AN ABSTRACT OF THE THESIS OF

William Russell Lamberson for the degree of Master of Science

in Animal Science presented on October 5, 1981

Title: The Effects of Inbreeding in a Flock of Hampshire Sheep

Abstract approved: Redacted for Privacy
David L. Thomas

A registered flock of Hampshire sheep that had been predominantly closed for approximately 30 years was utilized to study the effects of inbreeding on productivity of the 1980 and 1981 lamb crops. Five generation pedigrees for ewes and rams were used to calculate inbreeding coefficients. The median inbreeding coefficient of 598 lambs was 10.7% and coefficients ranged from 1.4 to 29.6%. The median inbreeding coefficient of 212 ewes was 4.3% and coefficients ranged from 0.0 to 28.1%. Regression techniques were used to determine the effects of ewe inbreeding on six month fleece weight and ewe breeding weight and the effects of ewe and lamb inbreeding on days from ram introduction to conception, fertility, prolificacy, lamb survival to 7 and 90 days, weight of lamb at birth, 30, 60 and 90 days and weight of lamb weaned per ewe exposed. A one percent increase in lamb inbreeding reduced ($P<.01$) survival to 7 days by 1.1%, reduced ($P<.01$) survival to 90 days by 1.3% and reduced ($P<.05$) weight of lamb weaned per ewe exposed by .59 kg. A one percent increase in ewe inbreeding decreased ($P<.10$) ewe breeding weight by .27 kg, increased ($P<.10$) days from ram introduction to conception by .35 days and decreased ($P<.05$) fertility by .56%. The effect of ewe inbreeding on six month fleece weight and of lamb and ewe inbreeding on prolificacy and lamb weight at

birth, 30, 60 and 90 days were not significantly different from zero. Weight of lamb weaned per ewe exposed was composed of fertility, prolificacy, lamb survival to 90 days and 90 day weight. Using the percentage deviation method the negative effect of lamb inbreeding on weight weaned per ewe exposed was attributed as follows: 11% to its effect on fertility, 6% to its effect on prolificacy, 80% to its effect on survival and 3% to its effect on 90 day weight.

THE EFFECTS OF INBREEDING IN A FLOCK OF HAMPSHIRE SHEEP

by

WILLIAM RUSSELL LAMBERSON

A THESIS

Submitted to

Oregon State University

in partial fulfillment of

the requirements for the

degree of

MASTER OF SCIENCE

Completed October 5, 1981

Commencement June 1982

APPROVED:

Redacted for Privacy

Assistant Professor of Animal Science in charge of major

Redacted for Privacy

Head of Department of Animal Science

Redacted for Privacy

Dean of Graduate School

Date thesis is presented Oct 5, 1981

Typed by Toshie N. Gordon for William Russell Lamberson

ACKNOWLEDGEMENTS

I sincerely thank Dr. David L. Thomas, my advisor, for his advice and guidance during my study period and for his continuing friendship.

I thank my committee members, Drs. William D. Hohenboken and Kenneth Rowe, for their assistance with statistical problems and writing.

I thank Steve Clarke, Paul Bellatty and my other friends in the basement for their willingness to discuss problem and ideas.

I appreciate the financial assistance provided by the Oregon State University Agricultural Experiment Station for support of this study.

My love and gratitude go to my wife, our parents and our children whose support and encouragement allowed me to complete this work.

Most of all, I wish to thank Ronald and Glenn Hogg who allowed me to collect data for this study. It has been a privilege to know and learn from these great livestock producers. I dedicate this thesis to them, their dedication to livestock breeding should be an inspiration to us all.

TABLE OF CONTENTS

LIST OF TABLES

The Effects of Inbreeding in a Flock of Hampshire Sheep

CHAPTER I

INTRODUCTION

Breeders of livestock have made use of inbreeding primarily in two ways. First, inbred lines have been developed for selection and crossing (in sheep, Hazel and Terrill, 1945 and 1946a) with the intent of duplicating the success of corn breeders who have used this method to produce high-yielding hybrids (East and Jones, 1919). These attempts by livestock breeders have, however, been notably unsuccessful (Dickerson, 1972).

The second use of inbreeding has been that of closing a line or herd and then using mass selection to remove undesirable types. This method was used by Bateson and Colling to develop breeds nearly two centuries ago (Johannson and Rendel, 1968). Most livestock producers are deterred from extensive mating within their herds because of the known detrimental effects of inbreeding. It must be remembered, however, that no matter what decline in appearance and performance results from close mating within a closed lined, the line carries only those genes present in their ancestors when the line was closed (Fisher, 1965). It should also be remembered that the decline in performance due to inbreeding will be recovered when the line is mated to unrelated animals (Dickerson, 1972).

Many studies have documented the effects of inbreeding in lines formed for crossing and in flocks in which inbreeding was incidental to other factors being studied (and was therefore at low levels)

(Hazel and Terrill, 1945, 1946a and 1946b; Terrill et al., 1947 and 1948; Morley, 1954; Doney, 1957 and 1966; Glembockii, 1956; Bogart 1961; Carter et al., 1961; Brown et al., 1961; Carter et al., 1961; Pattie, 1965; Lax and Brown, 1967 and 1968; Ercanbrack and Knight, 1981; and Galal et al., 1981). Few studies have dealt with the effects of inbreeding in the elite closed line (Ragab and Asker, 1954 and Liebenberg and John, 1973). This study examines the effects of inbreeding on production traits in a prominent flock of Hampshire sheep established for over 50 years and predominantly closed for 30 years.

LITERATURE REVIEW

Inbreeding. Inbreeding results from mating individuals that are more closely related than the average of the population. The consequence of inbreeding, according to Falconer (1960), is that two related individuals may carry replicates of a gene possessed by an ancestor common to both. When the related individuals mate, they may each pass their replicate of the gene to their offspring. The offspring then carries two replicates of what was one gene in a previous generation. The two genes are said to be identical by descent and the locus in the offspring is homozygous due to inbreeding.

The inbred individual is homozygous at loci which are identical by descent in addition to, but independent of, regular homozygosity. Wright (1922a) provided the inbreeding coefficient, F, to measure the increase in homozygosity due to inbreeding. Malecot (1969) alternatively defined the inbreeding coefficient as the probability that two genes at a locus are identical by descent. The inbreeding coefficient implies a comparison of the proportion of identical loci between the current population and a specified base population in which it is assumed that no loci have genes identical by descent.

Inbreeding Depression. The important result of inbreeding for the livestock producer or animal breeder is that increased homozygosity leads to a decline in vigor known as inbreeding depression. Inbreeding depression is effected through changes in genotypic frequencies which result in a higher proportion of homozygotes and a lower proportion of heterozygotes. A character's mean value will change only if it is affected by loci at which there is some degree of dominance. At these loci, when genotypic frequencies change the mean value will change in the direction of the recessive alleles.

Inbreeding depression was first shown experimentally by Darwin (1885) in a number of plant species. Later, Wright (1922b) examined the effects of inbreeding in guinea pigs. Since that time studies have been performed in many livestock and laboratory species. Findings have generally shown that inbreeding results in lowered performance for fitness characters such as survival, reproductive rate and body weight.

Turner and Young (1969) suggest that traits should be linearly affected by degree of inbreeding if epistatic effects are not important. This theoretical observation has generally been confirmed by experimental results, at least when inbreeding is at low to moderate levels. Two exceptions are the results from a comprehensive study of effects of inbreeding in beef cattle by Brinks and Knapp (1975) and results from a study by Bogart (1961) in sheep.

Brinks and Knapp (1975) found significant quadratic effects of dam's inbreeding on offspring growth traits, especially in male calves. Bogart (1961) presented data which suggested quadratic effects of inbreeding on prolificacy and survival in Suffolks. Unfortunately, Bogart (1961) presented no statistical analysis to confirm these apparent trends.

Effects of inbreeding on wool production and fleece characteristics have been studied extensively in both the United States and Australia. Hazel and Terrill (1945, 1946a and 1946b), Terrill et al. (1947 and 1948) and Ercanbrack and Knight (1981) presented results from selected inbred lines of Western Whitefaced range sheep in the United States.

The effects of inbreeding on fleece characters in Australian Merinos were reported by Morley (1954) who worked with a selected flock with low levels of inbreeding. Doney (1957) studied inbreeding effects on fleece traits of highly inbred lines of Peppin Merinos, and Lax and Brown (1967) examined fleece characters in a randomly selected control population of Peppin Merinos. Liebenberg and John (1973) reported the effects of inbreeding on fleece characters in elite flocks of German Mutton Merinos selected for meat traits.

Reports of these workers are summarized in Table 1 for greasy fleece weight, Table 2 for clean fleece weight, Table 3 for staple length and Table 4 for yield, fiber diameter, fleece density and crimps per centimeter. The reported effects of individual inbreeding on greasy fleeces declined .015 kg per one percent increase in inbreeding and the weight of clean fleeces declined .013 kg per one percent increase in inbreeding as averaged over all reports. Lax and Brown (1967) reported mixed effects of dam's inbreeding on the two traits. Staple length has also generally been found to decline with increasing levels of inbreeding. The average over all reports summarized was a .004 cm decline per one percent increase in individual inbreeding. Again, the reported effects of dam's inbreeding were mixed. Effects of individual inbreeding on yield were not consistent from study to study. The average effect was -.01% per one percent increase in inbreeding. Dam inbreeding was found to decrease yield by an average of .17% per one percent increase in dam's inbreeding. The effect of inbreeding on fiber diameter was not consistent, but the effect on fleece density and crimps per centimeter was negative. The average decline in fleece density was .22 fibers/mm^2 per percent increase in individual inbreeding. The average decline in crimps per centimeter was .012 crimps/cm per one percent increase in inbreeding. Dam's inbreeding increased crimps per centimeter by .007 crimps/cm per one percent increase in dam's inbreeding.

Fleece weights of inbred Blackface lambs were found by Doney (1956) to be lower (P<.01) than those of non-inbred half-sibs. Inbred lines of Precoce were found by Glembockii (1956) to have lower fleece weights and longer staple length than contemporary non-inbred lines.

Many reports of effects of inbreeding on body size have also been published. Effects on weights at various ages have been reported for Western whitefaced range sheep by Hazel and Terrill (1945, 1946a and 1946b), Terrill et al. (1947 and 1948) and Ercanbrack and Knight (1981). Effects in Australian Merinos have been reported by Morley (1954), Pattie (1965) and Lax and Brown (1967 and 1968). Ragab and Asker (1954) reported the effects of dam and offspring inbreeding on several measures in Ossimi sheep. Glembockii (1956) reported that inbred lines of Precoce sheep had lower birthweights than non-inbred contemporaries. He also reported that dam inbreeding had a negative effect on lamb birthweight. Bogart (1961) found no difference between inbred (17.5%) and non-inbred lines of Suffolks for birthweight or mature size. Brown et al. (1961) reported that in inbred lines of Hampshires, lamb inbreeding reduced 30 and 120 day weights but there was little effect of ewe inbreeding. Carter et al. (1961), in another study of inbred Hampshires, showed non-inbred controls to be superior to contemporary highly inbred lines (average inbreeding was 37%) for birth and 120 day weights. Doney (1966) compared Blackface lambs from father-daughter matings to contemporary non-inbred half-sibs and found the non-inbred sheep to have higher (P<.01) birth, 30 day, weaning and mature weights. Liebenberg and John (1973) examined the effects of inbreeding on mature weight in German Mutton Merinos. Regression coefficients reported by these researchers are presented in Tables 5, 6 and 7. Averaged across the studies summarized, a one percent increase in individual inbreeding resulted in a decrease of .014 kg in birth weight, .102 kg in 120 day weaning weight and .168 kg in mature weight. The average effects of dam inbreeding were to decrease birth weight by .0086 kg, 120 day weaning weight by .015 kg and increase mature weight by .013 kg per one percent increase in inbreeding.

Doney (1957) studied body size measured as a size index and found that each increase of one percent in inbreeding resulted in a 170 cm^3 decrease (P<.001) in body size of inbred (avg. F=12.8%) Peppin Merinos. Brown et al. (1961) reported a non-significant increase of .331 days to reach 27 kg per one percent increase in lamb inbreeding and a .0244 day increase per one percent increase in inbreeding of ewe in inbred Hampshires. Non-inbred Hampshires were found to be superior to inbred lines in preweaning gains by Carter et al. (1961).

Western range sheep were scored from 1 to 5 for condition (fatness) and body conformation with one being the superior score. The effects of inbreeding on these traits were reported by Hazel and Terrill (1945, 1946a and 1946b), Terrill et al. (1947 and 1948) and Ercanbrack and Knight (1981) and are summarized in Tables 8 and 9. A one percent increase in inbreeding increased body type score .098 units and condition score .009 units. Carter et al. (1961) also reported that increased inbreeding resulted in poorer type scores and slaughter grades in Hampshires.

Effects of inbreeding on face cover and body wrinkles were examined in Western range sheep (Hazel and Terrill, 1945, 1946a and 1946b; Terrill et al., 1947 and 1948 and Ercanbrack and Knight, 1981) and Australian Merinos (Morley, 1954; Doney, 1957 and Lax and Brown, 1967 and 1968). Face cover was scored 1 to 5 with the lower score representing the more desirable open face. Wrinkle scores were assigned by different methods in each country. In all studies, however, lower scores represent fewer body and neck folds. Effects of inbreeding on face cover were not consistent. Results of reports on these two traits are summarized in Tables 10 and 11.

Fitness traits are known to be negatively affected by inbreeding. Negative effects of inbreeding on lamb survival have been reported by Morley (1954) and Lax and Brown (1968) in Merinos, Glembockii (1956) in Precoce, Bogart (1961) in Suffolks, Doney (1966) in Blackface and Galal et al. (1981) in Fleish Merino and two fat tailed breeds. Morley (1954) reported that average inbreeding of lambs that survived to 18 months of age was lower than those lambs not surviving to 18 months (average inbreedings of 4.0 vs. 5.4%), however, no statistical test was reported. Bogart (1961) reported the mortality rates for three levels of inbreeding in Suffolks. Sheep inbred 0 - 5% had 24% mortality, those inbred 6 - 15% had 22% mortality and those inbred greater than 15% had 37% mortality. Doney (1966) found greater neonatal deaths among inbred than among outbred lambs ($P<.02$) but there were not significant differences between groups in additional deaths to maturity. Lax and Brown (1968) reported regressions of single male and female lamb survival to weaning on lamb and dam inbreeding. The reported regression coefficients were for male lambs, -.003 lambs per one percent increase in dam inbreeding and -.007 lambs per one percent increase in lamb inbreeding; for female lambs, -.002 lambs per one percent increase in dam inbreeding and -.017 lambs per one percent increase in lamb inbreeding ($P<.01$). Galal et al. (1981) reported the effects of lamb and dam inbreeding on survival to 7, 30, 120 and 180 days. Levels of inbreeding were broken into five percent ranges from zero to greater than 25 percent. Although significant effects of lamb inbreeding were reported for survival to 7 and 120 days there was no trend apparent. There was a consistent downward trend in survival as inbreeding of dam increased but the effect was not significant.

Negative effects of ewe inbreeding on fertility have been reported by Bogart (1961) in Suffolks and Glembockii (1956) in Precoce. Neither of these researchers quantified their findings. Doney (1957) reported in Australian Merinos that 57.7% of non-inbred ewes that were bred actually lambed while only 24.6% of inbred ewes (average inbreeding = 24.2%) lambed.

Effects of inbreeding on fertility and prolificacy or the two traits combined into "reproductive rate" have been examined in several studies. Doney (1966) reported that inbred ewes were less likely to be fertile than non-inbred ewes (46% vs. 86%) and that their lambing percentage was somewhat lower (1.10 vs. 1.13). Lax and Brown (1968) found that for each increase of one percent in ewe inbreeding, there would be .009 fewer lambs born per ewe mated. The inbreeding of fetus also had a slight negative effect. Carter et al. (1961) reported from a study involving inbred Hampshires that inbred lines weaned 12 percent fewer lambs per ewe bred than non-inbred lines. Glembockii (1956), Bogart (1961) and Liebenberg and John (1973) also reported detrimental effects of ewe inbreeding on lambing rate although these authors did not quantify their results.

Several interesting interactions of inbreeding with other factors have been reported. Differential effects of inbreeding between sexes have been found for growth traits in beef cattle (Brinks and Knapp, 1975). Terrill et al. (1947 and 1948) reported that inbreeding depressed yearling weights in Columbia males more than in females, and there were also larger effects of inbreeding on yearling weights in Targhee males than females. Ragab and Asker (1954) found greater effects of inbreeding in male than in female Ossimi sheep for birth, four and six month weights. They also found that single lambs showed significant inbreeding depression but twins did not for the same traits. Lax and Brown (1968) reported the negative effects of inbreeding on lamb survival to weaning were greater in female than male Merino lambs.

Doney (1958) reported different production curves for inbred and non-inbred Peppin Merino ewes. Inbred ewes peaked in production at a later age than non-inbred ewes, and their peak production was lower than that of non-inbred ewes. This phenomena might be interpreted as an inbreeding x age interaction.

Results from the many studies reviewed confirm that increased levels of inbreeding consistently result in decreased production. Traits most affected are those with low to moderate heritabilities.

TABLE 1. EFFECTS OF INBREEDING ON GREASY FLEECE WEIGHT

Breed	Sex	Avg. F %	Age	Regr. coef. indiv.[a]	Regr. coef. dam[b]	Author
Rambouillet	F	4.5	13 mo	-.009 kg**		Hazel and Terrill, 1946b
Columbia	F	10.6	13 mo	-.010 kg*		Terrill et al., 1947
Targhee	F	8.4	13 mo	-.015 kg**		Terrill et al., 1947
Columbia	M	9.9	13 mo	-.006 kg		Terrill et al., 1948
Targhee	M	10.6	13 mo	-.010 kg		Terrill et al., 1948
Merino	M,F	3.8	22-23 mo	-.029 kg**		Morley, 1954
Merino	F	12.8	lifetime	-.016 kg*		Doney, 1957
Merino	F	1.8	15-16 mo	-.019 kg*	.010 kg	Lax and Brown, 1967
Merino	M	1.8	10-11 mo	-.023 kg**	.001 kg	Lax and Brown, 1967
Average		7.1		-.015 kg	.005 kg	

[a] Change in performance per one percent increase in individual inbreeding.

[b] Change in performance per one percent increase in dam's inbreeding.

* $P<.05$.

** $P<.01$.

TABLE 2. EFFECTS OF INBREEDING ON CLEAN FLEECE WEIGHT

Breed	Sex	Avg. F %	Age	Regr. coef. indiv.[a]	Regr. coef. dam[b]	Author
Rambouillet	F	4.5	13 mo	-.005 kg[c]		Hazel and Terrill, 1946b
Columbia	M	9.9	13 mo	-.004 kg[c]		Terrill et al., 1948
Targhee	M	10.6	13 mo	-.011 kg**[c]		Terrill et al., 1948
Merino	M,F	3.8	22-23 mo	-.020 kg**		Morley, 1954
Merino	F	12.8	lifetime	-.015 kg***		Doney, 1957
Merino	F	1.8	15-16 mo	-.011 kg	-.001 kg	Lax and Brown, 1967
Merino	M	1.8	10-11 mo	-.011 kg**	-.002 kg	Lax and Brown, 1967
Mutton Merino				-.024 kg		Liebenberg and John, 1973
Average		6.5		-.013 kg	-.001 kg	

[a]Change in performance per one percent increase in individual inbreeding.

[b]Change in performance per one percent increase in dam's inbreeding.

[c]Dried fleece.

*P<.05.

**P<.01.

***P<.001.

TABLE 3. EFFECTS OF INBREEDING ON STAPLE LENGTH

Breed	Sex	Avg. F %	Age	Regr. coef. indiv.[a]	Regr. coef. dam[b]	Author
Rambouillet	M,F	4.5	4 mo	-.003 cm*		Hazel and Terrill, 1945
Whiteface[c]	M,F	9.7	4 mo	.000 cm		Hazel and Terrill, 1946a
Rambouillet	F	4.5	13 mo	-.009 cm		Hazel and Terrill, 1946b
Columbia	F	10.6	13 mo	-.007 cm		Terrill et al., 1947
Targhee	F	8.4	13 mo	-.006 cm		Terrill et al., 1947
Columbia	M	9.9	13 mo	-.013 cm		Terrill et al., 1948
Targhee	M	10.6	13 mo	-.015 cm		Terrill et al., 1948
Merino	M,F	3.8	22-23 mo	-.012 cm		Morley, 1954
Merino	F	12.8	lifetime	.016 cm		Doney, 1957
Merino	F	1.8	15-16 mo	.015 cm	.021 cm	Lax and Brown, 1967
Merino	M	1.8	10-11 mo	-.001 cm	.001 cm	Lax and Brown, 1967
Mutton Merino				-.047 %		Liebenberg and John, 1973
Rambouillet	M,F	14-47[d]	4 mo	-.005 cm[n.t.]	-.002 cm[n.t.]	Ercanbrack and Knight, 1981
Columbia	M,F	24-36[d]	4 mo	-.015 cm[n.t.]	-.008 cm[n.t.]	Ercanbrack and Knight, 1981
Targhee	M,F	17-47[d]	4 mo	.001 cm[n.t.]	.000 cm[n.t.]	Ercanbrack and Knight, 1981
Average		12.3		-.004 cm	.002 cm	

[a] Change in performance per one percent increase in individual inbreeding.

[b] Change in performance per one percent increase in dam's inbreeding.

[c] Data pooled from lines of Columbia, Corriedate and Targhee lambs.

* P<.05.

[n.t.] Not tested for statistical significance.

[d] Range in average inbreeding of several lines from which data were pooled.

TABLE 4. EFFECTS OF INBREEDING ON FLEECE CHARACTERS

Trait	Breed	Avg. F %	Age	Regr. coef. indiv.[a]	Regr. coef. dam[b]	Author
Yield						
	Merino	3.8	22-23 mo	-.02 %		Morley, 1954
	Merino	12.8	lifetime	.00 %		Doney, 1957
	Merino	1.8	10-11 mo	.071 %	-.163 %	Lax and Brown, 1967
	Merino	1.8	15-16 mo	-.012 %	-.171 %*	Lax and Brown, 1967
	Average	5.1		-.010 %	-.167 %	
Fiber Diameter						
	Merino	12.8	lifetime	-.024		Doney, 1957
	Merino	1.8	10-11 mo	.012	.057	Lax and Brown, 1967
	Merino	1.8	15-16 mo	.021	.007	Lax and Brown, 1967
	Average	5.5		.003	.032	
Fibers/mm^2						
	Merino	12.8	lifetime	-.40		Doney, 1957
	Merino	1.8	10-11 mo	-.102	.186	Lax and Brown, 1967
	Merino	1.8	15-16 mo	-.156	-.087	Lax and Brown, 1967
	Average	5.5		-.219	.050	
Crimps/cm						
	Merino	3.8	22-23 mo	-.014		Morley, 1954
	Merino	1.8	10-11 mo	-.015	.004	Lax and Brown, 1967
	Merino	1.8	15-16 mo	-.006	.009	Lax and Brown, 1967
	Average	2.5		-.012	.007	

[a] Change in performance per one percent increase in individual inbreeding.

[b] Change in performance per one percent increase in dam inbreeding.

* $P<.05$.

TABLE 5. EFFECTS OF INBREEDING ON BIRTH WEIGHT

Breed	Sex	Avg. F %	Age	Regr. coef. indiv.[a]	Regr. coef. dam[b]	Author
Ossimi	M,F		birth	-.026 kg		Ragab and Asker, 1954
Hampshire	M,F	16,27[c]	birth	-.001 kg	-.005 kg*	Brown et al., 1961
Merino	M	1.8	birth	-.015 kg*	-.015 kg	Lax and Brown, 1968
Merino	F	1.8	birth	-.015 kg*	-.014 kg	Lax and Brown, 1968
Average		11.6		-.011 kg	-.007 kg	

[a]Change in performance per one percent increase in lamb inbreeding.

[b]Change in performance per one percent increase in dam's inbreeding.

[c]Range in average inbreeding of several lines from which data were pooled.

*$P<.05$.

TABLE 6. EFFECTS OF INBREEDING ON WEANING WEIGHT

Breed	Sex	Avg. F %	Age	Regr. coef. Lamb[a]	Regr. coef. Dam[b]	Author
Rambouillet	M,F	4.5	4 mo	-.171 kg**		Hazel and Terrill, 1945
Whiteface[c]	M,F	9.7	4 mo	-.137 kg**		Hazel and Terrill, 1946a
Ossimi	M,F		4 mo	-.100 kg		Ragab and Asker, 1954
Hampshire	M,F	16,27[d]	4 mo	-.138 kg	.001 kg	Brown et al., 1961
Merino[e]	M	2-3	3-5 mo	-.068 kg*		Pattie, 1965
Merino[f]	M	1	3-5 mo	-.036 kg		Pattie, 1965
Merino[g]	M	2-3	3-5 mo	-.082 kg		Pattie, 1965
Merino[e]	F	2-3	3-5 mo	-.086 kg		Pattie, 1965
Merino[f]	F	1	3-5 mo	-.082 kg		Pattie, 1965
Merino[g]	F	2-3	3-5 mo	-.177 kg***		Pattie, 1965
Rambouillet	M,F	14-47[d]	4 mo	-.091 kg	-.055 kg[n.t.]	Ercanbrack and Knight, 1981
Targhee	M,F	17-47[d]	4 mo	-.103 kg[n.t.]	-.075 kg[n.t.]	Ercanbrack and Knight, 1981
Columbia	M,F	24-36[d]	4 mo	-.055 kg[n.t.]	-.076 kg[n.t.]	Ercanbrack and Knight, 1981
Average		11.6		-.102 kg	-.051 kg	

[a]Change in performance per one percent increase in lamb inbreeding.

[b]Change in performance per one percent increase in dam inbreeding.

[c]Data pooled from lines of Columbia, Corriedale and Targhee lambs.

[d]Range in average inbreeding of several lines from which data were pooled

[e]Data from a line of Australian Merinos selected for high weaning weight.

[f]Data from a randomly selected line of Australian Merinos.

[g]Data from a line of Australian Merinos selected for low weaning weight.

*P<.05.

**P<.01.

***P<.001.

n.t.Not tested for statistical significance.

TABLE 7. EFFECTS OF INBREEDING ON POSTWEANING BODY WEIGHT

Breed	Sex	Avg. F %	Age	Regr. coef. indiv.[a]	Regr. coef. dam[b]	Author
Ossimi	M,F		6 mo	-.200 kg		Ragab and Asker, 1954
Merino	M	1.8	10-11 mo	-.246 kg**	-.050 kg	Lax and Brown, 1967
Merino	F	3.8	10-12 mo	-.132 kg**		Morley, 1954
Rambouillet	F	4.5	13 mo	-.126 kg**		Hazel and Terrill, 1946b
Columbia	F	10.6	13 mo	-.025 kg		Terrill et al., 1947
Targhee	F	8.4	13 mo	-.176 kg**		Terrill et al., 1947
Columbia	M	9.9	13 mo	-.147 kg**		Terrill et al., 1948
Targhee	M	10.6	13 mo	-.266 kg**		Terrill et al., 1948
Merino	F	1.8	15-16 mo	-.196 kg*	.076 kg	Lax and Brown, 1967
Mutton Merino	F		mature	-.58 %		Liebenberg and John, 1973
Average		6.4		-.168 kg	.013 kg	

[a]Change in performance per one percent increase in individual inbreeding.

[b]Change in performance per one percent increase in dam inbreeding.

*P<.05.

**P<.01.

TABLE 8. EFFECTS OF INBREEDING ON BODY TYPE SCORE

Breed	Sex	Avg. F %	Age	Regr. coef. indiv.[a]	Regr. coef. dam[b]	Author
Rambouillet	M,F	4.5	120 days	.011**		Hazel and Terrill, 1945
Whiteface	M,F	9.7	120 days	.009**		Hazel and Terrill, 1946a
Rambouillet	F	4.5	406 days	-.011**		Hazel and Terrill, 1946b
Columbia	F	10.6	402 days	.002		Terrill et al., 1947
Targhee	F	8.4	402 days	.011**		Terrill et al., 1947
Columbia	M	9.9	403 days	.008*		Terrill et al., 1948
Targhee	M	10.6	403 days	.016**		Terrill et al., 1948
Rambouillet	M,F	14-47[c]	120 days	.014[n.t.]	.003[n.t.]	Ercanbrack and Knight, 1981
Targhee	M,F	17-47[c]	120 days	.015[n.t.]	.011[n.t.]	Ercanbrack and Knight, 1981
Columbia	M,F	24-36[c]	120 days	.023[n.t.]	.015[n.t.]	Ercanbrack and Knight, 1981
Average		6.4		-.168	.013	

[a]Change in performance per one percent increase in individual inbreeding.

[b]Change in performance per one percent increase in dam inbreeding.

[c]Range in average inbreeding of several lines from which data were pooled.

*P<.05.

**P<.01.

[n.t.]Not tested for statistical significance.

TABLE 9. EFFECTS OF INBREEDING ON CONDITION SCORE

Breed	Sex	Avg. F %	Age	Regr. coef. indiv.[a]	Regr. coef. dam[b]	Author
Rambouillet	M,F	4.5	4 mo	-.009**		Hazel and Terrill, 1945
Whiteface[c]	M,F	9.7	4 mo	.007**		Hazel and Terrill, 1946a
Rambouillet	F	4.5	13 mo	.007**		Hazel and Terrill, 1946b
Columbia	F	10.6	13 mo	.002		Terrill et al., 1947
Targhee	F	8.4	13 mo	.006**		Terrill et al., 1947
Columbia	M	9.9	13 mo	.004		Terrill et al., 1948
Targhee	M	10.6	13 mo	.013**		Terrill et al., 1948
Rambouillet	M,F	14-47[d]	4 mo	.016[n.t.]	.004[n.t.]	Ercanbrack and Knight, 1981
Targhee	M,F	17-47[d]	4 mo	.024[n.t.]	.016[n.t.]	Ercanbrack and Knight, 1981
Columbia	M,F	24-36[d]	4 mo	.021[n.t.]	.030[n.t.]	Ercanbrack and Knight, 1981
Average		15.2		.009	.017	

[a]Change in performance per one percent increase in individual inbreeding.

[b]Change in performance per one percent increase in dam inbreeding.

[c]Data pooled from lines of Columbia, Corriedale and Targhee lambs.

[d]Range in average inbreeding of several lines from which data were pooled.

**P<.01.

n.t.Not tested for statistical significance.

TABLE 10. EFFECTS OF INBREEDING ON FACE COVER SCORE

Breed	Sex	Avg. F %	Age	Regr. coef. indiv.[a]	Regr. coef. dam[b]	Author
Rambouillet	M,F	4.5	4 mo	.006**		Hazel and Terrill, 1945
Whiteface[c]	M,F	9.7	4 mo	-.001		Hazel and Terrill, 1946b
Rambouillet	F	4.5	13 mo	.003		Hazel and Terrill, 1946b
Columbia	F	10.6	13 mo	-.004		Terrill et al., 1947
Targhee	F	8.4	13 mo	.002		Terrill et al., 1947
Columbia	M	9.9	13 mo	.0005		Terrill et al., 1948
Targhee	M	10.6	13 mo	.016**		Terrill et al., 1948
Merino	F	1.8	15-16 mo	-.022	-.004	Lax and Brown, 1967
Merino	M	1.8	10-11 mo	.006	.024	Lax and Brown, 1967
Rambouillet	M,F	14-47[d]	4 mo	-.001[n.t.]	.017[n.t.]	Ercanbrack and Knight, 1981
Targhee	M,F	17-47[d]	4 mo	-.022[n.t.]	.007[n.t.]	Ercanbrack and Knight, 1981
Columbia	M,F	24-36[d]	4 mo	.030[n.t.]	.021[n.t.]	Ercanbrack and Knight, 1981
Average		13.0		.0015	.013	

[a] Change in performance per one percent increase in individual inbreeding.

[b] Change in performance per one percent increase in dam inbreeding.

[c] Data pooled from lines of Columbia, Corriedale and Targhee lambs.

[d] Range in average inbreeding of several lines from which data were pooled.

** P<.01.

[n.t.] Not tested for statistical significance.

TABLE 11. EFFECTS OF INBREEDING ON WRINKLE SCORE

Breed	Sex	Avg. F %	Age	Regr. coef. indiv.[a]	Regr. coef. dam[b]	Author
Rambouillet	M,F	4.5	4 mo	-.009**		Hazel and Terrill, 1945
Whiteface[c]	M,F	9.7	4 mo	-.003*		Hazel and Terrill, 1946a
Rambouillet	F	4.5	13 mo	-.003		Hazel and Terrill, 1946b
Columbia	F	10.6	13 mo	.0002		Terrill et al., 1947
Targhee	F	8.4	13 mo	.001		Terrill et al., 1947
Columbia	M	9.9	13 mo	-.003		Terrill et al., 1948
Targhee	M	10.6	13 mo	.0002		Terrill et al., 1948
Merino		3.8	22 mo	-.044		Morley, 1954
Merino		12.8		-.072**		Doney, 1957
Merino	M	1.8	10 mo	-.167**	.017	Lax and Brown, 1967
Merino	F	1.8	15 mo	.00	-.006	Lax and Brown, 1967
Rambouillet	M,F	14-47[d]	4 mo	-.001[n.t.]	.003[n.t.]	Ercanbrack and Knight, 1981
Columbia	M,F	24-36[d]	4 mo	.005[n.t.]	.005[n.t.]	Ercanbrack and Knight, 1981
Targhee	M,F	17-47[d]	4 mo	-.007[n.t.]	-.005[n.t.]	Ercanbrack and Knight, 1981
Average		12.3		-.022	.003	

[a] Change in performance per one percent increase in individual inbreeding.

[b] Change in performance per one percent increase in dam inbreeding.

[c] Data pooled from lines of Columbia, Corriedale and Targhee lambs.

[d] Range in average inbreeding of several lines from which data were pooled.

* P<.05.

** P<.01.

n.t. Not tested for statistical significance.

The Effects of Inbreeding in a Flock of Hampshire Sheep

CHAPTER II

INTRODUCTION

Hazel and Terrill (1945, 1946a and 1946b), Terrill et al. (1947 and 1948), Morley (1954), Doney (1957), Pattie (1965), Lax and Brown (1967 and 1968) and Ercanbrack and Knight (1981) have reported the effects of inbreeding in on various performance traits in sheep. Most of these studies have dealt with lines developed for crossing or with flocks in which inbreeding was incidental to other experimental objectives. These studies have been conducted primarily in wool producing breeds such as the American Rambouillet, Corriedale, Targhee and Columbia or the Australian Merino and, consequently, have dealt primarily with fleece characters with some emphasis on body weight.

There is little information regarding inbreeding effects on economically important traits in meat type sheep. There have been some reports on growth characters (Bogart, 1961; Brown et al., 1961; Carter et al., 1961 and Liebenberg and John, 1973), but reports on inbreeding effects on reproductive traits are noticeably absent.

The purpose of this study was to examine the effects of inbreeding on production traits in a closed flock of Hampshire sheep.

MATERIALS AND METHODS

Flock Management. Data were collected during 1980 and 1981 from a privately owned flock of approximately 250 registered Hampshire ewes located near Salem, Oregon. This flock had been in existence for over

50 years and had been predominantly closed to outside breeding for the past 30 years.

The flock was managed for February-March lambing. It was pastured on wheat (Triticum aestivum), rape (Brassica napus) and perennial rye-grass (Lolium perenne) throughout the year with grain and hay supplementation during the winter. Primary income was derived from the sale of yearling rams and ewes.

There was no program of intense selection based upon production or pedigree records. Rams and ewes were selected as yearlings based on visual appraisal of type and size. Mating between selected rams and ewes was a corrective mating scheme with regard to conformation. This negative assortative mating may have resulted in a slower than expected increase in measurable inbreeding. Once ewes entered the breeding flock, there was little or no culling.

Inbreeding coefficients were calculated from pedigrees traced back to 1955 which, in most cases, was five generations. A computer program (Rowe, 1981) utilizing a co-ancestry matrix was used to calculate inbreeding coefficients.

Data Collection. Data were collected from the 1980 and 1981 lamb crops and from ewes present during that time period. During 1980, data collected included date of lambing, number of lambs born, sex of lambs and mortality records. Weights of all lambs were collected four times during the spring. The first weighing was 45 days after the beginning of the lambing season and subsequently at 30 day intervals thereafter. Six-month fleece weights of ewes were collected at the time that lambs were weaned. In September of 1980, ewes were weighed as they were assigned to breeding groups. During the 1981 lambing season, data collection was similar to that of 1980 except that birth weights were also taken. The flock was sold shortly after the first 30 day weighing in 1981 so later weights were not obtained.

Traits Studied. The lamb traits considered in this study were birth, 30, 60 and 90 day weights and survival of lambs to 7 and to 90 days of age. Ewe traits were 6 month fleece weight, breeding weight, days from ram introduction to conception, fertility, prolificacy, lamb survival to 90 days, lamb 90 day weaning weight and weight of lamb weaned per ewe exposed.

Lamb 30, 60 and 90 day weights were approximated by choosing the weight taken nearest to when a lamb was at that age, correcting for the lamb's birthweight and linearly adjusting for its age at weighing. Survival was scored as 1 for a lamb surviving to 7 or 90 days and 0 for not surviving.

Fertility was scored as 0 for not lambing and 1 for producing at least one lamb. Prolificacy was recorded as the number of lambs born to a ewe that lambed. Days from ram introduction to conception was calculated by subtracting a standard gestation length (147 days) from the number of days between ram introduction and lambing. Any differences in gestation length among ewes would be included in this variable.

Weight of lamb weaned per ewe was the total 90 day weight of all lambs raised by a ewe. All ewes exposed to rams are included for this trait. Ewes not lambing or ewes lambing but not weaning a lamb would have a zero recorded. This trait is a composite of fertility, prolificacy, lamb survival to 90 days and lamb 90 day weight. Since this is a ewe trait, lamb survival to 90 days and lamb 90 day weight were not adjusted for type of birth or rearing.

Statistical Procedures. All data were analyzed using least-squares analysis of variance and regression procedures (Harvey, 1975). Model type 1 was used for each analysis. The main effects included in the statistical models for lamb traits are presented in Table 12 and for ewe traits in Table 13. Appropriate two factor interactions and quadratic effects of inbreeding were also included in the models. Random effects were absorbed by least-squares.

The general analysis procedure was to fit the full model and then to conduct a step-down analysis to arrive at the final models for each trait. Several runs were made with each model, deleting the least significant of the insignificant effects each time. This step-down procedure continued until only effects which were or which approached significance and regressions on lamb and ewe inbreeding remained in the models (Tables 12 and 13). During the step-down procedure, all two-factor interactions and the quadratic effects of inbreeding were deleted. This procedure was used to assure that the most complete model was obtained to accurately estimate the inbreeding effects. It is recognized that the step-down procedure may result in models in which the significance levels at which hypotheses are tested are underestimated.

RESULTS AND DISCUSSION

Lamb Traits. Mean weights of lambs at birth, 30, 60 and 90 days are presented in Table 14. Effects of lamb inbreeding (Table 14) were positive for birth, 30 and 60 day weights and negative for 90 day weight, but effects were not significantly different from zero. Ewe inbreeding had negative (Table 14), but non-significant, effects at all ages.

The lack of detrimental effects of lamb inbreeding on early weights found in the present study may be due to a positive correlated response in these traits as a result of long term selection for body size in this flock. Positive response to selection could have masked any negative effects of inbreeding on these growth traits.

Negative effects of dam's inbreeding on lamb body weights found in this study (Table 14) are in agreement with those reported by other researchers. Brown et al. (1961) and Lax and Brown (1968) reported regression coefficients which averaged -.007 kg per one percent increase in dam's inbreeding for birth weight, which is the same as the regression coefficient found in this study. The regression coefficient for weaning weight on dam's inbreeding averaged from studies by Brown et al. (1961) and Ercanbrack and Knight (1981) was -.05 kg per one percent increase in inbreeding which is in general agreement with the regression coefficient found in this study (-.075 kg per one percent increase in inbreeding for 90 day weight).

Inbreeding of lamb had significant negative effects on lamb survival to 7 and 90 days (Table 14). Dam's inbreeding, however, had a small positive, but not significant, effect on lamb survival.

Negative effects of inbreeding on lamb survival have been reported by many researchers (Morley, 1954; Bogart, 1961; Doney, 1966 and Lax and Brown, 1968). Lax and Brown (1968) reported regression coefficients of lamb survival to weaning of -.007 male lambs per percent lamb inbreeding and -.017 female lambs per percent lamb inbreeding ($P<.01$).

Lax and Brown (1968) reported a small negative effect of dam's inbreeding on lamb survival which disagrees with the small positive effect found in this study.

Ewe Traits. Presented in Table 15 are partial regression coefficients of 6-month fleece weight and ewe breeding weight on ewe inbreeding. Both of these traits responded negatively to an increase in ewe inbreeding although only the regression for breeding weight was significantly different from zero.

A one percent increase in ewe's inbreeding resulted in a .007 kg decrease in her 6-month fleece weight. This value, when doubled, falls between the average regression coefficient of -.022 kg per percent inbreeding reported in Merinos by Australian researchers (Morley, 1954; Doney, 1957 and Lax and Brown, 1967) and the -.010 kg per percent inbreeding reported by researchers in the United States in whitefaced range sheep (Hazel and Terrill, 1946b; Terrill et al., 1947 and 1948) for 12-month fleece weight.

Ewe body weight has been shown to be positively related to the number of lambs born. Therefore, it is an important trait to be considered (Lax and Brown, 1968). A one percent increase in ewe inbreeding resulted in a .272 kg decrease ($P<.10$) in her body weight at breeding in the present study. This coefficient is larger than the average of regression coefficients (-.134 kg per one percent increase in inbreeding) reported by Hazel and Terrill (1946b), Terrill et al. (1947 and 1948) and Lax and Brown (1967). The difference in coefficients may be due to the greater body weight of the Hampshires in this study compared with the wool producing breeds previously studied (94.5 vs. 56.4 kg). The effect of inbreeding on ewe weight may be related to the negative effect of inbreeding on prolificacy which has been reported in several studies (Bogart, 1961; Carter et al., 1961; Lax and Brown, 1968 and Liebenberg and John, 1973).

Inbreeding of fetus and ewe had the effect of delaying date of lambing either due to a longer period from exposure to the ram to conception or due to a longer gestation interval. Although it seems unlikely that increased inbreeding would increase gestation period, this may be the case since increased inbreeding resulted in small increases in birth weights. Whichever mechanism was responsible, there was a .35 day delay ($P < .10$) for each one percent increase in ewe inbreeding and a .17 day delay for each one percent increase in lamb inbreeding.

Each one percent increase in ewe inbreeding resulted in .012 fewer ($P < .05$) ewes lambing per ewe exposed. Inbreeding of potential conceptus also had a slight negative effect on fertility (Table 15), however, the effect was non-significant. In addition to the negative effects of inbreeding on fertility, there were also non-significant, negative effects of fetal and ewe inbreeding on prolificacy. For each increase of one percent in fetal and ewe inbreeding, there were decreases of .0012 and .0003 lambs born per ewe lambing, respectively. These regression coefficients are similar in magnitude to those reported by Lax and Brown (1968) but are much smaller than the effects found by Doney (1966). The Blackface ewes studied by Doney (1966) may have been under less desirable conditions than the Hampshires in this study. Since inbreeding results in a general decline in vigor those sheep in a harsh environment will suffer more from the detrimental effects of inbreeding than those in a good environment.

Presented in Table 15 are regression coefficients of the effects of lamb and ewe inbreeding on total weight of lambs weaned at 90 days per ewe exposed. This trait is of great importance to many sheep producers. A one percent increase in lamb inbreeding resulted in a .59 kg decrease ($P<.05$) in weight weaned per ewe exposed. A one percent increase in ewe inbreeding resulted in a .1 kg increase in weight weaned, but this coefficient was not significant.

Weight of lamb weaned per ewe exposed is composed of four traits: fertility, prolificacy, survival to 90 days and 90 day weight. By expressing the regression coefficients as a percentage of the mean for each trait, Turner and Young's (1969) method of "percentage deviation" may be used to determine the contributiom of each of these traits to the overall effect on weight weaned (Hohenboken and Cochran, 1976). Using this technique, the negative effect of lamb's inbreeding on weight weaned per ewe exposed can be attributed follows: 11% to the effect lamb's inbreeding on fertility, 6% to the effect of lamb's inbreeding on prolificacy, 80% to the effect of lamb's inbreeding on survival and 3% to the effect of lamb's inbreeding on 90 day weight.

TABLE 12. LEAST-SQUARES ANALYSES OF VARIANCE FOR LAMB TRAITS

Source	Birth weight		30 day weight		60 day weight		90 day weight		Survival to 7 days		Survival to 90 days	
	df[a]	MS[b]	df	MS	df	MS	df	MS	df	MS	df	MS
Number born	1	76.68**	--		--		--		1	.26	1	2.51**
Type of birth/rearing	--		2	111.61**	2	229.00**	2	265.69**	--		--	
Sex	1	4.59†	1	6.53	1	1.84	1	45.13	n.s.[c]		n.s.	
Age of dam	n.s.		n.s.		n.s.		n.s.		n.s.		n.s.	
Regr. on date of birth	1	.15	1	139.14**	1	139.25**	1	50.72	1	1.59**	1	.39
Regr. on lamb inbreeding	1	1.83	1	.69	1	1.79	1	4.59	1	1.09**	1	1.62**
Regr. on ewe inbreeding	1	.26	1	2.03	1	27.26	1	24.91	1	.07	1	.40
Residual	212	1.24	263	7.48	169	24.94	165	37.30	300	.14	300	.23

[a] Degrees of freedom.

[b] Mean square.

[c] Non-significant and dropped from the model.

† $P<.10$.

** $P<.01$.

TABLE 13. LEAST-SQUARES ANALYSES OF VARIANCE FOR EWE TRAITS

Source	Fleece weight		Breeding weight		Days to conception		Fert.		Prolif.		Survival to 90 days		90 day weaning weight		Wt. weaned per ewe exposed	
	df[a]	MS[b]	df	MS	df	MS	df	MS	df	MS	df	MS	df	MS	df	MS
Number born	2	1.80**		--	2	499.73		--		--		--		--		--
Ewe age	2	.01	2	517.52**		n.s.[c]	2	.27*		n.s.		n.s.		n.s.		n.s.
Sex		--		--		--		--		--		n.s.		n.s.		--
Regr. on lambing date		--		--		--		--	1	.97*		--		--		--
Regr. on lamb inb.		--		--	1	161.69	1	.03	1	.01	1	1.92*	1	2.78	1	2413.39*
Regr. on ewe inb.	1	.17	1	206.01†	1	790.97†	1	.56*	1	.00	1	.33	1	14.17	1	47.63
Residual	190	.13		--	295	265.51	200	.11	296	.34	302	.24	169	40.19	208	515.45

[a]Degrees of freedom.

[b]Mean square.

[c]Non-significant and dropped from the model.

†P<.10.

*P<.05.

**P<.01.

TABLE 14. LAMB TRAIT LEAST-SQUARES MEANS AND PARTIAL REGRESSION COEFFICIENTS ON LAMB AND EWE INBREEDING

Trait	No. of observ.	Mean	± S E[a]	Lamb regr. coef.	± S E	Ewe regr. coef.	± S E
Birth weight (kg)	223	4.8	± 0.08	.022	± .018	-.007	± .015
30 day weight (kg)	269	10.9	± 0.17	.012	± .039	-.016	± .031
60 day weight (kg)	182	21.0	± 0.38	.024	± .090	-.075	± .072
90 day weight (kg)	178	30.3	± 0.48	-.039	± .111	-.075	± .092
Survival to 7 days (%)	305	81.6	± 2.7	1.1**	± 0.4	0.3	± 0.4
Survival to 90 days (%)	305	58.4	± 3.5	-1.3**	± 0.5	0.7	± 0.6

[a]S E = Standard error of the least-squares mean or regression coefficient.

**P <.01.

TABLE 15. EWE TRAIT LEAST-SQUARES MEANS AND PARTIAL REGRESSION COEFFICIENTS ON LAMB AND EWE INBREEDING

Trait	No. of observ.	mean	± S E[a]	Lamb regr. coef.	± S E	Ewe regr. coef.	± S E
Fleece weight (kg)	196	1.7	± 0.03			-0.007	± .006
Breeding weight (kg)	122	94.5	± 1.2			-0.272	± .146†
Days to conception (days)	299	20.9	± 0.95	0.168	± .215	0.346	± .203†
Fertility (%)	204	88.4	± 2.3	-0.3	± 0.5	-1.2*	± 0.5
Prolificacy (lambs)	299	1.77	± 0.03	-0.001	± 0.008	-0.0003	± 0.008
Survival to 90 days (%)	305	58.4	± 2.8	-1.4*	± 0.5	0.7	± 0.6
90 day weaning weight (kg)	178	30.3	± 0.49	-0.03	± .12	.06	± .10
Weight weaned (kg) per ewe exposed	211	25.2	± 1.6	-0.59*	± 0.27	0.10	± 0.33

[a] S E = Standard error of the least-squares mean or regression coefficient.

† $P < .10$.

* $P < .05$.

LITERATURE CITED

Bogart, Ralph. 1961. Effects of inbreeding on performance traits in Suffolks. Oregon State University Sheep and Wool Day Report, November 3, 1961.

Brinks, J. S. and B. W. Knapp. 1975. Effects of inbreeding on performance traits of beef cattle in the Western Region. Western Regional Research Publication, Technical Bulletin 123. Colorado State University Experiment Station, Fort Collins.

Brown, C. J., C. A. Baugus and Samuel Sabin. 1961. Evaluation of factors affecting the growth of spring lambs. Arkansas Experiment Station Bulletin 646.

Carter, R. O., R. C. Carter, J. A. Gaines and C. M. Kincaid. 1961. Evaluation of an inbred line of Hampshire sheep. J. Anim. Sci. 20:387 (Abstr.).

Darwin, Charles R. 1885. The Effects of Cross and self fertilization in the vegetable kingdom. D. Appleton and Company, New York.

Dickerson, Gordon E. 1972. Inbreeding and heterosis in animals. In Proceedings of the Animal Breeding and Genetics Symposium in honor of Dr. Jay L. Lush. ASAS, Campaign, Illinois.

Doney, J. M. 1957. Effects of inbreeding on four families of Peppin Merinos. Australian J. Agr. Res. 8:299.

Doney, J. M. 1958. Effects of inbreeding on four families of Peppin Merinos. II. The influence of inbreeding on age trends. Australian J. Agr. Res. 9:252.

Doney, J. M. 1966. Inbreeding depression in grazing Blackface sheep. Anim. Prod. 8:261.

East, E. and D. F. Jones. 1919. Inbreeding and outbreeding, their genetic and sociological significance. Washington Square Press, Philadelphia.

Ercanbrack, S. K. and A. D. Knight. 1981. Weaning trait comparisons among inbred lines and selected non-inbred and randomly bred control groups of Rambouillet, Targhee and Columbia sheep. J. Anim. Sci. 52:977.

Falconer, D. S. 1960. Introduction to quantitative genetics. The Ronald Press Company, New York.

Fisher, Ronald A. 1955. The theory of inbreeding. Academic Press, New York.

Galal, E. S. E., E. A. Afifi, I. S. El-Kimary, I. A. Ahmad and A. F. Shawar. 1981. Lamb survival as affected by inbreeding and crossbreeding. J. Agr. Sci. 96:1.

Glembockiĭ, Ja. L. 1956. Ispoljzovanie inbridinga v plemennoĭ rabote s tonkorunnymi ovcami. Bjull. mosk. Obšč. Ispyt. Prirod., Otd. biol. 61:23 (Anim. Breed. Abstr. 25, No. 1321).

Harvey, W. R. 1975. Least-squares analysis of data with unequal subclass numbers. USDA ARS H-4.

Hazel, L. N. and Clair E. Terrill. 1945. Effects of some environmental factors on weanling traits of range Rambouillet lambs. J. Anim. Sci. 4:331.

Hazel, L. N. and Clair E. Terrill. 1946a. Effects of some environmental factors on weanling traits of range Columbia, Corriedale and Targhee lambs. J. Anim. Sci. 5:318.

Hazel, L. N. and Clair E. Terrill. 1946b. Effects of some environmental factors on fleece and body characteristics of range Rambouillet yearling ewes. J. Anim. Sci. 5:382.

Hohenboken, W. H. and P. E. Cochran. 1976. Heterosis for ewe lamb productivity. J. Anim. Sci. 42:819.

Johannson, Ivar and Jan Rendel. 1968. Genetics and Animal Breeding. W. H. Freeman and Company, San Francisco.

Lax, J. and G. H. Brown. 1967. The effects of inbreeding, maternal handicap, and range in age on 10 fleece and body characteristics in Merino rams and ewes. Australian J. Agr. Res. 18:689.

Lax, J. and G. H. Brown. 1968. The influence of maternal handicap, inbreeding, and ewe's body weight at 15-16 months of age on reproduction rate in Australian Merinos. Australian J. Agr. Res. 5:305.

Liebenberg, O. and M. John. 1973. The effects, and extent, of inbreeding in the Mutton Merino - based on elite flocks in the Halle, Magdeburg and Leipzig areas. Archiv für Tierzucht 16:423. (Anim. Breed. Abstr. 43, No. 4572).

Malécot, Gustave. 1969. The Mathematics of Heredity. W. H. Freeman and Company, San Francisco.

Morley, F. H. W. 1954. Selection for economic characters in Australian Merino sheep. IV. The effect of inbreeding. Australian J. Agr. Res. 5:305.

Pattie, W. A. 1965. Selection for weaning weight in Merino sheep. I. Direct response to selection. Australian J. Exp. Agr. Anim. Husb. 5:353.

Ragab, M. T. and A. A. Asker. 1954. Effects of inbreeding on a flock of Ossimi sheep. J. Hered. 45:89.

Rowe, K. E. 1981. INBREED. Department of Statistics, Oregon State University, Corvallis.

Terrill, Clair E., G. M. Sidwell and L. N. Hazel. 1947. Effects of some environmental factors on yearling traits of Columbia and Targhee ewes. J. Anim. Sci. 6:115.

Terrill, Clair E., G. M. Sidwell and L. N. Hazel. 1948. Effects of some environmental factors on yearling traits of Columbia and Targhee rams. J. Anim. Sci. 7:181.

Turner, Helen Newton and Sydney S. Y. Young. 1969. Quantitative genetics in sheep breeding. Cornell University Press, Ithaca, New York.

Wright, Sewall. 1922a. Coefficients of inbreeding and relationship. Amer. Nat. 56: 330.

Wright, Sewall. 1922b. Effects of inbreeding and crossbreeding on guinea pigs. I. Decline in vigor. USDA Bul. 1090.