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Improvement of Prolificacy of U.S. and Israeli Sheep Populations Through Inclusion of the F Gene of the Booroola Merino

D.L. Thomas, E. Gootwine, R. Braw-Tal, P.J. Dziuk,
A. Bor, H.A. Lewin

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Improvement of Prolificacy of U.S. and Israeli Sheep Populations Through Inclusion of the F gene of the Booroola Merino

Investigators' Names (Principal listed first)	Investigators' Institutions
D. L. Thomas	University of Illinois
E. Gootwine	A.R.O., The Volcani Centre
R. Braw-Tal	A.R.O., The Volcani Centre
P. J. Dziuk	University of Illinois
A. Bor	A.R.O., The Volcani Centre
H. A. Lewin	University of Illinois

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Signature
Principal Investigator

Signature
Institution's Authorizing Official

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C. Abstract

The purposes of this project were: 1) to evaluate the joint effects of the high prolificacy F gene of the Booroola Merino breed and 1/2 Booroola Merino inheritance on productivity of sheep in Israel and the U.S. and 2) to develop methods and criteria by which F-gene carriers could be differentiated from non-carriers as an aid in transferring the F gene into domestic populations through backcrossing. Booroola Merino x Awassi and Booroola Merino x Assaf F_1 lambs and ewes heterozygous for the F gene (F+) were compared to pure Awassi and Assaf lambs and ewes in Israel. In the U.S., Booroola Merino x Rambouillet F_1 lambs and ewes heterozygous for the F gene were compared to pure Rambouillet lambs and ewes. Comparisons in the U.S. were also made among F_1 lambs and ewes produced by mating Booroola Merino, Finnsheep, Combo-6, St. Croix and Barbados rams to Suffolk and Targhee ewes. Booroola Merino F_1 ewes were superior to all other breeds and crosses for ovulation rate, fleece weight and fleece quality and were also generally superior for litter size at birth. However, Booroola Merino crosses were inferior to other genotypes for growth, carcass composition, age at puberty, ewe fertility, lamb survival, weight of lamb weaned per ewe exposed and dairy milk production. Results suggested that only the F gene of the Booroola Merino genome held potential for improving productivity of domestic sheep populations in Israel and the U.S. Transfer of the F gene to domestic breeds through backcrossing would be accelerated if female carriers could be differentiated from non-carriers at an early age. Results from experiments utilizing Booroola Merino F_1 (F+) and pure breed (++) ewe lambs suggested that relatively accurate criteria to separate carriers from non-carriers could be developed from basal FSH concentrations at 30 days of age and ovulation rates at 5 to 7 months of age induced with either PMSG or ovine pituitary extract.

D. Objectives of the Original Research Proposal

1. To study the prolificacy of F_1 ewes produced by mating homozygous (FF) Booroola Merino rams to mutton and dairy breeds, native in the U.S.A. and Israel.

2. To study the prolificacy of backcross ewes carrying the F gene.

3. To determine the effect of the F gene on hormone profiles, number of ovulations and litter size in mutton and dairy breeds common to the U.S.A. and Israel.

4. To develop accurate methods to differentiate among ++, +F and FF genotypes in males and females prior to breeding age.

E. Report of Research Results

1. Productivity of Booroola Merino Crossbred Lambs and Ewes

Methods. At the Volcani Centre in Israel, approximately 125 Assaf and 125 Awassi ewes were inseminated with semen from 5 homozygous (FF) Booroola Merino (BM) rams each year over a two-year period to produce heterozygous (F+) F_1 ewes. BM x Assaf and BM x Awassi F_1 rams were mated to Assaf and Awassi ewes, respectively, to produce backcross ewes of 3/4 Assaf and 3/4 Awassi breeding. Some backcross ewes also were produced by mating F_1 ewes to rams of the two local breeds. Lambs were removed from their dams within 24 hours of birth to an artificial rearing unit until weaning at one month of age or a weight of approximately 12 kg. After weaning, lambs were fed a high concentrate diet ad libitum. Lambs were weighed periodically and carcass data were obtained on a sample of the lambs. Reproductive, wool and milk traits were recorded on contemporary Assaf, Awassi, Assaf-BM cross and Awassi-BM cross ewes managed under an accelerated lambing program.

At the University of Illinois in the U.S., approximately 90 Suffolk and 110 Targhee ewes were mated to homozygous BM, Finnsheep, Combo-6, St. Croix and Barbados rams each year over a four year period (12 different rams per breed were used) to produce F_1 ewes. F_1 ewes were exposed to Dorset rams each autumn. Ewes were exposed to lamb first at approximately one year of age.

Also in the U.S., approximately 300 Rambouillet ewes were exposed to Rambouillet or homozygous BM rams over the same four year period. The contemporary Rambouillet and

BM x Rambouillet ewes were mated to Rambouillet rams to produce Rambouillet or 3/4 Rambouillet, 1/4 BM offspring, with the exception that a few BM x Rambouillet ewes were mated to BM rams to produce some 3/4 BM, 1/4 Rambouillet offspring. Ewes were mated to lamb first at two years of age.

In the U.S., lambs were weaned from their dams at approximately 56 days of age and fed a high energy diet ad libitum postweaning. Weaning weights were collected on all lambs and carcass data from a sample of ram lambs. Reproductive rate and wool production was collected on all ewes.

Growth and Carcass Merit. Body weights and growth rates for BM crossbred lambs and purebred and crossbred lambs of local breeds in Israel and the U.S. are presented in Tables 1, 2 and 3. Table 1 presents birth weight and growth rates up to 150 days of age for Assaf, BM x Assaf (F_1), F_1 x Assaf (3/4 A), Assaf x F_1 (3/4 A'), BM x F_1 (3/4 BM) and Assaf x 3/4 A (7/8 A) lambs. Birth weights tended to decrease as the proportion of BM inheritance increased. Further backcrosses to Assaf should result in birth weights similar to pure Assaf. Weight at 150 days of age of 3/4 Assaf and pure Assaf lambs were already very similar.

TABLE 1. GROWTH OF ASSAF, BOOROOLA MERINO X ASSAF AND BACKCROSS LAMBS IN ISRAEL

Sex	Breed	No.	Birth weight, kg	Growth rate, g/d Preweaning	Growth rate, g/d Postweaning	150 d weight, kg
M	Assaf	188	4.5[a]	243[a]	294[a]	48.3[a]
	7/8 A	60	3.8[b,c]	271[a,b]	315[a]	46.6[a]
	3/4 A[e]	170	4.3[a,b]	273[b]	307[a]	48.2[a]
	3/4 A'[e]	61	4.0[b]	232[a]	298[a]	45.6[a]
	F_1	67	4.1[a,b]	250[a,b]	321[a]	47.0[a]
	3/4 BM	21	3.6[c]	235[a]	236[b]	36.9[b]
F	Assaf	149	4.3[a]	252[a]	261[a]	41.1[a]
	7/8 A	54	3.5[b]	222[a,b]	269[a,b]	38.3[a,b]
	3/4 A[e]	167	4.1[a]	259[a]	254[a]	41.8[a]
	3/4 A'[e]	56	3.7[b]	236[a,b]	238[a,b]	38.7[a,b]
	F_1	54	3.6[b]	214[b]	263[a]	34.5[b]
	3/4 BM	11	3.3[b]	219[a,b]	202[b]	30.5[b]

[a,b,c] Means in a column and sex with no superscripts in common are different (P<.05).
[e] See text for breed composition.

Examination of the data indicates presence of a major gene for reduced weight at 150 days of age linked to the X chromosome of the BM. In males, the difference between Assaf and F_1 lambs was only 1.3 kg (X chromosomes in both groups originate from the Assaf),whereas in females, the difference between Assaf and F_1 lambs was 6.6 kg (F_1's had 1 X chromosome from the BM). This may also have been due to greater heterosis in males than females.

Presented in Table 2 is growth of Rambouillet, F_1 and backcross lambs. All lambs were weaned at 56±4 days of age. F_1 and backcross lambs were compared against contemporary Rambouillet lambs born the same year from dams of the same age. In all cases, the lambs with BM ancestory grew more slowly than pure Rambouillet lambs. This was true even for the 3/4 Rambouillet-1/4 BM lambs, indicating a large negative effect of BM genes on growth.

TABLE 2. GROWTH OF RAMBOUILLET, F_1 AND BACKCROSS LAMBS IN THE UNITED STATES.

Breed	No.	Birth weight, kg	Weaning weight, kg	Market age, d	Market weight, kg	Birth to market ADG[e], g
Rambouillet	1178	4.56[a]	16.60[a]	273.6[b]	60.46	208[a]
BM x Rambouillet	243	4.33[b]	15.39[b]	282.1[a]	52.83	177[b]
Rambouillet	60	4.42[a]	14.52[a]	244.5	61.72	235[c]
BM x (BM x Ramb.)	30	3.35[b]	12.15[b]	283.7	57.99	194[d]
Rambouillet	123	4.33[a]	16.72[a]			
Ramb. x (BM x Ramb.)	54	3.75[b]	14.91[b]			

[a,b]Means in a column and group with no superscripts in common are different (P<.01).
[c,d]Means in a column and group with no superscripts in common are different (P<.05).
[e]ADG = average daily gain.

Table 3 presents data on growth of F_1 lambs sired by BM, Finnsheep, Combo-6, St. Croix or Barbados sires and with either Suffolk or Targhee dams. BM-sired lambs were intermediate among the breed groups for growth. However, it must be remembered that the other four breeds are known to be inferior to most U.S. breeds for growth traits.

The results from both stations indicate that the BM is inferior to, or at best no different from, some domestic breeds in both the U.S. and Israel for growth. This suggests that producers wishing to utilize the F gene of the BM will wish to minimize the proportion of other BM genes incorporated into the flock.

TABLE 3. GROWTH OF F_1 LAMBS SIRED BY BOOROOLA MERINO (BM), FINNSHEEP (FN), COMBO-6 (C6), ST. CROIX (SC) OR BARBADOS (BA) RAMS AND OUT OF SUFFOLK AND TARGHEE DAMS IN THE UNITED STATES.

	Breed of sire				
Trait	BM	FN	C6	SC	BA
Number of lambs	178	179	202	198	199
Birth weight, kg	$4.6^{a,b}$	4.7^{a}	$4.5^{b,c}$	$4.3^{c,d}$	4.3^{d}
Weaning weight, kg	$17.0^{c,d}$	19.3^{a}	18.4^{b}	17.6^{c}	16.7^{d}

^{a,b,c,d} Means in a row with no superscripts in common are different (P<.05).

Carcass composition of ram lambs slaughtered in Israel and the U.S. is presented in Tables 4 and 5, respectively. Table 4 presents body composition of Awassi, BM x Awassi, Assaf and BM x Assaf lambs. The fat tail of the Awassi is significantly heavier (P<.001) than the tail of the BM x Awassi (2.5 vs. .8 kg, respectively). Fat tail appears to be a recessive or partially recessive trait. Weight of internal fat was greater for BM x Awassi than Awassi lambs. BM inheritance also increased internal fat weight when substituted for Assaf inheritance, but the

TABLE 4. BODY AND CARCASS COMPOSITION OF AWASSI (AW), BOOROOLA MERINO (BM) X AWASSI, ASSAF (AS) AND BOOROOLA MERINO X ASSAF RAM LAMBS IN ISRAEL.

Trait	AW	BM x AW		AS	BM x AS	
Number of lambs	10	7		6	6	
Days of age	137.1	160.3	**	154	197	**
Slaughter wt., kg	43.2	43.3		46.5	47.8	
Cold carcass wt., kg	18.7	19.5		23.6	22.9	
Unshorn pelt, kg	5.2	5.7		6.0	6.2	
Head, kg	2.6	2.9		2.8	2.9	
Feet, kg	1.3	1.1	**	1.4	1.2	**
Fat tail, kg	2.5	.8	**	.6	.3	
Internal body fat, kg	1.0	2.1	**	2.4	3.0	
Carcass composition, %						
Bone	18.9	16.0	***	16.7	15.5	
Muscle	57.9	51.5	***	54.4	51.9	
Total carcass fat	20.4	28.9	***	27.2	30.1	
Subcutaneous fat	10.6	14.2	**	13.3	12.7	
Intermuscular fat	9.8	14.7	***	13.9	17.4	*

*P<.05, **P<.01, ***P<.001.

difference was not significantly different from zero and was smaller than when BM inheritance was substituted for Awassi inheritance. Carcass composition of BM crosses was inferior to that of the local breeds, especially when compared to the Awassi. BM x Awassi carcasses had significantly less bone, less muscle and more fat than Awassi carcasses. All carcasses had the fat tail removed before carcass composition was determined. When the fat of the fat tail was considered as part of the carcass weight, the differences between the two groups in % fat, muscle and bone was somewhat less.

Carcass traits of BM F_1 and domestic breed F_1 lambs from the 1987 and 1988 lamb crops in the U.S. are presented in Table 5. As was the case in Israel, BM crosses produced carcasses with more fat than other breeds. BM crosses had greater (P<.05) subcutaneous fat depth than all other crosses, more (P<.05) internal kidney fat than two of the other four crosses and the lowest estimated yield of trimmed and boneless leg, loin, rack and shoulder.

TABLE 5. CARCASS TRAITS OF F_1 LAMBS SIRED BY BOOROOLA MERINO (BM), FINNSHEEP (FN), COMBO-6 (C6), ST. CROIX (SC) OR BARBADOS (BA) RAMS AND OUT OF SUFFOLK AND TARGHEE DAMS IN THE UNITED STATES.

	Breed of sire				
Trait	BM	FN	C6	SC	BA
Number of lambs	30	49	43	46	50
Quality grade^e	11.4^{a,b}	11.9^a	11.3^{a,b}	11.7^a	11.0^b
Rib eye area, cm^2	14.8^b	14.5^b	15.0^b	14.9^b	16.7^a
12th rib fat, cm	.59^a	.42^b	.41^b	.47^b	.41^b
Kidney fat, %	2.6^{a,b}	2.2^{c,d}	1.9^d	2.5^{b,c}	2.9^a
Leg conformation^e	11.6	11.6	11.7	11.4	11.7
Yield grade^f	3.24^a	2.73^b	2.60^b	2.97^{a,b}	2.89^{a,b}

^{a,b,c,d} Means in a row with no superscripts in common are different (P<.05).
^{e}11=average choice, 12=high choice.
^{f}Yield grade is an estimate of % of carcass weight in trimmed and boneless leg, loin, rack and shoulder; 2.6 = 46.2%, 2.8 = 45.8%, 3.0 = 45.4%, 3.2 = 45.1%.

The results indicate that the incorporation of BM inheritance would have a negative effect on body and carcass composition in Israeli and U.S. sheep populations.

Ovulation Rate and Lamb Production. Presented in Table 6 are the natural ovulation rates and number of lambs born per ewe (prolificacy) of the young ewes in Israel.

The F_1 BM ewes ovulated 1.11 to 1.41 more eggs and 3/4 local ewes ovulated .24 to .71 more eggs than purebred domestic ewes. Prolificacy of ewes lambing at one year of age was .40 to .53 greater for the F_1 and .48 to .30 greater for the 3/4 local ewes than the domestic ewes, and the superiority of the BM-cross ewes over the domestic ewes increased in lambings at older ages.

TABLE 6. PROLIFICACY AND OVULATION RATE OF YOUNG F_1 BOOROOLA MERINO AND PUREBRED EWES IN ISRAEL.

	1-yr-old ewes		2- to 4-yr-old ewes		1- to 3-yr-old ewes		
Genotype	n	Prolificacy	n	Prolificacy	No. ewes	No. records	Ovulation rate
Assaf	45	1.35	96	1.48	47	83	1.65
BM x Assaf	43	1.88	95	2.27	27	50	2.76
3/4 Assaf	97	1.83	70	1.97	58	115	1.89
Awassi	88	1.25	88	1.30	34	34	1.19
BM x Awassi	20	1.65	18	1.89	9	11	2.60
3/4 Awassi	77	1.55			30	45	1.90

Lamb production of young ewes in the U.S. is presented in Table 7. Performance of the F_1 ewes out of Suffolk and Targhee dams is presented for both ewe lambs and ewes 2 and 3 years of age. Rambouillet and BM x Rambouillet ewes were mated to lamb first at two years of age so no ewe lamb performance data are available for these groups. As was the case in Israel, BM F_1 ewes had significantly higher ovulation rates than all other breed groups. BM F_1 ewes also had a greater prolificacy than Rambouillet purebred ewes. However, the BM F_1 ewes were not always superior in prolificacy to F_1 ewes sired by Finnsheep, Combo-6, St. Croix and Barbados rams. As ewe lambs, BM-sired ewes were significantly superior for prolificacy to only Barbados- and Combo-6-sired ewes, and no significant differences were found among these ewe groups for prolificacy at two and three years of age.

Relative to the other breed groups, BM-sired ewes were inferior or mediocre for other traits contributing to weight of lamb weaned per ewe exposed (ewe productivity). BM-sired ewes had the lowest fertility of all breed groups, had the poorest lamb survival among 2- and 3-year-old ewes and weaned lambs that were either the lightest or not significantly different in weight compared to other breed groups. The cumulative effect of poor or mediocre performance for these traits resulted in the 2- and 3-year-old BM-sired ewes having the poorest ewe productivity of all breed groups.

TABLE 7. OVULATION RATE AND LAMB PRODUCTION OF YOUNG EWES IN THE U.S.

Breed of sire	Ovulation rate, no.	Fertility, %	Prolificacy, no.	Lamb survival, %	Lamb weaning weight, kg	Ewe productivity, kg
Ewe lambs						
Finnsheep[a]	2.31[d]	91.8	1.62[f,g]	73.9	15.14[f]	14.06
Combo-6[a]	1.67[e]	81.2	1.41[g,h]	77.1	13.14[f,g]	11.29
Booroola M.[a]	3.05[c]	76.4	1.70[f]	85.0	11.58[g]	12.36
St. Croix[a]	1.67[e]	90.4	1.48[f,g,h]	82.6	13.66[f]	15.75
Barbados[a]	1.60[e]	93.5	1.29[h]	78.8	13.82[f]	12.63
2- and 3-year-old ewes						
Finnsheep[a]	2.88[d]	95.1[c]	1.83	68.0[e]	15.34	17.87[c,d]
Combo-6[a]	2.01[e]	80.2[c,d]	1.65	88.5[c,d]	16.70	19.10[c]
Booroola M.[a]	3.71[c]	58.5[d]	1.73	75.5[d,e]	15.19	11.64[d]
St. Croix[a]	2.01[e]	89.0[c]	1.83	94.7[c]	15.24	24.09[c]
Barbados[a]	1.96[e]	92.1[c]	1.78	87.6[c,d]	14.96	20.80[c]
2- and 3-year-old ewes						
Rambouillet[b]	1.60[d]	92.9[c]	1.36[d]	84.8[f]	16.55[c]	16.92[f]
Booroola M.[b]	3.03[c]	81.1[d]	1.93[c]	73.5[g]	12.84[d]	14.79[g]

[a]Breeds of dam were Suffolk and Targhee.
[b]Breed of dam was Rambouillet.
[c,d,e] Means within a group and column with different superscripts are different ($P<.05$).
[f,g,h] Means within a group and column with different superscripts are different ($P<.10$).

Ovulation rate results from both locations indicate that BM F_1 ewes have the potential to significantly increase lamb production over several local purebreds and crossbreds, and that this superior ovulation rate results in a greater litter size relative to local breeds of low to medium prolificacy. However, the BM F_1 ewes may not give birth to more lambs than some of the more prolific local breeds. It also appears, at least under the conditions in Illinois, U.S., that BM-sired ewes have some major disadvantage in terms of fertility, lamb survival and lamb weaning weight which results in them being inferior to many breeds and crosses for weight of lamb weaned per ewe exposed (ewe productivity).

Wool Production. It is not surprising that the BM F_1 ewes had increased ($P<.05$) fleece weights compared to ewes of local genotypes (Table 8) since the Australian Merino is recognized as the premier wool producing breed in the world. Ewes of BM ancestory had wool of shorter staple length in Israel where this trait was measured.

Detailed quality measurements were taken on fleeces in Israel. Compared with Awassi and Assaf ewes, BM-cross ewes had fleeces with higher count grades, fewer hair fibers, more desirable character and handle, and fewer cotts.

BM inheritance will improve the fleece weight and quality of local breeds in both Israel and the U.S.

TABLE 8. GREASE FLEECE WEIGHT AND STAPLE LENGTH OF YOUNG EWES IN ISRAEL AND THE U.S.

	1-yr-old ewes		2- and 3-yr old ewes		1-yr-old ewes		2-yr-old ewes	
Breed of sire	n	Fleece wt., kg	n	Fleece wt., kg	n	Staple length, cm	n	Staple length, cm
Awassi[a]	39	1.6[f]	35	2.3[f]	36	11.1[e]		
Booroola M.[a]	16	2.0[e]	16	3.7[e]	12	9.3[f]		
Assaf[b]	19	2.0[f]	50	2.6[f]	27	9.4[e]	22	11.0[e]
Booroola M.[b]	15	3.0[e]	34	3.7[e]	17	6.7[f]	37	7.8[f]
Finnsheep[c]			34	3.3[f]				
Combo-6[c]			60	3.3[f]				
Booroola M.[c]			45	4.2[e]				
St. Croix[c]			71	2.0[g]				
Barbados[c]			47	2.0[g]				
Rambouillet[d]			109	3.7[f]				
Booroola M.[d]			39	4.1[e]				

[a]Breed of dam = Awassi, [b]Breed of dam = Assaf, [c]Breed of dam = Suffolk or Targhee, [d]Breed of dam = Rambouillet.

Milk Production. Table 9 presents milk yield of Awassi and BM-Awassi ewes in Israel. Both 1/4 and 1/2 BM inheritance resulted in a large decrease in milk yield compared to pure Awassi. Owners of Awassi dairy herds wishing to make use of the high reproductive rate of the F gene will wish to minimize the proportion of other BM genes that are transferred to their sheep given the large negative effect BM inheritance appears to have on dairy milk production.

TABLE 9. LACTATION LENGTH AND YIELD (± S. D.) FOR EWES IN ISRAEL.

	First lactation			Second lactation		
Genotype	n	Length, d	Yield, liters	n	Length, d	Yield, liters
Awassi	26	184±61	402±220	20	214±50	567±161
BM x Awassi	13	163±51	249±127	11	169±45	238±137
Awassi	52	191±38	412±141			
3/4 Awassi	42	168±42	259±98			

Other Traits. Age at puberty for those ewe lambs reaching puberty by approximately nine months of age were collected for some of the ewes in the U.S. (Table 10). BM-sired ewes were older at puberty than all other breed groups but the increased age was significant only from Finnsheep-sired ewes. BM-sired ewes had lighter weights at breeding than all breed groups except Barbados-sired ewes (Table 10).

TABLE 10. AGE AT PUBERTY AND BREEDING WEIGHT OF EWES IN THE U.S.

Breed of sire	Age at puberty, d	Breeding weight, kg: 1-yr-old ewes	Breeding weight, kg: 2- and 3-yr-old ewes
Finnsheep[a]	194.8[f]	53.2[c]	49.3[c,d]
Combo-6[a]	210.8[e]	55.8[c]	53.6[c]
Booroola M.[a]	217.2[e]	47.6[d]	45.9[d]
St. Croix[a]	211.9[e]	53.0[c]	51.5[c]
Barbados[a]	208.2[e]	45.2[d]	45.8[d]
Rambouillet[b]			53.2[c]
Booroola M.[b]			44.7[d]

[a]Breed of dam = Suffolk or Targhee, [b]Breed of dam = Rambouillet.
[c,d](P<.05), [e,f](P<.10).

Conclusions. F_1 ewes containing 1/2 BM inheritance and heterozygous for the F gene ovulated more eggs, generally gave birth to larger litters and produced heavier and higher quality fleeces relative to the purebred and crossbred local breeds included in this study. The F1 BM lambs, however, grew slower and had poorer carcass composition, and F1 BM ewes were older at puberty, were lighter in body weight at breeding, had lower fertility, had reduced lamb survival, weaned lighter lambs, weaned less weight of lamb per ewe exposed and produced less dairy milk than contemporary lambs and ewes of domestic breeds and crossbreds.

Given the relatively low value of wool to the Israeli and U.S. sheep industries, it appears that the BM has little to offer these industries except the potential for large litters through the positive effect of the F gene on ovulation rate. Methods to efficiently move the F gene from the BM to well-adapted local breeds that have desirable levels of performance for growth, wool production or meat production should be developed.

2. Physiological Characteristics

Basal FSH Concentrations. Blood samples were collected from Assaf, BM x Assaf, Awassi and BM x Awassi ewe lambs between ages of one to fifteen weeks in Israel, and FSH concentration was determined in plasma by homologous radioimmunoassay using a kit supplied by NIAMDD. All values were expressed in ng NIAMDD-oFSH-RP-1/ml plasma.

Different patterns of plasma FSH concentrations as a function of age were observed (Figures 1 and 2). Assaf showed low and constant plasma FSH level throughout the period studied, Awassi were characterized by low basal plasma FSH level up to six weeks of age that increased toward the end of the period, while BM x Assaf and BM x Awassi had elevated FSH level in plasma between 3 and 6 weeks of age. The most significant difference between Assaf and BM x Assaf and between Awassi and BM x Awassi was observed at 3 to 5 weeks of age.

In a similar study conducted in the U. S., 28 Rambouillet and BM x Rambouillet ewe and ram lambs (7 lambs per breed group x sex subclass) were bled at approximately 30, 45 and 60 days of age, and the serum was assayed for FSH. BM x Rambouillet ewe lambs had significantly higher FSH concentrations than Rambouillet ewe lambs at 30 and 45 days of age with the greatest difference at 30 days (Figure 3).

Ram lambs had significantly lower FSH concentrations than ewe lambs. BM x Rambouillet ram lambs had greater FSH concentrations than Rambouillet ram lambs at all ages, but the differences were small and not significant (Figure 4).

The data from both locations indicate that basal plasma or serum FSH concentrations of ewe lambs at approximately one month of age may be useful in detecting the F gene. An FSH concentration of 4 ng/ml or greater at this age may be a useful criterion for presence of the F gene. If this criterion were used on the U. S. data, 57% (4/7) of the BM x Rambouillet ewe lambs would have been correctly identified as carriers of the F gene and 86% (6/7) of the Rambouillet ewe lambs would have been correctly identified as non-carriers of the F gene (Figure 5). The data from Israel also supports the 4 ng/ml or greater concentration of FSH as a criterion for presence of the F gene. However, some caution is advised in extrapolation of these results to other populations. Since the F_1s differ from the purebreds in not only the presence of the F gene but also in 1/2 BM inheritance, the value of plasma FSH concentrations, or any other trait, in detecting the F gene must be determined in populations of the same breed composition but with the F gene segregating.

Plasma FSH Following GnRH Administration. Six Awassi and 6 BM x Awassi ewe lambs (40 - 45 days of age) were administered 30 µg of a synthetic GnRH analog (Fertagyl, Intervet) twice at an 80 minute interval. Blood samples were taken at 20 minute intervals before and after each injection and assayed for plasma FSH concentration.

The effect of GnRH treatment on plasma FSH concentration is shown in Figure 6. GnRH administration resulted in an increase in plasma FSH within 20 to 40 minutes in ewe lambs of both genotypes, however BM x Awassi lambs showed a significantly greater response than Awassi lambs. The increase in FSH concentration above the basal value (maximal FSH concentration following GnRH injection minus mean FSH concentration in two samples taken prior to any GnRH treatment) was two-fold higher in BM x Awassi than in Awassi ewe lambs.

These results indicate that GnRH may be used to increase the difference in FSH concentrations between carriers and non-carriers of the F gene and thus increase the accuracy of identifying individual carriers in populations where the F gene is segregating.

Ovarian Morphology. Ovaries were removed from 4 Awassi and 4 BM x Awassi ewe lambs when the lambs were 30 to 46 days old. Ovaries of Awassi ewe lambs were large and the weight of paired ovaries was 600 mg. They contained many preantral and antral follicles. Ovaries of BM x Awassi ewe lambs were significantly smaller and weighed 132.5 mg ($P<.05$). Only one of the BM x Awassi ewe lambs had ovaries with antral follicles. The ovaries of the other 3 BM x Awassi ewe lambs had only preantral follicles. Ovaries of Assaf ewe lambs of similar age also were much larger and had more antral follicles than those of BM x Assaf ewe lambs. Thus follicular development is impaired in young BM-cross ewe lambs.

FIG. 1 Basal plasma FSH in Awassi (dashed line) and Booroola-Awassi (solid line) ewe lambs. Each value represents mean ± SEM of 9-16 or 6-14 (Booroola-Awassi) determinations. Significant difference between the genotypes is indicated: *$P < 0.05$, **$P < 0.01$, ***$P < 0.0001$.

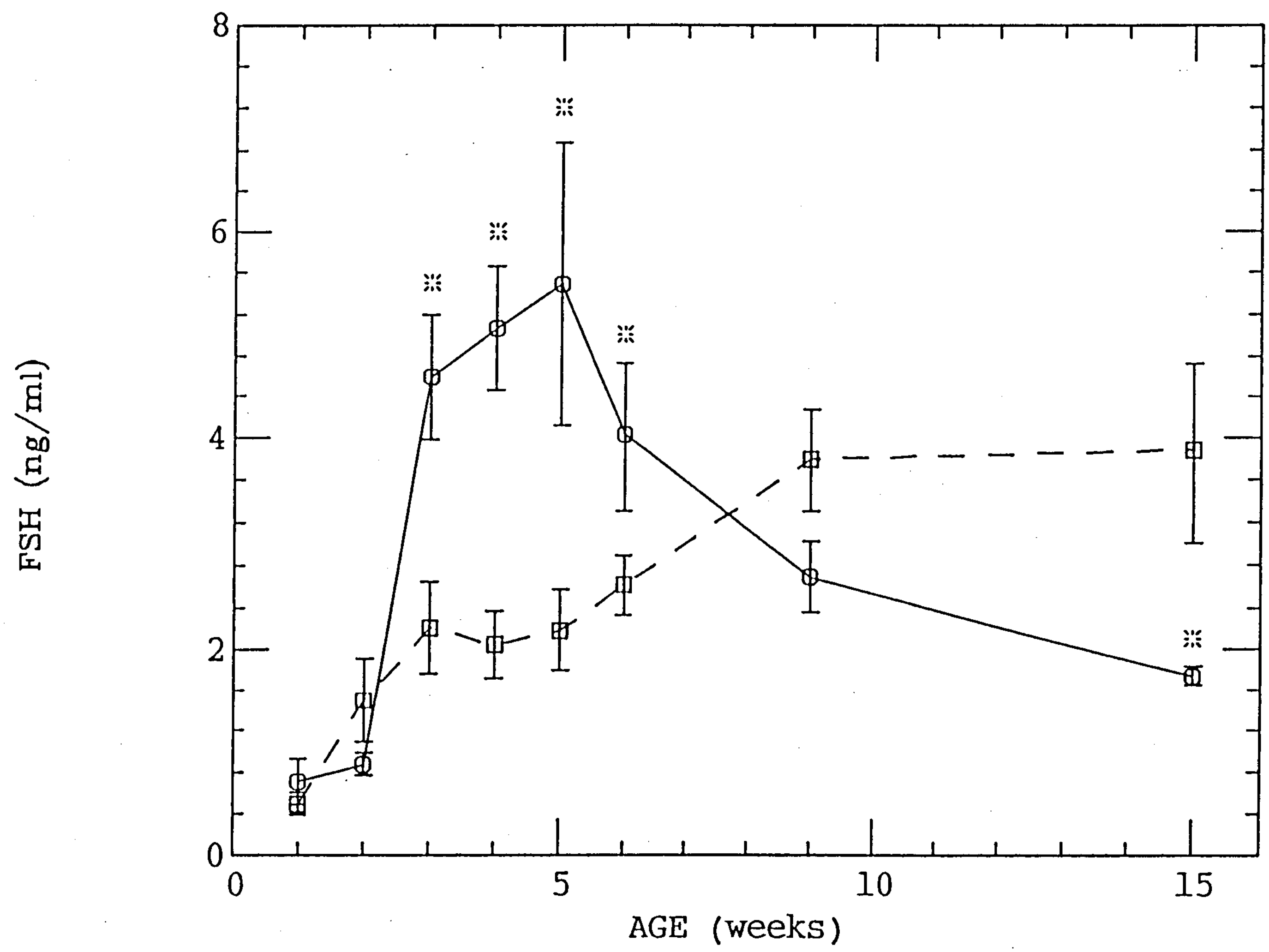


FIG. 2 Basal plasma FSH in Assaf (dashed line) and Booroola-Assaf (solid line) ewe lambs. Each value represents mean ± SEM of 9-14 (Assaf) or 6-15 (Booroola-Assaf) determinations. Significant difference between the genotypes is indicated: *P < 0.05, **P < 0.01, ***P < 0.001.

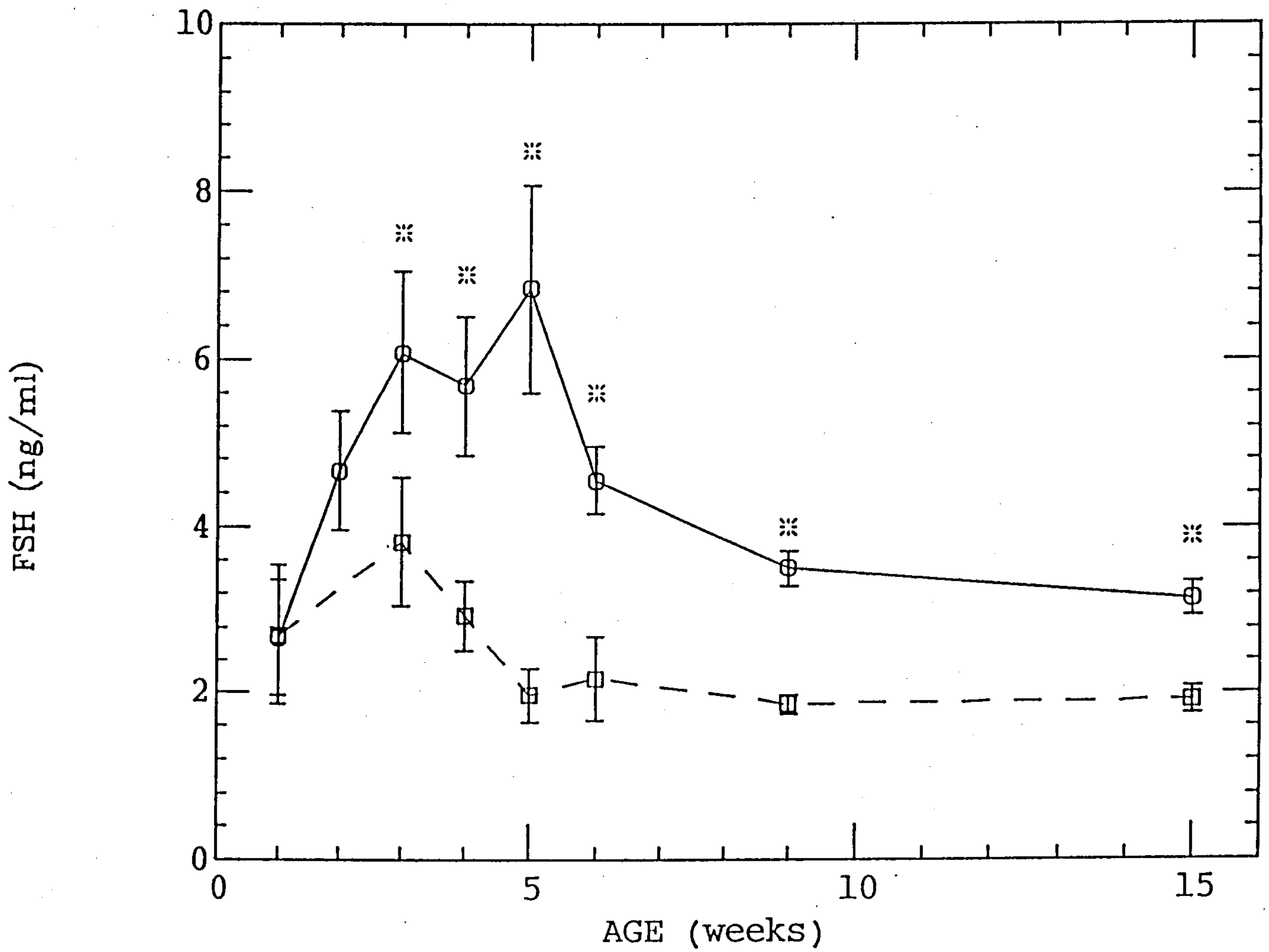


FIG. 3 Mean FSH concentrations in ewe lambs of both genotypes at 30, 45, and 60 d of age. SEM denotes standard error of difference of means. An asterisk indicates the difference between two genotypes was significantly different at least at the .05 level.

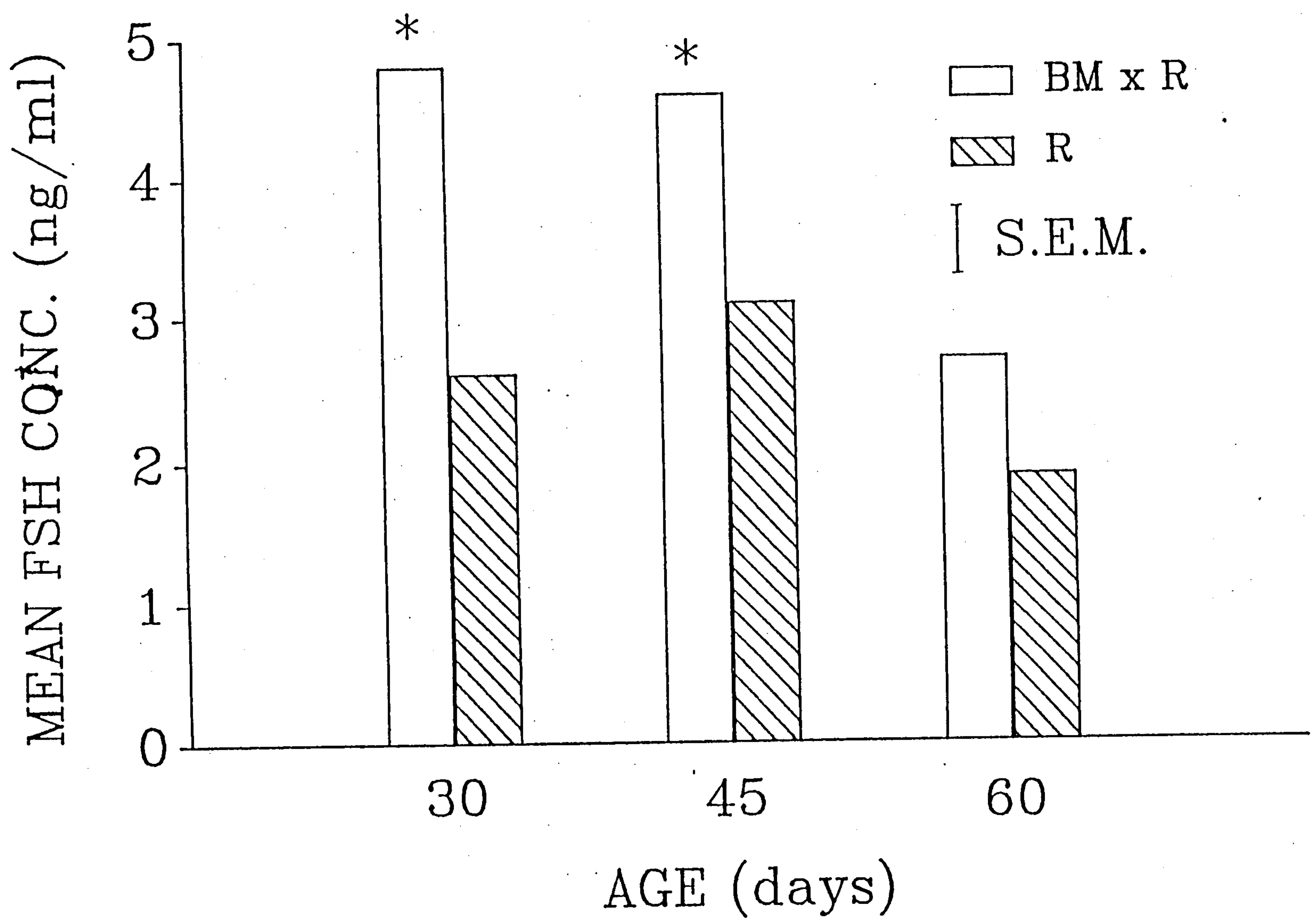


FIG. 4 Mean FSH concentrations in ram lambs of both the genotypes at 30, 45, and 60 d of age. SEM denotes standard error of difference of means.

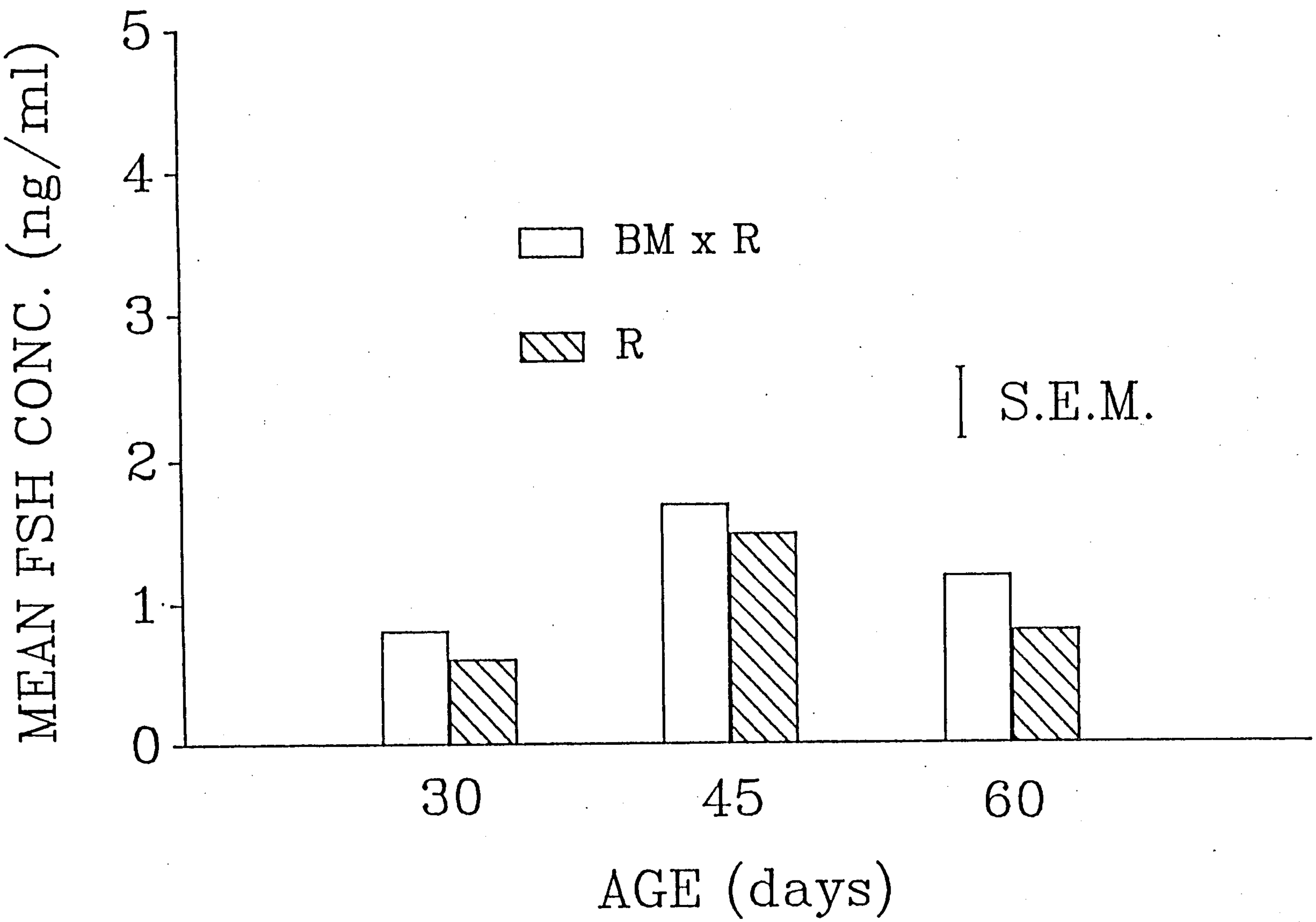


FIG. 5 Mean FSH concentrations of individual ewe lambs of both genotypes at 30, 45 and 60 d of age.

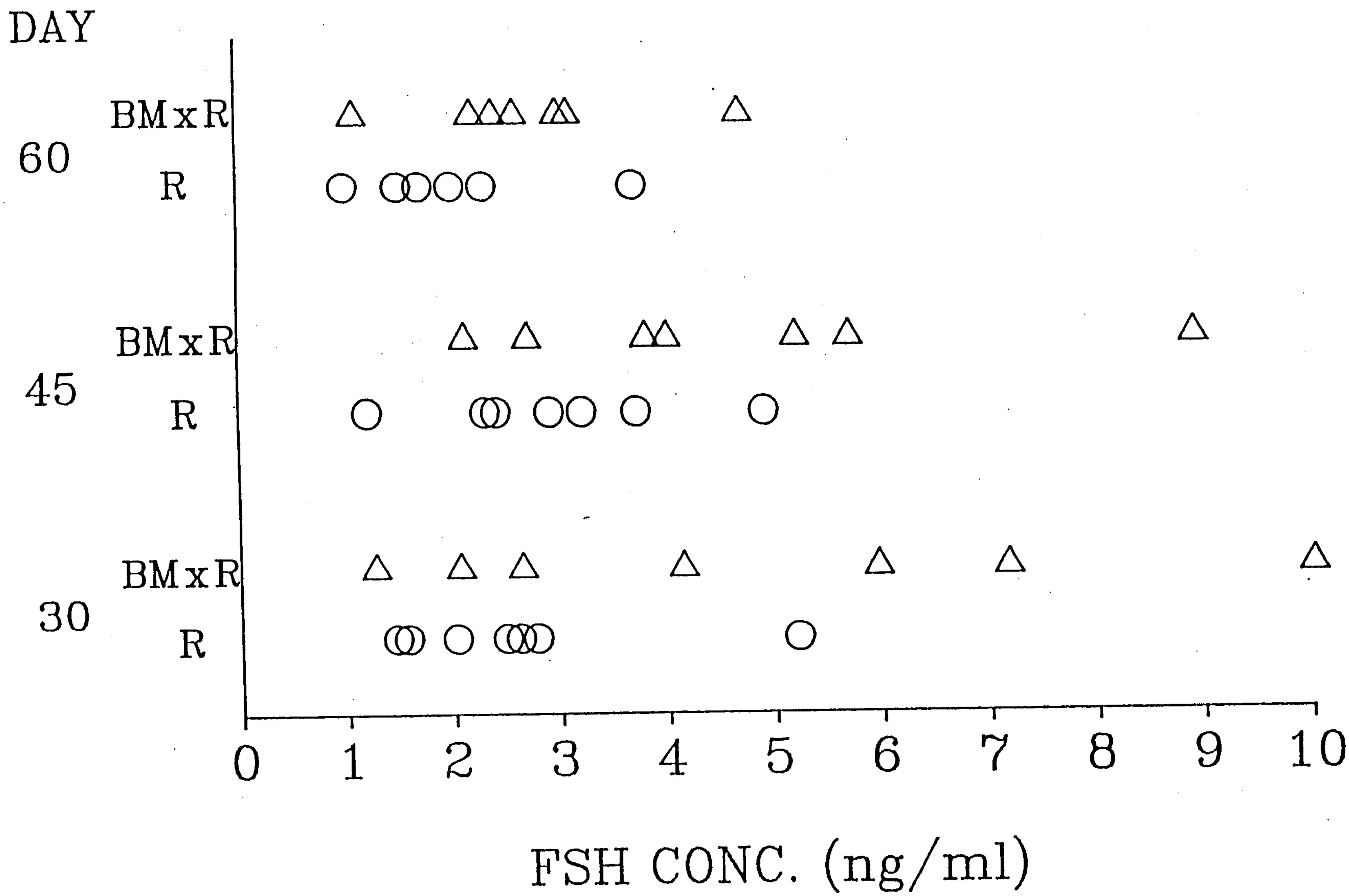
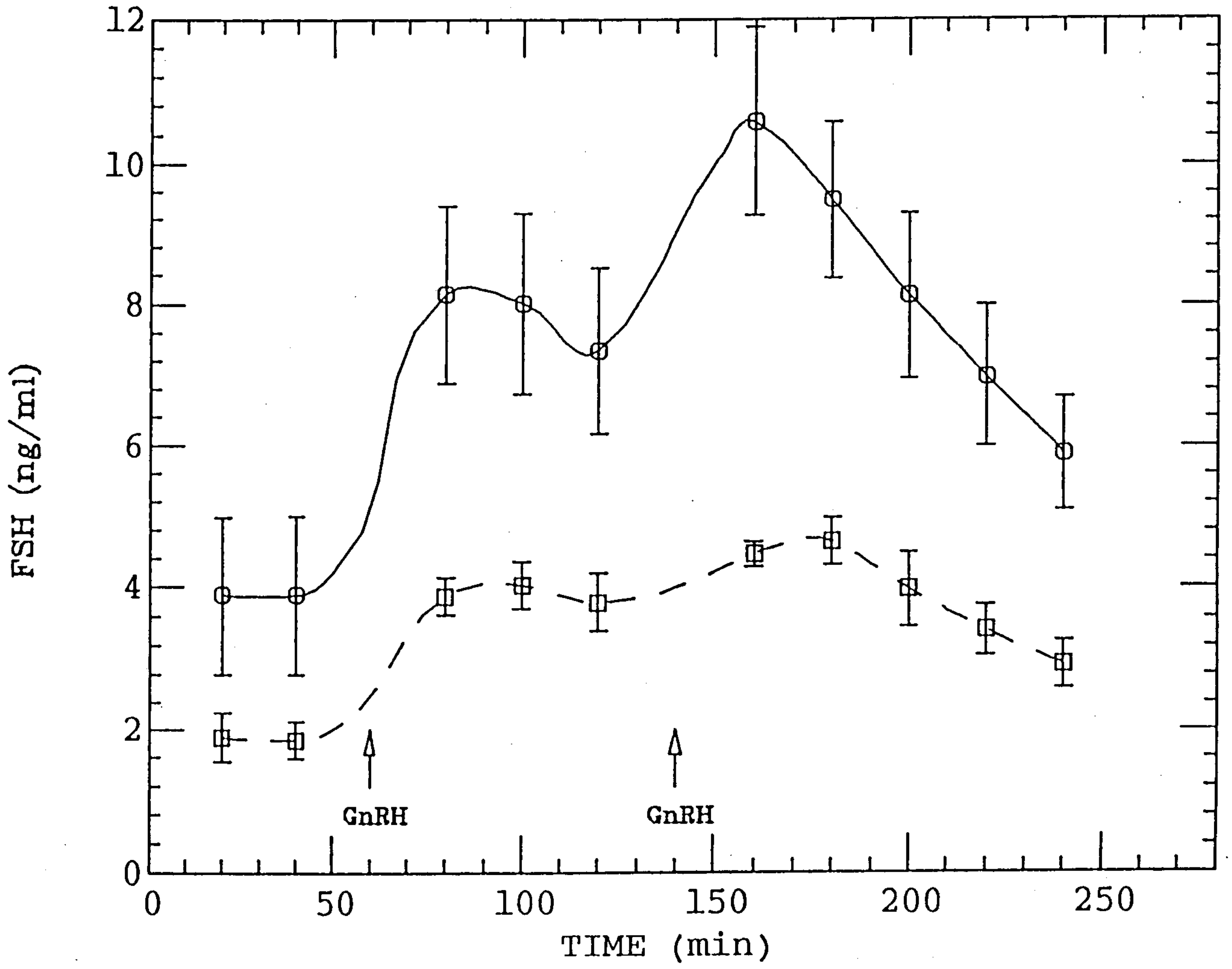


FIG. 6 Plasma FSH response to GnRH administration in 40-45 day old Awassi (dashed line) and Booroola-Awassi (solid line). GnRH was injected as indicated. Each value represents mean $\pm$ SEM of six determinations. Significant differences ($P < 0.05$) between genotypes were for all values following GnRH treatment.



Induced Ovulation Rate. The induction of ovulation and subsequent determination of ovulation rate in prepubertal ewe lambs may allow for identification of the presence of the F gene in young females. Presented in Table 11 is distribution of number of ovulations and mean ovulation rate for several genotypes treated with 400 i.u. PMSG in Israel at approximately 5 months of age. The rank of the genotypes for induced ovulation rate is similar to their expected rank for natural ovulation rate and litter size.

A criterion of 2 or more induced ovulations for presence of the F gene may be useful in a mixed population of BM x Awassi and Awassi or of BM x Assaf and Assaf ewe lambs. If such a criterion were used, 86% and 73% of the Awassi and Assaf ewe lambs, respectively, would have been classified correctly as non-carriers (++) and 60% and 65% of the BM x Awassi and BM x Assaf ewe lambs, respectively, would have been classified correctly as carriers (F+). This criterion would not be useful in differentiating between Finn x Awassi and BM x Awassi for presence of the F gene.

TABLE 11. DISTRIBUTION OF OVULATION RATE AND MEAN OVULATION RATE (± S.E.) OF PREPUBERTAL EWE LAMBS OF DIFFERENT GENOTYPES TREATED WITH 400 I.U. PMSG IN ISRAEL.

Genotype	n	Number of ewe lambs with an ovulation rate of: 0	1	2	3	4	5	6	7	Mean ovulation rate
Awassi	28	11	13	4						.75 ± .13
Assaf	34	7	18	7	2					1.12 ± .14
Finn x Awassi	22	4	8	7	2	1				1.45 ± .22
Booroola x Awassi	10	2	2	4	2					1.60 ± .33
Booroola x Assaf	23	4	4	5	4	2	3	-	1	2.43 ± .39

Prepubertal Rambouillet and BM x Rambouillet ewe lambs in the U.S. were administered several different compounds in different trials to induce ovulations.. Presented in Table 12 is the distribution of numbers of ovulations induced by a single injection of 500 i.u. of PMSG in trials conducted in 1987 and 1989. F_1 BM (F+) ewes had a greater ovulation rate than Rambouillet (++) ewes. When the criterion of 2 or more ovulations was used to distinguish ewes with the F gene, 64% of F+ ewes would have been classified correctly as carriers and 77% of ++ ewes would have been classified correctly as non-carriers.

TABLE 12. OVULATION INDUCED IN PREPUBERTAL EWE LAMBS WITH PMSG.

Breeding %	Trial	N	Ovulation distribution, no. 0	1	2	3	4..	10	Ovulation rate	2 or more ovulations,
BM x R[a]	1987-1[b]	13	4	2	3	2	2		1.69	53.8
	1987-2	11	3		4	1	3		2.09	72.7
	1989-1	6	1		3	2			2.00	83.3
	1989-2	26	6	4	8	2	5	1	2.15	61.5
	All	56	14	6	18	7	10	1	2.02	64.3
Ramb.	1987-1	9	7	1	1				.33	11.1
	1987-2	12	7	4	1				.50	8.3
	1989-1	5	2	2	1				.80	20.0
	1989-2	42	15	14	11	2			1.00	31.0
	All	68	31	21	14	2			.81	23.5
					P<.005[c]					P<.005[d]

[a]BM=Booroola Merino=F+, R=Ramb.=Rambouillet=++.
[b]Year of trial and replication within year.
[c]Significance level for difference between breeds in overall distribution of ovulations.
[d]Significance level for difference between breeds in overall distribution of ovulations in the two categories: 0,1 vs 2 or more.

Table 13 presents the results from 1987 using a single injection of 750 i.u. of hCG. The results were not promising with 60% of ewes of both breeds failing to ovulate. The chi square test did not detect a significant difference between breeds for distribution of number of ovulations or proportion of ewes with 2 or more ovulations.

TABLE 13. OVULATION INDUCED IN PREPUBERTAL EWE LAMBS WITH HCG.

Breeding %	Trial	N	Ovulation distribution, no. 0	1	2	3	4	5	Ovulation rate	2 or more ovulations,
BM x R[a]	1987-1[b]	14	10		2		1	1	.93	28.6
	1987-2	11	5	2	1	2	1		1.27	36.4
	All	25	15	2	3	2	2	1	1.08	32.0
Ramb.	1987-1	14	9	2	3				.57	21.4
	1987-2	11	6	4	1				.55	9.0
	All	25	15	6	4				.56	16.0
					P<.25[c]					P<.25[d]

[a,b,c,d]See Table 11.

In the trial in 1988, ewe lambs were given a single injection of 500 i.u. of PMSG followed 2 days later by a single injection of 250 i.u. of hCG. Results are presented in Table 14. Whereas a minority of ewes of both genotypes ovulated to hCG alone in the previous trial, the combination of PMSG and hCG resulted in a high percentage of ewes of both genotypes ovulating. The combination of both compounds induced too high an ovulation response in the ++ ewes to allow them to be accurately differentiated from the F+ ewes.

TABLE 14. OVULATION INDUCED IN PREPUBERTAL EWE LAMBS WITH A COMBINATION OF PMSG AND HCG.

			Ovulation distribution, no.								Ovulation	2 or more
Breeding	Trial	N	0	1	2	3	4	. . .	6	7	rate	ovulations, %
BM x R[a]	1988[b]	19	3	3	6	2	3		1	1	2.42	68.4
Ramb.	1988	24	5	9	7	3					1.33	41.7
						P<.25[c]						P<.10[d]

[a,b,c,d]See Table 11.

In an effort to mimic more natural post-pubertal endocrine conditions, ewe lambs were injected with a total of 4, 6 or 8 mg of an ovine pituitary extract in 6 equal doses every 12 hours. There was little difference in response from the 4, 6 and 8 mg doses so results from all doses were pooled in Table 15. These doses resulted in only 14.3% of ewes ovulating and were of little value in differentiating between the genotypes.

TABLE 15. OVULATION INDUCED IN PREPUBERTAL EWE LAMBS WITH 4 OR 8 MG OF OVINE PITUITARY EXTRACT.

			Ovulation distribution, no.				Ovulation	2 or more
Breeding	Trial	N	0	1	2	3	rate	ovulations, %
BM x R[a]	1989[b]	20	16	1	2	1	.40	15.0
Ramb.	1989	36	33	3			.08	0.0
				P<.25[c]				P<.025[d]

[a,b,c,d]See Table 11.

In 1989, an evaluation of 20 or 40 mg of ovine pituitary extract was conducted. The compound was administered by injection in 6 equal doses every 12 hours. These two doses each gave similar results, and results were pooled across doses in Table 16. Distribution of number of ovulations was markedly different between the genotypes. Eighty-one percent of F+ ewes ovulated with an average ovulation rate of 1.77 compared to 23% of ++ ewes ovulating with an average ovulation rate of .27. Approximately 65% of F+ ewes had 2 or more ovulations compared with only 4% of ++ ewes.

TABLE 16. OVULATION INDUCED IN PREPUBERTAL EWE LAMBS WITH 20 OR 40 MG OF OVINE PITUITARY EXTRACT.

Breeding %	Trial	N	Ovulation distribution, no. 0	1	2	3	4	Ovulation rate	2 or more ovulations,
BM x R[a]	1989[b]	26	4	5	11	5	1	1.77	65.4
Ramb.	1989	26	20	5	1			.27	3.8
					P<.005[c]				P<.005[d]

[a,bc,d]See Table 11.

From these studies, the most accurate treatments for differentiating among F+ and ++ individuals were PMSG (400 i.u. used in Israel and 500 i.u. used in U.S.) or 20 to 40 mg of ovine pituitary extract. When the criterion of 2 or more ovulations is used to determine presence of the "F" gene, PMSG treatment resulted in correct classification of approximately 63% of F+ ewes and 79% of ++ ewes. However, ovine pituitary extract at levels of 20 to 40 mg may be more accurate in differentiating between F+ and ++ genotypes than PMSG. Accuracy of detecting F+ individuals (65%) was similar to that obtained with PMSG, however, accuracy of detecting ++ individuals was considerably higher with pituitary extract (96%) than with PMSG.

Conclusions. In prepubertal ewe lambs, basal or GnRH-induced FSH concentrations at approximately 30 days of age or number of ovulations induced by PMSG or 20 to 40 mg of ovine pituitary extract appear to hold the most promise for differentiating between F+ and ++ individuals. However these techniques need to be tested in animals of the same breed composition where the F gene is segregating before their real worth can be determined.

3. Genetic Markers for the F Gene

In the U.S., linkage studies between the F gene and the R-O, A, B, C, D and M blood group systems, hemoglobin, carbonic anhydrase, X protein, transferrin and esterase have been conducted on a small scale. Preliminary results (1 sire and 9 daughters) suggest that a linkage between the R-O blood groups and the F gene is possible.

Several DNA probes were used in Israel on BM-Assaf and BM-Awassi crosses, and a RFLP was observed at the growth hormone locus. Also, a few VNTR probes were used and showed a high level of polymorphism. These probes can be used in future analyses to search for a linkage with the F gene.

F. Description of Cooperation

Research protocols at both locations were jointly discussed prior to the start of each study so that maximum use could be made of previous results at one location in the design of an appropriate experiment at the other location. In the early months of the project, scientists in the two countries maintained frequent contact via FAX and mail. In later months, electronic mail via computers was used to maintain an almost continuous line of communication, sometimes on a daily basis, between research groups.

A number of person-to-person contacts among scientists from the two locations were made during the project. Dr. Elisha Gootwine, team leader from Israel, spent 2 weeks at the University of Illinois in July, 1987 revising the proposal's budget and visiting with the University of Illinois team (Drs. David L. Thomas, Philip J. Dziuk and Harris A. Lewin) on specifics of experimental plans. Detailed plans for the two initial studies on induced ovulation rate, one conducted in Israel and the other in the U.S., were decided during this meeting. Dr. Gootwine also presented a seminar to the Department of Animal Sciences, University of Illinois on some preliminary work with the Booroola Merino and his plans for the future, and he attended the Field Day at the Dixon Springs Agricultural Center with Dr. Thomas where most of the experimental animals for this project are maintained. Drs. Gootwine, Thomas and Dziuk also attended the 1987 Annual Meeting of the American Society of Animal Science at Utah State University in August, 1987 where discussions concerning the project were continued.

Drs. Gootwine, Dziuk and Thomas attended the IIIrd World Congress on Sheep and Beef Cattle Breeding in Paris in June, 1988 where they discussed results from the first year of the project, data and information to be included in the First Annual BARD Report and proposed work for the remainder of the project.

Dr. Ruth Braw-Tal, from Israel, spent a week at the University of Illinois in July, 1989 visiting with the University of Illinois team on specifics of experimental plans and discussing the material to be incorporated in the Second Annual BARD Report. Dr. Braw-Tal presented a seminar to the Department of Animal Sciences, University of Illinois on her work on physiological treatments to identify presence of the F gene.

Dr. Harris Lewin spent a week in July, 1990 with the Israeli group at the Volcani Centre discussing their work in molecular genetics with the Booroola Merino and beginning the writing of a proposal which has been since submitted to BARD to continue work with the Booroola Merino.

Drs. Gootwine, Braw-Tal and Thomas presented papers on work accomplished under the BARD project at the International Workshop on Major Genes for Reproduction in Sheep held in Toulouse, France in July, 1990. While at the workshop, these scientists continued developing the proposal that has since been submitted to BARD for continuation of this work. Drs. Gootwine, Lewin and Gootwine also attended the 4th World Congress on Genetics Applied to Livestock Production in Edinburgh, Scotland in July, 1990. Drs. Gootwine and Thomas presented papers concerning results from the current project and continued the development of the proposal for continuation.

As a result of this project, scientists from Israel and the U.S. that previously had not known one another became scientific colleagues conducting truly cooperative research for the benefit of sheep producers in both countries.

G. Evaluation of Research Achievements

Considerable data were collected in comparing F_1 BM ewes heterozygous for the F gene (F+) with pure Awassi, Assaf and Rambouillet ewes and F_1 ewes sired by Finnsheep, Combo-6, St. Croix and Barbados rams. BM F_1 ewes ovulated more eggs and generally gave birth to more lambs than the domestic breeds to which they were compared. This can be attributed to the positive effect of the F gene on ovulation rate. BM F_1 ewes were also superior to ewes of domestic breeding for all measures of fleece quantity and quality. However, BM-cross lambs had lower survival rates to weaning, poorer growth rates, a higher percentage of carcass fat and a lower percentage of carcass lean than did lambs of domestic breeding. BM F_1 ewes were also older at puberty, had lower fertility, weaned less weight of lamb per ewe exposed and produced less dairy milk than ewes of domestic breeding. These results strongly suggest that infusion of 1/2 BM inheritance into domestic flocks in the U.S. and Israel will result in decreased lamb and dairy milk production.

Even though 1/2 BM inheritance is generally undesirable, the F gene, transferred to a domestic breed with good growth, milk or wool production, may result in increased efficiency of production. Transfer of the gene through backcrossing would be facilitated if carriers of the gene could be identified at an early age. Results from this project suggest that basal FSH concentrations of 30-day-old ewe lambs (higher in BM F_1 (F+) than domestic breed (++) ewes) can be used to separate carriers from non-carriers with a reasonable degree of accuracy, and this accuracy may be increased if determination is made on FSH concentrations after GnRH administration. Induced ovulation rate in prepubertal ewe lambs (5 to 7 months of age) is higher in BM F_1 than domestic breed ewes and can be used with a high degree of accuracy to determine genotype. Ovulation rate induced with PMSG or ovine pituitary extract was 60 to 65% accurate in identifying carriers and 80 to 95% accurate in identifying non-carriers.

In summary, the major achievements of this project have been: 1) the determination that the F gene has potential to increase the litter size of Israeli and U.S. sheep populations but the remainder of the Booroola Merino genome is undesirable due to its negative effects on other production traits and 2) development of techniques to discriminate between carriers of the F gene and non-carriers in young females to facilitate the transfer of the F gene through a backcrossing program into domestic breeds.

The results suggest that research groups in both countries should move ahead with the development of domestic stocks with the F gene, while continuing to search for more accurate methods to differentiate between carriers and non-carriers which, if found, would accelerate this development.

H. List of Publications

Braw-Tal, R., A. Bor and E. Gootwine. 1988. Plasma FSH and ovarian follicular population in prepubertal Booroola-Awassi and Booroola-Assaf ewe lambs. Proc. IIIrd World Cong. on Sheep and Beef Cattle Breeding. Institut National de la Recherche Agronomique, Paris, France. 2:661-663.

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Thomas, D. L., R. M. Bunge and T. G. Nash. 1990. Productivity of Suffolk and Targhee ewes mated to prolific- and hair-breed rams. W. G. Hill, R. Thompson and J. A. Woolliams (Ed.). Proc. 4th World Cong. on Genet. Appl. to Livestock Prod. Edinburgh, Scotland. 15:119-122.

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I. Three Copies of Each Publication Resulting from the Project (Enclosed)