Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.

A STUDY OF SOME FACTORS AFFECTING THE RESISTANCE OF NEWBORN LAMBS TO COLD-STRESS WITH PARTICULAR REFERENCE TO STARVATION AND EXPOSURE MORTALITY

A thesis presented in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy
in Animal Science
at Massey University

STUART NORMAN McCUTCHEON

1981

ABSTRACT

Newborn lambs (less than 48 hours old) were exposed to a range of environments and their responses to cold-stress examined. The study centred on Romney lambs, with Merinos and Drysdale-Romney crosses used for comparative purposes. Experiments were conducted in a climate chamber, the design of which is described. Environmental components examined were ambient temperature (5 to 30^{o}C), airspeed (0.0 to 1.9 m sec^{-1}) and wetness. The two main indices of resistance to cold-stress, together with their repeatabilities, were heat production (r = 0.53 to 0.59) and rate of decline in rectal temperature (r = 0.62 to 0.84).

The summit metabolic rate of Romney lambs was 18.03 ± 0.63 W kg^{-1}. Wet lambs became hypothermic at ambient temperatures as high as 15^{o}C but dry lambs did not approach the limit of their ability to control body temperature. Air movement increased heat production by 7 to 20% over conditions of still air.

Twin lambs exhibited a lower resistance to cold-stress than singles, this being a function of their lower bodyweight, poorer birthcoat insulation and possibly lower summit metabolic rate. Female lambs were less resistant to cold-stress than males in only one experiment. This effect could not be accounted for solely by between-sex differences in body weight.

Age effects were small and were mainly related to drying of the birthcoat. Unfed lambs less than 1 hour old had a similar thermoregulatory ability to older fed lambs. Summit metabolism appeared

not to be affected by age or feeding.

Dry Romney and Drysdale-Romney cross lambs frequently failed to constrict blood vessels of the hind limb immediately upon entering the cold zone and had higher skin temperatures than Merino lambs. Wet lambs exhibited low skin temperatures consistent with the constriction of peripheral blood vessels having occurred. Skin temperature declined rapidly with age in lambs less than 1 hour old.

Genotype for face cover did not affect the lamb's resistance to cold-stress, skin temperature, bodyweight or coat characteristics (hip coat depth, midside coat depth, midside wool weight per unit area of skin).

Bodyweight was an important determinant of resistance to cold-stress. Heat production in cold conditions was proportional to bodyweight raised to the power 0.78 to 0.85.

Drysdale-cross lambs had greater coat depths and midside wool weight (per unit area of skin) than Romneys, and a superior resistance to cold-stress. Coat depth was moderately repeatable ($r = 0.43$ to 0.73) and was reduced by wetting only in the Drysdale-cross lambs. Sire of the lamb appeared to influence coat depth but not midside wool weight.

Heat production was negatively related to each of the coat characters, the relationships being curvilinear in one experiment. Midside wool weight and coat depth were largely independent in their control of metabolic rate. Coat insulation per unit of depth or midside wool weight was not influenced by wetting or air movement

(within the range available).

High coat depths and midside wool weight in the birthcoat were (phenotypically) associated with high greasy fleeceweight and staple length, slightly poorer colour, and a possible increase in fibre diameter and medullation, in the hogget fleece.

Application of the results is discussed with respect to available methods of selecting or managing lambs for an improved resistance to cold-stress and a reduced incidence of starvation-exposure mortality.

ACKNOWLEDGEMENTS

I wish to acknowledge the guidance and assistance given me by my supervisors, Dr M.F. McDonald, Dr C.W. Holmes and Professor A.L. Rae, during the course of this study.

Special thanks are due to; my colleagues at Massey University, particularly Dr G.A. Wickham, for their valuable advice and discussion; Messrs M.G. Divehall and C.G.R. Muir for skilled technical assistance; and to my fellow graduate students, particularly Hugh Blair and Bill McMillan.

Acknowledgement is also made to; Mr L.C.F. Brunswick for providing the Merino lambs; Dr F.R.M. Cockrem for face-grading the hoggets; Mr P.H. Whitehead and farm staff for care of the animals; Messrs B. Thatcher and M. Wycherly for evaluation of the hogget wool; Mr C.J. Oldershaw who drafted the climate chamber plans; and to Mr A.C. Lowe (No. 3 Dairy Unit) and Mr W.B. Parlane (Animal Physiology Unit) for their co-operation.

I am grateful to Mrs A.F. Barton and Mrs R.A. Vining for their skilled and careful typing of this thesis.

The project was generously supported by the Vernon Willey Trust.

Finally, I am indebted to Deborah, my wife, for her patience and encouragement throughout this study programme.

TABLE OF CONTENTS

Chapter		Page
	ABSTRACT	ii
	ACKNOWLEDGEMENTS	v
	LIST OF TABLES	xiv
	LIST OF FIGURES	xxiii
	LIST OF ABBREVIATIONS	xxiv
	LIST OF APPENDICES	xxv
I	INTRODUCTION	
	The Contribution of "Starvation and Exposure" Deaths to Neonatal Lamb Mortality	1
	Starvation and Exposure Mortalities : The Influence of Cold-Stress	3
	Factors Affecting the Resistance of Lambs to Body Cooling	7
	1. Birthweight and birthrank	7
	2. Heat production	8
	(a) Level of summit metabolism	8
	(b) Attainment and maintenance of summit metabolism	12
	3. Heat loss	13
	(a) Birthcoat characteristics	13
	(b) Pilomotor control	17
	(c) Peripheral vasomotor control	17
	(d) Subcutaneous fat	19
	Possible Selection Criteria for Reducing Starvation and Exposure Losses	20
	Purpose and Scope of the Investigation	24

TABLE OF CONTENTS (continued)

Chapter		Page
II	EXPERIMENTAL	
	Animals	27
	1. Management of ewes	27
	2. Management of lambs before testing	29
	Control of Environmental Conditions for Testing Lambs	30
	1. Construction of climate chambers	30
	2. Control of chamber air temperatures	33
	3. Control of chamber airspeeds	34
	4. Wetting of the lambs	34
	5. Precision of environmental control	35
	(a) Control of air temperature	36
	(b) Control of airspeed	39
	(c) Factors affecting the relative humidity of air in the chambers	42
	Measurements : In Newborn Lambs	49
	1. Heat production	49
	2. Rectal and skin temperatures	53
	(a) Rectal temperature	53
	(b) Skin temperature	54
	3. Characteristics of the birthcoat	56
	(a) Depth of birthcoat	56
	(b) Wool weight per unit area of skin	65
	(c) Total weight of the birthcoat	66
	(d) Weight of birthcoat on the limbs	66
	4. Lamb age and weight	66
	Measurements : In Older Lambs and Hoggets	68
	1. Face cover grade	68
	2. Characteristics of the hogget fleece	68
	(a) Greasy fleeceweight	68
	(b) Staple length and crimp frequency	69
	(c) Mean fibre diameter	69
	(d) Standard deviation of fibre diameter and proportion of medullated fibres	69
	(e) Colour	69

TABLE OF CONTENTS (continued)

Chapter		Page
II	3. Post-shearing hogget bodyweight	69
	General Experimental Procedure	70
	Methods of Analysis	71
	1. Computer packages	71
	2. Analysis of continuous data	71
	(a) Calculation of sums of squares	71
	(b) Analysis of variance	72
	(i) Models fitted	72
	(ii) Models in which all main effects and interactions are fixed	74
	(iii) Mixed models	74
	(iv) Single degree of freedom comparisons	75
	(v) Presentation of the data	75
	(c) Regression analysis	77
	(d) Analysis of covariance	78
	(i) Model fitted	78
	(ii) Hypotheses tested	78
	(e) Correlation analysis	79
	3. Analysis of discrete data	79
	4. Miscellaneous variables	80
	(a) Relative humidity	80
	(b) Thermal circulation index	81
	(c) Standard deviation of fibre diameter	81
	(d) Proportion of medullated fibres	81
	(e) Hogget wool colour	81
	5. Levels of statistical significance	82
III	SUMMIT METABOLISM IN YOUNG ROMNEY LAMBS	
	Introduction	83
	Experimental Design and Methods	83
	Results and Discussion	84
	1. Level of summit metabolism	84
	2. Effect of age	85

TABLE OF CONTENTS (continued)

Chapter		Page
III	3. Effect of bodyweight	85
	Chapter Summary	86
IV	RESPONSES OF ROMNEY AND DRYSDALE-ROMNEY CROSS LAMBS TO COMPONENTS OF THE THERMAL ENVIRONMENT	
	Introduction	87
	Experimental Design and Methods	88
	Results and Discussion - Part I. Responses to Cold-Stress at Each Ambient Temperature	90
	1. Heat production	90
	2. Rectal temperature	99
	3. Hind-limb skin temperature	106
	4. Metabolism of lambs in relation to summit conditions	114
	Results and Discussion - Part II. Relationships Between Heat Production at 5°C Ambient Temperature and Other Characteristics of the Lamb	116
	1. Age of the lamb	116
	2. Body temperatures	118
	(a) Rectal temperature	118
	(b) Hind-limb skin temperature	121
	3. Characteristics of the birthcoat	124
	(a) Depth of birthcoat at the hip position	124
	(i) Treatment effects on hip coat depth	124
	(ii) Heat production and hip coat depth	124
	(iii) Hip coat depth, bodyweight and gestation length	131
	(b) Depth of birthcoat at the midside position	134
	(i) Treatment effects on midside coat depth	134
	(ii) Heat production and midside coat depth	134
	(iii) Midside coat depth, bodyweight and gestation length	138

TABLE OF CONTENTS (continued)

Chapter		Page
IV	(c) Midside wool weight per unit area of skin	141
	(i) Treatment effects on midside wool weight	141
	(ii) Heat production and midside wool weight	142
	(iii) Midside wool weight, bodyweight and gestation length	146
	(d) Relationships between the birthcoat characteristics	151
	(i) Midside and hip coat depth	151
	(ii) Midside wool weight and the coat depths	151
	(iii) Possible mechanisms for the control of heat production by midside wool weight	156
	(iv) The curvilinear relationship between heat production and midside wool weight	158
	4. Bodyweight and gestation length	160
	(a) Treatment effects on bodyweight and gestation length	160
	(b) The relationship between bodyweight and gestation length	163
	(c) Heat production and bodyweight	163
	5. Relative humidity of air in the chambers	165
	(a) Treatment effects on relative humidity	165
	(b) Heat production and relative humidity	169
	Chapter Summary	169
V	THE EFFECTS OF SIRE, BIRTHRANK AND BIRTHCOAT TYPE ON THE RESPONSES OF LAMBS TO COLD-STRESS AT A SINGLE AMBIENT TEMPERATURE	
	Introduction	174
	Experimental Design and Methods	175

TABLE OF CONTENTS (continued)

Chapter		Page
V	Results and Discussion	178
	1. Proportion of lambs attaining summit metabolism	178
	2. Heat production	184
	3. Rectal temperature	188
	4. Characteristics of the birthcoat	198
	(a) Depth of birthcoat	198
	(i) Treatment effects on coat depth	198
	(ii) Heat production and coat depth	204
	(b) Midside wool weight per unit area of skin	208
	(i) Treatment effects on midside wool weight	208
	(ii) Heat production and midside wool weight	211
	5. Bodyweight	213
	(a) Treatment effects on bodyweight	213
	(b) Heat production and bodyweight	213
	6. Hind-limb skin temperature and the weight of wool on the limbs	217
	(a) Treatment effects on skin temperature	217
	(b) Heat production and skin temperature	224
	(c) Skin temperature and the weight of wool on the limbs	226
	(d) Weight of wool on the limbs, hip coat depth and midside wool weight	231
	Chapter Summary	234
VI	THE EFFECTS OF FACE COVER SELECTION AND AGE/FEEDING LEVEL OF THE LAMB ON ITS RESPONSE TO COLD-STRESS AT A SINGLE AMBIENT TEMPERATURE	
	Introduction	238
	Experimental Design and Methods	239
	Results and Discussion	241
	1. Proportion of lambs attaining summit metabolism	241
	2. Rate of decline in rectal temperature	244
	3. Characteristics of the birthcoat	246

TABLE OF CONTENTS (continued)

Chapter		Page
VI	(a) Depth of birthcoat	246
	(b) Midside wool weight per unit area of skin	251
	4. Hind-limb skin temperature	256
	(a) Treatment effects on skin temperature	256
	(b) Skin temperature and the weight of wool on the limbs	256
	(c) Skin temperature and bodyweight	259
	(d) Skin temperature and age	265
	5. Distribution of face cover grades	267
	Chapter Summary	269
VII	THE RELATIONSHIP BETWEEN THE RESISTANCE OF THE NEWBORN LAMB TO COLD-STRESS AND ITS FACE COVER GRADE AT THREE MONTHS OF AGE	
	Introduction	272
	Experimental Design and Methods	272
	Results and Discussion	275
	1. Proportion of lambs attaining summit metabolism	275
	2. Heat production	275
	3. Hind-limb skin temperature	275
	Chapter Summary	280
VIII	THE REPEATABILITY OF RESISTANCE TO COLD-STRESS AND OF ASSOCIATED CHARACTERS IN YOUNG LAMBS	
	Introduction	282
	Experimental Design and Methods	282
	Results and Discussion	284
	1. Progeny Test lambs	284
	(a) Proportion of lambs attaining summit metabolism	284
	(b) Heat production and rate of decline in rectal temperature	284
	(c) Bodyweight	287
	(d) Depth of birthcoat	288
	(e) Hind-limb skin temperature	289

TABLE OF CONTENTS (continued)

Chapter		Page
VIII	2. Lambs sired by single-N rams	290
	(a) Proportion of lambs attaining summit metabolism	290
	(b) Heat production and rate of decline in rectal temperature	290
	(c) Bodyweight	292
	(d) Depth of birthcoat	293
	(e) Hind-limb skin temperature	294
	Chapter Summary	294
IX	RELATIONSHIPS BETWEEN SOME CHARACTERISTICS OF THE BIRTHCOAT AND OF THE HOGGET FLEECE	
	Introduction	297
	Experimental Design and Methods	297
	Results and Discussion	298
	1. Greasy fleeceweight	298
	2. Staple length	300
	3. Mean fibre diameter	303
	4. Crimp frequency	303
	5. Standard deviation of fibre diameter	306
	6. Proportion of medullated fibres	306
	7. Wool colour	311
	Chapter Summary	311
X	DISCUSSION AND CONCLUSIONS	314
	APPENDICES	328
	BIBLIOGRAPHY	335

LIST OF TABLES

Chapter	Table		Page
II	1	Effect of Temperature Setting, Airspeed Setting, Wetness and Chambers on Measured Chamber Air Temperature	37
	2	Effect of Airspeed Setting and Chambers on Measured Chamber Airspeed	41
	3	Effect of Temperature Setting, Airspeed Setting, Wetness and Chambers on Measured Relative Humidity of Air in the Chambers	44
	4	Test of Differences Between the Estimates of Heat Production Provided by the Formula of McLean (1972) and the Reduced Formula of Brouwer (1965)	52
	5	Effect of Birthcoat Grade, Skins within Grade, Position and Wetness on Birthcoat Depth	60
	6	Correlations Between Measured Birthcoat Depth and Mean Skin Birthcoat Depth at Each of Ten Positions on the Skin	64
IV	7	Effect of Sire Breed, Wetness, Airspeed and Sex on the Heat Production of Lambs at Six Ambient Temperatures	91
	8	Effect of Sire Breed, Wetness, Airspeed and Sex on the Rectal Temperatures of Lambs at Six Ambient Temperatures	100
	9	Effect of Sire Breed, Wetness, Airspeed and Sex on the Hind-Limb Skin Temperatures of Lambs at Six Ambient Temperatures	107
	10	Effect of Wetness, Airspeed and Sex on the Thermal Circulation Indices of Lambs at Six Ambient Temperatures	111

LIST OF TABLES (continued)

Chapter	Table		Page
IV	11	Test of Homogeneity of the Within-Class (Sire Breed) Regressions of Heat Production at 5°C Ambient Temperature on Age of the Lamb	117
	12	Test of Homogeneity of the Within-Class (Sire Breed) Regressions of Heat Production on Rectal Temperature at 5°C Ambient Temperature	120
	13	Test of Homogeneity of the Within-Class (Wetness) Regressions of Heat Production on Hind-Limb Skin Temperature at 5°C Ambient Temperature	123
	14	Effect of Sire Breed, Wetness, Sex and Bodyweight on Hip Birthcoat Depth	125
	15	Test of Homogeneity of the Within-Class (Sire Breed) Regressions of Heat Production at 5°C Ambient Temperature on Hip Birthcoat Depth	128
	16	Test of Curvilinearity in the Relationship Between Heat Production at 5°C Ambient Temperature and Hip Birthcoat Depth	129
	17	Test of Homogeneity of the Within-Class (Sire Breed) Regressions of Hip Birthcoat Depth on Gestation Length	133
	18	Effect of Sire Breed, Wetness, Sex and Bodyweight on Midside Birthcoat Depth	135
	19	Test of Homogeneity of the Within-Class (Sire Breed) Regressions of Heat Production at 5°C Ambient Temperature on Midside Birthcoat Depth	137
	20	Test of Curvilinearity in the Relationship Between Heat Production at 5°C Ambient Temperature and Midside Birthcoat Depth	139
	21	Test of Homogeneity of the Within-Class (Sire Breed) Regressions of Midside Birthcoat Depth on Gestation Length	140

LIST OF TABLES (continued)

Chapter	Table		Page
IV	22	Effect of Sire Breed, Sex and Bodyweight on Midside Wool Weight Per Unit Area of Skin: Lambs at First Test	143
	23	Test of Homogeneity of the Within-Class (Sire Breed) Regressions of Heat Production at 5°C Ambient Temperature on Midside Wool Weight Per Unit Area of Skin	144
	24	Test of Curvilinearity in the Relationship Between Heat Production at 5°C Ambient Temperature and Midside Wool Weight Per Unit Area of Skin	145
	25	Test of Homogeneity of the Within-Class (Sire Breed) Regressions of Midside Wool Weight Per Unit Area of Skin on Gestation Length : Lambs at First Test	148
	26	Ordered Fitting of the Partial Within-Class (Sire Breed) Regressions of Midside Wool Weight Per Unit Area of Skin on Bodyweight and Gestation Length : Lambs at First Test	149
	27	Ordered Fitting of the Partial Within-Class (Sire Breed) Regressions of Heat Production at 5°C Ambient Temperature on Midside and Hip Birthcoat Depth	152
	28	Test of Homogeneity of the Within-Class (Sire Breed) Regressions of Midside Wool Weight Per Unit Area of Skin on Midside and Hip Birthcoat Depths : Lambs at First Test	154
	29	Ordered Fitting of the Partial Within-Class (Sire Breed) Regressions of Heat Production at 5°C Ambient Temperature on Midside Birthcoat Depth and Wool Weight Per Unit Area of Skin	155

LIST OF TABLES (continued)

Chapter	Table		Page
IV	30	Effect of Sire Breed and Sex on Gestation Length : Lambs at First Test	161
	31	Effect of Sire Breed, Sex and Gestation Length on Bodyweight : Lambs at First Test	162
	32	Test of Homogeneity of the Within-Class (Sire Breed) Regressions of Log Total Heat Production at 5°C Ambient Temperature on Log Bodyweight	164
	33	Effect of Sire Breed, Wetness, Airspeed and Sex on Measured Relative Humidity of Air in the Chambers	166
	34	Test of Homogeneity of the Within-Class (Wetness) Regressions of Heat Production on Relative Humidity of the Climate Chamber Air at 5°C Ambient Temperature	168
V	35	Effect of Birthcoat Type, Birthrank and Sex on the Proportion of Lambs Attaining Summit Metabolism	181
	36	Effect of Metabolic Rate, Skin Temperature, Pre-Test Rectal Temperature, Bodyweight and Birthcoat Characteristics on the Proportion of Lambs Attaining Summit Metabolism	183
	37	Effect of Sire, Birthcoat Type, Birthrank, Airspeed and Sex on the Heat Production of Lambs at 10°C Ambient Temperature	185
	38	Effect of Sire, Birthcoat Type, Birthrank, Airspeed and Sex on the Rectal Temperatures of Lambs at 10°C Ambient Temperature	189
	39	Effect of Sire, Birthcoat Type, Birthrank and Sex on Pre-Test Rectal Temperature	192
	40	Effect of Sire, Birthcoat Type, Birthrank, Air-	

LIST OF TABLES (continued)

Chapter	Table		Page
		speed and Sex on the Rate of Decline in Rectal Temperature in Two Measurement Periods	193
V	41	Effect of Sire, Birthcoat Type, Birthrank, Airspeed and Sex on the Rectal Temperatures of Lambs at 10°C Ambient Temperature : Non-Summit Lambs	196
	42	Effect of Sire, Birthcoat Type, Birthrank, Sex and Bodyweight on Hip Birthcoat Depth	199
	43	Effect of Sire, Birthcoat Type, Birthrank, Sex and Bodyweight on Midside Birthcoat Depth	201
	44	Test of Homogeneity of the Within-Class (Birthcoat Type) Regressions of Heat Production at 10°C Ambient Temperature on Hip Birthcoat Depth	205
	45	Test of Homogeneity of the Within-Class (Birthcoat Type, Sex) Regressions of Heat Production at 10°C Ambient Temperature on Midside Birthcoat Depth	207
	46	Effect of Sire, Birthcoat Type, Birthrank, Sex and Bodyweight on Midside Wool Weight Per Unit Area of Skin	209
	47	Test of Homogeneity of the Within-Class (Sex) Regressions of Heat Production at 10°C Ambient Temperature on Midside Wool Weight Per Unit Area of Skin	212
	48	Effect of Sire, Birthcoat Type, Birthrank and Sex on Bodyweight	214
	49	Test of Homogeneity of the Within-Class (Airspeed) Regressions of Log Total Heat Production at 10°C Ambient Temperature on Log Bodyweight	216

LIST OF TABLES (continued)

Chapter	Table		Page
V	50	Effect of Sire, Birthcoat Type, Birthrank, Airspeed and Sex on the Hind-Limb Skin Temperatures of Lambs at 10°C Ambient Temperature	218
	51	Effect of Sire, Birthcoat Type, Birthrank, Airspeed and Sex on the Thermal Circulation Indices of Lambs at 10°C Ambient Temperature	220
	52	Effect of Sire, Birthcoat Type, Birthrank, Airspeed and Sex on the Rate of Decline in Hind-Limb Skin Temperature	222
	53	Test of Homogeneity of the Within-Class (Sex) Regressions of Heat Production on Hind-Limb Skin Temperature at 10°C Ambient Temperature	225
	54	Effect of Birthcoat Type and Birthrank on the Weight of Wool on the Limbs in Forty Lambs	227
	55	Test of Homogeneity of the Within-Class (Airspeed) Regressions of Hind-Limb Skin Temperature on Limb Wool Weight in Forty Lambs	228
	56	Test of Homogeneity of the Within-Class (Birthcoat Type) Regressions of Rate of Decline in Skin Temperature on Limb Wool Weight in Forty Lambs	229
	57	Test of Homogeneity of the Within-Class (Birthrank) Regressions of Limb Wool Weight on Hip Coat Depth in Forty Lambs	232
	58	Test of Homogeneity of the Within-Class (Birthrank) Regressions of Limb Wool Weight on Midside Wool Weight Per Unit Area of Skin in Forty Lambs	233
VI	59	Effect of Face Cover Group, Feeding Level and Sex on the Proportion of Lambs Attaining Summit Metabolism	242

LIST OF TABLES (continued)

Chapter	Table		Page
VI	60	Effect of Face Cover Group, Feeding Level and Sex on the Heat Production of Lambs at 10°C Ambient Temperature	243
	61	Effect of Face Cover Group, Feeding Level and Sex on the Rate of Decline in Rectal Temperature (Whole Experiment Period)	245
	62	Effect of Face Cover Group, Feeding Level and Sex on Hip Birthcoat Depth	247
	63	Test of Homogeneity of the Within-Class (Feeding Level) Regressions of Rate of Decline in Rectal Temperature on Hip Birthcoat Depth : Summit Lambs	249
	64	Test of Homogeneity of the Within-Class (Feeding Level) Regressions of Heat Production at 10°C Ambient Temperature on Midside Birthcoat Depth : Non-Summit Lambs	250
	65	Effect of Face Cover Group, Feeding Level and Sex on Midside Wool Weight Per Unit Area of Skin	252
	66	Test of Homogeneity of the Within-Class (Feeding Level) Regressions of Rate of Decline in Rectal Temperature on Midside Wool Weight Per Unit Area of Skin : Summit Lambs	253
	67	Test of Homogeneity of the Within-Class (Feeding Level) Regressions of Heat Production at 10°C Ambient Temperature on Midside Wool Weight Per Unit Area of Skin : Non-Summit Lambs	255
	68	Effect of Face Cover Group, Feeding Level and Sex on the Hind-Limb Skin Temperatures of Lambs at 10°C Ambient Temperature	257

LIST OF TABLES (continued)

Chapter	Table		Page
VI	69	Effect of Face Cover Group, Feeding Level and Sex on the Thermal Circulation Indices of Lambs at 10°C Ambient Temperature	258
	70	Effect of Face Cover Group, Feeding Level and Sex on the Weight of Wool on the Limbs	260
	71	Test of Homogeneity of the Within-Class (Feeding Level) Regressions of Hind-Limb Skin Temperature on Limb Wool Weight	261
	72	Effect of Face Cover Group, Feeding Level and Sex on Bodyweight	262
	73	Test of Homogeneity of the Within-Class (Sex) Regressions of Hind-Limb Skin Temperature on Bodyweight	264
	74	Test of Homogeneity of the Within-Class (Feeding Level) Regressions of Hind-Limb Skin Temperature on Age	266
	75	Distribution of Face Cover Grades in Control and Face Cover Lambs	268
VII	76	Distribution of Face Cover Grades in Lambs Sired by Single-N Rams	274
	77	Effect of Face Cover, Birthcoat Type and Birthrank on the Proportion of Lambs Attaining Summit Metabolism	276
	78	Effect of Face Cover, Birthcoat Type, Airspeed and Sex on the Heat Production of Lambs at 10°C Ambient Temperature	277
	79	Effect of Face Cover, Airspeed and Birthrank on the Hind-Limb Skin Temperatures of Lambs at 10°C Ambient Temperature	279

LIST OF TABLES (continued)

Chapter	Table		Page
VIII	80	Effect of Successive Tests in a Cold Environment on the Proportion of Lambs Attaining Summit Metabolism : Progeny Test Lambs	285
	81	Effect of Successive Tests in a Cold Environment on the Proportion of Lambs Attaining Summit Metabolism : Lambs Sired by Single-N Rams	291
IX	82	Effect of Face Cover Group, Sex and Hip Birthcoat Depth on Hogget Greasy Fleeceweight	299
	83	Effect of Face Cover Group, Sex, Hip Birthcoat Depth and Midside Wool Weight Per Unit Area of Skin on Staple Length of Hogget Wool	301
	84	Effect of Face Cover Group, Sex and Hip Birthcoat Depth on Mean Fibre Diameter of Hogget Wool	304
	85	Effect of Face Cover Group, Sex and Midside Wool Weight Per Unit Area of Skin on Crimp Frequency of Hogget Wool	305
	86	Effect of Face Cover Group and Sex on the Standard Deviation of Fibre Diameter of Hogget Wool	307
	87	Effect of Face Cover Group, Sex and Midside Wool Weight Per Unit Area of Skin on the Proportion of Medullated Fibres in Hogget Wool	308
	88	Effect of Face Cover Group, Sex, Hip Birthcoat Depth and Midside Birthcoat Depth on Colour Grade of Hogget Wool	309
Appendix I	89	Effect of Breed Type on the Hind-Limb Skin Temperatures of Dry Lambs at Six Ambient Temperatures	330

LIST OF FIGURES

Chapter	Figure		Page
II	1	Plan View of Climate Chambers	31
	2	Side Elevation of Left Climate Chamber	32
	3	Positions of Measurement in Preliminary Analysis of Birthcoat Depth	58
IV	4	Cooling Curves for a Range of Environmental Conditions	97
V	5	Experimental Plan for Lambs Exposed to a Single Ambient Temperature	177

LIST OF ABBREVIATIONS

LENGTH	mm	millimetre
	cm	centimetre
	m	metre
	km	kilometre
VOLUME	ℓ	litre
MASS	mg	milligram
	g	gram
	kg	kilogram
ENERGY	J	joule
	kJ	kilojoule
	cal	calorie
	kcal	kilocalorie
POWER	W	Watt
TEMPERATURE	^{o}C	degree Celcius
	^{o}F	degree Fahrenheit
TIME	sec	second
	min	minute
	hr	hour
STATISTICAL TERMS	S.E.	Standard error of the mean
	d.f.	degrees of freedom

All other abbreviations are defined at appropriate points in the text.

LIST OF APPENDICES

Appendix		Page
I	A Comparison of the Hind-Limb Skin Temperatures of Dry Merino, Romney and Drysdale-Romney Cross Lambs in Still Air	328
II	Estimation of the Bulk Density of the Birthcoat in Romney Lambs	333

C H A P T E R I

INTRODUCTION

CHAPTER I

INTRODUCTION

The Contribution of "Starvation and Exposure" Deaths to Neonatal Lamb Mortality

Between 5 and 25% of all lambs born annually on farms in New Zealand die before weaning (McFarlane, 1955; Hight and Jury, 1970; Knight, Hight and Winn, 1979; Dalton, Knight and Johnson, 1980). Similar mortality rates have been recorded in Australia (Moule, 1954; Alexander, McCance and Watson, 1955; Davies, 1964; Obst and Day, 1968), the United Kingdom (Purser and Young, 1959; Gunn and Robinson, 1963; Houston and Maddox, 1974) and the U.S.A. (Venkatachalam, Nelson, Thorpe, Luecke and Gray, 1949; Safford and Hoversland, 1960; Shelton, 1964). In New Zealand a commonly-accepted average of 15% pre-weaning mortality would account for at least 6 million lambs annually (Scott, 1962) and therefore constitutes an important source of economic loss to the sheep industry in this country.

Neonatal lamb mortality may be attributed to a variety of causes. The relative importance of these causes has been estimated from post-mortem surveys in which dead lambs are collected in the field and classified according to their likely "time of death" (ante-parturient, parturient, post-parturient) and "cause of death" (usually dystocia, starvation, exposure, disease, misadventure) based on certain anatomical and histological features seen at autopsy. Standardized techniques for use in these studies have been described in detail by McFarlane (1965).

Upon examination many dead lambs are seen to exhibit lesions attributable to both starvation and exposure. Consequently, these

deaths are often combined into a single post-mortem classification which may include mortalities considered to have been due to simple starvation (exhaustion of body reserves in the absence of hypothermia), simple exposure (lethal hypothermia with minimal depletion of body reserves), and to the combined effects of exposure and starvation. Thus McFarlane (1955), in a study of over 2000 dead lambs, estimated that 31% of deaths were primarily due to "starvation and exposure". A similar estimate is suggested by the results of McFarlane (1966). Hight and Jury (1970) found that, of some 800 lamb deaths, 27% were apparently accounted for by "physiological starvation", a category which did not include deaths attributed to simple exposure. Other mortality classes shown to be important by Hight and Jury were dystocia (32% of lamb deaths), post-natal infection (12%) and pre-natal death (10%). These estimates are in general agreement with those of McFarlane (1955) and with the results from a number of subsequent trials (Meyer and Clarke, 1978; Knight et al., 1979; Dalton et al., 1980).

Since the incidence of prematurity in sheep is reportedly low in the absence of infectious disease problems (Watson, 1962) it appears that the majority of pre-weaning deaths occur in fully developed lambs. Most of these deaths are clearly due to physiological failure of the lamb, or its dam, since the provision of intensive assistance, food, and warmth to the newborn lamb virtually eliminates neonatal mortality (Alexander, Peterson and Watson, 1959; Alexander and Peterson, 1961). Thus a considerable potential exists for the reduction of New Zealand's annual loss of 2 million lambs by starvation and exposure through appropriate management and selection of the newborn lamb.

Starvation and Exposure Mortalities : The Influence of Cold-Stress

At birth the lamb is delivered in a physiologically advanced state from the warm uterine environment to an external environment which is, in most cases, cooler than its lower critical ambient temperature (Slee, 1977). As a result the lamb must immediately increase its rate of body heat production, by up to 15 times the foetal level (Dawes and Mott, 1959; Alexander, 1962b), to compensate for body heat loss to the environment and so ensure that deep body temperature is maintained.

When the lamb's maximum sustainable metabolic rate is exceeded by the rate at which body heat is lost, deep body temperature falls. Many lambs suffer a decline in deep body temperature immediately after birth (Alexander and McCance, 1958), although the decline is minimal if the lamb is delivered into a warm environment (Smith, 1961). The majority of these lambs subsequently regain normal deep body temperatures of 39 to 40^{o}C within a few hours of birth, but in some cases the decline continues, often rapidly, until death occurs at deep body temperatures below 30^{o}C (Alexander and McCance, 1958). It is likely that these exposure deaths involve a "vicious circle" of falling deep body temperature and falling heat production since the lamb's "summit metabolic rate" (the maximum sustainable rate of body heat production per unit bodyweight) declines proportionately with rectal temperature when the latter is less than 36^{o}C (Alexander, 1962b).

Cold-exposure may also predispose lambs to early mortality in the absence of lethal hypothermia. When the lamb experiences a very high rate of body heat loss the associated requirement for a high

metabolic rate results in a rapid utilization and, unless the lamb suckles, depletion of its limited body stores of thermogenic carbohydrates, fats and proteins (Alexander, 1962c). Thus, while the energy derived from the catabolism of body reserves is sufficient to permit lamb survival for 3 to 5 days in conditions of thermoneutrality, survival time may be markedly reduced in a cold environment. This may partly explain why most starvation-exposure deaths occur within 3 days of birth (McFarlane, 1961).

A second consequence of starvation is that the lamb's ability to sustain a high metabolic rate declines as the catabolism of its body reserves proceeds (Alexander, 1962b). Hence starved lambs, and particularly those suffering a severe depletion of body reserves, are likely to be more susceptible to hypothermia than lambs which are well fed. Clearly the replenishment of body reserves and the provision of thermogenic substrates by suckling is important for a variety of reasons. Successful suckling is not, however, an absolute guarantee of survival since many lambs assigned to the post-parturient mortality class (which comprises mainly starvation-exposure deaths) show evidence of having suckled (McFarlane, 1955, 1966).

The physiological effects of cold-exposure on the lamb's drive to suckle provide another important link between starvation and exposure mortalities. Alexander and Williams (1966a) demonstrated that the lamb's suckling reflex is markedly depressed when deep body temperature falls below about 37^{o}C so that even mild hypothermia, while in itself non-lethal, may predispose to death by starvation. In addition, Alexander and Williams (1966a) demonstrated a possible effect of "discomfort" due to cold-exposure which, while apparently

independent of the hypothermia effect, also decreases the vigour of the suckling drive. These effects are compatible with field observations that the average time from birth to first suckling is prolonged in lambs born in cold, windy conditions compared with those born in less severe environments (McBride, Arnold, Alexander and Lynch, 1967). Conversely the "reward" of first obtaining milk is a strong positive stimulus to continued suckling (Alexander and Williams, 1966b) which further enhances the importance of early suckling success.

The nature of these physiological interactions provides strong evidence that starvation and exposure deaths are linked through the debilitating effects of the cold environment experienced by the lamb at birth. It may also explain why lesions of both starvation and exposure are commonly observed in the same lamb at autopsy. As a result there has been a general acceptance of the view that the "starvation-exposure syndrome" is a primary cause of about 30% of lamb mortalities and that the effects of cold-stress are implicated to some degree in the majority of these deaths (Alexander, 1962c; Sykes, Griffiths and Slee, 1976; Slee, 1977).

An alternative hypothesis, proposed by Haughey (1973b, 1978) suggests that the starvation-exposure syndrome is merely a secondary cause of lamb mortality, the primary cause being damage to the lamb's central nervous system (CNS) sustained during the birth process. Haughey (1973b) has reported that approximately 60% of lambs assigned to the starvation-exposure mortality class exhibit lesions in or around the cranial and spinal meninges. These lesions occur during both assisted and unassisted births, probably as a result of anoxia or trauma (Haughey, 1973a, 1975).

In lambs which survive the birth process (i.e. do not die of dystocia), the primary effect of CNS damage is apparently a depression of the suckling drive. Neither the ability to regulate deep body temperature nor the ability to mobilize body reserves appear to be severely affected since injured lambs starved at low ambient temperatures survive for periods comparable with those of uninjured controls (Haughey, 1975). The depression of the suckling drive interacts with environmental effects, being most strongly expressed when the lamb is exposed to a cold environment. Thus Haughey (1975) demonstrated that whereas 60% of injured lambs failed to suckle at an ambient temperature of 1^{o}C, the failure rate was only 5% at 28^{o}C. This suggests that the effects of CNS damage may interact with the effects of hypothermia or "discomfort" on the suckling drive, although the conditions in which Haughey's lambs were tested (dry, cold, "still" air) were probably too mild to induce hypothermia (Haughey, 1979). It also seems likely that the effects of CNS damage may be minimized by providing the lamb with a benign environment at birth.

The contribution of CNS injury to starvation-exposure mortalities on New Zealand farms remains unclear. In a recent New Zealand study (Duff, 1981), only 34% of 103 lambs assigned to the starvation-exposure classification were found to exhibit cranial and/or spinal meningeal lesions. Severe lesions were not seen in these lambs. Further research is therefore required to establish whether CNS injury is an important factor in starvation-exposure deaths in New Zealand, as appears to be the case in Australia. If so, one method of reducing the incidence of starvation-exposure deaths might be to select and manage ewes and lambs with a view to minimizing CNS injury at birth.

An alternative approach to the problem would be to select or manage the ewe flock so as to improve the resistance of the newborn lamb to body cooling in a cold environment. Hypothermic lambs are likely to be particularly susceptible to starvation-exposure deaths due to the depression of heat production and of the suckling reflex which occur when deep body temperature falls below about 37°C. Hence lambs which are able to maintain normal deep body temperature in a cold environment can be expected to have increased survival rates. An improved ability to maintain body temperature may also reduce the lamb's susceptibility to the effects of CNS injury. Only this second approach to starvation-exposure mortality will be considered further in the present study.

Factors Affecting the Resistance of Lambs to Body Cooling

1. Birthweight and birthrank

The birthweight and birthrank of the newborn lamb exert significant effects on its survival in the immediate post-natal period. Both light and heavy lambs have higher mortality rates than lambs of average birthweights (Alexander, McCance and Watson, 1955; Hight and Jury, 1970), although even lambs in the "optimum birthweight range" may still have mortality rates in excess of 10% (Hight and Jury, 1970; Dalton *et al.*, 1980).

Multiple-born lambs are much more susceptible to starvation-exposure mortality than are singles (Hight and Jury, 1970; Meyer and Clarke, 1978). This effect is apparently due to birthweight differences between multiple- and single-born lambs rather than to an effect of birthrank *per se*, since singles and multiples of equal birthweights have a similar incidence of starvation-exposure

mortalities (Dalton et al., 1980).

The susceptibility of small lambs to the starvation-exposure syndrome is considered to be primarily due to their less favourable ratio of surface area to volume (Alexander, 1974). The rate of heat loss from the lamb's body is related to some function of its surface area which is, in turn, proportional to bodyweight raised to a power less than unity. Thus in a standard cold environment small lambs are expected to have a greater rate of heat loss per unit bodyweight than larger lambs. Furthermore, since the summit metabolism per unit bodyweight of newborn lambs is constant over a range of weights (Alexander, 1962b) small lambs are expected to become hypothermic in less severe environments than large lambs. This relationship is commonly used to explain the more rapid body cooling observed in light lambs immediately after birth (Alexander and McCance, 1958). In addition, small lambs may be disadvantaged by disproportionately low levels of body reserves and, in extreme cases, by retarded development of the birthcoat and of body tissues and organs (Alexander, 1974).

2. Heat production

(a) Level of summit metabolism

The level of summit metabolism attained by the newborn lamb is likely to be an important determinant of neonatal survival since it provides the limit to which body heat loss (per unit bodyweight) may increase before hypothermia occurs. Alexander (1962b) has estimated the mean summit metabolism of newborn Merino and Border Leicester-Merino cross lambs to be about 19.8 W kg^{-1} (17.0 kcal kg^{-1} hr^{-1}), this being similar in suckled and unsuckled lambs. Summit

metabolism is normally measured as the level of heat production attained by the lamb when exposed to environmental conditions which produce a small decline (0.03 to 0.05^{o}C min^{-1}) in body temperature. The requirement for a controlled decline in deep body temperature ensures that the lamb is at the limit of its ability to produce body heat but that body temperature does not fall so low as to affect metabolic rate (Alexander, 1962b).

Subjecting lambs to environmental conditions which evoke a summit response in heat production results in a number of metabolic changes including the elevation of plasma concentrations of glucose, free fatty acids (FFA), glycerol and lactate (Alexander, 1962b; Alexander, Mills and Scott, 1968; Alexander, Bell and Hales, 1972). Similar effects are observed in lambs exposed to less extreme cold (Alexander and Mills, 1968). The elevation of blood metabolite levels can be mimicked by the infusion of adrenaline and nor-adrenaline into lambs in a thermo-neutral environment and is largely abolished by treatment with α- and β- adrenergic blocking agents. It is therefore considered to reflect a sympathetically-mediated increase in body reserve mobilization (Alexander, Mills and Scott, 1968). Other changes which accompany the induction of a summit response in metabolism include the elevation of cardiac output, depth of respiration and blood pressure; disturbance of the blood acid-base status; and a redistribution of blood flow in favour of the thermogenic tissues (Alexander and Williams, 1970a; Alexander, Bell and Hales, 1972, 1973).

Shivering and (regulatory) non-shivering thermogenesis together contribute to the summit metabolic response of lambs less than one week old (Alexander and Williams, 1968). Non-shivering

thermogenesis appears to occur mainly in the brown adipose tissue which, while constituting most of the lamb's adipose tissue at birth, is gradually replaced by white adipose tissue in the first few weeks of life (Gemmel, Bell and Alexander, 1972). This change is accompanied by, and may be responsible for, a decline in the level of summit metabolism per unit bodyweight attained by the lamb as it ages (Alexander, 1962b).

Shivering thermogenesis occurs in the striated muscles of the body and is under somatic nervous control (Hemingway, 1963). Normally shivering becomes obvious only under conditions of extreme cold which has lead Alexander (1975) to suggest that, in the lamb, shivering may not be employed until non-shivering thermogenesis is approaching its full potential. However, since striated muscle may respond to increased requirements for body heat production simply by increasing muscle tone, "shivering" thermogenesis may occur even when shivering is not observed (Webster, 1974).

Although skeletal muscle has the capacity to produce up to 60% of the lamb's summit metabolic rate, its energy reserves (mainly in the form of carbohydrate) are small compared with the energy available from body fat (Shelley, 1960; Alexander, 1962c; Alexander and Bell, 1975b). It is therefore not surprising that skeletal muscle appears to utilize FFA mobilized from brown fat stores, as is indicated by the rise in plasma FFA concentration which follows the chemical paralysis of skeletal muscle in severely cold-stressed lambs (Alexander, Mills and Scott, 1968).

Attempts to identify factors which contribute to the considerable

variation in summit metabolism observed between lambs, and which might be manipulated to increase the level attained at birth, have met with only limited success. Alexander and Bell (1975a) were unable to relate summit metabolism to the weight of dissectible brown adipose tissue, weight of skeletal muscles, or amount of chemically-extractable lipid in the lamb's body. They also considered that neither the extent of liver/muscle glycogen stores, nor the circulating levels of glucose, FFA and glycerol, were likely to be limiting factors. Alexander (1969, 1970) infused, or injected, into lambs a variety of hormones and other substances which might have been expected to influence summit metabolism (either through a direct action on the thermogenic tissues or by altering the availability of energy substrates) and found them to be generally without effect. The important exceptions were adrenaline and noradrenaline (which produced small increases in summit metabolism in a proportion of the lambs tested) and lipid and tri-iodothyronine (which resulted in more consistent, but still small, elevations in metabolic rate). The effect of tri-iodothyronine was, however, evident only after 3 days of treatment. In this context, it should be noted that Alexander (1962b) has cited unpublished evidence of depressed summit metabolism in hypothyroid lambs, and that daily injection of thyroxine retards the decline in summit metabolism which is normally observed as the lamb ages (Alexander, Bell and Williams, 1970).

Other studies have suggested that summit metabolism may be limited by the supply of oxygen to the thermogenic tissues since it has been shown to be significantly correlated with such parameters as cardiac output, heart rate, and respiratory frequency (Alexander

and Williams, 1970a; Alexander and Bell, 1975a). However, the correlations are not consistent between different groups of lambs and causal relationships may be difficult to establish. Perhaps the best evidence for a limiting effect of oxygen supply to the thermogenic tissues was provided by Alexander and Williams (1970b) who demonstrated that increasing the oxygen content of air inspired by lambs resulted in an increased level of summit metabolism in some lambs and an improved ability to maintain summit metabolism in others. These effects tended to be reversed under conditions of hypoxia.

(b) Attainment and maintenance of summit metabolism

Lambs born in the field may suffer a considerable decline in rectal temperature during the first hours of life. In extreme cases this can exceed 10^{o}C in the first 30 minutes (Alexander and McCance, 1958; Sykes, Griffiths and Slee, 1976). It is therefore probable that the rapid attainment of a high level of summit metabolism during this period would greatly favour the lamb's viability. Little is known about factors affecting the rate at which summit metabolism is attained although Alexander (1962b) has commented that poor pre-natal nutrition of the lamb appears to lead to a slow attainment of high metabolic rates immediately after birth. The final level of summit metabolism achieved is, however, independent of pre-natal nutrition.

Many of the factors which influence the lamb's ability to maintain high levels of summit metabolism have already been discussed. To summarize, Alexander (1962b) has reported that declining summit metabolism (per unit bodyweight) may be associated with; falling deep body temperature (below 36^{o}C); increasing lamb age (the decline being retarded if the lamb is kept in a cold environment or administered thyroxine); and with prolonged starvation.

3. Heat loss

(a) Birthcoat characteristics

A number of field trials in the United Kingdom and Australia have demonstrated an association between lamb birthcoat type and neonatal survival. Purser (1967) and Purser and Karam (1967) classified newborn Welsh Mountain lambs into 6 birthcoat grades (based on the distribution of halo hairs across the body) and examined the mortality rates, to 14 days of age, of lambs in each grade. Mortality was strongly associated with birthcoat type, being lowest in lambs of the intermediate grades. Lambs with very fine coats had particularly poor viability, especially if born in "bad" weather (high winds, minimum ambient temperature less than $-4^{o}C$, and daily rainfall exceeding 6 mm) when their mortality rate exceeded 40% compared with 10% losses in the hairiest lambs and only 3% in lambs of the intermediate grade 4. Differences between the birthcoat grades were minimized in "good" weather.

A similar association between birthcoat grade and neonatal survival has been reported by Obst and Evans (1970) who classified Australian Merino lambs into three grades based primarily on the distribution and density of halo hairs across the back. As in the previous studies there were no significant effects of birthcoat grade on the mortality of lambs born in "good" weather. Among lambs subjected to "bad" weather (rain and windspeeds greater than 10 km hr^{-1}) during the first 6 hours of life, those with "coarse" birthcoats had considerably lower mortality rates than lambs of the "medium" or "fine" grades. This result differs from those of the British studies in which lambs of intermediate hairiness exhibited the best survival rates. However, comparisons between these studies

may not be valid because of differences in the grading systems used.

Neither Davies (1964) nor Mullaney (1966) were able to demonstrate an effect of birthcoat grade on the viability of newborn Merino, Corriedale and Polwarth lambs. However, in each of their trials, lambing occurred in relatively mild weather and it seems that differences between birthcoat types may be expressed only in more severely cold conditions.

An association between birthcoat type, haemoglobin type and neonatal survival appears to exist in some sheep breeds. Hall and Purser (1979) found that, in some years, the mortality rate of haemoglobin (Hb) type AA lambs (of the Welsh Mountain and Scottish Blackface breeds) was significantly lower than that of the Hb type BB lambs. Obst and Evans (1970) demonstrated a similar effect in Australian Merino lambs although the difference was not significant. There was, however, a significant interaction between the effects of dam Hb type and lamb birthcoat type on survival of the newborn. In high rainfall years the mortality of lambs with "fine" and "medium" coats born to type AA ewes was significantly lower than the mortality of similar lambs born to type BB ewes. Among the "coarse"-coated lambs, mortality was independent of the dam's haemoglobin type. While the mechanism of this effect is unknown, the nature of the interaction does suggest a relationship between the dam's Hb type and the lamb's resistance to cold-stress.

The effect of birthcoat type on the ability of the newborn lamb to regulate body temperature has been studied in more detail by Alexander (1961, 1962a) and Slee (1978). Using the same grading

system as Obst and Evans (1970), Alexander identified lambs with "hairy" (coarse) and "fine" birthcoats (i.e. the two extremes of the grading system) and compared the insulative values of their coats. When the lambs were dry and in still air, the external (coat plus air) insulation of the fine-coated lambs was estimated to be approximately 60% that of the "hairy" lambs (Alexander, 1961). Exposure to a wind of 550 cm sec^{-1} halved the estimated external insulation of each coat type so that the superiority of the hairy coat was maintained. The effects of wetting the coat on its insulative value are unknown, but observations by Alexander (1962a) suggest that the birthcoats of lambs which have dried, but are then re-wetted, tend to trap air better than the coats of lambs still wet with amniotic fluid. The drying of the coat immediately after birth may therefore have important consequences for its insulative value.

Slee (1978) studied the "cold-resistance" (defined as the time required for deep body temperature to fall $1^{o}C$ under standard environmental conditions) of three breeds of lamb (Scottish Blackface, Tasmanian Merino and Welsh Mountain). Differences between the breeds, and between long- and short-coated strains within the Welsh Mountain breed, were highly significant and reflected the breed, or strain, differences in mean birthcoat depth (measured as the distance from the skin surface to the outer margin of the coat). Clipping the lambs resulted in a much greater decrease in cold-resistance among the long-coated lambs than among those with short coats, further evidence that superior pelage insulation was conferred by the deeper birthcoats. Between-breed differences in cold-resistance of the clipped lambs were smaller, but still significant, and were mainly due to corresponding breed effects on birthweight. The superior

cold-resistance of the Blackface lambs compared with the Merinos (before and after clipping) is consistent with field observations of their relative abilities to regulate deep body temperature (Sykes et al., 1976) which suggests that climate chamber tests may be useful predictors of viability in the field.

Studies with older sheep, in which a linear relationship has been demonstrated between fleece depth and external insulation (Joyce, Blaxter and Park, 1966; Webster and Blaxter, 1966), support the view of Slee (1978) that birthcoat insulation may be strongly dependent upon coat depth. However, the role of other characteristics of the coat has not been evaluated. Comparisons of Cheviot, Suffolk and Blackface sheep have suggested that, at low airspeeds, fleece characteristics other than depth do not significantly affect external insulation (Armstrong, Blaxter, Clapperton, Graham and Wainman, 1960; Webster and Blaxter, 1966). Conversely, estimates of fleece insulation per unit depth derived from a number of breeds and summarized by Joyce et al. (1966) may indicate that the Merino fleece is superior in this respect, evidence perhaps of an effect of fibre diameter or fibre number per unit area of skin on coat insulation. Doney (1963) found that the weight changes of cold-exposed, non-pregnant Blackface ewes were associated with their fibre number and midside wool weight per unit area of skin, as well as with fleece depth. Since the weight changes were considered to reflect individual differences in fleece insulation, these results may provide further evidence that coat insulation is not simply a function of depth, although the extent to which the measured fleece characteristics were correlated in that study is not known.

(b) Pilomotor control

Piloerection has been shown to increase the external insulation of cold-exposed cattle (Blaxter and Wainman, 1961, 1964; Gonzalez-Jimenez and Blaxter, 1962), but no comparable effect appears to have been reported in sheep, probably because of species differences in skin structure. In cattle all the follicles producing the coat hairs are associated with an arrector pili muscle (Carter and Dowling, 1954), whereas in sheep only the primary follicles, which produce less than 25% of the fibres in most fleeces, have an arrector muscle attached (Carter, 1955). Furthermore these follicles lie almost perpendicular to the skin surface and the arrector muscle is connected to the middle region of the follicle rather than at its base (Wildman, 1932). As a result, contraction of the arrector pili muscle, which has been shown to occur in response to in vitro catecholamine stimulation (Chapman, 1965), would result in only minimal erection of the primary fibres. It therefore appears unlikely that piloerection could make a significant contribution to the external insulation of the newborn lamb.

(c) Peripheral vasomotor control

Lambs exposed to severe cold exhibit a marked decline in peripheral blood flow (Alexander, Bell and Setchell, 1972) which results in the skin temperature of the extremities approaching ambient temperature (Alexander, 1961, 1962a). Based on his earlier observations, Alexander (1964) concluded that "the peripheral vasomotor mechanisms are as well developed at birth as in the adult sheep", but little is known about the extent to which lambs vary in their ability to control peripheral blood flow and the consequences of such

variation for body heat loss. Alexander, Bell and Hales (1973) demonstrated that some variation does exist between lambs in the rate of blood flow to the vasoconstricted tissues of the leg and ear but this information is a limited value since only 5 lambs were involved in the study.

Peripheral vasoconstriction is widely regarded as being an "all-or-none" phenomenon which is activated prior to the onset of cold-induced thermogenesis in environments just cooler than the lower critical temperature. This conclusion has been reached in studies of lambs (Alexander, 1961, 1962a) and older sheep (Armstrong et al., 1960; Joyce and Blaxter, 1964) based on evidence that calculated tissue insulation is constant once vasoconstriction has occurred and that the relationship between heat production and ambient temperature is linear in the "cold zone". However, other studies have suggested that peripheral vasoconstriction may be controlled in a more continuous manner. Webster and Johnson (1968) reported that cold-stressed sheep may show increased respiration rates (presumably associated with increased thermogenesis) before vasoconstriction has been fully employed. Similar evidence of a continuous response in cattle has been presented by Gonzalez-Jimenez and Blaxter (1962).

Slee (1964, 1968) compared the vasoconstrictor responses of Scottish Blackface and Tasmanian Merino rams subjected to increasingly cold environments. When in full fleece the Blackface rams vasoconstricted at higher ambient temperatures, and exhibited lower skin temperatures (on the hind-limbs and ears), than did rams of the Merino breed. However, when the rams were completely shorn and then re-cooled, both the timing and intensity of the skin temperature

response were more uniform between the breeds. It was therefore suggested that the breed differences were due to the Merinos having superior fleece insulation on the whole body (and thus entering their "cold zone" at lower ambient temperatures), or on the extremities (so that conservation of heat by vasoconstriction in these regions was of lesser importance in this breed).

Open-faced sheep have been shown to be more productive than sheep with woolly faces, especially in characters concerned with growth and reproduction (Cockrem and Rae, 1966). These differences may be associated with a poorer ability of woolly-faced sheep to control peripheral blood flow and therefore body temperature (Cockrem, 1967). The possibility that similar genetically-controlled differences in vasomotor activity might contribute to variation in the cold-resistance of the newborn lamb does not appear to have been studied. Cockrem and Rae (1966) found that the mortality of lambs born to open-faced ewes was lower than among the progeny of woolly-faced ewes, but the difference was not statistically significant and might not have been a function of lamb genotype. Nonetheless Cockrem (1967) has shown that the differential "effects" of face cover on body temperature control occur in lambs during the first year of life and further study of peripheral vasomotor control in the newborn lamb may well be warranted.

(d) Subcutaneous fat

In mature animals of many species the resistance to heat flow provided by the subcutaneous fat constitutes a considerable proportion of the individual's tissue insulation (Mount, 1979). However, the newborn lamb has virtually no subcutaneous fat (Alexander and Bell,

1975b) and it therefore appears unlikely that variation in this character could significantly contribute to variation in resistance to cold-stress during the neonatal period.

Possible Selection Criteria for Reducing Starvation and Exposure Losses

The nature of the physiological mechanisms involved in the starvation-exposure syndrome suggests that, if maternal behaviour is adequate, the susceptibility of newborn lambs to starvation and exposure may be greatly reduced provided that they maintain deep body temperature above about 37^{o}C. Thus the identification of, and selection for, heritable characteristics which confer upon the lamb a high resistance to body cooling may help to reduce current lamb losses. Evidence of breed and strain differences in body cooling support the view that resistance to hypothermia is to some extent heritable (Sykes et al., 1976; Slee, 1978; Slee, Griffiths and Samson, 1980), but the characteristics which contribute to these differences remain largely unidentified.

An ability to attain high levels of summit metabolism during the first few days of life would clearly be of benefit to the newborn lamb. However, while there is considerable variation between lambs in the level of summit metabolism attained at birth (Alexander, 1962b) no evidence exists that this variation is genetically based. Thus Alexander and Bell (1975a) were unable to detect significant differences between 5 breeds and crosses of lamb (Merino, Border Leicester, B.L. - Merino cross, Corriedale, Dorset Horn) in the level of summit metabolism. A study of lambs from breeds which evolved in more extreme climates might, however, identify such differences. The

rapid attainment of high levels of summit metabolism immediately after birth is also desirable but again there is no evidence that this trait is genetically controlled.

An effect on lamb survival of haemoglobin type, which is simply inherited (Evans, King, Cohen, Harris and Warren, 1956), has been described by Obst and Evans (1970) and Hall and Purser (1979). The mechanism of this effect is unknown but it may be partially explained by the greater twinning rate of haemoglobin Type B ewes (Hall and Purser, 1979) whose lambs also have the highest mortality rate. If there is an effect of haemoglobin type independent of the differential twinning rates it is likely to be mediated through poorer cold-resistance of the Type B lambs, especially those with fine birth-coats (Obst and Evans, 1970).

Susceptibility to starvation and exposure is clearly dependent on the birthweight of the newborn lamb. However, while the mortality rate of very small lambs may be high, their incidence in the flock is generally low and they may make only a limited contribution to overall mortality rates. For example, Duff (1981) found that 83% of lambs dying of starvation and exposure were in the 3 to 5 kg birthweight range, the range of birthweights at which lambs are normally considered to have minimum mortality rates per 100 lambs born (Hight and Jury, 1970; Dalton et al., 1980). It is therefore questionable whether starvation-exposure mortalities could be substantially reduced even if pregnant ewes were managed so that they all produced lambs in the "optimum birthweight range".

The role of CNS injury in the starvation-exposure syndrome requires further study. Although a proportion of dead lambs may

exhibit CNS lesions, the lesions show varying degrees of severity and the extent to which this determines their effects on the lamb's suckling drive is unknown. The mechanism by which the effects of CNS injury on the sucking reflex apparently interact with the effects of cold-exposure also requires further study.

Selection for specific birthcoat types has promise as a means of improving the resistance of the newborn lamb to cold-stress. Birthcoat "type" appears to be strongly inherited (Dry, 1955; Schinkel, 1955), but to date the grading systems used in birthcoat studies have been based on halo hair distribution rather than on the insulative value of the coat. Further research is required to identify those characteristics of the birthcoat which confer an insulative advantage and to examine the manner in which they are inherited.

The insulation provided by the vasoconstricted tissues of the newborn lamb is of the same magnitude as the external insulation in lambs with fine birthcoats (Alexander, 1961). It is, therefore, an important source of resistance to cold-stress. Since subcutaneous fat is of little importance, variation between lambs in tissue insulation will primarily be a function of variation in peripheral blood flow. At present little is known about the extent to which such variation exists, or whether it is genetically controlled. Studies with older sheep have suggested the possibility of heritable variation in peripheral vasomotor control (Joyce and Blaxter, 1964; Slee, 1964, 1968) which may be reflected in facial wool growth (Cockrem, 1967), but results are inconclusive.

While the selection of lambs with a good resistance to body cooling may be a desirable method of reducing mortalities due to starvation and exposure, further study of many aspects of this problem will be required before firm recommendations for selection procedures can be made. As a first step, it will be necessary to identify those traits which contribute to variation in the ability of lambs to regulate body temperature in a cold environment. Although the desirability of certain traits, such as the rapid attainment of a high level of heat production, is self-evident, those characters which affect the rate of heat loss from the lamb's body are yet to be examined in detail. It will then be necessary to establish that these traits are heritable, and that they can be easily measured with a good degree of repeatability. Finally, consideration must be given to the economic implications of selecting for these traits with respect to the likely returns from this selection and its effects on subsequent production in the ewe flock.

Purpose and Scope of the Investigation

The main purpose of this study was to identify characters which might be utilized in a selection programme to improve the resistance of the newborn lamb to body cooling. Characters associated with resistance to body heat loss were of particular interest. Investigations centred on lambs of the Romney breed, since this breed is numerically the most important in New Zealand, but Drysdale-Romney cross and Merino lambs were also examined for comparative purposes.

Two possible indices of cold-stress were considered for use in the study. The first, "rate of decline in rectal temperature", has been used in studies in the United Kingdom (Slee, 1978; Slee *et al.*, 1980) and relates most closely to the problem being considered. However, it has the major disadvantage that it depends not only on the rate at which heat is lost from the lamb's body, but also on the maximum level of heat production attained by the individual (i.e. the summit metabolic rate). It may be further influenced by the rate at which summit metabolism declines with rectal temperature when the lamb is severely hypothermic. The alternative index, "level of heat production required to maintain a constant deep body temperature" was therefore preferred. Since the lamb's body heat storage capacity is low (Alexander, 1961), this index more accurately estimates the rate of body heat loss when rectal temperature is constant. The use of this index did, however, place constraints on the environments in which the lambs could be tested. While it was desirable that the lambs be tested in cold conditions, it was also necessary to ensure, as far as possible, that they did not attain summit metabolism. Accordingly, the preliminary experiments involved the measurement, in

Romney lambs, of summit metabolic rate and of the environmental conditions which were likely to elicit a summit response in metabolism.

Characters concerned with birthcoat insulation were examined in some detail in this study because the insulation provided by the birthcoat is an important component of total body insulation, and because birthcoat type is related to the survival of lambs in the field. The Romney lambs were compared with Drysdale-Romney cross lambs which, although genetically similar to the Romneys, have birthcoats containing a high proportion of long coarse fibres (Dry, 1955). In lambs of these two "breeds", the relationship between coat insulation and various characteristics of the coat was examined, as were the effects of wetting and air movement on the insulative value of the birthcoat. Sources of variation in birthcoat depth (between- and within- coat types) were studied and the repeatability of measured coat depth was estimated in each "breed" of lamb. Some consideration was also given to the relationship between characteristics of the birthcoat and those of the hogget fleece.

The lamb's birthweight is considered to be an important determinant of its metabolic response to cold-stress (Alexander, 1964, 1973; Slee, 1977) due to surface area-volume relationships which have been discussed. Alexander (1962b) predicted the environmental conditions in which small and large lambs were likely to become hypothermic and so demonstrated a strong effect of birthweight. However, these predictions were based on the assumption that the lamb's body surface area is proportional to bodyweight $^{0.59}$. This exponent was derived by Lines and Peirce (1931) using data from slaughtered sheep whose bodyweights were in the range 3.8 to

50.4 kg. It is therefore questionable whether such an exponent is suited to the prediction of the thermoregulatory limits likely to be experienced by lambs of different birthweights. Accordingly, a second aim of this study was to examine the relationship between heat production and bodyweight in newborn lambs, and to derive experimentally an appropriate exponent relating bodyweight to "effective" body surface area (Brody, 1945).

The degree of face cover exhibited by hoggets may be a useful indicator of their ability to control body temperature (Cockrem, 1967). An hypothesis that face cover "effects" may also be expressed at birth was therefore examined by comparing the thermoregulatory ability of lambs from two flocks, one of which has been selected only for a reduced degree of face cover and the other maintained as a random-bred control group.

Finally, some sources of variation in skin temperature were examined in this study. The lamb's tissue insulation provides an important component of its resistance to body heat loss, and is likely to be mainly a function of peripheral blood flow. In some circumstances peripheral blood flow may be estimated by the measurement of skin temperature on the extremities (Fetcher, Hall and Shaub, 1949). A number of other factors may also contribute to variation in skin temperature (Molnar and Rosenbaum, 1963) and so introduce errors into the estimation of blood flow. Consequently, the final component of this study involved an examination of the extent to which these effects were likely to mask differences between lambs in the rate of blood flow to peripheral tissues.

C H A P T E R I I

EXPERIMENTAL

CHAPTER II

EXPERIMENTAL

Animals

1. Management of ewes

Most of the lambs used in the trials were the progeny of New Zealand Romney ewes mated to Romney, Drysdale or Drysdale-Romney cross (single-N) rams. The ewes, which were 2 to 6 years old at lambing, were individually identified by numbered brass and plastic eartags. Approximately 80% of them were bred on the University farms and the balance purchased from commercial farms in the Manawatu region.

Mating commenced in the second week of March each year and continued for 8 weeks. In order to extend the lambing period, and to control the distribution of lambing, the ewes were initially held in a non-mating mob and a proportion of them transferred to their respective mating groups at weekly intervals. By the seventh week of mating, all ewes were running with the ram. The rams were fitted with mating harnesses and crayon colours were changed at fourteen-day intervals. Tupping marks were recorded daily or weekly and expected lambing dates calculated on the basis of these records. The ewes were wintered on grass pasture on the University farms with some hay being fed during the last month of gestation.

The remaining lambs were born to N.Z. Merino ewes and were sired by Booroola Merino-N.Z. Merino cross rams. The ewes, which were 3 to 7 years old, were on loan from the Wairakei Experimental Station of the Ministry of Agriculture and Fisheries. They were mated at Wairakei and transported to Massey University when about 3 months

pregnant. Individual tupping records were not available for these ewes.

The ewes were transported to the Animal Physiology Unit 3 to 7 days before their expected lambing dates. Most of them were penned on wooden slats in air temperatures of approximately 15°C. Some ewes remained in these pens for up to 20 days before they lambed but the majority had lambed within a week of arriving at the Unit.

One group of ewes, members of the "Progeny Test" flock (Chapter VI), appeared to be highly susceptible to viral pneumonia and so were separated from the main flock. They were held outside the Unit in an open-sided haybarn protected by 1.5 metre-high walls constructed of hay bales. Air temperatures in the barn fluctuated between 2°C and 15°C.

In all experiments the ewes were offered average daily rations of approximately 0.5 kg dry matter (DM) of good quality pasture hay and 1.0 kg DM of freshly cut ryegrass/white clover pasture. About 20% (by weight) of this ration, mainly dead and stalky pasture material, was refused by the ewes. Average intakes were therefore 1.2 kg DM per day and were close to current feeding recommendations for pen-fed pregnant ewes as summarized by Jagusch and Coop (1971). However, because only limited pen space was available, it was often necessary to pen the ewes in groups of 2 to 3 and precise control of individual intakes was not possible. The same situation applied to ewes held in the haybarn. All ewes had continuous access to fresh water.

On entering the Unit some ewes did not eat for 24 to 48 hours and a few appeared to suffer from pregnancy toxaemia. They were

successfully treated by drenching with "Ketol" (Veterinary Ethicals Ltd., Auckland). Lambs born to ewes showing symptoms of pregnancy toxaemia or viral pneumonia were excluded from subsequent analyses.

From the time they arrived at the Unit, the ewes were inspected hourly between 7 a.m. and midnight for signs of impending parturition and, when considered necessary, lambing assistance was given. After lambing, all ewes (including those which lambed in the haybarn) were individually penned with their lambs in the Unit and their ration was changed to freshly cut pasture available *ad libitum*. Once testing of the lambs had been completed, the ewes and their lambs were returned to the University farms.

2. Management of lambs before testing

As soon as possible after birth each lamb was tagged with a serially numbered brass eartag and its sex, birthrank, date and time of birth, eartag number and dam number were recorded. If lambing had occurred between midnight and 7 a.m., and had therefore not been observed, the lamb's time of birth was estimated to the nearest hour from the degree of wetness of its birthcoat and from its progress towards standing and suckling.

In most trials the metabolic rate of each lamb was measured in order to estimate its rate of body heat loss and to study the extent to which variation in heat loss was determined by such factors as breed, sex, bodyweight and birthcoat type. Because of the need to test a large number of lambs in a short period of time, some lambs did not receive their first test until they were 25 to 30 hours old. It was therefore considered desirable that any possible effects of

starvation on the lamb's ability to produce body heat, as have been demonstrated by Alexander (1962b), should be avoided by allowing them to suckle before they were tested. This also avoided a confounding of the effects of age and starvation which would have arisen had suckling been prevented. As a general rule, therefore, the lamb was allowed unrestricted access to the dam's udder from the time of birth until about 20 minutes before its test began. The exception was an experiment in which half the lambs were tested within an hour of birth and before they had suckled (Chapter VI).

Control of Environmental Conditions for Testing Lambs

1. Construction of climate chambers

The lambs were tested in 2 climate chambers, the dimensions of which are shown in Figure 1 and Figure 2. Each chamber was constructed of 4 mm hardboard on a steel frame and its floor and ceiling were lined with 25 mm expanded polystyrene.

Oxygen consumption was measured in a ventilated hood in an open-circuit system similar to that described by Holmes (1971). The hood, of sealed hardboard construction, was mounted in the front of the climate chamber and was fitted with a clear perspex window which allowed the lamb's head to be observed from outside the chamber. A plastic collar fitted into the hood was fastened around the lamb's neck to seal the hood during the test period.

Air was drawn into the hood through a 25 mm diameter polyvinyl-chloride (PVC) pipe in the lower front corner of the hood. The pipe was connected to a two-litre "Air Intake Chamber" which buffered the system against movement of expired air out of the hood and which drew

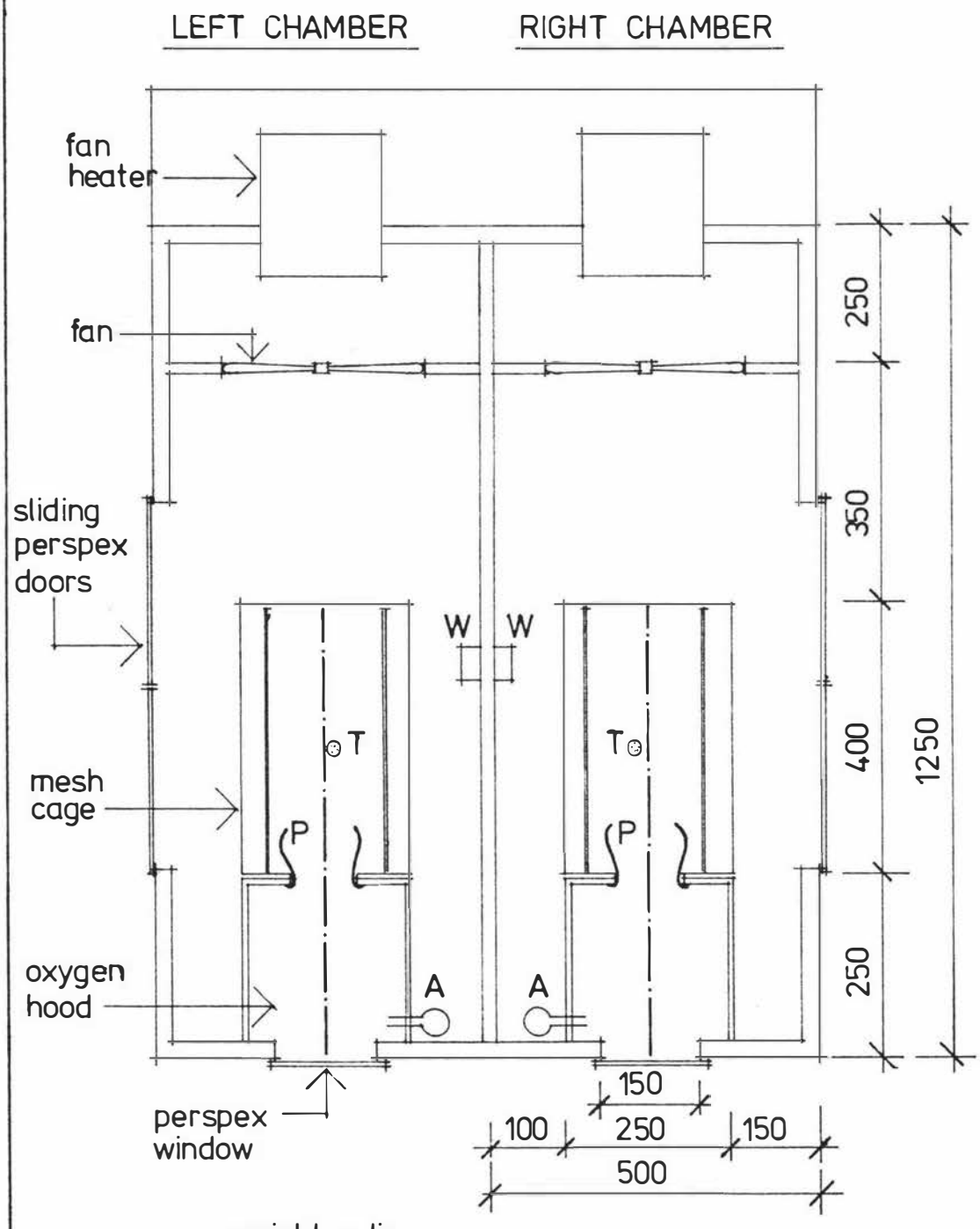

FIGURE 1: PLAN VIEW OF CLIMATE CHAMBERS

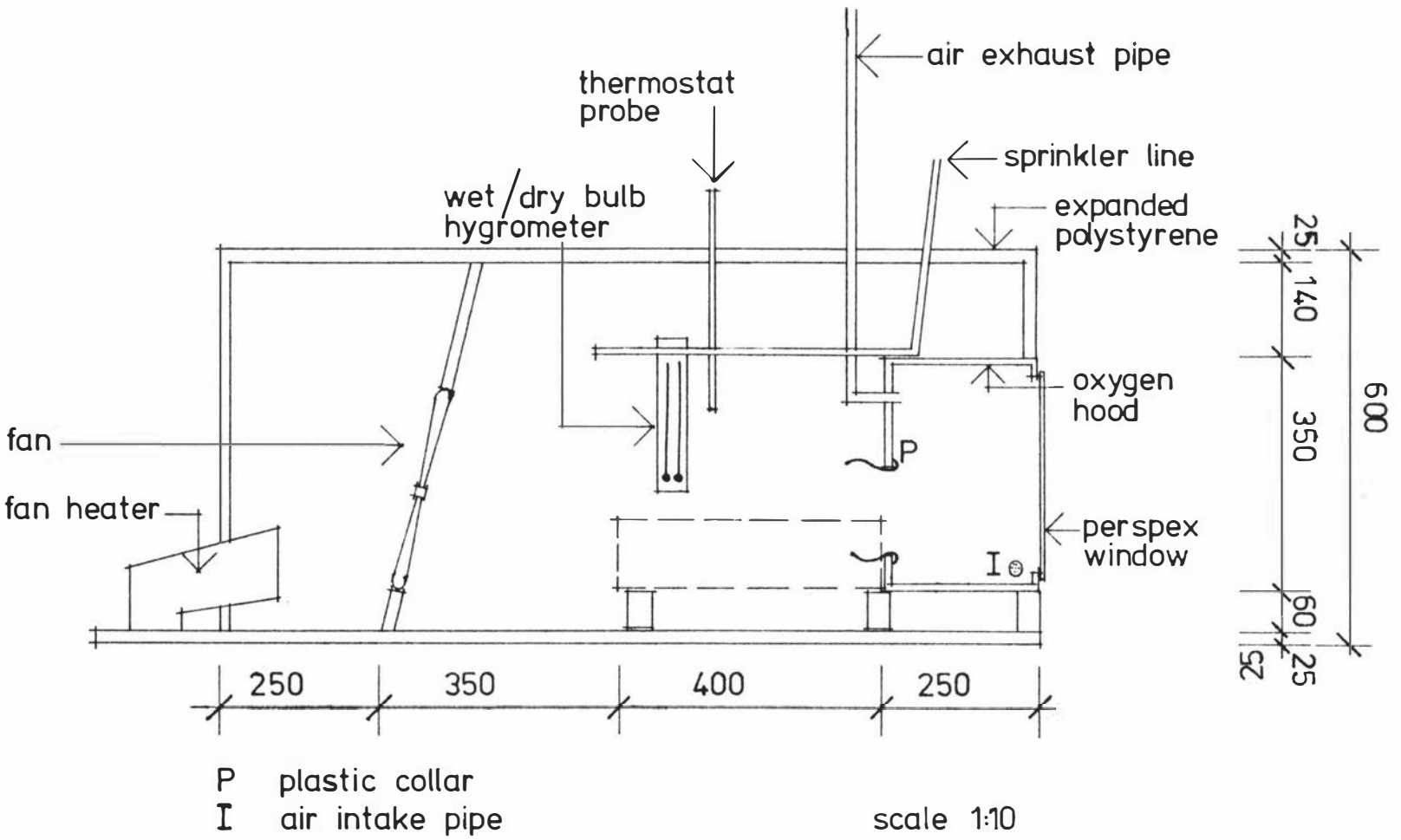

FIGURE 2: SIDE ELEVATION OF LEFT CLIMATE CHAMBER

air from within the climate chamber. Air was drawn out of the hood through a 25 mm diameter "Air Exhaust Pipe" to the gas meters and oxygen analyser (see "Measurements : Heat production").

The lamb was held within the climate chamber in a cage constructed of 30 mm steel mesh with a 20 mm mesh floor. Both the cage and hood were raised 6 cm from the chamber floor to allow air to circulate beneath the lamb. Two steel bars placed longtitudinally in the cage supported the lamb in a normal sitting position; it was then prevented from standing or turning by 2 additional bars passing through the mesh and across its back.

Two sliding perspex doors, each measuring 30 cm wide by 35 cm high, were built into the side of each chamber. These allowed observation of the lamb, adjustment of equipment, and recording of readings on the Mason's wet/dry bulb hygrometer (fixed to the inside wall of the chamber) with minimum interference to temperature control.

2. Control of chamber air temperatures

The climate chambers were located in an insulated room, the air temperature of which was maintained at 2°C by mechanical refrigeration. Air temperatures within each chamber were controlled over the range 5°C to 30°C by a two-kilowatt commercial fan heater ("Tang-ray", H.E. Shacklock Ltd., Dunedin) mounted at the rear of the chamber and connected to an electronic thermostat (Model DE-7973, Design Electronics Ltd., Palmerston North). The thermostat sensor was located directly over the lamb, 25 cm behind the oxygen hood and 25 cm above the floor of the cage.

Nominal air temperatures used in the experiments ranged from

5.0°C to 30.0°C in increments of 5.0°C. The relationship between nominal and actual air temperatures is discussed in a subsequent section (see "Precision of environmental control").

3. Control of chamber airspeeds

Variable airspeeds were provided by a 315 mm diameter electric fan (General Electric Company (N.Z.) Ltd., Wellington) located towards the rear of each climate chamber and connected to a variable fan-speed controller (Model DE-5001, Design Electronics Ltd., Palmerston North). Each fan was mounted on a steel frame at an angle of 75° to the chamber floor (Figure 2). Nominal airspeeds used in the experiments were 0.0, 1.0, 1.5 and 2.0 m sec^{-1}. Actual airspeeds are discussed in the later section "Precision of environmental control".

4. Wetting of the lambs

Lambs which were to be tested while wet were immersed in a bath of warm water (approximately 20°C) and water was rubbed well into the coat. They were then allowed to stand in a warm room for 5 minutes (until excess water had drained from the coat) before being placed in the climate chambers.

During the test procedure, wetness was maintained by an overhead sprinkler line placed directly above the lamb. A series of 20 G (0.9 mm external diameter) hypodermic needles inserted into this line at 6 cm spacing allowed water to drip continuously on to the lamb at a rate of approximately 5 ℓ hr^{-1}. This was subjectively judged to be sufficient to keep the lamb's coat saturated with water. Excess water drained through holes in the chamber floor.

Water flowed to the overhead line from a heading tank (mounted 2 m above the floor of the climate chamber) through 6 m of 6 mm (internal diameter) plastic tubing coiled in a water bath. The temperature of the water bath was thermostatically controlled so that water dripping on to the lamb was at approximately the same temperature as air in the climate chamber. Water temperature could not be adjusted as rapidly as could air temperature but was generally within 2 to 3^{o}C of nominal air temperature when the lamb's heat production was measured.

No attempt was made to control the degree of wetness of the lamb, individuals being tested either "wet" (saturated) or "dry" (to the touch). When necessary, young lambs, whose coats were still wet with amniotic fluids, were dried in a stream of warm air prior to being tested.

5. Precision of environmental control

The precision with which the climate chamber environment could be controlled was examined by measuring chamber air temperature, relative humidity and airspeed for various combinations of nominal temperature and nominal airspeed settings of the respective control equipment. The effect of chamber "wetness" (i.e. whether or not the equipment for wetting the lambs was in use) was also included as a factor in this study, the purpose of which was to determine;

(i) the "true" or measured values of temperature and airspeed at each of the respective nominal settings of the control equipment.

(ii) the existence of any interactions between the control mechanisms.

(iii) the extent to which the relative humidity of air in the chambers was influenced by airspeed, temperature and wetness. This information was required because relative humidity of the air could not be controlled but was likely to be related to evaporative heat loss from the lamb's body.

(iv) any between-chamber differences in air temperature, relative humidity or airspeed.

(a) Control of air temperature

The control of air temperature was studied in an experiment of four-way cross-classified design with interaction (see "Methods of Analysis"). The 4 main effects studied, and their respective levels, are shown in Table 1. All main effects were treated as fixed (since all the levels of these main effects which would be of interest in subsequent experiments were included in the model). There were 4 replicates per cell, a total of 384 observations.

Air temperature was measured to 0.5^{o}C with a mercury thermometer (G.H. Zeal Ltd., London, England) placed alongside the thermostat sensor and supported so that the mercury bulb was 6 cm above the floor of the lamb cage. The accuracy of the thermometer was checked against 2 other thermometers of the same type by simultaneous immersion in water of various temperatures.

The analysis of variance presented in Table 1 shows that the effects of temperature setting and airspeed setting were both highly significant, while the interaction between them was also significant ($P < .05$). Differences between the chambers and between the levels

TABLE 1: EFFECT OF TEMPERATURE SETTING, AIRSPEED SETTING, WETNESS AND CHAMBERS ON MEASURED CHAMBER AIR TEMPERATURE

Classification	Measured Air Temperature (°C) Mean ± S.E.			
	Nominal airspeed (m sec^{-1})			
Nominal temperature (°C)	0.0	1.0	1.5	2.0
5.0	5.34 ± 0.19 (16)	5.59 ± 0.16 (16)	4.94 ± 0.18 (16)	5.28 ± 0.12 (16)
10.0	10.06 ± 0.27 (16)	9.38 ± 0.23 (16)	10.00 ± 0.23 (16)	9.78 ± 0.22 (16)
15.0	14.44 ± 0.23 (16)	14.66 ± 0.23 (16)	14.06 ± 0.17 (16)	14.19 ± 0.26 (16)
20.0	19.59 ± 0.35 (16)	19.75 ± 0.28 (16)	18.91 ± 0.22 (16)	19.19 ± 0.22 (16)
25.0	24.38 ± 0.36 (16)	24.69 ± 0.22 (16)	24.47 ± 0.26 (16)	24.72 ± 0.29 (16)
30.0	30.66 ± 0.31 (16)	30.47 ± 0.26 (16)	29.25 ± 0.19 (16)	29.31 ± 0.25 (16)

Classification	Measured Air Temperature (°C) Mean ± S.E.	
Nominal temperature (°C)		
5.0	5.29 ± 0.09	(64)
10.0	9.80 ± 0.12	(64)
15.0	14.34 ± 0.11	(64)
20.0	19.36 ± 0.14	(64)
25.0	24.56 ± 0.14	(64)
30.0	29.92 ± 0.14	(64)
Nominal airspeed (m sec^{-1})		
0.0	17.41 ± 0.88	(96)
1.0	17.42 ± 0.88	(96)
1.5	16.94 ± 0.86	(96)
2.0	17.08 ± 0.86	(96)
Wetness		
Dry	17.12 ± 0.62	(192)
Wet	17.30 ± 0.61	(192)
Climate chamber		
Left	17.27 ± 0.61	(192)
Right	17.16 ± 0.61	(192)

...../continued

TABLE 1, continued

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Temperature setting (Temp.)	5	5446.12	5557.27 ***
Airspeed setting (Asp.)	3	5.67	5.79 ***
Wetness	1	3.28	3.35 †
Chambers	1	1.20	1.22 NS
Temp. x Asp.	15	1.97	2.01 *
Temp. x Wetness	5	0.86	0.88 NS
Temp. x Chambers	5	0.87	0.89 NS
Asp. x Wetness	3	0.52	0.53 NS
Asp. x Chambers	3	0.53	0.54 NS
Wetness x Chambers	1	0.55	0.56 NS
Temp. x Asp. x Wetness	15	0.93	0.95 NS
Temp. x Asp. x Chambers	15	0.74	0.76 NS
Temp. x Wetness x Chambers	5	0.23	0.23 NS
Asp. x Wetness x Chambers	3	1.24	1.27 NS
Error	303	0.98	

Quadratic Components

Source of Control	% Control of Variation in Measured Air Temperature
Temperature setting (Temp.)	98.76
Airspeed setting (Asp.)	0.06
Wetness	0.01
Chambers	0.00
Temp. x Asp. Interaction	0.07
Error	1.10
	100.00

of wetness were not significant.

The significant effect of airspeed was associated with a tendency for measured air temperature to decrease as nominal airspeed increased, particularly at the highest nominal temperature. It seems likely that this was due to greater amounts of cold air being drawn into the climate chambers at the higher airspeeds, which may have limited the ability of the temperature control equipment to maintain the higher air temperatures. However, this effect was not consistent across the airspeeds and part of the temperature x airspeed interaction may have been due to different patterns of air movement within the chambers at each airspeed.

Although the airspeed effect and its interaction with temperature setting were significant, an analysis of quadratic components (Table 1) shows that they contributed little to the total variation in measured air temperature. Nevertheless, within each temperature setting the mean measured air temperature varied with airspeed setting by up to $1.4^{o}C$. As a consequence, any comparison of airspeeds includes not only a direct effect of air movement on heat loss from the lamb's body but also a small effect on the rectal temperature - air temperature gradient experienced by the lamb. This effect was not, however, considered to be of major importance. In most of the experiments comparisons were made only at the 2 lowest nominal air temperatures where the mean measured air temperature varied with airspeed by only 0.4 to $0.7^{o}C$ (or 1 to 2% of the expected rectal temperature - air temperature gradient).

(b) Control of airspeed

The control of airspeed was examined in an experiment of two-way

cross-classified design with airspeed setting and chambers as main effects (both treated as fixed effects). There were 5 replicates per cell, a total of 40 observations.

Airspeeds were measured to 0.1 m sec^{-1} with a low-torque cup anemometer ("Rimco", Rauchfuss Instruments and Staff Pty. Ltd., Victoria, Australia). This was placed 20 cm behind the oxygen hoods with the centre of the anemometer cups 6 cm above the floor of the cage. Measurements were made over successive five-minute intervals.

The analysis of variance (Table 2) shows a highly significant effect of airspeed setting. This main effect controlled more than 98% of the variation in measured airspeed (see "Quadratic Components", Table 2) but measured airspeeds were lower than the corresponding nominal values. All other effects were non-significant.

The cup anemometer has a poor sensitivity to very low airspeeds and so an additional method of estimating the rate of air movement at 0.0 m sec^{-1} nominal airspeed was required. Using a standard unsilvered Kata thermometer (C.F. Casella and Co. Ltd., London) the mean rate of air movement in "still air" conditions was estimated to be 0.010 ± 0.001 m sec^{-1} from 10 observations in each chamber.

The degree to which air movement in climate chambers of this type approximates the corresponding situation in the field is, of course, questionable. In the field situation air movement could be expected to more closely approach a laminar flow, although turbulence would be induced by such factors as the roughness of the pasture cover. For the purposes of the present study, however, it was necessary to test the lambs in relatively small climate chambers in

TABLE 2: EFFECT OF AIRSPEED SETTING AND CHAMBERS ON MEASURED CHAMBER AIRSPEED

Classification	Measured Airspeed ($m\ sec^{-1}$) Mean ± S.E.	
Nominal airspeed ($m\ sec^{-1}$)		
0.0	0.00 ± 0.00	(10)
1.0	0.93 ± 0.02	(10)
1.5	1.41 ± 0.02	(10)
2.0	1.91 ± 0.02	(10)
Climate chamber		
Left	1.08 ± 0.16	(20)
Right	1.04 ± 0.16	(20)

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Airspeed setting (Asp.)	3	6.60	1100.33 ***
Chambers	1	0.01	2.00 NS
Asp. x Chambers	3	0.00	0.50 NS
Error	32	0.01	

Quadratic Components

Source of Control	% Control of Variation in Measured Airspeed
Airspeed setting	98.66
Chambers	0.45
Error	0.89
	100.00

which ambient temperature could be altered rapidly. The turbulent air flow patterns which would have been produced in the chambers were therefore an unavoidable consequence of this requirement, and results from the studies of the effects of air movement are likely to have only limited application in the field.

(c) Factors affecting the relative humidity of air in the chambers

Control of the relative humidity (RH) of air in the climate chambers was not possible with the available equipment. It was therefore important to determine the extent to which RH was affected by other components of the chamber environment.

The study involved a four-way cross-classified design model with the same main effects (and levels of these effects) as in the "Control of air temperature" experiment. Again all main effects were treated as fixed and there were 4 replicates per cell, a total of 384 observations.

Relative humidity was calculated to 1% from temperature readings (to $0.5^{o}C$) on the Mason's wet/dry bulb hygrometers (G.H. Zeal Ltd., London, England) using hygrometric tables provided by the manufacturer. Before the experiment commenced, the hygrometers were mounted together in one chamber and exposed to air of varying RH to ensure that their readings were in agreement with one another.

The data were fitted in all models as decimals and were not transformed to normality. Transformation was considered unnecessary because the data, although in percentage form, appeared to approximate a normal distribution. This assumption was confirmed by comparing

the F-ratios from analyses of variance on the non-transformed and transformed (by Arcsin transformation) data (see "Methods of Analysis").

The analysis of variance (Table 3) shows that all the main effects were significant, although 2 of these (temperature setting and wetness) controlled over 75% of the variation in measured RH. Three of the first-order interactions were also significant.

The analysis of variance must be interpreted with care because of the possibility that some of the main effects influenced not only the true RH of air in the chambers but also the estimates provided by the hygrometers of the humidity. This is particularly important when studying the effects of airspeed. Penman (1958) stated "It is a fact of experience that wet-bulb temperature does depend on ventilation rate, the 'wet-bulb depression' ..... being least in calm air and increasing to a steady upper limit as ventilation rate increases". In order to overcome this problem, standard tables provided for the conversion of wet- and dry-bulb thermometer readings to RH are based on the assumption that the rate of air movement over the hygrometer will be in the range 1.0 to 1.5 m sec^{-1}. The tables used in the present study were of this type (Honnor, pers. comm.). Since these tables overestimate RH if used for temperatures measured in still air, and underestimate RH if the hygrometers are strongly ventilated, the tendency for measured RH to decline as airspeed increased (Table 3) may have been a consequence of measurement errors rather than of a true change in humidity of the air. This would suggest that the best estimates of RH at each nominal temperature are likely to have been those obtained at the intermediate airspeeds. If an effect of

TABLE 3: EFFECT OF TEMPERATURE SETTING, AIRSPEED SETTING, WETNESS AND CHAMBERS ON MEASURED RELATIVE HUMIDITY OF AIR IN THE CHAMBERS (Relative humidity means and their standard errors are expressed as decimals)

Classification	Measured Relative Humidity - Mean ± S.E.					
	Nominal airspeed ($m\ sec^{-1}$)				Wetness	
Nominal temperature (^oC)	0.0	1.0	1.5	2.0	Dry	Wet
5.0	0.768± 0.050 (16)	0.671± 0.034 (16)	0.710± 0.028 (16)	0.742± 0.036 (16)	0.628± 0.024 (32)	0.818± 0.018 (32)
10.0	0.683± 0.034 (16)	0.601± 0.025 (16)	0.560± 0.029 (16)	0.533± 0.025 (16)	0.514± 0.016 (32)	0.674± 0.018 (32)
15.0	0.592± 0.027 (16)	0.447± 0.028 (16)	0.429± 0.026 (16)	0.422± 0.023 (16)	0.392± 0.016 (32)	0.553± 0.017 (32)
20.0	0.506± 0.022 (16)	0.370± 0.023 (16)	0.341± 0.024 (16)	0.330± 0.021 (16)	0.321± 0.015 (32)	0.453± 0.017 (32)
25.0	0.423± 0.019 (16)	0.313± 0.021 (16)	0.296± 0.023 (16)	0.291± 0.024 (16)	0.269± 0.014 (32)	0.392± 0.014 (32)
30.0	0.334± 0.017 (16)	0.273± 0.020 (16)	0.273± 0.026 (16)	0.238± 0.017 (16)	0.244± 0.016 (32)	0.315± 0.012 (32)
Climate chambers						
Left	0.550± 0.030 (48)	0.480± 0.026 (48)	0.470± 0.027 (48)	0.453± 0.028 (48)		
Right	0.552± 0.025 (48)	0.411± 0.025 (48)	0.399± 0.027 (48)	0.399± 0.029 (48)		

...../continued

TABLE 3, continued

Classification	Measured Relative Humidity - Mean ± S.E.	
Nominal temperature (^{o}C)		
5.0	0.723 ± 0.019	(64)
10.0	0.594 ± 0.016	(64)
15.0	0.472 ± 0.016	(64)
20.0	0.387 ± 0.014	(64)
25.0	0.331 ± 0.013	(64)
30.0	0.279 ± 0.011	(64)
Nominal airspeed (m sec^{-1})		
0.0	0.551 ± 0.019	(96)
1.0	0.446 ± 0.018	(96)
1.5	0.435 ± 0.019	(96)
2.0	0.426 ± 0.020	(96)
Wetness		
Dry	0.395 ± 0.012	(192)
Wet	0.534 ± 0.014	(192)
Climate chamber		
Left	0.488 ± 0.014	(192)
Right	0.440 ± 0.014	(192)

...../continued

TABLE 3, continued

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Temperature setting (Temp.)	5	1.814	342.17 ***
Airspeed setting (Asp.)	3	0.327	61.70 ***
Wetness	1	1.869	352.64 ***
Chambers	1	0.226	42.58 ***
Temp. x Asp.	15	0.013	2.51 **
Temp. x Wetness	5	0.027	5.15 ***
Temp. x Chambers	5	0.002	0.38 NS
Asp. x Wetness	3	0.010	1.94 NS
Asp. x Chambers	3	0.028	5.38 **
Wetness x Chambers	1	0.020	3.83 †
Temp. x Asp. x Wetness	15	0.004	0.83 NS
Temp. x Asp. x Chambers	15	0.005	0.91 NS
Temp. x Wetness x Chambers	5	0.002	0.38 NS
Asp. x Wetness x Chambers	3	0.001	0.23 NS
Error	303	0.005	

Quadratic Components

Source of Control	% Control of Variation in Measured R.H.
Temperature setting (Temp.)	57.3
Airspeed setting (Asp.)	6.8
Wetness	19.7
Chambers	2.3
Temp. x Asp. Interaction	1.0
Temp. x Wetness Interaction	1.4
Asp. x Chambers Interaction	1.0
Error	10.6
	100.1

airspeed on true RH did exist, it would presumably have occurred through a tendency for the fans to draw increasing amounts of comparatively dry air into the chambers as airspeed increased.

The significant between-chamber differences in measured RH may also be related to the airspeed effect. As is shown in Table 3 the hygrometers produced essentially the same estimate of mean relative humidity (pooled over temperature and wetness) when in still air. However, when the fans were in operation the right chamber hygrometer produced consistently low estimates of mean RH which suggests that its wet bulb was more exposed to air movement than that of the left chamber hygrometer. A possible explanation for this difference may be found in the climate chamber construction. The hygrometers were provided with the wet bulb fixed to the right of the dry bulb. Thus when they were mounted on the chamber walls (Figure 1), the wet bulb of the right chamber hygrometer may have been more exposed to air movement (from the fans) than that of the left chamber hygrometer (which may have been partially sheltered by the dry bulb). Alternatively the difference could have been due to differing patterns of air movement within the chambers. However this effect was not important in subsequent experiments since lambs were randomly assigned to chambers across all treatments.

The temperature and wetness effects are considered to have been true effects on relative humidity. Use of the sprinkler system resulted in the formation of a pool of water on the floor of the chambers, evaporation from which would have increased the moisture content of the air. Conversely the temperature effect would have occurred primarily as a result of the decreased water-holding

capacity of cold air.

An examination of the temperature x wetness cell means in Table 3 shows that this interaction occurred because, as air temperature fell, RH in wet conditions increased at a faster rate than in dry conditions. Thus although the total rate of evaporation from the free water pool was expected to be reduced at low air temperatures, it constituted a greater RH difference ("wet" less "dry") because the amount of water required to saturate the air declines exponentially with air temperature.

The temperature x airspeed cell means (Table 3) suggest that at zero airspeed, RH was consistently overestimated by the hygrometers and that this effect was most pronounced at the intermediate nominal temperatures. One of the effects of poor ventilation is that the cool damp air immediately surrounding the wet bulb is incompletely replaced by the relatively warm dry air in the environment at large so that the wet bulb depression is reduced and RH is overestimated (Penman, 1958). It is therefore reasonable to expect that at low ambient temperatures, when air in the chambers was near saturation level, the effect of incomplete replacement would have been minimized compared with that at higher temperatures when the "replacement air" had a relatively lower humidity. However this does not explain why the difference between the estimates of RH in still and moving air was also relatively small at the highest ambient temperature. Clearly some other mechanism was operating at this end of the temperature scale.

Although a complete explanation of these interactions is not possible, it should be noted that they contributed, in total, to less than 5% of the variation in measured RH. As such they are relatively unimportant effects compared with the control of variation in RH exerted by temperature setting and wetness. Moreover, since most of the interactions, and probably also the airspeed effect, appear to have involved an effect on the measurement of RH rather than on the true relative humidity of air in the chambers, they would not be reflected in the environment actually experienced by the lamb. Consequently the main effects "nominal air temperature" and "wetness" would probably have controlled much more than 75% of the variation in true (as opposed to measured) relative humidity of the air in the climate chambers.

Measurements : In Newborn Lambs

1. Heat production

The lamb's heat production was calculated from measurements of its oxygen consumption made in a ventilated hood in an open-circuit system. Air was drawn into the hood from within the climate chambers at a rate of 15 to 20 $\ell\ min^{-1}$ which ensured that the oxygen content of the exhaust air did not fall below 19%. The exhaust air was cooled to $5^{o}C$ and then rewarmed to $23^{o}C$ before passing through dry gas meters. Total gas flow rates were calculated separately for each lamb test and volumes were corrected to Standard Temperature and Pressure (STP) of dry gas. The oxygen concentration of small dried samples of the ingoing and exhaust air was measured by a paramagnetic analyser (Model OA 137, Servomex and Company, England) with a range of 19 to 21% oxygen concentration. The output of the

analyser was connected to a potentiometric chart recorder (Electronik 194, Honeywell, England) and the oxygen concentration in the exhaust gases was read from the recorder chart when the lamb's oxygen consumption was considered to have been stable for a period of at least 5 minutes. Stability of oxygen consumption was determined by continuous observation of the recorder chart. Upon exposure of the lamb to cold, its oxygen consumption showed an initially rapid increase but eventually reached a plateau and did not change by more than ±5% (a deviation of 2 to 6 mm on the recorder chart) over long periods of time. Once this steady-state situation had been reached, the lamb's oxygen consumption was considered to have stabilized. The stable rate of oxygen consumption was then calculated as the product of the ventilation rate (corrected to STP) and the difference in percentage oxygen concentration between the ingoing and exhaust air samples. The oxygen analyser and chart recorder were calibrated daily against gases of known oxygen concentration.

A variety of formulae are available for the calculation of heat production from oxygen consumption and other metabolic chemical exchanges. The most commonly used is that of Brouwer (1965), here expressed in kilojoules by Webster (1974);

$$H = 16.170\ (O_2) + 5.021\ (CO_2) - 2.167\ (CH_4) - 5.987\ (N)$$

where H = heat production (in kilojoules)

(O_2) = litres of oxygen consumed

(CO_2) = litres of carbon dioxide produced

(CH_4) = litres of methane produced

(N) = grams of urinary nitrogen excreted.

Webster states that the methane term is applicable only to

ruminants and that the nitrogen correction can be applied only when measurements are continued for at least 24 hours. Thus in short-term tests (up to 3 hours) on newborn lambs (which are metabolically non-ruminant), Brouwer's equation may be reduced to the terms in oxygen and carbon dioxide. The error from neglecting the methane and urinary nitrogen corrections is reportedly less than ±2% (Webster, 1974).

A simple equation for calculating heat production from oxygen consumption alone has been given by McLean (1972). As expressed in kilojoules by Webster this equation is of the form:

$$H = 20.46\ (O_2)$$

McLean calculated that the estimates of heat production provided by this equation are unlikely to differ from those provided by the full Brouwer equation by more than ±2% when heat production is measured in an open-circuit calorimeter, "except under severely abnormal feeding conditions".

In order to determine which of the formulae should be used in subsequent trial work, and hence whether measurements of carbon dioxide production would be required, a preliminary trial was undertaken to compare the estimates of heat production provided by the formula of McLean and that of Brouwer (reduced to terms in O_2 and CO_2). Five newborn lambs were each exposed to 4 sets of environmental conditions, a total of 20 observations. Gas flow rates and oxygen concentrations were measured over a ten-minute period as previously described. The carbon dioxide concentration of the ingoing and exhaust air was measured by an infra-red gas analyser

TABLE 4: TEST OF DIFFERENCES BETWEEN THE ESTIMATES OF HEAT PRODUCTION PROVIDED BY THE FORMULA OF McLEAN (1972) AND THE REDUCED FORMULA OF BROUWER (1965)

Formula	Number of estimates	Estimated Heat Production (kJ) Mean ± S.E.
McLean (1972) $H = 20.46\ (O_2)$	20	26.55 ± 1.61
(Reduced) Brouwer (1965) $H = 16.170\ (O_2) + 5.021\ (CO_2)$	20	26.50 ± 1.61

Paired t-test: $t_{19} = 0.40$, NS

$s_{\bar{d}} = 0.11$

(Model SB2, Grubb Parsons, England) calibrated daily against gases of known carbon dioxide concentration.

An analysis, by the paired t-test, of the estimates of heat production provided by each formula showed that they were not significantly different (Table 4). In no case did the difference between the estimates exceed 4% of the Brouwer estimate and the decision was made to use McLean's formula in all subsequent calculations of heat production. Routine measurement of carbon dioxide production was therefore not required since respiratory quotients were not of interest in this study. The rate of heat production, calculated by McLean's formula, was expressed in Watts per kilogram of bodyweight ($W\ kg^{-1}$).

2. Rectal and skin temperatures

(a) Rectal temperature

In the initial experiments rectal temperatures were measured to $0.5^{o}C$ with copper-constantan thermocouples (wire diameter 0.3 mm) encased in 4 mm (external diameter) plastic tubing. These were inserted 5 cm into the rectum of the lamb and held in place by flexible straps attached to the cage.

One thermojunction of each thermocouple was fixed in a constant reference junction (Associated Electrical Industries Ltd., England), the temperature of which was maintained at $40^{o}C$. The thermocouples were connected through a motorized Rotary Selector Switch (Type SP2, Croydon Precision Instrument Company, England) to a potentiometric chart recorder (Model SP-G3, Riken Denshi Co. Ltd., Japan) giving readings on each thermocouple for 20 seconds at two-minute intervals.

The thermocouples were calibrated at regular intervals by immersion in water of varying temperatures in the range 10 to 40°C. Water temperatures were measured to 0.5°C with mercury thermometers (G.H. Zeal Ltd., England).

In later experiments, where greater accuracy was required, rectal temperatures were measured to 0.1°C with prismatic-type clinical thermometers ("Phoenix", Japan) inserted 6 cm into the rectum for a period of 1 minute. When not in use the thermometers were stored in a dilute antiseptic solution. Before the trials, all thermometers to be used were simultaneously immersed in water of varying temperatures to ensure that they gave consistent readings.

(b) Skin temperature

Hind-lamb skin temperature was measured to 0.5°C with copper-constantan thermocouples (wire diameter 0.3 mm) encased in a single layer of thin plastic adhesive tape. An area on the outside of the hind leg, 4 cm long by 2 cm wide and 3 cm above the hoof, was clipped free of wool. The thermocouple was fixed in place with a 3 cm-wide, 1.3 mm-thick, vinyl strap fastened around the leg. One thermojunction of each thermocouple was fixed in the same reference junction as for the rectal temperature thermocouples and they were connected in the same manner to the potentiometric chart recorder. Calibration of the thermocouples was similarly by immersion in water of various temperatures.

An important constraint in the skin temperature studies was that, because a large number of lambs was to be tested, it was not possible to allow sufficient time in each test for skin temperature to equilibrate with environmental temperature. Preliminary studies

showed that when lambs were exposed to a cold environment, skin temperature declined rapidly at first but then more slowly as it approached environmental temperature. This presumably occurred because heat was lost from the limb across the skin temperature-ambient temperature gradient, which declined with skin temperature. Considerable periods of time were therefore required for skin temperature to equilibrate completely with environmental temperature. As a compromise, skin temperature was measured once heat production had stabilized, at a time when it was approaching, but had not quite attained, equilibrium with the environment.

A danger inherent in this approach was that if treatments affected the period of time required for lambs to attain stable heat production, they might exert a confounding effect on skin temperature (through an effect on the period available for skin temperature to equilibrate). For this reason skin temperature was measured, not as soon as heat production stabilized, but rather at (as far as possible) a fixed time interval after the lamb was exposed to the cold environment. As a safeguard this time interval was recorded for each lamb and preliminary analyses were conducted to determine whether this was influenced to any degree by treatments which significantly affected skin temperature. No such relationships were found in any of the experiments.

Some of the sources of error associated with the measurement of skin temperature have been discussed by Molnar and Rosenbaum (1963). In particular, they noted that the tendency for thermocouples to under-estimate true skin temperature increases with air velocity and with the temperature gradient between the skin and the external

air. This effect is due to an increasing transfer of heat away from the thermocouple as both airspeed and the temperature gradient increase. It seems likely that wetting the lamb would have a similar effect, due to heat loss (from the thermocouple area) associated with the evaporation of water lying on the vinyl strap, although this effect would probably be small. While some evidence exists that the use of a vinyl strap to secure the thermocouple in place would have reduced the magnitude of these errors compared with those associated with an exposed thermocouple (Molnar and Rosenbaum, 1963), it was not possible to actually measure the size of these errors experimentally. Thus, when comparing the skin temperatures of lambs exposed to different environments, it must be remembered that environmental conditions, and the method of measurement, may have produced errors in measured skin temperature.

3. Characteristics of the birthcoat

(a) Depth of birthcoat

The depth of the birthcoat (defined as the distance from the skin surface to the outer margin of the coat) was considered likely to be a major determinant of its insulative value. A preliminary study of the variation in birthcoat depth between- and within-coat types was therefore made to determine the positions at which the depth should be measured in subsequent experiments.

Six tanned Romney lamb skins, 2 each of hairiness grades III, V and VII (Dry, 1955), were used in the study. These grades are based primarily on the distribution and density of long medullated "halo hairs" across the back of the lamb; the lower the density of halo hairs, the lower is the hairiness grade. Unfortunately the

age of the lambs at the time of death was not known precisely but it was reasonable to assume that they were less than 2 weeks old, based on the size and appearance of the skins, and the information that Dry, who had originally graded these skins, generally did so when the lambs were only a few days old (Dry, 1955). However, the possibility of some error due to changes in birthcoat structure with age could not be entirely discounted.

Birthcoat depth was measured to 1 mm with a pair of modified dial calipers (Mitutoyo Co., Japan) at 10 standard positions on each skin. The positions were initially chosen at random on one skin, identified relative to their site in the whole lamb, and the corresponding positions marked on the other skins thus:

Position code	Site (Figure 3)
A	Base of the tail over the spine
B	Over the spine, in line with the hipbones (tuber coxae)
C	Over the spine, posterior to the shoulder blades (scapulae)
D	Over hipbone
E	On the neck, below and behind the ear
F	On the rump, in line with midside positions (G, H)
G	Midside, over the last rib
H	Midside, over the sixth rib
I	Hind leg, immediately above the "knee" joint
J	Above and behind the axilla of the front leg.

Depth measurements were made both when the coat was dry and after it had been thoroughly wetted with tap water. There were

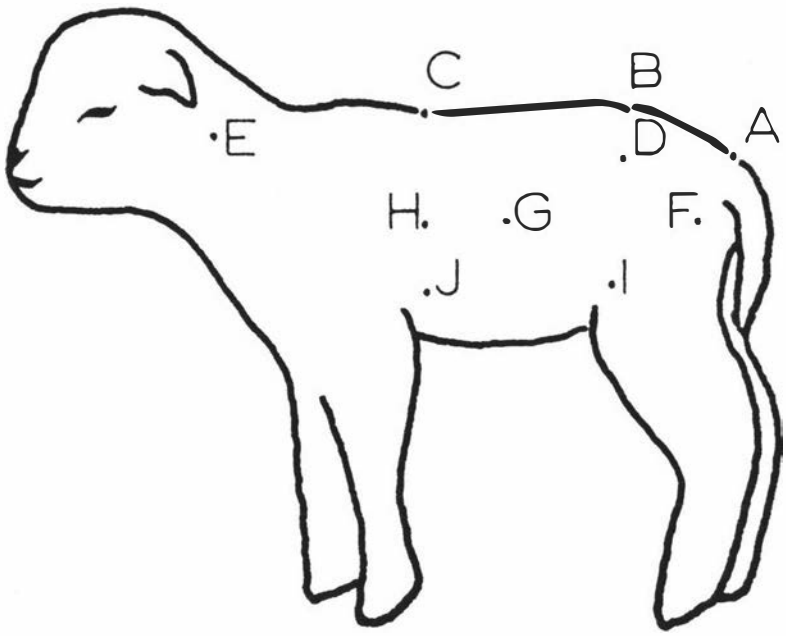

FIGURE 3: POSITIONS OF MEASUREMENT IN PRELIMINARY ANALYSIS OF BIRTHCOAT DEPTH

4 replicates per cell, a total of 480 observations.

The analysis of variance is presented in Table 5. Main effects "grade" and "wetness" were treated as being fixed while "position" and "skin within grade" were considered to be random effects.

The significant effect of birthcoat grade was to be expected since the classification of lambs into grades is based primarily on the distribution and density of long halo hairs in the birthcoat. Thus as the birthcoat grade (and therefore the density of halo hairs) increased, there was a corresponding increase in the depth of the coat. However the grades are broad classifications only and there was considerable variation in birthcoat depth between lambs (skins) within each grade.

The grade x position cell means (Table 5) show that, as birthcoat grade increased, there was a sequential increase in depth which, in general terms, occurred first at the positions along the back (positions A to F) and then at those on the side (G to J). This relationship. which corresponds with the pattern of halo hair development described by Dry (1955), accounts for the significant grade x position interaction. Across all grades the tendency for the "back" positions to have a greater depth than those on the side persisted, although differences between the positions were not significant. It should be noted, however, that differences between the positions would have been significant (at the 5% level) had "position" been treated as a fixed effect.

Wetting of the skins resulted in a significant reduction in their mean birthcoat depth but there was considerable variation in the

TABLE 5: EFFECT OF BIRTHCOAT GRADE, SKINS WITHIN GRADE, POSITION AND WETNESS ON BIRTHCOAT DEPTH

(Four observations contribute to each wetness x position x skin within grade cell mean. For other means the number of observations is shown in parentheses)

Classification	Birthcoat Depth (mm) Mean ± S.E.											
Grade:	Grade III				Grade V				Grade VII			
Skin[a]:	Skin 1		Skin 2		Skin 1		Skin 2		Skin 1		Skin 2	
Wetness:	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
Position:												
A	12.3	11.5	11.5	9.0	20.5	15.8	16.0	14.5	29.5	21.0	23.3	16.0
	±0.3	±0.9	±0.3	±0.6	±0.7	±0.6	±0.7	±0.3	±0.7	±2.0	±0.8	±1.5
B	12.0	11.0	11.5	10.0	18.5	15.0	18.0	15.0	28.0	22.3	19.3	17.0
	±0.4	±0.4	±0.3	±0.0	±1.2	±0.4	±0.4	±0.0	±0.7	±0.9	±0.5	±1.5
C	10.3	12.3	11.5	8.8	13.3	14.8	15.3	12.8	30.0	24.3	19.3	18.3
	±0.3	±0.9	±0.3	±0.5	±0.6	±0.3	±0.6	±0.6	±0.6	±0.8	±0.3	±1.4
D	12.5	11.3	12.0	8.8	15.3	14.3	13.0	12.0	27.0	23.8	21.5	17.0
	±0.5	±0.5	±0.0	±0.3	±0.3	±0.3	±0.9	±0.4	±0.7	±0.3	±0.3	±1.4
E	14.0	12.3	11.5	8.0	15.8	13.8	14.3	14.3	34.5	20.0	21.8	16.8
	±0.4	±0.8	±0.3	±0.4	±0.5	±1.1	±0.3	±0.9	±1.2	±0.4	±0.3	±1.2
F	11.0	9.3	12.0	8.5	16.0	16.0	16.0	14.8	30.0	19.0	21.5	17.5
	±0.7	±0.8	±0.4	±0.3	±0.0	±0.4	±1.1	±0.6	±0.4	±0.4	±0.7	±1.3
G	11.5	10.0	11.5	7.5	14.0	13.0	12.8	12.0	28.0	25.0	21.0	15.8
	±0.3	±0.4	±0.3	±0.3	±1.1	±0.4	±0.6	±0.4	±1.1	±1.5	±0.7	±0.6
H	12.8	10.3	11.0	7.3	10.3	11.8	11.8	10.8	36.0	21.3	24.0	18.3
	±0.6	±0.5	±0.0	±0.5	±0.8	±0.5	±0.6	±0.3	±1.7	±1.8	±0.7	±1.3
I	13.8	9.8	11.3	7.3	11.5	9.0	12.8	10.8	30.8	24.0	22.8	15.5
	±0.5	±0.9	±0.5	±0.3	±1.0	±1.1	±0.5	±0.3	±0.9	±1.3	±1.2	±0.7
J	12.5	10.0	12.3	6.5	9.5	9.0	13.0	10.3	24.5	19.3	22.3	18.8
	±0.5	±0.7	±0.3	±0.3	±0.3	±1.4	±1.2	±0.9	±0.7	±1.1	±0.5	±0.8

[a] Skin within grade

...../continued

TABLE 5, continued

Classification		Birthcoat Depth (mm) Mean ± S.E.		
		Wetness		
Grade	Skin within grade	Dry	Wet	Dry and Wet
Grade III	Skin 1	12.3 ± 0.2 (40)	10.8 ± 0.2 (40)	11.5 ± 0.2 (80)
	Skin 2	11.6 ± 0.1 (40)	8.2 ± 0.2 (40)	9.9 ± 0.2 (80)
Grade V	Skin 1	14.5 ± 0.6 (40)	13.2 ± 0.4 (40)	13.8 ± 0.4 (80)
	Skin 2	14.3 ± 0.4 (40)	12.7 ± 0.3 (40)	13.5 ± 0.3 (80)
Grade VII	Skin 1	29.8 ± 0.6 (40)	22.0 ± 0.5 (40)	25.9 ± 0.6 (80)
	Skin 2	21.7 ± 0.3 (40)	17.1 ± 0.4 (40)	19.4 ± 0.3 (80)
All Grades and Skins		17.4 ± 0.4 (240)	14.0 ± 0.3 (240)	

	Birthcoat grade			
Position	Grade III	Grade V	Grade VII	All Grades
A	11.1 ± 0.4 (16)	16.7 ± 0.6 (16)	22.4 ± 1.4 (16)	16.7 ± 0.9 (48)
B	11.1 ± 0.2 (16)	16.6 ± 0.5 (16)	21.6 ± 1.1 (16)	16.5 ± 0.8 (48)
C	10.8 ± 0.4 (16)	14.0 ± 0.4 (16)	22.9 ± 1.3 (16)	15.9 ± 0.9 (48)
D	11.1 ± 0.4 (16)	13.6 ± 0.4 (16)	22.3 ± 1.0 (16)	15.7 ± 0.8 (48)
E	11.4 ± 0.6 (16)	14.5 ± 0.4 (16)	23.3 ± 1.8 (16)	16.4 ± 1.0 (48)
F	10.2 ± 0.4 (16)	15.7 ± 0.3 (16)	22.0 ± 1.3 (16)	16.0 ± 0.8 (48)
G	10.1 ± 0.4 (16)	12.9 ± 0.4 (16)	22.4 ± 1.3 (16)	15.2 ± 0.9 (48)
H	10.3 ± 0.6 (16)	11.1 ± 0.3 (16)	24.9 ± 1.9 (16)	15.4 ± 1.2 (48)
I	10.5 ± 0.7 (16)	11.0 ± 0.5 (16)	23.3 ± 1.5 (16)	14.9 ± 1.0 (48)
J	10.3 ± 0.7 (16)	10.4 ± 0.6 (16)	21.2 ± 0.7 (16)	14.0 ± 0.8 (48)
All positions	10.7 ± 0.2 (160)	13.7 ± 0.2 (160)	22.6 ± 0.4 (160)	

...../continued

TABLE 5, continued

Analysis of Variance

Source of Variation	d.f.	Mean Square	F	
Grade	2	6175.19	9.61[a]	*
Position	9	32.79	0.93[b]	NS
Wetness	1	1363.50	22.57[c]	**
Skin within Grade (Skin: Grade)	3	607.79	10.45[d]	*
Grade x Position	18	35.91	1.91[e]	*
Grade x Wetness	2	254.35	4.34[f]	†
Position x Wetness	9	12.58	1.03	NS
Grade x Position x Wetness	18	12.20	1.53	NS
Position x Skin: Grade	27	10.76	1.35	NS
Wetness x Skin: Grade	3	48.19	6.03	**
Position x Wetness x Skin: Grade	27	8.00	3.47	***
Error	360	2.31		

Note: F - ratios and degrees of freedom by method of Satterthwaite (1946);

a. F = 6185.95/643.70 = 9.61; d.f. = 2.0, 3.4

b. F = 44.99/48.49 = 0.93; d.f. = 15.8, 26.4

c. F = 1371.50/60.77 = 22.57; d.f. = 1.0, 4.7

d. F = 615.78/58.96 = 10.45; d.f. = 3.1, 4.5

e. F = 43.91/22.96 = 1.91; d.f. = 26.1, 42.0

f. F = 262.35/60.39 = 4.34; d.f. = 2.1, 4.7

Quadratic Components

Source of Control	% Control of Variation in Birthcoat Depth	
Birthcoat Grade	60.68	
Position	0.00	(-0.11%)
Wetness	9.61	
Skins within Grade (Skin: Grade)	12.27	
Grade x Position Interaction	3.05	
Grade x Wetness Interaction	4.52	
Wetness x Skin: Grade Interaction	1.75	
Wetness x Position x Skin: Grade Interaction	1.96	
Error	6.15	
	99.99	

response to wetting among the various grades, skins and positions. However, these interactions contributed little to the total variation in coat depth ("Quadratic Components", Table 5), over 80% of the variation being associated with the effects of coat grade, wetness and skins within grades. Moreover a good degree of repeatability in measurements at a particular site is indicated by the high ($r = 0.94$) intra-class correlation of the repeated estimates.

The criteria for choosing the sites at which birthcoat depth would be measured in subsequent experiments were that;

(i) over all birthcoats (lamb skins), measured depth (wet and dry) at the chosen position in each coat should be highly correlated with the corresponding mean birthcoat depth, and

(ii) the position should be easily located in the live lamb.

The correlations between measured depth and mean depth of the coat at each position are presented in Table 6. For only 3 positions (C, D, G) was the correlation greater than 0.90 although all correlations were highly significant ($P < .001$). Position C was discarded because it was considered likely that location of this site, and measurement of birthcoat depth at it, would present some difficulties to an operator working alone with a restrained lamb. Thus, in subsequent experiments, birthcoat depth was measured to 1 mm over the hipbone and on the midside over the last rib. However, in view of the non-significance of the differences between positions, and the negligible contribution of "position" to variation in birthcoat depth (Table 5), it is likely that little accuracy would have been lost had any of the other positions been chosen.

TABLE 6: CORRELATIONS BETWEEN MEASURED BIRTHCOAT DEPTH AND MEAN SKIN BIRTHCOAT DEPTH AT EACH OF TEN POSITIONS ON THE SKIN

Position Code and Site	Correlation Between Measured Depth and Mean Birthcoat Depth [a]
A. (Base of the tail over the spine)	0.82 ***
B. (Over spine, in line with hipbones)	0.88 ***
C. (Over spine, posterior to shoulder blades)	0.95 ***
D. (Over hipbone) [b]	0.94 ***
E. (On the neck, below and behind ear)	0.84 ***
F. (On the rump, in line with positions G, H)	0.85 ***
G. (Midside, over the last rib) [b]	0.94 ***
H. (Midside, over the sixth rib)	0.87 ***
I. (Hind leg, immediately above "knee" joint)	0.90 ***
J. (Above and behind axilla of front leg)	0.85 ***

[a] Correlation of measured birthcoat depth at a given position with overall mean depth of the birthcoat (skin); calculated over all grades, skins within grades, levels of wetness and replicates; 48 observations per correlation.

[b] Positions which were finally chosen.

In the live lamb it was found that the measurement of birthcoat depth was complicated by movement of the lamb, particularly by respiratory movements at the midside position. To compensate for this a small area of skin was close-clipped alongside each measuring position to help ensure that the calipers were placed firmly on the skin surface but did not press into the skin.

(b) Wool weight per unit area of skin

The weight of wool per unit area of skin was measured by clipping the wool from a measured area of skin on the midside, immediately anterior to the last rib. Because insufficient lamb skins were available for a detailed analysis of variation in this trait (as was performed for birthcoat depth), the site of measurement was chosen on the basis that it was easy to locate and was adjacent to one site at which coat depth was to be measured. It is also a site commonly used for fleece-sampling in mature sheep.

The area of skin clipped was a standard 4 cm wide and its length (generally 4 to 5 cm) was measured to 0.1 cm with the modified dial calipers after the skin had been stretched just sufficiently to remove any wrinkles. The wool was clipped to 1 mm of the skin surface.

The midside wool samples were stored in numbered screw-capped bottles and, at the completion of the trial, were allowed to come to equilibrium with a controlled environment of 68% relative humidity (i.e. regained) over a period of 3 days. They were then weighed to 10 mg and the weights expressed as mg (greasy) wool per cm^2 skin surface.

(c) Total weight of the birthcoat

The total weight of the birthcoat was measured in a few lambs by clipping the coat to 1 mm of the skin surface. The wool was stored in numbered nylon gauze bags and regained at 68% relative humidity for 3 days before being weighed to 0.1 g. Birthcoat weight was then expressed as g (greasy) birthcoat wool per kg pre-clipping bodyweight.

(d) Weight of birthcoat on the limbs

The weight of the birthcoat on the limbs was measured by clipping the wool, again to 1 mm of the skin, from one each of the fore- and hind-limbs. On the fore-limbs, the wool was clipped below the level of the olecranon process while on the hind-limbs it was clipped to the level of the femuro-tibial junction. After clipping, the wool was stored in numbered nylon gauze bags and regained at 68% RH for 3 days before being weighed to 0.1 g. The weight of regained wool was then doubled before being expressed as g limb wool per kg pre-clipping bodyweight.

4. Lamb age and weight

A brief discussion of the measurement of the lamb's weight and the calculation of its age is warranted because of the potential errors involved. For lambs born between 7 a.m. and midnight, age at test could be calculated with confidence to within 15 minutes. However, if the lamb had been born during the night (and this applied to about 40% of the lambs) its time of birth could be estimated only to the nearest hour, and an error of the same magnitude was inherent in the calculation of age at test.

Because maximum accuracy in the estimation of age was desirable, particularly for lambs tested in the first few hours of life, the age calculation was performed as if the time of birth was known exactly (i.e. age was "calculated" to the nearest 0.25 hours) for all lambs. It should therefore be noted that the true error was somewhat larger for a proportion of the lambs and that the size of this error was confounded with the time of birth.

Prior to each test the lamb was weighed to 0.02 kg on a set of pan scales (Salter, Model 236). No allowance was made for errors in the measurement of weight due to gut-fill or moisture content of the birthcoat. In lambs which were permitted to suckle before being tested every effort was made to ensure that successful suckling was established, so that errors in weight were due only to the amount of milk ingested. It is therefore likely that these errors were age-dependent.

Alexander (1956) estimated that, in Merino lambs whose total (wet) birthweights were 3 to 4 kg, drying of the birthcoat resulted in an average weight reduction of 260 g (or 6 to 9% of total birthweight). In the present study no account was taken of this error, although lambs which were to be tested when wet were generally weighed before they were wetted with tap water. Thus, while the birthcoats of the Romney and Drysdale-cross lambs used in this study may have had a greater water-holding capacity than those of Alexander's Merinos, measured bodyweights were unlikely to have overestimated dry bodyweights by more than 10%.

Measurements : In Older Lambs and Hoggets

1. Face cover grade

In some experiments lambs surviving to 3 months of age were face-graded at this age with a view to retrospectively studying the relationship between face grade and resistance to cold-stress. The grading system was based on the distribution of visible wool growth on the face and around the eyes, and was similar to the system described by Cockrem and Rae (1966).

Initially each lamb was assigned to one of 4 grades (1, 1+, 2, 2+) where lower grades denote an increasing area of wool growth on the face. However it was not possible to fit all these grades in the statistical models being used to describe the experiments and so the grades were subsequently combined into two groups thus;

Group	Grades
Woolly faced	1, 1+
Open faced	2, 2+

2. Characteristics of the hogget fleece

In an attempt to relate characteristics of the birthcoat to those of the hogget fleece, lambs from one experiment which survived to 12 months of age were shorn and a number of their fleece characteristics were measured. The characteristics of interest and their method of measurement were as follows:

(a) Greasy fleeceweight

Greasy fleeceweight was measured by weighing the fleece to 0.01 kg immediately off the shears and prior to skirting of the fleece.

(b) Staple length and crimp frequency

The length of a staple drawn from the midside wool sample was measured to 0.5 cm. The number of crimps in this staple was then counted and the crimp frequency expressed as number of crimps per cm of staple length.

(c) Mean fibre diameter

The mean fibre diameter of the wool was estimated using the air-flow technique (Ross, 1958) on replicated samples of 2g of clean scoured wool from the midside sample. Fibre diameter was measured to 0.1 microns.

(d) Standard deviation of fibre diameter and proportion of medullated fibres

The diameter of 150 fibres from the scoured and regained midside wool sample was measured by the projection microscope technique. Snippets from the fibres were mounted on a glass slide in paraffin oil and the number of medullated fibres was counted at the same time. The standard deviation of fibre diameter in the sample was calculated from the 150 measured diameters, and the number of medullated fibres expressed as a proportion of the total counted.

(e) Colour

The colour of the scoured midside sample was assessed by assigning to it a subjective colour grade (range 1 to 9) where a high grade denotes good colour.

3. Post-shearing hogget bodyweight

Immediately after hogget shearing the ewe and ram hoggets were weighed to 0.5 kg.

General Experimental Procedure

Each lamb was separated from its dam 10 to 20 minutes before it was to be tested, and its age and weight were recorded. The lamb was then placed on its side in a specially designed restraining crate which held it firmly but allowed the operator free access to the midside and hip areas. The midside wool sample was removed, the lower hind limb clipped (in preparation for fixing the skin thermocouple) and birthcoat depth measured over the midside and hipbone areas. Where lambs were to be tested wet, they were immersed in warm water and then allowed to stand for 5 minutes before birthcoat depths were measured.

Measurements of hind-limb skin temperature, midside wool weight and coat depth were always made on the side of the lamb which would be presented to an observer standing outside the climate chamber (i.e. on the right side of the lamb if it was to be tested in the left chamber). The restraining crate was therefore reversible so that either side of the lamb could be presented to the operator.

Once clipping and birthcoat measurements had been completed, the lamb was given a subcutaneous injection (neck region) of 10 mg per kg bodyweight oxytetracycline (Terramycin Q-100, Pfizer Laboratories Ltd., Auckland) and its umbilical stump was sprayed with iodine wound disinfectant (Salsbury Laboratories, Christchurch). These were precautionary measures against respiratory diseases and navel-ill respectively. The lamb was then carried to the refrigerated room where it was placed in the climate chamber, the temperature of which had previously been set at the required level. The plastic collar

of the oxygen hood was fastened around the lamb's neck, the skin and (where required) rectal thermocouples fixed in place, and the lamb restrained by the 2 steel bars. The fans and water line were switched on where appropriate and testing began.

Once testing had been completed the lamb was removed from the chamber. If its rectal temperature had declined, it was re-warmed under an infra-red lamp or fan heater before being returned to its dam.

Methods of Analysis

1. Computer packages

Analysis of the data was carried out on the Massey University Burrough's B6700 computer using 2 statistical packages. Most of the analysis, including the analysis of variance, covariance, deviance (discrete data) and regression analysis was performed using the "GLIM" (General Linear Interactive Modelling) package (Nelder, 1975) which utilizes the linear model approach described by Nelder and Wedderburn (1972). A second package (Statistical Package for the Social Sciences or "SPSS") was used for simple correlation analysis and for the calculation of treatment means and standard errors in balanced models.

2. Analysis of continuous data

(a) Calculation of sums of squares

The sums of squares attributable to each effect were calculated as the reduction in the GLIM sums of squares (deviance) associated with removing the effect from the fully fitted model, subject to

the requirements of marginality in the GLIM package (Nelder, 1975). If any main effect or interaction in a model is a subset of another term, it is said to be marginal to that term (i.e. main effects A, B are marginal to the A x B interaction). In GLIM, terms may not be deleted from a model containing effects to which they are marginal. Thus in the analysis of variance for a three-way cross-classified model with interaction, the appropriate reductions are as follows:

Main effect	Appropriate reduction for effect sums of squares
A	R (A/μ, B, C)
B	R (B/μ, A, C)
C	R (C/μ, A, B)
Interaction	
A x B (A.B)	R (A.B/μ, A, B, C, A.C, B.C)
A x C (A.C)	R (A.C/μ, A, B, C, A.B, B.C)
B x C (B.C)	R (B.C/μ, A, B, C, A.B, A.C)
A x B x C (A.B.C)	R (A.B.C/μ, A, B, C, A.B, A.C, B.C)

where R (W/μ, X, Y, Z) denotes the reduction from eliminating the W effect from a model containing terms in W, X, Y and Z, together with the general mean (μ).

(b) Analysis of variance

(i) Models fitted

Most of the models fitted were for cross-classified (factorial) designs with interaction. These models may be generally described as follows:

$$y_{ijkl} = \mu + a_i + b_j + c_k + ab_{ij} + ac_{ik} + bc_{jk} + abc_{ijk} + e_{ijkl}$$

where, μ = the general mean

a_i = the effect of the i^{th} level of treatment a (and similarly for b_j, c_k)

ab_{ij} = the effect of the interaction between the i^{th} level of treatment a and the j^{th} level of treatment b (similarly for ac_{ik}, bc_{jk})

abc_{ijk} = the effect of the interaction between the i^{th} level of treatment a, the j^{th} level of treatment b and the k^{th} level of treatment c

e_{ijkl} = random error term peculiar to the y_{ijkl} observation.

The second type of model fitted in the analysis of variance was the nested model which may be described thus:

$$y_{ijkl} = \mu + a_i + b_j + c_{jk} + ab_{ij} + ac_{ijk} + e_{ijkl}$$

where, μ and e_{ijkl} are as described above

a_i = the effect of the i^{th} level of treatment a (similarly for b_j)

c_{jk} = the effect of the k^{th} level of treatment c nested within the j^{th} level of treatment b

ab_{ij} = the effect of the interaction between the i^{th} level of treatment a and the j^{th} level of treatment b

ac_{ijk} = the effect of the interaction between the i^{th} level of treatment a and the k^{th} level of treatment c nested within the j^{th} level of treatment b.

These equations describe, in general, all models which were fitted

in the analysis of variance. The particular main effects fitted in each model are described in the table presenting the analysis of variance pertinent to that model.

(ii) Models in which all main effects and interactions are fixed

For the models containing only fixed effects, testing procedures were as described by Snedecor and Cochran (1967) with all treatment and interaction mean squares being tested against the error term.

(iii) Mixed models

A number of the models which were used included fixed and random effects, and simple testing procedures did not exist for some of the terms in these models. In the case of mixed models which were balanced, the method of Satterthwaite (1946) was employed for testing those terms for which no denominator mean square was directly available. In this method, linear combinations of two or more mean squares are used to produce an approximate denominator mean square which has the correct expectation for the effect being tested. The expectation of each mean square was derived by the method of Henderson (1969).

In unbalanced designs, the problem was further complicated by the fact that the sums of squares, and hence the mean squares, attributable to the effects were not unique. The testing procedure for these designs was therefore as follows. All second order interactions (the highest order interactions fitted) were tested against the error term as for the balanced case. First-order interactions were tested against the mean squares of significant second-order interactions to which they were marginal, or against the error term if no such second-order

interactions existed. Similarly, main effects were tested against significant interactions to which they were marginal, or against the error mean square.

(iv) Single degree of freedom comparisons

In most of the experiments described in this study only two-level main effects were employed. An important exception was the experiment involving 4 levels of airspeed (still air and 3 rates of air movement) described in Chapter IV. In the analysis of this experiment it became apparent that much of the difference between the airspeeds was due to differences between "still air" and "moving air" rather than between the 3 higher airspeeds. This hypothesis was tested by single degree of freedom comparisons as described by Steel and Torrie (1960).

(v) Presentation of the data

For balanced models, treatment and interaction cell means (and their standard errors) were calculated using the SPSS computer package. In the case of unbalanced designs, the corresponding means and their standard errors were calculated by the method of fitting constants (Yates, 1934). Cell means are presented only for those interactions which were significant ($P<.05$) and, unless otherwise stated, the number of observations contributing to each mean is indicated (in parentheses) in the body of the table.

In most of the analyses, tests for the significance of differences between the component means of significant interactions were made using the Least Significant Difference or "LSD" (Snedecor and Cochran, 1967). This test was not, however, applied to all possible comparisons of cell means, the comparisons being made

as follows. For the component means of an interaction denoted by $A_i\ B_j$ (where i = 1...m, j = 1...n), comparisons tested by the LSD were:

A_1B_j vs A_2B_j vs A_3B_j...A_mB_j for all i within each j

A_iB_1 vs A_iB_2 vs A_iB_3...A_iB_n for all j within each i

Since in most experiments only two-level main effects were employed (i.e. m = n = 2) the usual comparisons were A_1B_1 vs A_1B_2, A_2B_1 vs A_2B_2, A_1B_1 vs A_2B_1 and A_1B_2 vs A_2B_2 (but not A_1B_1 vs A_2B_2 or A_2B_1 vs A_1B_2). A similar procedure was adopted for second-order interactions. Within these constraints, cell means which are presented in the following tables and which do not have common superscripts are significantly different ($P<.05$) by the LSD test.

The least significant difference was not applied to the significant interactions in the preliminary experiments concerned with the sources of variation in climate chamber environmental conditions and in birthcoat depth (this chapter). In these experiments, all of which were balanced designs, the control of variation in the independent variable by the main effects and interaction terms was of primary importance. Hence quadratic components were calculated to indicate the contribution of these effects to total variation in coat depth or components of the chamber environment. The calculations involved equating the mean squares for these effects to their expectations as derived by the method of Henderson (1969). It was assumed that the model was based on all the main effects in the analysis of variance, but only those interactions which were significant

($P<.05$). Non-significant interactions were included in the error term.

(c) Regression analysis

Where appropriate, overall regression coefficients (calculated across all main effects) were derived using the GLIM package and have been presented as the regression coefficient together with its standard error (i.e. $b \pm s_b$). The hypothesis that the regression coefficient had zero slope was tested using the two-tailed t-test ($t_{n-2} = b/s_b$, where n observations contribute to the regression). The absolute value of t is presented in each case, together with the level of significance.

A special case in the analysis of regression involved the relationship between the lamb's heat production and its bodyweight. Since heat production was expressed on a per unit bodyweight basis, simple regression was not appropriate because the errors in the dependent and independent variables would have been correlated. In this case, therefore, the regression was calculated on a double-logarithm basis relating the lamb's total heat production (a variable measured directly and from which heat production per unit bodyweight was calculated) to an exponent of bodyweight. Thus:

$$THP = \alpha\, WT^{\beta}$$

$$\log_e THP = \log_e \alpha + \beta \log_e WT$$

where THP = total heat production (in Watts)

WT = bodyweight (in kilograms)

e = the base of natural logarithms

α,β = the regression intercept and coefficient respectively.

The double-logarithm regression then proceeds as previously

described with the null hypothesis being $H_o : \beta = 0$.

(d) Analysis of covariance

(i) Model fitted

The model for the analysis of covariance may be generally described as follows:

$$y_{ijkl} = \mu + a_i + b_j + c_k + ab_{ij} + ac_{ik} + bc_{jk} + abc_{ijk} + \beta(X_{ijkl} - \bar{X}) + e_{ijkl}$$

where, β = the regression coefficient of Y on X

X_{ijkl} = the observed value of the covariate

$\bar{X}$ = the population mean value of the covariate

and where all other terms in the model are as described previously for the analysis of variance.

(ii) Hypotheses tested

The analysis of covariance was fitted according to the method of Searle (1971) with two hypotheses being tested (for an example of the presentation of the analysis of covariance, refer to Table 11). The F-ratio for the term "Pooled within-class" regression tests the hypothesis that this regression coefficient has zero slope, while the F-ratio for the "Difference" term tests whether the particular intra-class regression coefficients have equal slope. In both respects the terminology used is identical to that of Searle (1971).

For each analysis of covariance model studied, all possible intra-class regressions were fitted and the hypothesis of equality of the regression coefficients was tested in each case. However these analyses have generally been presented only where heterogeneity of the intra-class regression coefficients was detected. In certain other cases, where all the intra-class regression

coefficients were homogeneous, but where it was desirable to indicate the significance of the pooled within-class regression coefficient, the analyses presented incorporate the intra-class regressions for which the "Difference" mean square was greatest. When heterogeneity of the intra-class regression coefficients was apparent, the hypothesis of zero slope in each regression coefficient was examined using the t-test as described previously.

(e) Correlation analysis

Simple correlation coefficients were calculated using the SPSS computer programme and are presented as the value of the correlation (r) together with the test of zero correlation in the population. Where appropriate, intra-class correlations were calculated as described by Snedecor and Cochran (1967).

3. Analysis of discrete data

The analysis of discrete data (which primarily involved the proportion of lambs attaining summit metabolism) was accomplished using the GLIM logit transformation (Nelder, 1975). This transformation has the advantage that it provides valid tests of significance where the data are distributed in a binomial manner, including situations in which the treatment proportions approach the limits of the binomial range (i.e. 0% or 100% success). Chi square-distributed deviances were calculated from the reductions in the GLIM deviances as described for the analysis of variance. These are presented in the appropriate analysis of deviance tables.

Logit-transformed means and their standard errors were again calculated by the method of fitting constants (Yates, 1934) subject

to the assumption of unitary variance in the logit transformation. From these means the re-transformed percentage "successes" were calculated by the formula:

$$P = \frac{e^{Y}}{1 + e^{Y}} \qquad \text{(Nelder, 1975)}$$

where, P = probability of "success" (expressed as %)

Y = logit-transformed class mean

e = base of natural logarithms

The relationship between the proportion of lambs attaining summit metabolism and other characteristics of the lamb was examined by regression analysis on the logit scale. Only the overall regressions were fitted and the results are presented in terms of the regression coefficient and intercept on the transformed scale. Since the regression equation is of the form $Y = a + bX$ it follows from the above that the proportion of lambs expected to attain summit metabolism at a given value (X) of the independent variate may be calculated as:

$$P = \frac{e^{a + bX}}{1 + e^{a + bX}} = \frac{e^{bX}}{e^{-a} + e^{bX}}$$

4. Miscellaneous variables

(a) Relative humidity

Relative humidity data were calculated as decimals from the temperature readings on the Mason's wet/dry bulb hygrometers. The data were not, however, subjected to any transformation prior to analysis since an examination of the data suggested that they were approximately normally distributed. This was confirmed by comparing the F-ratios from analysis on the non-transformed and Arcsin-trans-

formed (Snedecor and Cochran, 1967) data. Transformation exerted little effect on the F-ratios and no effect on the conclusions drawn from the analyses of variance.

(b) Thermal circulation index

The thermal circulation index was calculated as:

$$TCI = \frac{T_S - T_A}{T_R - T_S}$$ (Burton and Edholm, 1955)

where T_A = ambient temperature

T_R = rectal temperature

T_S = hind-limb skin temperature

Since the thermal circulation index was used only as a guide to the interpretation of skin temperature changes, no analysis was performed on these data and the TCI values are presented as arithmetic means and standard errors for the appropriate treatment groups.

(c) Standard deviation of fibre diameter

The standard deviation of fibre diameter in the hogget wool samples was treated as being a normally-distributed random variable.

(d) Proportion of medullated fibres

The proportion (%) of medullated fibres in the hogget wool was analysed in the same manner as relative humidity. Transformation of the data (by Arcsin) did not influence the conclusions drawn from the analyses. Consequently the analyses presented are based on the un-transformed data.

(e) Hogget wool colour

The colour of the scoured midside wool samples was subjectively assessed on a scale of 1 to 9. This grading system was devised in

such a way that the colour grades from a population of sheep are expected to be approximately normally distributed (Wickham, pers. comm.). The colour grade was therefore treated as a random normal variable and was not transformed prior to analysis.

5. Levels of statistical significance

Throughout the text, the following symbols have been used to indicate various levels of significance:

Level of significance	Symbol
$P < .001$	***
$.001 < P < .01$	**
$.01 < P < .05$	*
$.05 < P < .10$	†
$.10 < P$	NS.

C H A P T E R I I I

SUMMIT METABOLISM IN YOUNG ROMNEY LAMBS

CHAPTER III

SUMMIT METABOLISM IN YOUNG ROMNEY LAMBS

Introduction

For reasons which have previously been discussed, the metabolic rate of the lamb was considered to be the most appropriate index of cold-stress for use in this study. However, the use of this index imposes constraints on the environments in which lambs may be tested, and in particular requires that the lambs should not attain summit metabolism (so that heat production remains a useful indicator of heat loss). Although summit metabolic rates have been measured in lambs of a number of breeds in Australia (Alexander, 1962b; Alexander and Bell, 1975a) no such measurements have been undertaken with New Zealand Romney lambs.

This chapter describes an introductory study in which the summit metabolism of young Romney lambs was estimated, both for the purpose of comparison with estimates obtained from other breeds and as an aid to the selection of appropriate environmental conditions for testing lambs in subsequent experiments. The effects of bodyweight and age on summit metabolism were also examined.

Experimental Design and Methods

Sixteen straightbred Romney lambs (8 of each sex) were selected at random from a larger group for the determination of summit metabolism. All had suckled prior to being tested and in most cases their birthcoats had been partially or completely removed by clipping to facilitate heat loss. Many had been exposed to mildly cold

conditions during the previous three-hour period but, when the determination of summit metabolism commenced, all had rectal temperatures in excess of 38.5°C.

The lambs were tested while wet at an air temperature of 2°C (the lowest air temperature that could be achieved with the temperature control equipment). Measurement of heat production and of rectal temperature (by thermocouple) commenced as soon as the lamb was settled in the climate chamber. The airspeed was then gradually increased until the lamb's rectal temperature began to fall by 0.5 to 1.5°C over intervals of approximately 20 minutes. Heat production initially increased with airspeed but eventually stabilized prior to the onset of hypothermia and showed little change thereafter. Summit metabolism was measured as the mean rate of heat production (per kg bodyweight) during the 15 to 20 minute period immediately after stability of metabolic rate was achieved.

Results and Discussion

1. Level of summit metabolism

The mean (± S.E.) summit metabolism of the 16 Romney lambs was 18.03 ± 0.63 Watts per kilogram of bodyweight. This estimate is 1.5 to 4.0 W kg^{-1} lower than those derived in a similar manner from lambs of a number of breeds in Australia (Alexander, 1962b; Alexander and Bell, 1975a). Within all the breeds, however, there exists a considerable variation in ability to produce body heat. Among the Romney lambs, summit metabolism ranged from 11.95 to 21.85 W kg^{-1}, a degree of variation which might be expected to have a considerable impact upon survival in the field. It may also

vindicate the use of metabolic rate, rather than rate of decline in deep body temperature, as the index of cold-stress when studying individual lambs. Among the 5 breeds and crosses examined by Alexander and Bell (1975a), summit metabolism ranged from 14.0 to 30.2 W kg^{-1}.

Although summit metabolism was not measured in any unfed newborn Romney lambs, Alexander (1962b) has reported that the estimates of summit metabolism obtained from unfed lambs less than 6 hours old differed little from estimates obtained when the same lambs were 18 to 28 hours old and had suckled. It therefore seems likely that the summit metabolic rates of unfed newborn Romney lambs would be similar to those of the older fed lambs studied here.

2. Effect of age

The overall regression coefficient of summit metabolism on age at test was b = 0.01 ± 0.09 W kg^{-1} hr^{-1} which was not significantly different from zero (t_{14} = 0.12, NS.). Thus over the range of ages studied (6 to 36 hours) summit metabolism was independent of age, a result which is consistent with Alexander's (1962b) data from lambs less than 2 days old. However, in the longer term, summit metabolism may tend to decline with advancing age (Alexander, Bell and Williams, 1970).

3. Effect of bodyweight

The relationship between summit metabolism and bodyweight was examined by regression analysis on a double logarithm scale as described in Chapter II (see "Methods of Analysis"). Thus:

$$\log_e THP = \log_e \alpha + \beta \log_e WT$$

where THP = total heat production (in Watts)

= summit metabolic rate (W kg^{-1}) x bodyweight (kg)

and where all other terms are as previously defined.

The overall regression coefficient of $\log_e$ THP on $\log_e$ WT was $b = 0.91 \pm 0.21$ which was highly significant ($t_{14} = 4.42$, $P<.001$). Thus "Total Heat Production" was proportional to bodyweight raised to the power 0.91 which suggests that summit metabolism (per kg bodyweight) declined slightly with increasing weight. However, the exponent was not significantly different from a value of unity so that, over the range of bodyweights studied (3.3 to 7.2 kg), these results are generally compatible with the hypothesis of Alexander (1962b) that summit metabolism (per unit bodyweight) is independent of the lamb's weight.

Chapter Summary

Summit metabolic rate was measured in 16 suckled New Zealand Romney lambs which were 6 to 36 hours old. Mean summit metabolism was 18.03 ± 0.63 Watts per kilogram of bodyweight which is 1.5 to 4.0 W kg^{-1} lower than the estimates derived from a number of breeds in Australia. Even within a small sample of Romney lambs there was a considerable variation in capacity for body heat production. The results are generally in agreement with Alexander's (1962b) assertion that summit metabolism per unit bodyweight is independent of the age or weight of the lamb over the range of ages and weights studied.

CHAPTER IV

RESPONSES OF ROMNEY AND DRYSDALE-ROMNEY CROSS LAMBS TO COMPONENTS OF THE THERMAL ENVIRONMENT

CHAPTER IV

RESPONSES OF ROMNEY AND DRYSDALE-ROMNEY CROSS LAMBS TO COMPONENTS OF THE THERMAL ENVIRONMENT

Introduction

When the newborn lamb is subjected to a cold environment it responds by increasing its metabolic rate to compensate for the loss of body heat to that environment. The rate of heat loss, and hence the metabolic response, is a function of the lamb's body insulation and of the cooling power of the environment. Although some information is available about the degree to which components of the thermal environment (such as rainfall, wind speed and ambient temperature) affect its cooling power (Alexander, 1961, 1962a), those studies were based mainly on lambs of the Merino breed. The results may therefore not be applicable to Romney lambs which have different birthcoat characteristics. As a consequence, the environmental conditions in which Romney lambs will become hypothermic are not well defined.

In this experiment lambs were exposed to a range of environmental conditions in order to measure their responses (in terms of heat production, rectal temperature and hind-limb skin temperature) to different components of the thermal environment. "Cooling curves" were produced to estimate the combined effects of air movement, wetting and ambient temperature on the lamb's metabolic response. A comparison of these curves with the estimates of summit metabolism derived in the previous chapter then identified the environmental conditions in which the lambs were likely to attain summit metabolic rates and become hypothermic. Finally, relationships between the

metabolic response and other characteristics of the lamb were examined at the lowest ambient temperature.

Experimental Design and Methods

The experiment involved 66 newborn lambs, 30 of which were exposed to a cold environment on 2 occasions. The interval between exposures was 1.5 to 22.0 hours and lambs were randomly assigned to environmental treatment groups at each test to avoid any possible bias associated with the order of test. (see addendum, page 334a)

The lambs were all born to Romney ewes and were sired by Romney and Drysdale rams, these breeds being used to produce a range of birthcoat types similar to that described in Chapter II. There were 2 sires per breed but single-sire mating was not practised. The ewes' mating dates were recorded daily and gestation length was calculated for each of the lambs.

Approximately 90% of the lambs were single-born, the ewes having been mated in a very dry autumn when feed was scarce and ryegrass staggers prevalent. No account was taken of the lamb's birthrank in the experimental design.

The experiment was of an unbalanced four-way factorial design (with sire breed, sex, airspeed and wetness as main effects) and was repeated over 6 ambient temperatures. The levels of the main effects are presented in Table 7. All were treated as being fixed effects.

Having been assigned to its treatment group, each lamb was subjected to a fixed sequence of declining ambient temperatures (from

30°C to 5°C) as shown in Table 7. This sequence was utilized because it allowed the physiological changes associated with an increasingly cold environment to be monitored. The fixed sequence was also considered preferable to a random order of ambient temperatures since preliminary observations had shown that, under the latter system, the lamb's heat production was slow to stabilize at each new ambient temperature. This was particularly evident when the ambient temperature was increasing as, in these circumstances, the lamb's heat production often remained elevated for some time after the ambient temperature had been increased. Thus the time required to test each lamb was prolonged. The main disadvantage of the fixed sequence approach was that the effects of each ambient temperature were confounded with time and with the effects of exposure to the previous temperatures. Simple comparisons between the ambient temperatures are therefore not possible.

The experimental procedure was generally as described in Chapter II. The lamb's age was recorded and its weight and birthcoat characteristics measured prior to each test, the exception being mid-side wool weight per unit area of skin which was measured only once on each lamb (before the first test). The lamb was then placed in the climate chamber at an ambient (nominal air) temperature of 30°C. Once its heat production had stabilized, rectal temperature and hind-limb skin temperature were measured (to 0.5°C) as was the RH of the chamber air. These measurements were usually made within a period of 3 to 5 minutes. The temperature control equipment was then adjusted to maintain the next ambient temperature in the sequence and the process was repeated for each of the 5 remaining ambient temperatures.

The climate chamber air temperature generally stabilized at the new setting in 10 to 15 minutes, although the period required for adjustment increased as the temperature setting declined. The lamb's heat production stabilized after a further 10 to 15 minutes, so that the maximum interval between temperature settings was about 30 minutes. Consequently, the total time required to test each lamb was about 3 hours.

The effects of sire breed, sex, airspeed and wetness on heat production and other components of the lamb's response to cold were studied by analysis of variance at each ambient temperature. These results were used to estimate the proportion of lambs attaining summit metabolism at the lowest ambient temperature. Relationships between heat production and a variety of other parameters were then studied at this ambient temperature by analysis of covariance.

Results and Discussion

Part I : Responses to Cold-Stress at Each Ambient Temperature

1. Heat production

The analyses of variance for heat production at each ambient temperature are presented in Table 7. Wet lambs had a significantly higher metabolic rate than dry lambs at all ambient temperatures, the increase in metabolic rate associated with wetness ranging from 70% at 30^{o}C ambient temperature to almost 100% at 5^{o}C. The mean metabolic rate of the wet lambs at 5^{o}C (14.68 ± 0.29 W kg^{-1}) was within the range of summit metabolic rates for Romney lambs measured in Chapter III (12 to 22 W kg^{-1}). However, the relatively low metabolic rates of the dry lambs, even at the lowest ambient temperature,

TABLE 7: EFFECT OF SIRE BREED, WETNESS, AIRSPEED AND SEX ON THE HEAT PRODUCTION OF LAMBS AT SIX AMBIENT TEMPERATURES

Classification		Heat Production (W kg^{-1}) Mean ± S.E.					
		Nominal air temperature (°C)					
		30.0	25.0	20.0	15.0	10.0	5.0
Sire breed							
Romney	(53)	7.99± 0.23	8.13± 0.24	8.93± 0.24	10.13± 0.25	11.24± 0.24	12.14± 0.27
Drysdale	(43)	6.42± 0.26	6.43± 0.27	6.81± 0.27	8.13± 0.27	9.20± 0.27	10.17± 0.30
Wetness							
Dry	(48)	5.33± 0.24	5.51± 0.25	5.93± 0.25	6.60± 0.26	7.18± 0.25	7.63± 0.28
Wet	(48)	9.09± 0.24	9.05± 0.25	9.81± 0.25	11.66± 0.26	13.26± 0.26	14.68± 0.29
Nominal airspeed (m sec^{-1})							
0.0	(24)	6.36± 0.34	6.43± 0.36	6.80± 0.36	8.35± 0.36	9.52± 0.36	11.72± 0.40
1.0	(24)	7.10± 0.34	6.94± 0.36	7.79± 0.36	9.06± 0.36	10.25± 0.36	12.52± 0.40
1.5	(24)	7.50± 0.34	7.68± 0.36	8.45± 0.36	9.63± 0.36	10.64± 0.36	12.79± 0.40
2.0	(24)	7.87± 0.34	8.07± 0.36	8.45± 0.36	9.47± 0.37	10.32± 0.36	12.31± 0.40
Sex							
Male	(48)	6.93± 0.24	6.94± 0.25	7.67± 0.25	8.98± 0.26	10.16± 0.25	11.38± 0.28
Female	(48)	7.49± 0.25	7.62± 0.26	8.07± 0.26	9.27± 0.26	10.28± 0.26	11.52± 0.29

.../continued

TABLE 7, continued

Analysis of Variance

(Note that for clarity of presentation only the mean squares and significance are given. However, since the model is fully fixed in each case all mean squares are tested against the error term.)

Source of Variation	d.f.	Mean Square and Significance					
		Nominal air temperature (°C)					
		30.0	25.0	20.0	15.0	10.0	5.0
Sire Breed (Breed)	1	56.36***	66.22***	102.97***	91.60***	95.72***	87.97***
Wetness (Wet.)	1	340.12***	299.48***	359.50***	614.75***	886.87***	1191.95***
Airspeed (Asp.)	3	10.05*	12.92*	14.64**	7.76†	5.39 NS	4.98 NS
Moving vs. still air	1	22.98**	23.11*	36.81**	19.34*	14.04†	12.10†
Within moving air	2	3.59 NS	7.82†	3.56 NS	1.97 NS	1.06 NS	1.42 NS
Sex	1	7.24 NS	10.91†	3.83 NS	2.02 NS	0.33 NS	0.46 NS
Breed x Wet.	1	0.00 NS	0.11 NS	2.13 NS	1.15 NS	0.46 NS	0.04 NS
Breed x Asp.	3	1.17 NS	0.46 NS	1.62 NS	1.92 NS	1.72 NS	3.25 NS
Breed x Sex	1	0.82 NS	0.08 NS	0.70 NS	0.39 NS	3.58 NS	7.89 NS
Wet. x Asp.	3	7.09†	7.56†	3.71 NS	0.03 NS	0.85 NS	3.17 NS
Wet. x Sex	1	1.34 NS	0.88 NS	0.12 NS	0.13 NS	0.03 NS	0.02 NS
Asp. x Sex	3	1.00 NS	0.26 NS	1.66 NS	1.82 NS	2.04 NS	4.17 NS
Breed x Wet. x Asp.	3	7.83†	7.87†	6.79 NS	4.99 NS	2.39 NS	0.60 NS
Breed x Wet. x Sex	1	0.20 NS	0.59 NS	0.76 NS	0.74 NS	2.95 NS	5.54 NS
Breed x Asp. x Sex	3	0.90 NS	0.50 NS	0.18 NS	0.99 NS	1.12 NS	3.10 NS
Wet. x Asp. x Sex	3	0.39 NS	0.92 NS	1.21 NS	2.44 NS	1.28 NS	3.19 NS
Error	67	2.89	3.30	3.30	3.63	3.60	4.17

suggest that these lambs are unlikely to attain their summit metabolic rate and become hypothermic in the field unless air temperatures are much lower than 5°C. A similar conclusion may be drawn from the results of Alexander (1962b).

The metabolic rate of the Drysdale-cross lambs was 20% lower than that of the Romney lambs at all ambient temperatures, the difference being highly significant ($P<.001$) in each case. At the lower ambient temperatures this effect can presumably be attributed to differences between the "breeds" in birthcoat characteristics and is in general agreement with observations on the effects of birthcoat type in other breeds (Alexander, 1961, 1962a; Slee, 1978). However, the "breed" difference also persisted at the higher ambient temperatures. At 30°C ambient temperature the mean metabolic rate of the dry Drysdale-cross lambs in still air (i.e. the least cold-stressed group) was 3.63 ± 0.44 W kg^{-1} which is similar to Alexander's (1961) estimate of basal metabolic rate (3.96 W kg^{-1}) in unfed Merino lambs. By contrast, the mean metabolic rate of the Romney lambs under the same environmental conditions was 5.32 ± 0.43 W kg^{-1}. It therefore appears that, at 30°C ambient temperature, the Romney lambs were already in the cold zone whereas the Drysdale-crosses were at thermoneutrality. This difference between the "breeds" was probably also a consequence of the Romney lambs' poorer coat insulation but the possibility that the Romneys ingested more milk prior to the test, and so had elevated metabolic rates even at the highest ambient temperatures (Alexander, 1961), cannot be entirely discounted.

It will be noted from Table 7 that the mean metabolic rates of

the Romney lambs varied little when the ambient temperature was reduced from 30°C to 25°C. However, this should not be interpreted as indicating that these lambs, like the Drysdale-crosses, were at thermoneutrality because the "breed" means in Table 7 are pooled over both levels of wetness. As is demonstrated in Figure 4 it was the wet Romney lambs whose metabolic rates varied little over the first 2 ambient temperatures. The metabolic rates of the dry Romney lambs in fact showed a generally linear increase as the ambient temperature was reduced, and are consistent with these lambs being in the cold zone. Possible reasons for this difference between the wet and dry lambs will be discussed later.

The effect of airspeed on metabolic rate was most pronounced at the higher ambient temperatures and was a function of differences between still and moving air rather than between the 3 highest airspeeds. In Chapter II, the RH of air in the chambers was shown to increase as ambient temperature declined. Accordingly, it might be suggested that the reduced airspeed effect at low ambient temperatures was due to the high RH inhibiting the effects of air movement on evaporative heat loss. However, in a subsequent experiment (Chapter V), in which lambs of similar birthcoat types were exposed to a single low ambient temperature (10°C), an effect of airspeed was apparent despite the chamber air again having a very high relative humidity. Indeed the only major difference between these experiments (in this respect) was that in the latter case a much shorter time elapsed before heat production was measured at the low ambient temperature. The non-significance of the airspeed effect at low ambient temperatures in the present study (Table 7) may therefore have been related in some

way to the time spent in the climate chambers by the lambs (this being obviously confounded with ambient temperature). One possibility might be that, had the overhead wetting line failed to maintain the level of coat wetness achieved by the initial immersion procedure (Chapter II), the potential for evaporation from the coat by air movement would have declined as the test proceeded. In the dry lambs a similar reduction in the moisture content of the coat could have occurred over time. Although these lambs were subjectively assessed as being dry, many were tested when only a few hours old and it is quite likely that their coats still contained a considerable amount of fluid. The wetness x airspeed interaction, which approached significance only at the higher ambient temperatures (Table 7), lends some support to this hypothesis since it reflects a greater effect of airspeed on the heat production of the wet lambs than on those tested when dry. Alternatively, the lambs exposed to moving air may have made postural adjustments which minimized the effects of air movement at low ambient temperatures. However, it seems likely that any such adjustments would have depended on the ambient temperature to which the lambs were exposed, rather than on the time spent in the climate chambers. Hence the effects of these adjustments would have been expressed in the experiment described in Chapter V as well as in this study.

Increasing airspeeds exerted a similar effect on each birthcoat type as is indicated by the non-significant sire breed x airspeed interaction. While a significant interaction might have been expected (through a tendency for the high airspeeds to more readily open up the fine shallow Romney coat), it must be remembered that the airspeeds available in this study were relatively low (a maximum of

1.9 m sec^{-1} compared with 5.5 m sec^{-1} used by Alexander). They may therefore have been too low to penetrate the birthcoat structure. In addition, the turbulence of air movement within the chambers would presumably have reduced the degree to which the coat structure was penetrated. Thus it seems likely that the major effect of air movement on "coat plus air" insulation was the removal of the boundary layer of still air over the coat, this effect being similar in the 2 birthcoat types.

The combined effects of air movement, wetting and ambient temperature on the cooling power of the environment are demonstrated in Figure 4. In the calculation of the mean metabolic rates, data were pooled across the sexes since sex of the lamb did not significantly affect its heat production at any ambient temperature. Similarly, since differences between the 3 levels of moving air were not significant, the mean metabolic rates are plotted for lambs grouped according to whether they were exposed to "still air" (0.0 m sec^{-1}) or "moving air" (1.0, 1.5 and 2.0 m sec^{-1}).

As has already been mentioned, the wet lambs of each "breed" exhibited little change in metabolic rate when the ambient temperature was reduced from 30°C to 25°C (Figure 4). This suggests that, at 30°C ambient temperature, these lambs were producing more body heat than was required to maintain body temperature. The increased rectal temperatures of these lambs, compared with those tested when dry, support the hypothesis that this occurred in response to stresses associated with the initial wetting treatment (see Table 8).

Figure 4 also illustrates the major effect of wetting on the level

KEY TO FIGURE 4

Sire breed : R = Romney

N = Drysdale

Wetness : D = Dry

W = Wet

Airspeed : S = Still air

M = Moving air

-·-·-·-·- Mean summit metabolism of Romney lambs (Chapter III)

--------- Lower limit of summit metabolism of Romney lambs (Chapter III)

The number of observations contributing to each series of means is indicated in parentheses

The vertical bars represent the standard error of the mean

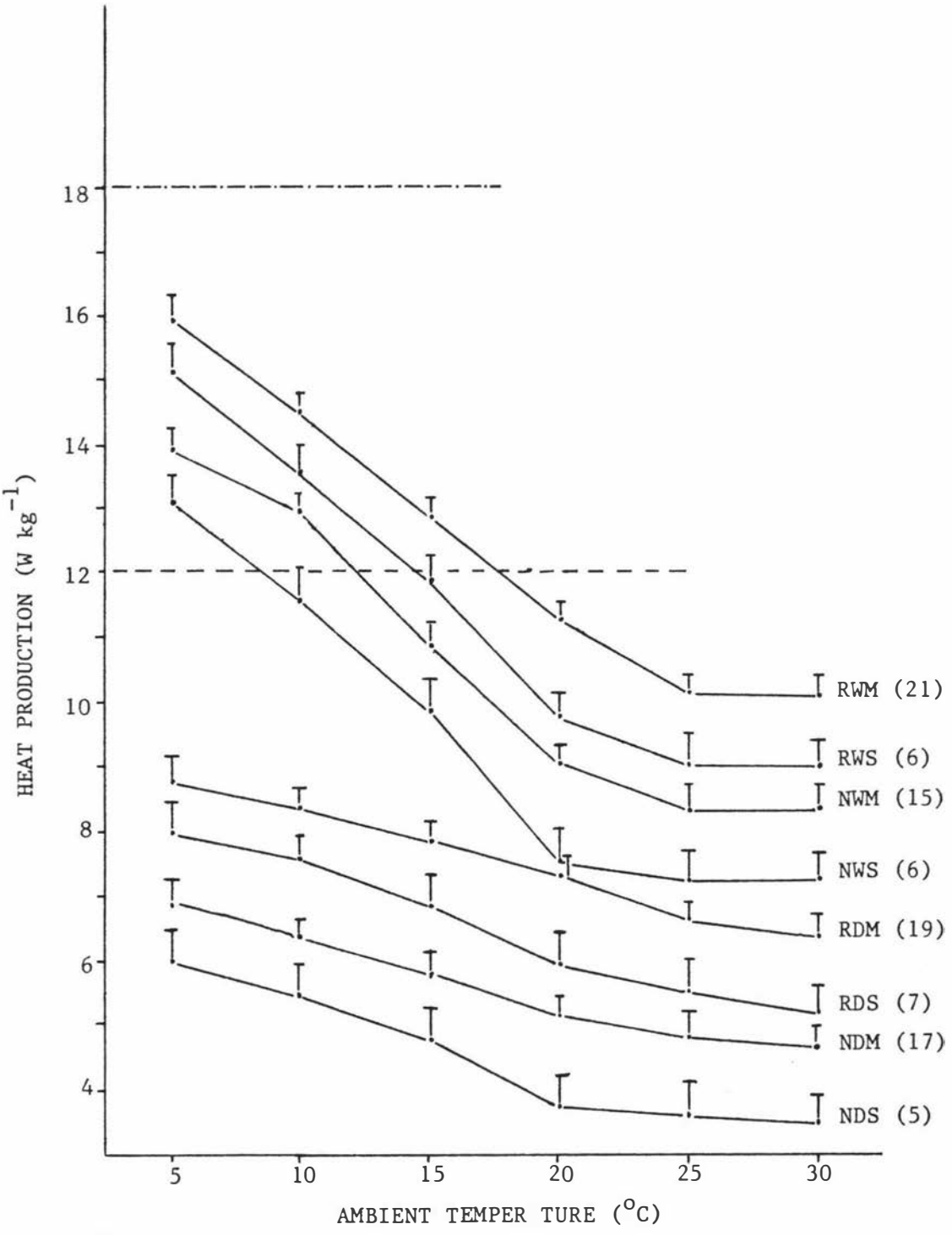

FIGURE 4: COOLING CURVES FOR A RANGE OF ENVIRONMENTAL CONDITIONS

of cold-stress experienced by the lamb. This effect was so large that attempts to estimate "effective ambient temperatures" (Sykes et al., 1976) for wet lambs involve an unacceptable degree of extrapolation from the curves for dry lambs. Nevertheless, the relative cooling powers of a range of environments can be estimated from these curves. For example, it can be estimated that conditions of wetness, air movement, and an ambient temperature of $5^{o}C$ constitute an environment which is approximately twice as cold (as indicated by the response in metabolic rate) as conditions of dryness and still air at the same ambient temperature. These estimates may, however, be subject to some error when dealing with environmental conditions in which a proportion of the lambs might be expected to attain summit metabolism. In this context, Figure 4 also illustrates the advantage of a high summit metabolic rate.

2. Rectal temperature

The only treatments which exerted significant effects on the rectal temperatures of the lambs were wetness and breed of sire (Table 8). Wet lambs had significantly higher rectal temperatures than dry lambs at all except the lowest ambient temperature, while the Romneys exhibited generally higher rectal temperatures than the Drysdale-cross lambs. However, the latter differences were not always significant.

The significant effect of wetness on rectal temperature is unusual because the wet lambs, which were apparently experiencing a greater degree of cold-stress than the dry lambs (as indicated by their higher metabolic rates), also had the greater rectal temperatures. Furthermore, this difference was established at the highest ambient

MASSEY UNIVERSITY
LIBRARY

TABLE 8: EFFECT OF SIRE BREED, WETNESS, AIRSPEED AND SEX ON THE RECTAL TEMPERATURES OF LAMBS AT SIX AMBIENT TEMPERATURES

Classification		Rectal Temperature (°C) Mean ± S.E.					
		Nominal air temperature (°C)					
		30.0	25.0	20.0	15.0	10.0	5.0
Sire breed							
Romney	(53)	39.53± 0.09	39.44± 0.10	39.53± 0.10	39.65± 0.10	39.56± 0.13	39.29± 0.16
Drysdale	(43)	39.24± 0.09	39.28± 0.11	39.23± 0.11	39.30± 0.13	39.09± 0.14	38.98± 0.18
Wetness							
Dry	(48)	39.11± 0.09	39.12± 0.10	39.07± 0.10	39.14± 0.12	38.92± 0.13	38.97± 0.17
Wet	(48)	39.65± 0.09	39.60± 0.10	39.69± 0.11	39.80± 0.12	39.73± 0.13	39.30± 0.17
Nominal airspeed ($m\ sec^{-1}$)							
0.0	(24)	39.54± 0.13	39.43± 0.14	39.34± 0.15	39.51± 0.17	39.44± 0.18	39.26± 0.24
1.0	(24)	39.33± 0.13	39.41± 0.14	39.43± 0.15	39.42± 0.17	39.22± 0.19	39.28± 0.24
1.5	(24)	39.31± 0.13	39.35± 0.14	39.43± 0.15	39.53± 0.17	39.33± 0.19	39.11± 0.24
2.0	(24)	39.33± 0.13	39.26± 0.14	39.33± 0.15	39.43± 0.17	39.32± 0.19	38.89± 0.24
Sex							
Male	(48)	39.39± 0.12	39.37± 0.10	39.41± 0.10	39.47± 0.12	39.46± 0.13	39.29± 0.17
Female	(48)	39.38± 0.12	39.35± 0.10	39.35± 0.11	39.47± 0.12	39.21± 0.14	38.97± 0.17

.../continued

TABLE 8, continued

Classification	Rectal Temperature (°C) Mean ± S.E.	
	Sire breed	
	Romney	Drysdale
At Nominal Air Temperature 30°C:		
Wetness		
Dry	39.13 ± 0.13[a] (26)	39.09 ± 0.14[a] (22)
Wet	39.93 ± 0.14[b] (27)	39.37 ± 0.14[a] (21)
At Nominal Air Temperature 10°C:		
Sex		
Male	39.48 ± 0.17[a] (22)	39.41 ± 0.15[a] (26)
Female	39.65 ± 0.13[a] (31)	38.76 ± 0.20[b] (17)

.../continued

TABLE 8, continued

Analysis of Variance

(Note that only mean squares are presented. The model is fully fixed in each case so all mean squares are tested against the error term.)

Source of Variation	d.f.	Mean Square and Significance					
		Nominal air temperature (°C)					
		30.0	25.0	20.0	15.0	10.0	5.0
Sire Breed (Breed)	1	2.06*	0.60 NS	1.99†	2.78*	4.70*	2.29 NS
Wetness (Wet.)	1	7.70**	5.67***	9.19***	10.43***	14.29***	2.73 NS
Airspeed (Asp.)	3	0.29 NS	0.15 NS	0.06 NS	0.07 NS	0.14 NS	0.77 NS
Moving vs. still air	1	0.85 NS	0.15 NS	0.06 NS	0.05 NS	0.40 NS	0.50 NS
Within moving air	2	0.01 NS	0.15 NS	0.06 NS	0.08 NS	0.01 NS	0.91 NS
Sex	1	0.01 NS	0.01 NS	0.07 NS	0.00 NS	0.93 NS	2.37 NS
Breed x Wet.	1	1.66*	0.59 NS	0.11 NS	0.48 NS	0.59 NS	0.87 NS
Breed x Asp.	3	0.98†	0.89 NS	0.41 NS	0.92 NS	1.42 NS	1.01 NS
Breed x Sex	1	0.45 NS	0.55 NS	0.23 NS	1.38 NS	3.63*	1.39 NS
Wet. x Asp.	3	0.61 NS	1.16†	0.75 NS	0.65 NS	0.15 NS	1.00 NS
Wet. x Sex	1	0.23 NS	0.03 NS	0.00 NS	0.04 NS	0.02 NS	0.06 NS
Asp. x Sex	3	0.05 NS	0.09 NS	0.03 NS	0.18 NS	0.17 NS	0.37 NS
Breed x Wet. x Asp.	3	0.72 NS	0.84 NS	0.58 NS	0.09 NS	0.05 NS	0.32 NS
Breed x Wet. x Sex	1	0.22 NS	0.74 NS	1.64†	1.92†	1.68 NS	1.01 NS
Breed x Asp. x Sex	3	0.51 NS	0.34 NS	0.72 NS	0.78 NS	1.96†	2.99 NS
Wet. x Asp. x Sex	3	0.49 NS	0.35 NS	0.44 NS	0.11 NS	0.14 NS	0.88 NS
Error	67	0.38	0.47	0.55	0.69	0.85	1.48

temperature when the degree of cold-stress experienced by all lambs was relatively low and when the metabolic rates of the wet lambs appeared to be unusually high (Figure 4). Accordingly, these results cannot be considered to indicate a superior ability of the wet lambs to control deep body temperature, despite the fact that their rectal temperatures were close to an accepted "normal" mean of 39.5°C (Alexander and McCance, 1958; Slee, 1968; Cockrem and McDonald, 1969; Sykes et al., 1976).

A more likely explanation is that the wet lambs increased their metabolic rates above the level required to maintain body temperature (as a response to the initial wetting treatment) and consequently increased their deep body temperatures. This hypothesis would require that all the lambs be mildly hypothermic prior to half of them being wetted which is quite feasible in view of the rectal temperature changes which have previously been observed in lambs immediately after birth (Alexander and McCance, 1958; Smith, 1961). Similar increases in rectal temperature upon initial exposure to cold have been demonstrated in mature sheep (Slee, 1966) and in Merino lambs (Alexander, 1961). However, it is not clear whether this apparent "over-compensation" in rectal temperature occurs in response to the increased rate of body heat loss which accompanies the initial exposure to cold, or to non-environmental stresses associated with the sudden change in the environment.

The presence of this effect may further complicate the interpretation of changes in metabolic rate and rectal temperature. It is apparent that, at 30°C ambient temperature, the relatively high metabolic rates of the wet lambs cannot be interpreted as simply

indicating the level of heat production required to maintain body temperature (since a component of this heat production was probably devoted to increasing deep body temperature). However the difference in mean rectal temperature between the wet and dry lambs was established by the time rectal temperature was first measured and remained relatively constant until the lowest ambient temperature. Consequently, the lambs' metabolic rates should still be reasonable estimates of their rates of body heat loss at ambient temperatures of 25°C and below. At the lowest ambient temperature, the non-significant effect of wetness appears to have been due to the declining rectal temperatures of the wet lambs which were associated with the attainment of summit metabolism in some members of this group.

The effect of sire breed on rectal temperature was similar to the wetness effect in that the group of lambs which apparently experienced the greater degree of cold-stress (Romneys) also had higher rectal temperatures. In the initial stages of the experiment this was due to the wet Romney lambs exhibiting a much greater increase in rectal temperature (compared with those tested dry) than did the Drysdale-crosses (Table 8). At the lower ambient temperatures the wet Drysdale-cross lambs had apparently increased their rectal temperatures, as is indicated by the non-significant sire breed x wetness interaction, but the "breed" difference in rectal temperature (of about 0.3°C) persisted. However, it would be difficult to ascribe any survival advantage to the Romney lambs on the basis of their slightly higher rectal temperatures since the "breeds" exhibited an equal net decline in mean rectal temperature

during the course of the experiment.

In view of the significant effects of airspeed on heat production at the higher ambient temperatures (Table 7) it might have been expected that the lambs exposed to moving air, which were clearly more cold-stressed than those in still air, would also have exhibited increased rectal temperatures. As Table 8 shows, this did not occur. Alexander (1961) found that, as the degree of cold-stress to which the lamb is exposed increases, so too does the initial rise in rectal temperature. Since the between-airspeed differences in heat production were much smaller than between the levels of wetness, a greater difference in cold-stress than that which existed between the airspeeds may have been required to induce an "over-compensation" effect in rectal temperature.

The possibility that the wet lambs altered their metabolism, and consequently increased their rectal temperatures, in response to non-environmental stress associated with the initial wetting procedure has already been noted. It should be pointed out that other non-environmental stresses (such as handling and separation from the dam) could also have affected the metabolism of the lambs. Many of them showed signs of distress when separated from their dams and most struggled when first placed in the climate chambers, although they generally became settled after 5 to 10 minutes in the chambers and remained so for the duration of the test. However, while stress associated with the wetting treatment could have contributed to the elevated rectal temperatures of the wet lambs in this study, non-environmental stresses were unlikely to have been responsible for the other treatment effects on rectal temperature.

Comparisons of rectal temperatures across the ambient temperatures do not highlight major trends although there was a tendency for rectal temperatures to fall at the lowest ambient temperatures, particularly among the wet lambs. Since the mean metabolic rate of these lambs was within the range of summit metabolism for Romney lambs (Figure 4) it appears that this change was associated with the onset of hypothermia in some individuals (see "Metabolism of lambs in relation to summit conditions").

3. Hind-limb skin temperature

The analyses of variance for hind-limb skin temperature at each ambient temperature are presented in Table 9. When interpreting these analyses it should be noted that hind-limb skin temperatures (henceforth referred to simply as "skin temperatures") were measured shortly after the lamb's metabolic rate had stabilized. Since hind-limb skin temperature is slow to equilibrate with each change in ambient temperature (Alexander, 1961) some of the treatment differences may reflect varying rates of equilibration in limb temperature rather than variation in the degree to which peripheral blood flow was altered. In addition, the measurement of skin temperature by surface thermocouple may be subject to certain errors as was discussed in Chapter II.

As a further aid to the interpretation of treatment effects on skin temperature, thermal circulation indices were calculated for each of the lambs, thus:

$$TCI = \frac{T_S - T_A}{T_R - T_S}$$ (Burton and Edholm, 1955)

TABLE 9: EFFECT OF SIRE BREED, WETNESS, AIRSPEED AND SEX ON THE HIND-LIMB SKIN TEMPERATURES OF LAMBS AT SIX AMBIENT TEMPERATURES

Classification	Hind-Limb Skin Temperature (°C) Mean ± S.E.					
	Nominal air temperature (°C)					
	30.0	25.0	20.0	15.0	10.0	5.0
Sire breed						
Romney (53)	31.59± 0.62	30.36± 0.67	27.48± 0.76	24.78± 0.83	21.37± 0.89	18.01± 0.93
Drysdale (43)	31.69± 0.69	30.44± 0.75	28.35± 0.85	25.67± 0.92	22.85± 1.00	20.55± 1.04
Wetness						
Dry (48)	33.05± 0.64	32.19± 0.70	30.75± 0.79	29.35± 0.85	27.14± 0.93	25.49± 0.97
Wet (48)	30.23± 0.65	28.61± 0.70	25.08± 0.79	21.11± 0.85	14.13± 1.14	13.06± 1.19
Nominal airspeed (m sec^{-1})						
0.0 (24)	31.12± 0.91	31.07± 0.99	29.33± 1.12	27.72± 1.20	26.46± 1.30	21.17± 1.36
1.0 (24)	32.17± 0.91	30.67± 0.99	27.16± 1.12	24.47± 1.20	21.62± 1.32	17.51± 1.38
1.5 (24)	32.44± 0.91	31.29± 0.99	29.10± 1.12	25.50± 1.20	20.42± 1.30	16.61± 1.36
2.0 (24)	30.82± 0.91	28.57± 0.99	26.07± 1.12	23.22± 1.20	19.94± 1.29	14.76± 1.35
Sex						
Male (48)	30.68± 0.64	29.67± 0.70	26.84± 0.79	24.20± 0.88	21.08± 0.93	18.76± 0.97
Female (48)	32.59± 0.66	31.13± 0.71	28.99± 0.81	26.25± 0.87	20.19± 0.95	19.80± 1.00

.../continued

TABLE 9, continued

Classification	Hind-Limb Skin Temperature (°C) Mean ± S.E.	
	Wetness	
	Dry	Wet
At Nominal Air Temperature 15°C:		
Nominal airspeed (m sec^{-1})		
0.0	29.03 ± 1.69[b] (12)	26.42 ± 1.69[b] (12)
1.0	28.88 ± 1.67[b] (12)	20.07 ± 1.74[a] (12)
1.5	29.75 ± 1.69[b] (12)	21.24 ± 1.74[a] (12)
2.0	29.74 ± 1.67[b] (12)	16.70 ± 1.69[a] (12)
At Nominal Air Temperature 10°C:		
Sex		
Male	24.65 ± 0.67[b] (24)	17.52 ± 1.31[a] (24)
Female	29.64 ± 1.34[c] (24)	16.62 ± 1.33[a] (24)
At Nominal Air Temperature 5°C:		
Sex		
Male	23.21 ± 0.70[b] (24)	14.31 ± 1.38[a] (24)
Female	27.78 ± 1.40[c] (24)	11.82 ± 1.39[a] (24)

.../continued

TABLE 9, continued

Analysis of Variance

(Note that only mean squares are presented. The model is fully fixed in each case so all mean squares are tested against the error term.)

Source of Variation	d.f.	Mean Square and Significance					
		Nominal air temperature (°C)					
		30.0	25.0	20.0	15.0	10.0	5.0
Sire Breed (Breed)	1	0.23 NS	0.15 NS	17.21 NS	24.12 NS	37.70 NS	121.46 NS
Wetness (Wet.)	1	191.45**	307.74***	773.90***	1628.41***	2436.19***	3707.11***
Airspeed (Asp.)	3	14.95 NS	37.31 NS	58.84 NS	86.99†	214.09**	174.72*
Moving vs. still air	1	8.57 NS	14.36 NS	64.07 NS	198.80*	605.52***	428.07*
Within moving air	2	18.14 NS	48.78 NS	56.22 NS	31.08 NS	18.38 NS	48.04 NS
Sex	1	84.29*	48.83 NS	107.22†	99.95 NS	93.66 NS	22.90 NS
Breed x Wet.	1	1.70 NS	3.25 NS	2.80 NS	1.75 NS	0.95 NS	13.43 NS
Breed x Asp.	3	15.76 NS	13.80 NS	19.80 NS	23.40 NS	38.45 NS	26.26 NS
Breed x Sex	1	22.10 NS	75.06†	91.64†	39.65 NS	13.89 NS	14.98 NS
Wet. x Asp.	3	24.35 NS	59.05†	58.07 NS	116.39*	110.43†	87.67 NS
Wet. x Sex	1	22.09 NS	21.86 NS	18.82 NS	51.42 NS	202.10*	311.91*
Asp. x Sex	3	14.71 NS	28.62 NS	18.92 NS	9.42 NS	8.74 NS	16.40 NS
Breed x Wet. x Asp.	3	25.84 NS	15.69 NS	19.69 NS	14.49 NS	62.84 NS	47.44 NS
Breed x Wet. x Sex	1	1.83 NS	1.20 NS	0.02 NS	3.26 NS	29.58 NS	77.75 NS
Breed x Asp. x Sex	3	16.69 NS	37.73 NS	34.25 NS	35.93 NS	60.73 NS	57.29 NS
Wet. x Asp. x Sex	3	12.04 NS	0.80 NS	5.88 NS	18.95 NS	26.04 NS	34.05 NS
Error	67	20.74	22.67	31.30	37.80	40.35	46.24

where T_A = ambient temperature (from Table 1)

T_R = rectal temperature

T_S = skin temperature

Since sire breed did not significantly affect hind-limb skin temperature (Table 9) the data were pooled across "breeds". Similarly, since the only significant airspeed difference was that between still and moving air, the data from lambs exposed to the 3 highest airspeeds have been pooled in the calculation of thermal circulation indices. Arithmetic means of TCI and their standard errors are presented in Table 10.

Wet lambs had significantly lower skin temperatures than dry lambs at all ambient temperatures, the difference between the mean skin temperatures of the two groups increasing as ambient temperature declined (Table 9). Among the wet lambs, skin temperature declined very rapidly as the ambient temperature was reduced so that the skin temperature - air temperature gradient varied to only a small degree (from 0.2 to 8.1°C). Conversely, the dry lambs exhibited a very slow rate of decline in skin temperature so that their skin temperature - air temperature gradients increased from 3.1°C to 20.5°C as the test proceeded. The skin temperatures of the dry lambs were also very much higher than those of the Merino lambs examined by Alexander (1961) in similar environmental conditions.

The hind-limb skin temperatures of the dry lambs which were exposed to still air were found to be significantly higher (at ambient temperatures of 15°C and below) than those of a sample of 10 Merino lambs exposed to the same environment (Appendix I). It was

TABLE 10: EFFECT OF WETNESS, AIRSPEED AND SEX ON THE THERMAL CIRCULATION INDICES OF LAMBS AT SIX AMBIENT TEMPERATURES

Classification		Thermal Circulation Index - Mean ± S.E.					
		Nominal air temperature (°C)					
		30.0	25.0	20.0	15.0	10.0	5.0
Wetness							
Dry	(48)	1.72± 0.30	2.38± 0.33	3.01± 0.81	2.74± 0.51	2.42± 0.27	2.52± 0.30
Wet	(48)	0.27± 0.12	0.71± 0.17	0.63± 0.10	0.56± 0.10	0.49± 0.10	0.41± 0.09
Airspeed							
Still air	(24)	0.47± 0.18	1.44± 0.26	1.73± 0.33	1.80± 0.32	2.17± 0.43	2.08± 0.49
Moving air	(72)	1.17± 0.22	1.58± 0.25	1.85± 0.56	1.60± 0.36	1.22± 0.18	1.26± 0.19
Sex							
Male	(48)	0.78± 0.25	1.50± 0.32	1.96± 0.81	1.65± 0.52	1.25± 0.22	1.39± 0.28
Female	(48)	1.21± 0.25	1.59± 0.25	1.69± 0.26	1.64± 0.22	1.67± 0.27	1.53± 0.26

considered that this difference arose because a substantial proportion of the dry Romney and Drysdale-Romney cross lambs had failed to constrict peripheral blood vessels, even at the lowest ambient temperature.

A similar conclusion may be drawn from the results presented in Table 9. The significant effect of wetness on skin temperature cannot have been due solely to a greater rate of temperature equilibration in the vasoconstricted limbs of the wet lambs compared with those tested when dry. Rather, the very high skin temperatures of the dry lambs are consistent with their having failed to fully constrict peripheral blood vessels, despite the fact that they were apparently in the cold zone at ambient temperatures below 20^{o}C. Among the wet lambs, however, the more rapid decline in skin temperature (as ambient temperature declined) was compatible with peripheral vasoconstriction having been fully employed. Thus it appears that some Romney and Drysdale-Romney cross lambs may require a severe cold-stress to stimulate peripheral vasoconstriction. It is also clear that, in these lambs, the onset of cold-induced thermogenesis is not always accompanied by a maximal reduction in blood flow to the peripheral tissues.

Neither airspeed nor sire breed exerted a significant effect on hind-limb skin temperature at the higher ambient temperatures. This is again consistent with the view that lambs do not employ peripheral vasoconstriction as soon as they enter the cold zone, particularly since the Romney lambs appeared to attain their lower critical temperature at a higher ambient temperature than the Drysdale-cross lambs. Hence the effects of airspeed and sire breed on the level of

cold-stress experienced by the lamb may have been too small to induce differences in peripheral vasoconstriction which could be detected by the measurement of skin temperature. The significant effect of airspeed at the lower ambient temperatures may have been due, not to differences in the timing of peripheral vasoconstriction, but rather to an effect of air movement on the rate at which limb temperature equilibrated with the environment in those lambs which had constricted peripheral blood vessels.

At the highest ambient temperature, female lambs exhibited significantly greater skin temperatures than males, despite there being no difference between the sexes in metabolic rate. At the 2 lowest ambient temperatures, female lambs also exhibited higher skin temperatures than males, but only when the lambs were dry. These interactions may indicate that the female lambs constricted peripheral blood vessels to a lesser extent than did the males, but it is not clear why this difference should have been apparent only at the extremes of the temperature range.

The thermal circulation indices (Table 10) add little to the interpretation of changes in skin temperature. Among the dry lambs, TCI increased as ambient temperature declined which is again consistent with the view that most of these lambs had not experienced peripheral vasoconstriction. Conversely the TCI values of the wet lambs declined slowly with ambient temperature but did not exhibit sudden reductions which are considered to be indicative of peripheral vasoconstriction. This was presumably because most of these lambs had experienced constriction of the peripheral blood vessels prior to the onset of the test.

4. Metabolism of lambs in relation to summit conditions

One of the major aims of this experiment was to establish the relationships between the level of heat production required by the lamb to maintain body temperature, and certain physical and physiological characteristics such as birthcoat depth and body temperature. Ideally this was to be done at the lowest ambient temperature when the lambs were being subjected to the most severe level of cold-stress available. However, in order to satisfactorily accomplish this aim, it was first necessary to identify those lambs which were likely to have attained summit metabolism, and so were likely to introduce errors into regression analyses involving heat production. Since the mean metabolic rates of the wet lambs were in the lower half of the range of Romney summit metabolic rates (Figure 4) it was likely that a few of these lambs, and particularly the Romneys, would also have attained summit metabolism.

The assessment of whether or not each lamb had attained summit metabolism was based on the lamb's estimated rate of change in rectal temperature when the ambient temperature was reduced from $10^{o}C$ to $5^{o}C$. The interval between the measurement of rectal temperature at each of these ambient temperatures was assumed to be 25 minutes (which for individual lambs would have been accurate to within ± 5 minutes). Lambs were considered to have attained summit metabolism if they exhibited a rate of decline in rectal temperature greater than $0.025^{o}C\ min^{-1}$ over this period (Alexander, 1962b). The validity of using this "cut-off point" in the rate of decline in rectal temperature will be discussed further in Chapter V (which describes an experiment in which a greater proportion of the lambs appeared to

have attained summit metabolism than was the case here). For the purposes of this experiment, account was also taken of the degree to which the lamb increased its metabolic rate when the ambient temperature was reduced from 10°C to 5°C.

A total of 12 lambs (9 Romneys and 3 Drysdale-crosses) exhibited rates of decline in rectal temperature greater than $0.025^{o}C\ min^{-1}$ when the ambient temperature was reduced over this range. Five of the Romney lambs had rectal temperatures of 39.5°C or greater at 5°C ambient temperature. In view of the apparent "over-compensation" effect which occurred in the rectal temperatures of the wet lambs, it is doubtful whether these 5 lambs had in fact attained summit metabolism. Furthermore, all of them exhibited substantial increases in metabolic rate when the ambient temperature was reduced from 10°C to 5°C, in contrast to the remaining 7 lambs which showed little or no change in metabolic rate. Thus, at the lowest ambient temperature, only 7 of the lambs (4 Romney, 3 Drysdale-cross) were considered to have attained summit metabolic rates. The decision was therefore made to analyse the relationships between heat production and other parameters at this ambient temperature while accepting that in a few lambs heat production would be related not to the rate of body heat loss but to individual limitations in body heat production. As an added precaution these relationships were analysed before and after the exclusion of the lambs considered to have attained summit metabolism. Where important differences occurred between these analyses they have been reported.

Part II : Relationships Between Heat Production at 5°C Ambient Temperature and Other Characteristics of the Lamb

This section of the results is primarily concerned with identifying some characteristics of the lamb which affect the level of heat production that it requires to maintain body temperature. Relationships between heat production and these characteristics were examined by analysis of covariance at the lowest ambient temperature. However, in order to interpret these analyses it was first necessary to identify treatment effects on the independent variable (e.g. birthcoat depth). Where appropriate, the analysis of variance for the independent variable is presented before consideration is given to its relationship with heat production.

A number of the characteristics examined were found to be significantly related to heat production, so suggesting the possibility that they might have been interdependent in their control of the metabolic response to cold-stress. This hypothesis was also examined for certain of these characters, particularly those concerned with birthcoat insulation, bodyweight and gestation length.

1. Age of the lamb

The overall regression coefficient of heat production at 5°C ambient temperature on age was b = -0.07 ± 0.55 W kg^{-1} hr^{-1} which was not significant (t_{94} = 0.13, NS.). Thus across all treatments, and over the range of ages involved (1 to 30 hours), the level of heat production required by the lamb to maintain body temperature was independent of age at the commencement of the test. However, the within-sire breed regressions were significantly heterogeneous (Table 11), metabolic rate being related to age in the Drysdale-cross

TABLE 11: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (SIRE BREED) REGRESSIONS OF HEAT PRODUCTION AT 5°C AMBIENT TEMPERATURE ON AGE OF THE LAMB

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 7)	28	49.34	
Intra-class (sire breed) regression of heat production on age	2	15.42	4.03*
Pooled within-class	1	8.57	2.24 NS
Difference	1	22.27	5.82*
Residual error	65	3.83	

lambs ($b = -0.17 \pm 0.06$ W kg^{-1} hr^{-1}, $t_{41} = 2.82$, $P<.01$) but not in the Romneys ($b = 0.02 \pm 0.05$ W kg^{-1} hr^{-1}, $t_{51} = 0.34$, NS.).

The tendency for metabolic rate to decline with increasing age among the Drysdale-crosses appears to have been due to a superior birthcoat insulation in the older lambs. In this "breed", birthcoat depth at the midside and hip sites was positively and significantly correlated with age ($r = 0.36$ and $r = 0.37$ respectively, both $P<.05$). Among the Romney lambs, no such association existed. As will be demonstrated later, the birthcoat depth of the Drysdale-cross lambs was reduced by wetting, but this did not occur among the Romneys. The tendency for coat depth to increase with age only in the Drysdale-cross lambs may therefore have been a function of age-related drying of the coat. Among the dry lambs this would have lead to a direct effect on coat depth while the older wet lambs, whose coats had dried to a greater extent before they were immersed in water, may have suffered a lesser reduction in coat depth as a result of this treatment. Thus the combined effects of the increased coat depths in the older Drysdale-cross lambs, and the lower requirement for body heat production which occurred as a result of this greater depth (see "Characteristics of the birthcoat") were likely to have been responsible for the reduced metabolic rates in these lambs as they aged.

2. Body temperatures

(a) Rectal temperature

The overall regression coefficient of heat production on rectal temperature at 5°C ambient temperature was $b = 0.80 \pm 0.36$ W kg^{-1} $°C^{-1}$ which was significant ($t_{94} = 2.25$, $P<.05$). Hence metabolic rate was related to rectal temperature even in lambs which had generally not

attained summit metabolism. This result contrasts markedly with those of Alexander (1962b). However, the significance of this regression was apparently due to the effects of sire breed and wetting on both metabolic rate and rectal temperature. Having taken account of these treatment effects, the pooled within-class regression was not significant (Table 12).

The within-sire breed regressions of heat production on rectal temperature were significantly heterogeneous ($P<.001$, Table 12). Among the Romney lambs heat production was independent of rectal temperature ($b = -0.34 \pm 0.24$ W kg^{-1} $^{o}C^{-1}$, $t_{51} = 1.42$, NS.) whereas among the Drysdale-crosses a strong positive relationship existed ($b = 1.34 \pm 0.34$ W kg^{-1} $^{o}C^{-1}$, $t_{41} = 3.94$, $P<.001$). However, the 3 Drysdale-cross lambs which attained summit metabolism at 5°C ambient temperature, and whose rectal temperatures fell to about 36°C, were primarily responsible for the significant relationship within their "breed". These lambs were also characterised by particularly low metabolic rates at 5°C ambient temperature. When they were excluded from the analysis, the corresponding within-sire breed regressions of heat production on rectal temperature were $b = -0.32 \pm 0.24$ W kg^{-1} $^{o}C^{-1}$, $t_{51} = 1.33$, NS. (Romney) and $b = 0.58 \pm 0.47$ W kg^{-1} $^{o}C^{-1}$, $t_{38} = 1.23$, NS. (Drysdale-cross). Hence after the exclusion of these lambs there was no significant relationship between heat production and rectal temperature, a result which would normally be expected in lambs which are not severely hypothermic (Alexander, 1962b). It should be mentioned that 2 Romney lambs also exhibited very low rectal temperatures (35 to 36°C) but these were not associated with exceptionally low metabolic rates as was the case with the few Drysdale-cross lambs. This would suggest that the Romney lambs which

TABLE 12: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (SIRE BREED) REGRESSIONS OF HEAT PRODUCTION ON RECTAL TEMPERATURE AT 5°C AMBIENT TEMPERATURE

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 7)	28	49.34	
Intra-class (sire breed) regression of heat production on rectal temperature	2	28.70	8.40***
Pooled within-class	1	6.77	1.98 NS
Difference	1	50.62	14.80***
Residual error	65	3.42	

attained summit metabolism did so primarily because they experienced high rates of body heat loss rather than because of poor summit metabolic rates (their level of heat production at 5°C ambient temperature being 14.9 to 16.0 W kg^{-1}). Conversely, the 3 Drysdale-cross lambs which attained summit metabolism had much lower metabolic rates (9.8 to 10.3 W kg^{-1}) at the same ambient temperature which was likely to have been the major factor in their rapid rate of decline in rectal temperature. This difference may also explain why a similar proportion of the Romney and Drysdale-cross lambs exhibited rates of decline in rectal temperature consistent with their having attained summit metabolism, despite the apparently superior birthcoat insulation of the latter group.

(b) Hind-limb skin temperature

The effects of various components of the thermal environment on the hind-limb skin temperatures of these lambs have been examined in an earlier section of this chapter. Those analyses suggested that a substantial proportion of the dry lambs had not experienced peripheral vasoconstriction but that the wet lambs had done so. This difference is in turn likely to affect the interpretation of relationships between the lamb's skin temperature and the level of heat production which it requires to maintain body temperature.

The overall regression coefficient of heat production on skin temperature was $b = -0.25 \pm 0.04$ W kg^{-1} $°C^{-1}$ which was highly significant ($t_{94} = 6.86$, $P<.001$). This relationship presumably derives from the common effects of environmental treatments on both skin temperature and metabolic rate. In particular the very low skin temperatures and high metabolic rates of the wet lambs, compared

with those tested when dry, would have contributed to the negative slope of this regression.

As Table 13 indicates, the within-wetness regressions of heat production on skin temperature were significantly ($P<.01$) heterogeneous. Among the dry lambs, heat production was independent of skin temperature ($b = 0.05 \pm 0.04$ W kg^{-1} $^{o}C^{-1}$, $t_{46} = 1.25$, NS.) while among the wet lambs the relationship was again strongly negative ($b = -0.23 \pm 0.08$ W kg^{-1} $^{o}C^{-1}$, $t_{46} = 2.71$, $P<.01$). The independence of heat production and skin temperature within the dry lambs is to be expected since many of these lambs had apparently failed to constrict peripheral blood vessels completely (65% of them, for example, had skin temperatures greater than 25^{o}C at the lowest ambient temperature). Thus the majority of them had failed to derive any insulative advantage from reducing blood flow to the periphery.

Among the wet lambs, heat production was negatively related to skin temperature. Had low skin temperatures been indicative of a more intense vasoconstriction, it might have been expected that this would result in an improved tissue insulation and therefore in a lesser requirement for body heat production. In this situation, low skin temperatures would have been associated with a low, rather than a high metabolic rate. As the negative regression coefficient demonstrates, this was not the case. However, this relationship may indicate that both the rate of body heat loss and the rate at which skin temperature equilibrates with the environment are affected by physical characteristics of the lamb such as coat insulation. For example, if lambs with a poor birthcoat insulation also had a poor coat cover on the limbs, they might be expected to have a high

TABLE 13: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (WETNESS) REGRESSIONS OF HEAT PRODUCTION ON HIND-LIMB SKIN TEMPERATURE AT 5°C AMBIENT TEMPERATURE

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 7)	28	49.34	
Intra-class (wetness) regression of heat production on skin temperature	2	17.80	4.75*
Pooled within-class	1	0.17	0.05 NS
Difference	1	35.42	9.45**
Residual error	65	3.75	

rate of body heat loss (and hence a high metabolic rate) in addition to a more rapid equilibration of limb temperature with the environment. Alternatively the coat cover of the limbs may affect the degree to which thermoreceptors in the skin are stimulated by a cold environment and so influence the intensity of peripheral vasoconstriction. These hypotheses will be examined further in Chapter V.

3. Characteristics of the birthcoat

(a) Depth of birthcoat at the hip position

(i) Treatment effects on hip coat depth

An analysis of the effects of sire breed, sex and wetness on birthcoat depth at the hip position is presented in Table 14. As expected, the major source of variation in coat depth was the breed of sire, Drysdale-cross lambs having a coat approximately twice as deep as that of the Romney lambs.

Wetting produced a significant reduction in the birthcoat depths of the Drysdale-cross lambs but only a small and non-significant reduction in the depth of the Romney coats. This result is in general agreement with those from the preliminary study of lamb skins (Chapter II). It seems likely that these interactions arise because the halo hairs are more sensitive to a reduction in depth associated with wetting than are the remaining fibres of the birthcoat.

(ii) Heat Production and hip coat depth

At $5^{o}C$ ambient temperature, the overall regression coefficient of heat production on hip coat depth was $b = -0.29 \pm 0.07$ W kg^{-1} mm^{-1} which was highly significant ($t_{94} = 4.36$, $P<.001$). The magnitude of this regression suggests that much of the differ-

TABLE 14: EFFECT OF SIRE BREED, WETNESS, SEX AND BODYWEIGHT ON HIP BIRTHCOAT DEPTH

Classification	Hip Birthcoat Depth (mm) Mean ± S.E.		
	Sire breed		
	Romney	Drysdale	Both Breeds
Wetness			
Dry	10.5 ± 0.6[a] (26)	21.4 ± 0.7[c] (22)	15.9 ± 0.4 (48)
Wet	9.5 ± 0.6[a] (27)	17.7 ± 0.7[b] (21)	13.6 ± 0.5 (48)
Dry and Wet	10.0 ± 0.4 (53)	19.5 ± 0.5 (43)	
Sex			
Male	14.9 ± 0.4 (48)		
Female	14.6 ± 0.5 (48)		

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Sire Breed (Breed)	1	2079.19	218.99***
Wetness (Wet.)	1	115.82	12.20***
Sex	1	2.33	0.24 NS
Breed x Wet.	1	42.01	4.42*
Breed x Sex	1	8.39	0.88 NS
Wet. x Sex	1	0.32	0.03 NS
Breed x Wet. x Sex	1	11.59	1.22 NS
Error	88	9.50	

.../continued

TABLE 14, continued

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (above)	7	341.28	
Intra-class (sire breed) regression of hip coat depth on body weight	2	37.90	4.29*
Pooled within-class	1	49.63	5.62*
Difference	1	26.18	2.96†
Residual error	86	8.83	

ence in metabolic rate between the Romney and Drysdale-cross lambs can be accounted for by their different birthcoat depths.

The pooled within-class regression coefficient of heat production on coat depth at this position was significant only at the 10% level (Table 15) with a value $b = -0.14 \pm 0.08$ W kg^{-1} mm^{-1}. Although the within-sire breed regressions were not significantly different at the 5% level, this difference approached significance for all 3 birthcoat characteristics measured and is likely to represent a real effect. Among the Romney lambs the regression slope was $b = -0.38 \pm 0.16$ W kg^{-1} mm^{-1} which was significant ($t_{51} = 2.42$, $P<.05$). The magnitude of this slope is such that lambs with the highest hip birthcoat depths encountered among the Romneys (18mm) would require, on average, 4.2 W kg^{-1} less heat production to maintain body temperature than lambs with the lowest coat depths (7mm). This difference is approximately 25% of the mean summit metabolic rate measured in Chapter III and so is of considerable practical importance.

Among the Drysdale-cross lambs, heat production was apparently independent of coat depth, the regression coefficient being $b = -0.06 \pm 0.10$ W kg^{-1} mm^{-1} ($t_{41} = 0.59$, NS.). However, when the regression lines for the two "breeds" were considered together, there was some evidence of a curvilinear relationship between heat production and hip coat depth. The presence of curvilinearity was tested for by fitting the linear and quadratic terms in the regression of heat production on coat depth after a model excluding the "sire breed" main effect. As is shown in Table 16, the quadratic term was significant ($P<.05$) when fitted

TABLE 15: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (SIRE BREED) REGRESSIONS OF HEAT PRODUCTION AT 5°C AMBIENT TEMPERATURE ON HIP BIRTHCOAT DEPTH

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 7)	28	49.34	
Intra-class (sire breed) regression of heat production on hip coat depth	2	12.19	3.11†
Pooled within-class	1	12.24	3.12†
Difference	1	12.14	3.09†
Residual error	65	3.92	

TABLE 16: TEST OF CURVILINEARITY IN THE RELATIONSHIP BETWEEN HEAT PRODUCTION AT 5°C AMBIENT TEMPERATURE AND HIP BIRTHCOAT DEPTH

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Wetness (Wet.)	1	1206.36	323.79***
Airspeed (Asp.)	3	4.99	1.34 NS
Sex	1	6.22	1.67 NS
Wet. x Asp.	3	2.50	0.67 NS
Wet. x Sex	1	0.24	0.06 NS
Asp. x Sex	3	4.77	1.28 NS
Wet. x Asp. x Sex	3	2.46	0.66 NS
Pooled within-class regression of heat production on hip coat depth:			
Linear term	1	95.85	25.73***
Quadratic term	1	17.55	4.71*
Residual error	78	3.73	

after the linear term, indicating that the gain in insulation per unit of depth declines as hip birthcoat depth increases. This effect occurs partly because the surface area of the coat, which is presented to the cold environment, increases with coat depth. Since a greater surface area predisposes to high rates of heat transfer from the coat to the environment, coat insulation is not directly proportional to depth (Blaxter, 1962). Furthermore, the halo hairs, although sparsely distributed in the coat, protrude from it and determine its depth in the Drysdale-cross lambs. A unit depth of the "outer coat" formed by these fibres is therefore expected to provide less insulation than a corresponding depth of the more dense Romney coat. The magnitude of the partial regression coefficients for the linear and quadratic terms ($b = -0.60 \pm 0.20$ W kg^{-1} mm^{-1} and $b = 0.010 \pm 0.006$ W kg^{-1} mm^{-2} respectively) indicates that maximum coat insulation would be achieved at a coat depth of approximately 30 mm.

The within-wetness regression coefficients of heat production at $5^{o}C$ ambient temperature on hip birthcoat depth were not found to be significantly heterogeneous. Thus it appears that the amount of insulation provided by a unit depth of coat is similar in both wet and dry coats. Any effects of wetting on the insulation provided by the birthcoat must therefore have been mediated through a change in coat depth, this being most pronounced in the Drysdale-cross lambs. Similarly the within-airspeed regressions of heat production on coat depth had homogeneous slopes which reinforces earlier conclusions that the available airspeeds were not sufficiently high to penetrate the coat structure.

(iii) Hip coat depth, bodyweight and gestation length

It will be noted from the analysis of covariance in Table 14 that the pooled within-class regression coefficient of hip birthcoat depth on lamb bodyweight was significant ($P<.05$). The magnitude of this coefficient ($b = 0.96 \pm 0.41$ mm kg^{-1}) indicates that, at this position, heavier lambs benefit by approximately 1 mm coat depth (or 10% of the mean Romney coat depth) per extra kg of bodyweight. Thus heavy lambs may be favoured by an improved coat insulation as well as by surface area considerations.

Although the within-sire breed regressions of coat depth on bodyweight were heterogeneous only at the 10% level (Table 14), the difference again approached significance for all 3 birthcoat characteristics measured and so may represent a real effect. Among the Romney lambs, hip coat depth was independent of bodyweight ($b = 0.43 \pm 0.50$ mm kg^{-1}, $t_{51} = 0.86$, NS.) whereas among the Drysdale-cross lambs a strong relationship was evident ($b = 1.88 \pm 0.67$ mm kg^{-1}, $t_{41} = 2.80$, $P<.01$). Apparently coat depth was, in the Drysdale-cross lambs, more sensitive to bodyweight (and possibly also to the level of pre-natal nutrition received by the lamb), despite there being no significant effect of sire breed on bodyweight (Table 31). This difference may reflect the greater rate of wool growth, and hence the greater nutritional demand for wool production, in the Drysdale-cross lambs during the late gestation period.

The overall regression coefficient of hip birthcoat depth on gestation length was $b = 0.15 \pm 0.26$ mm day^{-1} ($t_{94} = 0.59$, NS.)

and the pooled within-class regression was similarly non-significant (Table 17). Nor were the regression slopes significantly different between the sire breeds (Table 17). Hence there was apparently no relationship between coat depth and gestation length, despite gestation length being significantly related to bodyweight (to be discussed later). This result probably indicates that the slightly superior coat depths of heavier lambs derive from common effects of pre-natal nutrition. Since birthweight is more sensitive to variation in pre-natal nutrition than is gestation length (Thomson and Thomson, 1948-49; Taplin and Everitt, 1964), small differences in the level of pre-natal nutrition received by the lambs may have lead to correlated effects on birthcoat development and birthweight, but not on gestation length. Conversely, it seems reasonable to expect that, had the lambs been subjected to a severe nutritional stress *in utero*, a relationship between coat depth and gestation length might also have been apparent.

Alexander (1964) has suggested that poor pre-natal nutrition of lambs is likely to reduce the insulative value of their birthcoats and so increase their susceptibility to death by starvation and exposure. The results from this study would seem to confirm that suggestion since they show that, even where lambs are adequately fed *in utero*, and have good mean birth weights, small lambs may still be disadvantaged by poor coat depth. This effect is likely to be most strongly expressed in lambs which are genetically predisposed to producing very deep coats.

TABLE 17: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (SIRE BREED) REGRESSIONS OF HIP BIRTHCOAT DEPTH ON GESTATION LENGTH

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 14)	7	341.28	
Intra-class (sire breed) regression of hip coat depth on gestation length	2	14.74	1.57 NS
Pooled within-class	1	22.16	2.36 NS
Difference	1	7.32	0.78 NS
Residual error	86	9.37	

(b) Depth of birthcoat at the midside position

(i) Treatment effects on midside coat depth

The effects of sire breed, wetness and sex on birthcoat depth at the midside position were similar to those at the hip site. Both sire breed and wetness exerted significant effects on midside coat depth, and the reduction in depth upon wetting was most pronounced in the Drysdale-cross lambs (Table 18). In fact the only major difference between the two positions was in the degree to which the wetting treatment reduced coat depth. At the hip site, wetting produced a 17% reduction in depth while at the midside position a 25% reduction occurred. The greater reduction at the latter site was also associated with a greater dry coat depth and thus reinforces the view that deeper coats may be more sensitive to the effects of wetting. Sex of the lamb did not significantly affect its coat depth at either of the 2 positions examined.

(ii) Heat production and midside coat depth

The overall regression coefficient of heat production at $5^{o}C$ ambient temperature on midside coat depth was $b = -0.26 \pm 0.05$ W kg^{-1} mm^{-1} which was of the same magnitude and significance ($t_{94} = 4.89$, $P<.001$) as the equivalent relationship for hip coat depth. Similarly, the pooled within-class regression coefficient ($b = -0.13 \pm 0.06$ W kg^{-1} mm^{-1}) was virtually identical in slope to that for hip coat depth but was more highly significant ($P<.05$, Table 19). The within-sire breed regressions were again significantly different only at the 10% level, being $b = -0.47 \pm 0.17$ W kg^{-1} mm^{-1} ($t_{51} = 2.71$, $P<.05$) and

TABLE 18: EFFECT OF SIRE BREED, WETNESS, SEX AND BODYWEIGHT ON MIDSIDE BIRTHCOAT DEPTH

Classification	Midside Birthcoat Depth (mm) Mean ± S.E.		
	Sire breed		
	Romney	Drysdale	Both breeds
Wetness			
Dry	10.6 ± 0.8[a] (26)	24.3 ± 0.8[c] (22)	17.5 ± 0.3 (48)
Wet	9.3 ± 0.8[a] (27)	18.2 ± 0.9[b] (21)	14.1 ± 0.6 (48)
Dry and Wet	10.0 ± 0.5 (53)	21.6 ± 0.6 (43)	
Sex			
Male	15.1 ± 0.6 (48)		
Female	16.4 ± 0.6 (48)		

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Sire Breed (Breed)	1	3074.58	205.14***
Wetness (Wet.)	1	245.04	16.35***
Sex	1	33.00	2.20 NS
Breed x Wet.	1	128.36	8.56**
Breed x Sex	1	5.52	0.37 NS
Wet. x Sex	1	47.65	3.18†
Breed x Wet. x Sex	1	10.47	0.70 NS
Error	88	14.99	

.../continued

TABLE 18, continued

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (above)	7	507.01	
Intra-class (sire breed) regression of midside coat depth on bodyweight	2	42.30	2.95†
Pooled within-class	1	39.58	2.76†
Difference	1	45.02	3.14†
Residual error	86	14.35	

TABLE 19: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (SIRE BREED) REGRESSIONS OF HEAT PRODUCTION AT 5°C AMBIENT TEMPERATURE ON MIDSIDE BIRTHCOAT DEPTH

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 7)	28	49.34	
Intra-class (sire breed) regression of heat production on midside coat depth	2	16.57	4.37*
Pooled within-class	1	18.25	4.82*
Difference	1	14.89	3.93†
Residual error	65	3.79	

$b = -0.08 \pm 0.07$ W kg^{-1} mm^{-1} ($t_{41} = 1.19$, NS.) for the Romney and Drysdale-cross lambs respectively. However, a test for curvilinearity in the relationship between heat production and midside coat depth across both "breeds" of lambs (Table 20) showed that the quadratic term in the regression was not significant. Thus the relationship was adequately represented by a straight line in contrast to the heat production - hip coat depth relationship which was apparently curvilinear.

The within-wetness and within-airspeed regressions of heat production on midside coat depth were homogeneous and again these results are compatible with those from the study of hip coat depth. Similar conclusions may be drawn about the effects of wetting and air movement (within the range available) on the insulation afforded by a unit depth of coat at the midside position.

(iii) Midside coat depth, body weight and gestation length

As the analysis of covariance in Table 18 indicates, the relationship between midside coat depth and body weight was less strong than for hip coat depth, the pooled within-class regression coefficient being significant only at the 10% level although the slope was of a similar magnitude ($b = 0.85 \pm 0.52$ mm kg^{-1}) to that for the hip site. The within-sire breed regression coefficients were again significantly different only at the 10% level, being $b = 0.17 \pm 0.64$ mm kg^{-1} ($t_{51} = 0.27$, NS.) and $b = 2.06 \pm 0.86$ mm kg^{-1} ($t_{41} = 2.39$, $P<.05$) for the Romney and Drysdale-cross lambs respectively.

The overall regression coefficient of midside coat depth on gestation length was $b = -0.06 \pm 0.32$ mm day^{-1} which was not

TABLE 20: TEST OF CURVILINEARITY IN THE RELATIONSHIP BETWEEN HEAT PRODUCTION AT 5°C AMBIENT TEMPERATURE AND MIDSIDE BIRTHCOAT DEPTH

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 16)	15	83.80	
Pooled within-class regression of heat production on midside coat depth:			
Linear term	1	103.61	27.73***
Quadratic term	1	8.95	2.39 NS
Residual error	78	3.74	

TABLE 21: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (SIRE BREED) REGRESSIONS OF MIDSIDE BIRTHCOAT DEPTH ON GESTATION LENGTH

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 18)	7	507.01	
Intra-class (sire breed) regression of midside coat depth on gestation length	2	6.33	0.42 NS
Pooled within-class	1	1.70	0.11 NS
Difference	1	10.96	0.72 NS
Residual error	86	15.19	

significant (t_{94} = 0.19, NS.). The pooled within-class regression was similarly non-significant and the within-sire breed slopes were homogeneous (Table 21). Thus the relationship between midside coat depth, bodyweight and gestation length appears to have been similar to the situation for coat depth at the hip site.

It is clear, therefore, that the 2 coat depths were related to other characteristics of the lamb in a very similar manner. As a result, it seems likely that the insulative value of the birthcoat could be as adequately described by measuring only one of the coat depths as by measuring both of them. This hypothesis will be further examined when consideration is given to the "Relationships between the birthcoat characteristics".

(c) Midside wool weight per unit area of skin

(i) Treatment effects on midside wool weight

The weight of wool per unit area of skin on the midside was measured only once on each lamb since it was considered unlikely to vary with time over the first 36 hours of life (during which the lambs were to be tested) or with environmental treatments such as wetting. The analyses for the effects of sire breed and sex on this trait (hereafter referred to as "midside wool weight"), and for its relationships with bodyweight and gestation length, were therefore performed only on data from the 66 lambs (34 Romney, 32 Drysdale-cross) at their first test.

As was described earlier in this chapter, lambs presented for a second test were re-randomized to environmental treatment groups without regard to their previous treatment, and so were

treated as being separate individuals at each of the tests. Analyses for the relationship between heat production and midside wool weight therefore involve all 96 "lambs".

The analysis of variance presented in Table 22 shows that the Drysdale-cross lambs had significantly ($P<.001$) greater midside wool weights than did the Romney lambs, while differences between the sexes were not significant. In this respect midside wool weight was similar to birthcoat depth.

(ii) Heat production and midside wool weight

Neither the overall ($b = -0.015 \pm 0.018$ W kg^{-1} mg^{-1} cm^2, $t_{94} = 0.90$, NS.) nor the pooled within-class (Table 23) regressions of heat production (at $5^{o}C$ ambient temperature) on midside wool weight were significant. However, the within-sire breed regressions were significantly different ($P<.05$) and the pattern was similar to that for birthcoat depth. Thus a significant relationship existed among the Romney lambs ($b = -0.072 \pm 0.036$ W kg^{-1} mg^{-1} cm^2, $t_{51} = 2.02$, $P<.05$) but not among the Drysdale-crosses ($b = 0.019 \pm 0.014$ W kg^{-1} mg^{-1} cm^2, $t_{41} = 1.36$, NS.). As with the birthcoat depths, particularly at the hip site, there was some evidence of curvilinearity in the relationship between heat production and midside wool weight. This was again tested for by fitting the linear and then quadratic terms in this regression after a model excluding the main effect "sire breed". The analysis of covariance presented in Table 24 shows that the quadratic term was significant ($P<.01$). It can be predicted from the magnitude of the linear and quadratic partial regression coefficients ($b = -0.129 \pm 0.041$ W kg^{-1} mg^{-1} cm^2, and

TABLE 22: EFFECT OF SIRE BREED, SEX AND BODYWEIGHT ON MIDSIDE WOOL WEIGHT PER UNIT AREA OF SKIN : LAMBS AT FIRST TEST

Classification	Midside Wool Weight/Unit Area (mg cm^{-2}) Mean ± S.E.
Sire Breed	
Romney	42.1 ± 4.0 (53)
Drysdale	69.4 ± 4.1 (43)
Sex	
Male	52.2 ± 4.1 (48)
Female	59.3 ± 4.0 (48)

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Sire Breed	1	11 983.23	22.27***
Sex	1	819.91	1.52 NS
Sire Breed x Sex	1	205.25	0.38 NS
Error	62	538.13	

Analysis of Covariance

Source of Variation	d.f.	Mean Square	F
Main effects model (above)	3	4113.04	
Intra-class (sire breed) regression of midside wool weight on bodyweight	2	3676.56	8.48***
Pooled within-class	1	2523.37	5.82*
Difference	1	4829.75	11.14**
Residual error	60	433.51	

TABLE 23: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (SIRE BREED) REGRESSIONS OF HEAT PRODUCTION AT 5°C AMBIENT TEMPERATURE ON MIDSIDE WOOL WEIGHT PER UNIT AREA OF SKIN

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 7)	28	49.34	
Intra-class (sire breed) regression of heat production on midside wool weight	2	12.15	3.10†
Pooled within-class	1	1.57	0.40 NS
Difference	1	22.73	5.79*
Residual error	65	3.93	

TABLE 24: TEST OF CURVILINEARITY IN THE RELATIONSHIP BETWEEN HEAT PRODUCTION AT 5°C AMBIENT TEMPERATURE AND MIDSIDE WOOL WEIGHT PER UNIT AREA OF SKIN

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 16)	15	83.80	
Pooled within-class regression of heat production on midside wool weight:			
Linear term	1	16.77	3.71†
Quadratic term	1	34.88	7.72**
Residual error	78	4.52	

b = 0.0007 ± 0.0002 W kg^{-1} mg^{-2} cm^{4} respectively) that maximum coat insulation would be achieved at a midside wool weight of about 90 mg cm^{-2}. As will be demonstrated later, this approximately coincides with the coat depth (30 mm) at which the greatest conservation of body heat by the coat was found to occur. It should also be noted that if the partial regression coefficients are applied to the full range of midside wool weights in these lambs (20 to 150 mg cm^{-2}), the predicted metabolic rate begins to increase beyond 90 mg cm^{-2}. However, little credence can be given to the view that very high midside wool weights predispose to a high metabolic rate (i.e. a high rate of heat loss) since only 4 lambs had midside wool weights in excess of 90 mg cm^{-2} and some extrapolation is therefore involved. A similar situation existed with the partial regression coefficients for hip coat depth.

The within-wetness and within-airspeed regressions of heat production on midside wool weight were again homogeneous. In this respect, midside wool weight was similar to the coat depths and it may be concluded that the insulative value of a unit of midside wool weight is not affected by wetting of the lamb or by air movement (within the range of airspeeds available in this study).

(iii) Midside wool weight, bodyweight and gestation length

As the analysis of covariance in Table 22 illustrates, the within-sire breed regressions of midside wool weight on lamb bodyweight were significantly ($P<.01$) heterogeneous. The relationships were similar to those for the birthcoat depths, midside

wool weight being significantly associated with bodyweight among the Drysdale-cross lambs ($b = 19.16 \pm 6.60$ mg cm^{-2} kg^{-1}, $t_{30} = 2.90$, $P<.01$) but not among the Romneys ($b = -2.40 \pm 4.53$ mg cm^{-2} kg^{-1}, $t_{32} = 0.53$, NS.). However, this trait differs from the coat depths since it was the only coat characteristic for which there was strong evidence of a differential "breed" response to bodyweight (recall that, for the coat depths, the within-sire breed regressions were significantly different only at the 10% level). While this difference between the coat characteristics could indicate that midside wool weight is more sensitive to pre-natal nutrition than are the coat depths, it is more likely to be a function of greater accuracy in the measurement of this trait. Midside wool weight, unlike the coat depths, was not subject to errors of measurement associated with the wetting treatment.

The overall regression coefficient of midside wool weight on gestation length was $b = 2.84 \pm 1.43$ mg cm^{-2} day^{-1} which approaches significance at the 5% level ($t_{64} = 1.99$). The pooled within-class regression was also significant ($b = 3.84 \pm 1.27$ mg cm^{-2} day^{-1}, $P<.01$) and the within-sire breed slopes were homogeneous (Table 25). In this respect midside wool weight differed markedly from the coat depths, both of which were independent of gestation length. However, as is demonstrated by the ordered fitting of the partial intra-sire breed regressions of midside wool weight on lamb bodyweight and gestation length (Table 26), gestation length did not exert a significant control of variation in midside wool weight when fitted after bodyweight. Hence it

TABLE 25: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (SIRE BREED) REGRESSIONS OF MIDSIDE WOOL WEIGHT PER UNIT AREA OF SKIN ON GESTATION LENGTH : LAMBS AT FIRST TEST

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 22)	3	4113.04	
Intra-class (sire breed) regression of midside wool weight on gestation length	2	2595.88	5.53**
Pooled within-class	1	4355.95	9.28**
Difference	1	835.80	1.78 NS
Residual error	60	469.54	

TABLE 26: ORDERED FITTING OF THE PARTIAL WITHIN-CLASS (SIRE BREED) REGRESSIONS OF MIDSIDE WOOL WEIGHT PER UNIT AREA OF SKIN ON BODYWEIGHT AND GESTATION LENGTH : LAMBS AT FIRST TEST

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 22)	3	4113.04	
Partial intra-class (sire breed) regressions of midside wool weight on bodyweight (S.WT) and gestation length (S.GL)			
R(S.GL/μ, M.E.M.[1])	2	2595.88	6.23**
R(S.WT/μ, M.E.M., S.GL)	2	1993.45	4.78*
R(S.WT/μ, M.E.M.)	2	3676.56	8.82***
R(S.GL/μ, M.E.M., S.WT)	2	912.77	2.19 NS
Residual error	58	416.99	

[1] M.E.M. = Main effects model (Table 22).

would seem that the apparent effect of gestation length was mediated through its correlation with bodyweight. Conversely, bodyweight was found to make a significant contribution to the control of variation in midside wool weight when fitted after gestation length. Thus bodyweight exerted an effect over and above that associated with gestation length, and in this respect midside wool weight was again similar to the coat depths.

Reference has been made, in this discussion, to the possibility that the relationships between bodyweight and the birthcoat characteristics were due to differences in the level of pre-natal nutrition received by the lambs. In this context the term "pre-natal nutrition" has been used only in a very general sense, particularly because it is not possible to pinpoint the source of any such differences. For example, variation in the level of pre-natal nutrition received by the lamb might have been due to differences in; the amount and quality of the ewe's feed intake; her ability to mobilize body reserves and make nutrients available to the lamb; the lamb's ability to absorb these nutrients, across the placenta, from the maternal circulation; and in the number of foetuses carried by the ewe. Nevertheless, studies in which nutritional restrictions have been imposed on pregnant ewes do suggest the likelihood of common effects of pre-natal nutrition on the lamb's birthweight and birthcoat development. For example, Taplin and Everitt (1964) found that Merino lambs which were poorly fed *in utero* had significantly lower midside wool weights, birthweights, and total birthcoat weights than well-fed controls, but that gestation length was not affected by the level of pre-natal nutrition.

(d) Relationships between the birthcoat characteristics

The preceding sections of this chapter have identified a number of similarities between the birthcoat characteristics in their relationships with other characteristics of the lamb such as body-weight, gestation length and the metabolic response to cold-stress. It is therefore important to assess the degree to which these characteristics act independently in controlling the metabolic response of the lamb, with a view to identifying the minimum number of characteristics which must be measured to adequately describe the insulative value of the birthcoat.

(i) Midside and hip coat depth

Birthcoat depths at the midside and hip position were, as expected, highly correlated both across the sire breeds ($r = 0.88$, $P<.001$) and within the "breeds" ($r = 0.66$ and $r = 0.67$ for Romney and Drysdale-cross lambs respectively, both $P<.001$). The hypothesis of interdependence in the control of heat production by the 2 coat depths was tested by examining the control of error variance achieved by an ordered fitting of the partial intra-sire breed regressions of heat production (at $5^{o}C$ ambient temperature) on hip and midside coat depth. As Table 27 shows, little additional control of error variance was achieved by fitting the second partial intra-class regression and this was largely independent of the order in which the regressions were fitted. It may therefore be concluded that, under the range of environmental conditions available in this study, the component of coat insulation which is related to depth may be adequately described by measuring depth at only one of these sites.

TABLE 27: ORDERED FITTING OF THE PARTIAL WITHIN-CLASS (SIRE BREED) REGRESSIONS OF HEAT PRODUCTION AT 5°C AMBIENT TEMPERATURE ON MIDSIDE AND HIP BIRTHCOAT DEPTH

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 7)	28	49.34	
Partial intra-class (sire breed) regressions of heat production on midside (S.MD) and hip (S.HD) coat depth			
R(S.MD/μ, M.E.M.[1])	2	16.57	4.33*
R(S.HD/μ, M.E.M., S.MD)	2	2.56	0.67 NS
R(S.HD/μ, M.E.M.)	2	12.19	3.18*
R(S.MD/μ, M.E.M., S.HD)	2	6.95	1.81 NS
Residual error	63	3.83	

[1] M.E.M. = Main effects model (Table 7).

(ii) Midside wool weight and the coat depths

The overall regression coefficients of midside wool weight on hip coat depth and midside coat depth were respectively $b = 2.28 \pm 0.45$ mg cm^{-2} mm^{-1} ($t_{64} = 5.03$) and $b = 1.95 \pm 0.36$ mg cm^{-2} mm^{-1} ($t_{64} = 5.45$), each of which was highly significant ($P<.001$). The pooled within-class regression coefficients were of a similar magnitude, being $b = 1.86 \pm 0.80$ mg cm^{-2} mm^{-1} and $b = 1.53 \pm 0.60$ mg cm^{-2} mm^{-1} respectively (Table 28) although the within-sire breed regressions were not heterogeneous. Thus a strong relationship existed between midside wool weight and the coat depths, although the slope of this regression did not differ between the birthcoat types.

The relationship between these characteristics again suggests the possibility that their individual control of the metabolic response may have been interdependent. This possibility was tested by examining the control of error variance achieved by an ordered fitting of the partial intra-sire breed regressions of heat production (at $5^{o}C$ ambient temperature) on midside coat depth and midside wool weight. As the analysis of covariance in Table 29 shows, a significant control of error variance was achieved by fitting the second partial intra-class regression in each case, irrespective of the order in which the regressions were fitted. Consequently, it would seem that the control of heat production exerted by midside wool weight is largely independent of that attributable to birthcoat depth, despite the obvious correlation between these characters. It should also be noted that the choice of midside coat depth over hip coat depth as a component of the analysis presented in Table

TABLE 28: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (SIRE BREED) REGRESSIONS OF MIDSIDE WOOL WEIGHT PER UNIT AREA OF SKIN ON MIDSIDE AND HIP BIRTHCOAT DEPTHS : LAMBS AT FIRST TEST

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Main effects model (Table 22)	3	4113.04	
Intra-class (sire breed) regression of midside wool weight on hip coat depth	2	1499.36	2.96†
Pooled within-class	1	2748.72	5.43*
Difference	1	250.01	0.49 NS
Residual error	60	506.09	
Main effects model (Table 22)	3	4113.04	
Intra-class (sire breed) regression of midside wool weight on midside coat depth	2	1621.83	3.23*
Pooled within-class	1	3162.49	6.30**
Difference	1	81.17	0.16 NS
Residual error	60	502.00	

TABLE 29: ORDERED FITTING OF THE PARTIAL WITHIN-CLASS (SIRE BREED) REGRESSIONS OF HEAT PRODUCTION AT 5°C AMBIENT TEMPERATURE ON MIDSIDE BIRTHCOAT DEPTH AND WOOL WEIGHT PER UNIT AREA OF SKIN

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 7)	28	49.34	
Partial intra-class (sire breed) regressions of heat production on midside coat depth (S.MD) and midside wool weight (S.WW)			
R(S.MD/μ, M.E.M.[1])	2	16.57	4.94*
R(S.WW/μ, M.E.M., S.MD)	2	17.45	5.20**
R(S.WW/μ, M.E.M.)	2	12.15	3.62*
R(S.MD/μ, M.E.M., S.WW)	2	21.87	6.52**
Residual error	63	3.36	

[1] M.E.M. = Main effects model (Table 7).

29 was entirely arbitrary; a similar conclusion is reached if hip coat depth is substituted for depth at the midside position.

(iii) Possible mechanisms for the control of heat production by midside wool weight

Since midside wool weight appears to contribute to birthcoat insulation independently of coat depth, it seems appropriate to examine possible mechanisms by which this effect may occur. Variation in midside wool weight per unit area of skin is determined by variation in 4 traits - fibre density (number of fibres per unit area of skin), mean fibre length, mean fibre diameter, and the specific gravity of the wool. Fibre length is clearly related in some way to birthcoat depth and this presumably accounts for the relationship between midside wool weight and coat depth. Indeed, it is likely that this relationship is even more significant than is indicated by the regressions discussed previously since, in those regressions, errors in the measurement of the independent variable (coat depth) included not only the normal errors of measurement but also those induced by coat wetness in some lambs. Accordingly it is probable that any effect of midside wool weight on insulation which is independent of depth must also be independent of mean fibre length.

Since the airspeeds available in this study were apparently too low to penetrate the birthcoat structure, the effect of increasing midside wool weights must have been to reduce the rate at which heat flowed through a unit depth of the still air layer of the coat. Heat flows through the still air layer mainly by natural convection currents (which are a consequence of thermal

gradients within the air), and the birthcoat fibres may have an important role in immobilizing the air and reducing the extent to which natural convection occurs (Burton and Edholm, 1955). In this connection both fibre density and fibre diameter might be expected to have an effect. Coats with a high fibre density are more likely to reduce convection currents by providing an increased frictional resistance to air movement within the coat. However, while variation in fibre density might have contributed to the relationship between heat production and midside wool weight within the Romney and Drysdale-cross "breeds", it is unlikely to have contributed greatly to the between-sire breed differences since fibre density is similar in Romney and Drysdale-Romney cross lambs (Ross, 1954; Cockrem, 1959; Stephenson, 1959).

Coarse fibres present a greater surface area (per unit length) to still air within the coat than do fine fibres and so can be expected to more efficiently retard air movement. Within the Romney coats this effect is likely to have been small because large changes in fibre weight (and hence in midside wool weight for a constant fibre density) would be associated with only small changes in surface area (the weight per unit length being proportional to the square of fibre diameter while surface area is linearly related to diameter). However a between-sire breed effect is possible because although the Drysdale-cross coats have a greater mean diameter than those of the Romneys, their very coarse fibres also have a lower specific gravity than the Romney wool. This is because the coarse fibres contain a hollow core of medulla (Ryder and Stephenson, 1968). Hence the gain in surface area per unit increase in midside wool weight is expected

to be much greater across the "breeds" than within the Romney breed.

It may therefore be concluded that the relationship between heat production and midside wool weight is likely to have been due to the effects of fibre density (per unit area of skin) and fibre diameter on the rate of convective heat loss through the still air layer of the birthcoat. No attempt has been made to estimate the relative contributions of these factors to coat insulation. Fibre density and diameter may also influence the ability of the coat to control radiant heat loss (by reflection) although this effect is likely to be of lesser importance than that associated with convective losses (Burton and Edholm, 1955).

(iv) The curvilinear relationship between heat production and midside wool weight

Two possible explanations may now be offered for the curvilinear relationship between heat production and midside wool weight. The first is that, at high levels of midside wool weight, heat loss by conduction through the birthcoat fibres cancels out the corresponding gain in coat insulation. According to Burton and Edholm (1955), conduction of heat by the fibres of the coat is unlikely to be important unless the bulk density of the material forming the coat exceeds 5 pounds per cubic foot (80 mg cm^{-3}). An estimate of the bulk density of the birthcoats of the lambs in this study may be derived using the midside wool weight data. For example, the mean midside wool weight of the Romney lambs was 42.1 mg cm^{-2} and the mean coat depth (midside and hip) approximately 1.0 cm. From this the mean bulk density is estimated to be 40 mg cm^{-3} (or 50% of the upper limit),

assuming that the midside wool weight accurately estimates the mean weight of birthcoat per unit area of skin across the whole body. This assumption appears to be reasonable, as is indicated by the data from 12 completely-shorn Romney lambs (Appendix II). The midside wool weight of these lambs averaged 41.4 mg cm^{-2} and the estimated bulk density of their coats (calculated from measured birthcoat weight and depth plus an estimate of body surface area) was 48 to 59 mg cm^{-3}.

The mean birthcoat depth of the Drysdale-cross lambs was approximately twice that of the Romneys, but their midside wool weight was only 60% greater. This no doubt reflects the lower specific gravity of the medullated fibres and their tendency to protrude from the coat (so adding depth but little extra weight). Moreover, since midside wool weight was positively correlated with coat depth, the Drysdale-cross lambs with very high midside wool weights(in excess of 90 mg cm^{-2}) also had deep coats. In no case did the estimated bulk density of the coats of these lambs exceed 70 mg cm^{-3}. It must therefore be concluded that the curvilinear relationship between heat production and midside wool weight was not due to increasing rates of conductive heat loss through the fibres of the birthcoat.

An alternative hypothesis would be that this relationship occurred because of the correlation between midside wool weight and coat depth. It may be that the benefits of increasing midside wool weights were gradually negated by the associated effects of increasing coat depth and surface area of the coat exposed to the external environment. Earlier in this chapter, maximum

coat insulation was predicted to occur at a coat depth of about 30 mm. By regression analysis it can be shown that, at this coat depth, the midside wool weight was approximately 92 mg cm^{-2}. This corresponds almost exactly with the midside wool weight at which maximum coat insulation was predicted, and so supports the second hypothesis for this effect.

4. Bodyweight and gestation length

(a) Treatment effects on bodyweight and gestation length

Although the lambs were re-weighed at each test, variation in weight between the tests was small and was not affected by the environmental treatments imposed during the test procedure. In this respect bodyweight was more like midside wool weight than like the coat depths which varied to a considerable degree with the environmental conditions, particularly among the Drysdale-cross lambs. Analyses for the effects of sire breed and sex on bodyweight and gestation length, and for the relationship between these traits, were therefore carried out using only the data from the 66 lambs at their first test.

Neither sire breed nor sex of the lamb exerted a significant effect on gestation length although the interaction between these treatments was significant ($P<.05$, Table 30). Female Romney lambs had a longer gestation period than males of the same breed (by an average of 1.6 days) whereas, among the Drysdale-cross lambs, gestation length was independent of sex. However, this interaction was not reflected in the bodyweights of the lambs since, although male lambs were significantly heavier than females (Table 31), the effects of sex and sire breed on bodyweight at first test were additive. Sire

TABLE 30: EFFECT OF SIRE BREED AND SEX ON GESTATION LENGTH : LAMBS AT FIRST TEST

Classification	Gestation Length (Days) Mean ± S.E.		
	Sex		
	Male	Female	Both Sexes
Sire Breed			
Romney	145.6 ± 0.6[a] (22)	147.2 ± 0.5[b] (31)	146.4 ± 0.5 (53)
Drysdale	146.7 ± 0.5[a] (26)	145.5 ± 0.6[a] (17)	146.1 ± 0.4 (43)
Both Breeds	146.1 ± 0.4 (48)	146.3 ± 0.4 (48)	

Analysis of Variance			
Source of Variation	d.f.	Mean Square	F
Sire Breed	1	1.53	0.32 NS
Sex	1	0.90	0.19 NS
Sire Breed x Sex	1	30.34	6.37*
Error	62	4.77	

TABLE 31: EFFECT OF SIRE BREED, SEX AND GESTATION LENGTH ON BODYWEIGHT : LAMBS AT FIRST TEST

Classification	Bodyweight (kg) Mean ± S.E.
Sire Breed	
Romney	4.96 ± 0.14 (53)
Drysdale	4.90 ± 0.14 (43)
Sex	
Male	5.15 ± 0.14 (48)
Female	4.72 ± 0.14 (48)

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Sire Breed	1	0.06	0.09 NS
Sex	1	3.00	4.84*
Sire Breed x Sex	1	0.86	1.39 NS
Error	62	0.62	

Analysis of Covariance

Source of Variation	d.f.	Mean Square	F
Main effects model (above)	3	14.15	
Intra-class (sire breed) regression of bodyweight on gestation length	2	3.23	6.06**
Pooled within-class	1	6.28	11.78**
Difference	1	0.18	0.34 NS
Residual error	60	0.53	

breed did not significantly affect bodyweight, a result consistent with the findings of Cockrem and Rae (1959).

(b) The relationship between bodyweight and gestation length

The overall regression coefficient of bodyweight on gestation length was b = 0.14 ± 0.04 kg day^{-1} (t_{64} = 3.43, P<.01) and the pooled within-class regression coefficient was of a similar order (b = 0.15 ± 0.04 kg day^{-1}) and significance (P<.01, Table 31). While it is obviously difficult to establish "cause and effect" relationships involving bodyweight (as an indicator of birthweight) and gestation length, it may be noted that these regression coefficients are similar in magnitude to estimates of growth rate in late pregnancy obtained by the serial slaughter of foetuses (Rattray, Garret, East and Hinman, 1974).

(c) Heat production and bodyweight

The role of bodyweight as a determinant of the metabolic response to cold-stress was examined by fitting exponential functions to the relationship between Total Heat Production (in Watts) and bodyweight (see "Methods of Analysis"). Preliminary analyses showed that the 3 Drysdale-cross lambs which experienced severe hypothermia, and which were notable for their very low summit metabolic rates, exerted a disproportionate influence on the regressions. They have therefore been excluded from the analyses presented here.

The overall regression coefficient of $\log_e$ total heat production (THP) on $\log_e$ bodyweight was b = 1.21 ± 0.25 which was highly significant (t_{91} = 4.90, P<.001). An exponent of this magnitude implies that heat production per unit bodyweight actually increases with body-

TABLE 32: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (SIRE BREED) REGRESSIONS OF LOG TOTAL HEAT PRODUCTION AT 5°C AMBIENT TEMPERATURE ON LOG BODYWEIGHT

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Sire Breed (Breed)	1	0.65	22.89***
Wetness (Wet.)	1	12.06	424.58***
Airspeed (Asp.)	3	0.12	4.20**
Sex	1	0.01	0.39 NS
Breed x Wet.	1	0.01	0.46 NS
Breed x Asp.	3	0.06	2.07†
Breed x Sex	1	0.03	1.16 NS
Wet. x Asp.	3	0.13	4.67**
Wet. x Sex	1	0.00	0.00 NS
Asp. x Sex	3	0.09	3.04*
Breed x Wet. x Asp.	3	0.06	2.02 NS
Breed x Wet. x Sex	1	0.00	0.06 NS
Breed x Asp. x Sex	3	0.10	3.37*
Wet. x Asp. x Sex	3	0.06	1.94 NS
Intra-class (sire breed) regression of $\log_e$ total heat production on $\log_e$ bodyweight	2	0.59	20.58***
Pooled within-class	1	1.10	38.71***
Difference	1	0.07	2.44 NS
Residual error	62	0.03	

weight. However, once treatment effects on heat production had been taken account of, the pooled-within class regression coefficient had a more conventional value of b = 0.79 ± 0.13 which was again highly significant (P<.001, Table 32). This exponent suggests that heat production per unit bodyweight declines as bodyweight increases, and is in accordance with the results from a later experiment (Chapter V). Further consideration will be given to the role of bodyweight in that chapter.

5. Relative humidity of air in the climate chambers

(a) Treatment effects on relative humidity

The effects of wetness, airspeed and ambient temperature on the RH of air in the empty chamber have already been described in Chapter II. When a lamb is placed in the climate chamber, it is to be expected that the humidity of the air will also be affected by the rate at which water evaporates from the lamb's birthcoat and skin surface. In this situation, measured RH may reflect the rate at which water evaporates from different types of coat, which may in turn be related to the level of heat production required by the lamb to maintain body temperature.

Wetness again exerted the major control of variation in RH (Table 33), and the mean RH of the air (pooled across all other treatments) was 7 to 10% higher when lambs were in the chambers than when the chambers were empty (Table 3). This occurred during wet and dry tests, no doubt as a consequence of extra evaporation from the lamb's body. Similarly, airspeed exerted a significant effect on measured RH as was the case in the preliminary experiment (Chapter II).

TABLE 33: EFFECT OF SIRE BREED, WETNESS, AIRSPEED AND SEX ON MEASURED RELATIVE HUMIDITY OF AIR IN THE CHAMBERS
(Relative humidity means and their standard errors are expressed as decimals)

Classification		Measured Relative Humidity - Mean ± S.E.	
Sire breed	Sex	Wetness	
		Dry	Wet
Romney	Male	0.773 ± 0.025[b] (10)	0.900 ± 0.020[c] (12)
	Female	0.732 ± 0.018[b] (16)	0.911 ± 0.018[c] (15)
Drysdale	Male	0.656 ± 0.018[a] (14)	0.905 ± 0.020[c] (12)
	Female	0.711 ± 0.025[ab] (8)	0.855 ± 0.023[c] (9)

Sire breed		
Romney	0.829 ± 0.009	(53)
Drysdale	0.782 ± 0.011	(43)
Wetness		
Dry	0.725 ± 0.011	(48)
Wet	0.893 ± 0.010	(48)
Nominal airspeed (m sec^{-1})		
0.0	0.818 ± 0.014	(24)
1.0	0.774 ± 0.015	(24)
1.5	0.830 ± 0.015	(24)
2.0	0.800 ± 0.014	(24)
Sex		
Male	0.809 ± 0.010	(48)
Female	0.802 ± 0.011	(48)

.../continued

TABLE 33, continued

Analysis of Variance			
Source of Variation	d.f.	Mean Square	F
Sire Breed (Breed)	1	0.053	10.53**
Wetness (Wet.)	1	0.781	155.37***
Airspeed (Asp.)	3	0.015	2.94*
Sex	1	0.001	0.12 NS
Breed x Wet.	1	0.012	2.39 NS
Breed x Asp.	3	0.001	0.15 NS
Breed x Sex	1	0.001	0.29 NS
Wet. x Asp.	3	0.009	1.84 NS
Wet. x Sex	1	0.002	0.33 NS
Asp. x Sex	3	0.006	1.20 NS
Breed x Wet. x Asp.	3	0.001	0.17 NS
Breed x Wet. x Sex	1	0.033	6.52*
Breed x Asp. x Sex	3	0.006	1.23 NS
Wet. x Asp. x Sex	3	0.003	0.56 NS
Error	67	0.005	

TABLE 34: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (WETNESS) REGRESSIONS OF HEAT PRODUCTION ON RELATIVE HUMIDITY OF THE CLIMATE CHAMBER AIR AT 5°C AMBIENT TEMPERATURE

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 7)	28	49.34	
Intra-class (wetness) regression of heat production on RH	2	11.33	2.87†
Pooled within-class	1	12.99	3.29†
Difference	1	9.67	2.45 NS
Residual error	65	3.95	

More important, however, was the significant effect of sire breed, the RH of air in the chambers being 4.7% higher for the Romney lambs than for the Drysdale-crosses. As is indicated by the significant sire breed x wetness x sex interaction (Table 33), this difference was particularly evident among the dry lambs. Hence it seems likely that, during the test, the dry Romney lambs experienced a somewhat greater rate of evaporation from the birthcoat than did the Drysdale-crosses. This effect would presumably have contributed to the higher metabolic rates of these lambs at this ambient temperature.

(b) Heat production and relative humidity

The overall regression coefficient of heat production on RH at $5^{o}C$ ambient temperature was b = 0.26 ± 0.02 Watts per kg per unit percentage RH which was highly significant (t_{94} = 10.69, P<.001), while the pooled within-class regression coefficient was not significant at the 5% level (Table 34). The significance of the former regression appears to have been a function of treatment (particularly wetness) effects on heat production and RH. This regression also demonstrates that, in an essentially closed environment, the relationship between heat production and RH derives not from a "cause and effect" situation, but rather from one in which both variables are influenced by a common factor (in this case evaporation from the lamb's body).

Chapter Summary

Heat production, rectal temperature and hind-limb skin temperature responses were measured in 66 lambs tested wet or dry in a range of airspeeds at 6 ambient temperatures. Thirty of the lambs were tested twice giving a total of 96 observations.

Wetting of the lambs caused large increases in metabolic rate and the results show that dry lambs are unlikely to become severely hypothermic unless ambient temperatures are well below 5°C. Drysdale-cross lambs had significantly lower metabolic rates than Romneys, the effects of sire breed being additive with those of wetness and airspeed. Evidence was presented that the lower critical temperature occurs at a higher ambient temperature for Romney lambs than for Drysdale-crosses. The level of airspeed to which the lamb was exposed exerted its most pronounced effect on metabolic rate at the higher ambient temperatures, but it appears that the maximum airspeeds available were insufficent to penetrate the coat structure of either "breed" of lamb.

Wet lambs had consistently greater rectal temperatures than dry lambs, despite being more severely cold-stressed (as indicated by the response in metabolic rate). It is suggested that this difference arose from an "over-compensation" in rectal temperature by the wet lambs when they were first exposed to the wetting treatment. In support of this hypothesis, the wet lambs appeared to have elevated metabolic rates at the highest ambient temperature (compared with their metabolic rates at 25°C). A similar initial rise in rectal temperature upon exposure to cold has previously been demonstrated in young lambs and older sheep. However, this effect does not appear to greatly complicate the interpretation of metabolic rate data since the difference in rectal temperature between the wet and dry lambs was established at 30°C ambient temperature and remained relatively constant throughout most of the test.

Drysdale-cross lambs exhibited generally lower rectal temperatures

than Romneys, again despite being less severely cold-stressed. At the highest ambient temperature this was due to the Romneys exhibiting a much greater increase in rectal temperature when first wetted. Subsequently the wet Drysdale-cross lambs showed a similar "over-compensation" in rectal temperature to the wet Romneys, but the "breed" difference in mean rectal temperature persisted. However, this difference is unlikely to indicate that the Romney lambs are better able to control body temperature since the two "breeds" of lamb exhibited a similar net decline in rectal temperature when the ambient temperature was reduced from 30°C to 5°C.

The analysis of hind-limb skin temperatures, together with the results from Appendix I, provided strong evidence that many of the dry lambs had not constricted peripheral blood vessels of the limb. The wet lambs, however, had skin temperatures consistent with vasoconstriction having occurred. Hence it seems likely that many Romney and Drysdale-cross lambs require a strong cold stimulus to induce a reduction in peripheral blood flow. Among the wet lambs, heat production was negatively related to skin temperature at the lowest ambient temperature which may indicate that heat production and the rate at which skin temperature equilibrates with the environment are determined by the correlated effects of the coat insulation on the body and on the limb.

A number of parameters were significantly related to the level of heat production required by the lamb to maintain body temperature. Age effects were generally small although it appeared that the heat production of Drysdale-cross lambs declined with advancing age due to drying of the coat and an increase in its depth.

Drysdale-cross lambs had significantly greater coat depths and midside wool weights than Romney lambs and even under conditions of good pre-natal nutrition, heavy lambs were favoured by superior birthcoat characteristics. This was particularly so in the Drysdale-cross lambs. Gestation length did not affect any of the birthcoat characteristics measured except in one case (midside wool weight) through its correlation with bodyweight. Wetting the birthcoat significantly reduced its depth among the Drysdale-crosses but produced only a small and non-significant reduction among the Romneys.

The lamb's requirement for body heat production was dependent upon its coat characteristics, there being an apparently curvilinear relationship between heat production and both coat depth and midside wool weight (across the sire breeds). As a consequence, heat production was more strongly related to these coat characteristics in the Romneys than in the Drysdale-crosses. It also appears likely that little gain in insulative value of the coat could be made by increasing coat depth beyond about 30 mm or midside wool weight beyond about 90 mg cm^{-2}. The effects of coat depth at the midside and hip positions on metabolic rate were interdependent and it appears that the insulative value of the coat could be as accurately described by measuring depth at only one of these sites as by utilizing both of them. Midside wool weight exerted an effect on metabolic rate independent of its correlation with coat depth. It is suggested that this was due to variation in fibre density (per unit area of skin surface) or fibre diameter. The insulation provided by a unit of coat depth or midside wool weight was not affected by wetting or (within the range available) by airspeed. It appears that the major

effect of wetting on total birthcoat insulation was a reduction in the depth of the coat (particularly in Drysdale-cross lambs) while increasing airspeeds (up to 1.9 m sec^{-1}) removed only the boundary layer of still air over the coat.

C H A P T E R V

THE EFFECTS OF SIRE, BIRTHRANK AND BIRTHCOAT TYPE ON THE RESPONSES OF LAMBS TO COLD-STRESS AT A SINGLE AMBIENT TEMPERATURE

CHAPTER V

THE EFFECTS OF SIRE, BIRTHRANK AND BIRTHCOAT TYPE ON THE RESPONSES OF LAMBS TO COLD-STRESS AT A SINGLE AMBIENT TEMPERATURE

Introduction

Twin-born lambs are known to be particularly susceptible to starvation-exposure mortality (Hight and Jury, 1970), an effect which is probably mediated through their having lower birthweights than single lambs (Dalton *et al.*, 1980). This chapter examines the effects of birthrank on the level of heat production required by the lamb to maintain body temperature, and on other traits (such as bodyweight and the coat characteristics) which were, in the previous chapter, found to affect this requirement. The experiment also provided the opportunity to progeny-test 2 sires with respect to their lambs' heat production, bodyweight and coat characteristics.

In Chapter IV the heat production of wet lambs, which appeared to have constricted peripheral blood vessels at low ambient temperatures, was found to be negatively related to hind-limb skin temperature. It was suggested that this relationship could have been due to the correlation between external insulation of the body and an effect of the birthcoat insulation of the limb on the degree to which skin thermoreceptors were stimulated by the cold environment, or on the rate at which the temperature of the vasoconstricted limb equilibrated with the environment. Slee (1964, 1968) has also suggested that, in mature sheep, variation in the insulative value of wool on the limbs may contribute to variation in skin temperature. In this experiment, therefore, the relationship between skin temperature and the amount of

wool on the limbs was further examined. An attempt was also made to measure the rate at which skin temperature continued to equilibrate with the environment after stable heat production had been achieved.

Experimental Design and Methods

The experiment involved 86 lambs, all of which were born to Romney ewes and sired by Drysdale-Romney cross (single-N) rams. These sires were used to again produce a range of lamb birthcoat types similar to that described in Chapter II, while eliminating any effects of sire breed not closely linked with the dominant N-gene which produces the hairy birthcoat. Two rams were used, each being single-sire mated to a randomly selected sample of 40 ewes. The rams were paternal half-brothers. The birthcoat types of the lambs are referred to in this chapter as "non-hairy" and "hairy" types but were similar to the Romney and Drysdale-cross coat types respectively as described in the previous chapter.

All the lambs were tested when wet since, as was demonstrated in Chapter IV, dry lambs are unlikely to approach the limits of their ability to regulate deep body temperature unless air temperature is much lower than freezing point. Because a high proportion of twin lambs was expected, the ewes having been well fed prior to mating, it was considered advisable to test the lambs under less severe conditions than the most extreme available (in order to avoid having a high proportion of them attain summit metabolism). They were therefore tested at an ambient temperature of $10^{o}C$ and were exposed to either still or moving (1.50 m sec^{-1}) air. Thus the experiment was of an unbalanced five-way cross-classified design with sire, birthcoat type,

birthrank, airspeed and sex as main effects. All but the first of these were treated as fixed effects.

The experimental procedure was modified in a number of ways from that described in the previous chapter. Immediately after the lamb was placed in the climate chamber its "pre-test rectal temperature" was measured to 0.1^{o}C with a clinical thermometer (Figure 5). Once heat production had stabilized the lamb's rectal temperature was again measured, as were its metabolic rate and hind-limb skin temperature. The lamb then remained in the climate chamber for a further 10 to 15 minutes at the end of which period the measurements of rectal temperature and skin temperature were repeated. In addition, the time intervals between each of these 3 sets of measurements were recorded. Thus the rate of decline in rectal temperature and in skin temperature could be calculated. The rate of decline in rectal temperature (RDRT) was calculated over 3 measurement periods as illustrated in Figure 5:

(i) RDRT over the "first period" was used to describe changes which lead to treatment differences in rectal temperature at stable heat production, and to assess whether lambs had attained summit metabolism

(ii) the "second period" RDRT was also used to assess which lambs had attained summit metabolism

(iii) when calculated across the "whole experiment period", RDRT was used as an index of the lamb's resistance to cold-stress (an alternative to heat production).

Within one day of the test being completed, the weight of birthcoat on the limbs was measured in 40 of the lambs as described in Chapter II.

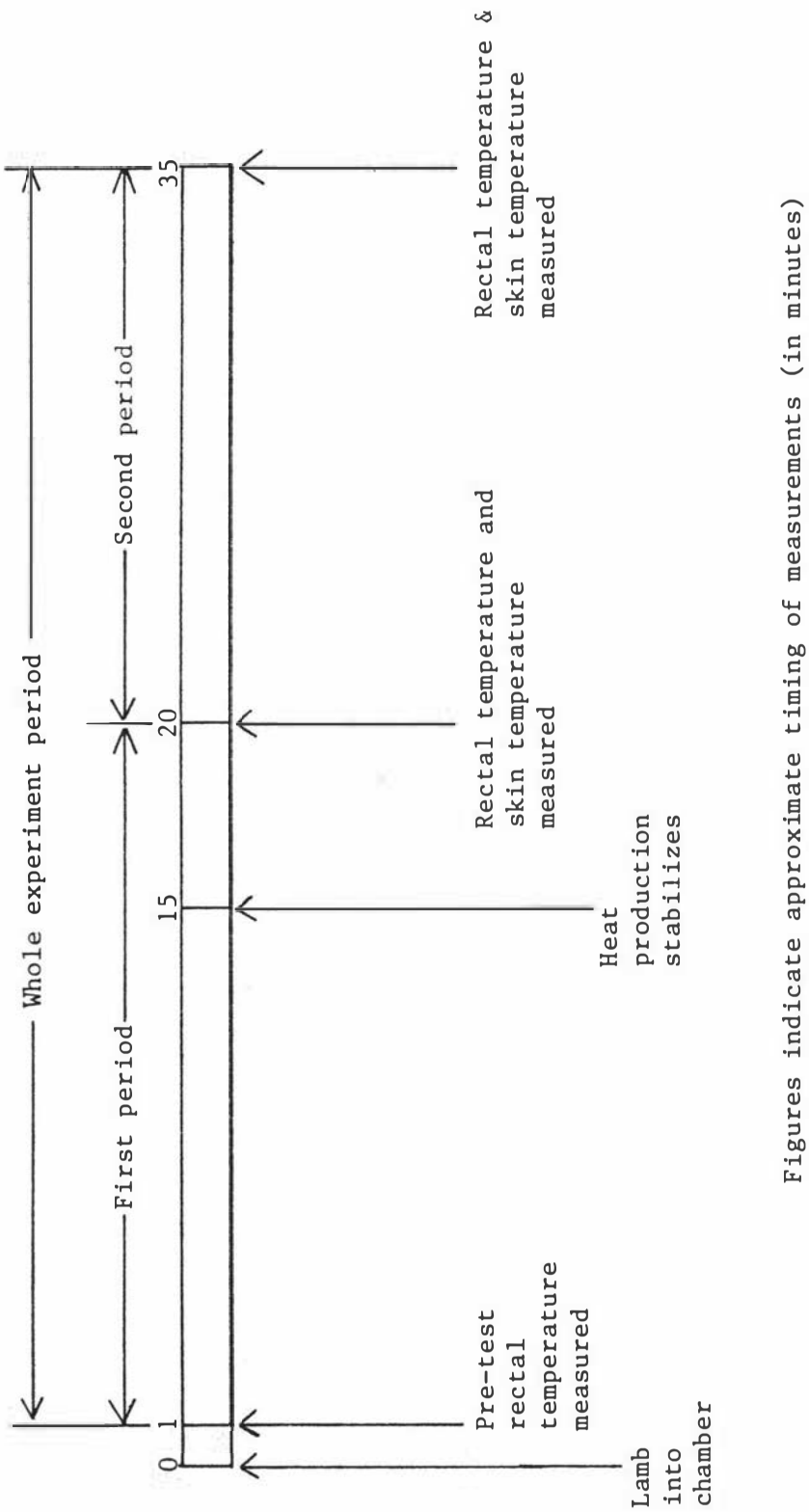

FIGURE 5: EXPERIMENTAL PLAN FOR LAMBS EXPOSED TO A SINGLE AMBIENT TEMPERATURE

Results and Discussion

1. Proportion of lambs attaining summit metabolism

Although these lambs were exposed to less severe environmental conditions than the wet lambs in the previous experiment, a considerable proportion of them exhibited rates of decline in rectal temperature consistent with their having attained summit metabolism. This, of course, creates some difficulty in the interpretation of metabolic rate data for reasons which have already been discussed. In particular, the presence of a high proportion of lambs which have attained summit metabolism may introduce an unacceptable degree of error into regressions involving metabolic rate since, in these lambs, heat production becomes a function of the individual's summit metabolism rather than of the independent variate in the regression. It may therefore be argued that the analysis of this data should involve only those lambs whose metabolic rates did not reach the summit level (hereafter referred to as the "non-summit" lambs). However, in order to analyse the data in this manner, it would be necessary to ignore those very lambs which are most likely to become hypothermic in the field (i.e. the "summit" lambs). Clearly, this too is undesirable. As a compromise the lambs were divided into 2 groups on the basis of whether or not they were considered to have attained summit metabolism. All data involving metabolic rate or parameters related to it were then subjected to dual analyses, one involving all the lambs and the other involving only the "non-summit" lambs. Where they occurred, differences between these analyses are discussed.

The attainment of summit metabolism was again assessed from the

rate of decline in the lamb's rectal temperature, the criterion being a rate in excess of $0.025^{o}C\ min^{-1}$. This figure, or indeed any figure, may be criticized on the basis that it is an arbitrary choice. However, in experiments in which lambs are compared under a standard set of environmental conditions (as opposed to the system described in Chapter III) it appears to be the only basis on which the attainment of summit metabolism can be defined. Moreover, an examination of the data from Chapter IV suggested that while some lambs may show small fluctuations in rectal temperature of up to $0.01^{o}C\ min^{-1}$ (even at high ambient temperatures), those with rates of decline in excess of $0.025^{o}C\ min^{-1}$ over periods of 20 to 30 minutes are likely to have reached the limit of their ability to produce body heat. An additional requirement, that this rate of decline should be sustained before and after the attainment of stable heat production, was also imposed. This was considered desirable because the lambs were being exposed to a single very cold environment rather than to a series of declining ambient temperatures as in Chapter IV. Hence lambs which showed the required rate of decline in rectal temperature prior to the measurement of heat production (i.e. while they were adjusting metabolic rate to the required level), but not in the subsequent period, were not considered to have attained summit metabolism.

A total of 25 lambs exhibited rates of decline in rectal temperature greater than $0.025^{o}C\ min^{-1}$ during the first period of measurement but 3 of these (1 hairy and 2 non-hairy types) exhibited stable rectal temperatures or very low rates of decline (approximately $0.01^{o}C\ min^{-1}$) in the second period. Twenty-two lambs (26% of lambs tested) therefore satisfied all criteria for the attainment of summit metabolism.

This contrasts with the previous experiment in which only 14% of the wet lambs attained summit metabolism, despite being exposed to the lower ambient temperature of $5^{o}C$.

Treatment effects on the proportion of lambs attaining summit metabolism were examined by analysis of deviance on the logit scale (see "Methods of Analysis") the results of which are presented in Table 35. In performing this analysis it was necessary to exclude some main effects to reduce the number of cells in which 0% or 100% of the lambs attained summit metabolism. Since a preliminary analysis showed that the effects of sire and airspeed were non-significant ($P>.05$) these main effects were excluded from the final analysis.

All the remaining treatment effects were found to be significant. Thus 37% of the non-hairy (Romney-type) lambs attained summit metabolism while only 8% of the hairy lambs did so. Similarly twin and female lambs were more likely to exhibit high rates of decline in rectal temperature than were single and male lambs respectively. All treatment effects were additive and, in most cases, treatment effects on the proportion of lambs attaining summit metabolism paralleled the corresponding effects on metabolic rate (Table 37). Hence treatment differences in metabolic rate are likely to be good indicators of the incidence of hypothermia in the field. This situation did not, however, apply to the birthrank effect and the reasons for this will be discussed later. Arithmetic proportions of lambs attaining summit metabolism in the treatments which did not exert significant effects were; sire D140/7 (29%), sire D46/7 (23%), this difference being significant at the 10% level in the full model ($\chi^2 = 2.71$); and

TABLE 35: EFFECT OF BIRTHCOAT TYPE, BIRTHRANK AND SEX ON THE PROPORTION OF LAMBS ATTAINING SUMMIT METABOLISM

Classification	Proportion of Lambs Attaining Summit Metabolism	
	Logit-Transformed Mean ± S.E.	Retransformed %
Birthcoat type		
Non-hairy	-0.52 ± 0.34	37.3 (45)
Hairy	-2.42 ± 0.56	8.2 (41)
Birthrank		
Single	-2.21 ± 0.53	9.9 (42)
Twin	-0.73 ± 0.36	32.6 (44)
Sex		
Male	-2.10 ± 0.58	10.9 (46)
Female	-0.84 ± 0.39	30.2 (40)

	Analysis of Deviance	
Source	d.f.	χ^2 Deviance
Birthcoat Type (Coat)	1	10.52**
Birthrank (Rank)	1	6.58*
Sex	1	4.95*
Coat x Rank	1	0.18 NS
Coat x Sex	1	0.08 NS
Rank x Sex	1	0.01 NS
Coat x Rank x Sex	1	1.06 NS
Error	78	76.01

0.0 m sec^{-1} airspeed (23%), 1.5 m sec^{-1} airspeed (28%).

Relationships between the proportions of lambs attaining summit metabolism and certain characteristics of the lamb (both physical and response-related) were examined by regression analysis on the logit scale. The overall regression coefficients and intercepts are presented in Table 36. Attainment of summit metabolism was most strongly related to bodyweight, the proportion of lambs expected to exhibit high rates of decline in rectal temperature decreasing as bodyweight increased. This relationship accords with the observed susceptibility of small lambs to hypothermia in the field (Alexander and McCance, 1958). By applying the regression equation to the mean bodyweights of single and twin lambs (Table 48) it can be shown that the between - birthrank difference in the attainment of summit metabolism was almost entirely accounted for by the corresponding difference in bodyweight. The same situation did not, however, apply to the sexes. Whereas the least-squares estimates of the proportions of male and female lambs attaining summit metabolism were 10.9% and 30.2% respectively (Table 35), the predicted difference was somewhat less (14.8% vs 26.1%) when calculated on the basis of mean bodyweight. Apparently part of the difference between the sexes in the frequency of attainment of summit metabolism was independent of the bodyweight effect. With respect to the birthcoat types, most of the difference between the hairy and non-hairy lambs appears to have been due to their different coat depths and midside wool weights.

Also of particular relevance to this study was the relationship with heat production. As is shown in Table 36, a high proportion of lambs attaining summit metabolism was associated with high, rather than

TABLE 36: EFFECT OF METABOLIC RATE, SKIN TEMPERATURE, PRE-TEST RECTAL TEMPERATURE, BODYWEIGHT AND BIRTHCOAT CHARACTERISTICS ON THE PROPORTION OF LAMBS ATTAINING SUMMIT METABOLISM

Independent Variate	Logit-Transformed Data	
	Overall regression coefficient ± S.E.	Intercept ± S.E.
Metabolic rate (W kg^{-1})	0.27 ± 0.11, t_{84} = 2.57, P<.05	-5.35 ± 1.72
Skin temperature (^{o}C)	-0.05 ± 0.06, t_{84} = 0.78, NS	-0.16 ± 1.17
Pre-test rectal temperature (^{o}C)	-0.74 ± 0.58, t_{84} = 1.27, NS	28.56 ± 23.37
Bodyweight (kg)	-1.58 ± 0.46, t_{84} = 3.45, P<.001	5.99 ± 1.99
Hip birthcoat depth (mm)	-0.16 ± 0.07, t_{84} = 2.27, P<.05	0.63 ± 0.75
Midside wool weight (mg cm^{-2})	-0.06 ± 0.02, t_{84} = 2.55, P<.05	1.71 ± 1.07
Age (hr)	-0.04 ± 0.04, t_{84} = 0.98, NS	-0.67 ± 0.46

low, metabolic rates. This is an important result since it indicates that the lambs which suffered high rates of decline in rectal temperature did so primarily because of their high rates of body heat loss (which were reflected in a requirement for high metabolic rates) rather than because of a poor ability to produce body heat (in which case a negative relationship might have occurred). The relationships with the birthcoat characteristics also support this view and confirm that the proportion of lambs becoming hypothermic in the field may be reduced by increasing the lamb's coat depth and midside wool weight. However it seems unlikely that the summit lambs exhibited their poor ability to regulate deep body temperature in the mild pre-test environment, as is indicated by the non-significant relationship between the proportion of lambs attaining summit metabolism and pre-test rectal temperature (Table 36). Similarly, since summit metabolic rate is independent of age (Alexander, 1962b and Chapter III), the lack of a relationship between the attainment of summit metabolism and age (Table 36) suggests that age exerted little effect on the rate of body heat loss in these lambs.

2. Heat production

The analysis of variance for heat production (all lambs) is presented in Table 37. The mean metabolic rates of these lambs were generally within the range of Romney summit metabolic rates (Chapter III) as might be expected given that at least 25% of the lambs had apparently attained summit metabolism. Moreover, their mean metabolic rates were approximately 2.0 W kg^{-1} greater than those of the wet lambs described in Chapter IV (at the same ambient temperature) and this may reflect their generally lower bodyweights (Table 48), birthcoat

TABLE 37: EFFECT OF SIRE, BIRTHCOAT TYPE, BIRTHRANK, AIRSPEED AND SEX ON THE HEAT PRODUCTION OF LAMBS AT 10°C AMBIENT TEMPERATURE

Classification		Heat Production (W kg^{-1}) Mean ± S.E.	
		Nominal airspeed (m sec^{-1})	
		0.0	1.5
Sire	Birthrank		
D140/7	Single	13.09 ± 0.65[a] (12)	16.66 ± 0.64[b] (12)
	Twin	15.09 ± 0.80[b] (9)	15.35 ± 0.74[b] (9)
D46/7	Single	15.30 ± 0.75[b] (9)	15.62 ± 0.75[b] (9)
	Twin	15.03 ± 0.62[b] (13)	16.58 ± 0.62[b] (13)

Sire		
D140/7	15.00 ± 0.35	(42)
D46/7	15.63 ± 0.34	(44)
Birthcoat type		
Non-hairy	16.25 ± 0.34	(45)
Hairy	14.45 ± 0.35	(41)
Birthrank		
Single	15.19 ± 0.34	(42)
Twin	15.51 ± 0.40	(44)
Nominal airspeed (m sec^{-1})		
0.0	14.59 ± 0.40	(43)
1.5	16.04 ± 0.36	(43)
Sex		
Male	14.75 ± 0.33	(46)
Female	15.88 ± 0.37	(40)

...../continued

TABLE 37, continued

Analysis of Variance			
Source of Variation	d.f.	Mean Square	F
Sire	1	8.82	0.35 NS
Birthcoat Type (Coat)	1	58.54	12.87***
Birthrank (Rank)	1	2.18	0.09 NS
Airspeed (Asp.)	1	55.34	2.23 NS
Sex	1	21.65	4.76*
Sire x Coat	1	5.21	1.15 NS
Sire x Rank	1	0.02	0.00 NS
Sire x Asp.	1	2.00	0.08 NS
Sire x Sex	1	14.91	3.28†
Coat x Rank	1	17.67	3.88†
Coat x Asp.	1	9.67	2.12 NS
Coat x Sex	1	0.95	0.21 NS
Rank x Asp.	1	14.12	0.57 NS
Rank x Sex	1	2.28	0.50 NS
Asp. x Sex	1	5.68	1.25 NS
Sire x Coat x Rank	1	1.34	0.29 NS
Sire x Coat x Asp.	1	12.97	2.85†
Sire x Coat x Sex	1	0.03	0.01 NS
Sire x Rank x Asp.	1	24.85	5.46*
Sire x Rank x Sex	1	1.38	0.30 NS
Sire x Asp. x Sex	1	10.54	2.32 NS
Coat x Rank x Asp.	1	2.51	0.55 NS
Coat x Rank x Sex	1	8.06	1.77 NS
Coat x Asp. x Sex	1	7.43	1.63 NS
Rank x Asp. x Sex	1	6.33	1.39 NS
Error	60	4.55	

depths (Tables 42, 43) and midside wool weights (Table 46). It may also have been related to the apparent tendency for the lambs in the previous experiment to dry out after some time in the climate chambers, an effect which would have reduced their requirement for body heat production compared with the lambs in this experiment.

Birthcoat type again exerted a significant effect on metabolic rate, the hairy lambs producing approximately 11% less body heat than the non-hairy group. This difference is somewhat smaller than that between the Romney and Drysdale-cross lambs in the previous experiment and is presumably a consequence of the limited heat production in the high proportion of non-hairy lambs which attained summit metabolism. In addition, the difference between the hairy and non-hairy lambs in birthcoat depth was found to be less than that between the corresponding groups in the previous study (Tables 42, 43).

Male lambs had significantly lower metabolic rates than the females which contrasts with the results of Chapter IV (in which differences between the sexes were not significant). This effect cannot be explained simply in terms of bodyweight differences since the between-sex differences in mean bodyweight were similar for these lambs (0.45 kg, Table 48) and for those in the previous chapter (0.43 kg, Table 31). Nor is it likely to be explained by a greater sensitivity of metabolic rate to bodyweight differences at lower bodyweights since these lambs were, on average, only 0.29 kg lighter than the lambs in Chapter IV. Birthrank did not significantly affect metabolic rate, despite its significant effect on the proportion of lambs attaining summit metabolism.

Although neither birthrank nor airspeed affected heat production, the interaction of these factors with sire of the lamb was significant ($P<.05$). Among the progeny of sire D140/7, single-born lambs exposed to still air had significantly lower metabolic rates than the twin lambs, but differences between the birthranks were not significant in moving air. In contrast, the effects of birthrank and airspeed were additive among the progeny of the other sire. The nature of this interaction suggests the possibility of non-additive effects of sire and birthrank on the lamb's birthcoat structure, but these effects were not identified by the analyses of birthcoat depth and midside wool weight (section 4 of this chapter). It should also be noted that the effect of airspeed would have been significant ($P<.001$) had the model been treated as being fully fixed.

An analysis of heat production data for only the non-summit lambs produced essentially the same results as that involving all the lambs. Sex and birthcoat type again exerted significant effects on heat production while the remaining treatments were non-significant. Differences between the treatment means were slightly reduced which is to be expected in view of the manner in which the summit lambs were distributed between the treatment groups.

3. Rectal temperature

In contrast to the Romney and Drysdale-cross comparison described in Chapter IV, differences between the birthcoat types were significant only at the 10% level and, in this experiment, the hairy lambs had the higher rectal temperatures when heat production stabilized (Table 38). Moreover, the 2 groups had virtually identical pre-test rectal temperatures (Table 39) which were 0.3 to 0.7^{o}C higher than those

TABLE 38: EFFECT OF SIRE, BIRTHCOAT TYPE, BIRTHRANK, AIRSPEED AND SEX ON THE RECTAL TEMPERATURES OF LAMBS AT 10°C AMBIENT TEMPERATURE

Classification	Rectal Temperature (°C) Mean ± S.E.		
	Nominal airspeed (m sec^{-1})		
	0.0	1.5	Both airspeeds
Sex			
Male	39.63 ± 0.16[ab] (23)	40.01 ± 0.16[b] (23)	39.82 ± 0.11 (46)
Female	39.76 ± 0.17[a] (20)	39.35 ± 0.17[a] (20)	39.56 ± 0.12 (40)
Both sexes	39.69 ± 0.12 (43)	39.68 ± 0.12 (43)	
Sire			
D140/7	39.65 ± 0.12 (42)		
D46/7	39.72 ± 0.12 (44)		
Birthcoat type			
Non-hairy	39.51 ± 0.12 (45)		
Hairy	39.86 ± 0.12 (41)		
Birthrank			
Single	39.95 ± 0.12 (42)		
Twin	39.42 ± 0.12 (44)		

.../continued

TABLE 38, continued

Analysis of Variance			
Source of Variation	d.f.	Mean Square	F
Sire	1	0.11	0.18 NS
Birthcoat Type (Coat)	1	2.37	3.78†
Birthrank (Rank)	1	5.57	8.91**
Airspeed (Asp.)	1	0.01	0.00 NS
Sex	1	1.42	0.47 NS
Sire x Coat	1	1.11	1.78 NS
Sire x Rank	1	0.37	0.59 NS
Sire x Asp.	1	0.00	0.01 NS
Sire x Sex	1	0.26	0.41 NS
Coat x Rank	1	0.02	0.04 NS
Coat x Asp.	1	0.01	0.01 NS
Coat x Sex	1	1.20	1.92 NS
Rank x Asp.	1	0.02	0.03 NS
Rank x Sex	1	0.07	0.11 NS
Asp. x Sex	1	3.00	4.80*
Sire x Coat x Rank	1	1.21	1.94 NS
Sire x Coat x Asp.	1	0.50	0.80 NS
Sire x Coat x Sex	1	1.72	2.75†
Sire x Rank x Asp.	1	0.19	0.31 NS
Sire x Rank x Sex	1	0.01	0.02 NS
Sire x Asp. x Sex	1	0.18	0.29 NS
Coat x Rank x Asp.	1	0.93	1.48 NS
Coat x Rank x Sex	1	0.03	0.05 NS
Coat x Asp. x Sex	1	0.01	0.01 NS
Rank x Asp. x Sex	1	0.56	0.89 NS
Error	60	0.63	

measured at stable heat production. Hence the lower rectal temperatures of the non-hairy lambs can be accounted for solely by their greater rate of decline in rectal temperature (RDRT) during this "first period" (Table 40). Treatment effects on the RDRT (first period and whole experiment) were, however, significant only at the 10% level, even for treatments which differed substantially in the proportion of lambs defined as having attained summit metabolism. While this was partly due to the arbitrary manner in which the attainment of summit metabolism was of necessity defined, it also reflects variation in the RDRT induced by lambs whose rectal temperatures increased by varying amounts upon initial exposure to cold. Nevertheless, the greater rate of decline in rectal temperature (over both measurement periods) among the non-hairy lambs is consistent with their higher metabolic rates and more frequent attainment of summit metabolism (as defined in this chapter).

The rectal temperatures of twin-born lambs (at stable heat production) were, on average, 0.5^{o}C lower than those of single lambs ($P<.01$, Table 38). Unlike the effect of birthcoat type, this difference partly reflects differences which existed at the commencement of the test. Thus the pre-test rectal temperatures of the single lambs were 0.34^{o}C greater than those of the twins ($P<.001$, Table 39). The rectal temperatures of the twins declined 50% faster than those of the singles, but the effect of birthrank approached significance ($P<.10$) only when RDRT was calculated over the "whole experiment" period (Table 40). However, despite having a greater RDRT over this period, and attaining summit metabolism more frequently, the twin-born lambs did not have a significantly greater metabolic rate than the singles (Table 37). This suggests that the twins may have had a slightly

TABLE 39: EFFECT OF SIRE, BIRTHCOAT TYPE, BIRTHRANK, AND SEX ON PRE-TEST RECTAL TEMPERATURE

Classification	Pre-Test Rectal Temperature (°C) Mean ± S.E.	
Sire		
D146/7	40.13 ± 0.06	(42)
D46/7	40.24 ± 0.06	(44)
Birthcoat type		
Non-hairy	40.19 ± 0.06	(45)
Hairy	40.18 ± 0.06	(41)
Birthrank		
Single	40.35 ± 0.06	(42)
Twin	40.01 ± 0.06	(44)
Sex		
Male	40.18 ± 0.08	(46)
Female	40.19 ± 0.06	(40)

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Sire	1	0.24	1.51 NS
Birthcoat Type (Coat)	1	0.00	0.01 NS
Birthrank (Rank)	1	2.29	14.38***
Sex	1	0.00	0.03 NS
Sire x Coat	1	0.62	3.88†
Sire x Rank	1	0.06	0.38 NS
Sire x Sex	1	0.05	0.34 NS
Coat x Rank	1	0.10	0.62 NS
Coat x Sex	1	0.16	1.02 NS
Rank x Sex	1	0.01	0.08 NS
Sire x Coat x Rank	1	0.37	2.29 NS
Sire x Coat x Sex	1	0.27	1.71 NS
Sire x Rank x Sex	1	0.00	0.00 NS
Coat x Rank x Sex	1	0.06	0.37 NS
Error	71	0.16	

TABLE 40: EFFECT OF SIRE, BIRTHCOAT TYPE, BIRTHRANK, AIRSPEED AND SEX ON THE RATE OF DECLINE IN RECTAL TEMPERATURE IN TWO MEASUREMENT PERIODS

Classification	Rate of Decline in Rectal Temperature ($^{o}C\ min^{-1}$) Mean ± S.E.		
	First period	Whole experiment	
Sire			
D140/7	0.022 ± 0.006	0.024 ± 0.006	(42)
D46/7	0.028 ± 0.006	0.030 ± 0.006	(44)
Birthcoat type			
Non-hairy	0.034 ± 0.006	0.036 ± 0.006	(45)
Hairy	0.016 ± 0.006	0.018 ± 0.006	(41)
Birthrank			
Single	0.020 ± 0.006	0.019 ± 0.006	(42)
Twin	0.030 ± 0.006	0.035 ± 0.006	(44)
Nominal airspeed ($m\ sec^{-1}$)			
0.0	0.020 ± 0.006	0.020 ± 0.006	(43)
1.5	0.029 ± 0.006	0.034 ± 0.006	(43)
Sex			
Male	0.016 ± 0.006	0.019 ± 0.006	(46)
Female	0.034 ± 0.005	0.035 ± 0.006	(40)

...../continued

TABLE 40, continued

Source of Variation	d.f.	Analysis of Variance (First Period) Mean Square	F	(Whole Experiment) Mean Square	F
Sire	1	0.001	0.37 NS	0.001	0.39 NS
Birthcoat Type (Coat)	1	0.007	3.54 †	0.007	3.96 †
Birthrank (Rank)	1	0.002	1.06 NS	0.005	2.90 †
Airspeed (Asp.)	1	0.002	0.85 NS	0.004	2.19 NS
Sex	1	0.006	3.38 †	0.005	2.81 †
Sire x Coat	1	0.004	2.22 NS	0.003	1.59 NS
Sire x Rank	1	0.000	0.11 NS	0.000	0.03 NS
Sire x Asp.	1	0.000	0.05 NS	0.001	0.26 NS
Sire x Sex	1	0.001	0.42 NS	0.000	0.15 NS
Coat x Rank	1	0.000	0.11 NS	0.000	0.00 NS
Coat x Asp.	1	0.002	1.00 NS	0.001	0.72 NS
Coat x Sex	1	0.001	0.32 NS	0.000	0.08 NS
Rank x Asp.	1	0.001	0.37 NS	0.001	0.71 NS
Rank x Sex	1	0.002	1.27 NS	0.003	1.66 NS
Asp. x Sex	1	0.002	1.27 NS	0.003	1.79 NS
Sire x Coat x Rank	1	0.001	0.58 NS	0.002	0.86 NS
Sire x Coat x Asp.	1	0.001	0.63 NS	0.002	1.29 NS
Sire x Coat x Sex	1	0.001	0.58 NS	0.002	1.23 NS
Sire x Rank x Asp.	1	0.001	0.32 NS	0.001	0.27 NS
Sire x Rank x Sex	1	0.000	0.02 NS	0.000	0.00 NS
Sire x Asp. x Sex	1	0.002	1.11 NS	0.001	0.48 NS
Coat x Rank x Asp.	1	0.001	0.32 NS	0.001	0.40 NS
Coat x Rank x Sex	1	0.000	0.05 NS	0.000	0.08 NS
Coat x Asp. x Sex	1	0.000	0.05 NS	0.000	0.07 NS
Rank x Asp. x Sex	1	0.001	0.48 NS	0.000	0.26 NS
Error	60	0.002		0.002	

poorer ability to produce body heat (i.e. a lower level of summit metabolism) than their single-born peers. A similar effect of birthrank on summit metabolism was reported by Alexander and Bell (1975a), although it was observed in only one of the breeds and crosses studied.

The rectal temperatures of female lambs declined twice as fast as those of the male lambs (Table 40). Although this difference was significant only at the 10% level it is again consistent with the effects of sex on heat production and on the proportion of lambs attaining summit metabolism. The mechanism of this effect is, however, unknown. It seems unlikely to have been related to bodyweight differences for reasons which have already been discussed. Nor can it be explained by differences in birthcoat insulation since, as will be discussed later, there were no effects of sex on any of the birthcoat characteristics measured.

Among the "non-summit" lambs, birthcoat type did not significantly affect rectal temperature at stable heat production (Table 41), so illustrating that the small difference shown in Table 38 was primarily due to the greater proportion of non-hairy lambs which attained summit metabolism. The birthrank effect was similarly non-significant although significance would have occurred had the model been fully fixed (i.e. had the birthrank mean square been tested against the error term rather than against the birthcoat type x birthrank x sex interaction). Thus even after the removal of the summit lambs, the singles still exhibited higher rectal temperatures than the twins by an average of $0.27^{o}C$.

TABLE 41: EFFECT OF SIRE, BIRTHCOAT TYPE, BIRTHRANK, AIRSPEED AND SEX ON THE RECTAL TEMPERATURES OF LAMBS AT 10°C AMBIENT TEMPERATURE : NON-SUMMIT LAMBS

Classification		Rectal Temperature (°C) Mean ± S.E.	
		Sex	
		Male	Female
Birthcoat type	Birthrank		
Non-hairy	Single	40.36 ± 0.13^{b} (12)	39.80 ± 0.19^{a} (7)
	Twin	39.73 ± 0.19^{a} (6)	40.07 ± 0.30^{a} (3)
Hairy	Single	40.12 ± 0.13^{ab} (12)	40.25 ± 0.22^{a} (5)
	Twin	39.85 ± 0.16^{a} (9)	39.77 ± 0.16^{a} (10)
Sire			
D140/7		40.16 ± 0.08^{b} (19)	39.79 ± 0.17^{a} (11)
D46/7		39.87 ± 0.11^{b} (20)	40.15 ± 0.14^{b} (14)

Sire		
D140/7	39.97 ± 0.15	(30)
D46/7	40.01 ± 0.15	(34)
Birthcoat type		
Non-hairy	39.99 ± 0.10	(28)
Hairy	40.00 ± 0.08	(36)
Birthrank		
Single	40.13 ± 0.09	(36)
Twin	39.86 ± 0.11	(28)
Nominal airspeed (m sec^{-1})		
0.0	39.94 ± 0.08	(33)
1.5	40.04 ± 0.10	(31)
Sex		
Male	40.02 ± 0.06	(39)
Female	39.97 ± 0.11	(25)

...../continued

TABLE 41, continued

Analysis of Variance			
Source of Variation	d.f.	Mean Square	F
Sire	1	0.00	0.00 NS
Birthcoat Type (Coat)	1	0.00	0.03 NS
Birthrank (Rank)	1	1.01	0.80 NS
Airspeed (Asp.)	1	0.30	1.47 NS
Sex	1	0.15	0.08 NS
Sire x Coat	1	0.03	0.15 NS
Sire x Rank	1	0.36	1.76 NS
Sire x Asp.	1	0.63	3.08†
Sire x Sex	1	1.82	8.90**
Coat x Rank	1	0.07	0.06 NS
Coat x Asp.	1	0.71	3.47†
Coat x Sex	1	0.20	0.16 NS
Rank x Asp.	1	0.34	1.66 NS
Rank x Sex	1	0.13	0.10 NS
Asp. x Sex	1	0.46	2.25 NS
Sire x Coat x Rank	1	0.53	2.59 NS
Sire x Coat x Asp.	1	0.03	0.15 NS
Sire x Coat x Sex	1	0.56	2.74 NS
Sire x Rank x Asp.	1	0.17	0.83 NS
Sire x Rank x Sex	1	0.02	0.10 NS
Sire x Asp. x Sex	1	0.01	0.05 NS
Coat x Rank x Asp.	1	0.00	0.00 NS
Coat x Rank x Sex	1	1.26	6.16*
Coat x Asp. x Sex	1	0.17	0.83 NS
Rank x Asp. x Sex	1	0.13	0.64 NS
Error	38	0.20	

4. Characteristics of the birthcoat

(a) Depth of birthcoat

(i) Treatment effects on birthcoat depth

In this experiment, as in Chapter IV, relationships between the birthcoat depths and other parameters were similar for both the sites examined (at the midside and hip positions). The analyses will therefore be discussed for only one of the positions (hip) except where important differences occurred.

Birthcoat type again exerted a highly significant effect on hip coat depth (Table 42) although the difference between the mean depths of the hairy and non-hairy lambs was smaller than between the wet Romney and Drysdale-cross lambs in the previous experiment. This was primarily due to the hairy lambs having a much lower hip coat depth (by 3 mm) than the wet Drysdale-crosses, and the difference was even more pronounced at the midside position. Whether this was due to genetic or nutritional differences is not clear. Evidence presented in the previous chapter that deeper coats may be more sensitive to nutritional restriction, together with the difference in bodyweight between lambs in the 2 experiments, suggests that a small nutritional effect might have been involved. However, in this experiment hip birthcoat depth was independent of bodyweight as is indicated by the non-significant overall ($b = 0.16 \pm 0.57$ mm kg^{-1}, $t_{84} = 0.27$, NS.) and pooled within-class regressions (Table 42). The relationship between coat depth at the midside position and bodyweight was similarly non-significant (Table 43).

Sire effects on hip birthcoat depth were not significant *per se* but did interact with the effects of birthcoat type.

TABLE 42: EFFECT OF SIRE, BIRTHCOAT TYPE, BIRTHRANK, SEX AND BODYWEIGHT ON HIP BIRTHCOAT DEPTH

Classification	Hip Birthcoat Depth (mm) Mean ± S.E.		
	Sire		
	D140/7	D46/7	Both sires
Birthcoat type			
Non-hairy	8.6 ± 0.5[a] (21)	7.8 ± 0.5[a] (24)	8.2 ± 0.3 (45)
Hairy	16.0 ± 0.5[c] (21)	13.2 ± 0.5[b] (20)	14.6 ± 0.4 (41)
Both birthcoat types	12.3 ± 0.4 (42)	10.5 ± 0.3 (44)	
Birthrank			
Single	12.0 ± 0.4 (42)		
Twin	10.8 ± 0.3 (44)		
Sex			
Male	11.3 ± 0.3 (46)		
Female	11.5 ± 0.4 (40)		

...../continued

TABLE 42, continued

Analysis of Variance			
Source of Variation	d.f.	Mean Square	F
Sire	1	66.02	2.74 NS
Birthcoat Type (Coat)	1	864.22	35.91***
Birthrank (Rank)	1	26.45	5.16*
Sex	1	0.70	0.14 NS
Sire x Coat	1	24.07	4.69*
Sire x Rank	1	3.48	0.68 NS
Sire x Sex	1	5.57	1.09 NS
Coat x Rank	1	9.17	1.79 NS
Coat x Sex	1	1.04	0.20 NS
Rank x Sex	1	5.85	1.14 NS
Sire x Coat x Rank	1	10.34	2.02 NS
Sire x Coat x Sex	1	2.79	0.54 NS
Sire x Rank x Sex	1	8.59	1.68 NS
Coat x Rank x Sex	1	6.21	1.21 NS
Error	71	5.13	

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (above)	14	74.81	
Intra-class (birthcoat type) regression of hip coat depth on body weight	2	3.39	0.65 NS
Pooled within-class	1	0.69	0.13 NS
Difference	1	6.09	1.18 NS
Residual error	69	5.18	

TABLE 43: EFFECT OF SIRE, BIRTHCOAT TYPE, BIRTHRANK, SEX AND BODYWEIGHT ON MIDSIDE BIRTHCOAT DEPTH

Classification	Midside Birthcoat Depth (mm) Mean ± S.E.	
Sire		
D140/7	12.2 ± 0.3	(42)
D46/7	11.4 ± 0.3	(44)
Birthcoat type		
Non-hairy	9.2 ± 0.3	(45)
Hairy	14.4 ± 0.3	(41)
Birthrank		
Single	12.4 ± 0.3	(42)
Twin	11.3 ± 0.3	(44)
Sex		
Male	11.7 ± 0.4	(46)
Female	11.9 ± 0.3	(40)

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Sire	1	15.21	3.68†
Birthcoat Type (Coat)	1	580.31	140.46***
Birthrank (Rank)	1	26.17	6.33*
Sex	1	0.80	0.19 NS
Sire x Coat	1	9.81	2.37 NS
Sire x Rank	1	0.67	0.16 NS
Sire x Sex	1	0.25	0.06 NS
Coat x Rank	1	0.58	0.14 NS
Coat x Sex	1	0.84	0.20 NS
Rank x Sex	1	6.12	1.48 NS
Sire x Coat x Rank	1	4.25	1.03 NS
Sire x Coat x Sex	1	8.12	1.96 NS
Sire x Rank x Sex	1	9.29	2.25 NS
Coat x Rank x Sex	1	4.99	1.21 NS
Error	71	4.13	

...../continued

TABLE 43, continued

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (above)	14	46.99	
Intra-class (birthcoat type) regression of midside coat depth on bodyweight	2	2.28	0.54 NS
Pooled within-class	1	3.24	0.77 NS
Difference	1	1.33	0.32 NS
Residual error	69	4.19	

While no significant difference existed between the non-hairy progeny of the 2 sires, the hairy progeny of sire D140/7 had coats which were, on average, 2.8 mm deeper than those of the hairy lambs sired by D46/7. In this experiment the progeny and their dams were managed in such a way as to satisfy the criteria of a progeny test (i.e. the dams were randomly assigned to sire group; they were managed identically except at mating; and the progeny were unselected). Hence the significant difference between the hairy progeny of each sire in hip birthcoat depth must represent a genetic effect. Across both coat types the progeny of sire D140/7 had hip coat depths approximately 1.8 mm greater than those of sire D46/7 and this difference would also have been significant ($P<.001$) had sires been treated as a fixed effect (Table 42).

At the midside position, the effects of sire and birthcoat type were additive (Table 43). Sire D140/7 again produced progeny with deeper birthcoats, their depth at the midside position being 0.8 mm greater than those of the other sire's progeny. While this difference was less than at the hip position it approached significance at the 5% level and is again likely to be genetic in origin.

It is perhaps not surprising that the effect of sire on lamb birthcoat depth was small, particularly since only 2 sires were involved and they were themselves paternal half-brothers. Nevertheless, the validity of the progeny test (both in terms of the management of ewes and lambs, and the number of progeny representing each sire) strongly suggests that the between-sire differences were genetically-controlled. Hence it seems likely

that a genetic basis might exist upon which selection plans could be developed for the improvement of birthcoat depth in newborn lambs.

The birthcoat depths of single-born lambs exceeded those of twins by just over 1 mm at each of the measurement sites ($P<.05$, Tables 42, 43). Although small in absolute terms, this difference is approximately 12% of the mean non-hairy coat depth and is therefore likely to represent a difference between the birthranks in that component of insulation which is related to depth. The lower birthcoat depth of the twin lambs was, as might be expected, associated with their lower bodyweight (Table 48) despite the non-significance of the regressions of coat depth on bodyweight.

(ii) Heat production and coat depth

The overall regression coefficient of heat production on hip birthcoat depth was $b = -0.25 \pm 0.06$ W kg^{-1} mm^{-1} which was of a similar magnitude and significance ($t_{84} = 4.03$, $P<.001$) to the corresponding relationship at $5^{o}C$ in Chapter IV. In contrast to the previous experiment, the within-birthcoat type regressions were significantly different at the 5% level, the regression coefficients being $b = -0.45 \pm 0.18$ W kg^{-1} mm^{-1} ($t_{43} = 2.44$, $P<.05$) for the non-hairy lambs and $b = 0.06 \pm 0.15$ W kg^{-1} mm^{-1} ($t_{39} = 0.39$, NS.) for the hairy group. When this analysis was repeated for only those lambs which did not attain summit metabolism, the overall regression of heat production on hip coat depth remained highly significant but the within-birthcoat type regressions were now homogeneous. This was presumably a consequence of the removal, from the analysis, of the summit lambs which tended to have high levels of heat production and low birthcoat depths

TABLE 44: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (BIRTHCOAT TYPE) REGRESSIONS OF HEAT PRODUCTION AT 10°C AMBIENT TEMPERATURE ON HIP BIRTHCOAT DEPTH

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 37)	25	11.63	
Intra-class (birthcoat type) regression of heat production on hip coat depth	2	13.01	3.06†
Pooled within-class	1	6.25	1.47 NS
Difference	1	19.78	4.65*
Residual error	58	4.26	

(Table 36). However, the apparent absence of heterogeneous within-birthcoat type regressions in this experiment does not negate the conclusions drawn about a curvilinear relationship between heat production and coat depth in Chapter IV. In that experiment the relationship was not altered by the exclusion of the few lambs which attained summit metabolism and the within-birthcoat type regressions were heterogeneous only at the 10% level (for 2 of the birthcoat characteristics). It is therefore not too surprising that the corresponding regressions were homogeneous among the non-summit lambs in this experiment, particularly since the difference in coat depth between the coat types was less than in the previous experiment.

The relationship between heat production and midside coat depth was essentially the same as that for the hip site, with one exception. In addition to the within-birthcoat type regressions being heterogeneous, the within-sex regressions were also significantly different when all lambs were included in the analysis (Table 45). Thus heat production was related to midside coat depth in the male lambs ($b = -0.46 \pm 0.19$ W kg^{-1} mm^{-1}, $t_{44} = 2.45$, $P<.05$) but not in the females ($b = 0.29 \pm 0.18$ W kg^{-1} mm^{-1}, $t_{38} = 1.62$, NS.). While this difference is superficially similar to that between the birthcoat types, it must be remembered that the sexes, unlike the coat types, did not have significantly different midside coat depths (Table 43). Hence the different within-sex regressions occurred over similar ranges of coat depth. Furthermore, the difference between these regressions was associated with a greater susceptibility of the female lambs to cold-stress (as indicated by their heat production, rate of decline in rectal

TABLE 45: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (BIRTHCOAT TYPE, SEX) REGRESSIONS OF HEAT PRODUCTION AT 10°C AMBIENT TEMPERATURE ON MIDSIDE BIRTHCOAT DEPTH

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 37)	25	11.63	
Intra-class (birthcoat type) regression of heat production on midside coat depth	2	20.08	5.00**
Pooled within-class	1	1.19	0.30 NS
Difference	1	38.96	9.71**
Residual error	58	4.01	
Main effects model (Table 37)	25	11.63	
Intra-class (sex) regression of heat production on midside coat depth	2	17.45	4.25*
Pooled within-class	1	1.19	0.29 NS
Difference	1	33.72	8.22**
Residual error	58	4.10	

temperature and attainment of summit metabolism) in complete contrast to the results from Chapter IV. It must therefore be concluded that the non-significant relationship between heat production and midside coat depth among the female lambs occurred not because variation in coat depth was unrelated to coat insulation but because a considerable proportion of the female lambs had attained summit metabolism. In support of this conclusion it was found that the within-sex regressions of heat production on midside coat depth were homogeneous when the summit lambs were excluded from the analysis.

(b) Midside wool weight per unit area of skin

(i) Treatment effects on midside wool weight

The analysis of variance for midside wool weight is presented in Table 46. Hairy lambs again had greater midside wool weights than the non-hairy lambs, but this difference was only significant at the 5% level since it was tested against the sire x birthcoat type x birthrank interaction. Similarly the effect of birthrank was non-significant although it would have been significant had the model been treated as fully fixed. As with the birthcoat depths, the effects of birthrank on midside wool weight paralleled those on bodyweight even though neither the overall ($b = 2.81 \pm 1.85$ mg cm^{-2} kg^{-1}, $t_{84} = 1.52$, NS.) nor the pooled within-class regressions (Table 46) of midside wool weight on lamb bodyweight were significant at the 5% level.

The effects of birthcoat type and birthrank interacted significantly with the sire effects ($P<.01$). Among the progeny

TABLE 46: EFFECT OF SIRE, BIRTHCOAT TYPE, BIRTHRANK, SEX AND BODYWEIGHT ON MIDSIDE WOOL WEIGHT PER UNIT AREA OF SKIN

Classification		Midside Wool Weight/Unit Area (mg cm^{-2}) Mean ± S.E.	
		Birthrank	
		Single	Twin
Sire	Birthcoat type		
D140/7	Non-hairy	43.0 ± 2.7^{ab} (13)	39.8 ± 3.5^{a} (8)
	Hairy	63.7 ± 2.0^{c} (11)	51.3 ± 3.1^{b} (10)
D46/7	Non-hairy	45.4 ± 3.0^{b} (11)	35.2 ± 2.9^{a} (13)
	Hairy	50.8 ± 3.0^{b} (7)	59.3 ± 2.7^{b} (13)
Sire			
D140/7		49.4 ± 1.5	(42)
D46/7		47.7 ± 1.4	(44)
Birthcoat type			
Non-hairy		40.9 ± 1.5	(45)
Hairy		56.3 ± 1.7	(41)
Birthrank			
Single		50.7 ± 1.2	(42)
Twin		46.4 ± 1.5	(44)
Sex			
Male		47.9 ± 1.4	(46)
Female		49.2 ± 1.6	(40)

.../continued

TABLE 46, continued

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Sire	1	15.11	0.01 NS
Birthcoat Type (Coat)	1	5930.03	5.35*
Birthrank (Rank)	1	489.18	0.44 NS
Sex	1	36.48	0.37 NS
Sire x Coat	1	15.45	0.01 NS
Sire x Rank	1	239.40	0.22 NS
Sire x Sex	1	1.16	0.01 NS
Coat x Rank	1	112.42	0.10 NS
Coat x Sex	1	8.07	0.08 NS
Rank x Sex	1	113.02	1.14 NS
Sire x Coat x Rank	1	1107.61	11.18**
Sire x Coat x Sex	1	203.26	2.05 NS
Sire x Rank x Sex	1	0.25	0.00 NS
Coat x Rank x Sex	1	1.91	0.02 NS
Error	71	99.08	

Analysis of Covariance

Source of Variation	d.f.	Mean Square	F
Main effects model (above)	14	565.41	
Intra-class (birthcoat type) regression of midside wool weight on bodyweight	2	227.55	2.39†
Pooled within-class	1	346.37	3.63†
Difference	1	108.73	1.14 NS
Residual error	69	95.36	

of sire D46/7, birthrank significantly affected the midside wool weights of non-hairy lambs but not of the hairy lambs, while among the progeny of the other sire the pattern was reversed. This effect cannot be explained in terms of bodyweight differences since, while birthcoat type was associated with bodyweight differences only among the progeny of sire D46/7 (Table 48), the effects of birthrank were additive. Nevertheless the nature of the sire x coat x rank interaction in midside wool weight does suggest the possibility that nutritional effects were involved.

Sire of the lamb did not significantly affect its midside wool weight and, in contrast to the coat depths, the difference would not have been significant had sires been treated as a fixed effect. Hence there was no evidence for an effect of sire on the lamb's midside wool weight.

(ii) Heat production and midside wool weight

The overall regression coefficient of heat production on midside wool weight was b= -0.072 ± 0.020 W kg^{-1} mg^{-1} cm^2 which, in contrast to the previous experiment, was highly significant ($t_{84} = 3.67$, $P<.001$). The within-birthcoat type regressions were not significantly different but, as with midside coat depth, the within-sex regressions were heterogeneous, although only at the 10% level (Table 47). Again heat production was related to this coat characteristic among the male lambs ($b = -0.090 \pm 0.033$ W kg^{-1} mg^{-1} cm^2, $t_{44} = 2.76$, $P<.01$) but not among the females ($b = 0.005 \pm 0.038$ W kg^{-1} mg^{-1} cm^2, $t_{38} = 0.14$, NS.). The within-sex regressions were not, however, significantly different when the summit lambs were excluded from the analysis and the

TABLE 47: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (SEX) REGRESSIONS OF HEAT PRODUCTION AT 10°C AMBIENT TEMPERATURE ON MIDSIDE WOOL WEIGHT PER UNIT AREA OF SKIN

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 37)	25	11.63	
Intra-class (sex) regression of heat production on midside wool weight	2	16.11	3.88*
Pooled within-class	1	15.65	3.77†
Difference	1	16.56	3.99†
Residual error	58	4.15	

explanation for this difference must be the same as for the corresponding situation with midside coat depth.

5. Bodyweight

(a) Treatment effects on bodyweight

Some of the treatment effects on the lamb's bodyweight at the time of testing have already been discussed in earlier sections of this chapter. As expected, male lambs were significantly ($P<.01$) heavier than females and single-born lambs were heavier than twins ($P<.001$, Table 48). The effects of sire and birthcoat type were not significant (in a mixed model analysis) but a significant ($P<.05$) interaction did exist between them. Thus the hairy progeny of sire D46/7 were heavier than the non-hairy progeny but no such differences existed among the progeny of the other sire. However this effect does not appear to be responsible for any of the corresponding treatment effects on birthcoat characteristics. In fact the hairy progeny of sire D46/7 had significantly lower coat depths (at the hip site) than the hairy progeny of D140/7 (Table 42) despite their significantly higher bodyweights.

(b) Heat production and bodyweight

The relationship between heat production and bodyweight was again examined by double-logarithmic regression of total heat production on bodyweight (as described in Chapter II). The overall regression coefficient of $\log_e$ total heat production on $\log_e$ bodyweight was $b = 0.78 \pm 0.11$ which was highly significant ($t_{84} = 7.15$, $P<.001$). The pooled within-class regression was similarly significant. When all the lambs were included in the analysis the within-airspeed regressions were heterogeneous (Table 49), but they were homogeneous when the same

TABLE 48: EFFECT OF SIRE, BIRTHCOAT TYPE, BIRTHRANK AND SEX ON BODYWEIGHT

Classification	Bodyweight (kg) Mean ± S.E.		
	Sire		
	D140/7	D46/7	Both sires
Birthcoat type			
Non-hairy	4.62 ± 0.13[a] (21)	4.68 ± 0.12[a] (24)	4.65 ± 0.09 (45)
Hairy	4.44 ± 0.13[a] (21)	4.97 ± 0.13[b] (20)	4.70 ± 0.09 (41)
Both birthcoat types	4.53 ± 0.09 (42)	4.82 ± 0.09 (44)	
Birthrank			
Single	5.11 ± 0.09 (42)		
Twin	4.24 ± 0.09 (44)		
Sex			
Male	4.90 ± 0.09 (46)		
Female	4.45 ± 0.09 (40)		

.../continued

TABLE 48, continued

Analysis of Variance			
Source of Variation	d.f.	Mean Square	F
Sire	1	1.71	1.16 NS
Birthcoat Type (Coat)	1	0.07	0.05 NS
Birthrank (Rank)	1	15.33	42.06***
Sex	1	4.12	11.29**
Sire x Coat	1	1.47	4.05*
Sire x Rank	1	0.09	0.24 NS
Sire x Sex	1	0.00	0.01 NS
Coat x Rank	1	0.24	0.65 NS
Coat x Sex	1	0.06	0.15 NS
Rank x Sex	1	0.05	0.15 NS
Sire x Coat x Rank	1	0.07	0.19 NS
Sire x Coat x Sex	1	0.01	0.04 NS
Sire x Rank x Sex	1	0.18	0.50 NS
Coat x Rank x Sex	1	0.21	0.58 NS
Error	71	0.36	

TABLE 49: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (AIRSPEED) REGRESSIONS OF LOG TOTAL HEAT PRODUCTION AT 10°C AMBIENT TEMPERATURE ON LOG BODYWEIGHT

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Sire	1	0.21	0.82 NS
Birthcoat Type (Coat)	1	0.22	0.86 NS
Birthrank (Rank)	1	0.55	2.10 NS
Airspeed (Asp.)	1	0.28	3.48†
Sex	1	0.02	0.24 NS
Sire x Coat	1	0.14	0.54 NS
Sire x Rank	1	0.01	0.03 NS
Sire x Asp.	1	0.01	0.07 NS
Sire x Sex	1	0.05	0.63 NS
Coat x Rank	1	0.15	0.56 NS
Coat x Asp.	1	0.06	3.46†
Coat x Sex	1	0.00	0.02 NS
Rank x Asp.	1	0.00	0.11 NS
Rank x Sex	1	0.00	0.24 NS
Asp. x Sex	1	0.00	0.01 NS
Sire x Coat x Rank	1	0.26	15.02***
Sire x Coat x Asp.	1	0.03	2.04 NS
Sire x Coat x Sex	1	0.00	0.04 NS
Sire x Rank x Asp.	1	0.03	1.63 NS
Sire x Rank x Sex	1	0.00	0.15 NS
Sire x Asp. x Sex	1	0.08	4.48*
Coat x Rank x Asp.	1	0.04	2.44 NS
Coat x Rank x Sex	1	0.02	1.37 NS
Coat x Asp. x Sex	1	0.00	0.01 NS
Rank x Asp. x Sex	1	0.00	0.21 NS
Intra-class (airspeed) regression of log total heat production on log bodyweight	2	0.34	19.74***
Pooled within-class	1	0.57	33.68***
Difference	1	0.10	5.79*
Residual error	58	0.02	

analysis was performed using the data from only the non-summit lambs. In this situation the pooled within-class regression coefficient was b = 0.82 ± 0.17 which was again highly significant (P<.001).

An examination of the overall and pooled within-class regression coefficients from both the analysis involving all the lambs, and that involving only the non-summit lambs, showed that all these coefficients lay in the range 0.78 to 0.85. It will be recalled from Chapter IV that the pooled within-class regression coefficient of $\log_e$ THP on $\log_e$ WT was also within this range (b = 0.79) in that experiment. It seems reasonable to suggest, therefore, that an appropriate exponent relating "effective surface area" (Brody, 1945) to bodyweight would lie in this range. Hence for the purposes of predicting the thermoregulatory limits of lambs of different bodyweights an exponent of this magnitude may be more appropriate than the lower figure (b = 0.59) used by Alexander (1962b).

6. Hind-limb skin temperature and the weight of wool on the limbs

(a) Treatment effects on skin temperature

As in the previous experiment, airspeed exerted a significant effect on skin temperature at stable heat production (Table 50), the lambs exposed to moving air having skin temperatures which were about 5°C lower than those of the lambs exposed to still air. Since the lambs in this experiment were being tested when wet, they were likely to have all experienced peripheral vasoconstriction. Accordingly, it is suggested that the airspeed effect was again due to differential rates of equilibration in the skin temperatures of the lambs exposed to the 2 levels of air movement. This difference may have been

TABLE 50: EFFECT OF SIRE, BIRTHCOAT TYPE, BIRTHRANK, AIRSPEED AND SEX ON THE HIND-LIMB SKIN TEMPERATURES OF LAMBS AT 10°C AMBIENT TEMPERATURE

Classification		Hind-Limb Skin Temperature (°C) Mean ± S.E.	
		Birthrank	
		Single	Twin
Sire	Birthcoat type		
D140/7	Non-hairy	19.94 ± 0.93[ab] (13)	19.26 ± 1.21[a] (8)
	Hairy	19.30 ± 1.02[a] (11)	17.40 ± 1.07[a] (10)
D46/7	Non-hairy	21.32 ± 1.04[b] (11)	17.04 ± 0.95[a] (13)
	Hairy	17.30 ± 1.30[a] (7)	19.41 ± 0.94[a] (13)

Sire		
D140/7	18.97 ± 0.54	(42)
D46/7	18.77 ± 0.53	(44)
Birthcoat type		
Non-hairy	19.39 ± 0.52	(45)
Hairy	18.36 ± 0.54	(41)
Birthrank		
Single	19.46 ± 0.55	(42)
Twin	18.28 ± 0.52	(44)
Nominal airspeed (m sec^{-1})		
0.0	21.43 ± 0.53	(43)
1.5	16.31 ± 0.53	(43)
Sex		
Male	18.61 ± 0.50	(46)
Female	19.13 ± 0.57	(40)

.../continued

TABLE 50, continued

Analysis of Variance			
Source of Variation	d.f.	Mean Square	F
Sire	1	0.01	0.00 NS
Birthcoat Type (Coat)	1	9.30	0.09 NS
Birthrank (Rank)	1	38.57	0.38 NS
Airspeed (Asp.)	1	468.76	39.58***
Sex	1	2.78	0.23 NS
Sire x Coat	1	0.02	0.00 NS
Sire x Rank	1	1.25	0.01 NS
Sire x Asp.	1	14.56	1.23 NS
Sire x Sex	1	3.04	0.26 NS
Coat x Rank	1	38.48	0.38 NS
Coat x Asp.	1	1.61	0.14 NS
Coat x Sex	1	0.17	0.01 NS
Rank x Asp.	1	30.37	2.56 NS
Rank x Sex	1	8.87	0.75 NS
Asp. x Sex	1	1.86	0.16 NS
Sire x Coat x Rank	1	102.05	8.62**
Sire x Coat x Asp.	1	21.80	1.84 NS
Sire x Coat x Sex	1	0.01	0.00 NS
Sire x Rank x Asp.	1	6.61	0.56 NS
Sire x Rank x Sex	1	5.27	0.45 NS
Sire x Asp. x Sex	1	0.04	0.00 NS
Coat x Rank x Asp.	1	20.27	1.71 NS
Coat x Rank x Sex	1	0.27	0.02 NS
Coat x Asp. x Sex	1	12.67	1.07 NS
Rank x Asp. x Sex	1	3.02	0.26 NS
Error	60	11.84	

TABLE 51: EFFECT OF SIRE, BIRTHCOAT TYPE, BIRTHRANK, AIRSPEED AND SEX ON THE THERMAL CIRCULATION INDICES OF LAMBS AT 10°C AMBIENT TEMPERATURE

Classification	Thermal Circulation Index - Mean ± S.E.	
Sire		
D140/7	0.51 ± 0.06	(42)
D46/7	0.49 ± 0.06	(44)
Birthcoat type		
Non-hairy	0.52 ± 0.05	(45)
Hairy	0.48 ± 0.07	(41)
Birthrank		
Single	0.57 ± 0.07	(42)
Twin	0.44 ± 0.05	(44)
Nominal airspeed (m sec^{-1})		
0.0	0.70 ± 0.07	(43)
1.5	0.30 ± 0.02	(43)
Sex		
Male	0.51 ± 0.07	(46)
Female	0.49 ± 0.05	(40)

mediated through an effect of air movement on the coat insulation of the limb, as will be demonstrated later in this chapter.

Sire, birthcoat type and birthrank were significantly interactive in their effects on skin temperature. Among the non-hairy progeny of sire D46/7, single lambs had significantly greater skin temperatures than did twins, but no effect of birthrank was apparent among the hairy progeny of this sire or among the progeny of sire D140/7. It might be expected that the vasoconstricted limbs of twin lambs would lose heat to the environment at a faster rate than those of single lambs since twins are generally smaller than singles and might therefore have a greater ratio of surface area to volume in the limbs. In this connection it may be noted that the effect of birthrank on skin temperature would have been significant at the 10% level had the model been treated as being fully fixed. However, it is not clear why the effect of birthrank should have been expressed in only one of the sire x birthcoat type groups.

The significant effect of airspeed on skin temperature was not paralleled by a corresponding effect on the rate at which skin temperature continued to decline after stable heat production was achieved (Table 52). This was probably because the skin temperature - air temperature gradient (at stable heat production) was about twice as high for the lambs exposed to still air as for those in moving air. The increased cooling power of the greater airspeed would therefore have been offset by this difference and, in any case, the lambs in still air would be expected to exhibit higher skin temperatures than those in moving air when skin temperature finally stabilized. Moreover, if part of the effect of airspeed on skin temperature was mediated through an in-

TABLE 52: EFFECT OF SIRE, BIRTHCOAT TYPE, BIRTHRANK, AIRSPEED AND SEX ON THE RATE OF DECLINE IN HIND-LIMB SKIN TEMPERATURE

Classification	Rate of Decline in Hind-Limb Skin Temperature ($^{o}C\ min^{-1}$) Mean ± S.E.		
	Nominal airspeed ($m\ sec^{-1}$)		
	0.0	1.5	Both airspeeds
Birthcoat type			
Non-hairy	0.098 ± 0.022[a] (23)	0.167 ± 0.023[b] (22)	0.134 ± 0.020 (45)
Hairy	0.154 ± 0.024[b] (20)	0.110 ± 0.023[b] (21)	0.134 ± 0.017 (41)
Both birthcoat types	0.128 ± 0.016 (43)	0.140 ± 0.016 (43)	
Sire			
D140/7	0.134 ± 0.017 (42)		
D46/7	0.134 ± 0.016 (44)		
Birthrank			
Single	0.110 ± 0.017 (42)		
Twin	0.159 ± 0.015 (44)		
Sex			
Male	0.129 ± 0.016 (46)		
Female	0.140 ± 0.017 (40)		

.../continued

TABLE 52, continued

Analysis of Variance			
Source of Variation	d.f.	Mean Square	F
Sire	1	0.00	0.02 NS
Birthcoat Type (Coat)	1	0.00	0.00 NS
Birthrank (Rank)	1	0.03	2.96†
Airspeed (Asp.)	1	0.01	0.06 NS
Sex	1	0.00	0.20 NS
Sire x Coat	1	0.01	0.43 NS
Sire x Rank	1	0.01	0.83 NS
Sire x Asp.	1	0.04	3.63†
Sire x Sex	1	0.00	0.01 NS
Coat x Rank	1	0.00	0.18 NS
Coat x Asp.	1	0.09	7.68**
Coat x Sex	1	0.00	0.16 NS
Rank x Asp.	1	0.03	2.80†
Rank x Sex	1	0.00	0.13 NS
Asp. x Sex	1	0.00	0.03 NS
Sire x Coat x Rank	1	0.04	3.51†
Sire x Coat x Asp.	1	0.00	0.10 NS
Sire x Coat x Sex	1	0.02	1.95 NS
Sire x Rank x Asp.	1	0.01	0.97 NS
Sire x Rank x Sex	1	0.00	0.05 NS
Sire x Asp. x Sex	1	0.00	0.19 NS
Coat x Rank x Asp.	1	0.02	1.98 NS
Coat x Rank x Sex	1	0.00	0.01 NS
Coat x Asp. x Sex	1	0.02	1.31 NS
Rank x Asp. x Sex	1	0.00	0.01 NS
Error	60	0.01	

creased tendency of the thermocouples to underestimate true skin temperature when exposed to moving air, this would not be expressed in a differential rate of decline in skin temperature.

A small effect of birthrank on the rate of decline in skin temperature was apparent, the skin temperatures of twin lambs falling approximately 45% faster than those of the single-born lambs ($P<.10$). This occurred despite the twins having slightly lower skin temperatures (at stable heat production) which were reflected in their lower thermal circulation indices (Table 51).

(b) Heat production and skin temperature

The overall regression coefficient of heat production on skin temperature was $b = -0.15 \pm 0.06$ W kg^{-1} $^{o}C^{-1}$ which was significant ($t_{84} = 2.32$, $P<.05$) but of a lesser magnitude than the corresponding regression coefficient in Chapter IV. The pooled within-class regression coefficient was, however, non-significant (Table 53). Although the within-sex regressions were heterogeneous, neither of them was significantly different from zero ($b = -0.14 \pm 0.08$ W kg^{-1} $^{o}C^{-1}$ and $b = 0.22 \pm 0.14$ W kg^{-1} $^{o}C^{-1}$ for male and female lambs respectively). Moreover, when the analysis was repeated for only the non-summit lambs, the within-sex regressions were homogeneous. Hence it may be concluded that heat production was essentially independent of skin temperature once account had been taken of the treatment effects (particularly those of airspeed) on both these variables. This situation differs from that in the previous experiment where heat production was negatively related to skin temperature among the wet lambs.

TABLE 53: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (SEX) REGRESSIONS OF HEAT PRODUCTION ON HIND-LIMB SKIN TEMPERATURE AT 10°C AMBIENT TEMPERATURE

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 37)	25	11.63	
Intra-class (sex) regression of heat production on skin temperature	2	10.66	2.46†
Pooled within-class	1	2.87	0.66 NS
Difference	1	18.46	4.25*
Residual error	58	4.34	

(c) Skin temperature and the weight of wool on the limbs

The weight of wool on the limbs was measured in a random sample of 40 of these lambs as described in Chapter II. Because of the small number of lambs involved it was not possible to fit the full model in the analysis of this trait (henceforth referred to as "limb wool weight"). Preliminary analyses showed that sire and sex exerted little effect on skin temperature and no effect on limb wool weight, so they were eliminated from the model. In fact none of the treatments significantly affected limb wool weight, even in the final model (Table 54).

The overall regression coefficient of skin temperature on limb wool weight was $b = 1.02 \pm 0.58$ $^{o}C\ g^{-1}$ kg which was significant only at the 10% level ($t_{38} = 1.75$). The within-airspeed regressions were, however, significantly heterogeneous (Table 55). Among the lambs exposed to still air, high skin temperatures were associated with high limb wool weights ($b = 2.00 \pm 0.61$ $^{o}C\ g^{-1}$ kg, $t_{18} = 3.24$, $P<.01$) but no significant relationship existed among the lambs in moving air ($b = -0.85 \pm 0.75$ $^{o}C\ g^{-1}$ kg, $t_{18} = 1.13$, NS.). Conversely, neither the overall ($b= -0.001 \pm 0.013$ $^{o}C\ min^{-1}\ g^{-1}$ kg, $t_{38} = 0.10$, NS.) nor the pooled within-class regression coefficients (Table 56) of rate of decline in skin temperature on limb wool weight were significant.

The relationship between skin temperature and limb wool weight would seem to have two possible explanations. Slee (1964, 1968) has suggested that sheep which have a superior coat coverage on the limbs may be less dependent on heat conservation by peripheral vasoconstriction than those whose limbs are poorly insulated from the cold. It may be, for example, that a poor insulation on the limbs results in a more

TABLE 54: EFFECT OF BIRTHCOAT TYPE AND BIRTHRANK ON THE WEIGHT OF WOOL ON THE LIMBS IN FORTY LAMBS

Classification	Weight of Wool on the Limbs (g kg^{-1}) Mean ± S.E.
Birthcoat type	
Non-hairy	8.87 ± 0.26 (20)
Hairy	8.93 ± 0.26 (20)
Birthrank	
Single	8.60 ± 0.27 (21)
Twin	9.20 ± 0.25 (19)

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Birthcoat Type (Coat)	1	0.04	0.03 NS
Birthrank (Rank)	1	3.51	2.59 NS
Coat x Rank	1	0.61	0.45 NS
Error	36	1.35	

TABLE 55: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (AIRSPEED) REGRESSIONS OF HIND-LIMB SKIN TEMPERATURE ON LIMB WOOL WEIGHT IN FORTY LAMBS

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Birthcoat Type (Coat)	1	12.53	1.38 NS
Birthrank (Rank)	1	47.48	5.23*
Airspeed (Asp.)	1	230.05	25.32***
Coat x Rank	1	9.96	1.10 NS
Coat x Asp.	1	2.61	0.29 NS
Rank x Asp.	1	22.29	2.45 NS
Coat x Rank x Asp.	1	0.01	0.00 NS
Intra-class (airspeed) regression of skin temperature on limb wool weight	2	53.56	5.90**
Pooled within-class	1	29.50	3.25†
Difference	1	77.67	8.55**
Residual error	30	9.09	

TABLE 56: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (BIRTHCOAT TYPE) REGRESSIONS OF RATE OF DECLINE IN SKIN TEMPERATURE ON LIMB WOOL WEIGHT IN FORTY LAMBS

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Birthcoat Type (Coat)	1	0.00	0.01 NS
Birthrank (Rank)	1	0.00	0.00 NS
Airspeed (Asp.)	1	0.00	0.09 NS
Coat x Rank	1	0.00	0.32 NS
Coat x Asp.	1	0.02	2.03 NS
Rank x Asp.	1	0.02	2.12 NS
Coat x Rank x Asp.	1	0.00	0.22 NS
Intra-class (birthcoat type) regression of the rate of decline in skin temperature on limb wool weight	2	0.01	0.98 NS
Pooled within-class	1	0.00	0.00 NS
Difference	1	0.02	1.95 NS
Residual error	30	0.01	

intense stimulation of peripheral thermoreceptors and so in a more intense vasoconstrictor response. The non-significant relationship between skin temperature and limb wool weight in the lambs exposed to the greater airspeed might then be explained by an increase in peripheral stimulation associated with the movement of cold air over the limb. However, this hypothesis would require a mechanism for peripheral vasomotor control which was continuously variable rather than an "all-or-none" response. While it is not possible to be certain that this did not occur, the generally linear relationships between heat production and ambient temperature among the wet lambs in Chapter IV suggest that the "all-or-none" response was more likely.

The second hypothesis, and the one which seems more tenable, is that the lambs vasocontricted in an "all-or-none" manner and that the rate at which their skin temperature equilibrated with the environment (i.e. the rate at which heat was lost from the limb) was then dependent upon the insulative value of the limb wool. Similarly, the final skin temperature achieved would have been related to the external insulation of the limb. The non-significant relationship between skin temperature and limb wool weight among lambs exposed to moving air could then be explained by a reduction in the insulative value of the limb wool in conditions of air movement. This supposes, of course, that the moving air was able to break down the coat structure on the limbs when it apparently did not do so on the body (Chapter IV). Such an effect could be explained only by differences in coat structure at these sites, or by different patterns of air movement over them. Alternatively, the increased rate of heat loss from the limbs which was associated with air movement may have been sufficiently large to mask variation in heat loss

associated with variation in limb wool weight.

(d) Weight of wool on the limbs, hip coat depth and midside wool weight

In the previous chapter, heat production was found to be negatively related to skin temperature in the wet lambs. It was therefore suggested that this relationship could have been due to the correlated effects of birthcoat insulation (of the body and the limbs) on heat loss and on the rate at which skin temperature equilibrated with the environment. Although metabolic rate and skin temperature were not related in the lambs examined in this experiment, some information may be provided about the relationship between limb wool weight and the birthcoat characteristics which were previously shown to affect external insulation.

The overall regression coefficient of limb wool weight on hip coat depth was b = 0.01 ± 0.05 g kg^{-1} mm^{-1} (t_{38} = 0.22, NS.). The within-birthrank regressions were heterogeneous (Table 57) being b = -0.23 ± 0.16 g kg^{-1} mm^{-1} (t_{19} = 1.48, NS.) and b = 0.19 ± 0.11 g kg^{-1} mm^{-1} (t_{17} = 1.73, P< .10) for single- and twin-born lambs respectively.

A similar situation existed with the regressions of limb wool weight on midside wool weight. The overall regression coefficient was non-significant (b = 0.01 ± 0.02 g kg^{-1} mg^{-1} cm^2, t_{38} = 0.82) but the within-birthrank regressions were heterogeneous (Table 58). Thus limb wool weight was again related to the birthcoat characteristic (midside wool weight) among twin lambs (b = 0.06 ± 0.02 g kg^{-1} mg^{-1} cm^2, t_{17} = 2.44, P< .05) but not among the singles (b = -0.03 ± 0.03 g kg^{-1} mg^{-1} cm^2, t_{19} = 0.89, NS.).

TABLE 57: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (BIRTHRANK) REGRESSIONS OF LIMB WOOL WEIGHT ON HIP COAT DEPTH IN FORTY LAMBS

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 54)	3	1.38	
Intra-class (birthrank) regression of limb wool weight on hip coat depth	2	3.21	2.58†
Pooled within-class	1	0.35	0.28 NS
Difference	1	6.07	4.88*
Residual error	34	1.24	

TABLE 58: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (BIRTHRANK) REGRESSIONS OF LIMB WOOL WEIGHT ON MIDSIDE WOOL WEIGHT PER UNIT AREA OF SKIN IN FORTY LAMBS

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 54)	3	1.38	
Intra-class (birthrank) regression of limb wool weight on midside wool weight	2	4.02	3.36*
Pooled within-class	1	2.09	1.75 NS
Difference	1	5.94	4.97*
Residual error	34	1.20	

It may therefore be concluded that, in this experiment, there was some small degree of relationship between limb wool weight and the birthcoat characteristics (at least among the twin lambs) but that heat production was not related to skin temperature. As a consequence it has not been possible to establish whether the hypothesis advanced for the negative heat production-skin temperature relationship in Chapter IV (i.e. that it occurs through the correlation between external insulation of the limb and that of the body as a whole) is tenable. Nevertheless it is clear that in neither experiment was there a significantly positive relationship between heat production and skin temperature. Variation in hind-limb skin temperature cannot, therefore, be interpreted as indicating a superior ability of some lambs to conserve body heat by more intense peripheral vasoconstriction.

Chapter Summary

In this experiment, responses to cold-stress were examined in 86 lambs with hairy and non-hairy birthcoats similar to those of lambs in the previous experiment. Approximately half the lambs were twin-born. All were tested while wet at an ambient temperature of $10^{o}C$, and were exposed to still air or moving (1.5 m sec^{-1}) air.

A substantial proportion (26%) of the lambs in this experiment were considered to have attained summit metabolism (based on a rate of decline in rectal temperature exceeding $0.025^{o}C\ min^{-1}$ before and after stable heat production was achieved). Relationships involving heat production were therefore subjected to dual analyses, once with all the lambs and again for only those lambs not attaining summit metabolism. The reasons for this type of analysis have been discussed.

Birthcoat type, sex and birthrank all significantly influenced the proportion of lambs attaining summit metabolism. The first 2 effects paralleled the corresponding treatment effects on metabolic rate and to a lesser degree on the rate of decline in rectal temperature. Birthrank did not,however, significantly affect metabolic rate. This may indicate that twin lambs have a slightly lower summit metabolism than singles (an effect which has been reported elsewhere). Differences between the sexes in resistance to cold-stress were much greater than in the previous experiment but cannot be readily explained in terms of between-sex differences in bodyweight or birthcoat characteristics.

The proportion of lambs expected to attain summit metabolism was positively related to metabolic rate which indicates that lambs were susceptible to severe hypothermia primarily because of poor body insulation rather than a poor ability to produce body heat. This view is confirmed by the negative relationships between the proportion of lambs expected to attain summit metabolism and the birthcoat characteristics.

The pre-test rectal temperatures of hairyand non-hairy lambs were virtually identical at about 40.2^{o}C. Upon exposure to the cold environment, non-hairy lambs exhibited a greater rate of decline in rectal temperature with the result that their rectal temperatures (at stable heat production) were significantly lower than those of the hairy lambs. These results contrast markedly with those from the corresponding lambs in Chapter IV and support the previously-expressed view that Romney-type and single-N lambs do not have inherently different "normal" rectal temperatures. Twin lambs also had lower rectal temperatures (at stable heat production) than singles but this was

partly due to their poorer ability to adjust to the mildly cold environment experienced prior to the test (as indicated by their low pre-test rectal temperatures).

In this experiment, as in Chapter IV, hairy lambs had significantly greater coat depths and midside wool weights than non-hairy lambs although the difference between the coat types was smaller than in the earlier experiment. Twin lambs also had significantly lower coat depths than singles and although there was no effect of birthrank *per se* on midside wool weight, the effects of birthrank, sire and birthcoat type were significantly interactive. The effects of birthrank on the birthcoat characteristics generally paralleled the corresponding effects on bodyweight, but there was no evidence of a strong relationship between the birthcoat characteristics and bodyweight.

The effect of sire of the lamb on midside coat depth was significant only at the 10% level, while for hip coat depth there was a significant interaction between sire and coat type. In the latter case the effect of sire was expressed only in the coat depths of the hairy lambs. Although the sire effects were small, the experiment did satisfy the criteria of a progeny test (both in terms of the number of progeny representing each sire, and the way in which the animals were managed). Hence, despite the small difference between the sires, these results do suggest that coat depth may be genetically controlled within birthcoat types. Indeed it is not surprising that the between-sire differences were small, particularly since the sires used were themselves paternal half-brothers. There was no evidence of a sire effect on midside wool weight.

Treatment effects on lamb bodyweight were generally as expected, the male lambs being heavier than females and singles heavier than twins. Sire and birthcoat type effects were not significant but did interact. Thus the hairy progeny of one sire were significantly heavier than the non-hairy progeny but no such effect was apparent among the progeny of the other sire. An analysis of metabolic rate - bodyweight relationships indicated that the level of heat production (per unit bodyweight) required to maintain body temperature declines as bodyweight increases, but not as rapidly as might be expected from the weight exponents used in previous studies.

The study of factors affecting hind-limb skin temperature was further extended in this experiment. Lambs were exposed to a single cold environment (thus eliminating variation in the "timing" of peripheral vasoconstriction) and the rate at which skin temperature continued to decline after the attainment of stable heat production was measured.

Thermal circulation indices were calculated for all treatment groups and were consistent with the lambs having constricted peripheral blood vessels. However the only treatment to significantly affect skin temperature was airspeed and this effect may again be related to the rate at which the limb temperature equilibrates with the environment. Aside from this effect, skin temperature was found to be most strongly related to the weight of birthcoat on the limbs, individuals with a high limb wool weight tending to have high skin temperatures (in still air). It was concluded that this effect was probably due to an influence of the limb wool weight on the rate at which heat is lost from the vasoconstricted limb and hence on the rate at which skin temperature equilibrates with the environment.

C H A P T E R V I

THE EFFECTS OF FACE COVER SELECTION AND AGE/FEEDING LEVEL OF THE LAMB ON THE RESPONSE TO COLD-STRESS AT A SINGLE AMBIENT TEMPERATURE

CHAPTER VI

THE EFFECTS OF FACE COVER SELECTION AND AGE/FEEDING LEVEL OF THE LAMB ON THE RESPONSE TO COLD-STRESS AT A SINGLE AMBIENT TEMPERATURE

Introduction

Open-faced sheep are known to have a faster growth rate and better reproductive ability than those with woolly faces (Cockrem and Rae, 1966), effects which may be mediated through a differential ability of these sheep to control peripheral blood flow and body temperature. The"effects" of face cover can be expressed in lambs during the first year of life (Cockrem, 1967) but it is not known whether the lamb's genotype for face cover influences its resistance to hypothermia immediately after birth. In this experiment the role of face cover was examined by measuring the responses to cold-stress of lambs from 2 selection flocks, one of which has been randomly bred and the other selected only for open faces. In a complementary experiment, described in Chapter VII, the "effects" of face cover were further examined by relating the responses to cold-stress of an unselected group of newborn lambs to their face cover grades at approximately 3 months of age.

The previous experiments have demonstrated that a strong relationship exists between the level of heat production which the lamb requires to maintain normal body temperature and certain characteristics of the birthcoat. However, in each case the lambs involved had dried naturally after birth and then had their coats artificially re-wetted. Slee (1977) has suggested that the influence of the birthcoat on total

body insulation is likely to be minimized in the very young lamb due to its being saturated with amniotic fluid. In this experiment, therefore, the lambs were first tested either when newborn (0.25 to 1.00 hours old) or when older (2.00 to 22.00 hours) to compare the effects, on coat insulation, of natural wetting with amniotic fluids and artificial wetting with tap water. Only the older lambs suckled prior to the test.

Experimental Design and Methods

The experiment involved 54 Romney lambs, all of which were drawn from the Massey University "Progeny Test" flock. This flock was randomly divided into 3 groups, each of approximately 80 ewes, in 1956 and since that time single-trait selection has been practised in 2 of the groups ("Face Cover" and "Fleeceweight"). The remaining group has been maintained as randomly-bred "Controls". Only lambs from the Face Cover and Control groups were used in this experiment. In the Face Cover group, selection of both ewes and rams has been based solely on the face cover grade (i.e. selection for more open faces) at the annual hogget shearing (generally in October). This group has been maintained at 80 ewes with 4 rams being single-sire mated to these ewes each year. The rams are used only once, at 18 months of age. Within the Control group, selection is random and the group structure is the same as for the other groups. Inbreeding coefficients for the Face Cover and Control groups have been estimated to be 0.09 and 0.10 respectively for lambs born in 1976 (Blair, 1981).

As previously noted, the lambs were tested either when newborn and unfed or when older and fed, so that the effects of age and feeding level were largely confounded. However, this was not considered to

present serious difficulties in the analysis since the ingestion of milk does not influence the lamb's capacity for heat production in cold climates (Alexander, 1962b). One problem with this treatment was that the assignment of lambs to levels of the treatment was not strictly at random, the unfed/newborn lambs becoming members of this group by virtue of being born at times when they could be tested immediately. As will be seen, this may have lead to some differences between the unfed/newborn and the fed/older lambs in certain characteristics. For convenience this treatment will be referred to as "Feeding Level" but the confounding with age, and the possible non-random assignment of lambs to the treatment levels, should not be ignored.

The twinning rate in the Progeny test flock was lower than among the ewes described in Chapter V, only 35% of the available lambs being twin-born. Preliminary analyses showed the birthrank effects to be small, and birthrank was therefore not fitted in the final analyses. Sex effects were fitted although they too were minor. Thus the experiment was of an unbalanced three-way cross-classified design with face cover group, feeding level and sex as main effects. All were treated as fixed effects.

The experimental procedure was similar to that described in Chapter V. All the lambs were tested when wet at an ambient temperature of $10^{o}C$ and were exposed to a nominal airspeed of 1.50 m sec^{-1}. The newborn lambs were separated from their dams immediately after birth and tested within 1 hour of separation while the remaining lambs were permitted to suckle until 20 minutes before the commencement of the test. Rectal temperature, skin temperature and limb wool weight were measured in all lambs as described in Chapter V.

Results and Discussion

1. Proportion of lambs attaining summit metabolism

The lambs in this experiment were considerably less resistant to hypothermia than the non-hairy lambs exposed to the same airspeed (1.5 m sec^{-1}) in Chapter V. Thus, while only 40.1% of the non-hairy lambs in moving air were considered to have attained summit metabolism, 64.8% of the Progeny Test lambs were affected in this manner. The poorer performance of these lambs was associated with their lower mean birthcoat depth at the hip site (6.9 ± 0.2 mm) than that of the non-hairy lambs (8.2 ± 0.3 mm). However, in addition to their lower resistance to body cooling, the Progeny Test lambs also had lower rates of heat production than the non-hairy lambs in the same environment (14.92 ± 0.37 vs 16.98 ± 0.41 W kg^{-1}) despite the almost identical bodyweights of the 2 groups. Hence it appears likely that the lambs in this experiment had a lower mean level of summit metabolism than those in Chapter V.

Treatment effects on the proportion of lambs attaining summit metabolism were again examined by analysis of deviance on the logit scale. None of the treatment effects was found to be significant (Table 59). The absence of an effect of sex conflicts with the results from the previous chapter in which a considerably higher proportion of females than males appeared to have attained summit metabolism. Similarly there was no effect of sex on the heat production of the Progeny Test lambs (Table 60), whereas a corresponding effect of sex was apparent in Chapter V.

The high proportion of lambs which attained summit metabolism

TABLE 59: EFFECT OF FACE COVER GROUP, FEEDING LEVEL AND SEX ON THE PROPORTION OF LAMBS ATTAINING SUMMIT METABOLISM

Classification	Proportion of Lambs Attaining Summit Metabolism		
	Logit-Transformed Mean ± S.E.	Retransformed %	
Face cover group			
Face cover	0.71 ± 0.41	67.1	(27)
Control	0.52 ± 0.40	62.7	(27)
Feeding level			
Unfed/newborn	0.53 ± 0.43	63.0	(24)
Fed/older	0.70 ± 0.39	66.9	(30)
Sex			
Male	0.81 ± 0.42	69.2	(26)
Female	0.42 ± 0.38	60.4	(28)

Analysis of Deviance

Source	d.f.	χ^2 Deviance
Face Cover Group (Group)	1	0.11 NS
Feeding Level (Feed.)	1	0.09 NS
Sex	1	0.45 NS
Group x Feed.	1	2.50 NS
Group x Sex	1	0.25 NS
Feed. x Sex	1	0.01 NS
Group x Feed. x Sex	1	3.21 †
Error	46	63.35

TABLE 60: EFFECT OF FACE COVER GROUP, FEEDING LEVEL AND SEX ON THE HEAT PRODUCTION OF LAMBS AT 10°C AMBIENT TEMPERATURE

Classification	Heat Production ($W\ kg^{-1}$) Mean ± S.E.	
Face cover group		
Face cover	14.95 ± 0.52	(27)
Control	14.81 ± 0.52	(27)
Feeding level		
Unfed/newborn	14.34 ± 0.55	(24)
Fed/older	15.42 ± 0.50	(30)
Sex		
Male	14.51 ± 0.54	(26)
Female	15.25 ± 0.51	(28)

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Face Cover Group (Group)	1	0.28	0.04 NS
Feeding Level (Feed.)	1	15.80	1.99 NS
Sex	1	7.49	0.95 NS
Group x Feed.	1	1.68	0.21 NS
Group x Sex	1	3.34	0.42 NS
Feed. x Sex	1	1.06	0.13 NS
Group x Feed. x Sex	1	1.27	0.16 NS
Error	46	7.93	

in this experiment again necessitated dual analyses separating the "summit" and "non-summit" lambs. In this case, however, the "summit" lambs comprised the greater proportion of the lambs tested. Since metabolic rate was not a useful indicator of resistance to cold-stress in these lambs it was necessary to use the rate of decline in rectal temperature as the main indicator, while accepting that some of the variation in this latter trait would have been due to variation in the level of summit metabolism achieved by the lamb. In contrast to the previous experiment, rate of decline in rectal temperature was calculated only over the whole experiment period (i.e. using the first and last measurements of rectal temperature). This was done because the trait was now being used entirely as an indicator of cold-stress and not to describe differences which lead to variation in rectal temperature at the time stable heat production was attained.

2. Rate of decline in rectal temperature

The analysis of variance for rate of decline in rectal temperature (whole experiment) is presented in Table 61. Only the feeding level treatment approached significance, the unfed/newborn lambs having a rate of decline in rectal temperature two-thirds that of the fed/older lambs ($P<.10$). This result is surprising, particularly in view of the very young age at which the unfed/newborn lambs were tested. These lambs had slightly deeper coats than the fed/older lambs (Table 62), which may have contributed to a superior birthcoat insulation. This difference must in turn have been at least partly responsible for the differential rates of decline in rectal temperature since feeding level did not affect metabolic rate.

TABLE 61: EFFECT OF FACE COVER GROUP, FEEDING LEVEL AND SEX ON THE RATE OF DECLINE IN RECTAL TEMPERATURE (WHOLE EXPERIMENT PERIOD)

Classification	Rate of Decline in Rectal Temperature ($^{o}C\ min^{-1}$) Mean ± S.E.	
Face cover group		
Face cover	0.059 ± 0.009	(27)
Control	0.053 ± 0.009	(27)
Feeding level		
Unfed/newborn	0.045 ± 0.009	(24)
Fed/older	0.068 ± 0.008	(30)
Sex		
Male	0.063 ± 0.009	(26)
Female	0.049 ± 0.009	(28)

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Face Cover Group (Group)	1	0.001	0.24 NS
Feeding Level (Feed.)	1	0.007	3.48 †
Sex	1	0.003	1.24 NS
Group x Feed.	1	0.001	0.29 NS
Group x Sex	1	0.001	0.38 NS
Feed. x Sex	1	0.004	1.81 NS
Group x Feed. x Sex	1	0.001	0.24 NS
Error	46	0.002	

Face Cover lambs did not differ significantly from the Control lambs in heat production, rate of decline in rectal temperature (RDRT) or in the attainment of summit metabolism. It is therefore apparent that, at least in the Progeny Test flock, selection for more open faces had not produced lambs which were better able to withstand severe cold at birth.

3. Characteristics of the birthcoat

(a) Depth of birthcoat

The mean birthcoat depth (at the hip site) of the unfed/newborn lambs was 1.0 mm greater than that of the fed/older lambs, a difference which was significant ($P<.05$, Table 62). This effect was largely due to the very high coat depths of the unfed/newborn Control group lambs and may indicate differences in the coat structure, of lambs of the 2 genotypes, which affected their response to the natural and artificial wetting treatments. However, the possibility also exists that this difference was a chance effect arising from the manner in which the lambs were assigned to the feeding level treatment. As will be discussed later in this chapter, certain other differences between lambs in the levels of this treatment appeared to be chance effects.

The role of the birthcoat characteristics as determinants of resistance to cold-stress was examined by dual regression analyses of heat production on the coat characters (for the lambs considered not to have attained summit metabolism) and of RDRT on the coat characters for the summit lambs. These analyses will be discussed separately.

(i) Lambs attaining summit metabolism

The overall regression coefficient of RDRT on hip birthcoat

TABLE 62: EFFECT OF FACE COVER GROUP, FEEDING LEVEL AND SEX ON HIP BIRTHCOAT DEPTH

Classification	Hip Birthcoat Depth (mm) Mean ± S.E.		
	Face cover group		
Feeding level	Face cover	Control	Both groups
Unfed/newborn	6.6 ± 0.4[a] (12)	8.2 ± 0.4[b] (12)	7.4 ± 0.3 (24)
Fed/older	6.8 ± 0.4[a] (15)	6.1 ± 0.4[a] (15)	6.4 ± 0.3 (30)
Both levels	6.7 ± 0.3 (27)	7.1 ± 0.3 (27)	
Sex			
Male	6.7 ± 0.3 (26)		
Female	7.1 ± 0.3 (28)		

Analysis of Variance			
Source of Variation	d.f.	Mean Square	F
Face Cover Group (Group)	1	1.04	0.48 NS
Feeding Level (Feed.)	1	12.60	5.82*
Sex	1	0.83	0.39 NS
Group x Feed.	1	17.08	7.89**
Group x Sex	1	2.31	1.07 NS
Feed. x Sex	1	0.14	0.06 NS
Group x Feed. x Sex	1	5.20	2.40 NS
Error	46	2.16	

depth was $b = -0.012 \pm 0.004^{o}C\ min^{-1}\ mm^{-1}$ which was significant ($t_{33} = 2.69$, $P<.05$). When account was taken of treatment effects on RDRT, the pooled within-class regression was significant only at the 10% level (Table 63) and the within-feeding level regressions were homogeneous ($P>.05$). At the midside position, neither the overall nor the pooled within-class regressions were significant and all within-class regressions were homogeneous. Hence, as was predicted at the commencement of this study, it was not possible to detect strong relationships between RDRT and the coat depths.

(ii) Lambs not attaining summit metabolism

Despite there being only 19 lambs which did not attain summit metabolism, the heat production of these lambs was significantly related to coat depth, particularly at the midside position. The overall regression coefficient of heat production on midside coat depth was $b = -0.79 \pm 0.29\ W\ kg^{-1}\ mm^{-1}$ which was significant ($t_{17} = 2.80$, $P<.05$). Because so few lambs were involved in this analysis, it was not possible to fit the within-feeding level regressions after the full model; they were therefore fitted after a model containing only the terms in face cover group and feeding level, together with their interaction. As Table 64 shows, the pooled within-class regression of heat production on midside coat depth was significant ($b = -0.96 \pm 0.33\ W\ kg^{-1}\ mm^{-1}$) but the within-feeding level regressions were homogeneous. At the hip site, the overall regression coefficient was not significant ($b = -0.57 \pm 0.35\ W\ kg^{-1}\ mm^{-1}$, $t_{17} = 1.62$) although it was of a similar magnitude to the corresponding regression at the midside position. The pooled-within class regression was significant only

TABLE 63: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (FEEDING LEVEL) REGRESSIONS OF RATE OF DECLINE IN RECTAL TEMPERATURE ON HIP BIRTHCOAT DEPTH : SUMMIT LAMBS

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Face Cover Group (Group)	1	0.000	0.16 NS
Feeding Level (Feed.)	1	0.009	8.80**
Sex	1	0.002	1.89 NS
Group x Feed.	1	0.002	1.89 NS
Group x Sex	1	0.000	0.38 NS
Feed. x Sex	1	0.001	1.32 NS
Group x Feed. x Sex	1	0.000	0.27 NS
Intra-class (feeding level) regression of RDRT on hip coat depth	2	0.004	3.50*
Pooled within-class	1	0.004	3.87†
Difference	1	0.003	3.12†
Residual error	25	0.001	

TABLE 64: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (FEEDING LEVEL) REGRESSIONS OF HEAT PRODUCTION AT 10°C AMBIENT TEMPERATURE ON MIDSIDE BIRTHCOAT DEPTH : NON-SUMMIT LAMBS

Analysis of Covariance

Source of Variation	d.f.	Mean Square	F
Face Cover Group (Group)	1	0.33	0.06 NS
Feeding level (Feed.)	1	3.28	0.57 NS
Group x Feed.	1	5.64	0.98 NS
Intra-class (feeding level) regression of heat production on midside coat depth	2	27.01	4.69*
Pooled within-class	1	53.04	9.21**
Difference	1	0.97	0.17 NS
Residual error	13	5.76	

at the 10% level and the within-feeding level regressions were again homogeneous.

(b) Midside wool weight per unit area of skin

As with coat depth there was a significant interaction between the effects of face cover group and feeding level on midside wool weight (Table 65). In this case, however, the interaction was due to the low midside wool weights of the unfed/newborn Face Cover lambs and so differs from the interaction in the birthcoat depths. Since the midside wool samples were weighed at a constant moisture content, the type of wetting applied to the coat (amniotic fluid or tap water) could not have been responsible for this interaction. Nor could the amount of solid material deposited in the coat (from the amniotic fluid) have contributed to this effect since the fed/older lambs, which lost much of this material during artificial wetting, had the higher midside wool weights. It therefore seems likely that this interaction reflects a chance effect. There was also a significant effect of sex, the female lambs having midside wool weights 27% greater than those of the males. This contrasts markedly with the results from the 2 previous experiments.

Within the summit lambs the overall regression coefficient of RDRT on midside wool weight was $b = -0.001 \pm 0.001$ $^{o}C\ min^{-1}\ mg^{-1}\ cm^{2}$ which was not significant ($t_{33} = 0.99$, NS.). The pooled within-class regression was significant only at the 10% level and the within-feeding level regressions were heterogeneous at the same level of significance (Table 66). In this respect the regression on midside wool weight was similar to the corresponding regression on hip coat depth.

TABLE 65: EFFECT OF FACE COVER GROUP, FEEDING LEVEL AND SEX ON MIDSIDE WOOL WEIGHT PER UNIT AREA OF SKIN

Classification	Midside Wool Weight/Unit Area ($mg\ cm^{-2}$) Mean ± S.E.		
	Face cover group		
	Face cover	Control	Both groups
Feeding level			
Unfed/newborn	30.0 ± 2.6[a] (12)	39.5 ± 2.6[b] (12)	34.7 ± 1.8 (24)
Fed/older	39.9 ± 2.3[b] (15)	38.8 ± 2.3[b] (15)	39.4 ± 1.6 (30)
Both levels	34.9 ± 1.7 (27)	39.1 ± 1.7 (27)	
Sex			
Male	32.6 ± 1.8 (26)		
Female	41.5 ± 1.7 (28)		

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Face Cover Group (Group)	1	166.35	2.13 NS
Feeding Level (Feed.)	1	284.00	3.64†
Sex	1	861.03	11.04**
Group x Feed.	1	332.39	4.26*
Group x Sex	1	80.44	1.03 NS
Feed. x Sex	1	13.53	0.17 NS
Group x Feed. x Sex	1	192.85	2.47 NS
Error	46	78.02	

TABLE 66: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (FEEDING LEVEL) REGRESSIONS OF RATE OF DECLINE IN RECTAL TEMPERATURE ON MIDSIDE WOOL WEIGHT PER UNIT AREA OF SKIN : SUMMIT LAMBS

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 63)	7	0.002	
Intra-class (feeding level) regression of RDRT on midside wool weight	2	0.004	3.63*
Pooled within-class	1	0.004	3.38†
Difference	1	0.004	3.88†
Residual error	25	0.001	

Among the lambs which did not attain summit metabolism, a much stronger relationship existed between heat production and midside wool weight, both the overall ($b = -0.16 \pm 0.05$ W kg^{-1} mg^{-1} cm^2, $t_{17} = 3.47$, $P<.01$) and the pooled within-class ($b = -0.21 \pm 0.04$ W kg^{-1} mg^{-1} cm^2, $P<.001$, Table 67) regressions being highly significant. The within-feeding level regressions were again homogeneous.

Two important points should be made about the preceding analyses involving the birthcoat characters. First it may be noted that the tests of homogeneity of the within-feeding level regressions of heat production on the coat characters lack power because only 19 lambs were involved in the analyses. This, of course, is a direct consequence of the high proportion of lambs which attained summit metabolism. Nevertheless, the overall and pooled within-class regressions of heat production on the coat characters were generally significant and an examination of the within-feeding level regression coefficients showed them to be similar in magnitude. These results therefore suggest that the naturally-wet coat of the newborn lamb and the artificially-wetted coat of the older lamb provide an equal amount of insulation per unit of depth or midside wool weight.

The second point is that the within-feeding level regressions of RDRT on both hip coat depth and midside wool weight were significantly heterogeneous at the 10% level. Since the difference reflected, in each case, a tendency for RDRT to be more strongly related to the coat character in the fed/older lambs than in the unfed/newborn group, it may have been a real effect. While such a relationship would suggest that coat insulation (and hence the rate of body heat loss) was more strongly related to these coat characters in the fed/older lambs, the

TABLE 67: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (FEEDING LEVEL) REGRESSIONS OF HEAT PRODUCTION AT 10°C AMBIENT TEMPERATURE ON MIDSIDE WOOL WEIGHT PER UNIT AREA OF SKIN : NON-SUMMIT LAMBS

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 64)	3	3.37	
Intra-class (feeding level) regression of heat production on midside wool weight	2	41.96	12.14**
Pooled within-class	1	83.30	24.10***
Difference	1	0.61	0.18 NS
Residual error	13	3.46	

information from the regressions involving heat production certainly does not support this hypothesis. The effect, if real, might have been mediated through other pathways such as an association between summit metabolic rate and hip coat depth or midside wool weight. However, relationships of this type could not be detected in these lambs.

4. Hind-limb skin temperature

(a) Treatment effects on skin temperature

Treatment effects on skin temperature were small and the lambs exhibited low skin temperature - air temperature gradients, indicating that peripheral vasoconstriction had occurred. The only treatment effect to approach significance was that of feeding level, the unfed/newborn lambs having skin temperatures 1.5^{o}C greater than those of the fed/older lambs ($P<.10$, Table 68). This conflicts with the results of Alexander (1961) who suggested that young unfed lambs had lower skin temperatures than older fed lambs. However, the comparison may not be valid since Alexander's "young" lambs appear to have been somewhat older than the unfed/newborn group in this experiment. There was also a significant face cover x feeding level x sex interaction in skin temperature. This was mainly due to the very low skin temperatures of the male fed/older lambs of the face cover group. Whether this reflects a superior ability of these lambs to constrict peripheral blood vessels is not known, but the interaction was not reflected in any of the other characteristics which have been shown to affect skin temperature.

(b) Skin temperature and the weight of wool on the limbs

The weight of wool on the limbs was measured in all 54 lambs in

TABLE 68: EFFECT OF FACE COVER GROUP, FEEDING LEVEL AND SEX ON THE HIND-LIMB SKIN TEMPERATURES OF LAMBS AT 10°C AMBIENT TEMPERATURE

Classification		Hind-Limb Skin Temperature (°C) Mean ± S.E.	
		Sex	
		Male	Female
Face cover group	Feeding level		
Face cover	Unfed/newborn	16.88 ± 1.30^{b} (4)	15.25 ± 0.92^{b} (8)
	Fed/older	12.69 ± 0.92^{a} (8)	17.00 ± 1.00^{bc} (7)
Control	Unfed/newborn	15.72 ± 0.99^{b} (7)	17.80 ± 1.17^{b} (5)
	Fed/older	15.43 ± 0.99^{bc} (7)	14.69 ± 0.92^{c} (8)

Face cover group		
Face cover	15.45 ± 0.52	(27)
Control	15.91 ± 0.51	(27)
Feeding level		
Unfed/newborn	16.41 ± 0.55	(24)
Fed/older	14.95 ± 0.48	(30)
Sex		
Male	15.18 ± 0.53	(26)
Female	16.19 ± 0.50	(28)

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Face Cover Group (Group)	1	5.12	0.75 NS
Feeding Level (Feed.)	1	21.65	3.17 †
Sex	1	15.93	2.33 NS
Group x Feed.	1	1.65	0.24 NS
Group x Sex	1	5.58	0.82 NS
Feed. x Sex	1	6.65	0.97 NS
Group x Feed.x Sex	1	61.28	8.96**
Error	46	6.84	

TABLE 69: EFFECT OF FACE COVER GROUP, FEEDING LEVEL AND SEX ON THE THERMAL CIRCULATION INDICES OF LAMBS AT 10°C AMBIENT TEMPERATURE

Classification	Thermal Circulation Index - Mean ± S.E.	
Face cover group		
Face cover	0.24 ± 0.03	(27)
Control	0.27 ± 0.03	(27)
Feeding level		
Unfed/newborn	0.29 ± 0.04	(24)
Fed/older	0.22 ± 0.03	(30)
Sex		
Male	0.22 ± 0.03	(26)
Female	0.28 ± 0.04	(28)

this experiment. The fed/older lambs had a greater limb wool weight than their unfed/newborn peers ($P<.05$, Table 70). As with the midside wool weight, this difference could not have been due to the degree of wetting of the coat or to the amount of solid material deposited in the coat from the amniotic fluid. It therefore almost certainly reflects a chance difference associated with the manner in which the lambs were assigned to the feeding levels.

Since the unfed/newborn lambs had lower limb wool weights than their fed/older peers, this difference clearly could not have accounted for their slightly higher skin temperatures. Indeed, this experiment was characterized by a general lack of relationship between skin temperature and limb wool weight, neither the overall ($b = 0.02 \pm 0.40$ $^{o}C\ g^{-1}$ kg, $t_{52} = 0.06$, NS.) nor the pooled within-class (Table 71) regressions being significant. All within-class regressions were homogeneous. This result is compatible with that from the previous experiment in which it was found that skin temperature was related to limb wool weight among lambs exposed to still air but not among those exposed to an airspeed of 1.50 m sec^{-1}. Since, in the present study, all the lambs were exposed to moving air, the absence of an association between skin temperature and limb wool weight is to be expected.

(c) Skin temperature and bodyweight

As the analysis of variance in Table 72 shows, the unfed/newborn lambs were significantly ($P<.05$) heavier than their fed/older peers, but other treatment effects were small. The feeding level effect (a difference of 0.51 kg) arose partly because the older lambs were weighed when dry (before artificial wetting) whereas the newborn lambs were weighed within 45 minutes of birth when their coats were still saturated

TABLE 70: EFFECT OF FACE COVER GROUP, FEEDING LEVEL AND SEX ON THE WEIGHT OF WOOL ON THE LIMBS

Classification	Weight of Wool on the Limbs ($g\ kg^{-1}$) Mean ± S.E.	
Face cover group		
Face cover	8.25 ± 0.19	(27)
Control	7.90 ± 0.19	(27)
Feeding level		
Unfed/newborn	7.77 ± 0.20	(24)
Fed/older	8.38 ± 0.18	(30)
Sex		
Male	7.93 ± 0.19	(26)
Female	8.22 ± 0.18	(28)

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Face Cover Group (Group)	1	1.58	1.65 NS
Feeding Level (Feed.)	1	4.94	5.14*
Sex	1	1.12	1.17 NS
Group x Feed.	1	0.16	0.16 NS
Group x Sex	1	0.47	0.49 NS
Feed. x Sex	1	1.04	1.08 NS
Group x Feed. x Sex	1	0.27	0.29 NS
Error	46	0.96	

TABLE 71: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (FEEDING LEVEL) REGRESSIONS OF HIND-LIMB SKIN TEMPERATURE ON LIMB WOOL WEIGHT

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 68)	7	17.01	
Intra-class (feeding level) regression of skin temperature on limb wool weight	2	1.32	0.19 NS
Pooled within-class	1	0.03	0.00 NS
Difference	1	2.62	0.37 NS
Residual error	44	7.09	

TABLE 72: EFFECT OF FACE COVER GROUP, FEEDING LEVEL AND SEX ON BODYWEIGHT

Classification	Bodyweight (kg) Mean ± S.E.	
Face cover group		
Face cover	4.69 ± 0.15	(27)
Control	4.83 ± 0.15	(27)
Feeding level		
Unfed/newborn	5.01 ± 0.16	(24)
Fed/older	4.50 ± 0.14	(30)
Sex		
Male	4.74 ± 0.15	(26)
Female	4.77 ± 0.15	(28)

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Face Cover Group (Group)	1	0.25	0.39 NS
Feeding Level (Feed.)	1	3.43	5.42*
Sex	1	0.02	0.03 NS
Group x Feed.	1	0.48	0.76 NS
Group x Sex	1	0.24	0.37 NS
Feed. x Sex	1	0.26	0.41 NS
Group x Feed. x Sex	1	0.20	0.32 NS
Error	46	0.63	

with amniotic fluids. Crude estimates of the amount of water which could be trapped by the coats of the older lambs were obtained by weighing 10 of these lambs before and after wetting. These estimates suggested that an additional 7.7% of the dry bodyweight would be added by the wetting treatment, a figure which agrees well with that from Alexander's (1956) study of Merino lambs. It is therefore likely that the mean bodyweight of the fed/older lambs would have been about 4.85 kg, had they been weighed after wetting. The balance of the difference in wet bodyweight between the 2 feeding levels (0.16 kg) may have been associated with dehydration or the catabolism of body reserves since the dams of these lambs appeared to produce less milk than other Romney ewes in the trials. This point is discussed further in Chapter VIII.

The overall regression coefficient of skin temperature on bodyweight was $b = 1.34 \pm 0.46\ ^{o}C\ kg^{-1}$ which was significant ($t_{52} = 2.67$, $P<.05$). The pooled within-class regression coefficient was of a similar magnitude and significance (Table 73) and all within-class regressions were homogeneous. In view of the non-significant relationships between skin temperature and limb wool weight, it is unlikely that heavy lambs had greater skin temperatures because of a greater amount of wool on the limbs. Hence the relationship between skin temperature and bodyweight may have resulted from physical effects of the size of the limb. As was suggested in Chapter V, if light lambs had a greater ratio of surface area to volume in the limb than their heavier peers, they would lose heat from the vasoconstricted limb more rapidly in a cold environment. It seems unlikely that the small lambs could have had lower skin temperatures because they experienced a more intense vasoconstriction. Although the small lambs would have been subjected to a greater degree of cold-stress in any environment, and hence might have been expected

TABLE 73: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (SEX) REGRESSIONS OF HIND-LIMB SKIN TEMPERATURE ON BODY WEIGHT

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 68)	7	17.01	
Intra-class (sex) regression of skin temperature on bodyweight	2	26.87	4.53*
Pooled within-class	1	35.28	5.95*
Difference	1	18.47	3.12†
Residual error	44	5.93	

to constrict peripheral blood vessels more intensely, other treatments which also affected the level of cold-stress experienced by wet lambs (e.g. birthcoat type) were not associated with differences in skin temperature in the previous experiments.

(d) Skin temperature and age

The overall regression coefficient of skin temperature on the age of the lamb was $b = -0.10 \pm 0.07\ ^{o}C\ hr^{-1}$ which was not significant ($t_{52} = 1.35$, NS.) and the pooled within-class regression coefficient was similarly non-significant (Table 74). By contrast, the within-feeding level regressions of skin temperature on age were heterogeneous ($P<.01$). Thus while skin temperature was independent of age among the fed/older lambs ($b = -0.02 \pm 0.10\ ^{o}C\ hr^{-1}$, $t_{28} = 0.22$, NS.), it declined markedly with age among their unfed/newborn peers ($b = -7.72 \pm 2.89\ ^{o}C\ hr^{-1}$, $t_{22} = 2.67$, $P<.05$). The latter relationship could not have been due to age-dependent effects on the coat insulation of the limb since, as has already been discussed, skin temperature was independent of limb wool weight at each of the feeding levels. Moreover, since the unfed/newborn lambs were not artificially wetted prior to their entry into the climate chambers, the older members of this group (up to 1 hour of age) would have had somewhat drier coats (including the wool on the limbs) than those tested immediately after birth. Hence, if an effect of limb wool insulation had existed, it would have been more likely to have resulted in a positive relationship between skin temperature and age. It may therefore be that the very rapid decline in skin temperature with advancing age among the unfed/newborn lambs (equivalent to a decline of $5.8^{o}C$ over the range of ages involved) reflects a poor ability of very young lambs to control peripheral blood flow. This may indicate that the lambs require an

TABLE 74: TEST OF HOMOGENEITY OF THE WITHIN-CLASS (FEEDING LEVEL) REGRESSIONS OF HIND-LIMB SKIN TEMPERATURE ON AGE

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (Table 68)	7	17.01	
Intra-class (feeding level) regression of skin temperature on age	2	22.11	3.60*
Pooled within-class	1	0.57	0.09 NS
Difference	1	43.65	7.10*
Residual error	44	6.14	

initial exposure to cold in order to fully stimulate the peripheral vasoconstrictor mechanism. Such an hypothesis is certainly tenable considering the nature of the environment in which the lamb spends the first 5 months of its life, and would also explain why the unfed/newborn lambs were found to have slightly higher skin temperatures (at stable heat production) than the fed/older lambs (Table 68).

5. Distribution of face cover grades

As a sequel to this study, the 44 experimental lambs which were present at 3 months of age were assigned face cover grades to provide some information about the extent to which the 2 groups of lambs differed in wool growth on the face. This examination, like the following experiment, suffered from the deficiency that 10 of the lambs did not survive to 3 months of age and so could not be assigned face grades. Accordingly, attempts to relate the face grades of the surviving lambs to those of the group as a whole may have been subject to some bias. This would be of particular importance if the failure of 10 of the lambs to survive was correlated with their genotype for face cover.

Although in most cases the cause of death in these lambs was not known, some relevant information may be provided about them. The deaths were equally divided between the face cover groups so that, in this respect, no bias existed. One of the lambs died at 3 days of age due to an intestinal obstruction and a further 2 lambs (twins) died, also at 3 days of age, apparently due to their dam's poor milk supply. The remaining deaths appeared to be due largely to a failure of the lambs to mother-up after they had been transported from the

TABLE 75: DISTRIBUTION OF FACE COVER GRADES IN CONTROL AND FACE COVER LAMBS

Face Cover Grade	Proportion of Group Lambs in Each Grade (%)	
	Control Group	Face Cover Group
1	31.8	4.5
1+	22.7	13.6
2	45.5	54.5
2+	0.0	27.3
Number of Lambs	22	22

Animal Physiology Unit to the University farms. However, with respect to their performance under test, the lambs which died did not appear to be a biased sample of the total group. For example, 70% of them had attained summit metabolism when tested, a proportion only marginally greater than that for the group as a whole. It therefore seems unlikely that the failure of these lambs to survive to 3 months of age could have seriously biased the following conclusions about the distribution of face grades among the face cover groups.

The face grades were assigned as described in Chapter II and are presented as the original grades. As Table 75 shows, approximately 50% of the lambs in each of the face cover groups were of grade 2 and the major difference between the groups lay in the distribution of lambs at the extremes of the grading scale.

Chapter Summary

This study involved 54 lambs drawn from the Massey University Progeny Test Flock which has been subjected to single-trait selection since 1956. Half the lambs were the progeny of a randomly-bred Control group and the balance were from the Face Cover selection group. The lambs were tested either when newborn (less than 1 hour old) and unfed or when older (2.00 to 22.00 hours) and suckled. All were tested when wet at a single ambient temperature ($10^{o}C$) and were exposed to a nominal airspeed of 1.50 m sec^{-1}.

The Progeny Test lambs exhibited a low resistance to hypothermia compared with Romney lambs from previous experiments, 65% of them attaining summit metabolism. This was associated with their more shallow birthcoats and lower summit metabolism than lambs in the

previous experiment.

Differences between the Face Cover and Control lambs in resistance to cold-stress and in associated characters were consistently small. Thus the 2 groups exhibited virtually identical frequencies of attainment of summit metabolism, rate of decline in rectal temperature, heat production, birthcoat characteristics, bodyweights and hind-limb skin temperatures. It therefore appears that the physiological effects of face cover genotype, which are so clearly expressed in older sheep, do not contribute to variation in the ability of newborn lambs to withstand a cold environment. This hypothesis is confirmed in the following chapter.

The confounded effects of feeding level and age were more apparent in this study. Unfed/newborn lambs were found to have a slightly lower rate of decline in rectal temperature than the fed/older group and this was associated with their greater coat depths but lower mid-side wool weight per unit area of skin. It is not clear, however, whether the latter differences are real effects or a consequence of the manner in which the unfed/newborn lambs were assigned to that treatment group. Moreover the newborn lambs had marginally greater hind-limb skin temperatures than their older peers and skin temperature declined rapidly with age during the first hour of life. This suggests that very young lambs become increasingly more able to restrict peripheral blood flow as they age and provides the only evidence so far available that wet lambs may vary in their ability to control peripheral blood flow.

Since a high proportion of the lambs attained summit metabolism

an attempt was made to use the rate of decline in rectal temperature (RDRT) as the main index of resistance to cold-stress. In regression analyses on the birthcoat characters this index was found to be unsatisfactory, RDRT showing little relationship with coat depth and midside wool weight. Conversely, in a smaller sample of non-summit lambs, much stronger relationships were found between heat production and the coat characters (in line with previous experiments). It is likely that RDRT is unsatisfactory because it is influenced to a considerable degree by the individual's level of summit metabolism. Thus when comparisons of RDRT are being made between lambs within breeds it would be desirable to also measure summit metabolic rate. Finally the results from the non-summit lambs suggest that the insulative value of a unit depth or midside wool weight of the naturally-wet coat is equal to that of the artificially wetted coat.

C H A P T E R V I I

THE RELATIONSHIP BETWEEN THE RESISTANCE OF THE NEWBORN LAMB TO COLD-STRESS AND ITS FACE COVER GRADE AT THREE MONTHS OF AGE

CHAPTER VII

THE RELATIONSHIP BETWEEN THE RESISTANCE OF THE NEWBORN LAMB TO COLD-STRESS AND ITS FACE COVER GRADE AT THREE MONTHS OF AGE

Introduction

In the experiment described in Chapter VI it was found that 23 years of single-trait selection for more open faces in a flock of Romney ewes had apparently not affected the ability of the newborn lambs to control deep body temperature in a cold environment. However, the lambs in that experiment exhibited a low resistance to body cooling compared with Romney-type lambs in the previous experiments. While some difference did exist between the Control and Face Cover groups in the average degree of face cover at 3 months of age, each group contained a substantial proportion of lambs in the intermediate face grades. A complementary analysis of the "effects" of face cover was therefore performed, using data from the unselected lambs described in Chapter V, to retrospectively examine the association between the newborn lamb's resistance to cold-stress and its face cover grade at 3 months of age.

Experimental Design and Methods

This analysis was again subject to a possible bias in that not all the lambs tested at birth (Chapter V) survived to 3 months of age. Of the 86 lambs tested at birth, 75 (87%) survived to the time of face grading, this being a slightly higher survival rate than among the Progeny Test lambs (81%). The deaths again appeared to be associated

mainly with mis-mothering and the 11 lambs which died included all members of 3 twin pairs. As in the previous experiment, the deaths were nearly evenly divided among the levels of the main treatment groups so that little bias could have existed in this respect. However, the lambs which died were atypical as regards their frequency of attainment of summit metabolism; 5 of them (45%) had attained summit metabolism at their first test compared with a frequency of 26% in the total group of 86 lambs tested. The possibility of some bias in the results cannot, therefore, be entirely discounted.

The four-level face grading system described in Chapter II was initially used in these lambs and the face grade distribution is presented in Table 76. As this table shows, the distribution of face grades in these lambs was intermediate between that of the Control and Face Cover groups in Chapter VI, but with a greater proportion of the lambs in grade 2 than either of these groups. However, because relatively few lambs were involved in the analysis it was obviously not possible to fit "face cover grade" as a four-level main effect. The lambs were therefore re-classified as being "woolly-faced" (grades 1, 1+) or "open-faced" (grades 2, 2+).

A second consequence of the low number of animals involved was that even a two-level "face cover" main effect could not simply be added to the five-way analysis of variance model used in Chapter V without incurring a considerable number of empty cells. To overcome this problem, models for the analysis of the independent variates included, in addition to "Face Cover", only those treatments which were found to exert a major effect on that variate in Chapter V. In all the analyses, "Face Cover" was treated as a fixed effect. Since

TABLE 76: DISTRIBUTION OF FACE COVER GRADES IN LAMBS SIRED BY SINGLE-N RAMS

Face Cover Grade	Proportion of Lambs in Each Grade (%)
1	17.3
1+	13.3
2	60.0
2+	9.3
Number of Lambs	75

the analyses were retrospective, the data on heat production, hind-limb skin temperature and the attainment of summit metabolism were, of course, a sample of the data analysed in Chapter V.

Results and Discussion

1. Proportion of lambs attaining summit metabolism

The lamb's phenotype for face cover at 3 months of age was not significantly associated with its tendency to attain summit metabolism (Table 77).

2. Heat production

In the analysis of variance for heat production (Table 78), no association was found between the lamb's level of heat production at $10^{o}C$ ambient temperature and the face cover group to which it was assigned. All interactions between face cover group and the other treatments fitted in the model were similarly non-significant. The remaining treatments were all significant which is generally compatible with the results from the analysis of heat production involving the full 86 lambs (Chapter V). An exception was the effect of airspeed which was not significant in the original analysis. However, this apparent difference between the analyses is simply a consequence of the model in Table 78 having been treated as fully fixed whereas in the original mixed model the airspeed effect was tested against an interaction which was very much larger than the error term.

3. Hind-limb skin temperature

Open-faced lambs exhibited a mean hind-limb skin temperature which was approximately $1.0^{o}C$ greater than that of the woolly-faced lambs,

TABLE 77: EFFECT OF FACE COVER, BIRTHCOAT TYPE AND BIRTHRANK ON THE PROPORTION OF LAMBS ATTAINING SUMMIT METABOLISM

Classification	Proportion of Lambs Attaining Summit Metabolism		
	Logit-Transformed Mean ± S.E.	Retransformed %	
Face cover			
Woolly-faced	-1.22 ± 0.54	22.8	(23)
Open-faced	-1.65 ± 0.41	16.1	(52)
Birthcoat type			
Non-hairy	-0.66 ± 0.37	34.0	(40)
Hairy	-2.20 ± 0.60	10.0	(35)
Birthrank			
Single	-2.19 ± 0.55	10.1	(37)
Twin	-0.68 ± 0.40	33.7	(38)

	Analysis of Deviance	
Source	d.f.	χ^2 Deviance
Face Cover	1	0.45 NS
Birthcoat Type (Coat)	1	5.95 *
Birthrank (Rank)	1	6.23 *
Face Cover x Coat	1	0.05 NS
Face Cover x Rank	1	0.01 NS
Coat x Rank	1	0.17 NS
Face Cover x Coat x Rank	1	1.00 NS
Error	67	67.37

TABLE 78: EFFECT OF FACE COVER, BIRTHCOAT TYPE, AIRSPEED AND SEX ON THE HEAT PRODUCTION OF LAMBS AT 10°C AMBIENT TEMPERATURE

Classification	Heat Production (W kg^{-1}) Mean ± S.E.	
Face cover		
Woolly-faced	15.69 ± 0.49	(23)
Open-faced	15.28 ± 0.32	(52)
Birthcoat type		
Non-hairy	16.23 ± 0.37	(40)
Hairy	14.74 ± 0.41	(35)
Nominal airspeed (m sec^{-1})		
0.0	14.55 ± 0.40	(36)
1.5	16.42 ± 0.38	(39)
Sex		
Male	14.85 ± 0.40	(39)
Female	16.11 ± 0.38	(36)

.../ continued

TABLE 78, continued

Analysis of Variance			
Source of Variation	d.f.	Mean Square	F
Face Cover	1	2.49	0.46 NS
Birthcoat Type (Coat)	1	40.16	7.48 **
Airspeed (Asp.)	1	65.37	12.18 ***
Sex	1	28.65	5.34 *
Face Cover x Coat	1	3.02	0.56 NS
Face Cover x Asp.	1	6.31	1.18 NS
Face Cover x Sex	1	0.00	0.00 NS
Coat x Asp.	1	9.37	1.75 NS
Coat x Sex	1	1.73	0.32 NS
Asp. x Sex	1	1.36	0.25 NS
Face Cover x Coat x Asp.	1	2.94	0.55 NS
Face Cover x Coat x Sex	1	5.29	0.99 NS
Face Cover x Asp. x Sex	1	4.68	0.87 NS
Coat x Asp. x Sex	1	2.35	0.44 NS
Error	60	5.37	

TABLE 79: EFFECT OF FACE COVER, AIRSPEED AND BIRTHRANK ON THE HIND-LIMB SKIN TEMPERATURES OF LAMBS AT 10°C AMBIENT TEMPERATURE

Classification	Hind-Limb Skin Temperature (°C) Mean ± S.E.	
Face cover		
Woolly-faced	18.71 ± 0.66	(23)
Open-faced	19.73 ± 0.44	(52)
Nominal airspeed (m sec^{-1})		
0.0	21.93 ± 0.56	(36)
1.5	16.52 ± 0.55	(39)
Birthrank		
Single	19.62 ± 0.53	(37)
Twin	18.83 ± 0.55	(38)

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Face Cover	1	16.48	1.60 NS
Airspeed (Asp.)	1	542.85	52.76***
Birthrank (Rank)	1	11.77	1.14 NS
Face Cover x Asp.	1	11.44	1.11 NS
Face Cover x Rank	1	0.20	0.02 NS
Asp. x Rank	1	17.85	1.74 NS
Face Cover x Asp. x Rank	1	0.13	0.01 NS
Error	67	10.29	

but this difference was not significant (Table 79). Thus there was no evidence of an association between face cover and hind-limb skin temperature, a result which is again compatible with the study of the Progeny Test lambs.

Chapter Summary

In this chapter an attempt was made to relate the lamb's phenotype for face cover at 3 months of age to its performance in a cold environment in the first hours after birth. For this purpose the 75 lambs which survived to face grading were classified as being woolly-faced (grades 1, 1+) or open-faced (grades 2, 2+). No association was found between the lamb's degree of face cover at this age and its heat production, hind-limb skin temperature or frequency of the attainment of summit metabolism. Since the most commonly-reported estimates of the heritability of face cover are in the range 0.4 to 0.5 (Cockrem and Rae, 1966; Blair, 1981) phenotypic face cover is expected to be a reasonable predictor of the individual's genotype for this trait. The results are thus entirely compatible with those from the previous experiment and with the hypothesis that the lamb's genotype for face cover is unlikely to affect its resistance to cold-stress during the neonatal period.

This analysis is, as has already been discussed, subject to some possible bias associated with the failure of 11 lambs to survive to 3 months of age. The bias could, however, be important only if their mortality was due to a poor resistance to cold-stress which was related to their genotype for face cover. Thus, for example, if the woolly-faced lambs had, as a group, been less able to survive in a cold

environment, it might be expected that a greater proportion of them would have succumbed in the field (i.e. that the majority of the lambs dying before three months of age would have been of one face cover group). Differences between the surviving lambs of each face cover level could then have been reduced to non-significance. However, such a mechanism obviously requires that there be a strong effect of weather conditions on the survival of these lambs once they had been removed from the Animal Physiology Unit. If that were the case it would be reasonable to expect differential mortality rates between the levels of the other treatments known to affect resistance to cold-stress in the climate chambers. Clearly this did not occur since the deaths were evenly divided between the levels of these treatments (particularly birthcoat type). This fact, together with the low proportion of lambs which died before 3 months of age, suggests that little bias could have existed in the analysis.

C H A P T E R V I I I

THE REPEATABILITY OF RESISTANCE TO COLD-STRESS AND OF ASSOCIATED CHARACTERS IN YOUNG LAMBS

CHAPTER VIII

THE REPEATABILITY OF RESISTANCE TO COLD-STRESS AND OF ASSOCIATED CHARACTERS IN YOUNG LAMBS

Introduction

The previous experiments have demonstrated that the resistance of the newborn lamb to cold-stress (as indicated by the level of heat production required to maintain body temperature or by the rate of decline in rectal temperature) may be related to its birthcoat characteristics and bodyweight. Studies in the United Kingdom have shown that resistance to cold-stress, when measured in a water bath test, is highly repeatable (Slee et al., 1980) but the repeatability of this trait in lambs chilled in cold air does not appear to have been determined. Nor is the repeatability of birthcoat depth in the live lamb known, although a high degree of repeatability was found in the study of tanned skins described in Chapter II. The repeatability of these traits was therefore examined in this experiment using lambs from some of the main genotypes described in the previous chapters.

Experimental Design and Methods

The lambs used in this experiment were drawn from the Progeny Test flock (whose first test was described in Chapter VI) and from the group sired by single-N rams (Chapter V). In the case of the Progeny Test lambs, only those individuals which had first been tested in the unfed/newborn state were used for this experiment. After the completion of their first test, the lambs were returned to their dams and permitted to suckle for between 2 and 20 hours. They were then tested again

under environmental conditions identical to those of the first test (i.e. wetness, 10°C ambient temperature, 1.50 m sec^{-1} nominal airspeed). Measurements of heat production, RDRT (whole experiment), skin temperature and birthcoat depth were made in exactly the same manner at each of the tests. In a departure from the methodology of the previous experiments, these lambs were weighed at the second test after they had been artificially wetted. This was done to give comparable estimates of bodyweight in the study of repeatability (the lambs having been naturally wet at their first test).

The hairy and non-hairy lambs (i.e. the progeny of single-N sires) were a sample drawn only from those lambs exposed to moving air (1.50 m sec^{-1}) at the first test. They were again returned to their dams after this test and permitted to suckle before being re-tested, in an identical environment, 2 to 20 hours later. Most of the traits of interest were measured in the same manner as for the Progeny Test lambs. The exception was bodyweight which was measured prior to artificial wetting at each test.

For continuous data the repeatability of the trait was assessed by calculating the correlation between performance at each of the tests. Differences between the tests were examined by the paired t-statistic, and such differences are discussed where they were significant. In both groups of lamb, RDRT was calculated over the whole experiment period.

For the discrete data (proportion of lambs attaining summit metabolism) the repeatability was assessed simply by examining the proportion of lambs attaining summit metabolism in the first test which

were similarly affected in the second test.

Results and Discussion

1. Progeny Test lambs

(a) Proportion of lambs attaining summit metabolism

Of the 24 lambs which were involved in the experiment, 15 (63%) attained summit metabolism (as defined previously) at the first test and 18 (75%) at the second. This difference, although not significant (Table 80), resulted from 4 lambs attaining summit metabolism only at the second test and 1 only at the first. Hence 19 of the lambs (79%) were consistent in their attainment of summit metabolism (or lack of it) at each of the tests. Among these lambs, the attainment of summit metabolism was less repeatable than for the lambs sired by single-N rams (section 2 of this chapter). However, in a number of cases the lambs which were not consistent between the tests had rates of decline in rectal temperature close to the criterion ($0.025^{o}C\ min^{-1}$) used to define the attainment of summit metabolism. Thus the between-test difference in these individuals was partly due to the manner in which the attainment of summit metabolism was defined.

(b) Heat production and rate of decline in rectal temperature

The heat production of these lambs increased significantly from a mean of $14.37 \pm 0.54\ W\ kg^{-1}$ at the first test to $15.86 \pm 0.39\ W\ kg^{-1}$ at the second ($t_{23} = 3.16$, $P < .01$). Despite this there was no significant change in the mean rate of decline in rectal temperature between these tests. Both these results are, as will be seen, consistent with those from the lambs sired by single-N rams, a much lower proportion of which attained summit metabolism. Among the Progeny Test

TABLE 80: EFFECT OF SUCCESSIVE TESTS IN A COLD ENVIRONMENT ON THE PROPORTION OF LAMBS ATTAINING SUMMIT METABOLISM : PROGENY TEST LAMBS

Classification	Proportion of Lambs Attaining Summit Metabolism		
	Logit-Transformed Mean ± S.E.	Retransformed %	
Test			
First	0.51 ± 0.42	62.5	(24)
Second	1.10 ± 0.47	75.0	(24)

Source	Analysis of Deviance d.f.	χ^2 Deviance
Test	1	0.88 NS
Error	46	58.75

lambs this change was associated with an increased heat production both in the lambs which had attained summit metabolism at the first test and in those which had not. The increased heat production (i.e. level of summit metabolism) of the summit lambs at the second test was unlikely to have been related to their increased age since summit metabolism is independent of age in Romney lambs (Chapter III) and in lambs of other breeds (Alexander, 1962b). It may therefore represent an acclimatization effect associated with the previous exposure to cold. Since the increased summit metabolic rate of these lambs did not result in a reduction in the rate of decline in rectal temperature, and since the non-summit lambs also had increased metabolic rates when tested a second time, the lambs' body heat loss must also have been increased at the second test. However, changes between the tests in characteristics which might account for this increased rate of heat loss (such as coat depth) could not be detected.

Among the Progeny Test lambs, both heat production ($r = 0.53$, $P<.01$) and the rate of decline in rectal temperature ($r = 0.62$, $P<.01$) were only moderately repeatable. These correlations are of a lesser magnitude than the repeatabilities of cold-stress (measured as the time required for rectal temperature to fall to $35^{o}C$ in a cold water bath) reported by Slee *et al*. (1980). However the data of Slee *et al*. (1980) were from lambs of a number of quite different breeds which is likely to have contributed to their greater correlations. Thus a four-fold difference existed in the mean resistance to cold-stress of 7 breeds and crosses which they examined and a considerably greater degree of variation could be expected between the individual lambs of the 10 breeds used in their repeatability study. When this is compared with the relatively small range over which the indices of cold-

stress in the Progeny Test lambs lay (for example 10.13 to 20.00 W kg^{-1} of heat production), the lower correlations found in these lambs are not too surprising. Moreover, the water bath test appears to be less sensitive to differences in birthcoat characteristics (between animals and presumably also between tests) than are tests conducted in cold air (Slee et al., 1980). This would also tend to minimize the variation between tests and hence improve the repeatability. Nevertheless, the relatively low repeatabilities of heat production and RDRT found among the Progeny Test lambs do indicate that resistance to cold-stress, measured when the lamb is at least 2 hours old and artificially wetted, is only a moderately good indicator of its ability to withstand the effects of a cold environment in the newborn, naturally-wet state.

(c) Bodyweight

The lamb's bodyweight at each test was, as expected, highly repeatable. Thus among the Progeny Test lambs the correlation between the bodyweights (i.e. between birthweight and bodyweight at the second test after artificial wetting) was $r = 0.97$ which was highly significant ($P < .001$). It is clear, therefore, that variation in weight between the tests could not have contributed greatly to the mediocre repeatabilities of resistance to cold-stress. The high repeatability of bodyweight also suggests that variation in such factors as the amount of milk ingested by the lamb could have made little contribution to variation in bodyweight. There was, however, a marked tendency for bodyweight to decline between the tests, the mean bodyweights at the first and second tests being 5.01 ± 0.17 kg and 4.84 ± 0.17 kg respectively. This difference was, by the paired t-test, significant at the 5% level. An important point about this decline in weight

(0.17 kg) is that it is almost exactly equal to the estimated difference in wet-coat bodyweight (0.16 kg) between the unfed/newborn and fed/older lambs of Chapter VI. This supports the previously-expressed view that the bodyweight difference between these groups could have been due to dehydration or the catabolism of body reserves as a consequence of the poor milk production of the dams of the Progeny Test lambs. In contrast, the lambs sired by single-N rams did not suffer a reduction in weight between the tests.

(d) Depth of birthcoat

Like the indices of cold-stress, birthcoat depth was only moderately repeatable in the Progeny Test lambs. At the midside position the correlation between depth at the 2 tests was $r = 0.43$ ($P < .05$) while at the hip site the correlation was somewhat higher ($r = 0.65$, $P < .001$). The greater repeatability at the hip position was also found to exist among the lambs sired by single-N rams.

These results again indicate that, at least among Romney lambs, coat depth in the artificially-wetted lamb is not a particularly good predictor of depth at the same site when the lamb's coat is naturally wet with amniotic fluids. However the poor repeatability does not appear to have been due to the effects of the different wetting treatments since, as will be seen in section 2 of this chapter, the repeatability of coat depth was no better in the non-hairy lambs which were wetted in the same manner (with tap water) on both occasions. Variation between the coat depths at each test, which contributed to the only moderate repeatability, may have been due to a variety of effects including grooming by the dam and changes in depth associated with the degree of wetting. Handling of the lamb prior to the second test could also

have contributed to variation in coat depth between the tests, although every care was taken, when handling the lambs, to avoid sites at which depth was measured.

It should also be pointed out that there was no significant change in the coat depths of these lambs between the tests. This result would seem to confirm that the significant effect of feeding level on coat depth in Chapter VI (Table 62) was, as suggested, a consequence of the manner in which the lambs were assigned to the levels of that treatment (i.e. a chance effect). In addition it illustrates that the saturation of the newborn Romney's coat with amniotic fluids is unlikely to influence its insulative properties through an effect on its depth (compared with the coat of the artificially wetted lamb).

(e) Hind-limb skin temperature

Hind-limb skin temperature was the least repeatable of the traits examined in the Progeny Test lambs, the correlation between skin temperature at the first and second tests being $r = 0.40$ ($P = .05$). It is not possible to determine whether the variation between the tests was due to changes in blood flow to the limb or to variation in the rate at which skin temperature equilibrated with the environment. Since these lambs were exposed to moving air at each test, variation in the insulative value of wool on the limbs is unlikely to have contributed to this effect. It is also difficult to imagine that bodyweight-related effects on skin temperature could have contributed to variation between the tests. Thus the possibility of small differences in blood flow might be seen to exist, particularly in view of the apparently poor control of blood flow among these lambs at their first test (Chapter VI). However, the hairy and non-hairy lambs,

which were not tested when newborn and did not exhibit any real evidence of variation in ability to control peripheral blood flow, also had a low repeatability of skin temperature.

2. Lambs sired by single-N rams

(a) Proportion of lambs attaining summit metabolism

Twenty of the hairy and non-hairy lambs sired by single-N rams (Chapter V) were involved in this assessment of repeatabilities. Of these, 19 (95%) were consistent in the attainment of summit metabolism at each test. Differences between the tests were not significant (Table 81). The exception was a non-hairy individual which attained summit metabolism at the first test but not at the second. The results from these lambs were therefore more consistent than from the Progeny Test lambs but, as has already been noted, the poorer "repeatability" among the latter group was due to a number of the lambs having rates of decline in rectal temperature close to the cut-off point. Thus the "attainment of summit metabolism", as defined in this study would seem to be a trait of good repeatability, despite the difficulties inherent in its use. It is also likely to be a useful indicator of the lamb's resistance to cold-stress, especially when considered in conjunction with metabolic rate and the rate of decline in rectal temperature.

(b) Heat production and rate of decline in rectal temperature

Among these lambs the changes in heat production and rate of decline in rectal temperature which accompanied the second test were consistent with those in the Progeny Test lambs. Thus heat production increased significantly from 16.17 ± 0.50 W kg^{-1} at the first test to 17.25 ± 0.54 W kg^{-1} at the second ($t_{19} = 2.29$, $P < .05$), but there was

TABLE 81: EFFECT OF SUCCESSIVE TESTS IN A COLD ENVIRONMENT ON THE PROPORTION OF LAMBS ATTAINING SUMMIT METABOLISM : LAMBS SIRED BY SINGLE-N RAMS

Classification	Proportion of Lambs Attaining Summit Metabolism		
	Logit-Transformed Mean ± S.E.	Retransformed %	
Test			
First	-1.10 ± 0.27	25.0	(20)
Second	-1.39 ± 0.31	20.0	(20)

Analysis of Deviance		
Source	d.f.	χ^2 Deviance
Test	1	0.14 NS
Error	38	42.51

no significant change in the rate of decline in rectal temperature. Since there was also no change in the proportion of lambs attaining summit metabolism, this result again suggests that the lambs experienced a greater rate of body heat loss at the second test. However, as with the Progeny Test lambs, changes in other characteristics of the lamb which might account for this increased rate of body heat loss could not be detected. Neither birthcoat depth nor bodyweight exhibited significant changes between the tests, and the cause of the between-test difference in heat production remains to be identified.

The repeatability of heat production of the hairy and non-hairy lambs was of a similar magnitude to that in the Progeny Test group ($r = 0.59$, $P<.01$). Rate of decline in rectal temperature was much more repeatable at $r = 0.84$ ($P<.001$). Indeed this level of repeatability is virtually identical to that derived by Slee et al. (1980) from one of their water bath tests. The greater repeatability of RDRT in the lambs sired by single-N rams (compared with the Progeny Test lambs) is no doubt a consequence of the much greater variation in this trait among these lambs. This was in turn due to their greater range of birthcoat depths and midside wool weights.

(c) Bodyweight

Bodyweight of the lamb was again highly repeatable, the correlation between bodyweight at each test being $r = 0.98$ ($P<.001$). In contrast to the Progeny Test lambs, however, the lambs sired by single-N rams did not suffer a reduction in weight between the tests. This is likely to have been due both to the greater age of these lambs when tested (so that they would have had more time to establish suckling prior to their second test) and to the apparently more plentiful milk

supply of their dams.

(d) Depth of birthcoat

Birthcoat depth was more highly repeatable in these lambs than in the previous group, the correlations between depth at each test being $r = 0.73$ ($P<.001$) at the midside position and $r = 0.77$ ($P<.001$) at the hip. Once again the apparently superior repeatabilities in these lambs were due in particular to their greater range of coat depths. Thus within the non-hairy lambs the correlations were similar to those of the Progeny Test lambs, being $r = 0.43$ and $r = 0.59$ for the midside and hip sites respectively. The significance of these correlations was, however, less than those in the Progeny Test group as a consequence of there being fewer lambs involved. Among the hairy lambs the repeatability of midside coat depth was particularly low ($r = 0.24$) and at the hip site the repeatability was somewhat improved ($r = 0.49$). Hence the tendency for depth at the hip to be more highly repeatable than at the midside was preserved in all 3 of the genotypes examined. In view of the low number of animals involved it is not possible to determine whether the lower repeatability of coat depth in the hairy lambs was a real difference. However, the nature of the birthcoat in these lambs, and the greater sensitivity of their coat depth to such treatments as wetting, would suggest that a real effect may have been involved.

The repeatability of midside wool weight was not examined in this study but some comments may be offered concerning its likely repeatability. Whereas considerable variation in coat depth between tests may be induced by handling, grooming and the degree of wetness of the coat (particularly among the single-N lambs), midside wool weight is

likely to be less sensitive to these treatments. Certainly it should not be affected by the degree of wetting if the midside wool samples are weighed at a constant RH of the air. Nor is grooming likely to influence the midside wool weight, except perhaps by the removal of solid material deposited in the coat from the amniotic fluid. This material would probably contribute only a small fraction of the total midside wool weight, and such variation could be eliminated by scouring the midside wool samples prior to weighing. One of the major sources of error in measuring midside wool weight appears to be that associated with the measurement of skin area. These errors have been discussed in detail by Henderson (1953).

(e) Hind-limb skin temperature

Skin temperature was again the least repeatable of the traits examined, with a correlation between skin temperature at the two tests of only $r = 0.40$ ($P<.10$). This repeatability estimate is identical to that derived from the study of the Progeny Test lambs.

Chapter Summary

The repeatability of resistance to cold-stress and of associated traits was examined in 24 of the Progeny Test lambs (Chapter VI) and in 20 of the lambs sired by single-N rams (Chapter V). The Progeny Test lambs were those which had been first tested in the newborn/unfed state while the hairy and non-hairy lambs were a sample of those exposed to moving air at the first test. In each case the lambs were returned to their dams and permitted to suckle for 2 to 20 hours before being re-tested in an environment identical to that used in the first test.

The attainment of summit metabolism by these lambs was quite

highly repeatable, 79% of the Progeny Test lambs and 95% of the group sired by single-N rams being consistent in whether or not they attained summit metabolism at each test. The lower repeatability of the Progeny Test lambs was due largely to a number of lambs whose rate of decline in rectal temperature was close to the criterion of $0.025^{o}C\ min^{-1}$ used to define the attainment of summit metabolism in this study. The difference between these groups in the repeatability of this trait was therefore primarily a function of the manner in which the attainment of summit metabolism was defined.

The 2 main indices of cold-stress used in this study, heat production and rate of decline in rectal temperature, exhibited moderate to good repeatabilities. For heat production the correlations were 0.53 to 0.59 and for RDRT 0.62 to 0.84. In each case the lambs sired by single-N rams exhibited the greater repeatabilities. For the rate of decline in rectal temperature the difference was associated with a greater variation in the trait among the hairy and non-hairy lambs. While these repeatability estimates are generally lower than those of Slee *et al*. (1980), this was probably due both to a lesser variability in the cold-stress indices among these lambs and to the water-bath test used by Slee *et al*. (1980) being less sensitive to differences in birthcoat insulation than were the cold air tests used here.

Birthcoat depth was only moderately repeatable, the correlations between the depths at each test ranging from 0.43 to 0.78. Repeatabilities were better in the lambs sired by single-N rams as a consequence of their greater range of coat depths. Depth at the hip site was consistently more repeatable than depth at the midside position. The repeatability of midside wool weight was not examined.

Hind-limb skin temperature was not highly repeatable, a correlation of 0.40 being found in each of the groups examined. The causes of the considerable between-test variation are not known, but it seems unlikely that variation in coat insulation on the limb was involved since all the lambs were exposed to moving air. Nor were bodyweight-related effects on skin temperature (such as were demonstrated in Chapter VI) likely to have been a contributing factor since bodyweight of the lamb was very highly repeatable.

CHAPTER IX

RELATIONSHIPS BETWEEN SOME CHARACTERISTICS OF THE BIRTHCOAT AND OF THE HOGGET FLEECE

CHAPTER IX

RELATIONSHIPS BETWEEN SOME CHARACTERISTICS OF THE BIRTHCOAT AND OF THE HOGGET FLEECE

Introduction

Since the level of heat production required by the lamb to maintain body temperature is related to some characteristics of its birthcoat, and since these characteristics can be measured with a reasonable degree of repeatability, the selection of newborn lambs for improved birthcoat insulation appears to be a possibility. It has not been within the scope of this study to estimate the heritability of these characteristics. However, some information may be provided about the possible effects of this selection (in the lamb's own lifetime) by examining relationships between characteristics of the birthcoat and those of the hogget fleece.

Experimental Design and Methods

The experiment involved only the Progeny Test lambs, all of whom were retained in the flock until hogget shearing (at approximately 13 months of age) as part of the ongoing experiment for which the flock was originally established. The ram and ewe hoggets were grazed separately from the time of weaning so some of the between-sex differences are likely to have been environmental effects (i.e. the "sex" treatment is actually a "sex-rearing" treatment). Fleece characteristics were measured at hogget shearing as described in Chapter II. The birthcoat depth data were those from measurements made after the lambs had been dried and re-wetted (i.e. from the first

test for the fed/older lambs and from the second test for the unfed/newborn group).

Of the 54 lambs tested at birth (Chapter VI), 41 were present at hogget shearing. Relationships between their birthcoat and hogget fleece characteristics were initially examined by simple correlation analysis within treatment groups and across all treatments. This analysis was used to identify relationships which were likely to be significant and these were then further examined by analysis of covariance.

Results and Discussion

1. Greasy fleeceweight

The analysis of variance for greasy fleeceweight of the hoggets is presented in Table 82. Male lambs produced fleeces which were 33% heavier than those of females, a difference which was highly significant ($P<.001$). There was also a small difference between the face cover groups in hogget fleeceweight. This difference was in favour of the more open faced hoggets but was significant only at the 10% level.

The pooled within-class regression coefficient of (hogget) greasy fleeceweight on (lamb) hip coat depth was $b = 0.07 \pm 0.04$ kg mm^{-1} which was significant ($P<.05$, Table 82). Thus increasing coat depth (and hence increasing coat insulation) was associated with an improvement in greasy fleeceweight. Over the range of hip coat depths encountered among these lambs (5 to 12 mm) this relationship would account for a difference of approximately 0.5 kg of greasy fleeceweight (or 14% of the mean fleeceweight of these hoggets). Significant

TABLE 82: EFFECT OF FACE COVER GROUP, SEX AND HIP BIRTHCOAT DEPTH ON HOGGET GREASY FLEECEWEIGHT

Classification	Greasy Fleeceweight (kg) Mean ± S.E.	
Face cover group		
Face cover	3.73 ± 0.10	(20)
Control	3.46 ± 0.10	(21)
Sex		
Male	4.12 ± 0.11	(17)
Female	3.08 ± 0.09	(24)

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Face Cover Group (Group)	1	0.74	4.26 †
Sex	1	10.75	61.74 ***
Group x Sex	1	0.62	3.56 †
Error	37	0.17	

Analysis of Covariance

Source of Variation	d.f.	Mean Square	F
Main effects model (above)	3	3.98	
Intra-class (sex) regression of greasy fleeceweight on hip coat depth	2	0.51	3.31 *
Pooled within-class	1	0.65	4.21 *
Difference	1	0.37	2.42 NS
Residual error	35	0.16	

relationships could not be detected between greasy fleeceweight and midside coat depth or wool weight per unit area of skin in the lamb.

2. Staple length

Hoggets of the Face Cover flock had a significantly greater mean staple length than their Control group peers ($P<.01$, Table 83) a result which contrasts markedly with the analysis of greasy fleeceweight. Sex of the lamb exerted only a small effect on its staple length.

Staple length in the hogget fleece was significantly associated with midside wool weight and, to a lesser extent, with hip coat depth. The pooled within-class regression coefficient of staple length on midside wool weight was $b = 0.09 \pm 0.03$ cm mg^{-1} cm^2 which was significant ($P<.05$, Table 83). Thus high midside wool weights in the lamb birthcoat were associated with increased staple lengths in the hogget fleece.

The relationship between staple length and hip coat depth was more complicated. The pooled within-class regression coefficient of staple length on hip coat depth was non-significant but the within-face cover group regressions were heterogeneous at the 10% level. Thus staple length was related to hip coat depth among the Face Cover lambs ($b = 0.47 \pm 0.25$ cm mm^{-1}, $t_{18} = 1.88$, $P<.10$) but not among the Controls ($b = -0.11 \pm 0.21$ cm mm^{-1}, $t_{19} = 0.51$, NS.). While this difference is of questionable significance, a similar pattern was detected in the relationship between fibre diameter and hip coat depth.

TABLE 83: EFFECT OF FACE COVER GROUP, SEX, HIP BIRTHCOAT DEPTH AND MIDSIDE WOOL WEIGHT PER UNIT AREA OF SKIN ON STAPLE LENGTH OF HOGGET WOOL

Classification	Staple Length (cm) Mean ± S.E.	
Face cover group		
Face cover	15.31 ± 0.42	(20)
Control	13.60 ± 0.41	(21)
Sex		
Male	14.99 ± 0.46	(17)
Female	13.92 ± 0.38	(24)

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Face Cover Group (Group)	1	29.82	8.54**
Sex	1	11.48	3.29†
Group x Sex	1	4.23	1.21 NS
Error	37	3.49	

.../continued

TABLE 83, continued

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (above)	3	14.83	
Intra-class (sex) regression of staple length on midside wool weight	2	10.15	3.26*
Pooled within-class	1	17.90	5.75*
Difference	1	2.39	0.77 NS
Residual error	35	3.11	
Main effects model (above)	3	14.83	
Intra-class (face cover group) regression of staple length on hip coat depth	2	6.31	1.89 NS
Pooled within-class	1	2.17	0.65 NS
Difference	1	10.45	3.14†
Residual error	35	3.33	

3. Mean fibre diameter

Fibre diameter was not strongly associated with any of the treatments or birthcoat characteristics of interest in this study. Neither face cover group nor sex of the lamb significantly affected mean fibre diameter (Table 84).

The pooled within-class regression coefficient of fibre diameter on hip coat depth was non-significant but the within-face cover group regressions were significantly heterogeneous, if only at the 10% level. Thus high coat depths were associated with coarse hogget wool among the Face Cover lambs ($b = 0.54 \pm 0.24$ microns mm^{-1}, $t_{18} = 2.20$, $P<.05$) but not among the Controls ($b = -0.09 \pm 0.20$ microns mm^{-1}, $t_{19} = 0.46$, NS.).

4. Crimp frequency

Although neither face cover group nor sex of the lamb exerted a significant effect on crimp frequency, the interaction between these treatments was significant ($P<.05$, Table 85). Thus the male hoggets of the group selected for open faces had a lower crimp frequency than the females, but no such difference existed among the Control animals.

The pooled within-class regression coefficient of crimp frequency on midside wool weight was significant at the 5% level with a value $b = -0.015 \pm 0.007$ crimps cm^{-1} mg^{-1} cm^{2} (Table 85). Since crimp frequency is an important factor in the subjective (quality count) assessment of wool fineness, this result indicates that increasing midside wool weights in the birthcoat are likely to be associated with increasing coarseness of the hogget fleece (when assessed visually).

TABLE 84: EFFECT OF FACE COVER GROUP, SEX AND HIP BIRTHCOAT DEPTH ON MEAN FIBRE DIAMETER OF HOGGET WOOL

Classification	Mean Fibre Diameter (micron) Mean ± S.E.	
Face cover group		
Face cover	32.67 ± 0.42	(20)
Control	32.19 ± 0.40	(21)
Sex		
Male	32.82 ± 0.45	(17)
Female	32.04 ± 0.37	(24)

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Face Cover Group (Group)	1	2.42	0.71 NS
Sex	1	6.12	1.79 NS
Group x Sex	1	1.09	0.32 NS
Error	37	3.42	

Analysis of Covariance

Source of Variation	d.f.	Mean Square	F
Main effects model (above)	3	3.14	
Intra-class (face cover group) regression of mean fibre diameter on hip coat depth	2	7.95	2.51 †
Pooled within-class	1	3.49	1.10 NS
Difference	1	12.42	3.93 †
Residual error	35	3.16	

TABLE 85: EFFECT OF FACE COVER GROUP, SEX AND MIDSIDE WOOL WEIGHT PER UNIT AREA OF SKIN ON CRIMP FREQUENCY OF HOGGET WOOL

Classification	Crimp Frequency (Crimps cm^{-1}) Mean ± S.E.		
	Sex		
	Male	Female	Both sexes
Face cover group			
Face cover	1.11 ± 0.13[a] (8)	1.48 ± 0.10[b] (12)	1.30 ± 0.08 (20)
Control	1.47 ± 0.12[b] (9)	1.37 ± 0.10[b] (12)	1.41 ± 0.08 (21)
Both groups	1.29 ± 0.09 (17)	1.43 ± 0.07 (24)	

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Face Cover Group (Group	1	0.07	0.54 NS
Sex	1	0.17	1.32 NS
Group x Sex	1	0.54	4.30*
Error	37	0.12	

Analysis of Covariance

Source of Variation	d.f.	Mean Square	F
Main effects model (above)	3	0.25	
Intra-class (face cover group) regression of crimp frequency on midside wool weight	2	0.28	2.37 NS
Pooled within-class	1	0.54	4.64*
Difference	1	0.01	0.10 NS
Residual error	35	0.12	

However, as has already been demonstrated, this does not hold true when fibre diameter is measured directly (by the airflow technique).

5. Standard deviation of fibre diameter

The standard deviation of fibre diameter in the hogget wool sample was not significantly influenced by the sex of the lamb or by the group history of selection for face cover (Table 86). Nor was it found to be associated with any of the birthcoat characteristics measured in this study.

Lockart (1956) found that the variability of fibre diameter in the fleece of two-tooth Merino ewes was significantly correlated with their birthcoat hairiness grade. Since birthcoat grade has been shown to be associated with coat depth in Romney lambs (Chapter II), it might have been expected that coat depth would also be related to the standard deviation of fibre diameter in the Progeny Test lambs. However, the range of birthcoat hairiness in these lambs was much smaller than was apparently the case in Lockart's study, which may account for the failure to identify any such relationships here.

6. Proportion of medullated fibres

The proportion of medullated fibres in the hogget midside sample was significantly affected by face cover group, the Control hoggets exhibiting a much greater frequency of medullation than their more open-faced peers (Table 87). There were, however, no strong relationships between the proportion of medullated fibres and characteristics of the birthcoat. The only evidence of such a relationship was in the heterogeneity (at the 10% level) of the within-face cover group regressions of percentage medullated fibres on midside wool weight.

TABLE 86: EFFECT OF FACE COVER GROUP AND SEX ON THE STANDARD DEVIATION OF FIBRE DIAMETER OF HOGGET WOOL

Classification	Standard Deviation of Fibre Diameter (microns)
Face cover group	
Face cover	6.46 (20)
Control	6.59 (21)
Sex	
Male	6.43 (17)
Female	6.61 (24)

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Face Cover Group (Group)	1	0.18	0.30 NS
Sex	1	0.33	0.55 NS
Group x Sex	1	0.02	0.03 NS
Error	37	0.60	

TABLE 87: EFFECT OF FACE COVER GROUP, SEX AND MIDSIDE WOOL WEIGHT PER UNIT AREA OF SKIN ON THE PROPORTION OF MEDULLATED FIBRES IN HOGGET WOOL
(Treatment mean proportions of medullated fibres and their standard errors are expressed as decimals)

Classification	Proportion of Medullated Fibres - Mean ± S.E.	
Face cover group		
Face cover	0.013 ± 0.009	(20)
Control	0.051 ± 0.009	(21)
Sex		
Male	0.036 ± 0.010	(17)
Female	0.028 ± 0.006	(24)

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Face Cover Group (Group)	1	0.014	7.98 **
Sex	1	0.001	0.45 NS
Group x Sex	1	0.001	0.68 NS
Error	37	0.002	

Analysis of Covariance

Source of Variation	d.f.	Mean Square	F
Main effects model (above)	3	0.005	
Intra-class (face cover group) regression of % medullated fibres on midside wool weight	2	0.004	2.06 NS
Pooled within-class	1	0.000	0.06 NS
Difference	1	0.007	4.07 †
Residual error	35	0.002	

TABLE 88: EFFECT OF FACE COVER GROUP, SEX, HIP BIRTHCOAT DEPTH AND MIDSIDE BIRTHCOAT DEPTH ON COLOUR GRADE OF HOGGET WOOL

Classification	Colour Grade - Mean ± S.E.	
Face cover group		
Face cover	5.3 ± 0.1	(20)
Control	5.5 ± 0.1	(21)
Sex		
Male	5.2 ± 0.2	(17)
Female	5.6 ± 0.1	(24)

Analysis of Variance

Source of Variation	d.f.	Mean Square	F
Face Cover Group (Group)	1	0.57	1.34 NS
Sex	1	1.70	4.02†
Group x Sex	1	0.07	0.16 NS
Error	37	0.42	

.../continued

TABLE 88, continued

Analysis of Covariance			
Source of Variation	d.f.	Mean Square	F
Main effects model (above)	3	0.76	
Intra-class (sex) regression of colour grade on hip coat depth	2	1.02	2.62†
Pooled within-class	1	1.23	3.15†
Difference	1	0.81	2.09 NS
Residual error	35	0.39	
Main effects model (above)	3	0.76	
Intra-class (sex) regression of colour grade on midside coat depth	2	1.37	3.72*
Pooled within-class	1	1.80	4.88*
Difference	1	0.95	2.56 NS
Residual error	35	0.37	

Among the open-faced hoggets the regression coefficient was significant at the 10% level with a value of b = 0.25 ± 0.13 percentage units mg^{-1} cm^2 (t_{18} = 1.78), while among the Control group the regression coefficient was not significant (b = -0.10 ± 0.10 percentage units mg^{-1} cm^2, t_{19} = 0.99).

7. Wool colour

Treatment effects on the colour grade of the hogget wool were small, there being a slight advantage in colour to the female lambs (P<.10, Table 88). However, colour grade was found to be related to coat depth at the midside position and, to a lesser extent, at the hip site. The pooled within-class regression coefficient of colour grade on midside coat depth was b = -0.13 ± 0.06 colour grade units (CGU) per mm depth which was significant at the 5% level (Table 88). At the hip site, the pooled within-class regression coefficient (b = -0.10 ± 0.06 CGU mm^{-1}) was significant only at the 10% level. Hence there was some tendency for high birthcoat depths at each site to be associated with poor colour in the hogget fleece.

Chapter Summary

Relationships between some characteristics of the birthcoat and of the hogget fleece were examined in 41 ewes and rams drawn from the Progeny Test flock. The birthcoat characteristics had been measured during the course of previous experiments (the coat depths after artificial wetting) when the lambs were less than 48 hours old. Hogget fleece characteristics were measured at hogget shearing when the animals were approximately 13 months of age.

Birthcoat depth at the hip site was positively associated with greasy hogget fleeceweight but negatively with the colour grade of the wool. At the midside position, only the negative relationship with colour grade was apparent. In addition hip coat depth was associated with staple length and mean fibre diameter (both positive regression coefficients), but only in the hoggets from the flock selected for open faces.

Midside wool weight per unit area of skin was positively associated with staple length and negatively with crimp frequency. The latter relationship indicates that lambs with high midside wool weights are likely to have a coarse hogget fleece where the diameter of hogget wool is subjectively assessed. However, midside wool weight was not associated with objectively-measured hogget fibre diameter. Finally, high midside wool weights were associated with an increased proportion of medullated fibres in the hogget fleece, but this again occurred only in the lambs from the open-face selection flock.

The results of this experiment must be interpreted with some care. Only a small number of animals was involved in the study and, more importantly, it has not been possible to establish genetic relationships between the birthcoat and hogget fleece characteristics. Hence some of the phenotypic relationships which were identified could have been due to common environmental effects at each stage of the animal's life. It does appear that, had the hoggets been selected on the basis of those characteristics which confer an improved coat insulation (i.e. high coat depth and midside wool weight), hogget fleece production in the current generation would not have suffered unduly. In some respects (e.g. staple length and greasy fleeceweight) the selected hoggets

would probably have been superior to the culled group, but one area of concern is the likely associated increase in medullation. However, the effects of such selection on hogget fleece production in future generations are yet to be identified.

C H A P T E R X

DISCUSSION AND CONCLUSIONS

CHAPTER X

DISCUSSION AND CONCLUSIONS

The main aim of this study was to examine characteristics of the newborn lamb which might influence its ability to resist the debilitating effects of a cold environment (and so might be manipulated to reduce the incidence of starvation and exposure mortality). During the course of the study certain problems were encountered in selecting the correct environmental conditions for testing the lambs. Since an incorrect choice may reduce the value of data generated in the experiment, some further discussion of the problem is warranted here.

In experiments which are concerned with examining the resistance to hypothermia of lambs (or any other homeotherms) it is clearly desirable that the animals be exposed to environments in which they will approach the limit of their ability to regulate deep body temperature. However, because there is considerable between-lamb variation in summit metabolic rate, some lambs will attain summit metabolism unless the group as a whole is exposed to a relatively warm environment. Accordingly, if the environmental conditions chosen for testing are to approximate the field situation (i.e. if the lambs are to be subjected to a severe cold-stress) it must be expected that a proportion of the lambs will attain their summit metabolic rate. In these animals, heat production will not be a useful index of resistance to cold-stress.

The first problem, then, is to identify those lambs which have attained summit metabolism. This is comparatively easy to do if they are exposed to an increasingly cold environment (as in Chapter III) and changes in their heat production and rectal temperature monitored

continuously. It is considerably more difficult if the lambs are exposed to a single very cold environment, in which case the attainment of summit metabolism can be defined only on the basis of some criterion in the rate of decline in rectal temperature. This has certain limitations, particularly for those lambs whose rate of decline in rectal temperature is very close to the chosen cut-off point. Nevertheless, treatment effects on the frequency of attainment of summit metabolism (as defined in this study) were found to correlate well with the corresponding effects on heat production, and the trait was fairly repeatable.

Having discriminated between the summit and non-summit lambs, it is then necessary to choose the appropriate index of resistance to cold-stress for use in the experiment. This is likely to be a particular problem if a substantial proportion of the lambs have attained summit metabolism. One possible approach is to use the rate of decline in rectal temperature (RDRT) as the main index, but attempts to relate this to traits such as coat depth may be confounded by variation in the summit metabolism of individual lambs. It is true that breed differences in RDRT may be related to corresponding differences in coat characteristics (Slee, 1978) presumably because differences between breeds in summit metabolism are small (Alexander and Bell, 1975a). Within-breed variation is much greater (for example 12 to 22 W kg^{-1} among the Romney lambs examined in Chapter III) and this will have considerable influence upon the RDRT. Thus if a high proportion of the lambs in an experiment attain summit metabolism, the available indices of resistance to cold-stress may be ineffective both for the summit lambs (for the reasons discussed) and for the non-summit group (because

only a few lambs are involved). This will be a particular problem if regression analyses are being attempted, as is illustrated by the experiment described in Chapter VI.

One way in which the appropriate environmental conditions can be selected is to expose the lambs to a sequence of declining ambient temperatures as described in Chapter IV. This permits the estimation of the number of lambs attaining summit metabolism at each ambient temperature and hence the selection of an environment in which the lambs are subjected to severe cold-stress but in which few become hypothermic. It has the major disadvantage that the time required to test each lamb is greatly prolonged (compared with exposure to a single environment) and that much of the data collected at the higher ambient temperatures may be irrelevant to the problem being considered. Other difficulties may also arise, such as the apparent tendency for the lambs' coats to dry out after some time in the climate chambers (Chapter IV).

In this study an attempt was made to use the data from lambs subjected to a series of declining ambient temperatures (Chapter IV) to select appropriate environmental conditions (at a single ambient temperature) for testing lambs in the subsequent experiments. This met with only limited success. In a number of cases lambs which were exposed to similar environments differed considerably in the frequency of attainment of summit metabolism, despite having similar bodyweights and birthcoat characteristics. Clearly the resistance to hypothermia of the newborn lamb is determined by factors not examined in this study, and until these are more fully understood there will be certain risks

inherent in exposing lambs to a single very cold environment. As a compromise it may be necessary to subject the lambs to more than one ambient temperature in the hope of avoiding the problems which are likely to occur when a high proportion of them attain summit metabolism.

The investigations described in this study centred on lambs of the Romney breed which is numerically the most important in New Zealand. Drysdale-cross lambs were used for comparative purposes and were, in each experiment, found to have a lower requirement for body heat production than the Romneys. It must be stressed, however, that a change to the Drysdale is not being advocated as a means of reducing lamb mortality. Lambs with the hairy birthcoat characteristic of the Drysdale were used simply to extend the range of coat depths and mid-side wool weights available in the study. Indeed, they present a unique opportunity to examine the effects of birthcoat characteristics because they are expected to be similar to the Romneys in most other respects (Dry, 1955).

The results of this study indicate that dry lambs are unlikely to become hypothermic unless the air temperature is well below freezing point or they are exposed to very high airspeeds. Conversely wet lambs, particularly those with low summit metabolic rates, could experience hypothermia at ambient temperatures greater than 15^{o}C. There would seem to be little that can be done in the field to minimize the detrimental effects of wetting, except perhaps the use of shelter or plastic coats to reduce the rate of evaporation from the lamb's body. Each of these approaches may have only limited application in extensive farming operations. Maternal grooming of the lamb seems likely to have a role in reducing the moisture content of the coat

(Alexander, Signoret and Hafez, 1974).

Airspeed effects were generally small, lambs exposed to moving air (1.0 to 2.0 m sec^{-1}) having rates of body heat production 7 to 20% greater than those in still air. There were no significant differences between the 3 levels of moving air, and it is suggested that the main effect of air movement on coat insulation was the removal of the boundary layer of still air over the coat. This view is further supported by the homogeneity of the within-airspeed regressions of heat production on coat depth and midside wool weight (Chapter IV). It must be remembered, however, that the airspeeds used in this study were relatively low, and that there would have been considerable turbulence within the chambers. Further research is required to establish the effects of higher airspeeds on the coat insulation of Romney lambs.

The study gives no clue as to why female lambs have a better survival rate in the field than do male lambs (Hight and Jury, 1970; Dalton et al., 1980). Differences between the sexes in resistance to cold-stress were apparent in only one experiment (Chapter V) where the female lambs had significantly greater rates of heat production than males and attained summit metabolism more frequently. These differences could not be accounted for solely by the between-sex difference in bodyweight. Since male lambs have greater birthweights than females they would be likely to suffer dystocia problems more frequently and it may be this difference which is largely responsible for their greater overall mortality in the field.

In the one experiment which examined birthrank effects, twin lambs

were seen to attain summit metabolism more frequently than singles, a difference which was almost entirely accounted for by their significantly lower bodyweights. This result is consistent with the findings of Dalton et al. (1980) that single- and multiple-born lambs of equal birthweights have an equal chance of survival. Despite attaining summit metabolism more frequently than singles, twin lambs did not have a significantly greater metabolic rate. Accordingly it is suggested that birthrank may exert a small effect on summit metabolism. Twin lambs were also handicapped by lower coat depths and midside wool weights than their single-born peers.

The resistance to cold-stress of the newborn lamb appears to improve little with increasing age over the first 2 days of life. In one experiment (Chapter IV) the heat production of lambs in a cold environment was found to decline with age, but only in the Drysdale-crosses. This effect was apparently due to an increase in the coat depth of these lambs as a consequence of age-related drying of the coat, and would presumably not apply to lambs born in wet weather. When the effects of age and feeding were considered simultaneously, newborn lambs which had not fed prior to their test were found to have a rate of heat production and frequency of attainment of summit metabolism similar to that of older suckled lambs. This contrasts with the recently-published findings of Eales and Small (1981) that feeding colostrum increases the summit metabolism of newborn lambs. Although summit metabolism was not measured directly in the unfed/newborn and fed/older lambs (Chapter VI), 65% were considered to have attained their summit metabolic rate. Among these individuals the heat production of the unfed/newborn lambs (14.52 ± 0.68 W kg^{-1}) was not

significantly different from that of the fed/older group (15.62 ± 0.62 W kg^{-1}, t_{33} = 1.18, NS.). When the unfed/newborn lambs were subjected to a second test (after they had suckled) their heat production was significantly greater than at the first test. However, this does not appear to have been due to the ingestion of colostrum or milk since another group of lambs, which had been fed at the first test, exhibited a similar increase in heat production when exposed to cold for a second time (Chapter VIII).

The study of hind-limb skin temperatures in newborn lambs produced some unexpected results. Skin temperatures of dry lambs were greater, and declined more slowly, than those of wet lambs over a range of ambient temperatures. Even at 5°C ambient temperature, after they had spent 3 hours in the climate chambers, 65% of the dry lambs had skin temperatures in excess of 25°C. Romney and Drysdale-cross lambs tested when dry and in still air also had significantly greater skin temperatures than Merinos in the same environment. It is therefore concluded that Romney and Drysdale-cross lambs do not necessarily constrict peripheral blood vessels immediately upon entering the cold zone (despite showing increases in metabolic rate), and that some may require a severe cold-stress to induce peripheral vasoconstriction. In Chapter VI very young lambs (less than an hour old at the commencement of the test) were found to exhibit a rapid decline in skin temperature with advancing age. It would seem that, at birth, lambs may have a poor ability to control peripheral blood flow (even in a very cold environment). However, they appear to develop this ability soon after birth and skin temperature was independent of age in lambs more than 2 hours old.

The relationship between heat production and skin temperature was examined in 2 experiments. If low skin temperatures were indicative of a more intense peripheral vasoconstriction, and if this resulted in an improved tissue insulation, it would be reasonable to expect a positive relationship between heat production and skin temperature. Such a relationship did not occur in either of the experiments (among wet lambs at low ambient temperatures). It is not known whether this was because the lambs varied little in the intensity of peripheral vasoconstriction or because skin temperature was not a good predictor of residual blood flow in the vasoconstricted limb. Skin temperature was also found to be influenced by the weight of wool on the limbs (in lambs exposed to still air) and by the lamb's bodyweight. This suggests that it was not a good indicator of peripheral blood flow, except for large differences such as those between dry and wet lambs.

The lamb's genotype for face cover does not appear to influence its resistance to cold-stress in the neonatal period. Cockrem (1967) has postulated that the observed relationships between facial wool growth and productive characters in mature sheep may be mediated through variation in ability to control peripheral blood flow and body temperature. Lambs from the Massey University Progeny Test flock were therefore examined to determine whether single-trait selection for more open faces (over a 25-year period) had altered their thermoregulatory ability. No differences were found between the Face Cover and Control lambs in the frequency of attainment of summit metabolism, rate of decline in rectal temperature, heat production or skin temperature. Nor were there any differences in bodyweight or birthcoat characters. Similarly when unselected hairy and non-hairy lambs (the progeny of

single-N sires) were assigned face cover grades at 3 months of age, no relationship could be found between the phenotype for face cover and their resistance to cold-stress at birth. Since face cover is moderately heritable, the results from both experiments are consistent with the view that the lamb's genotype for face cover does not influence its resistance to cold stress or its ability to control peripheral blood flow to the hind-limb.

The lamb's bodyweight has long been considered an important determinant of its resistance to cold-stress, a view supported by the results of this study. Thus in Chapter V the proportion of lambs attaining summit metabolism was found to be strongly related to bodyweight. The rate of heat production (per unit bodyweight) required to maintain body temperature in a cold environment was found to decline with increasing bodyweight. It did not, however, decline as rapidly as would be expected from the bodyweight exponent of 0.59 (Lines and Peirce, 1931) which has been widely quoted with respect to newborn lambs. In this study the experimentally-derived exponent was in the range 0.78 to 0.85 which was also very close to the exponent relating actual body surface area to bodyweight in foetal sheep (Malan and Curson, 1936).

A major component of this study concerned the role of the birthcoat as a determinant of resistance to cold-stress. Three coat characters were examined, these being the depth of the coat at the midside and hip positions, together with the weight of wool per unit area of skin on the midside. The sites at which coat depth was measured were chosen in a preliminary study of lamb skins on the basis that depth at these sites was highly correlated ($r = 0.94$) with overall mean coat

depth. The measurement of coat depth was highly repeatable in the preliminary study but less so (r = 0.4 to 0.8) in the live lambs.

Lambs with hairy birthcoats (i.e. the Drysdale-cross lambs of Chapter IV and the hairy lambs of Chapter V, all of which carried the single N gene) had significantly greater coat depths and midside wool weights than their non-hairy peers. The birthcoat depth of the hairy lambs was significantly reduced by wetting but no corresponding effect was apparent in the non-hairy group. It is suggested that this was due to a greater sensitivity of the long halo hairs to wetting, an effect which would have partially accounted for the poor repeatability of coat depth in the hairy lambs.

In Chapter V, single-born lambs were found to have greater coat depths and midside wool weights than twins. Although this effect of birthrank was paralleled by a corresponding effect on bodyweight, no association could be found between bodyweight and the coat characteristics in that experiment. Conversely, coat depth and midside wool weight did increase with bodyweight among the lambs described in Chapter IV. This relationship, which was particularly evident among the hairy lambs, would be expected to further compound the poor resistance to cold-stress of small lambs. There was no effect of gestation length on the coat characters except in one case (midside wool weight) through the correlation with bodyweight.

The level of heat production required by the lamb to maintain body temperature was strongly related to each of the coat characters. Although there was only a limited range of coat depths and midside wool weights in these lambs, particularly within the Romney breed, this was

associated with a considerable variation in the required metabolic rate.

Midside and hip coat depth were almost entirely interdependent in their control of the metabolic response to a cold environment, presumably as a consequence of the high correlation between the depth at each site. Thus the component of coat insulation which is a function of depth may be adequately described by measuring depth at only one site. Conversely, midside wool weight exerted a control of heat production over and above its correlation with the coat depths. It is suggested that this effect was due to lambs with high midside wool weights presenting a greater surface area of fibre (per unit area of skin) to retard convective air movement within the coat.

In one experiment (Chapter IV), heat production was found to be related to coat depth in a curvilinear fashion such that maximum coat insulation was attained at a depth of about 30 mm. This effect was considered to be due to the fact that deeper coats present a greater surface area to the environment than do shallow coats, and that the outer margins of very deep coats (Drysdale-cross lambs) consist mainly of sparsely-distributed halo hairs. The relationship between heat production and midside wool weight was also curvilinear, the maximum coat insulation being attained at a midside wool weight of about 90 mg cm^{-2}. It would appear that this occurred, not because of increased conductive heat loss in the coats of lambs with high midside wool weights, but rather through the correlation between midside wool weight and the non-linear coat depth relationships. Although the curvilinear relationships between heat production and the coat characters were not apparent in the subsequent experiment (which involved a smaller

range of coat depths and midside wool weights) they do indicate that the insulation provided by a unit depth or midside wool weight in the Romney is at least as good as that in the Drysdale-cross lamb.

The insulative value of the lamb's coat does not appear to be greatly affected by wetting, except in the hairy lambs whose coat depth is reduced by the wetting treatment. Thus the relationship between heat production and coat depth or midside wool weight was found to be similar for dry and (artificially) wet lambs. Nor do newborn lambs, whose coats are naturally wet with amniotic fluid, appear to have a poorer coat insulation than older artificially-wetted lambs. Similarly, the insulation provided by a unit depth or midside wool weight was not affected by the relatively low airspeeds in this study.

In conclusion it may be said that the selection for specific birthcoat types offers one of the potentially most useful methods of improving the resistance to cold-stress of the newborn lamb. Other possible approaches should not, however, be ignored. The control of birthweight is obviously important, small lambs being particularly susceptible to body cooling and to starvation-exposure mortality. In recent years much discussion has been devoted to the problem of how to reduce variation in birthweight and so improve survival. It must be stressed, however, that while the mortality of small lambs is particularly high, their incidence in the flock and contribution to the overall mortality rate are less so (Dalton et al., 1980; Duff, 1981). This fact, together with the tendency of ewes to buffer against bodyweight changes in the foetus by manipulating their own body reserves, means that attempts to reduce variation in birthweight may have only limited application as a means of improving lamb survival.

It has already been noted that, since the body of the newborn lamb contains little subcutaneous fat (Alexander and Bell, 1975b), tissue insulation is expected to vary with peripheral blood flow. Although there is some limited evidence that lambs vary in the rate of blood flow through vasoconstricted tissues (Alexander, Bell and Hales, 1973) it does not appear possible to detect this variation by the measurement of skin temperature. It seems likely that any such variation is so low as to contribute little to variation in the insulative properties of the body tissues. In this connection it may be noted that, although there is considerable between-breed variation in the cold-resistance of clipped lambs, much of this is accounted for by breed differences in bodyweight (Slee, 1978).

Attempts to improve the resistance of the newborn lamb to cold-stress by selection for specific birthcoat types hold some promise of success because the insulative value of the coat is an important determinant of total body insulation, and because the birthcoat characteristics are relatively easy to measure. The latter point applies more to midside wool weight than to the coat depths. Even so, given some experience the coat depths, particularly at the hip site, can be measured with a reasonable degree of repeatability within Romney-type lambs. Indeed the repeatabilities are quite high considering that coat depth can be measured to only 10% of the total range in lambs of this breed (i.e. to 1 mm in 10 mm). Moreover, it is apparent that even the small range of coat depths in these lambs is associated with a considerable saving in the level of heat production required to maintain body temperature.

While some genetic influences on birthcoat type are well docu-

mented (e.g. the effects of the N gene), selection for these genotypes is not applicable as a means of improving lamb survival because of the associated effects of these genes on the mature fleece. However, studies of other sheep breeds such as the Merino (Schinckel, 1955) and the Welsh Mountain (Roberts, 1926; Dry, 1975) have shown that a deep hairy birthcoat need not always be followed by a highly medullated adult fleece. The heritability of coat depth and midside wool weight within Romney lambs has not been estimated but evidence presented in this study of a small sire effect on coat depth (in sires that were themselves paternal half-brothers) suggests that this trait is genetically controlled to some extent. Nor have the consequences (with respect to the mature fleece) of selection for increased coat depth and midside wool weight been examined. The results of the experiment in Chapter IX suggest that high coat depths and midside wool weights are likely to be associated with increased greasy fleeceweight and staple length, and slightly poorer colour in the hogget fleece. There may also be an increased fibre diameter and proportion of medullated fibres. However, these are phenotypic relationships only, and the corresponding genetic correlations have not been examined. Nevertheless, it seems likely that if selection for improved birthcoat insulation can be implemented without detriment to the mature fleece, this would assist in improving the resistance of the newborn lamb to cold-stress and so reduce the incidence of starvation-exposure mortality.

A P P E N D I X I

A COMPARISON OF THE HIND-LIMB SKIN TEMPERATURES OF DRY MERINO, ROMNEY AND DRYSDALE-ROMNEY CROSS LAMBS IN STILL AIR

APPENDIX I

A COMPARISON OF THE HIND-LIMB SKIN TEMPERATURES OF DRY MERINO, ROMNEY AND DRYSDALE-ROMNEY CROSS LAMBS IN STILL AIR

Introduction

It was noted in Chapter IV that dry Romney and Drysdale-Romney cross lambs exposed to a sequence of declining ambient temperatures exhibited hind-limb skin temperatures which were considerably higher than those of the Merino lambs examined by Alexander (1961). This effect could have been due to the Merinos constricting peripheral blood vessels to a greater extent, or to their skin temperatures having been allowed to equilibrate more closely with ambient temperature. The 10 Merino lambs which were on loan from the Wairakei Experimental Station were used to test which of these factors was likely to have been the more important effect.

Experimental Design and Methods

The treatment of the Merino lambs was as described in Chapter IV with the lambs being exposed to the same sequence of declining ambient temperatures, and with hind-limb skin temperature measured as for the Romney and Drysdale-Romney cross lambs in that chapter. The Merinos were tested when dry and in still air, thereby removing any possible effect of air movement or wetting on the rate at which skin temperature equilibrated with the environment. Their hind-limb skin temperatures were compared with those of the 12 Romney and Drysdale-Romney cross lambs tested under the same environmental conditions in Chapter IV. No distinction was made between the latter 2 breeds since they had previously been shown not to differ in skin temperature. Hence the

experiment involved a simple comparison of the skin temperatures of 2 groups which will be referred to as "breed types" - the Merino lambs and the "Romney-type" (Romney and Drysdale-Romney cross).

Results and Discussion

The analyses of variance for skin temperature at each ambient temperature are presented in Table 89. Merino lambs exhibited consistently lower skin temperatures than the Romney-type lambs, although the difference was significant ($P < .05$) only at ambient temperatures of $15^{o}C$ and below. This was due to a more rapid decline in the skin temperatures of the Merino lambs as the test proceeded.

At the highest ambient temperature the mean skin temperature of the Merino lambs was $1.5^{o}C$ below the ambient temperature, while in the Romney-type lambs skin temperature exceeded ambient temperature by the same amount. Within each breed type, however, the lambs could be separated into 2 distinct groups on the basis of their skin temperatures at this ambient temperature. None of the Romney-type, and only one of the Merino lambs, exhibited skin temperatures between 26 and $33^{o}C$. The main difference between the breed types was in the proportion of lambs falling into each group; 60% of the Merino lambs exhibited skin temperatures lower than the $30^{o}C$ ambient temperature, while only 33% of the Romney-type lambs did so. Since all the lambs had been held at ambient temperatures of $2^{o}C$ to $15^{o}C$ prior to the test, this would appear to indicate that a greater proportion of the Merino lambs had constricted peripheral blood vessels at that time, but had experienced only limited vasodilation when exposed to the initially warm environment in the climate chambers.

TABLE 89: EFFECT OF BREED TYPE ON THE HIND-LIMB SKIN TEMPERATURES OF DRY LAMBS AT SIX AMBIENT TEMPERATURES

Classification		Hind-Limb Skin Temperature (°C) Mean ± S.E.					
		Nominal air temperature (°C)					
		30.0	25.0	20.0	15.0	10.0	5.0
Breed type							
Merino	(10)	28.55 ± 2.07	27.75 ± 2.11	25.65 ± 2.03	22.45 ± 2.28	20.00 ± 2.62	17.90 ± 2.92
Romney-type	(12)	31.48 ± 1.89	31.17 ± 1.93	30.46 ± 1.85	28.96 ± 2.08	28.38 ± 2.39	26.17 ± 2.66

Analysis of Variance

Source	d.f.	Mean Square and Significance		
		Nominal air temperature (°C)		
		30.0	25.0	20.0
Breed type	1	46.67 NS	63.67 NS	126.11†
Error	20	43.03	44.71	41.41
		15.0	10.0	5.0
Breed type	1	231.05*	382.59*	372.75*
Error	20	52.20	68.70	85.18

As the test proceeded (i.e. as the ambient temperature was reduced), the lambs which had high skin temperatures at 30°C ambient temperature frequently retained this difference over their peers. When the ambient temperature had been reduced to 5°C (2.5 hours after skin temperature was first measured) many of them still exhibited skin temperatures in excess of 25°C. Thus there was a highly significant correlation ($r = 0.73$, $P<.001$) between skin temperatures at 30°C and at 5°C ambient temperature (pooled across both breed types). This tendency for lambs to retain high skin temperatures was again most pronounced among the Romney-type lambs. Consequently the skin temperatures of these lambs declined much more slowly than did those of the Merino lambs.

The very high skin temperature - ambient temperature gradients exhibited by many of these lambs at the lowest ambient temperature strongly suggest that they had not fully constricted peripheral blood vessels. Since the skin temperatures of the Merino lambs (Table 89) declined more slowly than did those of the Merinos studied by Alexander (1961), the generally high skin temperatures of lambs in this study could partly reflect a failure of skin temperature to equilibrate with ambient temperature. However this does not explain why lambs within each breed type varied to a considerable degree in their ability to minimize the skin temperature - air temperature gradient. Moreover Alexander (1961) also found that some fed Merino lambs had very high skin temperatures, at ambient temperatures below 10°C, despite apparently allowing a longer period of equilibration than was the case in this study.

It must therefore be concluded that the Romney and Drysdale-cross

lambs were less adept at minimizing peripheral blood flow in a cold environment than were the Merino lambs. This factor, rather than problems of equilibration in skin temperature, appears to have been primarily responsible for the high skin temperatures of the dry Romney-type lambs.

A P P E N D I X I I

ESTIMATION OF THE BULK DENSITY OF THE BIRTHCOAT IN ROMNEY LAMBS

APPENDIX II

ESTIMATION OF THE BULK DENSITY OF THE BIRTHCOAT IN ROMNEY LAMBS

Introduction

The data described in this appendix are derived from 12 Romney lambs of a similar genetic background to those described in Chapter IV. The lambs were close-clipped to remove the entire birthcoat and the birthcoat characteristics (midside and hip coat depth, midside wool weight per unit area of skin and total birthcoat weight) were measured as described in Chapter II. Removal of the birthcoat was performed to facilitate heat loss during the measurement of summit metabolism (Chapter III).

Results

The mean bulk density of the birthcoats of these lambs was estimated as follows:

$$\text{Bulk density (mg cm}^{-3}) = \frac{\text{Total birthcoat weight (mg)}}{\text{Surface area (cm}^2) \times \text{Mean coat depth (cm)}}$$

where "mean coat depth" for each lamb refers to the mean of its hip and midside coat depth. The lamb's surface area was estimated from its bodyweight using the following formulae:

$A = 0.121\ W^{0.59}$ where A is the surface area in square metres and W the weight in kilograms (Lines and Peirce, 1931)

$A = 3.320\ W^{0.778}$ where A is the surface area in square centimetres and W the weight in grams (Malan and Curson, 1936)

While neither of these formulae provides an ideal estimate of surface area, the former having been calculated on data from sheep of newborn to mature post-natal age and the latter from foetuses of 28 to 149 days gestational age, it seems likely that the best available estimate of surface area would lie within the range of estimates provided by these equations.

The mean weight of these lambs was 5.40 ± 0.27 kg and mean surface area was therefore estimated to lie between 2 653 ± 104 cm^2 (by formula of Malan and Curson, 1936) and 3 260 ± 100 cm^2 (by formula of Lines and Peirce, 1931). Mean total birthcoat weight was 140.56 ± 7.63 g and birthcoat depth (calculated over both measuring sites) averaged 9.0 ± 0.3 mm. The mean bulk density of the lambs' birthcoats was therefore estimated to be in the range 48.0 ± 1.5 to 59.4 ± 1.8 mg cm^{-3}.

ADDENDUM : CHAPTER IV

It was noted by the examiners that no account had been taken of possible correlations between performance at each test for the lambs tested twice in Chapter IV. The data were therefore re-analysed as follows:

(a) for each of the 3 independent variables (heat production, rectal temperature and skin temperature) in the analysis of variance (Tables 7, 8, 9), and at each of the 6 ambient temperatures, residuals were calculated as the deviation of actual from predicted performance for each lamb test. The correlation between the residuals at first and second test was then calculated for the lambs tested twice. The correlations ranged from -0.01 to +0.48 with most of the values being between $r = 0.20$ and $r = 0.35$.

(b) analyses of variance, weighted to take account of the correlation (assumed to equal 0.30) between the repeated observations, were then undertaken and the results compared with those reported in the text. For heat production and rectal temperature the 2 analyses (at each ambient temperature) indicated the same levels of significance for all main effects and interactions. In the case of skin temperature, the revised analysis showed a slight increase in the F-ratios for the main effect of airspeed and for some interactions. The interpretation of these analyses was not, however, altered.

B I B L I O G R A P H Y

BIBLIOGRAPHY

Alexander, G. (1956) Changes in weight of lambs during the first thirty-six hours of life. Aust. vet. J., 32: 321-325.

Alexander, G. (1961) Temperature regulation in the newborn lamb. III. Effect of environmental temperature on metabolic rate, body temperatures, and respiratory quotient. Aust. J. agric. Res., 12: 1152-1174.

Alexander, G. (1962a) Temperature regulation in the newborn lamb. IV. The effect of wind and evaporation of water from the coat on metabolic rate and body temperature. Aust. J. agric. Res., 13: 82-99.

Alexander, G. (1962b) Temperature regulation in the newborn lamb. V. Summit metabolism. Aust. J. agric. Res., 13: 100-121.

Alexander, G. (1962c) Energy metabolism in the starved newborn lamb. Aust. J. agric. Res., 13: 144-164.

Alexander, G. (1964) Lamb survival : physiological considerations. Proc. Aust. Soc. Anim. Prod., 5: 113-122.

Alexander, G. (1969) The effect of adrenaline and noradrenaline on metabolic rate in young lambs. Biol. Neonate, 14: 97-106.

Alexander, G. (1970) Summit metabolism in young lambs. Effect of hormones and drugs that affect mobilization and utilization of substrate for cold-induced thermogenesis. Biol. Neonate, 15: 37-48.

Alexander, G. (1973) Heat loss from sheep. p. 173-203 in Proceedings of the 20th Easter School in Agricultural Science, University of Nottingham. Edited by Monteith, J.L. and Mount, L.E. Butterworth, London.

Alexander, G. (1974) Birth weight of lambs : influences and consequences. CIBA Foundation Symposium 27: 215-245.

Alexander, G. (1975) Body temperature control in mammalian young. Br. Med. Bull., 31: 62-68

Alexander, G. and Bell, A.W. (1975a) Maximum thermogenic response to cold in relation to the proportion of brown adipose tissue and skeletal muscle in the body and to other parameters in young lambs. Biol. Neonate, 26: 182-194.

Alexander, G. and Bell, A.W. (1975b) Quantity and calculated oxygen consumption during summit metabolism of brown adipose tissue in new-born lambs. Biol. Neonate, 26: 214-220.

Alexander, G., Bell, A.W. and Hales, J.R.S. (1972) The effect of cold exposure on the plasma levels of glucose, lactate, free fatty acids and glycerol and on the blood gas and acid-base status in young lambs. Biol. Neonate, 20: 9-21.

Alexander, G., Bell, A.W. and Hales, J.R.S. (1973) Effects of cold exposure on tissue blood flow in the new-born lamb. J. Physiol., Lond., 234: 65-77.

Alexander, G., Bell, A.W. and Setchell, B.P. (1972) Regional distribution of cardiac output in young lambs : effect of cold exposure and treatment with catecholamines. J. Physiol., Lond., 220: 511-528.

Alexander, G., Bell, A.W. and Williams, D. (1970) Metabolic response of lambs to cold. Effects of prolonged treatment with Thyroxine, and of acclimation to low temperatures. Biol. Neonate, 15: 198-210.

Alexander, G. and McCance, I. (1958) Temperature regulation in the newborn lamb. I. Changes in rectal temperature within the first six hours of life. Aust. J. agric. Res., 9: 339-347.

Alexander, G., McCance, I. and Watson, R.H. (1955) Some observations on losses among Merino lambs. Age at death, birth weight and duration of gestation of the lambs from one flock. Aust. vet. J., 31: 85-90.

Alexander, G. and Mills, S.C. (1968) Free fatty acids and glucose in the plasma of newly born lambs : effects of environmental temperature. Biol. Neonate, 13: 53-61

Alexander, G., Mills, S.C. and Scott, T.W. (1968) Changes in plasma glucose, lactate and free fatty acids in lambs during summit metabolism and treatment with catecholamines. J. Physiol., Lond., 198: 277-289.

Alexander, G. and Peterson, J.E. (1961) Neonatal mortality in lambs. Intensive observations during lambing in a flock of maiden Merino ewes. Aust. vet. J., 37: 371-381.

Alexander, G., Peterson, J.E. and Watson, R.H. (1959) Neonatal mortality in lambs. Intensive observations during lambing in a Corriedale flock with a history of high lamb mortality. Aust. vet. J., 35: 433-441.

Alexander, G., Signoret, J.P. and Hafez, E.S.E. (1974) Sexual and maternal behaviour. p. 222-254 in Reproduction in farm animals. Third Edition. Edited by Hafez, E.S.E. Lea and Febiger, Philadelphia.

Alexander, G. and Williams, D. (1966a) Teat-seeking activity in new-born lambs : the effects of cold. J. agric. Sci., Camb., 67: 181-189.

Alexander, G. and Williams, D. (1966b) Teat-seeking activity in lambs during the first hours of life. Anim. Behav., 14: 166-176.

Alexander, G. and Williams, D. (1968) Shivering and non-shivering thermogenesis during summit metabolism in young lambs. J. Physiol., Lond., 198: 251-276.

Alexander, G. and Williams, D. (1970a) Cardiovascular function in young lambs during summit metabolism. J. Physiol., Lond., 208: 65-83.

Alexander, G. and Williams, D. (1970b) Summit metabolism and cardiovascular function in young lambs during hyperoxia and hypoxia. J. Physiol., Lond., 208: 85-97.

Armstrong, D.G., Blaxter, K.L., Clapperton, J.L., Graham, N. McC. and Wainman, F.W. (1960) Heat production and heat emission of two breeds of sheep. J. agric. Sci., Camb., 55: 395-401.

Blair, H.T. (1981) Response to selection for open face and greasy fleece weight in Romney sheep. Thesis, Ph.D., Massey University.

Blaxter, K.L. (1962) The energy metabolism of ruminants. Hutchinson, London.

Blaxter, K.L. and Wainman, F.W. (1961) Environmental temperature and the energy metabolism and heat emission of steers. J. agric. Sci., Camb., 56: 81-90.

Blaxter, K.L. and Wainman, F.W. (1964) The effect of increased air movement on the heat production and emission of steers. J. agric. Sci., Camb., 62: 207-214.

Brody, S. (1945) Bioenergetics and growth. Reinhold, New York.

Brouwer, E. (1965) Report of subcommittee on constants and factors. p. 441-443 in Energy metabolism (Proceedings, 3rd symposium, European Association of Animal Production, Troon, Scotland, May 1964). Edited by Blaxter, K.L. Academic Press, London.

Burton, A.C. and Edholm, O.G. (1955) Man in a cold environment. Arnold, London.

Carter, H.B. (1955) The hair follicle group in sheep. Anim. Breed. Abstr., 23: 101-116.

Carter, H.B. and Dowling, D.F. (1954) The hair follicle and apocrine gland population of cattle skin. Aust. J. agric. Res., 5: 745-754.

Chapman, R.E. (1965) The ovine arrector pili musculature and crimp formation in wool. p. 201-232 in Biology of the skin and hair growth. Edited by Lyne, A.G. and Short, B.F. Angus and Robertson, Sydney.

Cockrem, F. (1959) Studies of the effects of the gene N on body growth and fleece development of the New Zealand Romney. II. The development of the fibre population. Aust. J. agric. Res., 10: 400-412.

Cockrem, F. (1967) The effects of temperature on body growth and other traits of open- and woolly-faced Romney lambs. Proc. N.Z. Soc. Anim. Prod., 27: 193-209.

Cockrem, F.R.M. and McDonald, M.F. (1969) An investigation of the relationships between body temperature and implantation and lambing rates in the New Zealand Romney ewe. Proc. N.Z. Soc. Anim. Prod., 29: 195-207.

Cockrem, F. and Rae, A.L. (1959) Studies of the effects of the gene N on body growth and fleece development of the New Zealand Romney. I. The body growth of the N-type lamb. Aust. J. agric. Res., 10: 387-399.

Cockrem, F. and Rae, A.L. (1966) Studies of face cover in the New Zealand Romney Marsh sheep. I. The relationships between face cover, wool blindness, and productive characters. Aust. J. agric. Res., 17: 967-974.

Dalton, D.C., Knight, T.W. and Johnson, D.L. (1980) Lamb survival in sheep breeds on New Zealand hill country. N.Z. Jl agric. Res., 23: 167-173.

Davies, H.L. (1964) Lamb losses in South-western Australia. Proc. Aust. Soc. Anim. Prod., 5: 107-112.

Dawes, G.S. and Mott, J.C. (1959) The increase in oxygen consumption of the lamb after birth. J. Physiol., Lond., 146: 295-315.

Doney, J.M. (1963) The effects of exposure in Blackface sheep with particular reference to the role of the fleece. J. agric. Sci., Camb., 60: 267-273.

Dry, F.W. (1955) Multifactorial inheritance of halo-hair abundance in New Zealand Romney sheep. Aust. J. agric. Res., 6: 608-623.

Dry, F.W. (1975) The architecture of lambs' coats : a speculative study. Massey University, Palmerston North

Duff, X.J. (1981) An investigation of perinatal lamb mortality in a flock of Romney ewes in the Wairarapa district of New Zealand. Dissertation, Diploma in Agricultural Science, Massey University.

Eales, F.A. and Small, J. (1981) Effects of colostrum on summit metabolic rate in Scottish Blackface lambs at five hours old. Res. vet. Sci., 30: 266-269.

Evans, J.V., King, J.W.B., Cohen, B.L., Harris, H. and Warren, F.L. (1956) Genetics of haemoglobin and blood potassium differences in sheep. Nature, Lond., 178: 849-850.

Fetcher, E.S., Hall, J.F. and Shaub, H.G. (1949) The skin temperature of an extremity as a measure of its blood flow. Science, N.Y., 110: 422-423.

Gemmel, R.T., Bell, A.W. and Alexander, G. (1972) Morphology of adipose cells in lambs at birth and during subsequent transition of brown to white adipose tissue in cold and warm conditions. Am. J. Anat., 133: 143-164.

Gonzalez-Jimenez, E. and Blaxter, K.L. (1962) The metabolism and thermal regulation of calves in the first month of life. Br. J. Nutr., 16: 199-212.

Gunn, R.G. and Robinson, J.F. (1963) Lamb mortality in Scottish hill flocks. Anim. Prod., 5: 67-76.

Hall, J.G. and Purser, A.F. (1979) Lamb production and haemoglobin type. Rep. Anim. Breed. Res. Orgn. : 9-12.

Haughey, K.G. (1973a) Vascular abnormalities in the central nervous system associated with perinatal lamb mortality. 1. Pathology. Aust. vet. J., 49: 1-8.

Haughey, K.G. (1973b) Vascular abnormalities in the central nervous system associated with perinatal lamb mortality. 2. Association of the abnormalities with recognised lesions. Aust. vet. J., 49: 9-15.

Haughey, K.G. (1975) Birth injury and cold exposure as components of perinatal lamb mortality. Proc. N.Z. vet. Assoc. Sheep Soc. : 79-88.

Haughey, K.G. (1978) Perinatal lamb mortality. Paper presented to "Sheep Health and Production" course, Faculty of Veterinary Science, Massey University, May 23-24, 1978.

Haughey, K.G. (1979) The effect of birth injury to the foetal nervous system on the survival and feeding behaviour of lambs. p. 109-111 in Reviews in rural science IV (Proceedings of a symposium held at the University of New England, Armidale, N.S.W., Australia, September 1979). Edited by Wodzicka-Tomaszewska, M., Edey, T.N. and Lynch, J.J.

Hemingway, A. (1963) Shivering. Physiol. Rev., 43: 397-422.

Henderson, A.E. (1953) Fleece development and wool growth on the Romney lamb. J. agric. Sci., Camb., 43: 12-53.

Henderson, C.R. (1969) Design and analysis of animal husbandry experiments. p. 1-35 in Techniques and procedures in animal science research. Second edition. American Society of Animal Science.

Hight, G.K. and Jury, K.E. (1970) Hill country sheep production. II. Lamb mortality and birth weights in Romney and Border Leicester x Romney flocks. N.Z. Jl agric. Res., 13: 735-752.

Holmes, C.W. (1971) The effect of milk given at various temperatures on the oxygen consumption of young calves. Anim. Prod., 13: 619-625.

Houston, D.C. and Maddox, J.G. (1974) Causes of mortality among young Scottish Blackface lambs. Vet. Rec., 95: 575.

Jagusch, K.T. and Coop, I.E. (1971) The nutritional requirements of grazing sheep. Proc. N.Z. Soc. Anim. Prod., 31: 224-234.

Joyce, J.P. and Blaxter, K.L. (1964) The effect of air movement, air temperature and infrared radiation on the energy requirements of sheep. Br. J. Nutr., 18: 5-27.

Joyce, J.P., Blaxter, K.L. and Park, C. (1966) The effect of natural outdoor environments on the energy requirements of sheep. Res. vet. Sci., 7: 342-359.

Knight, T.W., Hight, G.K. and Winn, G.W. (1979) The influence of sires on lamb survival. Proc. N.Z. Soc. Anim. Prod., 39: 87-93.

Lines, E.W. and Peirce, A.W. (1931) The basal (standard) metabolism of the Australian Merino sheep. Bull. Coun. sci. industr. Res. Aust. no. 55.

Lockart, L.W. (1956) Birthcoat of lambs and adult fibre diameter. Aust. J. agric. Res., 7: 152-157.

McBride, G., Arnold, G.W., Alexander, G. and Lynch, J.J. (1967) Ecological aspects of the behaviour of domestic animals. Proc. Ecol. Soc. Aust., 2: 133-165.

McFarlane, D. (1955) Neonatal lamb mortality in the Gisborne area. Proc. N.Z. Soc. Anim. Prod., 15: 104-119.

McFarlane, D. (1961) Perinatal lamb losses. Aust. vet. J., 37: 105-109.

McFarlane, D. (1965) Perinatal lamb losses. 1. An autopsy method for the investigation of perinatal losses. N.Z. vet. J., 13: 116-135.

McFarlane, D. (1966) Perinatal lamb losses. 2. A preliminary survey of New Zealand perinatal lamb losses in the areas surrounding Gisborne, Wairoa, Nelson, Rangiora and Ashburton. N.Z. vet. J., 14: 137-144.

McLean, J.A. (1972) On the calculation of heat production from open-circuit calorimetric measurements. Br. J. Nutr., 27: 597-600.

Malan, A.P. and Curson, H.H. (1936) Surface area in the foetus of the Merino sheep. Onderstepoort J. vet. Sci. Anim. Ind., 7: 251-259.

Meyer, H.H. and Clarke, J.N. (1978) Genetic and environmental effects on incidence and causes of lamb mortality. Proc. N.Z. Soc. Anim. Prod., 38: 181-184.

Molnar, G.W. and Rosenbaum, J.C. (1963) Surface temperature measurement with thermocouples. p. 3-11 in Temperature : its measurement and control in science and industry. Part 3, biology and medicine. Edited by Hardy, J.D. Reinhold, New York.

Monteith, J.L. (1973) Principles of environmental physics. Arnold, London.

Moule, G.R. (1954) Observations on mortality amongst lambs in Queensland. Aust. vet. J., 30: 153-171.

Mount, L.E. (1979) Adaptation to thermal environment : man and his productive animals. Arnold, London.

Mullaney, P.D. (1966) The relation of birth coat and lamb survival. Aust. J. exp. Agric. Anim. Husb., 6: 84-87.

Nelder, J.A. (1975) General linear interactive modelling. Royal Statistical Society, England.

Nelder, J.A. and Wedderburn, R.W.M. (1972) Generalized linear models. Jl R. statist. Soc. A, 135: 370-384.

Obst, J.M. and Day, H.R. (1968) The effect of inclement weather on mortality of Merino and Corriedale lambs on Kangaroo Island. Proc. Aust. Soc. Anim. Prod., 7: 239-242.

Obst, J.M. and Evans, J.V. (1970) Genotype-environment interactions in lamb mortality with particular reference to birth coat and haemoglobin type. Proc. Aust. Soc. Anim. Prod., 8: 149-153.

Penman, H.L. (1958) Humidity. Chapman and Hall, London.

Purser, A.F. (1967) Is lamb birthcoat type related to hardiness. Rep. Anim. Breed. Res. Orgn. : 26-34.

Purser, A.F. and Karam, H.A. (1967) Lamb survival, growth and fleece production in relation to birthcoat type among Welsh Mountain sheep. Anim. Prod., 9: 75-85.

Purser, A.F. and Young, G.B. (1959) Lamb survival in two hill flocks. Anim. Prod., 1: 85-91.

Rattray, P.V., Garret, W.N., East, N.E. and Hinman, N. (1974) Growth, development and composition of the ovine conceptus and mammary gland during pregnancy. J. Anim. Sci., 38: 613-626.

Roberts, J.A.F. (1926) Kemp in the fleece of the Welsh Mountain sheep. p. 1-17 in The British Research Association for the Woollen and Worsted Industries, Publication 59.

Ross, D.A. (1958) Rapid measurement of the fibre diameter of Romney cross-bred wool by the airflow apparatus. N.Z. Jl Sci., 1: 127-142.

Ross, J.M. (1954) Development of the follicle population in N-type sheep. Aust. J. agric. Res., 5: 484-489.

Ryder, M.L. and Stephenson, S.K. (1968) Wool growth. Academic Press, London.

Safford, J.W. and Hoversland, A.S. (1960) A study of lamb mortality in a western range flock. I. Autopsy findings on 1051 lambs. J. Anim. Sci., 19: 265-273.

Satterthwaite, F.E. (1946) An approximate distribution of estimates of variance components. Biometr. Bull., 2: 110-114.

Schinckel, P.G. (1955) Inheritance of birthcoats in a strain of Merino sheep. Aust. J. agric. Res., 6: 595-607.

Scott, J.D.J. (1962) Lamb mortality : determining main causes of losses. N.Z. Jl Agric., 105: 421.

Searle, S.R. (1971) Linear models. Wiley, New York.

Shelley, H.J. (1960) Blood sugars and tissue carbohydrate in foetal and infant lambs and Rhesus monkeys. J. Physiol., Lond., 153: 527-552.

Shelton, M. (1964) Relation of birthweight to death losses and to certain productive characteristics of fall-born lambs. J. Anim. Sci., 23: 355-359.

Slee, J. (1964) Comparative responses of Tasmanian Merino and Scottish Blackface sheep to a falling environmental temperature. Proc. Aust. Soc. Anim. Prod., 5: 188-189.

Slee, J. (1966) Variation in the responses of shorn sheep to cold exposure. Anim. Prod., 8: 425-434.

Slee, J. (1968) Body temperature and vasomotor responses in Scottish Blackface and Tasmanian Merino sheep subjected to slow cooling. Anim. Prod., 10: 265-282.

Slee, J. (1977) Cold exposure and survival in newborn lambs. Rep. Anim. Breed. Res. Orgn. : 11-16.

Slee, J. (1978) The effects of breed, birthcoat and body weight on the cold resistance of newborn lambs. Anim. Prod., 27: 43-49.

Slee, J., Griffiths, R.G. and Samson, D.E. (1980) Hypothermia in newborn lambs induced by experimental immersion in a water bath and by natural exposure outdoors. Res. vet. Sci., 28: 275-280.

Smith, I.D. (1961) Thermoregulation in the newborn Merino. Aust. vet. J., 37: 205-210.

Snedecor, G.W. and Cochran, W.G. (1967) Statistical Methods. Sixth Edition. Iowa State University Press, Ames, Iowa.

Steel, R.G.D. and Torrie, J.H. (1960) Principles and procedures of statistics. McGraw-Hill, London.

Stephenson, S.K. (1959) Wool follicle development in the New Zealand Romney and N-type sheep. V. The pre-natal relationships between growth, skin expansion, and primary follicle number. Aust. J. agric. Res., 10: 453-470.

Sykes, A.R., Griffiths, R.G. and Slee, J. (1976) Influence of breed, birthweight and weather on the body temperature of newborn lambs. Anim. Prod., 22: 395-402

Taplin, D.E. and Everitt, G.C. (1964) The influence of prenatal nutrition on postnatal performance of Merino lambs. Proc. Aust. Soc. Anim. Prod., 5: 72-81.

Thomson, A.M. and Thomson, W. (1948-49) Lambing in relation to the diet of the pregnant ewe. Br. J. Nutr., 2: 290-305

Venkatachalam, G., Nelson, R.H., Thorp, F., Luecke, R.W. and Gray, M.L. (1949) Causes and certain factors affecting lamb mortality. J. Anim. Sci., 8: 392-397.

Watson, W.A. (1962) Abortion and stillbirth in sheep. Vet. Bull., Weybridge, 32: 259-264, 335-341.

Webster, A.J.F. (1974) Physiological effects of cold exposure. p. 33-69 in Environmental physiology. Edited by Robertshaw, D. Butterworth, London.

Webster, A.J.F. and Blaxter, K.L. (1966) The thermal regulation of 2 breeds of sheep exposed to air temperatures below freezing point. Res. vet. Sci., 7: 466-479.

Webster, M.E.D. and Johnson, K.G. (1968) Some aspects of body temperature regulation in sheep. J. agric. Sci., Camb., 71: 61-66.

Wildman, A.B. (1932) Coat and fibre development in some British sheep. Proc. zool. Soc. Lond. : 257-285.

Yates, F. (1934) The analysis of multiple classifications with unequal numbers in the different subclasses. J. Am. statist. Ass., 29: 51-66.