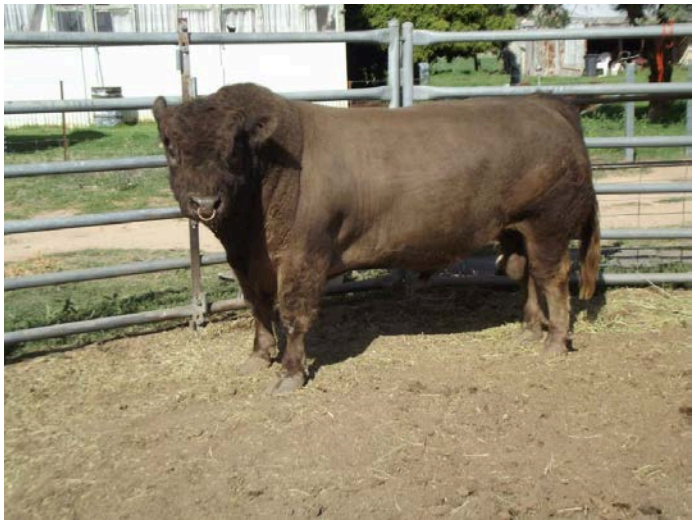
Dun Galloway Genetics;
a discussion of effect on phenotypical expression



Chocolate Dun Galloway Bull Mithaliam Destroyer, photo courtesy of Greenethorpe Galloways

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Discussion

Dun Galloways express in three primary phenotypes: Chocolate, Golden and Silver. Golden dun results from heterozygous codon deletion within the PMEL gene (p.Leu18del) PMEL +/del. Silver dun results from homozygous codon deletion within the PMEL gene (p.Leu18del) PMEL del/del. From a breeder aspect this simply means the dun trait within various Galloway populations is an autosomal incompletely dominant trait; .i.e it only takes a single dose for partial expression on phenotype.

To discuss scientific publication and make further assumptions based our results with dun genetics in Galloway Cattle, I think we need to first consider the overall picture in regards to solid color coat in Cattle.

In the following text we will deal with three of the six known locus that determine color coat in various breeds of cattle breeds found around the world; Extension (E), Agouti (A) and Dun (D).

Solid coat color in cattle results from the presence of absence of melanin (eumelanin “black” and phaeomelanin “red”) in hair coat. These melanocytes migrate from the neural crest during embryonic development. As hair grows, melanocytes are transferred to the follicles to produce pigment. Further traits can modify color coat in utero, shortly after birth or with aging.

Additional traits can further modify for spotting, pattern and dilution. While breeder opinions are diverse and may not concur, I think it is logical based on historical publications that Galloway populations in native locale were comprised of a diverse genotype (color / pattern)

prior to, or at least early on in domestication. For the sake of argument, all that follows will assume such, and that today's modern Galloway populations (herds) have been selected for varying degrees of reduction in diversity.

Extension

Black Galloway (E^D/E^D), photo courtesy R&S Waples Red Galloway (e/e), photo courtesy of Jeremy Perkins

Solid black, red and wild-type Cattle are the result of Extension (E) locus: E^D = black, E^+ = wild-type (black/red) and e = red in homozygous fashion. Though similar expression are possible in heterozygous states. One thing I always try to keep in mind is Galloway Cattle are historically referenced as having a "black coat with reddish tinge"; E^+/E^+ or E^D/E^+ in genotype. Many such cattle are still in existence and are of preferred type by pedigree breeders. Given, there have been several studies suggesting this expression being a result of copper deficiency or inability to absorb copper as a result of genotype. Given, many herds have been bred away from this phenotype to produce "jet black" coats more typical of Aberdeen Angus; E^D/E^D in genotype.

As a result, my thoughts have always leaned towards early solid Galloway's being the product of several combinations or types of genotype. With earliest references citing black animals having a reddish tinge being suggestive of E^+/E^+ or E^D/E^+ in genotype.

Color coat tests for Extension genotype are available; Melanocortin 1 Receptor (MC1R). When I first started to color test my Galloways and Belted Galloways for recessive red carriers in the early 1990's, results of homozygous wild-type E^+/E^+ and heterozygous wild-Type carriers E^D/E^+ were little understood and confused results. Advances in testing over the last two decades make the results available today much more comprehensive.

While cost prohibitive on a whole herd basis for most breeders, they can be affordable when used on select top end pedigree animals. Knowing your genotype can help in planning future breeding's with a reliable expectation of desired results. The three alleles found at the Extension locus (E^D, E^+ and e) determine and control production of black (eumelanin) and red (phaeomelanin) color pigments. All other traits can only dilute or reorganize melanocytes.

Wild-type Red Galloway (E+/e), photo courtesy Jeremy Perkins

Possible Wild-type Black Galloway (E^D/E^+), photo courtesy G & C Stuart

Expected test results:

E^D/E^D - homozygous dominant black, i.e. "jet black". ***(Phenotype; black)***
E^D/E^+ - dominant black & wild-type carrier. ***(Phenotype; predominantly black)***
E^D/e - heterozygous black & red carrier. ***(Phenotype; black)***
E^+/E^+ - wild-type. ***(Phenotype; predominantly red & black with Agouti influencing color)***
E^+/e - heterozygous wild-type & red carrier. ***(Phenotype; predominantly red)***
e/e - homozygous red. ***(Phenotype; red)***

Agouti

E^+ can be further modified by the Aougti (A) locus. Agouti comes in several forms and has distinct effects depending upon combination. It is not well understood or documented across cattle breeds. The existence of a recessive black Agouti allele (a) has been postulated with some recent supportive documentation, having the effect of modifying wild-type black/red E^+/E^+ or E^D/E^+ to jet black. Again as with Extension, it is possible Galloway's have more than one type of Agouti in genotype. To touch on briefly potential alleles found in Galloway Populations: A^+ wild-type (neutral allele). The suggested allele A^{bp} is epistatic (dominant) to E^D and hypostatic (subordinate) E^+. In combination with E^D, Agouti is not likely visible. In combination with E^+, Agout results in very dark wild-type; expressing not only varying degrees of red, but also locations of red on the body. The allele a^w is recessive and will remove red pigment; leading to the illusion of evenly distributed black melanocytes on the body of wild-type E^+, mimicking a black animal. A^{br} will produce brindle.

Brindle

As early as 1949 Berge (1949) reported brindle a result of co-expression of two distinct traits in Nordic cattle. More recently, Oulmouden (2000 & 2006) showed brindle to be the result of Agouti (A^{br}) in Normande Cattle. Thus, we now know brindle to be comprised of E^+/A^{br}. Brindle is a striping pattern distinct from spotting (S). Best visible on wild-type black animals, less so or nearly invisible on wild-type red, comprised of black and yellow / red color pigments.

With wild-type long present in Galloway populations, it should come as no surprise that this phenotype has been resurrected in the German Neanderthal Galloway herd of Hartmut Kindel.

Ultra DE0352356872, photo courtesy of H. Kindel

Dun

Silver Dun Galloway (left), Golden Dun Galloway (right), photos courtesy Michelle Blegen

It is possible dun is found in at least two forms in Galloway populations. Both standalone and possibly in co-expression of both. Dun is an incompletely dominant trait, and allow for partial expression in heterozygous form. In Galloway's the heterozygote (+/del) expressing as "Golden" and the homozygote (del/del) expressing as "Silver". While present in spotted (White Park) and patterned (Riggit & Brindle) Galloway's, the dun locus is only a mutation of solid color, i.e. black or red. The presence of spotting or pattern traits has no effect on the expression of dun.

There are distinct expressions of heterozygous Golden Dun phenotypes in birth coat colors. The first being a "golden" color and the second being a "blue/grey". The latter turns golden within 2-4 weeks. In Galloway's both are equally common. In North American Belted Galloway herds each type is easily traced by pedigree to initial importations from the UK.

With autosomal mutations of color across species, such as Agouti and dun, both recessive and incompletely dominant, variation of color (shading) is to be expected. This as a result of "autosomal concentration", .i.e a sort of cumulative effect. Just as an autosomal incompletely dominant trait has distinct impact on phenotype in both heterozygous and homozygous fashion, so does an autosomal recessive trait. Only in the latter it takes much observation to take note of the subtle differences presented.

At least one breeder has suggested the possibility of mtDNA contribution in variation among dun phenotypes. While worthy of consideration, it is unlikely to produce color variation among dun Galloway. Dun is an autosomal incompletely dominant trait passed by either or both sexes to offspring.

Chocolate Dun Discussion

So this now leaves us with the dilemma of the "Chocolate Dun" phenotype. There are two likely scenarios' to consider. 1. Chocolate Dun is the result of a "unique" allele. 2. Chocolate Dun is the result of combination of dun with various types of E and A alleles in co-expression. In either case, we can demonstrate normal Mendelian values for transmission of an autosomal incompletely dominant trait. We should be able to substantiate either hypothesis via available currently genetic testing of live animals and tracking of reliable pedigree's.

Aldermere Lopez (2987-D) ca. 1995 in WI, USA, photo by A. S. Bias

Heterozygous transmission is easily verified. In example we can use the Chocolate Dun Belted Galloway bull Aldermere Lopez (2987-D). His pedigree demonstrates a continuous, unbroken maternal descendancy from dun animals on at least one lineage: Ald. Venus (3254-D*****), Ald. Rusty (2622-D), Mochrum Jamie (1037-D), Boreland Champion 4th (151D), Boreland Champion 3rd (2077D). Review of his registered progeny reveals 40 calves; of which 20 are dun and 20 are black, a 50/50 ratio. Assuming non registered births also follow a similar parallel, this supports a 50% ratio expected for transmission of dun in Galloway's as an autosomal incompletely dominant trait. Autosomal transmission can be verified by the pedigree of Otokahe Promise (25690B), a black calf born of two Golden Dun parents. Further review of Lopez progeny will also reveal a far smaller number of Chocolate Dun vs. Golden Dun calves. This is supportive of

parental genotype consisting of random combinations of E (E^D/E^Dor E^+/E^+ or E^D/E^+) alleles with possible addition A (A^{bp} or A^w) alleles. It does not rule out the dun allele being epistatic to a distinct allele for Chocolate Dun.

Otokahe Promise (25690B), photo courtesy of Kris von Dohrmann

Conclusions

We have long known that both wild-type black (E^+/E^+) and wild-type red (E^+/e) cattle exist in Galloway Populations. We now know the brindle trait exists in wild-type (E^D/E^+ A^{br}, $E^+/$ E^+ A^{br}) Galloway Populations, thus showing that wild-type can be further modified by pattern and spotting traits. We have long known that dun is capable heterozygous and homozygous modification of expression in black (E^D/E^D +/del, E^D/E^D del/del), in red (e/e +/del, e/e del/del).

It is only logical to assume a corresponding dun mutation of wild-type black (E^+/E^+ +/del, E^+/E^+ del/del), and red (E^+/e +/del, E^+/e del/del) with or without Agouti. The most logical choice for this phenotype based on prior discussion is Chocolate Dun. If this hypothesis is true, than Chocoloate, Golden, and Silver dun all result from the same deletion within PMEL gene, should be easily verified with current available extension testing.

Footnotes:

***:** *Current CLRC listing does not indicate as being "dun". However, several printed pedigrees and oral history of Ald. Venus confirm as being a dun.*

***: Assuming Chocolate Dun has a similar mode of inheritance.*

Definitions:

GALLOWAY POPULATION - Domestic herds comprising total breed population.
ALLELES - alternate forms/varieties of a gene.
CARRIER - individual who is heterozygous for a trait.
DILUTION GENE - the expression of another gene in the phenotype.
GENES - units of inheritance. ***(used interchangeably with TRAIT in this writing from a breeders perspective)***
GENOTYPE - the genetic makeup of an individual.
HETEROZYGOUS - genotype consisting of two different alleles for a particular trait.
HOMOZYGOUS - genotype consisting of two identical alleles for a particular trait.

PHENOTYPE is the visible traits of an individual.
TRAIT – units of inheritance. ***(used interchangeably with GENE in this writing from a breeders perspective)***

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