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Effects of the FecB Gene in Half-sib Families of Rambouillet-cross Ewes

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Abstract

Records of Booroola-Rambouillet ewes (N = 94) were analyzed to estimate the difference between carriers (B+) and non-carriers of the FecB gene for ovulation rate, fertility, litter size, number of lambs weaned, fleece weight, and body weight within paternal half-sib families. The ewes were progeny of heterozygous (B+) Booroola-Rambouillet rams (n=5) mated to homozygous (++) Rambouillet ewes. Genotype at the FecB locus was predicted using DNA markers known to be linked to the FecB locus. The estimated differences between B+ and ++ ewes were +1.18 ± .12 ova/cycle (P=.0001) for ovulation rate, +.51 ± .16 lambs born/ewe lambing (P=.002), and +.18 ± .18 lambs weaned/ewe lambing (P=.34) in first-parity ewes. Estimated body weight differences between B+ and ++ ewes were –.88 ± .97 kg at 7 mo of age (P = .36) and –2.10 ± 1.15 kg at 18 mo of age (P = .07). Greasy fleece weights at 15 mo of age were not different between predicted FecB genotypes (P = .48). Assignment of genotype based on linked DNA markers effectively identified ewes that are heterozygous carriers and those that are non-carriers for FecB. Ewes predicted to be B+ had significantly greater ovulation rate and litter size compared to their ++ half-sibs. The difference between B+ and ++ ewes was generally not significant (P> .05) for other traits.

Key words: Sheep, Rambouillet, Booroola Merino, Reproduction, Marker assisted selection

Introduction

Improving the reproductive efficiency of sheep flocks can increase the efficiency of lamb production. Crossing Rambouillets, which are adapted to Western U.S. conditions, with more prolific breeds may increase lamb production but may also adversely affect other economically important traits, such as growth rate and wool production. The Booroola Merino's higher reproductive rate has been shown to be due to a single gene (Piper and Bindon, 1996), known as FecB. Therefore, introgressing FecB into Rambouillet flocks may increase reproductive rate without substantial changes in other economically important traits.

Heterozygous carriers and homozygous non-carriers of the FecB allele are designated with B+ and ++, respectively. Willingham et al. (1988) showed that Booroola x Rambouillet ewes classified as carriers (B+) of the FecB allele, based on pedigree, had a .91 ova increase in ovulation rate (2.45 vs. 1.54) compared to Rambouillet ewes (++). Meyer et al. (1994a) found that Booroola-cross ewes classified as B+, based on ovulation rate or pedigree, produced 1.1 more lambs at birth per ewe lambing than ++ ewes. At the time these projects were conducted, the methods used to predict FecB genotype were 1) observing either ovulation rate or litter size or 2) by pedigree (for progeny of known homozygous parent(s)). With the use of microsatellite markers (Montgomery et al., 1993) it became possible to predict FecB genotype in males and females prior to sexual maturity. Thus, the effect of the FecB allele could be estimated within paternal half-sib families. Comparing performance of paternal half-sibs predicted to be B+ with those predicted to be ++ will yield estimates of the phenotypic effects of the genotypes that are not influenced by breed or sire effects.

The objective of this study was to estimate the difference in performance between carriers (B+) and non-carriers (++) of the FecB allele for ovulation rate, fertility, litter size at birth and at weaning, fleece weight, and body weight within paternal half-sib families of Rambouillet-cross ewes with prediction of genotype based on segregation of microsatellite markers flanking the FecB locus.

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Materials and Methods

Animals and Management

Rambouillet - Booroola rams that had from 44% to 6% Booroola Merino ancestry were selected from a flock of sheep where the FecB gene is being introgressed into Rambouillet. The dams of the rams were ewes predicted to be B+ based on ovulation rate records. The rams (n=5) were initially predicted to be B+, based on their genotype at two flanking markers available at the time, OarAE101 and BM1329 (Lord et al., 1996). Rams were mated to Rambouillet ewes (++) from a different flock to produce Rambouillet - Booroola (RXB) ewes (N=94), which were either B+ or ++ at the FecB locus. The RXB ewes were produced over a 3-yr period (Table 1). All RXB ewes were born and raised to weaning on pasture at the Winters Ranch near Brady, Texas. At weaning they were brought to the Texas A&M University Agricultural Research and Extension Center, San Angelo, Texas. They were fed a growing diet (14% CP, 64% TDN) to 12 mo of age. Thereafter, they were managed on pasture and supplemented as needed.

Number of ewes in each family and age at weaning are shown in Table 1. One of the sires produced ewes in two years. Because of differences in management, the ewes born in different years were considered as different sire families in all analyses. Ovulation rate was observed at approximately 10 mo of age for families A and B and at approximately 18 mo of age for families C, D, E, and F because of management considerations. Families A and B were fall-born ewes while the remaining families were spring-born ewes. Few of the spring-born ewes were cycling at 10 mo of age. Therefore, in order to obtain two ovulation records prior to seasonal anestrus, recording of ovulation rate and exposure to rams were delayed until the following breeding season. All RXB ewes were exposed to vasectomized rams with marking harnesses for detection of estrus and a laparoscope was used for observation of ovulation rate 6 to 13 d after a ewe exhibited estrus (Lamberson and Thomas, 1982). After the first ovulation rate record was obtained, ewes were exposed to fertile rams, and ovulation rate was observed by the same procedure on a subsequent cycle. The ovulation data used for analysis were the average of the two ovulation rate records for each ewe. Ewes lambed in a barn at the Texas A&M University Agricultural Research and Extension Center at San Angelo. The number of lambs born to each ewe and lamb birth weights were recorded. Approximately 7 d after lambing, ewes and lambs were returned to large pastures until weaning. The number of lambs weaned was the number of lambs surviving to 60 d of age.

Body weights of RXB ewes were recorded at an average age of 7 mo and again at 18 mo of age. Because families A and B had an opportunity to lamb prior to 18 mo of age, their 18-mo weights were excluded from analysis to avoid bias from differences due to the effects of gestation and lactation. Greasy fleece weights were recorded at approximately 17 mo of age for Families A and B, and at approximately 12 mo of age for Families C, D, E, and F.

Assignment of FecB Status

Blood samples were taken from all ewes and their sires and DNA extracted by the procedure described by Montgomery and Sise (1990). Three commercially available markers (GenomNZ, Dunedin, New Zealand) that span a 10 cM region containing the Booroola locus (Lord et al., 1998) were genotyped. All sires were heterozygous at the three marker loci. Ewes were classified as B+ if they inherited the same complete marker haplotype found to be associated with the B allele in the female ancestors of the sires. At the time this project was conducted, a test for the FecB mutation (Wilson et al., 2001; Mulsant et al., 2001) was not available.

Statistical Analysis

The linear model used to estimate the difference between B+ and ++ ewes included fixed effects for sire family and predicted FecB genotype nested within sire family and, in the case of 7-mo body weight, a linear covariate for age. Results of preliminary analyses indicated that age and body weight of ewe when ovulation was recorded were not significant sources of variation for ovulation rate. PROC GLM of SAS was used for analyses. The Estimate statement of PROC GLM was used to estimate the mean within-family difference in performance between ewes receiving the paternal haplotype associated with the B allele and those receiving the paternal haplotype associated with the + allele.

Results and Discussion

The distribution of within-ewe means of ovulation rate from the two observations per ewe are shown in Table 2. While the distribution of ewes across mean ovulation rate categories is significantly different, (c^{χ} = 61.1; $P < .001$) there is also overlap. Nineteen (20%) of the 94 ewes had a mean ovulation rate of two. When genotype was predicted by the DNA markers, seven of these were predicted to be ++ and 12 were predicted to be B+. All but one of these ewes had two observations, each with two ovulations. If mean ovulation rate were used to predict FecB genotype of these ewes, some of these ewes would be classified incorrectly. Most previous estimates of production traits in different genotypes at the FecB locus have relied on genotype assignment based on ovulation rate. In this study, the genotypes were assigned based on the presence of DNA markers flanking the region containing the FecB locus. The markers span a 10 cM region and phase information for the alleles at the FecB and marker loci were determined for each sire from previous generations. In the future, FecB genotypes could be assigned to all ewes rather than using linked markers because the gene is identified (Wilson et al., 2001; Mulsant et al., 2001) and a direct test for the causative mutation is now available.

Ovulation Rate

The estimated difference between the FecB genotypes for ovulation rate is shown in Table 3. B+ ewes had an average ovulation rate 1.18 ova per cycle greater than the ++ ewes ($P = .0001$). Mean ovulation rate for B+ ewes was 2.71 ova and the mean ovulation rate for ++ ewes was 1.53 ova. Similar results were obtained by Piper et al. (1985) who reported that the FecB allele increased ovulation rate by 1.65 ova per ewe for each copy of the allele present. In a comparison of genotypic classes from different backcrosses of the Booroola Merino and Mérinos d'Arles, Bodin et al. (1991) showed that the differences between B+ ewes and ++ ewes for ovulation rate ranged from .92 to 1.72 ova with an average difference of 1.2 ova. Southey et al. (2002) reported an increase of 1.54 ova when comparing B+ ewes with ++ ewes. Piper et al. (1985) and Davis et al. (1991) suggested that the size of the effect of the FecB allele was not associated with the ovulation rate of the ++ ewes. Castonguay et al. (1990)

reported that Booroola x Finnsheep ewes (n=19) had ovulation rates 1.1 ova/cycle greater than Finnsheep ewes (n=14). But, Young and Dickerson (1991) found that Booroola x Finnsheep crossbred ewe lambs (n=136) had an ovulation rate .5 ova per cycle higher compared to purebred Finnsheep ewe lambs (n=183). The lower estimate of Young and Dickerson (1991) suggests that the effect of the FecB allele may not be as large in a Finnsheep background or may not be as large in ewe lambs. The close agreement between the estimate of +1.2 ova of the present study and most of the estimates reviewed by Davis et al. (1991) indicates that similar results are obtained when using phenotypes or marker genotypes to assign FecB genotype.

Fertility
There was not a significant difference in fertility (ewes lambing/ ewe exposed) between FecB genotypes (Table 3). Earlier reports have also shown no differences in fertility between B+ and ++ ewes within similar background genotype (Meyer et al., 1994a; Southey et al., 2002).

Body Weight of Ewes
The estimate of the difference between B+ ewes and ++ ewes was not significantly different from zero at 7 mo of age, when the mean body weight was 36.3 kg (Table 3). The mean body weight at 18 mo was 53.3 kg (Table 3). At 18 mo of age the B+ ewes were 2.10 ± 1.15 kg lighter than ++ ewes (P=.07). Only 65 ewes contributed to this estimate as families A and B were excluded because some ewes lambed prior to the time the 18-mo weight was recorded. The within-family estimates (data not shown) showed ++ ewes were significantly heavier in two of the four families analyzed for 18-mo weight. While several studies have reported that Booroola x local breed crosses were lighter than local breed contemporaries (Davis et al., 1991), these estimates were generally a function of the difference between Booroola-Merino background genotype and the genotype of the local breed. Southey et al. (2002) reported a non-significant difference in body weight at breeding due to the FecB allele. Visscher et al. (2000) reported no significant difference in ADG between B+ and ++ Booroola-Texel lambs, when feeding lambs to a predetermined live weight. Meyer et al. (1994b) reported B+ lambs were .4 kg lighter than ++ lambs at weaning (P < .1) within similar genotypes, but found FecB genotype had no influence on body weight of lambs at later ages. Southey et al. (2002) concluded that lighter body weights of the Booroola Merino crosses compared to Rambouillet ewes appear to be due to loci other than the FecB locus because ++ Booroola-cross ewes were lighter than Rambouillet ewes, and the difference between backcross B+ and backcross ++ for breeding weight was not significant. Piper and Bindon (1982) and Piper et al. (1988) reported that Booroola Merino crosses had similar body weight to several other strains of Australian Merino. Meyer et al. (1994b) also concluded that the observed differences in body weight were due primarily to Merino breeding rather than the presence of the FecB allele. Our result for body weight at 18 mo of age suggests that the FecB allele may have an effect on bodyweight. Visscher et al. (2000) reported that B+ lambs had a higher dressing percent, a higher fatness score, and greater internal carcass fat. However, the lack of consistent differences across studies that estimated the difference between B+ and ++ lambs with similar background genotype suggests that the FecB allele does not significantly affect body weight. However, few studies have had a design sufficient to estimate the difference between B+ and ++ animals free of sire or breed effects and further studies are needed to provide a definitive answer.

Litter Size
Litter size (lambs born / ewe lambing) was .51 lambs greater in B+ ewes compared to ++ ewes (P=. 002; Table 3). All records were of first parity, and perhaps this limited the number of lambs born. These results indicate that the FecB allele has a major effect on increasing ovulation rate but a smaller increase in litter size of first parity ewes. Southey et al. (2002) reported an increase of .65 lambs in litter size due to the FecB allele in ewes of mixed ages. It has been shown that embryo mortality increases with ovulation rate (Hanrahan, 1986). Therefore, it is expected that the ewes with a higher mean ovulation rate (B+) will have higher embryo mortality and the difference between FecB genotypes will be smaller for litter size compared to ovulation rate. The summary of Davis et al. (1991) reported an average increase of .6 lambs born for Booroola x local breed crosses as compared to the local breed. Teyssier et al. (1998) reported an increase of .9 lambs born/ewe lambing due to the presence of the FecB allele in Merino d'Arles-cross ewes.

Number of Lambs Weaned
Carriers (B+) of the FecB allele weaned .18 ± .18 (P = .34) more lambs than their non-carrier (++) half-sisters (Table 3). These first parity ewes had a mean litter size at weaning of 1.2 lambs/ewe lambing. The difference between B+ and ++ ewes for number of lambs weaned was smaller than for number of lambs born, reflecting lower survival in lambs born in larger litters. Survival to weaning was 86% for singles, 72% for twins, and 48% for triplets in this sample of ewes. Mean lamb survival was lower in B+ ewes because a greater proportion of their lambs were twins and triplets compared to the ++ ewes. When only lambs born as singles and twins were considered, the survival rate was similar for each genotype (.79 for B+ and .74 for ++).

Lamb survival has previously been shown to decrease as litter size increases, primarily because of effects of lower birth weight (Piper and Bindon, 1982). Similar to the present study, Piper and Bindon (1982) found no significant difference in lamb survival between Booroola-Merino and the control Merino for single-born or twin-born lambs. Meyer et al. (1994a) reported that despite greater litter size at birth, B+ ewes did not wean significantly more weight of lamb than ++ ewes, primarily due to higher mortality among lambs of B+ ewes. Thus, as a result of increased lamb losses, a smaller proportion of B+ ewes produced a lamb at weaning. Although the FecB allele dramatically increased litter size in Booroola-Merino crosses with longwool breeds, the high mortality under pasture conditions, of lambs born in litters of more than two, combined with poor growth rate of Merino-derived lambs offset much of the advantage in prolificacy. Meyer et al. (1994a) also found that among higher order births, B+ ewes producing triplets weaned only .25 more lambs than those producing twins, and ewes with litter size of four or greater weaned fewer lambs than those giving birth to triplets. High lamb mortality in large litters has also been reported by Hinch et al. (1985) for Booroola x Romney ewes and by Owens et al. (1985) for purebred Booroolas. Both studies attributed much of the increased mortality to the decline in birth weights observed with increasing litter size. The data suggest that the decreased lamb survival in lambs born to B+ ewes was a consequence of larger litter size and not a direct effect of the FecB allele. Under intensive management, Gootwine et al. (1995) reported survival of triplets of 77%, which was substantially greater than in the present study. Therefore, alternative management practices should be employed to improve lamb survival in large litters in order to realize more of the potential lamb production possible through the use of the FecB allele.

Fleece Weights

There was not a significant difference between greasy fleece weights of B+ and ++ ewes (Table 3). This estimate is in agreement with previously published studies. Meyer et al. (1994 b) concluded that fleece weights and wool characteristics of Booroola crosses with different breeds were dependent upon the other breed. Within similar crossbred genotypes, B+ lambs produced .07 kg less wool than ++ lambs ($P < .01$) but no difference was observed at the 12 to 14 mo shearing (Meyer et al., 1994 b). Ponzoni et al. (1985) observed no significant difference for sire FecB genotype in wool production and wool quality characteristics among Booroola-Merino x Merino sheep measured at 15 mo of age. Southey et al. (2002) reported that ++ ewes had greater fleece weights than B+ ewes, but the fleece weights included records of reproducing ewes and were not adjusted for litter size. The fleece weights used in the analysis of the present paper were recorded prior to gestation. Snowder and Shelton (1988) showed that each additional lamb weaned results in a decrease of approximately 3% in greasy fleece weight. Therefore, fleece weights of B+ ewes are expected to be smaller than those of ++ ewes when compared among reproducing ewes where the B+ ewes are producing more lambs.

The increased reproductive rate of the B+ ewes in this study indicates the potential for improved efficiency. However, in these first parity ewes, a significant difference in number of lambs weaned was not realized due to increased mortality of the lambs born in larger litters. A similar result was reported by Southey et al. (2002) where weight of lamb weaned was not significantly different between B+ and ++ ewes. However, in a summary of several studies, an advantage of 29% more lambs were weaned from Booroola-cross ewes when compared to the local breed with which the Booroola were crossed (Davis et al., 1991). They reported the greatest advantage was observed in intensively managed flocks. This suggests that more intensive management systems than were used for the present study may be required to realize the benefits of the greater reproductive rate of the B+ ewes.

Conclusions

The ability to predict FecB genotype with DNA markers or a direct test for the gene provides animal breeders with a tool to identify ewes with a substantially higher reproductive rate from within half-sib families prior to puberty. The use of the FecB allele in commercial sheep production has been hindered by an inability to differentiate between carriers and non-carriers. The use of DNA tests allows for direct comparisons among B+ and ++ daughters within paternal half-sib families. Introgression of the FecB allele into breeds that have desirable phenotypes for traits other than reproduction offers the potential to improve the efficiency of lamb production. The lack of a significant difference for number of lambs weaned is likely a consequence of using first-parity ewes. Dickerson et al. (1975) documented significantly lower lamb survival from first-parity ewes relative to mature ewes. The difference between mature B+ and ++ for number lambs weaned may be larger than for the young ewes used in this study. If so, more of the increase in ovulation rate could be realized as lambs weaned. Estimates of number of lambs weaned from mature ewes are needed to more fully assess the value of FecB for improving the efficiency of lamb production.

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Table 1. Number of ewes and age at weaning and observation of ovulation rate by sire family

Sire family	Year	Number of ewes All	Number of ewes (B+/++)	Mean age at weaning, d	Mean age at ovulation, d
1088 (A)	1995	14	8/6	109	301
1527 (B)	1996	15	10/5	155	348
1865 (C)	1996	10	7/3	106	440
2011 (D)	1996	12	7/5	106	442
2011 (E)	1997	30	18/12	78	461
2191 (F)	1997	13	6/7	79	459
Summary		94	56/38	105	414

Table 2. Number of ewes by mean ovulation rate from two observations/ewe by predicted FecB genotype (N=94).

	Mean ovulation rate						
Genotype	1.0	1.5	2.0	2.5	3.0	3.5	4.0
+	10	17	7	3	1	0	0
B	0	0	12	17	19	5	3

Table 3. Means and estimated differences between Fec^{B+} and Fec^{++} genotypes within half-sib families of Rambouillet-cross ewes

Trait	Mean B+	Mean ++	Estimated difference (B+ - ++)[a]	P
Ovulation rate, ova	2.71	1.53	+1.18 ± .12	.0001
Body weight at 7 mo, kg	35.86	36.74	-.88 ± .97	.36
Body weight at 18 mo, kg	52.21	54.32	-2.10 ± 1.15	.07
Fertility, %	80.7	88.1	-7.4 ± 8.4	.38
Number of lambs born	1.96	1.45	+.51 ± .16	.002
Number of lambs weaned	1.23	1.05	+.18 ± .18	.34
Fleece weight, kg	3.90	3.99	-.09 ± .13	.48

[a] A positive value indicates that the B+ ewes were superior, a negative value indicates that the ++ ewes were superior.