were present among the offspring of a mating, thus the wf and blue phenotypes had to be combined in the sta-

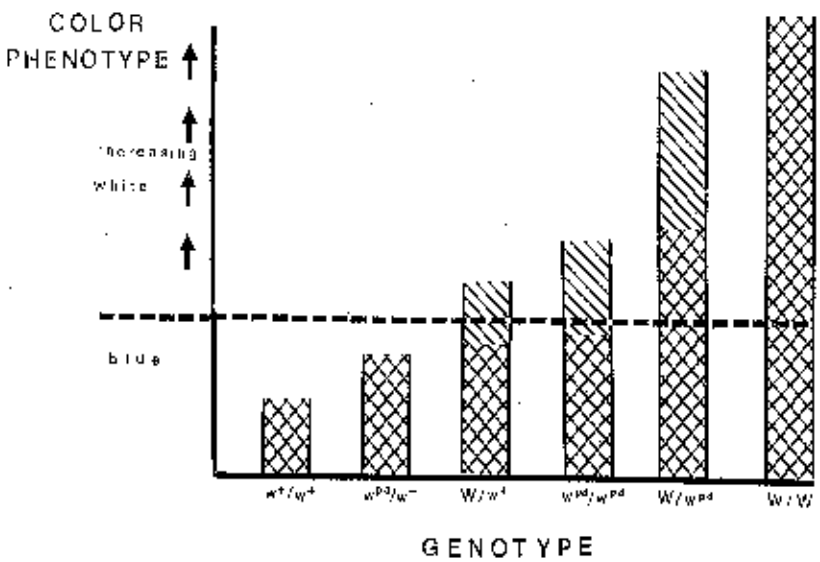

Figure 2. Graphic view of the interaction between the three alleles at this locus and feather pigmentation. The height of the crosshatched bars indicates increasing potential for white, while the diagonal portions indicate the range over which that genotype produces a varying phenotype.

Table 4. Genotypes, phenotypes, and penetrance in peafowl

Genotype	Phenotype	Penetrance (%)
W/W	White	100
W/w^{pd}	Pied	100
w^{pd}/w^{pd}	Dark pied/blue	79/21
W/w^+	Blue white-flight/blue	60/40
w^{pd}/w^-	Blue	100
w^+/w^+	Blue	100

tistical analyses to eliminate possible classification errors. It is easy to see how people in the past came up with different and in some cases conflicting results when working with these phenotypes. When one crosses white peafowl with blue "wild-type" in a flock containing both the *W* and w^{ml} alleles, there is the possibility that the blue "wild-type" could in fact be any one of four different genotypes (w^+/w^+, W/w^+, w^{ml}/w^{ml}, or w^{ml}/w). Needless to say, the results would be quite different in each case and very confusing to the person who was unaware of the makeup of this locus and the imperfect penetrance associated with its alleles. We hope this paper will aid in a better understanding of the workings of this locus.

Pied plumage patterns in poultry species (Crawford 1990) and white-spotting or piebaldness, as it is called when referring to coat colors in mammals (Searle 1968), are quite abundant. Some of these phenotypes are produced by recessive genes and others by dominant genes, but very few have the same type of inheritance as seen in this study (interaction of two mutant alleles at the same locus). Also, many of these examples in other species are associated with adverse pleiotropic effects (Searle 1968) that have not been seen to date in the peafowl.

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