Investigation of the Booroola (FecB) and Inverdale (FecXI) mutations in 21 prolific breeds and strains of sheep sampled in 13 countries

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Abstract

Twenty-one of the world’s prolific sheep breeds and strains were tested for the presence of the FecB mutation of BMPR1B and the FecX¹ mutation of BMP15. The breeds studied were Romanov (2 strains), Finn (2 strains), East Friesian, Teeswater, Blueface Leicester, Hu, Han, D’Man, Chios, Mountain Sheep (three breeds), German Whiteheaded Mutton, Lleyn, Loa, Galician, Barbados Blackbelly (pure and crossbred) and St. Croix. The FecB mutation was found in two breeds, Hu and Han from China, but not in any of the other breeds. The 12 Hu sheep sampled were all homozygous carriers of FecB (FecB/B/FecB⁺) whereas the sample of 12 Han sheep included all three genotypes (FecB/B/FecB⁺, FecB⁺/FecB⁺) at frequencies of 0.33, 0.58 and 0.08, respectively. There was no evidence of FecX¹ in any of the breeds sampled.

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1. Introduction

Recent discoveries have revealed that high prolificacy in Booroola sheep is the result of a mutation (FecB) in the bone morphogenetic protein receptor 1B (BMPR-1B) gene (Wilson et al., 2001; Mulsant et al., 2001; Souza et al., 2001) and that high prolificacy in Inverdale Romney sheep is due to a mutation (FecX¹) in the bone morphogenetic protein 15 (BMP15) gene (Galloway et al., 2000). Knowledge of these mutations has prompted researchers to screen other prolific sheep breeds to determine whether either of these mutations is responsible for their high prolificacy. A previous study of eight prolific breeds (Thoka, Woodlands, Olkuska, Garole, Javanese, Lacaune, Belclare and Cambridge) revealed that FecB was present in the Garole sheep of India and the Javanese sheep of Indonesia (Davis et al., 2002). FecX¹ was not present in any of these breeds although more recent research has shown that the Belclare breed has two different mutations of BMP15 (FecX¹B and FecX¹G) resulting in the same phenotype as FecX¹, while the Cambridge breed also has the FecX¹G mutation (Hanrahan et al., 2004).

This study extends the investigation of the FecB and FecX¹ mutations to 21 breeds and strains, which include some of the world’s most prolific breeds.

2. Materials and methods

2.1. Prolific sheep flocks

In this text litter size is defined as lambs born per ewe lambing. A summary of the breeds sampled is in Table 1. The Chinese Hu and Small-tailed Han sheep were sampled from commercial flocks in Jiangsu and Shandong provinces, respectively, by staff of Nanjing Agricultural University. The 12 Hu sheep sampled all had produced at least one set of triplets or quadruplets in their lifetime. Each of the 12 Han ewes had produced at least one set of triplets, quadruplets or quintuplets.
Table 1
Mean lifetime litter size records of tested sheep

<table>
<thead>
<tr>
<th>Breed</th>
<th>Country</th>
<th>No. tested</th>
<th>Mean no. lambings (±S.E.)</th>
<th>Mean litter size (±S.E.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lleyn</td>
<td>Wales</td>
<td>16</td>
<td>3.0 (±0.4)</td>
<td>3.4 (±0.2)</td>
</tr>
<tr>
<td>Romanov</td>
<td>Germany</td>
<td>11</td>
<td>3.4 (±0.4)</td>
<td>3.1 (±0.1)</td>
</tr>
<tr>
<td>Hu</td>
<td>China</td>
<td>12</td>
<td>2.8 (±0.2)</td>
<td>3.0 (±0.1)</td>
</tr>
<tr>
<td>D’Man</td>
<td>Morocco</td>
<td>15</td>
<td>6.3 (±0.3)</td>
<td>3.0 (±0.1)</td>
</tr>
<tr>
<td>Han</td>
<td>China</td>
<td>12</td>
<td>3.7 (±0.6)</td>
<td>2.9 (±0.1)</td>
</tr>
<tr>
<td>Loa</td>
<td>Iceland</td>
<td>12</td>
<td>5.2 (±0.6)</td>
<td>2.9 (±0.1)</td>
</tr>
<tr>
<td>Teeswater</td>
<td>England</td>
<td>12</td>
<td>2.7 (±0.7)</td>
<td>2.5 (±0.2)</td>
</tr>
<tr>
<td>Chios</td>
<td>Cyprus</td>
<td>12</td>
<td>3.9 (±0.3)</td>
<td>2.5 (±0.3)</td>
</tr>
<tr>
<td>Barbados Blackbelly</td>
<td>USA</td>
<td>7</td>
<td>3.6 (±0.5)</td>
<td>2.3 (±0.2)</td>
</tr>
<tr>
<td>St. Croix</td>
<td>USA</td>
<td>2</td>
<td>3.0 (±2.0)</td>
<td>2.2 (±0.2)</td>
</tr>
<tr>
<td>East Friesian</td>
<td>Germany</td>
<td>12</td>
<td>5.2 (±0.6)</td>
<td>2.1 (±0.1)</td>
</tr>
<tr>
<td>Barbados Blackbelly</td>
<td>USA</td>
<td>2</td>
<td>5.5 (±0.5)</td>
<td>2.0 (±0.2)</td>
</tr>
<tr>
<td>Blueface Leicester</td>
<td>Scotland</td>
<td>12</td>
<td>2.3 (±0.4)</td>
<td>2.0 (±0.2)</td>
</tr>
<tr>
<td>Mountain Sheep (brown)</td>
<td>Germany</td>
<td>8</td>
<td>3.0 (±0.0)</td>
<td>1.8 (±0.1)</td>
</tr>
<tr>
<td>Tyrolian Mountain Sheep</td>
<td>Austria</td>
<td>11</td>
<td>3.9 (±0.4)</td>
<td>1.8 (±0.1)</td>
</tr>
<tr>
<td>German Whiteheaded Mutton</td>
<td>Germany</td>
<td>15</td>
<td>3.1 (±0.3)</td>
<td>1.6 (±0.1)</td>
</tr>
<tr>
<td>Mountain Sheep (white)</td>
<td>Germany</td>
<td>11</td>
<td>4.4 (±0.9)</td>
<td>1.5 (±0.2)</td>
</tr>
<tr>
<td>Finn (high line)</td>
<td>Ireland</td>
<td>21</td>
<td>3.9 (±0.1)</td>
<td>4.5 (±0.1)*</td>
</tr>
<tr>
<td>Finn (control line)</td>
<td>Ireland</td>
<td>17</td>
<td>3.8 (±0.2)</td>
<td>2.4 (±0.1)*</td>
</tr>
</tbody>
</table>

* Finn records are ovulation rates as litter size records were unavailable.

The three Mountain Sheep (Bergschaf) breeds sampled had mean litter sizes ranging from 1.5 to 1.8 lambs. The 12 Tyrolian Mountain Sheep ewes were selected from flock book records on the basis of being unrelated for two generations. None of these ewes had records of litters larger than twins but 8 of the 12 had a parent or grandparent born as a triplet. The white German Mountain Sheep and brown German Mountain Sheep (brown and white are separate breeds) were sampled from flocks in Upper Bavaria. One ewe of each strain had a record of triplets but all others had singles and/or twins.

The 15 German Whiteheaded Mutton ewes were sampled by the Department of Animal Breeding and Genetics in Giessen and all had produced litters of singles and twins, with an average litter size of 1.6.

Eleven of the Romanov ewes were from a flock belonging to the Oberer Hardthof research farm of the Department of Animal Breeding and Genetics in Giessen and each had produced at least one triplet or quadruplet litter in their first four lambings. A 12th Romanov ewe from Giessen had no litter records. An additional 13 Romanov ewes from a commercial flock in Quebec, Canada were also sampled but no litter records were available from these ewes.

The 15 D’Man ewe samples came from the Institut Agronomique et Vétérinaire Hassan II in Morocco and each had at least two records of large litters (triplets, quadruplets, quintuplets or sextuplets).

The 12 Chios ewe samples came from the Agricultural Research Institute, Nicosia and included nine ewes that had produced at least two sets of triplets, quadruplets or quintuplets, and three ewes that had produced only singles or twins.
Eight of the East Friesian ewes sampled from flocks at the Oberer Hardthof research farm of the Department of Animal Breeding and Genetics in Giessen had produced at least one set of triplets or quadruplets, and four had produced a maximum of twins.

Seven of the Teeswater ewes sampled from two commercial flocks in England had produced at least one set of triplets or quadruplets, and five young ewes had only produced singles or twins.

Eight of the Bluefaced Leicester ewes sampled from a commercial flock in Scotland had produced at least one set of triplets or quadruplets, and the other four were young ewes with records of singles or twins.

Three Blackbelly, three Blackbelly × Hampshire, and four (St. Croix × Suffolk) × (Blackbelly × Hampshire) sheep were sampled from a flock in the USA. The Blackbellies included a ewe that had produced five sets of twins and one triplet litter, a ewe that had produced one single and four sets of twins, and a ram. The Blackbelly × Hampshire ewes were prolific full-sibs; each had produced at least two sets of triplets. The most prolific of the three sibs had litter records of 1, 3, 3, 4 and all of the four (St. Croix × Suffolk) × (Blackbelly × Hampshire) ewes were her daughters. Two of the daughters produced triplets.

Four St. Croix sheep from four different flocks in the USA were sampled. Two of these were rams, one was a ewe that had produced two sets of triplets and three sets of twins, and the other was a ewe that had produced twins at her only lambing.

Twelve Loa sheep from the Hafrfellstunga farm in northeast Iceland were sampled. Seven had produced at least one set of quadruplets and the remainder had produced at least one set of triplets.

Fifteen Galician ewes from three farms in the Galicia region of Spain were sampled. No litter size records were available for these sheep.

A line of Finns selected for high ovulation rate was established in Ireland in 1977 (Hanrahan, 1982). Over the last five years of the selection, programme (ewes born 1993–1997) the mean ovulation rates of the two lines differed by 2.0 (4.6 versus 2.6; (Hanrahan, 2003)). Twenty ewes from the high line and 17 from the control line were sampled.

The 16 Lleyn ewes sampled were from five commercial flocks in Wales. Each of the ewes had at least one record of triplets, quadruplets or quintuplets.

2.2. Sample collection

Blood samples were collected in 10 ml heparinised vacutainers from Romanov (Canada), Chios (Cyprus), Tyrolian Mountain Sheep (Austria), Teeswater (England) and Bluefaced Leicester (Scotland) sheep or as a few drops of blood on FTA® paper (Whatman BioScience Ltd., Cambridge, UK) embedded in easiTrace™ labels (Halley Labels, Christchurch, New Zealand) from D’Man (Morocco) and Loa (Iceland) sheep. Extracted DNA samples were sent to NZ from Han (China), Hu (China), East Friesian (Germany), Romanov (Germany), white and brown Mountain Sheep (Germany), German White-Headed Mutton (Germany), Finn (Ireland), Lleyn (Ireland), Galician (Spain), Barbados Blackbelly (USA) and St. Croix (USA). All samples, blood and DNA, were consigned to the AgResearch Molecular Biology Unit, Department of Biochemistry, University of Otago, Dunedin or the AgResearch commercial DNA testing laboratory (Genomnz™) at the Invermay Agricultural Centre
with the appropriate import approval from the New Zealand Ministry of Agriculture and Fisheries.

2.3. Preparation of blood on FTA® paper

For the blood samples on FTA® paper, DNA was extracted from each 2.0 mm punch using alkaline lysis at 75 °C as described by Rudbeck and Dissing (1998). The punches were incubated for 5 min in 20 μl 0.2 M NaOH and then 180 μl 0.04 M Tris–HCl, pH 7.5 was added. An aliquot of 1–5 μl of extract was used per PCR.

2.4. Forced restriction fragment length polymorphism PCR for FecB

PCR was carried out using a modification of the forced RFLP method described by Wilson et al. (2001). The primer TestR15 has been engineered to introduce a point mutation such that PCR products from the BMPR-IB gene with the Booroola mutation contain an AvaII (New England Biolabs, Beverly, MA) restriction site (G|GACC) whereas products from non-carriers of the mutation lack this site. Genomic DNA (~100 ng) was amplified as described by Wilson et al. (2001). For FTA® samples, punches (single 1.2 mm punch) were amplified in a 25 μl reaction volume using an alternative primer set: CCAGAGGA-CAATAGCAAAGCAAA, TestF2, and CAAGATGTITTTCATGCCTCATCAAACACGGTC (TestR15). The amplification was carried out using 35 cycles at 94 °C for 15 s, 60 °C for 30 s and 70 °C for 30 s, followed by 72 °C for 5 min and 99 °C for 15 min. The 190 bp product was then digested using AvaII. The resulting products were separated by electrophoresis on a 3.5% agarose gel and visualised with ethidium bromide. Products containing the FecB mutation yield 160 bp and 30 bp fragments, whilst non-carrier products remain uncut at 190 bp.

2.5. Forced restriction fragment length polymorphism PCR for FecXI

Analysis of samples for FecXI was carried out using the forced RFLP method described by Galloway et al. (2000). Primer 12 has been designed to generate a forced XbaI restriction enzyme site (T|CTAGA) in PCR products from carriers of the FecXI mutation in the BMP15 gene, whereas products from non-carriers of the mutation lack this site. Genomic DNA and FTA elutions were amplified using Primer 12 (GAAGTAACCAGTGTTCCCTC- CACCCTTTTCT) and Primer 13 (CATGATTGGGAATTGAGACC). The amplification was carried out using 35 cycles at 94 °C for 30 s, 60 °C for 40 s and 70 °C for 30 s, followed by 72 °C for 4 min. The 154 bp product was digested with XbaI (Roche Diagnostics New Zealand Ltd.), and the products were separated by electrophoresis on a 3.5% agarose gel and visualised with ethidium bromide. Products containing the FecXI mutation yield 124 bp and 30 bp fragments, whilst non-carrier products remain uncut at 154 bp.

3. Results

Table 1 shows the country where sheep were sampled, mean number of lambing records and mean litter size of the ewes sampled for each breed.
In addition to the sheep with litter size records (Table 1), other sheep without records that were also tested were Tyrolian Mountain Sheep—white (n = 1), German Mountain Sheep—brown (n = 4), Romanov from Germany (n = 1), Romanov from Canada (n = 13), Galician from Spain (n = 15) and Barbados Blackbelly (n = 1).

The Booroola FecB mutation in the BMPR1B gene was present in samples from the Chinese Hu and Han sheep. All of the Hu sheep were homozygous (FecB/FecB) for FecB. Their mean lifetime records of litter size was 2.95 (S.E. = 0.10). The FecB genotypes in the Han sheep included FecB/FecB (n = 4), FecB/FecB+ (n = 7) and FecB+/FecB+ (n = 1). Mean litter sizes were 2.99 (S.E. = 0.24) for the four FecB/FecB ewes and 2.73 (S.E. = 0.13) for the seven FecB+/FecB+ ewes. The FecB+/FecB+ ewe had a mean lifetime litter size of 3.50, with individual litter records of 3, 3, 3, 4, 5 and 3.

None of the other breeds sampled carried the FecB mutation, and none of the sheep sampled carried the Inverdale FecX mutation in the BMP15 gene.

4. Discussion

All of the breeds sampled are noted for their high prolificacy. The Chinese Hu sheep have a mean litter size of about 2.1 (individual litters range from 1 to 8) and the ability to lamb twice per year (Feng et al., 1996; Yue, 1996). The Small-tailed Han sheep from China are also highly prolific, averaging 2.4 lambs born per ewe lambing (Feng et al., 1996). The Mountain Sheep breeds from the alpine regions of Bavaria (Germany), Tyrol (Austria), Southern Tyrol (Italy) and Engadine (Switzerland) are described as having prolificacy ranging from 1.6 to 2.2 lambs born per ewe lambing depending on how they are managed (Farid and Fahmy, 1996). The mean litter size in German Whiteheaded Mutton sheep was reported to range from 1.8 to 2.1 (Farid and Fahmy, 1996). In a review of prolificacy in Romanov sheep, which originated in Russia, Fahmy (1996) presented litter size date from 17 published reports from nine countries; the mean litter size for mixed-age flocks was 2.9 (range = 2.2–4.4). D’Man sheep from Morocco have a mean litter size of about 2.1 (Boujenane, 1996) and high variation in ovulation rate has led to speculation that a single gene affecting prolificacy could be segregating in this breed (Lahlou-Kassi and Marie, 1985). The Chios breed originating in the Greek island of Chios, has an overall average litter size of 1.8, but in some flocks the litter size is as high as 2.3 (Hatziminaoglou et al., 1996). The Chios flock of the Cyprus Agricultural Research Institute, that the sampled ewes came from, has an average litter size of 1.9 (Papachristoforou et al., 2003), with individual litters ranging from 1 to 6. The East Friesian breed developed in the East Friesland region of Northern Germany and the East Friesian Islands has been described as the third most prolific breed in Europe, after the Finn and Romanov (Farid and Fahmy, 1996) but the animals require good care to fulfil this potential in prolificacy. The litter size of mature ewes of the rare Teeswater breed from Teesdale in England averages about 2.5 (Fahmy and Mason, 1996). The Bluefaced Leicester breed originated in Northumberland, England. Ewes average 2.2 lambs born per ewe lambing but in well-managed flocks this average can reach 2.5 lambs born per ewe lambing (Fahmy and Mason, 1996). Rastogi et al. (1980) reported that flocks of Barbados Blackbelly sheep on three research stations had mean litter sizes ranging from 2.0 to 2.3.
Prolificacy in St. Croix hair sheep ranges from 1.6 to 2.2 lambs born per ewe lambing, depending on season and feeding level (Godfrey et al., 2003). St. Croix sheep are also known as White Virgin Islands Sheep or Creole (Mason, 1980a), and studies of Creole sheep in the West Indies suggest that a major gene for prolificacy may be present (Mahieu et al., 1989). Loa sheep are a strain of the Icelandic breed where recent evidence suggests that a major gene increasing litter size by about 0.7 is segregating (Jonmundsson and Eythorsdottir, 2003).

The Galician breed, also known as Marinana, comes from the Galicia region of northwest Spain and has an average litter size of about 1.8, although in well-managed flocks it can exceed 2.8 (Fahmy and Mason, 1996). Litter size in Finns in Finland averaged 2.8 (Maijala, 1996), and this breed has been used widely in crossbreeding programmes in many countries. The Lleyn breed originated in Wales, and litter size ranges from 1.8 to more than 2.0 (Anon, 1998).

The discovery of the \textit{FecB} mutation in the Hu and Han breeds brings to five the number of breeds known to carry this mutation, excluding the numerous breeds into which \textit{FecB} has been introgressed from the Booroola Merino in the last 25 years (Davis et al., 1991). It appears that \textit{FecB} is fixed in populations of Garole (Davis et al., 2002) and Hu sheep but segregating in the Javanese (Davis et al., 2002), Booroola Merino (Piper et al., 1985) and Han breeds.

It is not known whether the 2 breeds, Hu and Garole in which \textit{FecB} is fixed, have common ancestry. Adult Hu ewes typically weigh 32–44 kg, the fat-tail is small with a triangular fat deposit near the base, the fleece is white and both sexes are polled. In contrast, the Garole are a microsheep weighing 11–14 kg, they have a short thin tail, the fleece is light brown, females are polled and males are horned. The ancient silk route ran westward from Shanghai, branched at the city of Kashi in Western China with one branch travelled south through Pakistan and India to Calcutta. Thus, the Garole sheep of Bengal and the Hu sheep of Jiangsu and Zhejiang provinces are each farmed near a terminus of the silk route and it is possible that sheep carrying \textit{FecB} once travelled along this trade route. Although Garole and Hu sheep have markedly different phenotypes, both breeds are reported to have some individuals with an earless phenotype (Bose et al., 1999; Mason, 1980b), which may also suggest that these breeds are distantly related. The earless phenotype is present in Javanese Garut sheep (Mason, 1980c), which have also been reported to have \textit{FecB} segregating in the population (Davis et al., 2002).

Early reference to the prolificacy of Hu (Shanghai) sheep was made by Charles Darwin (Darwin, 1883). Both the Hu and Han breeds are descended from Mongolian sheep (Chang, 1979). Records show that traders brought Mongolian sheep to Zhejiang, Jiangsu, Hebei, Henan and Shandong provinces as early as the 5th century AD (Feng et al., 1996) and it is in these provinces where the Hu (Zhejiang and Jiangsu) and Han (Hebei, Henan and Shandong) sheep are concentrated today.

The presence of the three different \textit{FecB} genotypes in the Han samples shows that the gene is not fixed in this breed. A recent study by Liu et al. (2003) also showed that the three \textit{FecB} genotypes were present in the Han breed and they found a frequency of 0.74 for the \textit{FecB} gene in a sample of 164 Han ewes. Although the sample size in this study was too small for reliable comparisons of litter, the 12 \textit{FecB}^{BB}/\textit{FecB}^{BB} Hu ewes had a similar mean litter size to the four \textit{FecB}^{BB}/\textit{FecB}^{BB} Han ewes (2.95 versus 2.99). Liu et al. (2003) reported a litter size of 2.47 in first parity \textit{FecB}^{BB}/\textit{FecB}^{BB} Han ewes and 3.17 at later parities.
The consistently large litters from the one non-carrier Han ewe in the present study (four sets of triplets, one set of quadruplets and one set of quintuplets) suggests that other genes causing high prolificacy may also be present in Han sheep. Recent studies in Small-tailed Han sheep of the ovine melatonin receptor 1a gene (MTNR1A) located on ovine chromosome 26 have shown an association between a polymorphism at nucleotide position 604 of exon 2 and prolificacy (Chu et al., 2003). The effect in adult ewes (second parity) was large. In that study, the A/A genotype had a mean litter size that was 1.06 and 0.94 higher than the A/B and B/B averages, respectively.

In the present study, tests were carried out only for the Inverdale FecXI mutation. There are five known mutations of the BMP15 gene that produce the same phenotype of increased ovulation rate in heterozygous ewes and infertility in homozygous ewes (Galloway et al., 2000; Bodin et al., 2003; Hanrahan et al., 2004). However, as all five mutations cause infertility in homozygous ewes and there is an absence of reports of infertility among the breeds sampled except the Lleyn, it seems unlikely that genes causing infertility are segregating among these breeds. The Lleyn is one of the founder breeds of the Cambridge and Belclare breeds. The FecXG mutation of BMP15 causing infertility among homozygous ewes has been identified in Cambridge and Belclare breeds (Hanrahan et al., 2004). A high incidence of ovarian hypoplasia has been reported in a Lleyn flock by Vaughan et al. (1997) and their description of the ovaries was very similar to the small streak ovaries observed in homozygous Inverdale ewes. Recently Mullen et al. (2003) confirmed that the FecXG mutation of BMP15 is present in Lleyn sheep.

Although all of the breeds sampled are highly prolific, there are big differences in the husbandry systems in which they have evolved and this could affect whether a spontaneous mutation leading to large litters is retained or lost. An example of one extreme is the Tyrolian Mountain Sheep run in an alpine environment where it is difficult for ewes to rear more than two lambs, and at the other are Hu sheep which have been described as a barn-yard breed (Chang, 1979) because they are typically managed in very small flocks that are penned all year. Selection in the Tyrolian Mountain Sheep has been for short lambing intervals but would be against large litters such as occur in many ewes carrying the FecB mutation whereas the intensive management of Hu sheep would favour selection for large litters, which could have eventually led to the fixation of FecB with its large effect on prolificacy in this breed.

5. Conclusion

A previous study had suggested that the presence of FecB in Booroola Merino and Javanese sheep probably traced back to the Garole sheep of Bengal. The discovery of the FecB mutation in the Chinese Hu and Han breeds might be because the mutation arose spontaneously in two separate events in the Garole and Hu breeds or because these breeds share a common ancestor. The absence of the FecB and FecXI mutations in the other prolific breeds does not preclude major gene effects on prolificacy in some of these breeds, and more extensive screening is required as tests for newly discovered mutations are developed.
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