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Short Communication

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Historical analysis of Newfoundland dog fur colour genetics

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Abstract
This article makes use of digitized historic newspapers to analyze Newfoundland dog fur colour genetics, and fur colour variations over time. The results indicate that contrary to the accepted view, the 'Solid' gene was introduced into the British population of Newfoundland dogs in the 1840s. Prior to that time, the dogs were white and black (Landseer) or white and brown, and thus spotted/spotted homozygotes. Due to 'Solid' being dominant over 'spotted', and selective breeding, today the majority of Newfoundland dogs are solid black. Whereas small white marks on the chest and/or paw appears to be a random event, the historical data supports the existence of an 'Irish spotted' fur colour pattern, with white head blaze, breast, paws and tail tip, in spotted/spotted homozygotes.
Keywords: Fur colour genetics, Irish spotting, Landseer Newfoundland, MITF, Newfoundland dog.

Introduction

The Newfoundland is one of the most majestic and distinctive breeds of dog (Waters, 2006; Bondeson, 2012). Originating in Newfoundland, these dogs were exported, mainly to Britain, as early as the 1730s, for use as ship's dogs. By the 1780s, the Newfoundland dogs had become fashionable as pets, and Britain had a considerable population of them (Bondeson, 2012). According to recent breed monographs, the original Newfoundland dogs were solid black (Fig. 1). These publications also allege that the white and black spotted Newfoundland dogs became popular for a while in the 1820s and 1830s, after being portrayed by Sir Edwin Landseer, who had a great liking for these animals, but they then sank back into obscurity (Booth Chern, 1975; Drury, 1978; Barlowe, 2001; Kosloff, 2006). Since the 1880s, these white and black dogs have been known as 'Landseer Newfoundlands', a name coined not by any kennel club or dog breeding association, but by the eccentric Victorian dog fancier Dr William Gordon Stables (Stables, 1875,1880).

Sir Edwin Landseer was one of many British or continental European painters from the first half of the nineteenth century to have depicted white and black spotted Newfoundland dogs; his production does not include any solid black, or solid brown, specimens (Fig. 2). Landseer portrayed many solid black dogs of other breeds, and it is not conceivable that a painter of his talent would be unable to depict a black Newfoundland, if these dogs had been common in his time (Mellencamp, 1976, 1978; Waters, 2006). Inventories of Newfoundland dog iconography demonstrate that from the 1740s until the 1840s, there were many paintings and drawings of white and black [and also some white and brown] Newfoundland dogs, but no convincing illustrations to support the existence of solid black [or brown] dogs at the time, in Britain or on the European continent (Conlon, 1989; Matenaar, 1989; Waters, 2006; Bondeson, 2011, 2012).

The accepted facts of Newfoundland dog fur colour genetics are that the basic colour of a Newfoundland dog is determined by what is known as the B locus, with 'Black' colour being dominant over 'brown'. Thus, the BB homozygotes will be black, as will the Bb heterozygotes; only the bb homozygotes will be brown. Then there is the D locus, with 'Non Dilute' dominant over 'dilute'. The DD and Dd dogs will be black, whereas the dd homozygotes will be grey, or diluted black. There are some grey Newfoundland dogs in the United States, but very few elsewhere. The regulation of solid colour versus spotting in Newfoundland dogs is controlled by the S locus, where 'Solid' colouring is dominant over 'spotted'. Thus the SS homozygotes and the Ss heterozygotes will be solid black (or brown), whereas the ss homozygotes will be spotted. In Newfoundlands, there are several different patterns of spotting, ranging from dogs that are white with a few black spots, to dogs that are black with white feet, chest and tail tip. Dr Charles Little constructed a model with an allelic series where S is Solid, s^i is 'Irish spotting' with white head blaze, breast, paws and tail tip, s^p piebald spotting with coloured plates, separated or confluent, and s^w extreme-white piebald spotting. He discussed the possibility of plus and minus modifiers affecting the type of spotting, and also the putative existence of a 'pseudo-Irish' spotting pattern that might occur in Solid/spotted heterozygotes in some breeds of dogs (Little, 1957). Dr Øjwind Winge preferred a simpler model with two alleles at the locus for white mottled: T for solid coloured or nearly so, and t for white mottled (Winge, 1950). The various loci discussed above are of course not proper genes,

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Fig. 1. A solid black Newfoundland and a Landseer, from Rawdon Lee's *History and Description of the Modern Dogs of Great Britain and Ireland.*

Fig. 2. A print of Landseer's painting of the Newfoundland dog Lion.

resulting from genotyping or genomic sequencing, but rather interpretations of breeding results.

Later, a model of polygenic inheritance was applied to the piebald spotting patterns in Landseer Newfoundland dogs and Holstein-Friesian cattle (Pape, 1990). The Landseers were divided into three classes: the dark dogs with white legs, chest, tail and head blaze (Mantel), the white and black spotted dogs with white legs and tail (Medium), and the nearly all white dogs with a black face-mask and a few black sports on the body (Light). It was postulated that the recessive major spotting gene worked with at least two modifiers, which he termed s_2 and s_3. Dogs that were S_3S_3 homozygotes, and either S_2S_2 homozygotes or S_2s_2 heterozygotes, were dark (Mantel). Dogs that were s_2s_2 homozygotes, and either s_3s_3 homozygotes or S_3s_3 heterozygotes, were nearly all white (Light). All other combinations resulted in the traditional white and black spotted dogs (Medium). This model was tested in large populations of cattle (n=1118), and a much smaller population of dogs (n=110), and proved to work quite well, according to a combined sum and Fisher test (Pape, 1990), it would have been interesting to see it evaluated in a larger population of dogs.

The same paper also addressed the problem of the inheritance of small white marks in Newfoundland dogs (Pape, 1990). Although most Solid/spotted heterozygotes were solid black or brown, it was presumed that modifier genes might again be playing a part in the 'pseudo-Irish' spotting, as well as in the inheritance of other patterns of small white markings. In Pape's classification system, there were solid-coloured dogs without white marks (Class I), solid-coloured dogs with some white on the chest (Class IIA), dogs with small white marks on the chest and one or more paws (Class IIB), and 'Irish spotted' dogs with white on the head, chest, belly, paws and tail tip (Class III). Again, a model of two modifiers determining these spotting patterns was constructed, and tested using a database of stud book material. This theory worked reasonably well, with the exception that the number of 'Irish spotted' pups was underestimated when dogs from Class I were mated either with each other, or with dogs from Class II. When dogs from Class I were mated together, the expected values of Class I, II and III pups were 1740, 250 and 9, respectively; the observed values were 1765, 234 and 0, respectively, quite possibly indicating that solid-coloured dogs do not have 'Irish spotted' pups. In matings with dogs from Class I with dogs from Class II, the expected values of Class I, II and III pups were 641, 293 and 16, respectively; the observed values were 627, 320 and 3, respectively. Again the underestimation of the number of 'Irish spotted' pups casts some doubt on the validity of this inheritance model.

In 2007, the gene 'Microphtalmia associated transcription factor' (MITF) was recognized as causing one or more spotting patterns in dogs, including Landseer Newfoundlands. The insertion of a short interspersed nucleotide element (SINE) in the MITF start codon was linked with random spotting in many dog breeds (Karlsson *et al*., 2007). A later population study indicated that dogs homozygous for the SINE had white markings comparative to those in Pape's three classes of Landseer Newfoundlands. In most breeds, dogs heterozygous to the SINE insertion were either solid coloured or had minimal white markings, but in certain breeds, the dogs had the 'pseudo-Irish' pattern discussed by Little (Schmutz *et al*., 2009).

Results and Discussion

To investigate the historical variation of Newfoundland dog fur colour, the 'Times Digital Archive' (Gale Databases) database of the advertisements for lost or stolen dogs in the *Times* newspaper was used. For these advertisements to be useful, they needed to contain a good description of the animal in question, thus helping to eliminate the potential bias due to

carelessness or journalistic license. Many of the descriptions of the dogs are sufficiently detailed, such as this one from 1785:

"LOST on Saturday last, May 28th, a large Black Newfoundland Dog, has White Feet, a little White in the Forehead, the end of his Tail White, answers to the Name of Lyon".

Advertisements that did not describe the fur colour of the dogs in question, or that concerned mongrels were excluded, resulting in a total of 134 advertisements to recover lost or stolen Newfoundland dogs from 1785 until 1890. Further excluding a grey Newfoundland advertised for in 1814, and a white and yellow 'Newfoundland' dog advertised for in 1839, the remaining 132 dogs belonged to the fur colour patterns that are recognized today (Table 1). Prior to the year 1840, there was not a single advertisement describing a solid black (or brown) Newfoundland, but 15 dogs that were obvious white and black (or brown) spotted. Most of these Landseers belonged to the 'Medium' and 'Light' subgroups. Between 1840 and 1850, solid black dogs begin appearing in the *Times* advertisements, and in the time period 1850-1859, they were nearly as frequently described as the other fur colour variations. In the time period 1860-1890, solid black dogs were in the majority. Thus it appears as if solid black Newfoundland dogs were very scarce in Britain prior to 1840, before ultimately becoming the most common fur colour variant.

Using Pape's classification system (Pape, 1990), it was clear that the 'III' pattern of fur colour was represented in many early (pre-1840) dogs. The 'IIA' and 'IIB' dogs were all post-1850, however, and thus appeared after the 'Solid' gene had been introduced. This supports the hypothesis that small white marks on the chest and paws are a random event rather than the result of a specific allele. During embryogenesis, the melanocytes, the cells producing pigment, migrate down from the spinal column. But not all the dogs complete this process by birth or thereafter, and this incomplete migration results in a white toe or a white spot on the chest in an otherwise solid-coloured animal (the'IIB' and 'IIA' classes, respectively). Table 1 provides no support for the existence of a 'pseudo-Irish' spotting phenomenon in Newfoundland dogs, but instead supports Little's original hypothesis of an 'Irish spotting' allele. Since 8 Newfoundland dogs with the 'III' fur colour pattern were described in the time period 1785-1839 (Table 1), before the 'Solid' gene had been introduced, this would indicate that the 'III' for colour pattern occurs in spotted/spotted homozygotes. The role of modifiers in regulating this fur colour pattern remains unclear.

Table 1. Fur colour variation in Newfoundland dogs over time, from the 'Times Digital Archive' database, 1785-1890.

Time period	*Landseer*	*White/ Brown*	*IIA*	*IIB*	*III*	*Black*	*Brown*
1785-1799	1	1	0	0	1	0	0
1800-1819	2	1	0	0	2	0	0
1820-1839	8	2	0	0	5	0	0
1840-1849	9	1	0	0	6	4	1
1850-1859	10	1	4	3	4	17	1
1860-1869	6	0	5	2	5	20	1
1870-1890	1	0	2	0	0	6	0

It was also possible to use a second online newspaper database, the 'Nineteenth Century British Library Newspapers' (Gale Databases). This database covers a large number of historic London and provincial UK papers, although it was a concern that the descriptions of the dogs (for sale, for auction, and lost or found) were often much less detailed than those in the Times Digital Archive. Since advertisement quality seemed to decline over time, it was not possible to continue past 1839. It should be noted that where the dogs have been pointed out to be solid black, rather than just 'black', they have been put in a special 'solid black' category. Out of a total of 149 advertisements in the British Library database, there were two solid white dogs and one red and white dog; the remainder fitted into the present-day classification system (Table 2). The tallied results were much the same as for the Times Digital Archive, although the British Library database indicates that there were a few solid black dogs in Britain prior to 1840. This discrepancy in solid black dog may be a result of a lack of cynological sophistication in the provincial newspapers of the time. Not only was the definition of a Newfoundland dog somewhat vague in Georgian times, but a brief advertisement such as 'For sale by auction, a black Newfoundland dog' does not rule out that the animal had some white markings. Still, a few of the advertisements for solid black 'Newfoundlands' appear bona fide, perhaps indicating that although the larger, white and black or white and brown spotted Newfoundland dogs were preferred by the dog fanciers, a few of the smaller, solid-coloured, retriever-like black dogs were imported from Newfoundland at the time. However, these dogs would not appear to have been interbred with the spotted Newfoundland dogs to any extent prior to the 1840s, when solid black dogs became fashionable.

In late Victorian times, there was much interest in dogs and their doings: kennel clubs were founded, breed standards established, and large dog shows held. The late Victorian dog fancy sometimes rewrote the history of their favourite breeds: for example, the original purpose of the Bulldog as a bull-baiting dog was conveniently 'forgotten', and emphasis was instead put on its pure and ancient English stock, and its friendly and affectionate nature (Ritvo, 1986).

Table 2. Fur colour variation in Newfoundland dogs over time, from the 'Nineteenth Century British Library Newspapers' database, 1760-1839.

Time period	*Landseer*	*White/Brown*	*IIA*	*IIB*	*III*	*Solid Black*	*Black*	*Brown*
1760-1769	1	2	0	0	0	0	1	0
1770-1779	20	2	0	0	9	1	2	0
1780-1789	10	4	0	0	3	0	3	0
1790-1799	12	2	0	0	1	0	0	1
1800-1809	14	1	0	0	4	0	0	1
1810-1819	12	0	0	0	4	0	1	0
1820-1829	14	1	0	0	1	0	1	0
1830-1839	16	0	0	0	2	1	0	0

A prime mover in the late Victorian Newfoundland dog fancy was Dr William Gordon Stables, a former naval surgeon who had left medical practice and established himself as a writer of juvenile fiction (Fig. 3). He wrote at least a hundred novels, as well as countless articles for the *Boy's Own Paper* and other periodicals (Graham, 2006; Bondeson, 2012). He also wrote a number of books on animals, including *Our Friend the Dog* that went through a number of editions. Although having no academic education in the fields of zoology and veterinary medicine, and possessing only an outdated medical degree, Dr Stables fancied himself as an expert on all canine matters. He considered the Newfoundland to be the most sagacious of all dog breeds, and himself kept a number of these dogs over the years; an irresponsible dog owner, he was fond of watching dog fights involving his own animals, and on occasion even set his dogs on human beings. For some reason or other, possibly that his own favourite Newfoundland champion 'Theodore Nero' had been solid black, Dr Stables made up his mind that the solid black variety was the original breed of the Newfoundland dog. The white and black spotted dogs had briefly been fashionable in the time of Sir Edwin Landseer, who liked to paint them, but now they were again in a decline (Fig. 4). When interviewed in 1875, Dr Stables said that the white and black Newfoundland dog should be called the Landseer, since they had so often been included in his paintings (Stables, 1875). In an 1880 article, Dr Stables proclaimed that "The black-and-white breed is now generally called the 'Landseer Newfoundland', a name the writer originated a few years ago" (Stables, 1880). The denomination 'Landseer Newfoundland' thus does not originate with any dog breeding association, or knowledgeable expert on dogs, but with a Victorian eccentric who wrote silly children's books, and who liked to scatter German marching bands with his mischievous Newfoundland dog. The views of Dr Stables on Newfoundland fur colour were also widely regurgitated at the time, and are still quoted with approval today.

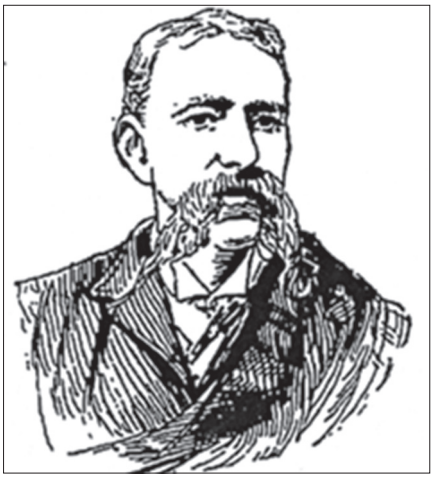

Fig. 3. Dr William Gordon Stables, from the *Penny Illustrated Paper*, March 19, 1892.

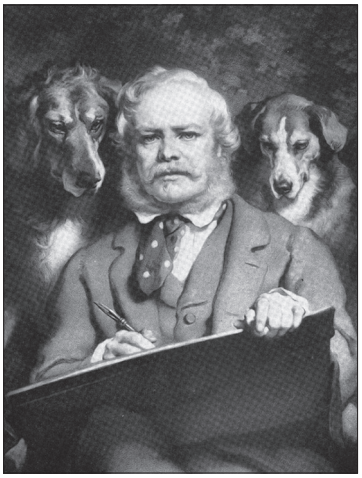

Fig. 4. An 1865 print of Landseer's 'The Connoisseurs': a self-portrait with two of his dogs.

The best way of studying dog colour genetics is by way of recording breeding histories, but prior to the late Victorian dog fancy, there was very little interest in recording the breeding of dogs. Thus the historical

study of Newfoundland dog fur colour genetics would have to rely on contemporary descriptions of lost or stolen dogs, or dogs for sale or for auction. Based on the data described above, and the art history studies of fur colour variation in Newfoundlands, it is reasonable to suggest that the 'Solid' gene was introduced into the British population of Newfoundland dogs in the 1840s, quite possibly through importation of smaller, solid black dogs from parts of Newfoundland. Certain dog fanciers may have used these imported dogs in breeding experiments to produce solid black Newfoundland dogs with the same size and general phenotype as the finest white and black spotted specimens. Being dominant over 'spotted', the 'Solid' gene soon impacted on the Newfoundland dog phenotype, particularly since the solid black dogs became highly fashionable in late Victorian times. When Dr William Gordon Stables and other Victorian dog fanciers rewrote the history of the Newfoundland dog, they wrongly claimed that Landseer had a preternatural liking for white and black dogs, and that the solid black dogs were the original breed (Bondeson, 2012). This statement would appear to have originated in the good doctor's imagination rather than in factual observations, however, and it is time that the breed monograph 'accepted truth' about Newfoundland dog history is challenged.

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