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Aspects of Major Genes in Sheep Production

M. H. Fahmy
Agriculture and Agri-Food Canada, Dairy and Swine Research and Development Centre, P.O. Box 90, Lennoxville, Quebec, Canada, J1M 1Z3.

A modified version of this article was presented at the 49th Annual Meeting of the European Association of Animal Production in Warsaw, Poland, 24-27 August, 1998. Even though, several aspects have already been published in previous issues of the Sheperd, I feel that putting all the knowledge available on the subject under one heading will be useful to the Shepherd readers interested in the subject of major genes in sheep.

The concept of a major gene responsible for marked increase in prolificacy was first suggested by the Australian scientists Piper and Bindon in 1980, who later made a detailed description on the events leading to the recognition of the Booroola gene (FecB.) as a major gene for prolificacy in sheep (Piper and Bindon, 1996). However, as reported by Dr. Helene Newton Turner (1982), the origin of the Booroola gene may have been from the Bengal sheep which had shown exceptional prolificacy and which a modern relative, the Garole sheep, is believed to have a major gene for prolificacy (Ghalsasi et al. 1994).

In the last decade, several breeds showing high prolificacy were examined and several showed characteristics indicative of the possibility of a major gene segregating in the population. Among these breeds the Thoka, Belle-lle, Olkuska and Javanese are the ones most often identified, though not necessarily the most studied. In addition to these breeds where the higher prolificacy seemed to have developed naturally, most probably as a result of mutations, there are several breeds which were developed by screening populations of different breeds and subsequently by mating animals with exceptional prolificacy.

Although in most of the animals prolificacy was probably caused by quantitative inheritance, it is now believed that the high prolificacy of the Cambridge breed is caused by a major gene. So far, the majority of the genes identified show an inheritance indicative of their presence on autosomal chromosomes, however, a mutant gene located on the X chromosome (the inverdale gene) has been reported recently in Romney sheep, in New Zealand (Davis et al., 1991).

Recently, a different kind of major genes was discovered in the United States and Australia. These genes are responsible for a major improvement in carcass quality, manifested by an increase in leanness and a decrease in fatness. Although similar genes with large effect on leanness have been identified in cattle and swine, the callipyge and carwell genes are believed to be the first to be identified in sheep.

The present review presents the origin and performance of the most important breeds with confirmed major genes and a short reference to others where the presence o major genes is a strong possibility.

The Booroola gene (FecB).

The Booroola fecundity gene (FecB) is by far the most widely distributed, studied, and used in the sheep industries all over the world.

World distribution

The Booroola gene was first identified in Australia. New Zealand was the first country in 1972 to import Booroola from Australia before resolving that high prolificacy in Booroola Merinos (BM) is controlled by a single gene. Other importations followed between 1973 and 1980. (Davis and Fogarty 1996).

The first importation to USA was in 1982; Canada followed suit in 1985. Uruguay, Brazil, and Chile are so far the only countries in South America to import the BM gene. (Fahmy, 1996b).

In 1980, Hungary became the first European country to import BM. In France, INRA introduced BM rams from Australia, in 1981. Importations of the Booroola gene to UK consisted of 20 BM x Border Leicester ewes in 1981 and two BM x Coopworth and one BM x Leicester heterozygous rams imported by Scotland from NZ (Veress, 1996).

Czechoslovakia purchased seven BM rams from New Zealand. Germany's first importation of the BM gene consisted of 50 vials of frozen semen from NZ in 1988. In 1988 Poland imported from NZ 121 frozen BM embryos heterozygous for the FecB gene. The Netherlands imported in 1986 from the UK three crossbred BM x Trexel rams heterozygote for the FecB gene. Recently a private company in Spain imported BM sheep (Veress, 1996).

The only two importations of Booroola to sub-tropical countries of Africa and Asia were to Israel from NZ in 1985 and to South Africa from Australia in 1984, (Galal, 1996).

Investigations

A complete review of comparisons between Booroola and local breeds for production traits in different countries was prepared by Davis et al. (1990). Table 1 is a summary of the results presented for reproduction traits. Some additional recent results from various geographical areas are listed below.

Oceania: The initial utilization of the FecB gene was to introduce it by crossing into the Australian Merino industry. Numerous studies on Booroola crosses have assessed the effects of such crossings and also measured differences in lifetime productivity between animals with and without the FecB.

Results indicated that the BM was suitable for extensive wool production systems, even if mortality rate was much higher due to larger litters, and this is so provided that adequate ewe nutrition can be guaranteed to assure higher lamb weaning rates. At present, exploitation of FecB in Merino flocks is directed at increasing the gene frequency to the point where all rams have a high probability of being homozygous. The gene can then be introduced by sheep breeders to other Merino strains by backcrossing so that the desirable features of that strain are combined with the increased reproductive performance of the Booroola.

The economic benefits of increasing prolificacy in the prime lamb industry led

Table 1: Performance of Booroola cross compared to local breeds in different countries (Davis et al. 1990)

	Ovulation rate	Litter size	Lamb surviva 1%	Lamb weight in kg at:		Lambs weaned per ewe joined	
				Birth	Weaning	Number	Wt, kg
Booroola	2.56	1.99	77.0	3.31	15.2	1.45	22.04
Local breed	1.57	1.38	86.8	4.16	18.1	1.12	20.27
Difference	0.9	0.61	-9.8	-0.85	-2.9	0.33	1.77

to the utilization of FecB for improving reproductive efficency in Britrish breeds through crossing in order to achieve rapid and permanent increases in the lambing rate (Table 2). Piper et al. (1988), stated the following reasons as to why the major use of the FecB gene in Australia would be best through its incorporation into British breeds and their crosses.

Firstly, lamb survival and growth is better in British breeds and their crosses with Merinos than among pure Merinos, suggesting that the problems associated with triplet and higher order births would be reduced.

Secondly, depending on lamb prices, a higher net profit from prime lamb production means that increased costs incurred in rearing large litters are easier to justify; and,

Thirdly, prime lamb producers are committed to high reproduction rates.

The prime lamb industry in Australia is based on the use of Border Leicester Merino (BLM) ewes as the prime lamb dam mated to a terminal meat sire to produce three-way cross lambs. Utilization of FecB has the potential to increase the reproductive performance of the BLM by 10-30%. This may lead to increased revenue or a significant reduction in production costs. Ewe reproduction rate is a limiting factor in prime lamb profitability. Increasing the number of lambs sold per ewe mated increases the efficiency of production by distributing maintenance costs of the breeding flock across additional offsprings.

Poland: In Poland, BM were mated to Polish Merino, Wielkopolska, Kamieniecka and Uhruska. First-cross ewes from such matings had a prolificacy rate of about 1.82 lambs born, which is 55% higher than that of native Polish breeds (Table 3). However, as a result of low fertility and lamb survival up to weaning, their fecundity was no higher than 1.07 lambs weaned per ewe joined, or only 0.11 lambs higher than that of native breeds (Osikowski and Borys 1996).

Israel: The only trial with BM in the Middle East was conducted in Israel using native Awassi and Assaf sheep. Awassi and Assaf (100 ewes of each) were inseminated with semen from homogenous BM rams. The backcrosses were produced by mating F_1 rams to native ewes. Prolificacy of F_1 ewes, heterozygous for the FecB gene, was about 0.6 lambs higher than those of native breeds; with the backcrosses intermediate. Gootwine et al. (Personal communication) estimated that Awassi and Assaf ewes homozygous for the FecB gene will produce about one lamb more per parturition (Table 4). They suggested that the use of the newly developed prolific Awassi can be extended not only to intensively managed flocks, but also to extensive systems, where the traditional Awassi phenotype is preferred.

France: Bodin et al. (1990) reported a trial in which BM were systematically crossed with Merino D'Arles to produce a new synthetic and prolific line of Merino. They divided the animals into three possible genotypes: those with a high probability of carrying the FecB allele, those with a high probability of being non-carriers and those having equal probabilities of carrying or not carrying the FecB allele. Their results are summarized in Table 5. One copy of the gene resulted in an increase of 1.15 in

Table 2: Reproductive performance in Australia of crossbred ewes derived from Booroola and control Merinos

Breed of dam	Percentage of Ewes with ovulation rate					
	1	2	3	4	<4	Mean
BLB	7.7	31.3	26.4	20.3	14.2	3.07
BLM	19.4	66.7	13.9			2.13
DHB	9.3	37.2	37.2	8.5	7.7	2.75
DHM	38.7	57.5	3.8			1.73
	Litter size					
	1	2	3	4	<4	Mean
BLB	17.0	42.7	29.2	7.6	3.5	2.31
BLM	38.8	60.2	1.0			1.66
DHB	23.5	45.2	25.2	3.9	0.8	2.14
DHM	51.0	49.0				1.45

BLB=Border Leicester Booroola, BLM=Border Leicester Merino
DHB=Dorset Horn x Booroola, DHM=Dorset Horn x Merino

Table 3: Reproductive performance of first crosses between Polish breeds and BM (Osikowski and Borys 1996)

Native breed crossed	Fertility	Litter size at birth	%lambs weaned	Fecundity **
Polish Merino	79 (-7)*	1.95 (34)	81 (-9)	1.25 (13)
Polish Merino	90 (12)	1.64 (30)	87 (-6)	1.15 (28)
Wielkopolska	100 (!8)	2.0 (100)	79 (-21)	1.22 (67)
Kamienieska	62 (-38)	1.8 (26)	87 (7)	0.88 (-23)
Uhruska	95 (6)	1.5 (25)	83 (2)	1.19 (32)

* (% of native breed) **Lambs weaned per ewe joined

Table 4: Performance of Booroola Merino (BM) crosses with Awassi and Assaf. (% difference in brackets)

Breed group	Lambs Born/ewe lambing			Ovulation rate	
	1st crop	2nd crop	3rd crop	Mean	% ewes with <3CL*
BM x Awassi	1.6 (33)	1.8 (50)	2.1 (47)	2.8 (133)	0.88%
1/4 BM-3/4 Awassi	1.4 (17)	1.5 (25)	1.6 (14)	2.7 (125)	0.71%
BM x Assaf	1.9 (27)	2.1 (40)	2.5 (47)		
1/4 BM-3/4 Assaf	1.7 (13)	1.9 (27)	2.0 (18)		

* None of the Awassi ewes had <3 CL

ovulation rate and 0.68 lambs which correspond, in general, to the results obtained with BM mating other native breeds elsewhere.

USA and Canada: In USA and Canada most evaluations of BM crosses were done with other prolific breeds, mainly Finnsheep and Romanov. In USA, ovulation rate of first-cross Finnsheep ewe lambs was 0.2 to 0.4 eggs lower than that of first-cross BM. However, first-cross ewes had approximately 0.15 lambs more than first-cross Finnsheep (Table 6). In Canada, BM rams were mated to Finnsheep and Suffolk ewes to evaluate the effect of the fecundity gene in prolific and non-prolific sheep. When averaged across age groups and experiments, BM first-cross ewe lambs weaned fewer lambs than first-cross Finnsheep ewe lambs even though they gave birth to more lambs, (Castonguay et al. 1990). Fahmy (1995) compared the reproductive performance of first cross and backcross of Finnsheep and of Romanov to those of BM (Table 7). BM crosses were inferior in yearling fertility and litter weight at weaning, and in prolificacy, comparable to Finnsheep crosses but inferior to Romanov crosses. On the other hand, BM first cross registered the lowest perinatal and preweaning mortality.

The Javanese sheep gene (FecJ)

Origin

The sheep of Indonesia are of two distinct types, thin-tailed and fat-tailed. Their origin is not known, but presumably the thin-tailed type came originally from the Indian subcontinent, and the fat-tailed type came from west Asia. There has been some admixture of European breeds from the Netherlands, UK, Australia and New Zealand but these breeds have made only a minor contribution to the present gene pool. The most popular of the thin-tail type is the Javanese Thin-Tailed (JTT), also known as Priangan of western Java. Other strains include the Semarang from central Java, and the Sumatra type from the island of that name. The Javanese Fat-Tail (JFT) is found predominantly in eastern Java.

Performance

Mean litter sizes approach 2 and occasionally exceed it, indicating that these sheep are moderately prolific. However, the means are not consistent with reports of an exceptionally high frequency of litters of 3 or more. Obst et al. (1980) reported 16.8% of 262 litters with 3 to 5 lambs per litter, in a flock in which the most frequent litter size class was singles and the overall mean litter size was 1.71.

Table 5: Proportion of ewes with various ovulation rate and litter size (Bodin et al. 1990)

Genotype	1	2	3	4	>4	Mean
			Ovulation Rate			
++	91.4	8.1	0.4	-	-	1.09
++&F+	60.1	25.7	3.4	0.8	-	1.45
F+	12.9	57.6	22.9	5.7	1.0	2.24
			Litter size			
++	69.9	28.1	2.0	-	-	1.32
++&F+	48.0	45.0	7.0	-	-	1.61
F+	28.7	45.2	23.3	2.6	0.3	2.00

Table 6: Reproductive traits of BM crosses compared to F crosses in U.S.A.

Trait	1/2F	**1/2 BM**	*
Age at 1st estrus, d	194	**208**	3
Age at 1st estrus, d	183	**207**	2
OR: Ewe lambs	2.41	**2.89**	3
OR: Ewe lambs	1.69	**1.89**	2
CR: Ewe lambs	87	**78**	3
CR: Ewe lambs	81	**39**	2
CR: 2 and 3 year old	92	**99**	1
LS: Ewe lambs	1.58	**1.84**	3
LS: Ewe lambs	1.53	**1.53**	2
LS: Mixed ages	1.91	**2.04**	4
LS: 2 and 3 year old	2.00	**2.26**	1
Lambs weaned/ewe lambing	1.26	**1.02**	1
2 and 3 year old	1.82	**1.76**	1

* References: 1, 2 Young and Dickerson (1991a, 1991b); 3, Bunge et al. (1993); 4, Willingham et al. (1988

Table 7: Reproductive performance of BM crosses compared to Finnsheep and Romanov crosses, (Fahmy 1995)

	1/2F	1/4F	1/2R	1/4R	**1/2B**	**1/4B**
Fertility, %	84.4	73.0	91.6	95.2	**62.6**	**61.9**
Lambs born	1.86	1.44	1.99	1.63	**1.70**	**1.42**
Lambs weaned	1.64	1.40	180	1.50	**1.58**	**1.25**
Litter wt. at birth, kg	5.52	5.02	6.31	5.41	**5.17**	**5.23**
Litter wt. at weanig, kg	24	22	26	24	**20**	**21**
Lamb mortality:						
at birth, %	5.7	2.9	4.7	4.0	**3.5**	**4.0**
1-50 days, %	6.5	2.0	2.8	4.2	**1.7**	**5.6**

Segregation of a gene with large effect on ovulation rate is the possible explanation for this apparent anomalous pattern. The first indication was the unusually high repeatability of ovulation rate and litter size (Bradford et al., 1986; Reese et al., 1990; Iniguez et al., 1990). Subsequent breeding data supported the presence of such a gene (Bradford et al. 1991). The gene has been designated $FecJ^F$ and a single copy increases ovulation rate by 0.7 to 0.9. The effect on litter size is a little less especially in yearlings. Whether or not the FecJ is the same as FecB is not yet known. The similarity of the effect and the postulated origin of the FecB gene (Turner, 1982) suggest it may be.

Bradford et al.(1986) suggested that the $FecJ^F$ gene probably exists in all

Table 8: Lamb survival and litter weight at 90 days for ewes of three genotypes in two flocks differing in level of inputs

	Ewe Genotype		
	$FecJ^+$ $FecJ^+$	$FecJ^F$ $FecJ^+$	$FecJ^F$ $FecJ^F$
Lamb Survival (%)			
Low plan of nutrition			
Poorest - 4 yrs. (1)	74	58	41
Best - 5 yrs. (1)	89	75	59
High plan of nutrition			
3 yrs. (2)	93	78	81
Litter Wt. 90d (kg)			
Low plan of nutrition			
Poorest - 4 yrs. (1)	7.7	7.4	6.7
Best - 5 yrs. (1)	10.9	11.9	12.2
High plan of nutrition			
3 yrs. (2)	15.4	18.0	20.3

(1) From Inounu et al. (1993).
(2) From Subandriyo and Inounu (1994)

strains of Indonesian sheep but at a relatively low frequency, (0.05 to 0.25). They based their conclusions on the fact that litter size ranges from 1 to 6 in JTT ewes, 1 to 5 in JFT ewes, and 1 to 4 in a small sample of Semarang ewes and that repeated records of 3 and occasionally 4 were observed in a flock of Sumatran ewes with an average litter size of 1.54. Repeatability of litter size in a JTT flock in which the gene was segregating was 0.62 (Inounu et al., 1993).

Bradford et al. (1991) reported mean litter sizes of 1.23, 1.89 and 2.37 for first litters and 1.30, 2.11 and 2.83 for second and later litters, for ewes homozygous non-carriers, heterozygous and homozygous carriers of the mutant allele, respectively. Mean litter sizes for three additional years from the same flock were 1.15, 2.14 and 2.48, repectively (Subandriyo and Inounu, 1994).

The Thoka gene

Origin

A major gene for prolificacy has been recently identified in Icelandic sheep. The gene is given the name "Thoka" after the ewe orginally possessing the gene. That two flocks in southeastern Iceland contained sheep that produced an unusually high percentage of triplets in an area where twins were a rarity was an astonishing event. The pedigree of almost all ewes with multiple births could be traced back to the ewe Thoka, born in 1950. However, the gene might have existed earlier since Thoka's grandmother was claimed to have given birth to triplets around 1940 (Jonmundsson and Adalsteinsson, 1985). One son of Thoka used in a neighboring farm resulted in a significant increase in the number of triplets (8.7 vs. 1.4%) and quadruplets (0.7 vs. 0%).

Performance

Jonmundsson and Adalsteinsson (1985) confirmed the presence of a single major gene responsible for the increased prolificacy. They noted that in "normal" Icelandic sheep, non-carriers of the Thoka allele, ovulated on average, 1.59 ova, whereas the carriers ovulated 2.14, ($P<0.001$). In another group of ewes, Thoka allele-carrier ewes ovulated, on average, 3.34 ova compared with 2.20 for non-carriers ($P<0.001$) and fecundity was 2.29 vs 1.66 ($P<0.001$) (Eythorsdottir et al. 1990). The repeatability of ovulation rate for carriers averaged 0.69, whereas that of non-carriers averaged 0.24. Most of the results on the Thoka gene assume the existence of heterozygous animals. Scientists calculated that a copy of the gene may be responsible for an increase of 0.64 lambs per ewe lambing; the effect on ovulation rate is even greater (1.21 ova).

The Olkuska Gene

Origin

Olkuska is a breed orginating from the crossing of local long-wool Polish sheep with Pomeranian, Friesian and Holstein sheep at the beginning of the 20th century. As a result of intensive crossing with other breeds, the population of these sheep has declined drastically from almost 10,000 in 1960 to no more than 200 in 1986, (Grabowski et al., 1987). The use of lamb pelts in the fur industry is believed to have stimulated selection for high litter size. Recent results and analysis of production records suggest the presence of a major gene in the Olkuska (Martyniuk and Radomska 1990).

Performance

Average mature body weight is about 100 kg for rams and 60-70 kg for ewes. Ewes are good milkers and show excellent mothering abilities. Ewe lambs are usually mated for the first time at 10 months of age. The Olkuska sheep are prolific with fecundity rate of over 190 lambs per 100 ewes. Triplets and quadruplets are frequent and large litters of five and six are not rare. Olkuska rams were crossed intensively with Polish Merino, and the resulting F1 ewes showed increased prolificacy, 1.30-1.77(Grabowski et al., 1987). Ovulation rate of F1 Olkuska-Polish Merino ewes, 1, 2 and 3 years of age averaged 2.20, 1.95 and 1.74, respectively, compared to 1.15 and 1.06 for young and adult pure Polish Merino ewes, (Martyniuk, 1988).

The high prolificacy of the Olkuska may be the result of a major gene. Martyniuk and Radomska (1990) reported ovulation rates of 2.71 vs 1.67 and litter size of 2.10 vs 1.5 for suspected carriers and non-carriers of F1 Polish Merino x Olkuska ewes, whereas the 3/4 Olkuska suspected carriers averaged 2.83 and 2.16, respectively. Ovulation rate and litter size of suspected carriers of the mutant allele had 1.04 more ovulations and 0.60 more lambs than the non-carriers (Radomska et al., 1988). These estimates are remarkably consistent with those in breeds with confirmed presence of a major gene, (Martyniuk and Radomska, 1990; Knothe and Wierzchos, 1992). The repeatability of 0.45±0.03 estimated for litter size, may indicate the segregation of a major gene (Knothe and Grabowski, 1990).

A nucleus flock of Olkuska sheep was established at the Zelazna

Experimental Farm in 1992 to conserve this endangered breed (Martyniuk, 1996). Ovulation rate in this flock was recorded by laparoscopy over the 1992, 1993 and 1994 breeding seasons and ranged from 1 to 8 with a mean of 3.0 in each year. Litter size at birth varied from 1 to 5, with a mean for the flock of 2.14, 2.42 and 2.33 for the 3 years, respectively. It was estimated that, assuming a single gene to be responsible for fecundity, one copy of the putative gene in heterozygous carriers increased ovulation rate by 1.03 and litter size by 0.63 lambs.

The Belle-Ile sheep

Origin

The sheep population of the Belle-Ile island in nothern France is believed to be the surviving progeny of an old population of south Brittany sheep called "Race de Deux," i.e., Twin Breed (Malher and Denis, 1988). This breed is the result of a cross between the local population and a Dutch breed of sheep, called "Flandrin," which was introduced to the Vannes region in the middle of the 18th Century.

Performance

Mature weight of Belle-Ile ewes averages 40 kg. The average litter size in 132 litters of ewes 2 years old or older was reported at 2.26 lambs born, with 37% born triplet or higher. One ewe was reported to have produced 30 lambs in eight parturitions and two of her daughters produced 27 lambs in seven parturitions. Recent results by Malher and Le Chere (1998) indicated that ovulation varies between 1 and 8 with a mean of 2.54, whereas litter size varied between 1 and 7 with a mean of 2.23. Repeatability of ovulation rate was 0.8 and litter size 0.2. The high prolificacy of Belle-Ile sheep is suspected to be the result of a major gene segregating in this population (Malher and Le Chere, 1998). In presumed Homozygote, heterozygote and non-carriers, ovulation rate averaged 4.0, 2.4 and 1.6, and litter sizes averaged 2.7, 2.2 and 1.4, respectively. Thus, one copy of the gene results in an increase of about 1.2 in ovulation rate and 0.65 in litter size, again consistent with the results from other major genes.

The Garole sheep

Origin

These "microsheep" are found in Sundarbans, an area of West Bengal, India, south of Calcutta and extending eastwards into Bangladesh. Their population is about 50,000, raised in small flocks. Garole sheep graze year-round along field boundaries and on the sides of roads. The area is humid with rains every month of the year but mostly between May and October. In April and May, the maximum temperature averages 36° C, and in December and January the minimum temperature averages 13° C (Ghalsasi et al., 1994).

Performance

Garole sheep are very small, weighing 0.6-0.9 kg at birth, 6-7 kg at 6 months and 10-14 kg at maturity. Adult sheep are 45-50 cm long (from shoulder to pin bones), 44-50 cm height (at withers) and have a chest circumference of 56-61 cm. Males are usually horned and females polled. Ewes lamb for the first time at 11-13 months of age and can breed year-round with no specific breeding season. Information on litter size collected from19 flocks and involving 56 lambing records indicated that 91% of ewes produce multiple births, of which 64.3, 21.4 and 5.4% were twins, triplets and quadruplets, respectively. Average litter size was 2.23 lambs (Ghalsasi et al., 1994). Garole sheep are raised solely for meat and never shorn or milked. Wool is coarse, with mostly medullated fibres, (Singh and Bohra, 1996).

Researchers have speculated that ancestors of this prolific breed were imported into Australia from Calcutta in 1792 and 1793. These animals may have contributed to the prolificacy of the BM sheep of Australia (Turner, 1982). There are also evidence that the prolificacy in Javanese sheep may have been the result from introductions of Bengali sheep into Java.

Genes discovered by scanning populations

The Cambridge breed

Origin

The Cambridge breed was described in details by Owen (1996). The following is an extract from his paper. "The objective of developing the Cambridge sheep was to create a new damline to produce rams for siring prolific crossbred ewes for mating with terminal sires of meat breeds. The foundation group was selected by the screening of several British meat breeds for ewes of high prolificacy. The criterion of selection was that each ewe should have given birth to a minimum total of 9 lambs in the three lambings preceding selection. As a result of this screening 54 ewes from nine breeds and crosses were obtained. The ewes were mated in their first season to seven Finnsheep rams. Subsequently homebred F1 rams and rams from backcrosses to the original foundation ewes, were used as sires, until the establishement of the composite breed, with an approximate genetic contribution of 20-25% from the Finnsheep."

Performance

Ovulation rate: The first evidence that the high proilificacy of the Cambridge breed may be caused by a major gene was reported by Hanrahan (1990) after observations made earlier indicated a wide range of ovulations and a high coefficient of variation that would be expected with the segregation of major genes with a large effect (Owen et al., 1990). However, the distribution from a large data-set did not show the trimodal distribution expected with the segregation of one gene at a single autosomal locus (Fig. 1). The best explanation of the data is the segregation of major genes at two loci. One possible model is a gene at an autosomal locus and another from and X-linked locus. Another model incorporates a restricted gene, possibly at a single locus, wide causing wide variability to a basal distribution.

Lambing performance of the ewe and lamb survival: Table 9 shows the main aspects of lambing performance in the Bangor flock for recent years. Average

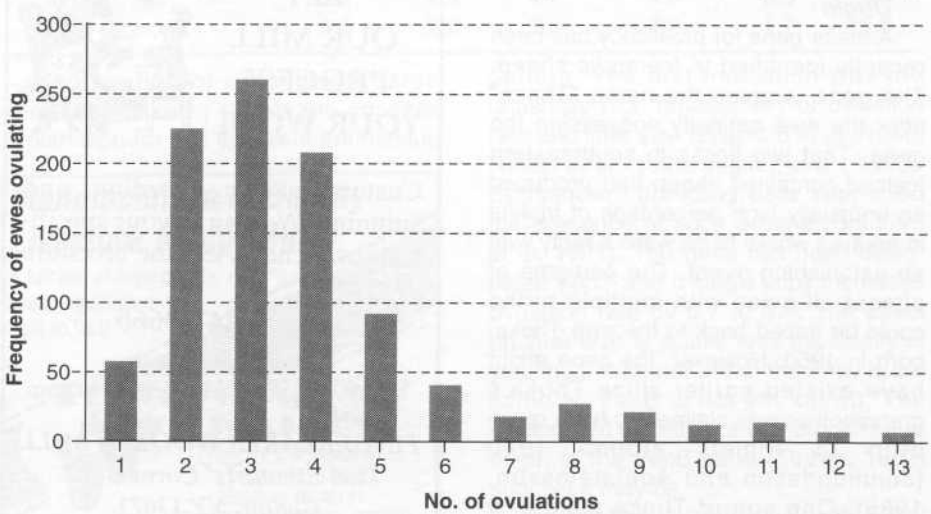

Fig. 1 Ovulation rate of Cambridge sheep (Owen, 1996)

the BM into existing populations of non-prolific breeds has been reported worldwide. The following are a few of those reported.

The Booroola Leicester (Australia)

Development began in 1981 by single sire matings of homozygous BM ewes with stud Border Leicester (BL) sires. Two years later the ewe progeny were mated to new BL sires to create 3/4 BL progeny. From this point onwoard ewes were selected on the basis of repeated ovulation rates and backcrossed again to new BL sires to create flocks (7/8 BL) that had the appearance of straightbred BL. To ensure a wide representation of BL blood, different rams were used at each mating. In 1992 the Booroola Leicester was accepted as an Appendix breed to the Flock book and a Breed Society was formed.

Hyfer (Australia)

The breeding program for Hyfer sheep was initiated in 1978 and involved two generations of crossing with subsequent selection. Rams from two high fertility Merino strains (BM and Trangie Fertility) were bred to Poll Dorset ewes. These breeds and strains combine high lambing rate and out-of-season breeding ability with good lamb growth, carcass quality and wool traits. Rams and ewes of the F1 crosses were reciprocally mated to produce a base population comprising 1/2 Poll Dorset, 1/4 Trangie Fertility Merino, 1/4 BM. The base population was interbred and ewes joined in an accelerated lambing system. Following three matings in their first two years, top performing ewes were selected into a nucleus flock to breed replacements. Selection was on the basis of total weight of lamb weaned (adjusted for age and sex) by ewes over the two years. Rams were selected primarily on their dam's performance (total weight of lamb weaned) with consideration given to growth, leanness and pollness (Davis et al. 1996). The recognition of FecB gene was made after the Hyfer breeding program was initiated. The gene frequency of FecB was subsequently estimated to be about 50% in the original Booroola sires used and about 10% in the base population.

The mean litter size of mature Hyfer ewes mated in late summer is 1.91. The distribution of litter size is approximately 30% single, 55% twin, 12% triplet and 3% higher order. Ewes mated under an accelerated 8-monthly lambing system achieve an average of 1.22 lambings per year, with fertility levels of 75 to 80% for a 6-week spring mating season. Average lambing rates under extensive grazing management are 1.98 lambs born and 1.45 lambs weaned/ewe mated/year.

Estimated heritability for mean performance (3 records) for litte size is 0.31 and for lambs born, lambs weaned and weight of lamb weaned, 0.19, 0.10 and 0.13±0.06, respectively (Fogarty et al., 1994).

Hungarian Prolific Merino (Hungary)

The breed was developed from a cross between BM rams and Hungarian Merino sheep. Animals carrying the fecundity allele were recognized as a new breed in 1992. The sheep are selected for frequent lambing, heavier mature weight, longer and finer wool fibres and pollness. Selection is also directed to establishing a nucleus population homozygous for the fecundity gene.

The new breed has the same physical appearance, the several physiological characteristics (late sexual maturity, prolonged breeding season, etc.) of the Merino sheep. The two strains differ in productivity. In sheep subjected to accelerated lambing, prolificacy averaged 1.98 and was found to vary according to lambing interval, from 1.77 for ewes with intervals less than 230 days to 2.12 for those with intervals of 261-290 days. The average number of lambs born and weaned per ewe per year is 2.45 and 1.91, respectively. Lamb mortality at birth is about 9% and from birth to weaning 14%. At present, the population of registered Hungarian Prolific Merino is about 2000 ewes concentrated on three farms (Veress, 1996).

Boolys (Canada)

A new breed of sheep was developed by introgressing the mutant Booroola allele (FecB) from BM sheep into the DLS breed. The development of that new breed was unique in that crossing and backcrossing was practiced to achieve a final combination of 3/8 Merino-5/8 DLS, then the animals were tested for the presence of the FecB allele. The animals with that mutation were subsequently multiplied to obtain a prolific population homozygous for the FecB gene.

Summarily the development was done in the following manner. The basic population of DLS was mated to rams homozygous for the Booroola locus. The F1, all heterozygous for the gene, were backcrossed to DLS rams; thus theoretically half the progeny were carriers of one copy of mutant gene. These progeny were mated to F1 rams heterozygous for the gene to obtain the final combination, which was then tested for the presence of FecB. In the first years of the study, the presence of animals with the mutant allele was determined from repeated laparoscopy and examination of litter size. In latter years, the more accurate procedure of gene markers was used. The results revealed that about 12% of the 3/8B-5/8BLS population is homozygous and 36% heterozygous for the FecB gene. These were close to the theoretical expectations and insures the possibility of creating a homozygous population.

The results on the productivity of the flock indicated that the ewes were capable of maintaining a lambing rythm of one parturition every 8 months and their prolificacy increased progressively with the increase in the frequency of the FecB gene in the flock. The productivity of the flock in terms of lambs weaned and kilograms weaned per ewe per year increased from 1.6 and 35 kg in 1990 to 2.3 and 64 kg in 1996, respectively. This represented an increase of 49 and 82%, respectively and indicates that not only the number of lambs weaned increased but also the average weight of lambs also increased. The increase in ewe productivity was not accompanied by an increase in mortaltiy which remained at th 20% level and was even lower for the younger ewes lambing their first two litters. (Fahmy and Castonguay, 1990).

Other breeds under development

Israel: introgression of FecB into Awassi.

France: introgression of FecB into Merinos D'Arles and Romanov.

New Zealand: intogression into FecB into Romney.

UK: introgressing FecB into, Dorset, Ile de France, North Country Cheviot, Romney March, Suffolk, Texel.

MAJOR GENES FOR IMPROVING CARCASS QUALITY

The *Callipyge* Gene

Origin

The *callipyge* gene is a newly discovered major gene that affects carcass

composition. It was identified in a flock of Dorset in Oklahoma, USA in the mid eighties. The effect of the gene is not apparent at birth, but by two months of age lambs carrying the callipyge allele and non-carriers can be identified easily. The gene is traced to the telomeric region of chromosome 18 between the markers CSSM18 and TGLA22 and exhibits peculiar inheritance suggesting dominant negative imprinting which was subsequently termed "polar overdominance" (Cockett et al. 1996).

Performance

The mutant allele has shown an exceptional effect on the degree of muscling and particularly on specific muscles in the loin and leg, thus improving the most valuable retail cuts of lamb carcasses. The *callipyge* allele causes a significant increase in the weight of leg and loin muscles and a marked decrease in the overall fatness in the carcass. Lambs with the *callipyge* allele dress between 3 and 4 percent more than normal lambs as shown in Table 10. The higher dressing percentage results from higher total lean content since fatness was found to decrease in *callipyge* lambs.

The area of *longissimus dorsi* muscle in lambs carrying the mutant allele increases by more than 40% (Table 11). Moreover, measures of subcutaneouseous and inter-muscular fat suggest that total fat decreases significantly in *callipyge* lambs. They also had about 0.7% less kidney fat than normal lambs (Table 12).

Dissection of lamb carcasses revealed that the total muscle mass increases while that of fat and bones decreases (Table 13). Therefore, the *callipyge* gene can potentially have a very large economic impact on the value of lamb carcasses and particularly in breeds deficient in leg muscling such as prolific breeds and crosses.

However, the carcasses with the *callipyge* gene are disadvantageously affected by the toughness of the longissimus muscle caused by hypertophy, and reduced intramuscular fat (marbling). Several studies using different approaches were conducted to resolve that problem, such as freezing then thawing prior to storage at -0.5°, or using calcium chloride injection to improve meat tenderness. Electrical stimulation of carcasses after slaughter has also been used as a method for tenderizing meat from *callipyge* lambs. A simple method to increase the tenderness of a muscle is to pro-long the aging process. Aging can be for a longer (80 d) or for a shorter period (1 to 24 d).

Table 10: Dressing percentage of *callipyge* (Cg) and normal (N) lambs

Reference	Breed	Sl. wt.	Cg	N	Cg-N
Fahmy, 1998	Rom, RX	43	52.4	49.5	2.9
Goodson et al. 1998	Crossbreds	52.3	61.6		
		56.7		56.9	
Jackson et al. 1997b	Ramb	52.5	57.3	53.9	3.4
Fernandez, 1996	Ramb X	37	62.7	59.3	3.4
Koohmaraie et al. 1995	Dorset	169d	53.6	51.3	2.3
Snowder et al, 1994	RambX	54.5	52.7	48.4	4.3
	ColumX	54.5	52.1	49.6	2.5
	SuffolkX	54.5	54.5	50.3	4.2

Table 11: Effect of the *Callipyge* allele on loin eye area and backfat

			Area of Loin-eye muscle, cm2			Backfat thickness mm		
Reference	Breed	C. wt	Cg	N	D%	Cg	N	D %
Fahmy, 1998	Rom, RX	21	18.5	13.1	41	4.1	6.1	-33
Goodson et al. 1998	Crosses	32	24.4	16.6	47	.30	.56	-46
Jackson et al. 1997b	Ramb	29.2	17.6		71*	5.9		-
		26.6		10.3			7.5	21*
Fernandez, 1996	Ramb X	26.3	20.9		95*	4.4		-
		22.6		10.7			7.1	38*
Koohmaraie et al. 1995	Dorset	28.5	19.8	14.8	32	4.4	6.3	-30
Snowder et al, 1994	RambX	28.6	21.6	14.3	51	1.5	2.2	-32
	ColumX	29.6	22.1	15.1	46	1.5	2.0	-25
	SuffolkX	26.2	20.3	15.9	28	2.2	2.0	10

Cg=*Callipyge,* N=Normal phenotypes, D=Cg-N/N,%, C and GR=over loin eye and 11 cm from mid point, respectively, *based on different carcass weights

Table 12: Weight of kidney fat/ (g) or % of kidney fat (between brackets)

Reference	Breed	Wt.	Cg	N	Cg-N/ N, %
Fahmy, 1998	Rom, RX	21	202	339	
			(0.9)	(1.6)	-0.7
Goodson et al. 1998	Crosses	32	343	532	
			(1.1)	(1.7)	-0.6
Jackson et al. 1997	Ramb	29	(1.9)		-1.0
		27		(2.9)	
Fernandez, 1996	Ramb X	26	(3.6)		-0.6
		23		(4.2)	
Koohmaraie et al. 1995	Dorset	28	456	566	
			(1.6)	(2.0)	-0.4

Other studies used combinations of two or more methods.

The Carwell gene

This gene was also discovered in the Dorset population in Australia. Its effect is similar to that of the *callipyge* gene but to a lesser extent. There are suggestions that the two genes are in fact the same. Work is underway in Australia and NZ to identify the gene, its location

and its effect. So far information available is scanty.

Conclusions

Major genes whether with large effects on reproduction or causing significant improvement in carcass quality are important tools to make sheep production more competitive and economically viable. As shown, some genes may have some undesirable "side effects," such as the streak ovaries and infertile ewes in Inverdale and Cambridge genes, or the toughness of certain muscles in the case of *callipyge* and carwell genes. Proper use of specific mating schemes to minimize the effect of the former and management and technological advances in meat science to reduce the effect of the latter genes can minimize the negative effects of these genes.

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