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Testing homology of loci for two plumage colors, “lavender ” and “ recessive white ”, with hybrids between chickens and Japanese quail hybrids

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breed varieties, which could well be accounted for by the small sample size per breed, although positive selection at a neighboring locus (Smith and Haigh 1974) or a founder effect (David and Cappy 1988; Irvin et al. 1998) may at least partially cause some of this reduced variation. Modern dog breeds are of recent origin and many popular breeds, such as Labrador retriever, expanded the effective population size shortly after the homogenization of the breed standard. Thus different ancient haplotypes should be conserved in those populations and reduce genetic drift to a negligible level (Nichols and Beaumont 1996). Therefore the observed overall variability most likely reflects the level of heterozygosity of an assumed large ancestral population (Vila et al. 1999). Breeds that have experienced several bottlenecks, like the Portuguese water dog, or have a small population size, like the standard schnauzer, show fewer alleles and reduced heterozygosity compared to other breeds or breed varieties (Table 1). However, the variability was not correlated with the number of registered dogs, although those numbers might be a rough estimate of the actual breeding populations within the United States. While extreme homogeneity might be a problem of single breeds or breed varieties (Jeffreys and Morton 1987), our study suggests that most breeds still retain high levels of heterozygosity, at least for some of the loci tested.

The recent common ancestry of *Canidae* species is reflected in the interspecies conservation of these three microsatellite loci. For each locus, genomic DNA from all members of the *Canidae* family tested could be PCR amplified, and sequencing of the amplicons confirmed the identity of the microsatellite motif. These microsatellites therefore also offer a suitable tool for evaluation of conservation and homology in this region within *Canidae*.

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Testing Homology of Loci for Two Plumage Colors, "lavender" and "recessive white," With Chicken and Japanese Quail Hybrids

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Homology for two plumage color loci was

studied by hybridization between chickens and Japanese quail. First, chicken-quail hybrids were produced from homozygous "lavender" chicken cocks and "bleu" Japanese quail, and all 30 hybrids had the same parental slaty blue plumage color. On the other hand, no hybrids with this plumage were obtained out of 18 progeny from the same cocks and wild-type quail. These results show that the slaty blue plumage color is determined by homologous loci in Japanese quail and chickens. Second, all ($n = 25$) chicken-quail hybrids hatched from homozygous "recessive white" cocks and "recessive white" ($n = 8$) or "wild-type" ($n = 17$) quail had the same pattern of plumage color, with white feathers on the ventral face and colored feathers elsewhere. These results indicate that the recessive white mutations are not homologous in Japanese quail and chickens.

Chickens and Japanese quail belong to the same family, the Phasianidae (Mason 1984). Interspecific cross is possible between chickens and Japanese quail, producing sterile chicken-quail hybrids in low frequency (Damme 1991; Ogasawara and Huang 1963; Silversides and Mérat 1991; Takashima and Mizuma 1981; Wilcox and Clark 1961), but the reciprocal cross to obtain quail-chicken hybrids was never successful (Mitsumoto and Nishida 1958; Sarvella and Marks 1970). Consequently the artificial insemination of quail with semen from cocks provides a simple way for testing homologies between loci with visible effect, like plumage color. Homologies between loci may be anticipated by comparing plumage color and mode of inheritance, and confirmed by observing phenotypes of chicken-quail sterile hybrids. This approach was used for the first time with avian species by Silversides and Mérat (1991), who established the homology of the *AL* locus in the chicken and in the Japanese quail.

In chickens, the "lavender" phenotype is due to an autosomal recessive mutation, *LAV*^L*, at the *LAV* locus (Brumbaugh et al. 1972). Plumage color of homozygous birds varies from slaty blue to beige depending on the relative abundance of eumelanin and pheomelanin in the feathers (Somes 1988). At first the cause for this dilution of plumage color appeared to be related to the presence of melanocytes with abnormal dendrite formation in the "lavender" chicken (Brumbaugh et al. 1972), because in the mouse, a similar color mutation, "leaden," was associated



Figure 1. (A) Homozygous “lavender” cock. (B) Homozygous “bleu” adult Japanese quail. (C, D) “Lavender” × “bleu” 5-week-old chicken-quail hybrids.

with fewer and thinner dendrites in melanocytes (Markert and Silvers 1956). However, later works indicated that dendrites were present in melanocytes of lavender chickens (Mayerson and Brumbaugh 1981), and that the site of action of the mutation in the mouse was in the melanocytes (Stephenson et al. 1985). Similar dilutions of feather color determined by recessive mutations were reported by Jaap and Milby (1944) in the turkey (“recessive slate”), by Levi (1957) in the pi-

geon (“milky”), by Hollander and Walther (1962) in the muscovy duck (“lavender”), and by Somes (1988) in the Japanese quail (“bleu”).

Recessive white feathering in the chicken (Bateson and Punnett 1906) and in the turkey (Robertson et al. 1943) is due to a mutation that prevents the expression of feather color by other loci. The albino mutation (C^*A) at the multiallelic “recessive white” locus C in the chicken is caused by a deletion at a copper-binding site of the

tyrosinase gene (Tobita-Teramoto et al. 2000). Corresponding biochemical defects for the C^*C allele (recessive allele for white plumage and pigmented eyes) have not yet been reported. A similar recessive mutation with a less complete expression (dark eyes and white feathering except for some colored feathers on the top of the head and on the back) has been reported in Japanese quail (Roberts et al. 1978).

The purpose of the present work was to test the possible homologies between loci for “lavender” chickens and “bleu” quail, and for “recessive white” chickens and quail by crossing male chickens and female quail homozygous for the corresponding recessive alleles.

Materials and Methods

We maintain a gene pool with small numbers of LAV^*L/LAV^*L and of C^*C/C^*C chickens and pure line stocks of “bleu” and “recessive white” Japanese quail at our INRA experimental unit in Nouzilly, France. Both quail stocks were started from single mutant birds which appeared spontaneously in the quail colony, and after initial crossing and backcrossing to the mutant parent, they were fixed for each mutation. To minimize inbreeding, each mutant line was crossed to a wild-type plumage quail line twice in the past 10 years, and all (about 200 per stock) F_1 birds had wild-type plumage. Birds with the mutant phenotype obtained in the following F_2 generation were then kept as parents of the mutant stock which bred true thereafter. Consequently recessiveness of the two mutations is well established. Visual comparison of “bleu” quail and “lavender” chickens in our experimental unit indicated that their plumage color was quite similar. On the other hand, eye pigmentation and mode of inheritance of our “recessive white” Japanese quail corresponded closely to those of C^*C/C^*C chickens, whereas the white plumage retained a few normally pigmented feathers in the quail but not in the chickens.

Mixed sperm from 8 to 10 LAV^*L/LAV^*L cocks (Figure 1A) was used to inseminate 32 “bleu” (Figure 1B) and 8 “wild-type” (control) Japanese quail. Several cocks also had a naked neck, a trait determined by a semidominant autosomal mutation (Somes 1990). Mixed sperm from 4 C^*C/C^*C cocks was used to inseminate 16 “recessive white” (Figure 2A,B) and 16 “wild-type” (control) Japanese quail. Each quail was inseminated twice a week, repeated 2-week egg collections were carried out, and

Table 1. Hybrids obtained from crosses between lavender chickens and bleu or wild-type Japanese quail

Sire phenotype	Dam phenotype	No. of eggs set	No. of fertile eggs (%)	No. of hatched eggs (%)	Lavender/bleu hybrids	Hybrids with other plumage colors
Lavender	Bleu	617	49 (7.9)	18 (2.9)	18 + 12 ^a	0
Lavender	Wild-type	1569	26 (1.7)	18 (1.1)	0	18

^a Dead-in-shell quail with visible plumage.

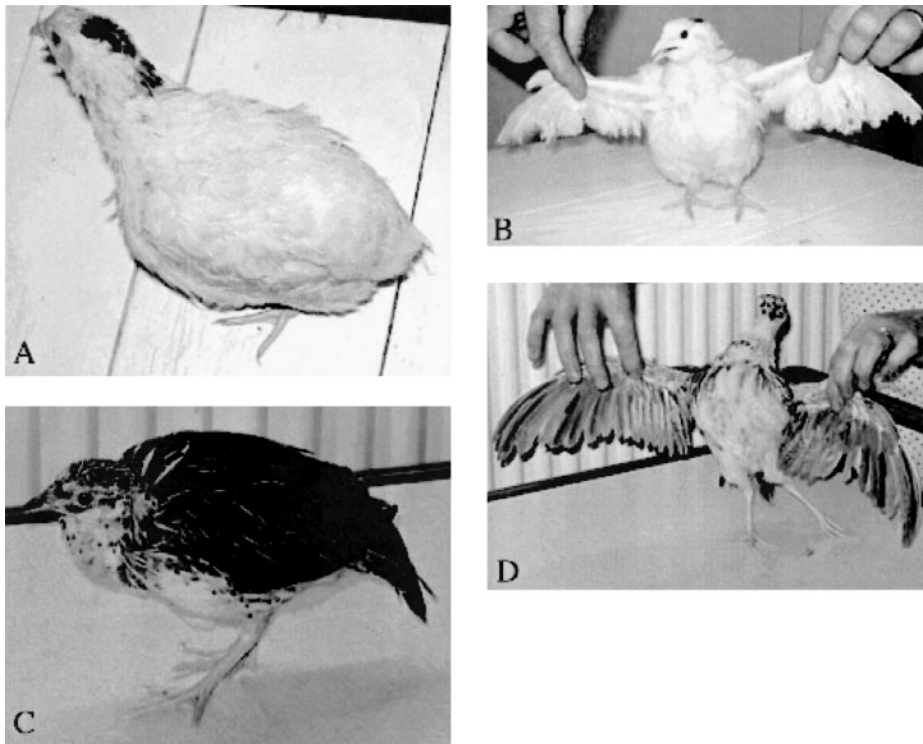


Figure 2. (A, B) "Recessive white" Japanese quail. (C, D) "Recessive white" × "recessive white" 6-week-old chicken-quail hybrids.

successive hatches were obtained. Eggs were candled at 13 days, and unhatched eggs at 20 days of incubation were opened to allow classification of down color.

Results and Discussion

At hatching, hybrid chicks were the size of quail chicks, but they had stronger chicken-like legs and were much more active. After a few days they were already outgrowing contemporary quail and showing a more erect chicken-like posture.

"Lavender" and "Bleu"

The results of the hybrid crosses are shown in Table 1. All 30 hybrids obtained from "bleu" quail had the lavender/bleu plumage color, with some variation of intensity (Figure 1C,D). Incidentally, 17 of them were also "naked neck" (Figure 1C). On the other hand, none of the 18 hybrids

obtained from "wild-type" quail had the lavender/bleu phenotype: their plumage had various proportions of black, wild-type quail, and white feathers, and six of them were "naked neck." These results show that the same gene determines the lavender and bleu phenotypes, because both mutations must be present in the hybrid to obtain the mutant plumage color. Since *LAV*L* was first used in chickens, and because this is the first report to show homology at this locus between the two species, it is proposed that the name "lavender" and symbol *LAV*L* be used in both species.

"Recessive White"

The results of the hybrid crosses are shown in Table 2. All 25 hybrids, whether they were hatched from "wild-type" or "recessive white" quail, had the same pattern of plumage color, with wild-type quail

feathers on the back, head, and wings, and white feathers on the ventral surface (Figure 2C,D). No "recessive white" hybrid was obtained. These results show that the "recessive white" phenotype is determined by different mutations in Japanese quail and in chickens. Since the name "recessive white" was given for chickens (Somes 1988) first, the white plumage phenotype of the Japanese quail and its corresponding mutation should be given specific names. We propose "white plumage" and *WHI*W*. The fact that "recessive white" chickens have no pigmented feathers (Smyth 1990), whereas their quail counterparts always have a few normally pigmented ones somewhere on their back from the head to the pelvic area (Cheng and Kimura 1990), was already an indication of this difference. The uniform white ventral plumage of all hybrids sired by "recessive white" cocks showed that the recessive chicken mutation *C*C* was somewhat expressed in the hybrid, although it was present in a single dose. This phenotype is analogous to that of the tuxedo quail (white feathers on the ventral face and brown feathers elsewhere), which is heterozygous at the Japanese quail recessive white locus and homozygous *EB*E/EB*E* for the mutant allele **E* at the "extended brown" locus *EB** (Cheng and Kimura 1990). A similar pattern of white plumage color was observed also in heterozygous guinea fowl obtained by crossing a pigmented line with a homozygous white line (Cauchard 1971). In all three instances the pattern of white feathers on the ventral face of the bird was associated with the heterozygous state of a "recessive white" locus.

This work has confirmed that hybridization is an appropriate tool to study homology in chickens and Japanese quail for genes with visible effects.

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Table 2. Hybrids obtained from crosses between recessive white chickens and recessive white or wild-type Japanese quail

Sire phenotype	Dam phenotype	No. eggs set	No. fertile eggs (%)	No. hatched eggs (%)	White hybrids	Hybrids with quail wild-type back and white ventral surface
Recessive white	Recessive white	1560	14 (0.9)	5 (0.3)	0	5 + 3 ^a
Recessive white	Wild-type	1578	20 (1.3)	11 (0.7)	0	11 + 6 ^a

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^a Dead-in-shell quail with visible plumage.

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