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Francis F. Minvielle, David Gourichon, Jean Louis Monvoisin. Effects of two-locus combinations, using the “ roux ”, “ lavender ” and “ beige ” mutations, on plumage color of Japanese quail. *Journal of Heredity*, 2003, 94 (6), pp.517-522. hal-02679361

HAL Id: hal-02679361

<https://hal.inrae.fr/hal-02679361>

Submitted on 31 May 2020

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Effects of Two-Locus Combinations, Using the Roux, Lavender, and Beige Mutations, on Plumage Color of Japanese Quail

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Abstract

The interactions between the effects of three plumage color mutations taken two-by-two (sex-linked recessive roux, autosomal recessive lavender, and autosomal dominant beige) were studied in Japanese quail by producing a total of 121 F₁ and 1118 F₂ quail from the three pure stocks. Three new plumage colors were obtained in F₂ quail: roux-diluted beige, cream, and lavender-diluted beige. Two of them, roux-diluted beige (from the roux and beige mutations) and cream (from the roux and lavender mutations) corresponded to double homozygotes or hemizygous birds, and could therefore be used to tag a quail line. On the other hand, an F₃ from F₂ birds with lavender-diluted beige plumage was necessary to show that quail with this plumage color were homozygous for the lavender mutation, but were either homozygous or heterozygous for the beige gene. In all three F₂s, observed segregation of plumage colors fit simple two-locus Mendelian inheritance.

Plumage color mutations of Japanese quail have been described extensively in the recent past (Somes 1988) and additional reports on several new mutations have been published since then (e.g., Ito and Tsudzuki 1994; Tsudzuki et al. 1993), but interactions of plumage color genes at different loci have been studied only for a few mutations (Cheng and Kimura 1990). One of the most striking interactions is between the recessive white mutation and the extended brown locus, with the tuxedo plumage color (dark brown back and white belly) of quail which are homozygous for the recessive white mutation and heterozygous at the other locus (Chikamune and Kanai 1978; Truax and Johnson 1979).

From a genetic standpoint, systematic study of epistasis between color mutations might contribute new phenotypic evidence for unknown underlying genetic interactions which could then be further analyzed with modern molecular tools to search for the corresponding causal mechanisms. From a practical standpoint, obtaining new plumage colors or patterns from combining different mutations into the same stock will help tag commercial quail lines visibly, to help the breeder manage lines or the

consumer identify a specific origin. Single mutations are being used already for those purposes. For example, the recessive white and fawn mutations were fixed, respectively, in the English White and Australian Fawn commercial quail strains (Cheng and Kimura 1990), and the roux mutation was introgressed into a broiler quail strain (Minvielle et al. 1999).

In our Nouzilly experimental unit, we maintain a dozen plumage color variants, three of which, the roux, beige, and lavender mutations, have a special interest. Recently we (Minvielle et al. 2000) showed that the roux sex-linked recessive mutation belonged to the brown locus *BR**, and that it could be used commercially for early sexing of cross-breds (Minvielle et al. 1999). From the description of the Australian Fawn quail (Somes 1984) and the mode of inheritance of the fawn mutation (Nichols and Cheng 1988), it is likely that our dominant beige mutation belongs to the same locus as the fawn mutation which is common in commercial stocks. Finally, by producing lavender/bleu chicken-quail hybrids (Minvielle et al. 2002), we have shown that the rare bleu Japanese quail was homozygous for a gene, *LAV*^L*, which is homologous to the autosomal recessive

lavender mutation reported in the chicken (Brumbaugh et al. 1972). Because the beige, fawn-like mutation was already present in commercial stocks, because the roux gene might become widely used for sexing, and since little was known about the lavender mutation in quail, we undertook to study the interactions between these three genes and to describe the corresponding plumage colors in an F_1 , F_2 experiment with the three purebred stocks taken two at a time.

Materials and Methods

For all three mutations studied in the present work, each mutant stock kept at the Unité Expérimentale de Génétique Avicole, INRA Nouzilly, was fixed for only one color mutation, and it was homozygous for the wild-type allele at the other two plumage color loci. The beige stock (female plumage in Figure 1, top left) has not been described previously. Before this work it was crossed reciprocally to wild-type stock every 10 generations to avoid the build up of inbreeding. Each time, all F_1 progeny and three-quarters of F_2 quail had beige plumage, which showed the mutation was autosomal and dominant over the wild-type allele. Because the plumage color (Cheng K, personal communication) and the mode of inheritance of the beige mutation were quite similar to those reported for the fawn mutation, we supposed that it belonged to the fawn locus, and we named it *FAW*BE* in this article. Symbols used for the roux and lavender genes were, respectively, *BR*R* and *LAV*L* (Crittenden et al. 1996).

In a single hatch following a 3-week egg collection, F_1 quail for experiments 1, 2, and 3 were obtained by crossing roux males and beige females (experiment 1), roux males and lavender females (experiment 2), lavender males and beige females and reciprocally (experiment 3). There were, respectively, five, five, three, and three single-pair matings. Each F_1 bird was identified at hatching. At 1 month of age, adult plumage color and sex were recorded. Next, F_2 birds were produced for each experiment in three successive hatches from single-pair matings of F_1 quail. Full-sib mating was prohibited. There were 12, 11, and 12 F_2 full-sib families produced, respectively, in experiment 1 (interaction of the roux and beige mutations), experiment 2 (interaction of the roux and lavender mutations), and experiment 3 (interaction of the lavender and beige mutations). Down color was recorded at hatching, and four types of color were found in each F_2 . At 1 month of age adult plumage color was recorded, and the match between the assignment to a color class at hatching and the plumage color at 1 month was perfect. The frequencies of the observed phenotypes were compared to expectations under two-locus genetic models of inheritance by chi-square analysis. In experiment 2 and experiment 3, an F_3 generation was produced. For experiment 2, it was obtained by six single-pair matings of 12 F_2 birds which had a new, cream

plumage color (Figure 1, bottom left). For experiment 3, the F_3 generation was produced by 12 single-pair matings of 19 F_2 birds (7 males and 12 females) chosen among those which exhibited another, new plumage color (Figure 1, bottom right), and later, the 19 F_2 parents were genotyped at the beige locus by performing a test cross with the pure lavender stock.

Results and Discussion

Experiment 1: Interaction Between the Roux and Beige Mutations

All 19 F_1 males had the beige plumage color and all 20 F_1 females had a roux-diluted beige plumage color (Figure 1, top center) without the usual dark spots found in all beige quail (Figure 1, top left). No bird with a roux plumage (Figure 1, top right) was obtained. The genotype of the F_1 was *BR*N/BR*R*; *FAW*N/FAW*BE* for males, and *BR*R/W*; *FAW*N/FAW*BE* for females, where *W* stands for the sex chromosome in females and **N* stands for a wild-type allele. It appears then that the roux mutation in the hemizygous female was effective in diluting the dark dots on feathers in the presence of a single dose of the beige mutation, but that it could not induce the typical roux phenotype. Consequently one might suppose that *BR*R/BR*R*; *FAW*N/FAW*BE* males should also have a similar plumage color, but the phenotype resulting from beige homozygotes could only be inferred from analyzing the F_2 . Incidentally, results from the F_1 showed also that crossing roux and beige quail stock produced autosex progeny, but the color difference between males and females was less obvious than with the cross between roux and wild-type quail (Minvielle et al. 2000).

The segregation of plumage color among the 416 F_2 progeny (hatching rate 85%) is shown in Table 1, and four colors were observed: wild-type, roux, beige, and roux-diluted beige (beige without dark dots). Two hypotheses were tested regarding the beige homozygotes, and the hypothesis that the roux mutation diluted the dots in the plumage of both homozygous and heterozygous beige individuals (hypothesis A) could not be falsified: there was indeed some interaction between the effects of the two genes when the quail were homozygous or hemizygous for the roux mutation.

Experiment 2: Interaction Between the Roux and Lavender Mutations

All 28 F_1 males had the wild-type plumage color and all 26 F_1 females had the roux plumage color (Figure 1, top right). The genotype of the F_1 was *BR*N/BR*R*; *LAV*N/LAV*L* for males, and *BR*R/W*; *LAV*N/LAV*L* for females. In this experiment again, crossing roux and lavender quail produced autosex progeny.



Figure 1. Plumage colors of Japanese quail. **Top** (left to right): beige, rous-diluted beige, rous. **Bottom** (left to right): cream, lavender, lavender-diluted beige.

Table 1. Segregation of plumage color in F₂ from roux and beige quail (experiment 1)

Plumage color and genotypes under hypotheses A and B	Observed	Expected ratio	Expected number
Wild-type			
<i>BR*N/BR*R</i> ; <i>FAW*N/FAW*N</i> and <i>BR*N/W</i> ; <i>FAW*N/FAW*N</i>	62	A and B: 1/8	52
Roux			
<i>BR*R/BR*R</i> ; <i>FAW*N/FAW*N</i> and <i>BR*R/W</i> ; <i>FAW*N/FAW*N</i>	58	A and B: 1/8	52
Beige			
<i>BR*N/BR*R</i> ; <i>FAW*BE/FAW*BE</i> and <i>BR*N/BR*R</i> ; <i>FAW*N/FAW*BE</i> and <i>BR*N/W</i> ; <i>FAW*BE/FAW*BE</i> and <i>BR*N/W</i> ; <i>FAW*N/FAW*BE</i>	155	A: 3/8	156
<i>BR*N/BR*R</i> ; <i>FAW*BE/FAW*BE</i> and <i>BR*N/BR*R</i> ; <i>FAW*N/FAW*BE</i> and <i>BR*N/W</i> ; <i>FAW*BE/FAW*BE</i> and <i>BR*N/W</i> ; <i>FAW*N/FAW*BE</i> and <i>BR*R/BR*R</i> ; <i>FAW*BE/FAW*BE</i> and <i>BR*R/W</i> ; <i>FAW*BE/FAW*BE</i>		B: 4/8	208
Roux-diluted beige			
<i>BR*R/BR*R</i> ; <i>FAW*BE/FAW*BE</i> and <i>BR*R/BR*R</i> ; <i>FAW*N/FAW*BE</i> and <i>BR*R/W</i> ; <i>FAW*BE/FAW*BE</i> and <i>BR*R/W</i> ; <i>FAW*N/FAW*BE</i>	141	A: 3/8	156
<i>BR*R/BR*R</i> ; <i>FAW*N/FAW*BE</i> and <i>BR*R/W</i> ; <i>FAW*N/FAW*BE</i>		B: 2/8	104

Hypothesis A: the roux mutation dilutes the dark dots in the plumage of both homozygous and heterozygous beige individuals. Chi-square statistics = 4.1 < chi-square (3, 0.01) = 11.3.

Hypothesis B: the roux mutation only dilutes the dark dots in the plumage of heterozygous beige individuals. Chi-square statistics = 29.3 > chi-square (3, 0.01) = 11.3.

The segregation of plumage color among the 315 F₂ progeny (hatching rate 74%) is shown in Table 2, and four colors were observed: wild-type, roux, lavender (Figure 1, bottom center), and cream (Figure 1, bottom left), which is a new plumage color. Proportions obtained were in agreement with the hypothesis that both mutations were fixed in cream quail.

This was confirmed by the observation of 52 F₃ progeny from F₂ cream quail, which all showed the cream plumage. To a certain extent, the roux gene is epistatic to the lavender one because cream quail had a very pale roux plumage due to the lavender mutation, which further diluted the wild-type color already diluted by the roux mutation, but the typical slaty color of the lavender mutation (Minvielle et al. 2002) did not show in cream birds except for slight undertones (Figure 1, bottom left).

Experiment 3: Interaction Between the Lavender and Beige Mutations

All 28 F₁ quail had the same beige plumage, and the genotype of the F₁ males and females was *LAV*N/LAV*L*; *FAW*N/FAW*BE*, which gave no information on possible interactions between the two mutations.

The segregation of plumage color among the 387 F₂ progeny (hatching rate 77%) and the corresponding postulated two-locus genotypes are shown in Table 3. Four colors were observed: wild-type, beige, lavender, and lavender-diluted beige, which is another new plumage color (Figure 1, bottom right). From the known modes of action (recessiveness and dominance) of the two autosomal mutations, we could suppose that all *LAV*L/LAV*L*; *FAW*N/FAW*BE* quail had lavender-diluted beige

Table 2. Segregation of plumage color in F₂ from roux and lavender quail (experiment 2)

Plumage color and genotypes	Observed	Expected ratio	Expected number
Wild-type			
<i>BR*N/BR*R</i> ; <i>LAV*N/LAV*N</i> and <i>BR*N/BR*R</i> ; <i>LAV*N/LAV*L</i> and <i>BR*N/W</i> ; <i>LAV*N/LAV*N</i> and <i>BR*N/W</i> ; <i>LAV*N/LAV*L</i>	135	3/8	118
Roux			
<i>BR*R/BR*R</i> ; <i>LAV*N/LAV*N</i> and <i>BR*R/BR*R</i> ; <i>LAV*N/LAV*L</i> and <i>BR*R/W</i> ; <i>LAV*N/LAV*N</i> and <i>BR*R/W</i> ; <i>LAV*N/LAV*L</i>	117	3/8	118
Lavender			
<i>BR*N/BR*R</i> ; <i>LAV*L/LAV*L</i> and <i>BR*N/W</i> ; <i>LAV*L/LAV*L</i>	35	1/8	39
Cream			
<i>BR*R/BR*R</i> ; <i>LAV*L/LAV*L</i> and <i>BR*R/W</i> ; <i>LAV*L/LAV*L</i>	28	1/8	39

Chi-square statistics = 6.0 < chi-square (3, 0.01) = 11.3.

Table 3. Segregation of plumage color in F₂ from lavender and beige quail (experiment 3)

Plumage color and genotypes under hypotheses A and B	Observed	Expected ratio	Expected number
Wild-type <i>FAW*^N/FAW*^N; LAV*^N/LAV*^N and FAW*^N/FAW*^N; LAV*^N/LAV*^L</i>	78	A and B: 3/16	73
Beige <i>FAW*^{BE}/FAW*^{BE}; LAV*^N/LAV*^N and FAW*^{BE}/FAW*^{BE}; LAV*^N/LAV*^L and FAW*^N/FAW*^{BE}; LAV*^N/LAV*^N and FAW*^{BE}/FAW*^N; LAV*^N/LAV*^L</i>	236	A: 9/16	218
<i>FAW*^{BE}/FAW*^{BE}; LAV*^N/LAV*^N and FAW*^{BE}/FAW*^{BE}; LAV*^N/LAV*^L and FAW*^N/FAW*^{BE}; LAV*^N/LAV*^N and FAW*^{BE}/FAW*^N; LAV*^N/LAV*^L and FAW*^{BE}/FAW*^{BE}; LAV*^L/LAV*^L</i>		B: 10/16	242
Lavender <i>FAW*^N/FAW*^N; LAV*^L/LAV*^L</i>	24	A and B: 1/16	24
Lavender-diluted beige <i>FAW*^N/FAW*^{BE}; LAV*^L/LAV*^L and FAW*^{BE}/FAW*^{BE}; LAV*^L/LAV*^L FAW*^N/FAW*^{BE}; LAV*^L/LAV*^L</i>	49	A: 3/16 B: 2/16	73 48

Hypothesis A: the lavender mutation dilutes the dark dots and the beige color in the plumage of homozygous and heterozygous beige individuals. Chi-square statistics = $9.7 < \chi^2$ (3, 0.01) = 11.3.

Hypothesis B: the lavender mutation only dilutes the dark dots and the beige color in the plumage of heterozygous beige individuals. Chi-square statistics = $0.5 < \chi^2$ (3, 0.01) = 11.3.

plumage color. But no a priori information on the plumage color of double homozygous *LAV*^L/LAV*^L; FAW*^{BE}/FAW*^{BE}* birds was available. It might as well have been lavender-diluted beige (some epistasis of *LAV*^L*: hypothesis A) or beige (some epistasis of *FAW*^L*: hypothesis B). Chi-square tests (Table 3) could falsify neither hypothesis A nor hypothesis B.

In the nine full-sib F₃ families obtained from lavender-diluted beige F₂ quail, not a single bird had beige plumage color. Quail were either lavender-diluted beige ($n = 139$) or lavender ($n = 25$). Under hypothesis B, however, matings between lavender-diluted beige quail to produce the F₃ should have taken place only among *LAV*^L/LAV*^L; FAW*^N/FAW*^{BE}* F₂ birds, and consequently 25% of their progeny should have had beige plumage. Therefore hypothesis B was wrong. Moreover, the test cross of F₂ birds, parents of the F₃, with pure lavender quail stock produced only lavender ($n = 57$) and lavender-diluted beige ($n = 108$) birds, thereby confirming that lavender-diluted beige F₂ quail were either heterozygous or homozygous for *FAW*^{BE}*. The lavender mutation modifies the plumage color of all carriers of the beige mutation in the same way.

This work describes three new Japanese quail plumage colors that result from two-locus interactions. In all cases, segregation in the F₂ was found to fit simple Mendelian two-locus expectations. It might be worthwhile, however, to study the combined effects of any two of these mutations on embryonic mortality because the observed number of quail with the new plumage color appeared to be less than expected in the three experiments. Only two colors, diluted beige and cream, correspond to homozygous or hemizygous birds, and could then be used to tag a line, as they will breed true under

pure line matings. Moreover, our observations showed that the roux mutation could be used for early sexing in crosses with fawn stock. Finally, we found that the beige/fawn mutation, which is dominant over the genes for wild-type plumage color, was not epistatic to the lavender and roux mutations.

Acknowledgments

Special thanks to Claude Bouchot (Station de Recherches Avicoles, INRA Nouzilly) for taking the photographs of the different plumage colors and for producing the color plate, and to Chantal Moussu (Unité Expérimentale de Génétique Avicole, INRA Nouzilly) for taking good care of the experimental birds.

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Received January 27, 2003

Accepted July 31, 2003

Corresponding Editor: Susan J. Lamont