

**GENETIC EVALUATION OF THE EFFECTS OF DIVERGENT
FEATHERING SELECTION AND MAJOR FEATHERING
GENES ON GROWTH PERFORMANCES AND
CARCASS TRAITS IN BROILER CHICKENS**

By

MENGLIANG LOU

**(B.Sc. and M.Sc. Zhejiang Agricultural University,
People's Republic of China)**

**Scottish Agricultural College
Poultry Science Department
Auchincruive, Ayr**

**A thesis submitted for the degree of Doctor of Philosophy in the
Faculty of Science in the University of Glasgow, November, 1994**

ProQuest Number: 11007896

All rights reserved

INFORMATION TO ALL USERS

The quality of this reproduction is dependent upon the quality of the copy submitted.

In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if material had to be removed, a note will indicate the deletion.



ProQuest 11007896

Published by ProQuest LLC (2018). Copyright of the Dissertation is held by the Author.

All rights reserved.

This work is protected against unauthorized copying under Title 17, United States Code
Microform Edition © ProQuest LLC.

ProQuest LLC.
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106 – 1346

Thesis
10,000
Copy 1

GLASGOW
UNIVERSITY
LIBRARY

CONTENTS

LIST OF TABLES	vii
LIST OF FIGURES	x
ACKNOWLEDGEMENTS	xii
SUMMARY	xiv
CHAPTER 1. INTRODUCTION	1
CHAPTER 2. LITERATURE REVIEW	3
2.1. FEATHERS AND THEIR DISTRIBUTION IN THE DOMESTIC CHICKENS	3
2.1.1. Genes That Control the Rate of Feathering	4
2.1.1.1. Major genes	4
a) The K locus	4
b) The T locus	5
2.1.1.2. Polygenes that control feather growth	5
2.1.1.3. Sexual dimorphism	6
2.1.2. Genes That Control the Distribution of feathers--The Naked Neck Gene	8
2.2. EFFECTS OF FEATHERING AND TEMPERATURE ON BROILER GROWTH	9
2.2.1. Feathering and Broiler Growth	9
2.2.1.1. Early feathering (kk & k/w) and late feathering (KK, Kk & K/w)	9
2.2.1.2. Other Feathering Genes on Broiler Growth	12
2.2.1.2.1. The naked neck gene in normal temperature	12
2.2.1.2.2 Feathering Score and Body Weight	13
2.2.2. Temperature, Feathering and Body Weight	15
2.2.2.1. Temperature and K-k genotype on growth	15
2.2.2.2. Temperature and Na/na allele on growth	15
2.2.2.3. Temperature and feathering polygenes on body growth	17
2.3. GENETICS OF FEED EFFICIENCY	18
2.3.1. Genetic Variability of FCR	19
2.3.2. Component Traits of Feed Efficiency	21
2.3.2.1. Effect of behaviour on feed efficiency	21
2.3.2.2. Feathering effect on feed efficiency	22
2.3.2.2.1. Major genes	23

a). Early vs. late feathering	23
b). The naked neck gene	24
2.3.2.2.2. Effect of feathering selection	25
2.3.2.2.3. Feathering response on FCR selection	26
2.4. BROILER CARCASS, MEAT YIELD, AND CHEMICAL COMPOSITION	26
2.4.1. Factors Influencing Carcass and Meat Yields	27
2.4.1.1. Breed and strain differences in carcass and meat yields	27
2.4.1.2. Effect of body weight, age and sex	28
2.4.1.3. Nutritional factors	29
2.4.1.4. Feathering effects	31
2.4.1.5. Effects of interactions between factors on carcass traits	32
2.4.2. Chemical Composition of Broiler Carcass	33
2.4.2.1. Effects of genetic selection on the chemical composition	34
2.4.2.2. Effects of age and sex	35
2.4.2.3. Effect of feathering on carcass composition	35
2.4.2.4. Effect of temperature on carcass composition	36
2.5. GENETIC PARAMETERS AND THEIR ESTIMATION	36
2.5.1. Heritability and Its Estimation	37
2.5.1.1. Definition	37
2.5.1.2. Methods of heritability estimation	37
2.5.2. Genetic Correlation and the Estimation	38
2.5.3. Estimates of Genetic Parameters for Body Weight and Feathering	39
CHAPTER 3. GENERAL MATERIALS AND METHODS	41
3.1. OBJECTIVES OF THE EXPERIMENTS	41
3.2. DESCRIPTION OF THE LINES	42
3.2.1. Feathering Selection Lines	42
3.2.1.1 Origin and selection procedures	42
3.2.1.2. Replacement stock management	43
3.2.2. The Line with the Naked Neck Gene	44
3.3. THE DESIGNED EXPERIMENTS	45
3.3.1. Chicks Used in the Experiments	45
3.3.1.1. Experiment 1	45
3.3.1.2. Experiment 2 and 3	45
3.3.2. General Management of the Chicks	46
3.3.3. Measurements and Procedures	47
3.3.3.1. Feather length measurements	48

3.3.3.2. Body weight and feed consumption	48
3.3.3.3. Procedure of slaughter and dissection	48
3.3.3.4. Sample preparation for chemical analysis	50
3.3.3.5. Protein determination	51
3.3.4. Statistical Analysis	52
3.4. GENETIC PARAMETER ESTIMATION	52

CHAPTER 4. EFFECTS OF FEATHERING GENOTYPES, TEMPERATURE AND SEX ON CARCASS PROTEIN CONTENT AND PARTITION OF CHICKEN TO FORTY DAYS OF AGE

53

4.1. INTRODUCTION	53
4.2. MATERIALS AND METHODS	54
4.3. RESULTS	56
4.4. DISCUSSION	58
4.4.1. Dry Matter Contents	58
4.4.1.1. Dry matter of the plucked carcass	78
4.4.1.2. Dry matter in parts	79
4.4.1.3. Dry matter with age	80
4.4.2. Protein Contents	80
4.4.2.1. Protein content in the starved body	81
4.4.2.2. Protein content in the plucked carcass	81
4.4.2.3. Protein content in carcass parts	82
4.4.2.3.1. Protein content of the dry feather	82
4.4.2.3.2. Protein contents in the meat, viscera and residual	83
4.4.2.4. Age effect on the protein content	83
4.4.3. Protein Partition	84
4.4.3.1. Whole body protein partition to feather, meat, viscera and residual	84
4.4.3.1.1. To feathers	84
4.4.3.1.2. To meat	85
4.4.3.1.3. Protein partition to the residual	85
4.4.3.2. Protein partition of the plucked carcass to meat, viscera and residual	86
4.4.3.2.1. To meat	86
4.4.3.2.2. To the viscera	86
4.4.3.2.3. To the residual	86
4.4.3.3. Effects of interactions on body and carcass protein partition	87
4.5. CONCLUSIONS	89

CHAPTER 5. EFFECTS OF NAKED NECK GENE, Na, EARLY (kk) OR LATE (Kk) FEATHERING AND FAST (F) OR SLOW (S) FEATHERING ON BROILER GROWTH PERFORMANCES AND CARCASS TRAITS	90
5.1. INTRODUCTION	90
5.2. MATERIALS AND METHODS	91
5.2.1. Stock	91
5.2.2. Housing and the Layout of the Experiment	91
5.2.3. Diets	92
5.2.4. Procedure and Measurements	92
5.3. RESULTS	94
5.3.1. Feather Measurements	95
5.3.2. Body Weight and Weight Gain	96
5.3.3. Feed Consumption	99
5.3.4. Feed Conversion Ratio (FCR)	100
5.3.5. Carcass Measurements	101
5.3.6. Chemical Analysis and Protein Partition	106
5.4. DISCUSSION	110
5.4.1. Effects of Feathering Genes on Feather Growth	110
5.4.2. Effects of Feathering Genes on Growth and Feed Consumption	111
5.4.2.1. The Na gene	111
5.4.2.2. K genotype and line	111
5.4.3. Effects of Feathering Genotype on FCR	112
5.4.4. Interrelationships among BW, FC, FCR and Feathering	115
5.4.5. Effects of Feathering Genes on the Carcass Traits	115
5.4.5.1. The Na gene on carcass traits	115
5.4.5.2. K genotype, line and carcass traits	117
5.4.6. Effects of Feathering Genes on Carcass Chemical Composition and Protein Partition	118
5.4.6.1. Na gene	118
5.4.6.2. Effects of K genotypes and line	119
5.5. CONCLUSIONS	120

**CHAPTER 6. THE RELATIONSHIP BETWEEN FEATHER GROWTH AND FEED CONVERSION RATIO IN BROILERS--
--- A STUDY ON THE INDIVIDUAL BASIS----** 121

6.1. INTRODUCTION	121
6.2. MATERIALS AND METHODS	122
6.2.1. Chicks and the Mating Plan	122
6.2.2. Diets	122
6.2.3. Bird Management	124
6.2.4. Records and Procedures	126
6.2.5. Models for Data Analysis	126
6.3. RESULTS	128
6.3.1. The Rearing Period	128
6.3.2. Feathering	129
6.3.3. Body Weight and Feed Consumption	132
6.3.4. Carcass Traits	137
6.4. DISCUSSION	139
6.4.1. Feather Measurements	139
6.4.2. Body Weight, Body Weight Gain, Feed Consumption and FCR	140
6.4.3. Carcass and Meat Yields	141
6.5. Conclusions	143

CHAPTER 7 ANIMAL MODEL ANALYSIS OF THE SELECTION EXPERIMENT FOR FEATHERING IN BROILER CHICKS AT THREE WEEKS OF AGE 144

7.1. INTRODUCTION	144
7.2. MATERIALS AND METHODS	144
7.2.1. Data	144
7.2.2. Data analysis	146
7.2.2.1. Outline of the statistical model and analysis procedures	146
7.2.2.2. Analyses of the data sets	148
7.2.2.2.1. Univariate analyses	148
7.2.2.2.2. Bivariate analysis	149
7.3. RESULTS	150
7.3.1. Change of the Means by the Selection	150
7.3.1.1. Change in tail feather length	150

7.3.1.2. Body weight changes	156
7.3.2. REML Estimation of the Genetic Parameters	159
7.3.2.1. Estimation of the heritabilities from the univariate analyses	159
7.3.2.2. Bivariate analysis	164
7.4. DISCUSSION	166
7.4.1. Selection Response	166
7.4.1.1. Tail feather length	166
7.4.1.2. Body weight	166
7.4.2. Genetic Parameters	167
7.5. CONCLUSIONS	169

CHAPTER 8. GENERAL DISCUSSIONS AND CONCLUSIONS 170

8.1. DISCUSSION	170
8.1.1. The Control of Feathering	170
8.1.2. The Consequences of the Feathering Selection on the Broiler Traits	171
8.1.3. The Roles of Major Feathering Genes in Broiler Production	171
8.1.4. The Joint Effects of Feathering Genes on Broiler Production	172
8.1.5. Analysis of the Selection Data	173
8.2. CONCLUSIONS	174

APPENDICES

Appendix 2.1. Energy preservation by feathers in chicks	176
Appendix 4.1. Feed composition of the starter and grower (g/kg) used in Experiment 1	178
Appendix 4.2. Body weight and portional weights (g) of the birds used for the chemical analysis at different ages in Experiment 2	179

REFERENCES	180
-------------------	-----

LIST OF TABLES

Table 4.1. Dry matter contents (g/kg) of meat, viscera and carcass residual	56
Table 4.2. Crude protein contents (g/kg) in samples of feathers(dry), meat, viscera and carcass residual	57
Table 4.3. Body protein partition among feathers, meat, viscera and the residual across the age (g/kg body protein)	58
Table 4.4. Significance levels for the effects of temperature, sex, naked neck gene, feathering selection line and their interactions on dry matter and protein contents, and the protein partition of the whole body and plucked carcass among feathers, meat, viscera and residuals in the simplified three way variance analysis	59-60
Table 4.5. Effects of interactions between sex and line on body protein partition in meat and feathers, and plucked carcass protein partition in meat (g/kg)	78
Table 5.1. Feed composition of the starter, grower and finisher/withdrawal (g/kg) in the second experiment	93
Table 5.2. Effects of the feathering genotypes on the feather growth(mm) and dry feather weight (g) at 52 days, all adjusted for body weight at the measurement.	94
Table 5.3. Test of significance for the effects of the feathering genes and line on feathering adjusted for body weight	95
Table 5.4. Means of the body weight and weight gain as affected by the feathering genes and the line	97
Table 5.5. Test of significance for the effects of the feathering genes and line on the body weight and body weight gain at the age or period shown	97
Table 5.6a. The effect of interaction between the naked neck gene and K gene on the body weight at 34 days of age (g)	98
Table 5.6b. The effect of interaction between the naked neck gene and K gene on the body weight gain between 17 and 34 days of age (g)	98
Table 5.7. Effects of feathering on the cumulative feed consumption to the days shown or within the period indicated	99
Table 5.8. Test of significance for the effects of the feathering genes and line on feed consumption to the age or within the period shown in the table	99
Table 5.9. The effects of interaction between the line and K gene on feed consumption during different periods of time	100
Table 5.10. Effects of feathering on the cumulative feed conversion ratio to the days shown or within the period indicated	100

Table 5.11. Test of significance for the effects of the feathering genes and line on the cumulative feed conversion ratio to the age or within the period indicated	101
Table 5.12. The starved live body weight dressed carcass weight, and dissected yields of the sampled birds and the weight loss during dissection (g) at 52 days of age (see text for full explanation of the dissection losses)	102
Table 5.13. Feathering genotype effects on the relative carcass and meat yields in g/kg starved live body weight	103
Table 5.14. Test of significance for the effects of feathering genotype on the relative carcass and meat yields in g/kg starved live body weight	104
Table 5.15. Feathering genotype effects on the relative carcass and meat yields in g/kg NYD	105
Table 5.16. Test of significance for the effects of feathering genotype on the relative carcass and meat yields in g/kg dressed carcass weight	106
Table 5.17. Effects of feathering on the chemical composition (g/kg wet sample) of the carcass parts and the protein partition among the various parts of the bled-carcass with feathers and of the dressed carcass	107
Table 5.18. Test of significance for the effects of feathering genotype on the chemical composition of the carcass and its parts and on the total bled-carcass protein partition into the four parts and the total dressed carcass protein into the three dissected parts	108
Table 6.1. Composition of feed used during FCR measurements (from 21 days onwards)	123
Table 6.2. The grouped body weight, body weight gain, feed intake and feed conversion ratio of the early and late feathering male chicks in the rearing period of 21 days	128
Table 6.3.1. (Trial 1) The effects of feathering genotype (kk early and Kk late) and family on the primary, secondary, tail and back feather length measurements at the ages of 21, 28, 35 and 45 days in mm, and on the dry weight of flight feathers and other body feathers at 46 days	130
Table 6.3.2. (Trial 2) The effects of feathering genotype (kk early and Kk late) and family on the primary, secondary, tail and back feather length measurements at the ages of 21, 28, 35 and 45 days in mm, and on the dried weight of flight feathers and other body feathers at 46 days	131
Table 6.3.3. Tests for the statistical significance of the effects of the K genotype, family and their interactions on various feathering measurements in trials 1 and 2	132

Table 6.4.1. (Trial 1) Effect of early and late feathering genotype and sire family on body weight, body weight gain, feed consumption and FCR at various ages (24, 31, 38 and 45 days) or during the different periods of time	134
Table 6.4.2.2. (Trial 2) Effect of early and late feathering genotype and sire family on body weight, body weight gain, feed consumption and FCR at various ages (24, 31, 38 and 45 days) or during the different periods of time	135
Table 6.4.3. Test of significance by analysis of variance for the effects of K genotype, family and their interaction on the broiler performance traits in Trial 1 and Trial 2	136
Table 6.5. Results from the combined analysis of (co)variance for the overall FCR data (from 24 to 45 days of age) with models 2 - 6	137
Table 6.4. Means of the Carcass Traits in different sire families in Trial 1 and Trial 2 in g/kg NYD	138
Table 7.1. Number of records in the fast and slow feathering selection lines and the control line for the present analysis from the base population to generation eight	145
Table 7.2. The means and standard deviations of tail feather length in the fast and slow feathering selection lines, and the control line in G1-8	151
Table 7.3. Realised selection differentials of the tail feather length weighed according to the contributions of the breeding birds to the next generation in the fast and slow feathering lines throughout the generations	153
Table 7.4. Realised heritabilities estimated from the regression of selection response to the cumulative selection differential in the fast and slow feathering lines	154
Table 7.5. Means and standard deviations of body weight (g) of the males and females in the three lines from the base population to the eighth generation	156
Table 7.6. REML estimates of additive genetic, error and phenotypic components for the tail feather length from different lines and sets of data	161
Table 7.7. REML estimates of additive genetic, error and phenotypic components for body weight from different lines and sets of data	162
Table 7.8. REML estimates of heritabilities for the tail feather length and body weight from different sets of data (generations and lines) with various options	163
Table 7.9. REML estimates from the bivariate analyses for the tail feather length and body weight: variance and covariance components and the resulting heritabilities and the genetic, residual and phenotypic correlations between the two traits	165

LIST OF FIGURES

Fig 4.1. Effects of temperature, sex, Na gene and line on the dry matter content in the plucked carcass	61
Fig 4.2. Effects of temperature, sex, Na gene and line on meat dry matter content	62
Fig 4.3. Effects of temperature, sex, Na gene and line on viscera dry matter content	63
Fig 4.4. Effects of temperature, sex, Na gene and line on residual dry matter content	64
Fig 4.5. Changes of dry matter and protein contents in the whole body and its dissected parts with age	65
Fig 4.6. Effects of temperature, sex, Na gene and line on the protein content of the starved body	66
Fig 4.7. Effects of temperature, sex, Na gene and line on the protein content of the plucked carcass	67
Fig 4.8. Effects of temperature, sex, Na gene and line on dry feather protein content	68
Fig 4.9. Effects of temperature, sex, Na gene and line on meat protein content	69
Fig 4.10. Effects of temperature, sex, Na gene and line on viscera protein content	70
Fig 4.11. Effects of temperature, sex, Na gene and line on residual protein content	71
Fig 4.12. Protein partition among feather, meat, viscera and carcass residual of the whole body and plucked carcass	72
Fig 4.13. Effects of temperature, sex, Na gene and line on whole body protein partition to feathers	73
Fig 4.14. Effects of temperature, sex, Na gene and line on whole body protein partition to meat	74
Fig 4.15. Effects of temperature, sex, Na gene and line on whole body protein partition to residuals	75
Fig 4.16. Effects of temperature, sex, Na gene and line on plucked carcass protein partition to meat	76
Fig 4.17. Effects of temperature, sex, Na gene and line on plucked carcass protein partition to residual	77
Fig 5.1. Effect of major gene and line on the tail feather length at various ages	96
Fig 5.2. Relationship between tail feather length at 28 days and cumulative feed conversion ratio to 51 days adjusted for the effect of Na gene	114

Fig 6.1. The cage allocation in the environment controlled room for birds after 21 days in Trial 1	125
Fig. 6.2. Growth pattern of the primary and secondary feathers in the early and late feathering males from 21 to 45 days	129
Fig 7.1. Tail feather length changes of the males in the three lines during the generations of divergent feathering selection	151
Fig 7.2. Tail feather length changes of the females in the three lines during the generations of divergent feathering selection	152
Fig. 7.3. Deviations of tail feather length of the two selected lines from the control line (Males)	152
Fig. 7.4. Deviations of tail feather length of the two selected lines from the control line (Females)	153
Fig 7.5. Cumulative selection differential and response in tail feather length of the fast feathering line (males+females)	155
Fig 7.6. Cumulative selection differential and response in tail feather length in the slow feathering line (males+females)	155
Fig 7.7. Body weight changes of males in the three lines during the generations of selection for feathering	157
Fig 7.8. Body weight changes of females in the three lines during the generations of selection for feathering	157
Fig 7.9. Responses of body weight (deviations from the control line) in the two lines to the feathering selection (males)	158
Fig 7.10. Responses of body weight (deviations from the control line) in the two line to the feathering selection (Females)	158

ACKNOWLEDGEMENTS

This thesis has recorded the results of research undertaken of one who has been supported by many. Without their full-hearted help, neither the research work nor the compiling of thesis would ever been completed. Therefore, I express my sincere thanks to those who have helped me.

I am most grateful to the Chinese government and The British Council who enabled me to study in the University of Glasgow by providing the scholarship.

My sincere thanks are due to Dr W. K. Smith, my supervisor, for his continuous encouragement, advice and criticism both in conducting the experiments and in the preparation of the thesis. My gratitude is also due to Mr P. Dun, Head of the Poultry Science Department, the Scottish Agricultural College, Auchincruive, for his kind comments and advice.

The skillful help in the management of the experimental birds and data collection of Mr D. Brown, the scientific officer in the Poultry Science Department, must be acknowledged. I am also grateful to Mrs A. Alexander for her guidance and advice in my poultry carcass dissection work.

I wish to express my thanks to Dr. J. Dixon, Mr. Dunsmuir and other members of staff in the Analytical Services Unit for their help in chemical analyses of the diets, and their guidance in preparing and analysing the carcass samples.

My thanks have to go to the following as well:

Mr. D. Arnot, Head of Computing and Information Technology Department, who has not only provided me with the access to the JANET system for my genetic data analyses, but also has written the program to recode the pedigree data.

Dr R. Thompson in AFRC Edinburgh, Roslin, for his introduction to the DFREML program; Dr R. Crump, SAC, Edinburgh, Genetics and Behaviour Sciences Department, for his great patience in giving me instructions and advice in running the DFREML program.

Mr. A. Sword, the Scottish Agricultural Statistical Services, for his advice on the data analyses in the designed experiments.

I would like to thank all of other members of staff in Poultry Department for their kindness and friendship, staff of the library for their help in providing most of the reading materials during the preparation of the thesis.

Finally, I would like to express my extreme gratitude to my wife, Zhang, who has most strongly supported me throughout my research undertaking in the UK and accompanied me in this country for most of the years, and who also has helped type part of the thesis, and to our parents who have given us a lot of moral support.

SUMMARY

The general objectives of the research undertaken were firstly to demonstrate the possibilities in feathering manipulation of chicks by means of quantitative feathering selection or by means of introducing major genes, and secondly to elucidate the consequences of different methods of genetic feathering manipulation for broiler production. With these, a divergent feathering selection program has been proceeded to the eighth generation. The breeders in different generations were used in various matings with other lines carrying different major feathering genes. The chicks so produced were tested in the series experiments for the feathering measurements, broiler growth performance, carcass traits and body protein partition.

EXPERIMENT 1

The females from the fifth generation of fast (F) and slow (S) feathering selection lines were mated by a group of early feathering (k) males, which were heterozygous for the naked neck gene (Na). The resulting progeny had the following four different feathering genotypes from both of the lines: males, NanaKkF/S, nanaKkF/S, all late feathered; females, NanakwF/S and nanakwF/S, all early feathered. These chicks were raised in a high (30°C) and normal (20°C) post-brooding temperature and analysed for their carcass composition and body protein partition at the ages of 10, 20, 30 and 40 days. The results were as follows:

1) The dry matter (DM) content of broiler carcass and its dissected parts was not significantly affected by feathering. Carcass DM at 30 days of age was significantly ($P < 0.05$) increased from 285 to 301 g/kg by increased temperature from 20 to 30 °C.

2) Protein content of the plucked carcass was not affected by the factors studied, but the whole body protein content was significantly ($P < 0.05$) higher in the normally feathered birds (209 g/kg), birds from the fast feathering line (208 g/kg) and those raised in the high temperature (208 g/kg) than the naked neck birds (203 g/kg), slow feathering line (204 g/kg) and birds kept at normal temperature (204 g/kg), respectively, at 40 days of age. Protein content in the dried feathers was higher in the more mature feathers.

3) The naked neck gene significantly increased the amount of whole body protein in

meat from 380 to 413 g/kg ($P < 0.05$), but reduced protein in the feathers from 164 to 135 g/kg ($P < 0.001$) at 40 days of age. On the plucked carcass basis, the naked neck bird still had more protein in meat ($P = 0.083$), but less in the carcass residuals ($P = 0.100$). Apart from reduced the feather protein in the slow line, feathering selection did not significantly affect body protein partition. High temperature had an unfavourable effect on meat protein deposition. The males generally had less body protein in feathers and carcass residuals, but more in meat than the females.

4) The proportion of meat protein in carcass increased with age at the expense of both offal and residual. Feather protein of the whole body also increased with age.

EXPERIMENT 2

Normal feathering special males with a heterozygous late feathering genotype (nanaKk) were first produced from the mating between the males of the selection lines and the females of the heterozygous naked neck early feathering females (Nanakw). The two groups of special males were mated back to the same naked neck population in the next generation. This mating resulted in the following four major gene genotypes of the male chicks for both the fast and slow lines: Nanakk, NanaKk, nanakk and nanaKk. These eight feathering genotypes were tested for the genotypic effects on feather growth, broiler performance, carcass traits and chemical composition of the dissected carcass parts. The feathering measurements were made at 7, 17, 28, 38, and 48 days of age and the group body weight and feed consumption was taken at 17, 34 and 51 days. At day 52, birds were slaughtered for carcass and chemical composition measurements. The post-brooding temperature was held at 25°C. The following results were obtained:

1). The rate of feathering, as measured by the length of the primary, tail and back feathers, was dependent on the major gene genotype in the K locus, the polygene genotype (line) modified by the feathering selection, and the interaction between them. The polygenes influence on the feathering rate in late feathering birds did not show their effect in the kk early feathering birds. Although it reduced the 52-day feather weight by 21%, the naked neck gene did not affect feathering rate.

2). The naked neck males had an equal body weight (2000g) to the normally feathered counterparts (2003g) at 51 days of age, although they had significantly lower body weight by 28g at 34 days. In the slow feathering line, but not the fast feathering line, the early feathering males had lower a body weight than the late feathering ones at both 34 and 51 days.

3). Later or slower feather development, as measured by the tail feather length at 28 days, was related to higher overall feed conversion ratio (FCR) by a factor of 0.00163/mm. By contrast, the naked neck birds required 50 g less feed to reach the same body weight at 51 days than their fully feathered brothers.

4). Relative to the starved body weight (g/kg), the naked neck birds have significantly ($P < 0.05$) higher yields of the dressed carcass (902.4 vs. 890.4), eviscerated carcass (682.1 vs. 671.9), breast meat (146.6 vs. 138.6), thighs (142.6 vs. 139.0), thigh meat (107.2 vs. 103.2), and the total edible portion (406.0 vs. 390.7), but significantly low yields of dry feathers (28.4 vs. 35.7) and total skin (76.0 vs. 80.6) than the normally feathered ones. On the dressed carcass basis, the naked neck birds had significantly higher yields of breast meat, thigh meat and total edible portion, but very highly significantly less total skin.

5). The early and late feathering genotypes did not differ in carcass traits. The slow feathering line had significantly ($P < 0.05$) higher yields of drumsticks, meat of the drumsticks and total meat, but lower yield of the frame than the fast line on the starved body weight basis. The slow line also had a slightly ($P < 0.1$) higher yield of breast meat, but lower yields of the abdominal fat and the residuals.

6). The skin and carcass residual, but not the meat, of the naked neck birds contains more moisture than the normally feathered counterparts. The patterns of the naked neck gene effect on the body protein partition agreed with Experiment 1. Although the naked neck gene reduced the total skin weight, it did not alter the amount of body protein deposited in skin owing to the higher protein density than the skin of normal feathering birds. The late feathering birds and slow feathering line had significantly ($P < 0.05$) more carcass protein in meat than their respective early feathering and fast feathering counterparts.

EXPERIMENT 3

In order to evaluate the quantitative relationship between feathering and feed conversion ratio, two batches of the early feathering and late feathering male chicks were raised in the individual cages after 21 days of age. They were produced from a similar two-step mating as in Experiment 2, but involving the special males from the slow feathering line only. Individual records for feathering and FCR between 25 and 45 days were obtained. The following results were obtained.

1). The early feathering chicks had lower FCR than the late feathering half-brothers during the 21-day brooding period (1.201 vs. 1.227 in Trial 1 and 1.218 vs. 1.251 in Trial 2). In the individual cages, the early feathering birds again had a lower overall FCR than the late feathering ones in both of the trials (2.17 vs. 2.26 in Trial 1 and 2.27 vs. 2.34 in Trial 2 respectively). The final body weight was the same for the two feathering genotypes.

2). FCR between 24 and 45 days was negatively related to the tail feather length at 28 days both phenotypically and genetically. The genetic correlation (-0.623) between these two traits was stronger than the phenotypic (-0.240) one according to the preliminary restricted maximum likelihood (REML) bivariate analysis fitting an individual animal model.

3). Sire families differed significantly in FCR, the yield of frame and in several feathering traits. Family differences also existed ($P < 0.1$) in the yields of abdominal fat and breast meat.

SELECTION DATA ANALYSIS

The tail feather length and body weight data collected from eight generations of the fast and slow feathering selection were summarised for the direct response in feathering and correlated response in body weight to the feathering selection. In order to draw both the practical and theoretical implications from the selection program, these data were also subjected to the REML analyses. The variance and covariance components and genetic parameters were estimated both for the base population and later generations based on data from different lines and combinations of generations. The results obtained were:

1). Quantitative selection has been effective in manipulating the feathering trait. After eight generations of selection, the fast feathering line had a three-week tail feather length more than two times of that in the control line, and from four to five times that in the slow feathering line.

2). The base population had high heritabilities for both tail feather length and body weight. The combined estimates were 0.54 and 0.56 for the tail feather length, and 0.54 and 0.47 for body weight based on data of generations 1-2 and generations 1-3, respectively. Estimates for the later generations were lower, and were 0.32 and 0.33 for the tail feather length, and 0.51 and 0.35 for body weight with data including generations 4-8 and generations 6-8, respectively.

3). The control line had higher heritabilities for both of the traits than the selected lines in the later generations. Compared with the control, feathering selection reduced the genetic variance of this trait by about two thirds (23.5 vs. 7.57), after four rounds of intensive selection in the slow line, but not the fast line (21.9).

4). Treating parents without records as fixed effects might help to account the bias in heritability estimation caused by intensive selection before and within the assumed base generation. However, this option should be used with caution.

5). In the base population, the tail feather length had a moderate positive genetic correlation with body weight at 24/25 days (0.49, 0.48 and 0.35 for the data from the fast, control and slow feathering lines, respectively). This correlation could be reduced rapidly by random drift and especially directional selection.

CHAPTER 1

INTRODUCTION

The outer-most layer of a chick, feathers, play very important roles in protecting the body from injury and preventing it from excessive heat loss. As the broiler grows faster, these protection needs are becoming ever more demanding, especially at an early age. Furthermore, broiler farmers may want feathers to grow earlier and faster for various reasons. One consideration is that earlier feather development may reduce the need to provide heat for brooding, so as to reduce the fuel cost. Another consideration is that earlier feather development may help plucking. Finally, a better feathering condition of a finished broiler always gives a healthy image. Poorly feathered bird may also cause welfare concerns of the public. However, feather growth is not without cost. The keratinised feather protein can not be easily degraded and recycled. Therefore, feather proteins are mostly wasted from the livestock production system. Further more, feather insulation might become a burden to the bird's survival in a high temperature (Smith and Lee, 1977). Cahaner et al. (1993) argued that a slow rate of heat dissipation (partially caused by feather insulation) might have been a limiting factor for additional weight gain of fast-growing broilers even at a temperature of 20-24°C.

A selection program for fast and slow feathering was initiated in 1986 by Edriss et al. (1988) in the Scottish Agricultural College at Auchincruive to test the possibility of genetic manipulation of feathering in the background of late feathering broiler population. Since then, the pure lines have been extensively tested for the growth performance of the broiler progeny (Edriss, 1988); growth of different feather series, breeder performance, energy and protein metabolism (Priyono, 1991); broiler growth performance and carcass traits (Ajang et al., 1993). However, a pure line is unlikely to be used for commercial broiler production. Therefore, the designed experiments in the present research program used the progeny from the various matings of the fast / slow feathering lines with other lines of poultry. This arrangement was not only closer to the real commercial broiler breeding program, but also provided the opportunities to allow the effects of other major genes to be studied on a broader background of feathering.

The naked neck gene has been known to give beneficial effect on growth of chicks at high temperatures and to increase the yields of broiler carcass and meat (Merat, 1986). At present, at least two poultry breeding companies, each with a very small share of the international market, are offering the naked neck birds for commercial uses. However,

the effect of this gene was mostly studied in the layer-type chicks (Merat, 1986). Also most of the reported studies concerning the effect of this gene were carried out in a single genetic background of feathering. Although better carcass and meat yield of the naked neck birds has been observed in many studies (Merat, 1986; Cahaner et al., 1992, 1993), a full balance sheet for the relative yields of different parts of the body and carcass has not so far been provided by researchers.

The effect of early (kk, kw) vs. late feathering (K-) genotypes on their effect on the growth performance of chicken has been controversial ever since Warren and Payne (1945) reported a larger weight of birds classified as early feathering (Chambers et al., 1993/1994). The possible effect of the sex-linked K gene genotype needs to be clarified with thoroughly, because this gene series plays the central role in the feathering sexing of the day old chicks.

A series of experiments were carried out to investigate the opportunities to manipulate feather growth by different genetic means, and the consequences of this manipulation in terms of broiler production. The first two experiments looked at the effects of the feathering selection, the naked neck gene, early / late feathering genes and other related factors on broiler growth, carcass traits and the body protein partition among different parts. The third experiment focused on the quantitative relationship between the feathering traits and broiler feed conversion ratio.

Finally, a summary was completed of the result of the divergent feathering selection program from the base population to the eighth generation and to estimate the genetic parameters in different lines and in different combinations of generations with the Derivative Free Restricted Maximum Likelihood (DFREML) program. By this undertaking, the practical implications of the feathering selection in different directions were hoped to be outlined. Similar effort was made by Edriss (1988) in the first two generations with Harvey's maximum likelihood program.

CHAPTER 2

LITERATURE REVIEWS

2.1. FEATHERS AND THEIR DISTRIBUTION IN THE DOMESTIC CHICKENS

Feathers in the adult chicken can be broadly categorised into three types (Deschutter and Leeson, 1986), the contour feathers (flight feathers), down feathers (plumes) and the filoplumes, although more categories are possible (Lucas and Stettenheim, 1972). Structurally, the contour feathers are the most developed type of feathers characterised by a strong and long shaft and interlocking barbules between the adjacent barbs of the vane. The plumes are the most prominent type of feathers in chicken, and are featured by lack of the interlocking barbules with a smaller shaft than the contour feathers. The filoplumes are hairlike feathers with barbs confined to the apex. The contour feathers are mainly for body protection and flight, plumes for insulation, and the filoplumes may have some kind of sensory function. The insulation function of the plumes is far more important in the domestic chicken than the other functions in terms of poultry production.

Feathers are not evenly distributed over the body, and are organised into tracts or pterylae. According to the distribution or the surface area the feathers cover over the body, there are nine pterylae in most of the domestic chicken breeds (Lucas and Stettenheim, 1972), which can be further subdivided into about a hundred tracts. The space of bare skin left between the feather tracts and between the adjacent feathers within a tract are collectively termed as apteria. Normally the apteria carries scattered downs and filoplumes.

The first adult plumage is the result of three cycles of moults, though some of the feathers in certain tracts may have fewer moults to reach their adulthood, as the moult could be incomplete over the whole body surface (Lucas and Stettenheim, 1972).

Although the genetic variability of feather distribution in a normal feathering chicken is unknown, they can certainly be altered by several major genes. For instance, the presence of the naked neck gene can eliminate feathers nearly completely around the neck area and reduce the feather distribution in many of the pterylae over the body.

Apart from the naked neck gene, five others, including the scaleless gene, have been described to reduce the normal feather coverage in different degrees at certain ages of the bird (Somes Jr., 1990). Not only the feather distribution, but also the time of feather emergence or feather growth rate is controlled by different feathering genes.

2.1.1. Genes that Control the Rate of Feathering

2.1.1.1. Major genes

a) The K locus

There are at least four alleles in the sex-linked K locus with the slower or later feathering gene being more dominant over the faster or earlier feathering gene.

Serebrovsky (1922) showed that a single pair of sex-linked genes were responsible for the early and late feathering trait with the late feathering being dominant to the wild-type of early feathering. Later, Warren (1925) confirmed this important discovery, and Hertwig and Rittershaus (1929) proposed the symbol K to designate this gene.

The late feathering chicks, even the heterozygous males, have a significantly shorter tail feathers than the early feathering genotypes at ten days of age (Hays, 1952). The status of the tail feather development at about ten days was used as the main criteria to separate the two phenotypes of feathering by the early researchers (Warren and Payne, 1945; Glazener and Jull, 1946; Godfrey and Farnsworth, 1952). However the industry uses the relative length of the primary (and secondary) feathers to their coverts to sex day-old chicks. The early feathering chicks show a longer primaries than the coverts (Darrow and Warren, 1944).

Apart from the earlier primary, secondary and tail feather development of the early feathering chickens, these birds also show earlier moulting of the above feathers (Warren and Gordon, 1935; Mueller and Moultrie, 1952) and better back score at eight and twelve weeks of age (Hays, 1951).

Detailed study by Siegel et al. (1957 b) revealed that the late feathering gene might be incompletely dominant to the early feathering gene, and the homozygous and heterozygous late feathering male chicks can be separated from each other by sight at hatching with an accuracy of over 80%. However the accuracy was not high enough to

replace the occasional need of progeny test to confirm the genotype of the late feathering males.

The two other alleles of the K locus, K^n and K^s were reported by Somes (1969) and McGibbon (1977), respectively. Birds carrying the K^n gene develop feathers extremely slowly. The K^n gene was shown to be dominant to both the late (K) and early (k) feathering genes (Somes, 1969). Birds with the K^s gene showed a bare-back at 6 weeks of age. The order of dominance was suggested as $K^n > K^s > K > k$ (McGibbon, 1977).

The late feathering gene K has been found to be tightly linked with the *ev21* in the sex chromosome Z (Bacon et al., 1988) and this linkage was suggested to be the major reason for the lower egg production rate and higher mortality in the laying stock produced from the late feathering dams (Harris et al., 1984; Havenstein et al., 1989; O'Sullivan et al., 1991 b). The *ev21* encodes a complete viral particle (Smith and Fadly, 1988), which can provoke susceptibility to avian leucosis virus infection by interfering with the immune response system.

b) The T locus

An autosomal recessive feathering gene, retarded (t^s), was reported by Warren (1933) to reduce the feathering rate in the early feathering birds up to 6 weeks of age but not in the late feathering birds. Another allele at this locus, tardy t, was found to reduce the feathering rate even further than the retarded birds (McGibbon and Halpin, 1946; Jones and Hutt, 1946). The tardy gene, t, is recessive to both the retarded, t^s , and the normal feathering, T.

2.1.1.2. Polygenes that control feather growth

Apart from the major gene effects, feathering rate can also be altered by polygenes. Experiments carried out within populations in which one or the other feathering gene in the K locus has been fixed clearly showed this point.

Siegel (1963 a, 1963 b) measured the percentage of the back covered by feathers at eight weeks of age in two different selection experiments for breast angles and body weight respectively. The same base population with the early feathering gene fixed (Siegel, 1963 a) were involved in both of the selection experiments. The coefficient of variation of the back feathering score was about ten percent in both of the cases. The estimated heritability of the feathering score ranged from 0.01 to 0.53 with an overall average of 0.20, when direct selection was made on breast angles in the first

experiment. It ranged from 0.13 to 0.53, with an overall mean of 0.34, when the direct selection was made on body weight in the second experiment. The results indicated that the time or age of feather emergence and subsequent growth can be manipulated by genetic selection in the early feathering population.

After 4 years of selection within a population with only the late feathering gene, Radi and Warren (1938) established a well feathered and a poor feathered strain, which as broilers differed genetically in the degree of feathering. Although the authors suggested that the difference between the strains might be the result of the modifying factors, it did indicate that the feathering condition can be altered by selection within the slow feathering population.

Edriss (1988) successfully developed a fast and a slow feathering line by selection from the same base population with only the late feathering gene (KK in the males and K/W in the females). Three generations of direct selection produced a large response in feathering rate (Ajang et al., 1993). However, some interaction between the major feathering genes and polygenes might exist as indicated by our previous experiment (Lou et al., 1992). In the early feathering females, the feathering rate difference between the two line origins was not observed.

2.1.1.3. Sexual dimorphism

Sex dimorphism in feathering rate has been observed for a long time: females generally develop their juvenile feathers more quickly than males. However, some of the sex dimorphism in feathering observed by early researchers might be attributed to the sex-linked major gene effect in the K locus. The proportion of females showing early feathering phenotype will be always higher than that of the males as long as the population is segregating both the early and late feathering gene. In the extreme situation, all of the females could show early feathering while all of the males show the late feathering phenotype, if all the sires are early feathering and the dams are late feathering, which is, in fact, the genetic basis to produce feathering-sexable day-old chicks.

Sex dimorphism in feathering rate was reported in both the early and the late feathering populations, with the early feathering gene (k) or the late (K) feathering gene being fixed.

Hays (1952) compared the tail feather length of males and females in the early feathering Rhode Island Red breed (RIR) and White Leghorn (WL)-RIR cross at ten

days of age. In the RIR flock, the males had a mean tail length of 1.60 cm, while females had an average of 1.92 cm. A similar result was found in the hybrid flock: the males had a mean tail length of 1.87 cm and that of the females was 2.08 cm. In both of the flocks the difference between sexes was highly significant.

While undertaking a genetic study for feathering in the early feathering White Plymouth Rocks (WPR), Siegel et al., (1957) observed significant differences between the two sexes in terms of 10-day back score, 10-day breast score, and percentage of back area covered with feathers at 5-, 7-, and 10-weeks of age. In all of the cases, the females were superior to the males in feathering. In later studies, better feathering condition was consistently found at eight weeks of age in terms of the back area covered by feathers (Siegel, 1963 a, b).

In a pure slow feathering commercial stock of Hubbard, McDougald and Keshavarz (1984) found that the females had longer primary, secondary and back feathers, and better back feather scores than the males before 31 days of age. However, the males grow their wing feathers at a faster rate than the females, so that at 31 days of age, the wing feathers were of the same length in the two sexes.

Edriss (1988) also observed sexual dimorphism in feathering in populations carrying only the slow feathering gene. The least- squares means of the feathering measurements in the random-bred control line at 24/25 days of age are shown in the following table for the zero generation (base population), and generations 1 (G1) and 2 (G2).

Feather score or length (mm) of the control line

Gen.	Back Score		Primary		Secondary		Tail	
	male	female	male	female	male	female	male	female
Base	1.80	2.34	76.6	77.8	52.4	61.8	/	/
G1	2.71	4.58	84.0	88.5	61.6	78.7	18.8	30.2
G2	3.11	3.70	79.9	80.6	55.4	65.0	14.7	20.2

In the later generations, a similar sexual dimorphism was consistently found in Edriss' (1988) lines (Priyono, 1991; Ajang et al., 1993). The primary, secondary, tail, back, breast, cape and ventral feathers were longer in the females than in the males up to 30 days of age (Priyono, 1991). Also the tail feathers appeared earlier in the females, at least in the slow feathering line (Priyono, 1991). Sexual dimorphism is more

profound in the slow feathering line than in the fast feathering line (Priyono, 1991; Ajang et al., 1993).

2.1.2. Genes That Control the Distribution of Feathers--the Naked Neck Gene

The peculiar features of birds caused by the naked neck gene was first described by Davenport in (1914). This author also found that this trait is controlled by a single dominant gene. However, later studies showed that the naked neck gene is incompletely dominant because the homozygous birds can be distinguished by sight from the heterozygous according to Crawford (1976) and Scott and Crawford (1977) and further supported by Merat (1986).

Greenwood (1927) reported that the apteria in the naked neck birds are completely devoid of feathers. The head tract is absent except for just around the comb. There are no feathers on the dorsal surface of the neck except those of the anterior spinal tract. The ventral tract is absent except for two small patches on each side above the crop.

The above description suits the heterozygous naked neck bird according to Crawford (1976), because in the homozygous naked neck bird, the tuft of several dozens of feathers above the crop shown in the heterozygous naked necks is absent or reduced to a few units. The areas of other apteria in the naked neck birds are enlarged as well, apart from those around the neck, especially in the homozygous birds. Merat (1986) suggested that it could be used as an additional criterion for the separation of the two kinds of naked neck birds that the extension of apteria on the ventral surface of the thighs and on the breast was larger in the homozygous naked neck birds than in the heterozygous ones.

In 1986, Merat summarised various sets of data of his own and others on the effect of naked neck gene on feathering. The average reduction in feather weight as a percentage of the live body weight was 2.9 in NaNa, and 1.7 in the Nana, or about 30% and 25% respectively in NaNa and Nana in absolute feather weight compared with the nana normal feathering birds.

2.2. EFFECTS OF FEATHERING AND TEMPERATURE ON BROILER GROWTH

2.2.1. Feathering and Broiler Growth

Many reports exist concerning the effect of feathering on body growth of the poultry. Most of the early comparisons were made between early and late feathering birds because, among other things, of the obvious commercial importance in sexing day-old chicks. However in more recent years, the effects of some other feathering genes have also been investigated in the hope of finding the best feathering genotypes for the different poultry production systems.

2.2.1.1 Early feathering (kk and k/w) and late feathering (KK, Kk and K/w)

Warren and Payne (1945) first reported the effect of early or late feathering phenotype on body growth in a New Hampshire (NH) flock subjected to different diets with the early feathering gene segregating at a frequency of about 0.72. The birds were kept in low winter temperature although no figure was given. At twelve weeks of age, both the male and the female early feathering birds were consistently heavier than the late feathering counterparts. An average difference of 6% was observed.

Subsequently, Glazener and Jull (1946) reported that the early feathering groups (of males) tended to be heavier than the late feathering groups. However, in this experiment not only was the number of birds small but the opposite 'tendency' recorded in the females was ignored.

Goodman and Muir (1965) presented a set of data from their breeding program showing that the early feathering birds were not only 'highly significantly' heavier, but also 'highly significantly' more uniform up to the weight of about 1.5 kg. However the way of their data manipulated can be criticised in several aspects. Firstly, the body weight data were recorded as deviations from the average of the sex within hatch, and then 1000 was added to avoid a negative deviation, and then pooled over sexes. Therefore the two important factors, sex and hatch, went missing, and moreover, the reported averages (g) were neither the real averages, nor the deviations from the common mean. Secondly, since the variances of body weight deviations between the two feathering types were highly significantly different from each other, a common variance assumption was violated in the analysis of variance, and this would have affected at least the calculation of the probabilities to check the significance. Thirdly, as the recessive early feathering gene was in a high frequency (1475 early : 407 late),

most of the late feathering birds would have been the males, and the body weight variance could be larger in males than in the females because of the larger weight. Therefore, the conclusion regarding the uniformity is questionable. However by referring to the report by Hurry and Nordskog (1953) and their calculation based on the data of Glazener and Jull (1946), this effect might be true. Nevertheless, one should bear in mind that the late feathering males were not uniform genetically, as they included both the homozygous (KK) and heterozygous (Kk) genotypes in all of the above mentioned reports in this section, and the proportions of the two are dependent on the gene frequency and the mating system.

Many researchers, on the other hand, were not able to find much difference between the early and late feathering birds.

Hays (1951) found no body weight difference between early and late feathering males or females in RIR (selected for fecundity) at 8 or 12 weeks of age. Godfrey and Farnsworth (1952) conducted an experiment with broilers from Silver Oklabars, NH, and Barred Plymouth Rock (BPR), to compare the body weight between early and late feathering birds at ten weeks of age. Although the progeny from relatively comparable matings seemed to favour early feathering in the males, the authors concluded that body weight was not related to feathering and the early or late feathering effect was limited to the feather follicles.

While analysing the genetic relationships between feathering and growth rate in BPR and NH, Hurry and Nordskog (1953) found no difference in weight between early and late feathering birds at 8 week of age, though the late feathering males, but not the females, were significantly more variable than the early feathering counterparts.

Sheridan and McDonald (1963) analysed the effect of feathering on 5- and 10-week body weight of broilers in a selection program. The results showed significant effects for all of the factors considered, i.e. sire, sex, and hatch, except the feathering phenotype. However, these authors tried to put forward a nutrient competition theory between body and feather growth at the early age, based on an 'interesting' but non-significant trend. The late feathering birds tended to be heavier at 5 weeks but lighter at 10 weeks of age than the early feathering ones.

Dunnington and Siegel (1986) assessed the same sex-linked feathering alleles in chicks from three different genetic lines, one selected for high body weight, one for low body weight and the other for high antibody response to sheep erythrocytes, raised to 31 days of age. Although the early feathering k/w females were slightly heavier than

the late feathering females ($P < 0.10$) at 21 and 31 days of age, no body weight difference in males was reported. Later O'Sullivan et al. (1991 a) extended the above assessment to 63 days of age in a more complex experiment, in which no heterozygous Kk slow feathering male was involved. It was reported that the late feathering chicks were heavier than the early feathering ones from hatch to 21 days of age, after which body weight were similar, differences reappeared at 63 days of age, when the early feathering chicks were heavier than the late feathering ones (2606 vs. 2499 g). However no test of statistical significance or other details were provided concerning the body weight comparison.

It can be concluded from the above reports scattered from the forties to early nineties that the sex-linked early feathering gene has either no effect or a small beneficial effect on growth, to the broiler age. The importance of the early feathering gene seems to be a minor feature only in terms of growth itself in most of the circumstances in a modern broiler selection program featured by a large population size and rapid progress in growth performance. Superior broilers could be selected in both early and late feathering stocks. However, if the early feathering gene was associated with uniformity, or the late feathering gene was associated with increased phenotypic variance of body weight, as indicated by Hurry and Nordskog (1953), and Goodman and Muir (1965), the gene frequency of K vs. k+ might have real genetic implications, as it would alter the heritability of body weight. There is no literature so far available to assess this point.

It should be noted however that Lowe and Merkley (1986) observed significant differences in body weight and weight gain among the all three possible feathering genotypes, KK, Kk and kk, in the males, and differences were 'generally in favour of slower feathering genotypes'. A scrutiny of the report revealed that the homozygous KK late feathering males were produced from a slightly different genetic background, at least as indicated by a significantly higher hatch-weight than all of the other groups, although the authors tried to justify the inclusion of this genotype in the analyses. In the report the sex effect was not separated from the genotypic effect. This confounding might have some effect on the probability calculations for the multiple comparisons. Nevertheless the tendency in body weight and weight gain in favour of Kk slow feathering males over kk early feathering males observed in this experiment would not change. The relatively high rearing temperature might have favoured the late feathering males as will be discussed later.

2.2.1.2 Other Feathering Genes on Broiler Growth

2.2.1.2.1. The naked neck gene in normal temperature

Merat (1986) reviewed literature extensively to evaluate the effects of the naked neck gene on the performances of the poultry. For most of the traits recorded, the heterozygous naked neck birds are in between the two homozygous genotypes.

Early observations made on the 'light type' birds with the naked neck gene in the 'normal' post-brooding temperature demonstrated a reduced body weight at 8- or 10-weeks of age compared with the normal feathering birds. Bordas et al. (1978) reported a 4.1% and 5.1% reduction in 10-week body weight of the heterozygous and homozygous naked neck birds, respectively, compared with the normal feathering ones. Merat (1979) recorded the average body weight of 789g for the heterozygous naked neck males at 8 weeks of age compared with an average of 803g for the normal feathering males at the same age when reared at 15-20°C. Although the genotypic effect was non-significant, Hammade et al. (1987) provided data to show a small reduction in body weight of the naked neck males at 8 weeks of age reared at 18°C. The respective body weights were 1562g (nana), 1548g (Nana), and 1534g (NaNa).

The juvenile body weight traits are more relevant in heavy birds for broiler production, and the conclusions concerned with the naked neck gene effect reached in the light birds might not necessarily be applicable to the heavy broilers.

Hanzl and Somes (1983) evaluated the naked neck gene effect on broiler growth performance at 8-weeks of age. The authors incorporated this gene into a WPR broiler strain by four generations of repeated backcrossing before the heterozygous naked neck parents were used to produce the three genotypes of broilers for the evaluation in two temperatures. In the cool room at 21°C, the 8-week body weight of the heterozygous males was comparable to the normal feathering males, but the rest of the naked neck birds (Nana females, NaNa males and females) were all considerably below the 'normal' standards. The differences were between 7.3 and 15.8%.

El-Attar and Merat (1985) mated the normal feathering Cornish males with the heterozygous naked neck females to produce Nana and nana progeny in assessing the effect of this gene on body growth. Temperature was not well controlled in the experiment, but averaged at about 20°C (Merat, 1986). The two genotypes were very close to each other for their eight-week body weight within hatch and sex. Over the

two hatches, 8-week body weights for males were 2025g (Nana) and 1966g (nana), and for the females were 1678g (Nana) and 1692g (nana), respectively.

However, in a recently published report, Eberhart and Washburn (1993 a) found that the body weight of the F2 generation naked neck birds (sexes combined) in both of the small body weight population and heavy broiler population were significantly higher than the normal feathered counterparts at 21°C. Cahaner et al. (1993) recently also reported that the naked neck birds which had high growth potential grew significantly better than their normally feathering counterparts at 23 °C.

From the above conflicting results, it is difficult to draw a general conclusion on the effect of the naked neck gene at a normal temperature condition. However it seems to be reasonable to say that in the broiler type males, no inferior effect of heterozygous naked neck gene on body weight can be detected at about 20°C. However heterozygous naked neck females and the homozygous naked neck birds of either sex should be treated with caution for commercial uses.

2.2.1.2.2 Feather score and body weight

Feathering score is usually judged for the degree of the feather covering condition at a certain age. Different researchers used several different scoring systems to suit different purposes and to avoid subjectivity to the best knowledge of the researchers. The back region of the birds was most often used site for scoring presumably for its importance and also to certain degree for the convenience of operation in the live bird.

Martin (1929) measured the feathering condition in one, two and three month old BPR with a four grade system. It was found that better feathering at three months of age was closely related to higher body growth in the males, and in the females very poor feathering was related to poor body growth.

Jaap and Morris (1937), with their 3-grade feather-scoring system, found a significant correlation coefficient of 0.33 between 8-week feather score and body weight within group (breed or cross) and sex, indicating a positive relationship between feathering and body growth.

Hays (1951) however, could only find a linear relationship between the four-grade feathering score at eight weeks of age and weight at eight or twelve weeks in the female RIR. In the males, there was no significant correlation between degree of

feathering and body weight at 8 weeks of age, and the 12-week body weight was only slightly related with the 8-week score.

Hurry and Nordskog (1953) reported a phenotypic correlation of 0.45 in the BPR and 0.33 in NH between their nine-grade feathering score and body weight at 8 weeks of age. The genetic correlation based on full-sib analysis was 0.24 and 0.78 respectively. These authors therefore concluded that any selection for improved growth rate would automatically bring about some improvement in feathering, and vice versa.

Siegel (1963 b) used the percentage of the back covered by feathers as a measure of feathering condition at eight weeks in two lines of WPR, divergently selected for or against 8-week body weight. The genetic correlations between body weight and feathering estimated from the first three generations were all positive, from 0.08 to 0.30 for the females, and from 0.11 to 0.23 for the males. However, the genetic correlation calculated in the fourth generation was essentially zero for both the males and females. Because the heritability estimation for both body weight (Siegel, 1962) and feathering (Siegel, 1963 b) did not show such a decline, it seems that the correlated response in back feathering, while selection is being made on body weight only, might be a short term phenomenon. Were improvement in back feathering required, therefore, due attention would have to be paid to this trait. It is especially so when the improved body weight to age resulted in earlier slaughter.

Edriss (1988) undertook a divergent selection program on broiler feathering in the genetic background of slow feathering KK (males) and K/w (females). The six-grade feather score at 24/25 days of age was found to have a genetic correlation of 0.45 with body weight at the same age. This author also argued that the tail feather length measurement was a better alternative to back feather scoring for its simplicity, objectiveness, and efficiency. The tail feather length measurement was also found to have a positively genetic correlation with body weight of 0.605 in the second generation of selection.

In conclusion, feather growth is positively correlated with body growth at juvenile ages. Selection for body growth is expected to bring about improvement in feathering to age, or vice versa. However, it is not clear if the genetic correlation is sustainable for a population subjected to selection of only one of the two traits. Furthermore, it is not clear what amount of selection pressure has to be diverted to feathering selection to keep the feathering condition unchanged to a specific market weight while continuous improvement is being made in weight to age.

2.2.2 Temperature, Feathering and Body Weight

The effect of temperature on broiler performance, including growth is well documented (Howlider and Rose, 1987) in the literature, and is generally in good agreement. However the combined effect of different temperatures and different feather coverage on broiler performance has received less attention by researchers and consequently is rather poorly understood.

2.2.2.1 Temperature and K-k genotype on growth

While seeking the possible reasons for the observed better growth rate in the early feathering birds than in the late feathering counterparts, Warren and Payne (1945) suggested that the low winter temperature might have favoured a well covered body at an early age. This suggestion is reasonable from the common sense. It however implies an important possible interaction between feathering genotype and ambient temperature. Although the above suggestion was made almost half a century ago, direct evidence to support or oppose this hypothesis is scarce in literature. However it may serve as indirect evidence that a relatively high temperature was applied within the specific period in both of the experiments reviewed in section 2.2.1.1. in which the slow feathering birds had a higher body weight (Lowe and Merkley, 1986; O'Sullivan et al., 1991 a). Lowe and Merkley (1986) kept the room temperature at 35°C in the first week, and then reduced at the rate of 2.8°C each week to a minimum of 24°C. O'Sullivan et al. (1991 a) also maintained the ambient temperature at 35±1°C during the first 7 days and gradually reduced it to 20°C by 35 days of age. The late feathering chicks were heavier than the early feathering ones from hatch to 21 days of age only in the experiment of O'Sullivan et al. (1991 a). However, Dunnington and Siegel (1986) were not able to find any significant interaction between temperature regime and the K genotype towards the end of the experiment (27 days) in terms of body weight, either in males or in females, kept in two temperatures.

It can be concluded that the interaction between the practical temperature regime and K genotype, if any, is small, and is not easily detected. Therefore the practical importance of this possible interaction is rather limited.

2.2.2.2 Temperature and Na/na allele on growth

The stimulus for the study of naked neck gene effect on the poultry production in high temperature comes from the report by Smith and Lee (1977) who observed a higher fertility for the naked neck males than the normal feathering males (87.8 vs.

79.7%) and greater survival rate of the naked neck chicks under heat stress. Both of the results have important practical implications.

As reviewed in the previous section, the growth performance of the naked neck birds in the normal temperature of 20°C could be either slightly inferior to or comparable with the normal feathering birds. However in a high temperature (30°C or over), birds carrying one or two naked neck genes grow substantially better, especially in the heavy broilers (Eberhart and Washburn, 1993b) mainly due to the ease of heat dissipation (Merat, 1986; Cahaner et al., 1992, 1993) and less nutrient required for feather growth.

Bordas et al. (1978) individually caged male chicks from 2 to 10 weeks at 31°C. Higher body weights were reported for the naked neck birds at 10 weeks of age: 1014g for NaNa, 988g for Nana, and 888 g for nana.

Monnet et al. (1979) raised female chicks in both 20 and 31°C, and males in 31°C. Significantly higher body weights were observed at 8 and 10 weeks in the females in 31°C, which caused a significant genotype × temperature interaction. In the males, a significant genotype effect was found for 10-week body weight: 1070g for nana, 1174g for Nana, 1192g for NaNa.

Hanzl and Somes (1983) caged chicks in 38°C in one room and 21°C in the other. Higher 8-week body weights for the NaNa males, and especially for the females were recorded, which together with a lower body weight for the naked neck birds in 21°C, resulted in a highly significant genotype × temperature interaction. Unfortunately, the Nana chick, which was suggested by Merat (1986) as the more likely candidate for use in commercial production, did not show a higher body weight than the normal feathering birds at 38°C in this particular experiment.

Cahaner et al. (1992) compared naked neck chicks with normally feathered ones under standard Israeli commercial management conditions. Chicks were produced from three different ways of cross mating, and the comparison was made five times in different seasons. The overall result showed that the heterozygous naked neck birds had a higher 7-week body weight than the normal feathering sibs by about 3%. Another experiment was carried out in controlled chambers under a high temperature of 30-32°C (Cahaner et al., 1992). Sibs with one naked neck gene reached 1924g at 8 weeks of age, which was 8.23% heavier ($P < 0.001$) than the normal feathering sibs. Later, these same authors (Cahaner et al., 1993) reported again that the homozygous naked neck birds (2018g) was significantly heavier than the heterozygous ones (1835g),

which in turn was significantly heavier than the normally feathered birds (1723g) kept in a constant high temperature of 32°C to eight weeks of age.

Eberhart and Washburn (1993 a) reported that under chronic heat stress of 32°C, the naked neck birds from both the light and heavy populations grew significantly better to 4-, 6-, and 8-weeks of age than the normal feathered ones. The pooled 8-wk body weight over two experiments were 748g (Na-), and 654g (nana) in the small weight population, and 1195g (Na-) and 1099g (nana) in the broiler population.

To conclude with this section, the naked neck birds are superior in growth to the normally feathered birds under high temperature conditions. However the degree of realisation of the benefit of being naked neck depends on the actual environmental condition (temperature), and also likely to certain degree, on the genetic background of the stock. Obviously, more research work is required in both of these aspects to fully realise the benefit of this gene at high temperatures and to avoid potential detrimental effect on growth and efficiency in the normal or moderate temperatures.

2.2.2.3. Temperature and feathering polygenes on body growth

Very few experiments have so far been conducted to study the effects of feathering polygenes in different temperatures or in a high temperature on body growth.

After two rounds of divergent feathering selection, Edriss (1988) compared the growth performance of the fast and slow feathering lines at 49 days of age in 30 and 20°C. Body weight was depressed by high temperature to a similar degree in both of the lines. However the males were more sensitive to high temperature than the females (-26.4% in males vs. -17.9% in females). Later these two lines were compared again under the same two temperatures, together with the effect of the naked neck gene (Lou et al., 1991, and for more details see Quoi, 1991). The fast feathering males always had higher body weight at 40 days of age both with or without carrying the naked neck gene under both temperatures. Surprisingly, body weight depression by high temperature was slightly higher in the slow feathering males, especially in the group with the least feather covering (slow feathering males with the naked neck gene).

It seems that there might be an optimum level of feather covering even for birds in high temperatures, in other words, it might not be the case that the less feather covering, the better the growth will be in high temperatures. In support of this hypothesis is that high temperature favours the better feathered sex, the females, in terms of growth performance (Edriss, 1988; Cahaner and Leenstra, 1992). However,

much more research work needs to be done before the optimum levels of feathering, if they do exist, to suit the different temperatures can be defined.

2.3. GENETICS OF FEED EFFICIENCY

Feed efficiency, the ratio of body weight (gain) to feed consumption, or feed conversion ratio (FCR), the ratio of feed consumption to body weight (gain), is a trait that cannot be measured directly. Because it is a ratio between two traits, any factor that can affect body weight and feed consumption either separately or in different proportions will influence the ratio, e.g. temperature, feed energy and protein levels. For a genetic study, fluctuations in environment or nutrition should be avoided or controlled to the minimum, except in the controlled study of the interactions between genetics and such factors.

In the literature, there has been some debate about the optimum way to measure and express the efficiency trait. One consideration is that the feed efficiency and FCR may have different genetic parameters apart from the opposite signs for correlations with other traits (Robinson and Berruecos, 1973). The second is that neither feed efficiency, nor FCR reflects the true biological efficiency of the animal, because of the inclusion of feed cost for non-productive purposes (mainly for maintenance). The third is the choice of a proper reference scale for body weight and feed consumption measurements. There are three possible alternatives available, i.e. age-constant, body weight-constant, and feed allowance-constant measurements. Each of these has its own pros and cons. However the age-constant measurement is the most commonly used and most easily obtained.

For the first consideration, Robinson and Berruecos (1973) tended to advocate the use of FCR for its higher heritability and lower coefficient of variation than feed efficiency based on their swine data. In poultry, both FCR and feed efficiency are in use, though the former is more prevalent. The second consideration lead to the introduction of the residual feed consumption concept in layers by Nordskog et al. (1972), and its wide application in layer selection programs (Arboleda et al., 1976; Wing and Nordskog, 1982). The theory behind it is to find a measure for efficiency more or less independent of the maintenance requirement and level of production, e.g. independent of body weight and egg mass. However, adjustment for maintenance in feed efficiency has rarely been undertaken in broilers, probably for the difficulties in estimating the maintenance requirement accurately for the fast growing bird.

Up to now the most commonly used reference scale for FCR measurement is the time scale, that is the age constant measurement. However the industry practice is to sell the broiler birds according to the market weight, but not to a specific age. Theoretically, the age constant measurement of feed efficiency might impose a penalty to the faster growing bird for its higher maintenance requirement. Therefore the suitability to measure FCR on the age constant basis has been challenged in recent years, and the body-weight constant measurement has been attempted by Pym and Nicholls (1979), Sorenson (1984), and Chambers and Lin (1988). However, in following this practice, body weight needs to be monitored continuously, for body weight could not be 'pre-set' like age, and even a day-to-day handling for both body weight and feed consumption is practised, body weight still needs to be adjusted to constant by mathematical means. It is always somewhat questionable to use an unstable reference scale for any kind of measurement, in the present case, the FCR. One alternative is to use the total feed allowance as the reference, for it is closer to the industry practice, and yet easier to control. Although the feed scale is rarely used by animal scientists, it is commonly used by agro-economists to demonstrate the diminishing return law, and to establish the response functions (Heady and Bhide, 1984).

The following discussion concerns mainly results of feed efficiency or FCR on the basis of the age-constant measurements, except otherwise indicated.

2.3.1 Genetic Variability of FCR

Differences in FCR between strains and crosses were noticed as early as in the 1940's by Hess et al. (1941). However a systematic selection procedure to reveal the genetic variability and possibly to exploit it within a population was not applied until the late 1960's, mainly because of the hope that selection for increased body weight would automatically improve the feed efficiency for savings made on maintenance requirement. The predicted amount of feed saving from reducing one day to reach the same target broiler weight has been recently given by Pasternak and Shalev (1983). The commercial breeders have already succeeded a great deal in taking advantage of this relationship between growth rate and feed efficiency. Therefore what the breeders might be most interested in is the variability of FCR independent of body weight.

Wilson (1969) selected birds for increased body weight gain or feed efficiency between 5 and 10 weeks, together with a randombred control line. After one round of selection, it was found that the additive genetic variation in feed efficiency was approximately 40% of the genotypic variation (or $h^2 = 0.40$), and direct selection for

weight gain was about three times as efficient in increasing the average daily gain as the correlated response to selection for feed efficiency. Conversely, selection for gain would be only 75% as efficient as direct selection in reducing FCR. It was also indicated from this short experiment that selection for gain would rapidly increase feed consumption, while selection for efficiency would not.

Guill and Washburn (1974) reported the results of FCR selection experiments in two different populations of chickens. Selection was carried out for three generations in a broiler line which had been selected previously for growth rate, and for one generation only in a randombred population. Apart from the respective control sublines, four sublines in each of the two populations were selected for high or low FCR with body weight either unrestricted or held constant. Although the estimated heritability was lower in the broiler line than in the randombred line (0.25 vs. 0.42), it is significant to note that the restriction in body weight did not hinder the progress in reducing FCR by selection in both of the populations. It is clear that not only the FCR has a moderate heritability, but it also has a substantial amount of variation independent of body growth.

Existence of variation in FCR independent of body weight also allowed Pym and Nicholls (1979) and Pym (1983) to gain consistent progress in reducing FCR by selection in the FCR selected line without bringing about any further change in feed intake between 5 and 10 weeks of age over five (Pym and Nicholls, 1979) and twelve (Pym, 1983) generations. The realised heritability up to the tenth generation in this selection line was 0.26 (Pym, 1983).

After undertaking four generations of selection for increased 40-day live weight or reduced 18- to 40-day FCR on either a normal diet or low protein diet, Sorenson (1984) compared feed efficiency on both a fixed age and a fixed weight bases. FCR differences were substantially less with the weight-constant comparison than the age-constant comparison. Nevertheless, the FCR selected line was still significantly more efficient than the weight selected line on the weight constant basis. A similar result was also reported by Pym (1983) when comparisons were made between the weight selected line and the FCR selected line on both constant weight and constant age bases.

Leenstra and Pit (1987) compared the performance of two lines of chickens selected for four generations for either high 42-day body weight (after *ad libitum* feeding, GL line in the report), or low 21- to 42-day FCR, among other lines. The weight selected line had 228g higher 42-day body weight and 0.18 higher FCR than the FCR selected line.

In summary, the age-constant measure of FCR might not be the ideal way to express the efficiency trait. However, there is a large enough genetic variation of this trait even when the population has a history of intensive selection for body weight, and therefore substantial improvement can be made by selection. This age-constant FCR is only partially dependent on body weight, and improvement in age-constant FCR will usually result in improvement in weight-constant FCR, though the correlated response may be smaller than the direct response.

2.3.2. Component Traits of Feed Efficiency

Like most of other quantitative traits, it is difficult to decompose the variability in feed efficiency quantitatively into specific physiological and biological processes for a particular population. However, most of the possible component traits (direct and indirect) for feed efficiency have been described qualitatively in literature. Most of the following factors have been suggested to contribute the variability in feed efficiency (Pym, 1990): 1) behaviour factors; 2) maintenance requirement; 3) growth potential and feed consumption ability; 4) ability in feed digestion and energy metabolism; 5) genetic control over important biochemical processes in metabolism; 6) sensitivity to stress and disease infections.

Among the factors, only the contributions of behaviour and maintenance difference among birds to the variation in FCR will be reviewed in details in the present context.

2.3.2.1. Effect of behaviour on feed efficiency

There are at least two possible ways behaviour contributes to the variability in feed efficiency among birds. The first is the feeding behaviours influencing the amount of feed loss by spillage. The second is the behaviour which affects the non-productive energy requirement of the bird.

Substantial feed wastage in layers has been reported even for birds kept in modern cage systems combined with a low level of feed in the trough (Tauson, 1979). Heil and Hartmann (1980) estimated a heritability of 0.13 for feed wastage. The genetic basis for this kind of feeding behaviour in broilers was also indicated by Siegel et al. (1984). Because reasonably effective management procedures to prevent feed wastage are available, it is generally agreed that the contribution of the feeding behaviour to the feed efficiency in a well managed flock is unimportant in broilers. Since feed wastage measurement is very laborious and its accuracy is sometimes doubtful, any report on direct selection against it has not been found.

Behaviour affects the non-productive energy requirement of activity and of maintenance by clustering in colony raised chicks.

Van Kampen (1976) reported that heat production was 25% higher in a hen during the first 30 minutes of standing, and 37% higher in an eating hen than a sitting one. It was also reported (Anonymous, 1982, ARC Poultry Research Centre) about 25% of between-bird variation in metabolic rate of broiler strains was due to differences in activity. Boa-Amponsem, Dunnington and Siegel (1991) compared the feeding behaviour between males from two broiler lines differing in growth potential. Males from the faster growing line were observed to eat and drink more often to support their growth, but to stand and rest less often, than the slower growing males. Barbato et al. (1980) studied the so called non-consuming feeding behaviour in two divergently selected lines for body weight, and found that it occupied only 297 minutes for the high weight line, but 450 minutes for the low weight line within a 24 h period.

Wathes and Clark (1981) reported that the flock raised chicks spent about 2/3 of their time in a cluster, and the sensible heat loss of those in the cluster was only between 30 and 60% of those individuals not in the cluster. Although there is no evidence to support that clustering behaviour has a genetic basis, the practice to measure feed consumption and feed efficiency in the individually caged birds for selection purposes might bring about serious genetic \times environment interactions because of the prohibition of the clustering behaviour (having an equivalent effect of lowering temperature). Selection for individual feed efficiency would over-emphasise the importance of feather insulation. Existing evidence points out that this is highly possible. Pym (1983) reported that after 12 generations of selection, birds in both the low FCR- and high weight-selected lines were exclusively homozygous for early feathering (kk and k/W), while the high feed consumption-selected line had become homozygous for extremely slow feathering (K^n was suggested). Both the early and late feathering genes were segregating in the randombred control line. To overcome the possible bias for caging, the room temperature needs to be raised to compensate the extra sensible heat loss for the individual birds compared with the flock raised chicks.

2.3.2.2 Feathering effect on feed efficiency

Apart from protecting the bird from injuries, the main function of feathers in broilers is to give insulation to the bird, thereby reducing the maintenance energy requirement. The degree of insulation to prevent heat loss from the body is a function of the amount of feather covering over the body (Wathes and Clark, 1981). The direct

effect of feathering on feed efficiency therefore will be dependent on the balance between the cost of feather growth and the savings (mainly energy) from its protection and insulation functions.

Presumably, the nutrient cost for feather synthesis does not change with age. Thus the amount of net energy saving or loss for feathering is only dependent on the amount of saving. If we take the duration from when a feather starts to have the insulation function to the end of life of the feather or the bird (slaughtered) as the *effective life span of the feather*, then the amount of saving is mainly a function the effective life span and the environment temperature. It is obvious that more energy can be saved in a cold environment than in a warm one. Earlier feathering in broilers usually makes the effective life longer; later slaughter or cessation of the experiment also makes the life longer for those feathers which are still alive at the point of slaughtering, but not for those which have already been shed. These two factors considered together can explain most of the discrepancies in results concerning the effect of feathering on body growth reviewed above.

There is insufficient data available to allow detailed calculations on the nutrient and energy balances for feather growth between costs and savings. However the following guideline can be provided from the energy balance data provided by Prijono (1991), and by assuming 1) the juvenile feather contains 50% of dry matter (Cahaner et al., 1987 and our own unpublished data obtained by difference); 2) dry feather contains 24.0 MJ/kg gross energy (MAFF, 1990) with an estimated energy deposition efficiency of 60%, then the energy cost for feather synthesis could be recovered by insulation saving within about 5 days in 20-22°C (see details in Appendix 2.1). However, there is no such simple guideline that can be provided concerning the effect of feathering on the feed efficiency, for the latter is not a simple direct function of energy balance. Therefore, the effects of different feathering genes on FCR still need to be evaluated empirically even without pleiotropic effect of the feathering gene (e.g. direct effect of feathering gene on the body weight.).

2.3.2.2.1. Major genes

a). Early vs. late feathering

Most of the early reports were only focused on the effect of the feathering genotype on body weight. The effect of K genotype on the feed efficiency was rarely recorded.

Lowe and Merkley (1986) assessed the effect of rate of feathering on broiler feed conversion ratio. In the males, FCR to 28 days of age was only slightly but non-significantly better in the slower feathering groups. FCR in the later period (28-52 days) and the cumulative FCR to 52 days of age were essentially the same for all of the comparable feathering genotypes (males were better in FCR than the females). Therefore the statement in the summary that 'means among the male genotypic groups differed significantly ($P < 0.05$) for feed conversion' and 'differences were generally in favour of the slower feathering genotypes' seems to be misleading as far as FCR is concerned.

O'Sullivan et al. (1991 a) also recorded feed efficiency for the early (kk, k/-) and late (KK, K/-) feathering broilers (sexes mixed) up to 62 days of age. Feed efficiency was slightly higher (better) in the early feathering birds than the late feathering ones. The respective feed efficiency values were 0.64 vs. 0.61, 0.60 vs. 0.57, and 0.52 vs. 0.49 to the age of 28, 41, and 62 days. Unfortunately, no statistical analysis for feed efficiency was conducted as the genotypic effect was confounded with pen effect in the experiment.

To summarise, the effect of rate of feathering on FCR seems to be not large. However, more work still needs to be done before a conclusion can be reached.

b). The naked neck gene

As with the body weight, the effect of the naked neck gene on FCR is also largely dependent on the environment temperature. Generally, birds with the naked neck gene tend to have a reduced feed efficiency or increased FCR at a temperature of 20°C or below, but tend to have a higher feed efficiency at a temperature of 30°C or higher.

An inferior feed efficiency of the naked neck birds was reported by Monnet et al. (1979) and Hanzl and Somes Jr. (1983) at a temperature of 21°C or below. However similar FCR values were recorded by Zein-El-Dein et al. (1984) at 24°C, Eberhart and Washburn (1993 a) at 21°C for both the light body weight and broiler populations, and Cahaner et al. (1993) at 23°C.

A better or similar feed efficiency was consistently found in the naked neck birds compared with the normally feathered birds at higher (29°C or over) temperatures (Bordas et al., 1978; Monnet et al., 1979; Hanzl and Somes Jr., 1983; Cahaner et al., 1992, 1993 and Eberhart and Washburn, 1993 a).

Only a few studies so far have addressed the interaction between the genotypes and temperatures for FCR. Hanzl and Simes Jr. (1983) found that the interaction between the three genotypes (NaNa, Nana, and nana) and the two temperatures (21 and 38C) in their experiment was non-significant. The naked neck birds seems to be more sensitive to the change in temperature than the normal feathering birds, however a consistent significant interaction was not found by Quoi (1991) for FCR who assessed both of the naked neck birds (Nana) and the normal feathering birds in the post-brooding temperature of 20 and 30°C. Significant interactions were found in both the broiler strain and the light Athens-Canadian randombred stock in a recently published study by Eberhart and Washburn (1993 a). The nature of the interaction in the broiler population seemed to be slightly different from the light type birds. In the broiler population, the normal feathering birds had a higher FCR in the constant high temperature of 32°C than in the normal temperature of 21°C, while the naked neck birds from the same parents had the same FCR in the two temperatures. In the light Athens-Canadian chicks, a lower FCR at high temperature than at the low temperature was found in both naked neck and normal feathering birds. The difference between the two temperatures was, however, much larger in the naked neck birds than in the normal feathering counterparts.

2.3.2.2.2. Effect of feathering selection

Direct selection for fast or slow feathering in the genetic background of late feathering gene K (Edriss, 1988) has resulted in changes in body weight, carcass traits and possibly FCR (Ajang et al., 1993). The overall FCR to 48 days of age across the high, medium and low protein diets was essentially the same for both of the lines. However the week by week data seems to favour the slow feathering up to four weeks of age (under the brooding conditions). Thereafter the early feathering line had lower FCR at least numerically. The former might have reflected the difference between the lines in the cost of feather growth, and the latter might have reflected the extra energy saving achieved by better insulation. In this regard, if the experiment had proceeded for a longer period of time, more saving could have been made by the fast feathering line compared with the slow feathering line.

The very small difference in FCR between the above two lines indicates that the contribution of the feathering genes to the variation of FCR might not be very large. This is indirectly supported by the fact that consistent gains in feed efficiency are still possible after the FCR selected line had been fixed or nearly fixed in the K locus by the early feathering gene k (Pym, 1983).

As reviewed in section 2.2.1.2.2, a few reports pointed out that the feathering condition was positively associated with body weight. However, the association between feathering polygenes and FCR has not been extensively studied.

2.3.2.2.3. Feathering response on FCR selection

Selection for feed efficiency has resulted in different correlated responses in feathering under different environment conditions.

Pym (1983) reported that twelve generations of selection for low FCR between 5 and 9 weeks of age resulted in the fixation of the early feathering gene k^+ indicating that this gene might have contributed to the better feed efficiency in this line under the normal temperature. On the other hand, Cahaner et al. (1987) found that in the efficiency selected commercial broiler sire line, the amount of feather covering was significantly less than the other commercial line in their experiment. If the temperature condition under which the selection program was carried out was similar to that of the reported experiment, the more efficient line might have been selected in a hot environment, and therefore effectively favoured the less feathered birds.

It can be summarised that variation in feathering condition contributed to the variation of feed efficiency. But the magnitude and even the direction of this contribution is dependent on environment temperature, and also on the average effective life span of the feathers, or the period and duration of FCR measurement.

2.4. BROILER CARCASS, MEAT YIELD, AND CHEMICAL COMPOSITION

Different standards are being used to evaluate the value of the broiler or meat products in different levels of processing and retailing, and different forms of consumption (Chambers, 1990).

The commercial value of a broiler carcass is first accessed by carcass yield, the percentage weight of carcass of the (starved) live body weight. However a few different definitions of carcass exist. The plucked-bled carcass, often called New York Dressed (NYD), is the carcass after killing, bleeding and defeathering; the eviscerated carcass or empty carcass is the carcass after all of the viscera, including the head, neck, and claws with parts of shanks, but excluding the kidneys and a part of the neck skin,

are removed; and the oven-ready carcass is usually the eviscerated carcass together with the neck, heart, liver and gizzard with or without the lungs. If the carcass is going to be further processed, its value will be determined either by the yields of the specific parts/cuts with different values, e.g. breast, back, wings, thighs, drumsticks, giblets, or by the yield of specific tissues from different parts, muscle, skin, fat and bone. The yields of portions or the dissected tissues from them are usually expressed in g (weight) or g/kg of carcass weight, or live weight.

One of the recent industry concerns of the carcass traits, though not listed above, has been the excessive yield of abdominal fat for its detrimental effect on both the broiler production efficiency and carcass quality (Leenstra, 1986).

The nutritive value of poultry meat is however mainly determined by the chemical composition of the carcass, usually by proximate analysis in terms of moisture, protein, lipid and ash contents, because it is generally believed that the quality of protein from poultry meat is stable.

2.4.1. Factors Influencing Carcass and Meat Yields

The following factors will be discussed in turn for their effects on the carcass and meat yields: breed/strain; age and sex; nutrition; feathering; and the interactions among the above factors.

2.4.1.1. Breed and strain differences in carcass and meat yields

Differences in carcass and meat yields between breeds or strains have long been noticed. Superior carcass, breast meat and the total edible meat yields were reported in Cornish strains by Hathaway et al. (1953) and confirmed by Orr (1955). Better eviscerated carcass yield was reported in the WPR or their crosses in a study with large number of different pure-breds and crosses without Cornish (Jaap et al., 1950). However some of the differences observed by the early researchers might have partially contributed to the differences in body weight. Comparisons were often made among breeds and their crosses with large differences in growth potentials to the same age. But many of the carcass traits are positively related with body weight and age (Jaap et al., 1950; Bouwkamp et al., 1973). Commercial broiler stocks are often subjected to detailed study of carcass traits. Most of the studies revealed differences among strains or combination of strains in terms of yields of portion or/and meat (Bouwkamp et al., 1973; Merkley et al., 1980; Orr et al., 1984; Wabeck et al., 1984; Acar et al., 1991; Renden et al., 1992). These differences among the commercial

broiler strains probably reflect the differences in line development and improvement history (Chambers, 1990) and also indicate that substantial genetic variation exists in carcass traits. The two most variable, which yet may be the most important carcass traits as well, are the relative abdominal fat yield and breast meat yield. The existence of large variations in abdominal fat yield has stimulated intensive studies to reduce its deposition. Contrarily, little published work has been found concerning the potential of increasing the breast meat yield by selection, and the genetic consequences of the selection.

2.4.1.2. Effect of body weight, age and sex

The growth of a component part of the body relative to the whole can be described by the allometric function in the form of $Y=aX^b$, where Y is the weight of the component part, X is the whole weight, i.e. the body weight or the whole carcass weight. Theoretically, a is the proportional weight of the component when the whole weight is of one unit; b, the allometric growth coefficient, is the measure of the growth rate of the component relative to the whole. When b is greater than unity, the component part is growing faster than the whole, which usually means an increasing proportional yield with age for the part concerned. When b is smaller than unity, then the component part is growing slower than the whole, and the part will lose its relative yield as the whole grows.

As a general rule, Prescott (1985) reported that the nutritionally demanding parts of broiler males (e.g. leg muscle, breast muscle, feathers and fat) up to the adult age had their allometric growth coefficients greater than 1, while the supplying organs (heart, liver, and alimentary tract) had coefficients smaller than 1. The allometric growth coefficient of eviscerated carcass was also greater than 1. This agreed with the observation of Jaap et al. (1950) that larger cockerels had higher dressed and eviscerated yields. The effect of age on the carcass traits can be looked as another form of body weight effect because broilers grow on a time scale. Therefore if the allometric coefficient of a component is greater than unity, the relative yield of the component will increase to the older age, otherwise it will decrease.

The allometric growth feature of the body components tends to interfere with the accurate evaluation for the yields of carcass, portions and the dissected tissue of the portion to a particular age when the breed, strain or even individuals have different growth rates, as suggested by Bouwkamp et al. (1973). Therefore comparisons of carcass traits between different stocks should be ideally made at a common market weight. While comparisons among individuals within a population at a strict common

weight is usually not practical, an adjustment for body weight difference should be attempted just as in the case of feed efficiency comparison as proposed by Chambers and Lin (1988).

While so many of the experiments concerned with the carcass traits were carried out in the male broilers only, the effect of sex should not be overlooked. Existing data suggest that the females might have different allometric growth patterns from the males for many of the body components. Female broiler chickens are usually smaller than their male counterparts. They tend to have a higher proportional yield of breast (meat) (Hayse and Marion, 1973; Bouwkamp et al., 1973; Seemann, 1981; Broadbent et al., 1981; Tawfik et al., 1989), but lower yields of thighs and drumsticks (Hayse and Marion, 1973; Bouwkamp et al., 1973; Broadbent et al., 1981; Tawfik et al., 1989). The female broilers also tend to have higher yield of the abdominal fat (Leenstra, 1986).

2.4.1.3. Nutritional factors

A high capacity of an animal to store the surplus energy in the body as fat when food supply is abundant was essential for it to survive in the evolution history. Fat deposition in animals, including the broiler chicken, responds readily to the quality and quantity of food supply. When unlimited food is supplied, such as the situation in broiler production, the major determinants for fat deposition or fatness of an animal are the supply of nutrients per unit of energy (Fisher, 1984), or the energy level and especially the ratio between feed energy and feed protein, or the ratio between energy and the limiting nutrient in the diet (Fisher, 1984). Both high energy and a high ratio, separately, or together, tend to result in more fat deposition. Broilers respond to other factors as well in terms of fat deposition, such as crude fibre and fat contents in the diet, the form of feed supplied, and interactions among nutritional factors (Leenstra, 1986).

Apart from the relatively easy response in body fat and body weight itself, nutritional effects on carcass traits seem to be not large, and many of the alterations in carcass traits by nutritional factors may actually be the 'side effect' or the consequences of an increase or a decrease in proportional fat yield.

Salmon (1983) was not able to find a clear response of carcass traits to the starter diets when the protein content ranged from 205 to 242 g/kg. The total meat seemed to respond to the increasing protein content in the finisher. Actually only the breast meat yield increased from 193 to 207 g/kg eviscerated carcass when the finisher protein was

raised from 166 to 227 g/kg. A similar response of the breast meat yield to the diet protein was observed previously (Salmon et al., 1981).

A reduced breast yield was reported by Summers et al. (1988) due to a low diet protein level or improper amino acid balance. However, Leeson et al. (1988) was only able to find a significant response in breast meat yield to very high diet protein content (28, 24, and 22 % in the starter, grower and finisher respectively) in the males. No significant response to the large difference of protein content was detected in the females.

A few experiments have been conducted to study the response of carcass traits, especially breast (meat) yield to the dietary amino acid contents. Moran Jr and Bilgili (1990) reported that the relative weight of the breast cut in both sexes responded positively to the supplemental lysine in the base finisher diet (28-42 days, containing 0.85% lysine). A non-linear response in breast meat to a high level of lysine had been demonstrated by Hickling et al. (1990). Different strains of broilers may also respond differently to lysine content in terms of breast meat yield (Acar et al., 1991).

The relative yields of other portions are usually less sensitive to the dietary energy level (Mendes and Cury, 1986) and protein content (Salmon et al., 1983). However Ajang et al. (1993) found that both the leg meat and wing meat responded well to the dietary protein content in the range between 200 and 260 g/kg in the grower, while the breast meat did not respond to the protein content.

Restricted feeding up to 19% of voluntary feed intake during the last 12 days of the growing period was reported not only to reduce the carcass fat content and the back yield, but also significantly increase breast yield (Arafa et al., 1985).

In summary, carcass traits, especially the fat content, in broilers respond to both the feed specification and feeding level. However, to achieve less fat deposition and more lean production by nutritional means, e.g. increasing dietary protein and / or amino acid contents, extra cost will be inevitable. In the case of restricted feeding, possible reductions in growth may occur (Arafa, 1985) and extra feeding space may also be required. It is not surprising that Fisher (1984) suggested that the power of nutritional manipulation of fat content in broilers is rather limited, and only the genetic selection against fatness offers an effective way of ameliorating the (fat) problem. This has been stated many times in the literature (Leenstra, 1986; Cahaner et al., 1987; Whitehead, 1990).

2.4.1.4. Feathering effects

Both the rate and amount of feathering can affect the carcass traits. There might be three ways that the feathering effect is manifested. First of all, feathers are lost during plucking, and the higher the relative feather weight to the live body weight is, the lower the dressed yield will become. Secondly, better feathering provides better insulation against heat loss from the body, and makes more energy available for fat deposition. Therefore, with the same feed specification, a well feathered bird tends to have more fat deposition than a poor feathered one. And finally, since feathers consist mainly of proteins, a poorly feathered bird might have more protein available for lean growth than a well feathered bird, as long as energy is not the limiting factor for body growth in that poorly feathered one.

The naked neck gene, by reducing feather covering, increases eviscerated carcass yield by 0.9-2.4% (Merat, 1986). The difference in carcass yield between the early feathering and late feathering genotypes was small and non-significant at 52 days of age (Merkley and Lowe, 1988). However, three rounds of selection for fast and slow feathering resulted in a significant difference in eviscerated carcass yield (Ajang et al., 1993). The slow feathering line had a higher yield. A higher carcass yield was also observed in the scaleless chickens at 8 weeks of age (Somes, Jr and Johnson, 1982).

A high correlation between average feather score and abdominal fat yield among five feathering lines of chickens selected for or against heat loss was recorded by McAdam and cited by Emmans (1987). Better feathering at three weeks of age was related to the higher abdominal fat yield. Ajang et al. (1993) reported a similar result when comparing the fast and slow feathering lines in the third generation. However early feathering or late feathering genotypes do not seem to have much effect on the abdominal fat yield (Merkley and Lowe, 1988; O'Sullivan et al., 1991 a) except when the feed was severely restricted (O'Sullivan et al., 1991 a). The restricted early feathering birds had a higher abdominal fat yield. However, growth of the restricted birds was beyond an acceptable level, therefore, this exception does not have much practical implication.

While the naked neck gene has not been well evaluated for its effect on carcass traits for broiler production, existing data show that this gene does not have an abrupt effect on the abdominal fat yield (Merat, 1986). Zein-El-Dein et al. (1984) observed a slight decrease in abdominal fat yield brought about by this gene. Later El-Attar and Merat (1985) reported a higher abdominal fat yield in the naked neck bird than in the normal ones. Although none of these three comparisons were statistically significant,

seems to be unusual for the naked neck gene not to reduce the abdominal fat yield substantially while it eliminate feather growth by at least 20%. However the higher feed intake in the naked neck birds (El-Attar and Merat, 1985) was not observed in the late feathering (Lowe and Merkley, 1986) or the slow feathering birds (Ajang et al., 1993). This difference may explain at least in part the exceptional effect of the naked neck gene on abdominal fat deposition. The reduced number of feather follicles was thought to be the reason for reduced subcutaneous fat yield in the naked neck bird (Zein-En-Dein et al., 1984; El-Atar and Merat, 1985; Cahaner et al., 1993). The lower capacity of the subcutaneous site to hold fat in these birds may also force them to store more fat in the abdominal cavity.

The effect of feathering genes on meat yield has also been reported. The general tendency is that the less well feathered birds usually have higher meat yields. The naked neck gene (heterozygous) effect on total meat yield (% of eviscerated yield) has been well summarised by Merat (1986). The percentage difference between naked neck and normal feathering birds ranged from 1.8% to 5.1% (excluding the two extremes) with an average of 3.6%. With a same eviscerated weight of 1.5 kg, the difference between the two genotypes would be 54 g in favour of the naked neck genotype. Significantly higher breast meat but lower skin yields of the naked neck birds were reported recently by Cahaner et al. (1993) in both high and normal temperature conditions. Ajang et al. (1993) reported a significant feathering line effect on all of the meat yield traits. The slow feathering selected line had a significantly higher ($P < 0.001$) total meat (378.0 vs. 359.0), breast meat (154.3 vs. 142.3), leg meat (173.0 vs. 167.0) and wing meat (32.8 vs. 31.0) yields in g/kg NYD at 48 days.

It seems to be an exception that both Merkley and Lowe (1988) and O'Sullivan et al. (1991 a) were unable to find significant effect of the early vs. late feathering genotype on meat yield.

2.4.1.5. Effects of interactions between factors on carcass traits

Interactions between factors such as strain, sex, age and nutrition have been observed extensively for fat content in broilers. The literature on the interaction effects on other carcass traits are very limited, however. Thus this section will mainly focus on the fat issue.

True difference between two levels of a factor needs to be expressed gradually in time, and usually the differences accumulates over a period of time. Therefore within a certain limit, the older the bird is for comparison, the larger the difference between the

groups of birds becomes. In some other instances, a temporary difference between groups will disappear as time goes by. Either an accumulating or a diminishing difference between groups results in an interaction between age and the factor concerned. An example of the former is the sex effect on abdominal fat yield with age: females increase their abdominal fat content quicker than the males (Tawfik et al., 1988), and naturally, an increasing difference was observed between the two sexes with age. An example of the latter is the effect of small differences in nutritional concentration on fat deposition. ten Have and Scheele (1981) reported the effect of energy level with a constant ratio between energy and protein. At 6 weeks of age, birds on a 12 MJ/kg ME diet had less than 80% of the fat deposition of birds on 15 MJ/kg ME diet, while at 8 weeks of age, no apparent difference was found between the same two groups.

Sex differences in the ratio of thigh : breast is dependent on age as well. The ratio was the same at 35 days of age for both sexes, and then the males had an increasingly higher ratio than the females until 175 days of age (Grey et al., 1982).

Difference in the yield of breast muscle between two commercial strains of broilers was absent at hatch, small at 2 weeks of age, and reached the maximum at between 8 and 10 weeks of age (Acar et al., 1993).

The general existence of interactions between age and other factors on carcass traits further indicates the delicate situation in the choice of the reference scale for comparisons of carcass traits, as in the case of feed efficiency comparisons.

Interactions between other factors on carcass traits have occasionally been reported in the literature. However, satisfactory explanations and the practical implications are rarely found, except for an emphasis for the need to give more details in reporting the experimental procedures.

2.4.2. Chemical Composition of Broiler Carcass

Chemical composition determines the nutritive value of the broiler carcass. At present, the major concern of the poultry industry, and consumers alike, on carcass composition is the excessive fat content in the carcass.

The contents of the main chemical components in the carcass are closely related. According to Lewis and Perry (1991), the carcass fat content can be fairly accurately predicted from the carcass moisture content, because these two carcass components

were highly negatively correlated with each other. Summers et al. (1965) found that the carcass protein content can be estimated from the moisture content. However, the most variable component in broiler carcass is fat but not water (Leenstra, 1984). Furthermore, the composition of the fat-free tissue in animals was relative constant at a given age and was not affected by the degree of fatness of the animals (Lin, 1981). Therefore the fat content in the carcass is the major determinant of the whole carcass composition, although the moisture measurement is usually first taken in an analysis and used as the basis for further calculation for other components. It is understandable that the relationships between fat and moisture, and between fat and protein are both negative.

Factors which influence the abdominal fat deposition can affect the whole carcass fat content in a similar way, though the abdominal fat (c.v.=25-30%) is more variable than the total fat content (c.v.=15-20%) (Leenstra, 1984). Cahaner et al. (1986) reported that the amount of abdominal adipose tissue is highly correlated with the amount of adipose tissue elsewhere. This confirms that a high abdominal fat yield coincides with a high fat content of the whole carcass. Nutritional measures and / or feeding techniques are often adopted to manipulate broiler growth and also carcass fat, especially the abdominal fat content. Growth is not the concern in this section, and the effects of nutritional factors on the abdominal fat yield have already been detailed in the previous section.

2.4.2.1. Effect of genetic selection on the chemical composition

Genetic selection can profoundly alter the carcass composition. Selection against fatness have been shown not only to reduce carcass fat content, but to increase the relative amounts of protein and moisture at the same time (Leenstra and Pit, 1987; Whitehead, 1990; Keren-Zvi et al., 1990). Continual selection for body weight to age on the other hand, increased the carcass fat content and decreased the protein and moisture contents in the carcass (Chambers et al., 1981). Selection for high feed efficiency or low FCR also results in a decrease in carcass fat content and an increase in carcass protein and moisture in the broilers (Pym and Solvyns, 1979; Leenstra and Pit, 1987; Cahaner et al., 1987). Selection for fast feathering has resulted in an increased carcass fat and decreased protein and moisture contents compared with the selection for slow feathering (Ajang et al., 1993).

2.4.2.2. Effects of age and sex

The effect of age (and body weight change with age as well) on broiler carcass composition was detailed by Edwards et al. (1973) in both males and females and by Prescott et al. (1985) in the males. From one week old to the age of maturity, both males and female broilers increase their dry matter and fat contents in the carcass. However the changes in dry matter and fat contents is more dramatic in the females than in males. Therefore at the broiler age or older, females have a higher dry matter (lower moisture) and fat contents than the males (Edwards et al., 1973; Pym and Solvyns, 1979; Broadbent et al., 1981; Chambers et al., 1981; Ajang et al., 1993). The sex effect on carcass protein was not large. However males had higher carcass protein content numerically and occasionally significant than the females in most of the reports (Edwards, Pym and Solvyns, 1979; Broadbent et al., 1981; Chambers et al., 1981; Ajang et al., 1993).

2.4.2.3. Effect of feathering on carcass composition

The following feathering conditions have been studied for their relationship with the carcass composition: early vs. late feathering; scaleless feathering birds vs. feathered birds; naked neck birds vs. fully feathered and selected fast vs. selected slow feathering.

Merkley and Lowe (1988) was not able to find any significant effect of the early or late feathering gene in the male and female broilers on the moisture content in the eviscerated carcass and total lipid content in the dry samples of the carcasses . Apart from the sex effect, the genotype in this locus had no effect on the abdominal fat yield.

Somes Jr. and Johnson (1982) reported that birds showing the so called scaleless trait (scsc, nearly completely naked) had significantly higher moisture, protein and ash contents but lower fat content in the whole carcass at both 5 and 8 weeks of age.

Hanzl and Somes Jr. (1983) reported that the naked neck birds had significantly higher moisture and lower lipid contents in the whole (plucked) carcass. However, the carcass protein content was not affected by the naked neck gene. Zein-el- Dein et al. (1984) found that the percentage of subcutaneous and intermuscular adipose tissue was significantly lower in the naked neck birds than in the normally feathered chickens, which might suggest a lower fat content in the carcass of the naked neck birds than the normal feathering ones.

Very recently, Ajang et al. (1993) reported that birds from the fast feathering line had higher fat contents and lower water and protein contents in the carcass than birds from the slow feathering line. The higher fat content in the fast feathering line was at least partially explained by the fact that a higher proportion of the total retained energy was stored as fat and lower proportion of energy was stored as protein in the fast feathering line than the slow feathering line (Priyono, 1991).

2.4.2.4. Effect of temperature on carcass composition

Howliger and Rose (1987) summarised the relationship between rearing temperature and body composition based on data from several different sources. The adapted data show a strong linear positive relationship between temperature and abdominal fat and total fat contents, but a linear negative relationship between temperature and body moisture content. From the data collected, these authors, however, was not able to show any relationship between temperature and carcass protein content. As far as the carcass protein content is concerned, Hanzl and Somes Jr. (1983) found that birds raised in a high temperature had significantly lower protein in the 8-week-old broiler carcass. Somes Jr. and Johnson (1982) also reported that high temperature reared birds had lower protein contents in the carcass on the dry sample basis but not on the wet basis.

2.5. GENETIC PARAMETERS AND THEIR ESTIMATION

The most important genetic parameters are heritabilities of the quantitative traits in the narrow sense (Falconer, 1989) and the correlations (phenotypic, genetic and environmental) among them. These parameters are required in breeding practice for the prediction of selection responses (direct and indirect) and the estimation of breeding values of the individuals (Becker, 1984). They also help the choice of optimal population structure and different selection strategies. For instances, a trait with high heritability can be effectively altered by mass selection; a trait which is expensive or impossible to measure directly can be indirectly selected by means of an easily measured indicator trait which has a high genetic correlation with the target trait.

Other genetic parameters which might have some bearings in a selection program are dominance effect, maternal effect and effects of different interactions. The traditional methods are usually not efficient in handling these parameters since only a limited amount of links among the animals can be analysed and information abstracted. With the advances of technology, these effects can be considered with some efforts

(e.g. Meyer, 1989 in general; Meyer and Hill, 1991 for maternal effects in mice; Wei et al., 1993 for dominance in poultry). Because these kind of parameters have not been extensively estimated in the livestock populations and their practical importance is still largely undefined, the following will be mainly focused on the estimation of heritabilities and genetic correlations.

2.5.1. Heritability and Its Estimation

2.5.1.1. Definition

Heritability in the narrow sense is the ratio of additive genetic variance, or the variance of breeding values to the phenotypic variance (Falconer, 1989). It is a measure of degree of determination of phenotype by the genes (not the genotypes) transmitted from the parents, and is also a measure of reliability of the phenotypic value as a guide to the breeding value which is expected to be recovered in the successive generations. Falconer (1989) emphasised that heritability is a property not only to a character, but also to the population, to the environmental conditions and to the scale of the measurements for the trait. Becker (1984) on the other hand emphasised that a reference population to which the parameters pertain should be defined with every effort. In the reference population, genes affecting the trait under consideration can be assumed to be not linked; the individuals in this population are independent from each other with an inbreeding coefficient of zero; further more no selection is applied to the trait during the development of the lines from this reference population. However, the constraint on selection can be at least partially relaxed with the restricted maximum likelihood (REML) procedure for the data analysis.

2.5.1.2. Methods of heritability estimation

The estimation of heritability is usually dependent on the partition of the phenotypic variance into the additive variance and the rest. Traditionally, the partition of variance is carried out by the analysis of resemblance between relatives by means of variance analysis with the sires and dams treated as random effects (Falconer, 1989). Hill and Meyer (1988) reviewed the assumptions underlying the analysis, and pointed out that many of the assumptions could be violated for data collected from an animal selection program. The most noticeable two points were, firstly, the parents are bound to be related for a population which is not infinite in size; secondly, genetic variance are affected by selection in previous generations and among the parents of the group. Ignorance of the above points usually lead to the underestimation of additive genetic variance and hence heritability in the base population.

With the introduction of the animal model in REML, the relatedness of the animals in the pedigree can be resolved. Under this model, the random genetic and environmental components for animals from different generations are jointly described by a covariance matrix and the fixed effects are accounted for by an incidence matrix (Hill and Meyer, 1988). By maximising the (log) likelihood function, the parameters that fit the data set and the model best can be searched for directly (Meyer, 1989).

Directional selection reduces the variance of the parents and the covariance of sibs. Therefore selection results in a downwards bias for the heritability estimated by sib analysis or a reduction in the precision of heritability estimation based on the regression of offspring to parents (Falconer, 1989). With the animal model, however, use of the relationship matrix could account for both drift and selection (Sorenson and Kennedy, 1984) on the conditions that the genetic model is appropriate (infinitesimal gene effects and no linkage) and all of the information, upon which the selection decisions are based, are included in the analysis (Hill and Meyer, 1988). Furthermore, Graser et al. (1987) suggested that to account for the selection of animals in the base population (or animals in the later generation without tracing information from the back pedigree), these selected parents could be treated as fixed instead of random. As explained by Meyer and Hill (1991), regarding selected animals as fixed is equivalent to using only the proportion of variance among their progeny independent of the fixed parents to estimate the variance. This treatment of data was thought to be logically appealing and has been used to analyse of mice data (Meyer and Hill, 1991) as well as dairy data (van Vleck, 1985).

In a selection experiment, heritability can also be estimated by analysis of the regression of selection responses to the selection differentials (Falconer, 1989), or sometimes simply by the ratio of accumulated selection response to the accumulated selection differential. Heritability estimated in this way is referred to as realised heritability. The limitation for a valid estimation is that the number of generations of selection should not be large, so that the gene frequencies in the population have not been substantially changed by the selection.

2.5.2. Genetic Correlation and the Estimation

Genetic correlation is the correlation between the breeding values of individuals for the two traits concerned in a population. The main cause of the genetic correlation was thought to be the pleiotropic effect of the genes, though linkage is a cause of transient correlation, especially in populations derived from crosses between divergent strains or lines (Falconer, 1989). However, because breeding values are not directly measurable,

the estimation of genetic correlation is, like the estimation of heritability, dependent on the analysis of either the resemblance between relatives, or the correlated response to the directional selection of another trait in a selection experiment (Falconer, 1989) in a way analogous to the estimation of heritability. In the estimation of genetic correlation, the covariance of the two traits need to be partitioned into the genetic and environmental components apart from the partition of the variances of the corresponding traits.

With the REML, a multivariate animal model can be fitted for the estimation of the genetic parameters. However the computational demand to maximise the likelihood function even in a two-dimensional space (in the case of bivariate analysis) is so huge that some alternative strategies which reduce the computing requirement have to be found. One strategy often adopted in the multivariate analysis is to transform the data into the canonical scale, so as to convert the original data of the traits into so called canonical variables. These new variables are uncorrelated both genetically and phenotypically. After the transformation, therefore, a multidimensional search for the maximum likelihood can be carried out as a series of univariate analyses (Meyer, 1991). After the maximum has been located, the results are transformed back to the original scale.

2.5.3. Estimates of Genetic Parameters for Body Weight and Feathering

Estimates for the heritability of body weight in broilers are enormous in the literature. However, most of the estimates so far were based on the variance decomposition with the random sire and dam model. As summarised by Chambers (1990), the estimates based on the sire variance components were the lowest (0.4-0.6) and estimates base on the dam components were the highest with those based on the sire plus dam components being intermediate (0.5-0.6). Occasionally estimates were reported based on the regression of offspring on parent or based on the body weight response to the directional selection. These estimates were usually nearest to those based on the sire variance components (Chambers, 1990).

Heritability estimates for the feathering traits are scarce in the literature, let alone the genetic correlations between the feathering traits and other performance traits.

Hurry and Nordskog (1953) reported the heritability estimate for their nine-grade feathering score at eight weeks of age based on the full-sib components. The estimates were 0.42 and 0.33 for the BPR and NH population respectively.

Siegel et al. (1957 a) obtained the heritability estimates for six feathering traits in the early feathering WPR populations by the intrasire regression of offspring on dams. The chicks had been selected either for superior or inferior feathering. The heritabilities were 0.40, 0.32, 0.49, 0.39, 0.47, and 0.32 for ten-day back score, ten-day breast score, five-week and seven-week percentage of back area covered with feathers, ten-week pin feather score and the amount of body down present at ten weeks.

Edriss et al. (1988) reported the heritability estimates based on the full-sib variance components for four feathering traits at 24/25 days of age in the second generation of the fast and slow feathering selection program. The back score, primary feather length, secondary feather length and tail feather length had the heritability estimates of 0.458, 0.873, 0.833 and 0.568, respectively.

The genetic correlation between feather score and body weight was also estimated in the study of Hurry and Nordskog (1953). It was 0.24 for the BPR and 0.78 for the NH. The genetic correlation between body weight and the percentage of back area covered by feathers at eight weeks of age, estimated by Siegel (1963 b) has already been mentioned in section 2.2.1.2.2. The estimates were 0.23, 0.20, 0.11 and 0.00 in males and 0.15, 0.30, 0.80 and 0.00 in females for generation 1, 2, 3 and 4, respectively. The genetic correlation between body weight and feathering traits reported by Edriss et al., (1988) were 0.449 (back score), 0.274 (primary feather length), 0.367 (secondary feather length) and 0.605 (tail feather length) respectively. Although most of the above estimates were low, it is believed that feather growth as a part of body growth is positively correlated with broiler body weight.

CHAPTER 3

GENERAL MATERIALS AND METHODS

3.1. OBJECTIVES OF THE EXPERIMENTS

In the course of the research undertaken, three designed experiments have been carried out to evaluate the effects of the feathering selection, effects of major feathering genes and other related factors on broiler growth performance and carcass traits. The divergent feathering selection program initiated by Edriss (1988) and followed by Prijono (1991) to the fifth generation has been continued for three further generations. Changes in the tail feather length and body weight are analysed for their responses to the feathering selection. The genetic parameters involved in different generations are estimated with a DFREML program fitting an individual animal model.

The objectives of the three designed experiments are described as follows:

1. The first experiment was designed to evaluate the effects of feathering genotype, sex and temperature on the total body protein partition among feather growth, edible meat, non-edible parts and residual carcass. This was a joint project in which the growth performance and the carcass traits were reported by Quoi (1991).

2. The second experiment was carried out to evaluate the effects of the Na gene, early or late feathering genotype and six generations of feathering selection on broiler growth performances (body weight, feed intake, feed conversion ratio and feather length), carcass traits and chemical composition (protein contents) of the dissected parts of the carcass. The main objective was to define the optimum amount feather covering manipulated by genetic means for broiler production at a post-brooding temperature of 25 C.

3. The third experiment was based on the results of Experiment 2 which indicated a strong correlation between feathering rate and feed efficiency for the grouped birds. This experiment was designed to further demonstrate the relationship between feed efficiency and feather growth on the individual basis. Two rounds of the experiment

with the same design were undertaken, and each time records for feather growth, body weight, feed intake and feed conversion ration were obtained for 48 individually caged male chicks from 21 to 45 days. Carcass traits were measured for all of the individuals at the end of the experiment.

4) The analysis of the selection data was aimed at the demonstration of the efficacy of the selection program in manipulating the juvenile feathering condition in the late feathering chicken population and the genetic consequences of the selection in terms of changes of the means, variances, covariances and genetic parameters. Two approaches were taken for the analysis. First of all, the means of the tail feather length and body weight were computed and compared for the Fast, Control and Slow feathering lines over the generations. Secondly, the genetic parameters of the two traits were estimated from different lines and generations.

3.2. DESCRIPTION OF THE LINES

The divergent feathering selection program with a control line was started in 1986 and was carried out to the third generation by Edriss (1988). Later Prijono (1991) continued the work to the fifth generation. These lines have been maintained to the eighth generation. The selection procedure was detailed by Edriss (1988) and Ajang et al. (1993) to the third generation. The other broiler-type stock with the naked neck gene involved in the present research was purchased from the commercial breeders in early 1990, and it has been reproduced and managed together with the above three lines.

3.2.1. The Feathering Selection Lines

3.2.1.1 Origin and selection procedures

Six hundred male and 600 female day-old chicks which formed the base population, were from the female side male line in the commercial broiler breeding program of Ross Breeders Ltd. The stock were homozygous for the late feathering gene, K. At 24 days of age, the control line was first established by random selection of all chicks available. The fast and slow feathering lines were established by mass selection for or against the predicted back feather score. The equation for the prediction of the back feather score was based on the regression of the six-grade back score on the primary and secondary flight feather length, so that the "score" used as the selection criteria for the two lines was continuous, rather than discrete. Thirty male and 150 female chicks were selected for each of the three lines at this stage.

From generations 1 to 3, the two selection lines were mass selected for or against the predicted tail feather length, for its objectiveness and high genetic correlation with the back feather score (Edriss, 1988). The equations to predict the tail feather length were based on the within generation, line, sex and hatch regression of the tail length on the back feather score, primary and secondary flight feather lengths. Each line of the first two generations was reproduced from 16 males and 96 females by mating each sire to 6 non-sib random females.

From generation 3 onwards, the basic family structure and mating policy remained the same. However the number of sires for each line was reduced to 8-10 in different generations. Because the divergence in feathering had already been established between the two selection lines, with generation four and later, some selection pressure was exerted on body weight at three weeks of age. *Female breeders* were selected by independent culling levels for body weight and tail length within line and hatch. The general guideline for selection was that half of the culling was made for small body weight, and another half for short or long measured tail feather length (not the predicted one) in the fast or slow feathering line. However, because of the negative correlation between body weight and tail length (Edriss, 1989), slightly more selection pressure for body weight was put in the slow feathering line in order to keep a rough balance in body weight among the lines. In order to reduce the rate of the increase of inbreeding, *males* were selected within the families. Two male candidates within a sire family within hatch and line were first selected for high body weight, and then choose the one with longer or shorter tail length measurement in the fast or slow feathering line, so that more selection pressure had been put in upgrading body weight than in further feathering rate divergence. Once again a balance in body weight among the lines was considered for males.

In the control line, a similar selection pressure on body weight as the two feathering selection lines was made on both males and females. However, other cullings were made at random.

The progress of the selection program has been kept at the rate of one generation per year.

3.2.1.2. Replacement stock management

The fully pedigreed chicks were individually wing-banded and sexed after hatching and managed as broiler breeders. They were fed *ad libitum* with a commercial starter diet before the measurements were taken at 24/25 days of age for

the base population and from generation 1 to 4, and at 21 days from generation 5 onwards. Immediately after the measurements, chicks started a restricted feeding program. The lighting period per day was 23 hours before the measurements, and then gradually reduced to 8 hours with an intensity of about 5 lux. Selection was usually made within two days following the measurements except on a few occasions in which the day-old chicks were not sexed, and the selection had to be made at a later age when sex was determined visually. No further selection was attempted thereafter except for the normal culling of the disqualified birds throughout their life. The small number of non-layers were also replaced by the spare birds before the artificial insemination for stock regeneration.

At 20-22 weeks of age, all of the males and females were transferred from the floor to the individual cages. To ease the replacement process of the whole stock for the next generation, and also to minimise the disturbance both to the birds and egg production records, the grouping of the females for a family structure were set up at this stage in most of the generations. Seventeen hours of light per day was provided in the laying house.

The age of breeders when the first insemination for stock replacement was made ranged from 30 weeks to 50 weeks of age in different years, mainly related to the availability of the rearing houses and other arrangements.

3.2.2. The Line Carrying the Naked Neck Gene

The stock carrying the naked neck gene was on a non-strain specific background with its body weight in between layer and broiler breeds. It might be regarded as early 1980's broiler. This stock carries only the early feathering gene (k) in the K locus, and no feathering rate selection has so far been attempted.

After its introduction, this stock has been managed together with the existing three lines. Body weight measurement was also taken at three weeks of age. Chicks in the first generation were selected for body weight (mass selection for females, and within sire family selection for the males) within the population. In order to match the body weight of the existing lines quickly, a group of early feathering commercial broiler parent stock males were used to mate the females from this line in producing the second generation in 1991. Therefore the first weight-improved birds were in service while producing chicks for the third experiment in early 1993.

3.3. THE DESIGNED EXPERIMENTS

3.3.1. Chicks used in the Experiments

3.3.1.1. Experiment 1

For the chemical analysis of broiler carcasses in the first experiment, chicks were produced from the mating between 14 heterozygous naked neck males (with pooled semen) from the base population of the naked neck stock (Nanakk) and the females from the fast feathering (F) selected (nanaK/wF) and slow feathering (S) selected lines (nanaK/wS) in the fifth generation. The day-old chicks were feather sexable: all of the females were early feathered, and the males were heterozygous late feathered. Four distinct feathering genotypes (together with sex difference) were created from each of the two female lines. Males: NanaKkF, nanaKkF, NanaKkS, nanaKkS; Females: Nanak/wF, nanak/wF, Nanak/wS, and nanak/wS.

One bird each was randomly chosen at the age of 10, 20, 30 and 40 days of age from all of the genotype and temperature combinations for dissection and for chemical analyses of the feather, meat, non-edible parts and residual carcass (see details in section 3.3.3.3.)

3.3.1.2. Experiment 2 and 3

In order to have a combined evaluation of all of the feathering genes available in the selection program in experiment 2, the mating plan was divided into two steps in two successive generations.

The first step was to produce two groups of special males. This was done by mating individually nine males each from the fast and slow feathering lines to three of the heterozygous naked neck females. The males used were in the fifth generation of feathering selection, and females in the base population of the naked neck line. From the above pedigreed mating, one normally but late feathered male chick (nanaKkF from the fast feathering line males and nanaKkS from the slow feathering line males) from each of the 9 sire families per line was selected and raised to maturity.

The second step involved backcrossing the above special males to the heterozygous naked neck females in the following generation (generation 1 of the naked neck line). Each male was mated to six females this time. Again the chicks were pedigree hatched (recorded to the sires only). They were vent-sexed at hatching,

and the male chicks were used for the experiment. Therefore the chicks had two different grand sire origins, with two pairs of feathering genes segregating together. The expectations were that the naked neck chicks and normal feathering chicks; and early feathering (kk) and heterozygous late feathering (Kk) chicks both had ratios of 1:1. So, eight distinct feathering genotypes with a similar genetic background otherwise, were created as the material for the evaluation in the experiment with a split-plot design (Chapter 5).

In the preparation of chicks for the study of the relationship between feathering rate and feed efficiency (experiment 3, Chapter 6), the same two step procedures as in the second experiment were involved, except all of the breeding birds were one generation younger. Because this was a more focused study, a few more constraints about the choice of the experimental materials were imposed: only the special males from the slow feathering line were used in the backcross-mating, and only the normal feathering male chicks were used. The theory in the mating plan was to create a reasonably wide-spread distribution in feathering rate without the interference of the naked neck gene. Therefore the quantitative relationship between feathering rate and feed conversion ratio in the individuals could be isolated and studied in detail.

With 48 individual cages available, six chicks, three early feathering and three late feathering, from eight sires could be accommodated. The experiment was repeated twice using the same facilities over an interval of four weeks. The same eight sires were involved in the second mating. However, in order to avoid too many full brothers being involved in the two consecutive experiments, each male was mated to a different group of the females the second time. Thus when results from these two experiments are analysed together, the error term would not be correlated in different ways.

3.3.2. General Management of the Chicks

For the grouped chicks raised on the floor, the following general management procedures had been followed. Before the chicks were hatched, the house and the equipment were thoroughly washed with high pressure hot water with detergent, and then without detergent. After the pens were set to suit the needs of the specific experiment, new wood shavings was provided on the floor. Each pen was provided with at least one mini-drinker and one bell drinker, one or two tube feeders and two to five new egg trays according to the size of the pen and the number of chicks to be raised. Three to five days before the arrival of the chicks, the house was closed and fumigated, and opened again 24- 48 hours later. The rooms were heated to the

temperature of 32°C 24 hours before the arrival of chicks. All of the drinkers were cleared and checked again for their normal functioning. Feed was added on the egg trays and in the open base of the tube feeders before the chicks arrived.

From the beginning, chicks were encouraged to use the tube feeder by temporal removal of the top tube and with easier access by lowering the feeders partially into the shavings. After 5 to 7 days, the egg trays were gradually removed, and the mini-drinkers replaced by the bell drinkers.

In the third experiment, the house and facilities were prepared as before. During the first three weeks, chicks were raised on the floor. At 21 days of age, chicks were transferred to the individual cages. The cages were all in the same size, with 37.5 cm in depth and 52.5 cm in width. Each cage was equipped with a cup-drinker and an individual trough. A plastic container was used to hold the pre-weighed amount of feed for each individual.

Feed and water were provided *ad libitum* to all of the birds in the three experiments, except for the 12-16 hour period before the slaughter when only water was available. Twice daily, the drinkers and feeders were cleaned and feed was added when necessary.

For the purpose of disease prevention, the entrances of the houses were equipped with a foot bath in which a valid disinfectant at a correct concentration was kept and used on entry to and exit from the house. Apart from the withdrawal feed mixes, all feed mixes were medicated with a coccidiostat. Vaccines against infectious bronchitis (at day 1 by aerosol method) and infectious bursal disease (at day 18 and 25 through the drinking water) were routinely used for the broilers.

Lights were on for 23 hours per day throughout all of the experiments. Light intensity was controlled at about 20 lux for the first 5 days in the middle of the pens, and reduced to 5 lux thereafter.

3.3.3. Measurements and Procedures

During the experiments, measurements were taken for feather length, body weight feed consumption, and different carcass traits at various ages.

3.3.3.1. Feather length measurements

The lengths of the tail feather, primary and secondary flight feathers were taken as follows.

Tail feather length: the longest tail feather in a bird was measured from its base to the farthest point of emergence using a ruler trimmed precisely to zero mm.

Primary flight feather: the second primary flight feather on the right wing was measured from its base to the farthest point of emergence.

Secondary flight feather: the second one on the right wing was measured from its base to the farthest point of emergence.

3.3.3.2. Body weight and feed consumption

The individual **body weight** and the amount of feed consumed were always measured to the nearest gram in the beginning and at the end of a period. Grouped body weight was recorded to the nearest 10 grams.

Feed consumption was calculated as the difference between the sum of feed added to the group of birds in the pen or the individual in the cage and the amount left at the end of the specific period.

Body weight gain was calculated as the difference between the body weights at the end and in the beginning of the specific period of the group or the individual.

Feed conversion ratio (FCR) was the ratio of feed consumption to the corresponding body weight gain in the same unit of weight.

3.3.3.3. Procedure of slaughter and dissection

Feed withdrawal: 12-16 hours before slaughtering, feed was withdrawn, and only water was available.

Killing: in the first experiment, the birds were killed by suffocating with carbon dioxide, and the starved body weights were taken after the birds were killed for the handling ease. In the later experiments birds were weighed onto the slaughter line and stunned before killing by cutting through the jugular vein, oesophagus and trachea.

Blood was drained off for a minimum of 3 minutes before the carcass went through hot water bath to help the manual plucking. Feathers from the individuals were separately collected in the marked cotton bags and were dried in an oven at 60°C for 48 hours before being weighed to the nearest 0.1g.

The bled-plucked carcasses were allowed to drain off water for half an hour and then wrapped in the black plastic bags with 8 - 10 carcasses together. They were stored in the chill room at 4°C overnight before being eviscerated. All of the carcass and its parts were weighed to the nearest 0.1g.

Evisceration: Before the evisceration, the carcass weight was taken as New York Dressed (NYD). The head and claws were cut off after the separation of the oesophagus, and the crop and trachea from the opened neck. The viscera and the organs were then pulled out through a small cross-sectional opening near and around the cloaca. The abdominal fat pad together with the fat around the gizzard was collected as the abdominal fat. The neck was cut off transversely through the far front of the shoulders. The eviscerated carcass (empty carcass) was then weighed and recorded.

Dissection: A transverse incision was made through the dorsal skin cranial to the pelvis (ilium) and a longitudinal incision to the tail base. Then the back skin was cut loose up to the attachment of the two thigh muscles to the ischium. The skin was cut at the ventro-lateral side of the carcass between leg and body, from the base of tail up to the edge of transverse incision. The two thigh muscles (M. semimembranosus and M. semitendinosus) were cut loose from the ischium starting from the caudal end of the pubis. The hip joint was broken by pushing the leg in a dorsal direction and cutting the tendons and ligaments. By tearing the M. gluteous and M. iliotibialis from their attachments in a cranial direction, the leg was removed from the carcass. The back skin was cut off from the leg, and the thigh and drumstick were separated by cutting the joint of the femur and tibia to the area where the M. gastrocnemius pars interna, and the M. semimembranosus and M. semitendinosus cross. The thighs and drumsticks from both sides were weighed together.

The wings were removed by holding the knife parallel to the M. scapulotriceps edges of the wing, thus cutting the tendons of the joint.

The breast skin was cut and pulled to the sides. The breast meat (M. pectoralis major and M. supra corcoideus) was cut at the rim of fat. Then both sides of the breast meat were torn off together in cranial direction, detaching the clavicle

(wishbone) from sternum. The clavicle was separated from the breast meat later. The carcass frame was what was left after the legs, wings and breast meat were removed.

The trimmed meat left around the coracoid were removed in experiment 1 and 2 and was add to the total meat. All of the skin left on the frame was also separated in experiment 2.

Finally, the skin, meat and bones from both sides (experiment 1 and 2) or one side (experiment 3) of thighs, drumsticks and wings were separated (wings were not deboned in experiment 3).

In the course of dissection, the following items were separated and weights recorded.

1. NYD, the bled-plucked carcass;
2. Eviscerated carcass (EVC, without offal and neck);
3. Abdominal fat pad;
4. Thighs and the skin, meat and bones;
5. Drumsticks and the skin, meat and bones;
6. Breast meat;
7. Wings (and the meat, experiment 1 and 2);
8. Frame;
9. Total meat (breast meat + thigh meat + drumstick meat + heart, liver and gizzard; trimmed meat and wing meat were also included in Experiment 1 and 2, but not 3);
10. Non-edibles viscera (gastrointestinal tracts, lungs and other non-edible organs eviscerated, experiment 1 only)
11. Dissection residual in Experiment 1 (frame, skin, fat, bones, head, neck, feet).
12. Total residual without skin in Experiment 2 (non-edible viscera + items in 11 without skin).
13. Total skin (experiment 2 only).

3.3.3.4. Sample preparation for the chemical analysis

Feather sample preparation was relatively straight forward. About 15 g of the finely mixed dry feather samples (if less than 15 g, then the whole lot was used) were cut into fine particles by a pair of scissors. After mixing, the samples are ready to be analysed. The carcass samples were prepared in the following procedure of sampling, freeze drying, and freeze milling.

If the respective part of carcass material from an individual bird was less than about 75 g, the whole sample was chopped manually into small pieces and dried in an aluminium container in the freeze drier. If the material was more than 100 g, the whole material was chopped and minced in a chopping bowl until a homogeneous sample of about 100 g could be weighed out.

The collected samples were then placed into a freeze drier for 120 hours (-4°C) before being weighed again, and dry matter content calculated. The dried samples were then stored in plastic bags at -20°C. They were ready to be ground in the freeze miller with liquid nitrogen at low speed to prevent the fat from melting. The milled samples were stored in plastic jars inside the plastic bags at -20°C again until analysis for crude protein.

3.3.3.5. Protein determination

An adapted Kjeldahl method, called indophenol blue method (Spillane, 1966) was adopted for protein determination in all of the samples. The procedure involves the following two steps. The first step is the digestion of protein into ammonia and then the second step is to quantify the ammonia in the spectrophotometer (see below for details). The chemicals used were as follows (all chemicals are of "Analar" quality):

Sulphuric acid reagent: 40 g selenium dioxide + 100 ml distilled water + 2 litres concentrated sulphuric acid.

Hydrogen peroxide: 100 volumes strength.

Reagent (A+B): 31.26 g phenol + 3.75 g sodium hydroxide + 0.156 g sodium nitroprusside and then made up to 5 litres with distilled water.

Reagent C: 99.4 g trisodium orthophosphate + 11.69 g disodium hydrogen orthophosphate + 15.6 g sodium hydroxide + 31.2 ml sodium hypo-chlorite and made up 2.5 litres with distilled water.

The procedure of protein determination described below was followed:

Weigh 1.000g of freeze dried, milled material into a 250 ml digest tube, add 22.5 ml of sulphuric acid reagent and allow the acid to wet the sample thoroughly. Carefully add 9 ml of hydrogen peroxide in 1 ml aliquots, allow the reaction to subside and place in the digest block. Digest for 60 minutes and if solution is clear,

allow to cool and make up to a volume of 225 ml with distilled water. If solution is still dark, add 1 ml of hydrogen peroxide and re-digest for 15 minutes. Mix the solution and allow to cool -- the solution is now ready for the colorimetric procedure.

Dilute 0.05 ml of the digest solution with 10 ml of reagent (A+B), add 5 ml of reagent C, mix thoroughly and allow to sit for 60 minutes at room temperature. Standard solutions of known protein concentrations are diluted at the same time as the samples. When the indophenol blue colour has developed, the solutions are read on the spectrophotometer at 661 nm - the instrument being set to give the appropriate concentration range.

3.3.4. Statistical Analysis

In analysing the data from all of the designed experiments, a general statistical package, GENSTAT 5.2 (1990) was used for the variance and covariance analysis. The linear models for the analyses are given in each individual sections. However the multiple regression analyses were performed using MINITAB (release 8, 1990).

3.4. GENETIC PARAMETER ESTIMATION

The body weight and tail feather length data were collected and organised from eight generations of divergent feathering selection. These data were subjected to the genetic analyses. The derivative free restricted maximum likelihood (DFREML) algorithm invoking an animal model suggested by Graser et al. (1987) was adopted for the estimation of variance-covariance components. The simplex method was used to allocate maximum of the likelihood functions. The DFREML program resided in the ESAVAX machine at the SAC computing centre, Edinburgh, was accessed through the computer network. More details are given in Chapter 7.

CHAPTER 4

EFFECTS OF FEATHERING GENOTYPES, TEMPERATURE AND SEX ON THE PROTEIN CONTENT AND PROTEIN PARTITION OF CHICKEN TO FORTY DAYS OF AGE

4.1. INTRODUCTION

From the nutritional point of view, the effect of feathering on broiler growth performance and carcass traits is dependent on the balance between the amount of nutrient resources required for the development and growth of the feathers and the nutritional benefit that a bird can get from the proper insulation provided by feathers. As it has been reviewed in section 2.3.2.3 and appendix 1, the amount of energy that can be saved from a better insulation provided by feathers can be calculated based on the data obtained by Prijono (1991). However, the effects of feathering on the protein metabolism and the consequences of different amounts of feather covering and feathering rate has not yet been fully investigated. With the vast range of different feathering genotypes available, the present research project was undertaken to elucidate how the feathering genotypes influence the growth performance and the carcass traits, and furthermore, to investigate how the feathering genotypes affect the protein partition among the various parts of the body. As a part of the integrated research program, this experiment was conducted to address the latter part of the question. The results concerning the assessment of the feathering genotype effects on feather length measurements, body weight and meat production have already been detailed by Quoi (1991), and summarised by Lou et al. (1992).

4.2. MATERIALS AND METHODS

Six hundred and thirty three chicks with eight different feathering genotypes were hatched for the experiment and were individually wing banded at day old. The eight feathering genotypes to be compared in the experiment were NanaKkF, NanaKkS, nanaKkF, nanaKkS in males and Nanak-F, Nanak-S, nanak-F, nanak-S in females. The mating plan to produce these genotypes has been described in Chapter 3, section 3.1.1. The chicks were housed in four controlled environment rooms, with 6 pens each. Two temperature treatments were applied in the experiment. The two rooms in the middle (room 2 and 3) were kept at 30°C, and the temperature in other two rooms at the ends of the house (room 1 and 4) were gradually reduced from 32°C at day old to the normal temperature of 20°C at 21 days of age.

Random representatives of the four feathering genotypes of females were housed in rooms 1 and 3, and of males in rooms 2 and 4 in separated pens. With 6 pens available in each room, the two genotypes with the naked neck gene in both males and females were replicated in the hot rooms, and the two genotypes without the naked neck gene were replicated in the normal temperature rooms. Therefore the factorial layout of the experiment was half replicated.

Birds were given a purpose-formulated starter diet for the first twenty days and a grower diet thereafter. Both of the diets had a calculated metabolisable energy level of 12.7 MJ/kg and balanced amino acid profiles according to the NRC (1984) guidelines. The starter contained 240g/kg crude protein, and the grower 230g/kg (Appendix 4.1).

For meat yield and other carcass trait assessments (Quoi, 1991), two birds from each pen were randomly selected at the end of each ten-day period up to 50 days of age. Among them, one healthy bird from each of the 4 genotypes × 2 sexes × 2 temperatures combinations were randomly selected for chemical analysis. After killing by suffocation with CO₂ (without loss of blood), they were manually plucked and further dissected into three main parts, i.e. total meat, viscera and residual (see items 9, 10 and 11 in Chapter 3 section 3.3.3.). No bird was selected for chemical analysis at 50 days of age, owing to a severe ascites problem at this age (Quoi, 1991). As one of the bases for the calculations of the results, body weight and yields of the dissected parts for the birds used in the chemical analysis are provided in Appendix 4.2. For detailed accounts of performance data of the grouped birds, see Quoi (1991).

Samples of feathers were dried and cut into fine particles; samples of meat, viscera

and carcass residual were dried and milled as described in Chapter 3. These samples were analysed for dry matter and crude protein contents.

The statistical analyses of the data sets were first carried out (not presented) with the following full fixed model for a 2×2×2×2 factorial design:

$$Y=U+T+S+N+L+T*S+T*N+T*L+S*N+S*L+N*L+T*S*N+T*S*L+T*N*L+r$$

where Y is the variable in question; U, the overall mean; T, the effect of temperature; S, sex; N, Na gene; L, line; r, the residual; and the rest are the terms of two-way and three-way interactions between and among the above factors.

Because only one bird was chosen in each of the group and age combinations, the residual term is equivalent to the four way interaction with only one degree of freedom. In the analysis that follows, the factor with the least major effect was dropped off from the model, and then a simplified model for 2×2×2 factorial design was adopted and results are reported here.

4.3. RESULTS

The dry matter and protein contents of the meat, viscera and the residual are shown in Tables 4.1 and 4.2 respectively. Means of the whole body protein partitioned to feather, meat, viscera and the residual are presented in Table 4.3. The effects of the single factors on various traits together with their general trend with age are visualised in 17 figures (Fig 1 - Fig 17). The statistical significances of the factors are presented in Table 4.4 and are also indicated in the figures with *(P<0.05), **(P<0.01) and ***(P<0.001). The probabilities between 0.5 and 0.1 are indicated by # sign in the figures. The two way interactions between the factors which showed some consistency across the ages are presented in Table 4.5.

Table 4.1. Dry matter contents (g/kg) of meat, viscera and carcass residual

age days	Normal Temperature								High Temperature							
	Males				Females				Males				Females			
	Naked neck		Normal		Naked neck		Normal		Naked neck		Normal		Naked neck		Normal	
	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow
Meat																
10	240	255	252	243	266	232	245	246	248	235	241	234	238	248	243	251
20	250	242	252	251	250	253	243	245	253	253	264	258	257	246	250	252
30	240	255	237	242	229	253	244	240	260	251	239	254	247	249	243	248
40	248	250	253	245	243	245	254	244	240	250	262	246	272	244	251	244
Viscera																
10	240	245	229	240	262	239	240	230	240	231	242	236	223	242	228	254
20	244	248	227	245	233	255	238	259	262	238	228	232	261	261	241	234
30	245	240	229	231	216	243	234	220	259	254	248	243	237	263	230	275
40	232	237	248	231	233	230	247	256	225	259	219	228	268	231	226	243
Residual																
10	291	321	298	294	345	310	335	337	331	299	308	283	290	312	314	354
20	321	318	341	327	331	347	327	334	338	338	324	323	380	331	334	354
30	349	355	332	321	296	336	336	338	354	378	332	347	347	325	380	369
40	347	340	374	325	348	339	365	357	313	359	366	324	380	355	363	367

Table 4.2 Crute protein contents (g/kg) in samples of dry feather, meat, viscera and carcass residual

age days	Normal Temperature								High Temperature							
	Males				Females				Males				Females			
	Naked neck		Normal		Naked neck		Normal		Naked neck		Normal		Naked neck		Normal	
	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow
Dry feather																
10	860	902	878	881	854	852	868	874	863	873	886	871	884	843	857	839
20	895	863	885	853	900	882	893	866	887	857	888	856	889	891	888	882
30	891	887	890	882	901	901	910	907	882	885	869	864	889	881	887	880
40	888	896	893	898	891	903	905	897	885	888	903	898	898	883	901	899
Meat																
10	183	207	185	198	205	174	194	185	186	187	189	184	177	196	187	182
20	203	198	197	202	200	194	192	205	206	208	207	208	192	187	207	203
30	192	199	195	203	191	196	199	190	197	193	196	199	195	200	186	192
40	210	197	199	207	197	205	209	175	201	201	212	211	220	209	214	206
Viscera																
10	148	174	138	142	157	143	145	152	132	145	139	127	133	138	152	141
20	159	157	159	173	154	152	152	158	166	160	152	161	142	156	145	143
30	152	155	142	158	148	144	155	140	153	154	154	149	137	165	143	170
40	154	161	155	165	153	161	156	145	157	145	144	155	144	141	143	166
Residual																
10	173	177	173	173	174	169	172	173	174	175	165	170	162	170	165	175
20	185	187	186	194	185	185	179	183	202	196	191	186	176	200	185	192
30	178	201	183	185	175	191	165	173	177	177	187	186	186	182	198	191
40	176	189	187	188	184	183	189	193	194	195	190	205	179	172	178	183
Starved body with feathers																
10	180	188	177	171	195	176	189	183	173	167	175	171	173	188	182	187
20	188	190	192	192	190	187	190	194	201	197	195	191	184	194	195	203
30	184	195	195	188	191	200	196	189	192	190	202	195	199	198	206	203
40	204	201	207	204	201	202	217	198	207	202	210	215	207	199	212	211

4.4. DISCUSSION

4.4.1 Dry Matter Contents

The dry matter (DM) content is not only the basis for the calculation of the contents of other chemical components, but the whole carcass DM itself is a strong indicator of the whole carcass fat content (Lewis & Perry, 1991), *i.e.* high DM is related to high fat content.

Table 4.3 Body protein partition among feathers, meat, viscera and the residual across the age (g/kg body protein)

age days	Normal Temperature								High Temperature							
	Males				Females				Males				Females			
	Naked neck		Normal		Naked neck		Normal		Naked neck		Normal		Naked neck		Normal	
	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow
Protein in the Feathers																
10	111	48	121	51	133	137	143	117	64	11	107	72	136	136	98	150
20	67	70	99	77	91	95	133	108	89	63	113	70	126	97	126	151
30	107	73	141	104	136	127	160	149	126	117	155	99	145	126	126	159
40	150	123	165	113	142	109	188	176	138	124	165	139	145	148	182	181
Protein in the Meat																
10	351	382	322	372	357	311	338	339	374	388	341	353	324	328	341	336
20	391	408	386	396	371	392	360	391	357	400	339	404	382	356	373	361
30	404	383	354	400	415	402	396	399	394	392	356	395	358	369	369	356
40	408	423	380	406	403	453	394	339	381	381	371	372	424	430	394	382
Protein in the Viscera																
10	94	120	118	133	113	108	108	101	99	118	117	108	108	98	132	91
20	89	81	75	81	85	79	80	81	80	78	84	92	79	83	74	67
30	71	72	76	70	72	62	71	68	68	75	59	70	59	68	68	67
40	65	59	57	62	67	67	58	64	62	61	61	71	58	60	63	63
Protein in the Residuals																
10	444	451	439	445	397	444	411	443	463	483	435	466	432	439	429	422
20	454	441	440	447	453	434	427	419	474	459	465	435	413	465	428	422
30	419	472	429	426	377	408	373	385	412	416	431	436	438	437	436	417
40	377	396	398	419	389	371	360	421	420	434	404	418	373	363	361	374

Table 4.4 Significance levels for the effects of temperature(Temp), sex, naked neck gene (Na), feathering selection line and their interactions on dry matter and protein contents, and the protein partition of the whole body and plucked carcass among feathers, meat, viscera and residual in the simplified three way variance analysis

Factors	Age	Temp	Sex	Na	Line	T*S	T*N	T*L	S*N	S*L	N*L	TSN	TSL	TNL	SNL
Dry matter content															
Meat	10			/		/		/		/	/	/	*	/	/
	20	.062		/		/		/		/	/	/	/	/	/
	30	*	/	.100	*	/		/	/	/	/	/	/	**	/
	40		/			/		/	/	/	/	/	/	/	/
Viscera	10				/			/		/	/	/	/	/	/
	20	/		.062		/	/	/		/	/	/	/	/	/
	30	*	/			/		/	/	/	/	/	/	/	/
	40	/				/	/	/		/	/	/	/	/	.081
Residual	10		.057		/			/	.100	/	/	/	/	/	/
	20		.098		/			/	/	/	/	/	/	/	/
	30	.089	/			/		/	/	/	/	/	/	/	/
	40	/	*			/	/	/		/	/	/	/	/	/
Carcass	10		.052	/		/		/	/	/	/	/	*	/	/
	20		/			/		/	/	/	/	/	/	/	/
	30	*	/			/		/	/	/	/	/	/	/	/
	40	/				/	/	/		/	/	/	/	/	*
Protein content															
Feather	10	/	*			/	/	/				/	/	/	/
	20	/	**	.063	***	/	/	/		*		/	/	/	/
	30	***	**	/		/		/	/	/	/	/	/	/	/
	40			*	/			/	/	/	/	/	/	/	/
Meat	10				/			/	/	/	/	/	/	/	/
	20		*	.098	/			/	.096	/	/	/	/	/	/
	30			/		/		/	/	/	/	/	/	/	/
	40	/				/		/	/	/	/	/	/	/	/
Viscera	10	*			/			/	.085	/	/	/	/	/	/
	20		*	/		/		/	/	/	/	/	/	/	/
	30			/	*	/		/	/	/	/	/	***	/	/
	40			/		/		/	/	/	/	/	/	/	/
Residual	10	.071		/		/		/	/	/	/	/	/	/	/
	20	.073	.092	/		/		/	/	/	/	/	.063	/	/
	30		/			.059	/	/	/	/	/	/	/	/	/
	40	/	.086			/	/	/		/	/	/	/	/	/
W. body	10	.097	*	/		/		/	/	/	/	/	*	/	/
	20	/				/		/	/	/	/	/	/	/	/
	30	*	.052	/		/		/	/	/	/	/	/	/	/
	40	*	/	**	*	/	/	/		/	/	/	/	/	*
Carcass	10		/			/		/	/	/	/	/	/	/	/
	20		*	/		/		/	/	/	/	/	/	/	/
	30		/	.075	.052	/		/	/	/	/	/	/	/	/
	40		/			/		/	/	/	/	/	/	/	/
Factors	Age	Temp	Sex	Na	Line	T*S	T*N	T*L	S*N	S*L	N*L	TSN	TSL	TNL	SNL

to be continued...

Table 4.4 (con'd) Significance levels for the effects of temperature(Temp), sex, naked neck gene (Na), feathering selection line and their interactions on dry matter and protein contents, and the protein partition of the whole body and plucked carcass among feathers, meat, viscera and residuals in the simplified three way variance analysis

Factors	Age	Temp	Sex	Na	Line	T*S	T*N	T*L	S*N	S*L	N*L	TSN	TSL	TNL	SNL
Whole body protein partition															
Feather	10	/	***		.056	/	/	/		*		/	/	/	
	20	/	**	*		/	/	/				/	/	/	
	30	/	*	.062	.052	/	/	/		.071		/	/	/	
	40	/	*	***	**	/	/	/	*			/	/	/	
Meat	10	/	**			/	/	/	*	*		/	/	/	
	20	**	**	/	***		/		/	**	/	/	***	/	/
	30	.061	/			/			/	/		/	/	/	
	40			*	/	.096		/		/	/		/	/	/
Viscera	10				/			/		/	/		/	/	/
	20				/			/		/	/	*	/	/	/
	30			/			/	*	/		/	/	/	/	/
	40	/				/	/	/				/	/	/	
Residual	10	*	***	/	**		/		/		/	/	*	/	/
	20		.051		/		/			/	/		/	/	/
	30	.063	*	/		**	/		/		/	/	/	/	/
	40	/	*			/	/	/				/	/	/	/
Plucked carcass protein partition															
Meat	10	/				/	/	/	.090			/	/	/	
	20	*		/	*		/		/	*	/	/	*	/	/
	30	*			/	**		/		/	/		/	/	/
	40	/	.066	.083		/	/	/				/	/	/	
Viscera	10		/			/			/	/		/	/		/
	20			/			/		/		/	/		/	/
	30		/			/		*	/	/		/	/		/
	40	/				/	/	/				/	/	/	
Residual	10		/			/			/	/		/	/		/
	20		/			/			/	/		/	/		/
	30	*		/	**	/		/	/	/		/	/	/	/
	40	/	*	.100		/	/	/				/	/	/	/
Factors	Age	Temp	Sex	Na	Line	T*S	T*N	T*L	S*N	S*L	N*L	TSN	TSL	TNL	SNL

Note: * P<0.050; **P<0.010; *** P<0.001; probabilities between 0.100 and 0.050 are denoted with actual figures; and a blank space means that the probability is > 0.100. A slash (/) denotes a factor with the least effect on the trait concerned, and the interactions involved with this factor were not applicable in the three way variance analysis.

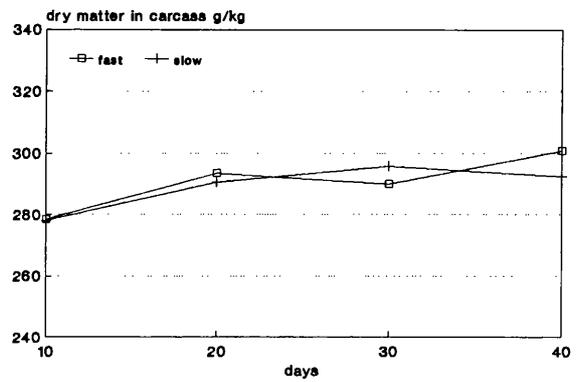
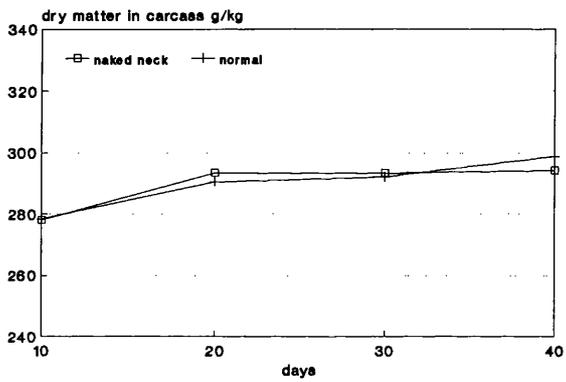
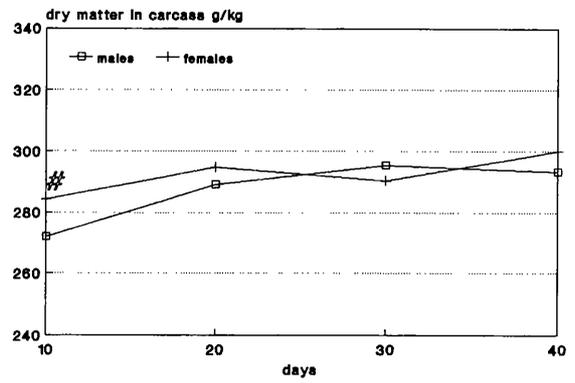
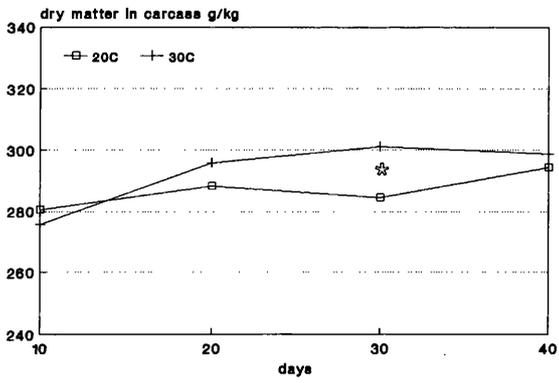


Fig 4.1. Effects of temperature, sex, Na gene and line on the dry matter content in the plucked carcass

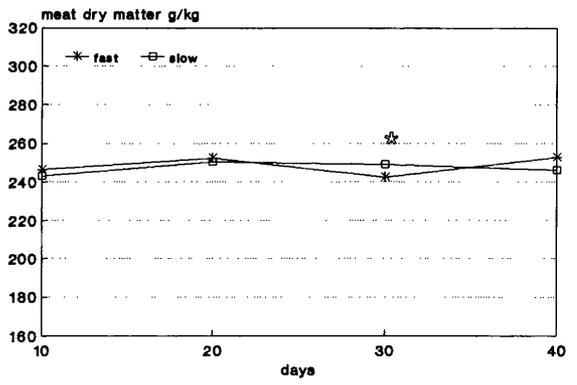
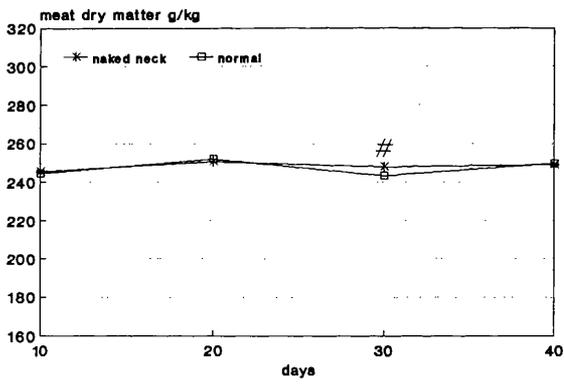
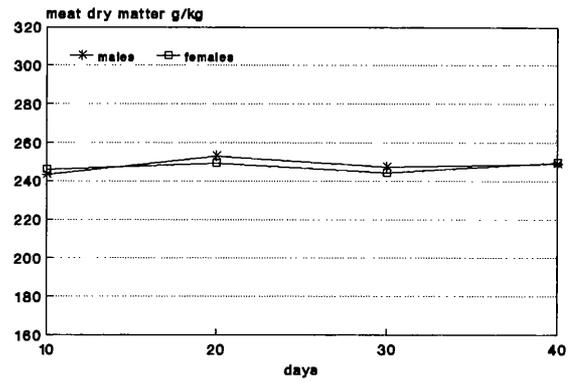
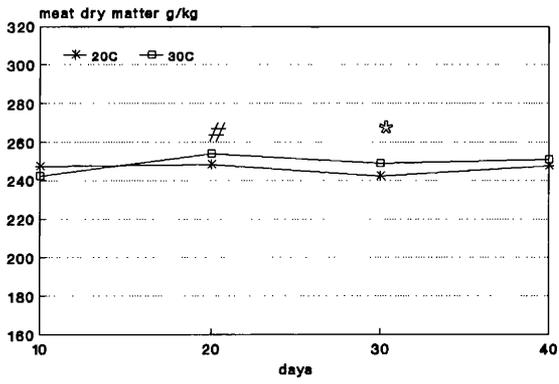


Fig 4.2. Effects of temperature, sex, Na gene and line on meat dry matter content

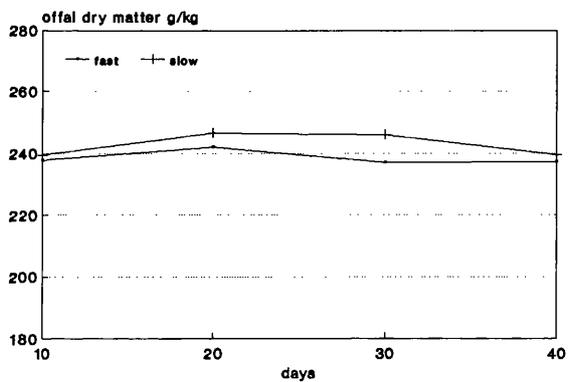
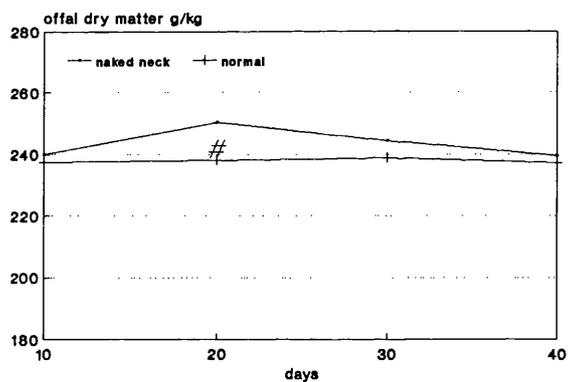
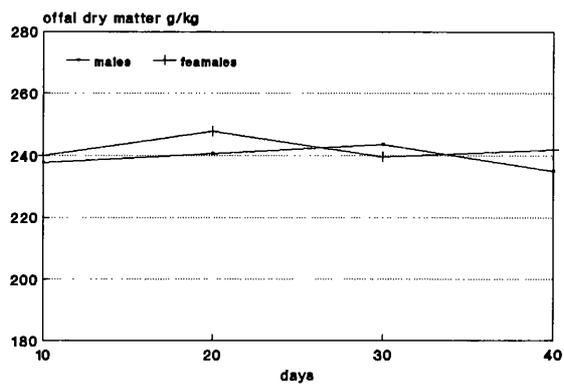
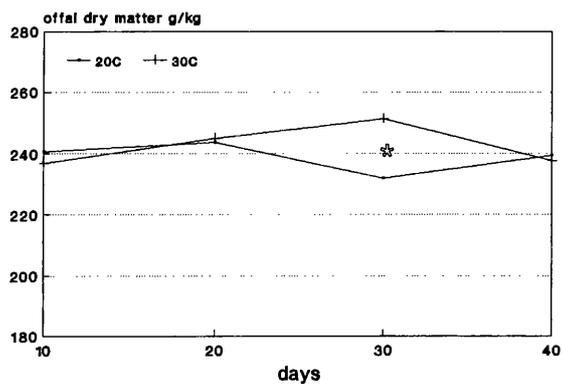


Fig 4.3. Effects of temperature, sex, Na gene and line on viscera dry matter content

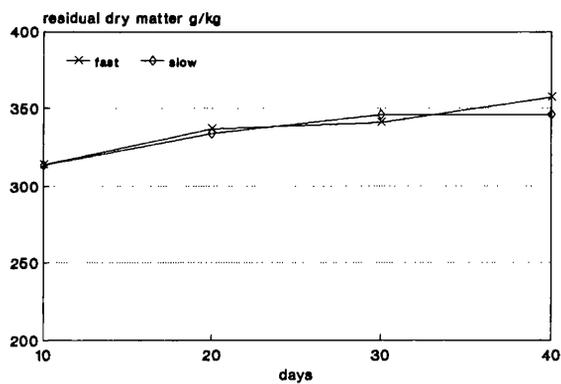
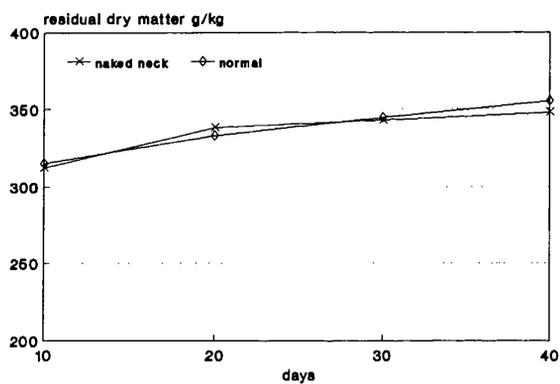
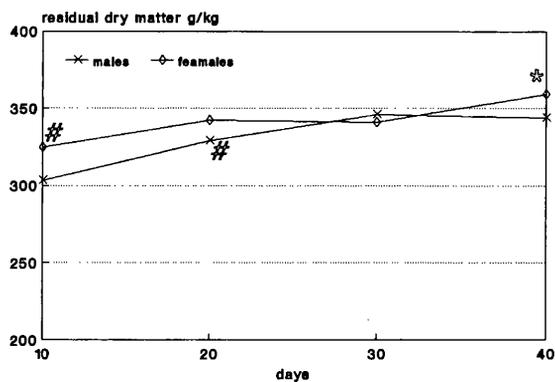
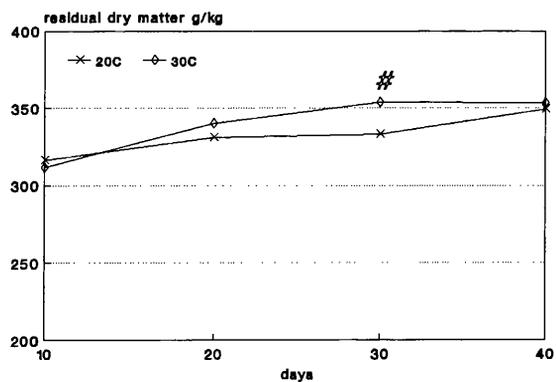


Fig 4.4. Effects of temperature, sex, Na gene and line on residual dry matter content

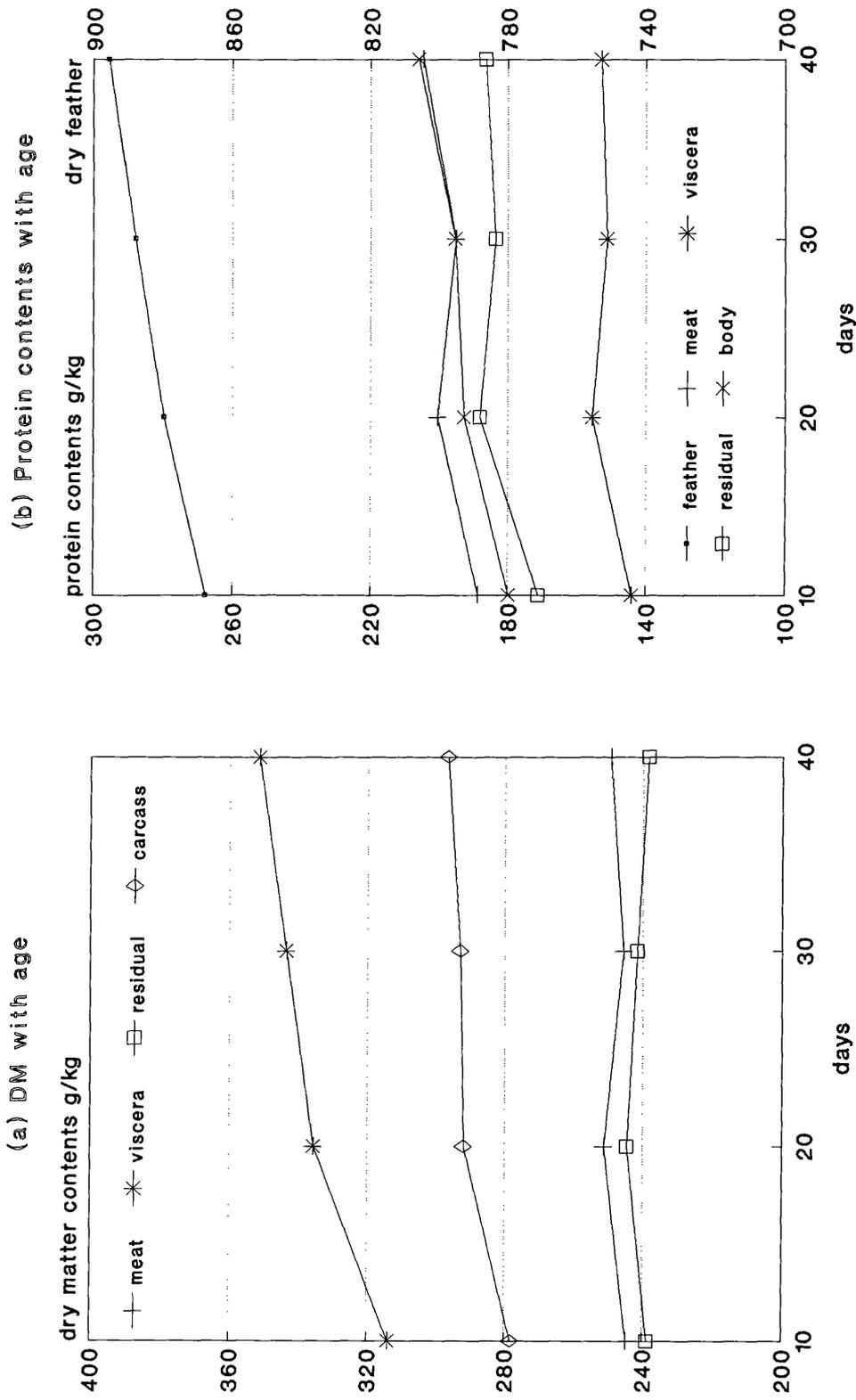


Fig 4.5. Changes of dry matter (a) and protein contents (b) of the carcass (whole body) and the dissected parts with age

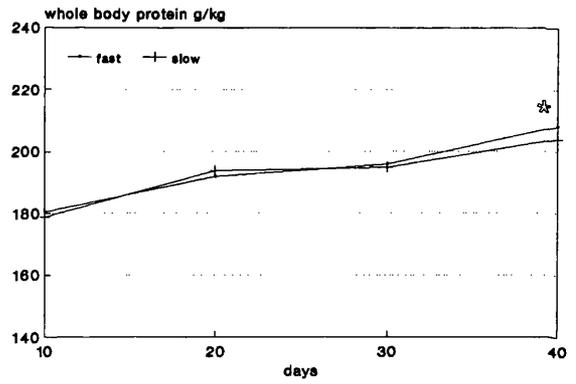
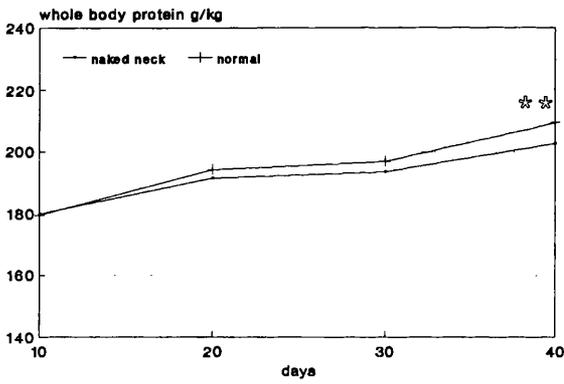
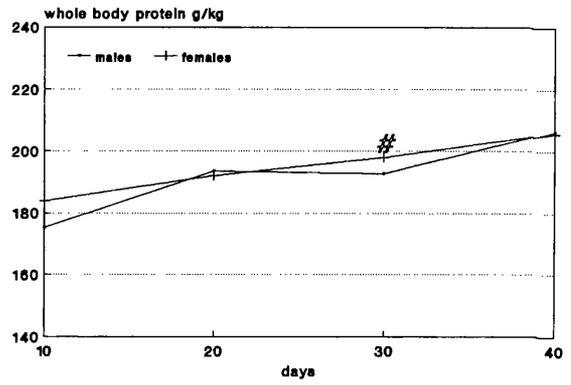
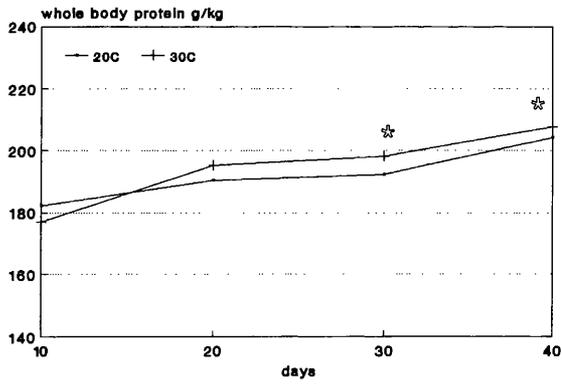


Fig 4.6. Effects of temperature, sex, Na gene and line on the protein content of the starved body

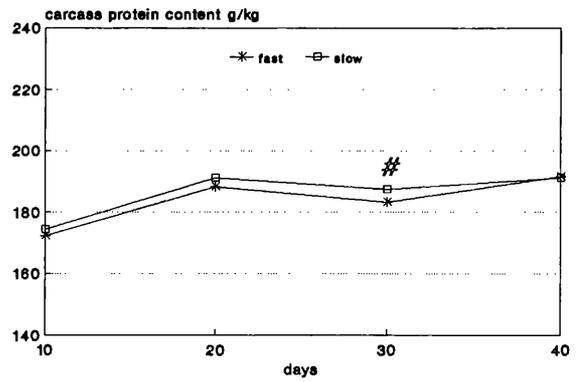
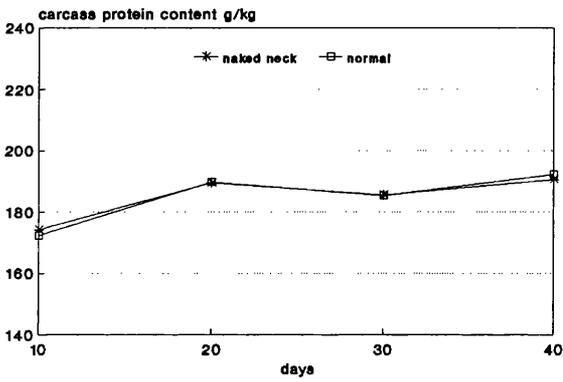
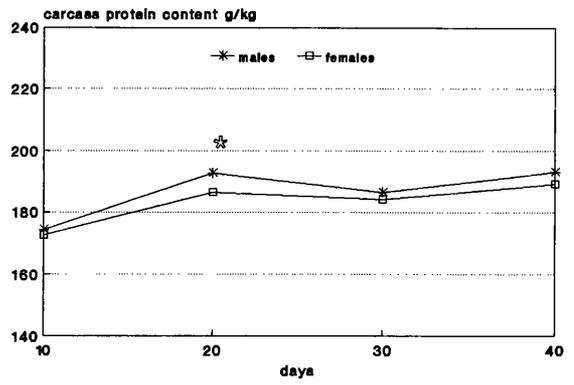
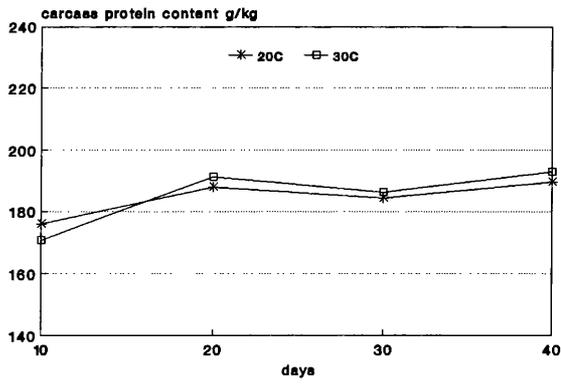


Fig 4.7. Effects of temperature, sex, Na gene and line on the protein content of the plucked carcass

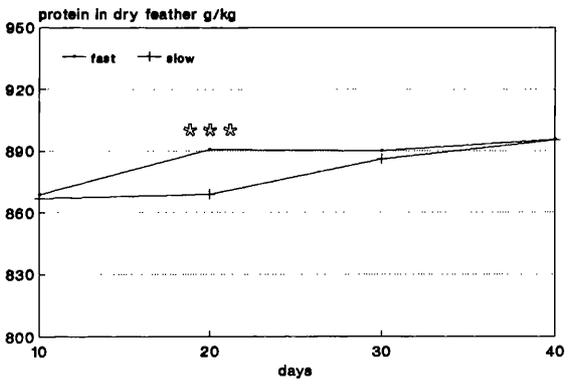
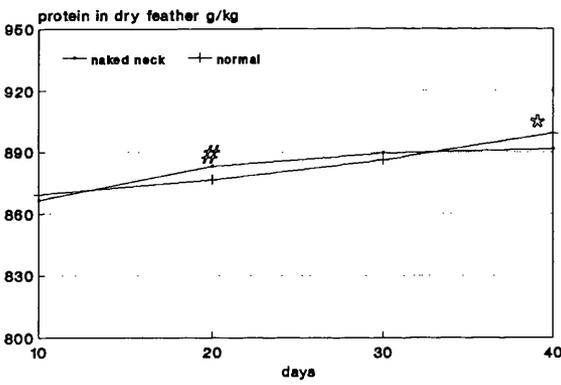
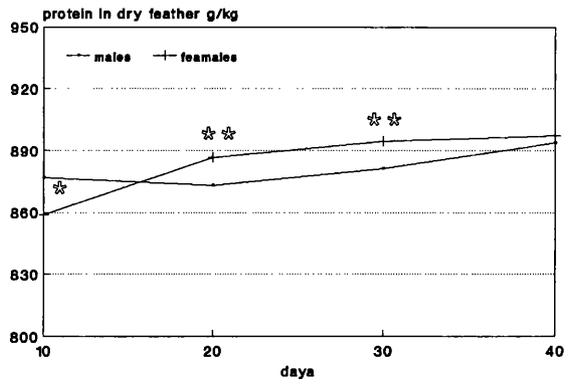
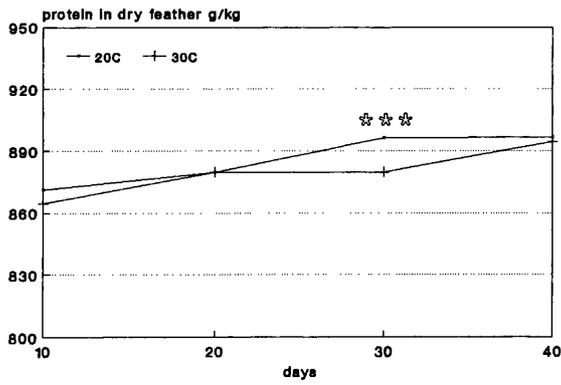


Fig 4.8. Effects of temperature, sex, Na gene and line on dry feather protein content

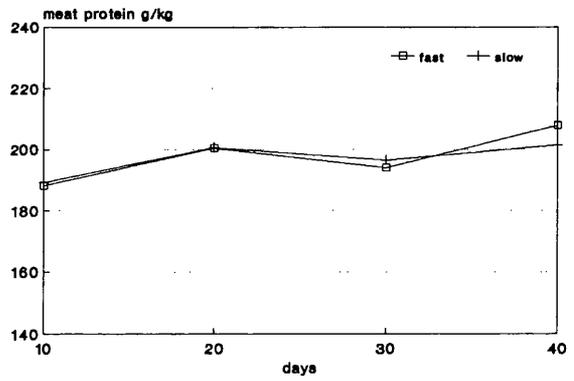
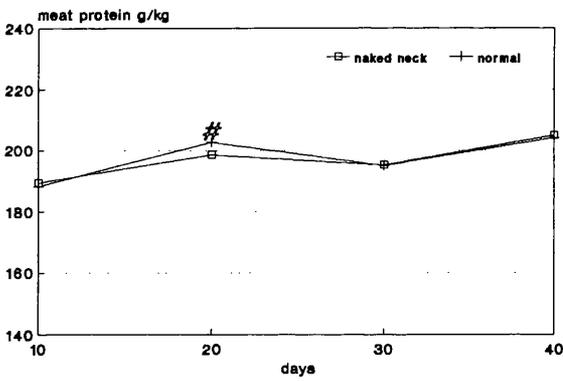
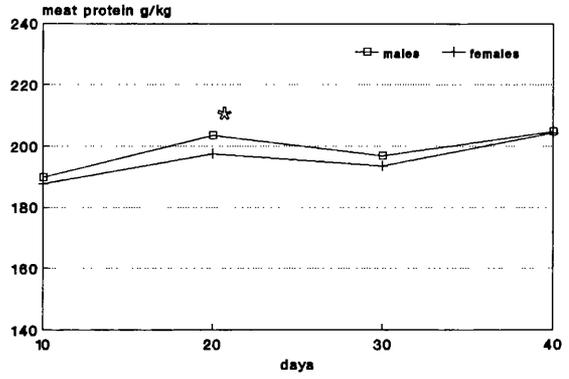
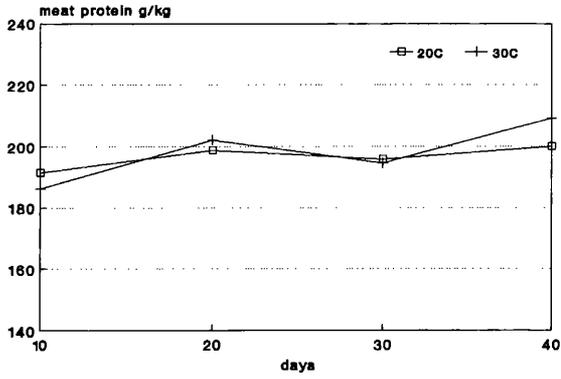


Fig 4.9. Effects of temperature, sex, Na gene and line on meat protein content

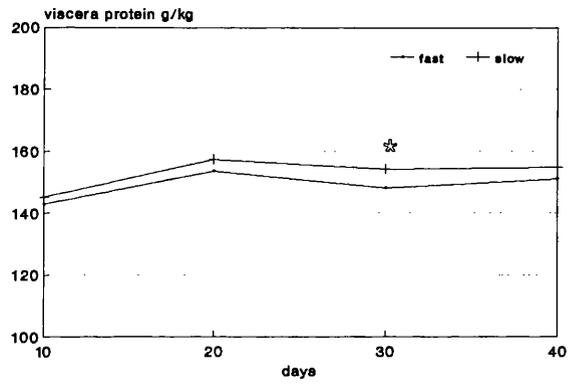
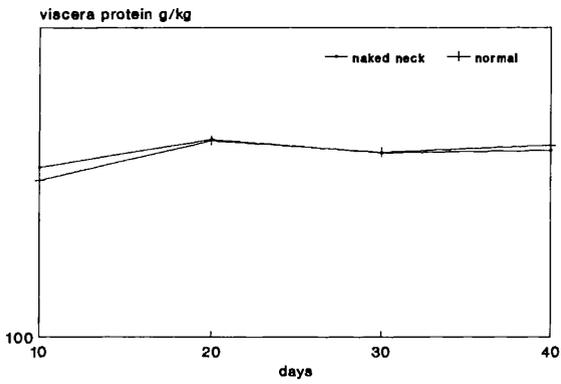
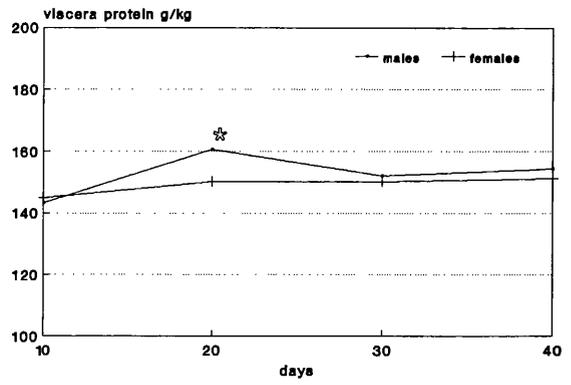
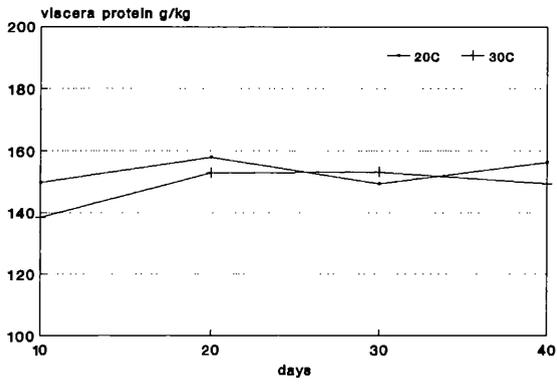


Fig 4.10. Effects of temperature, sex, Na gene and line on viscera protein content

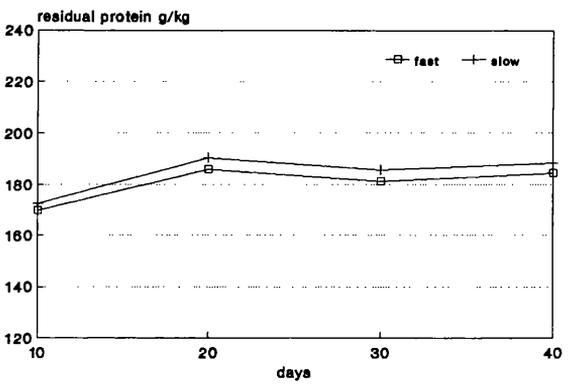
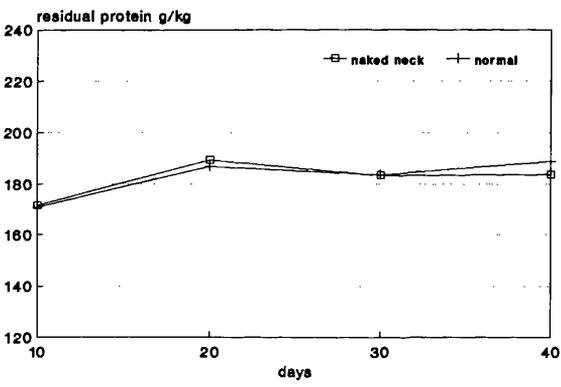
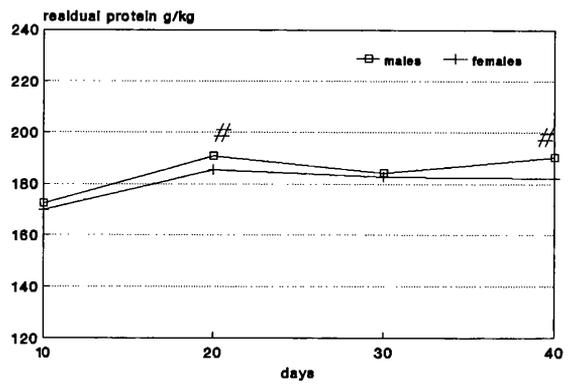
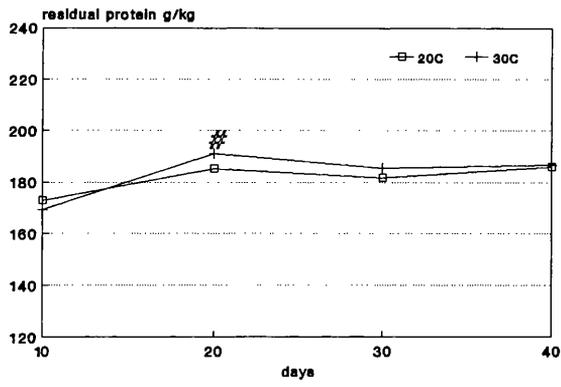


fig 4.11. Effects of temperature, sex, Na gene and line on residual protein content

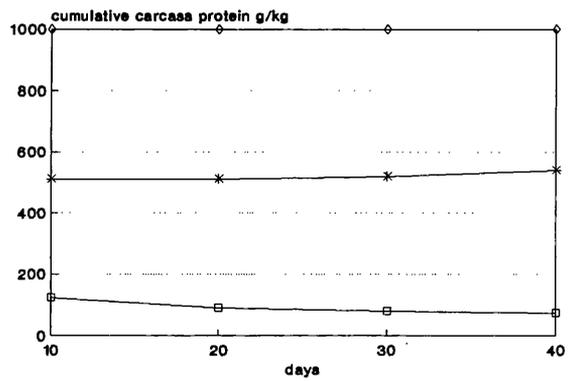
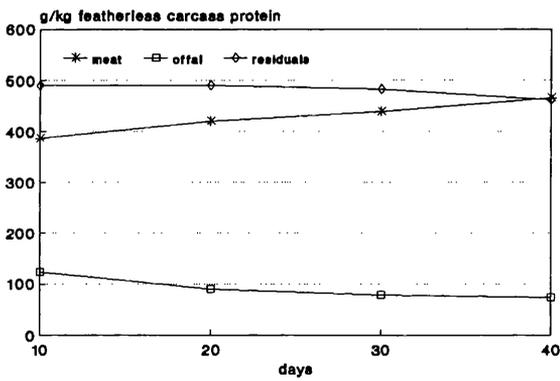
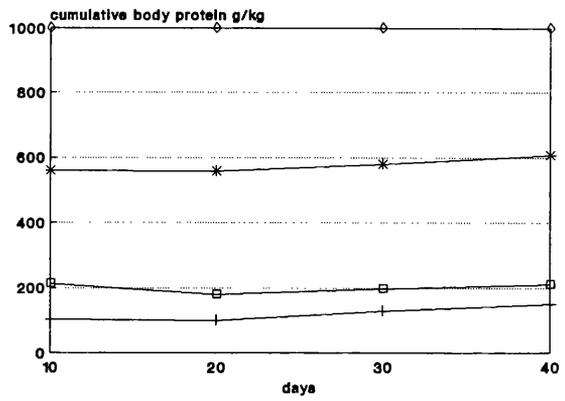
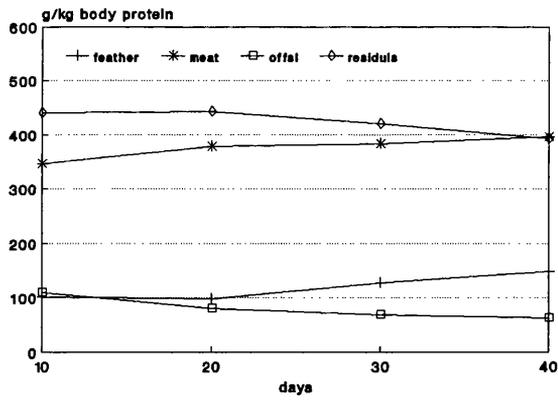


Fig 4.12. Protein partition among feather, meat, viscera and residuals of whole body (above) and plucked carcass (below) (The cumulation order is feather, viscera meat and residual)

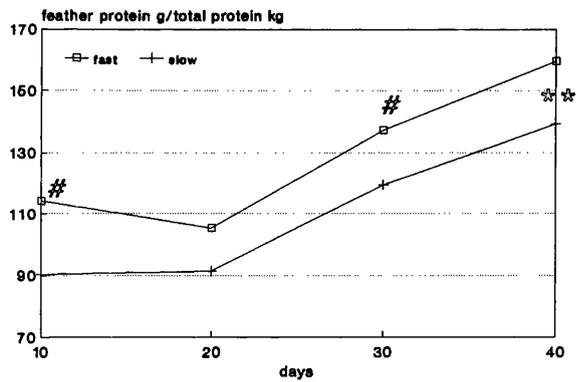
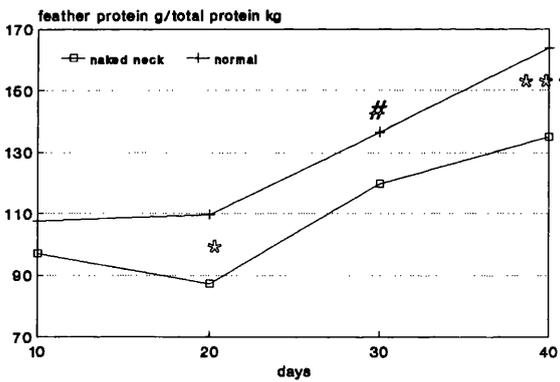
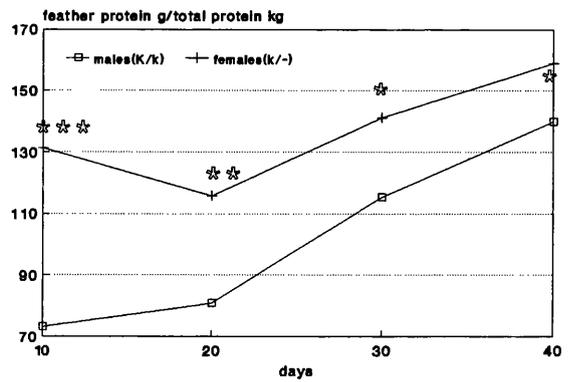
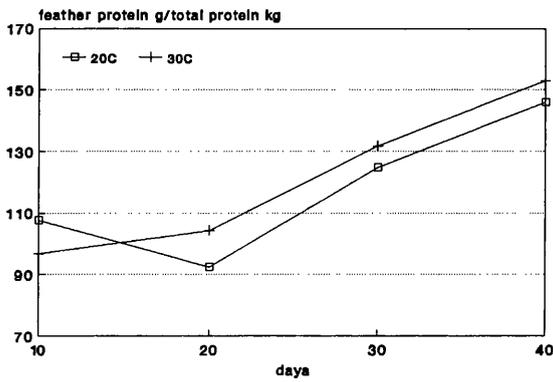


Fig 4.13. Effects of temperature, sex, Na gene and line on whole body protein partition to feathers

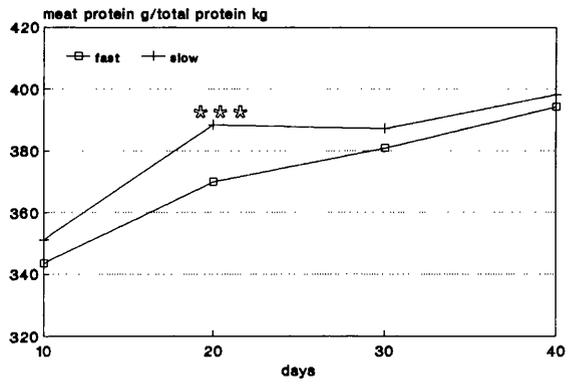
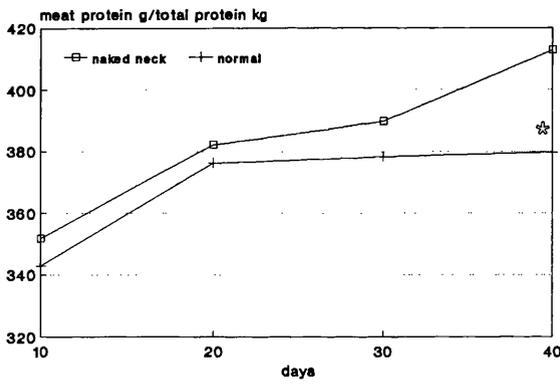
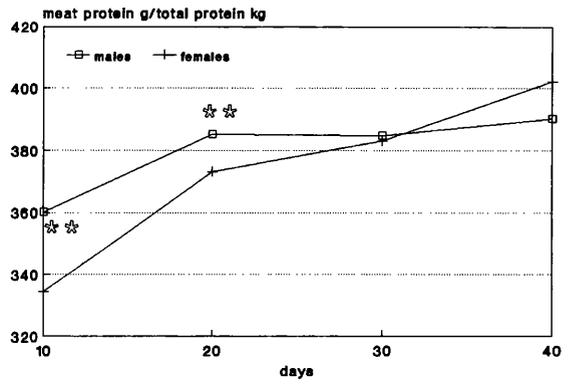
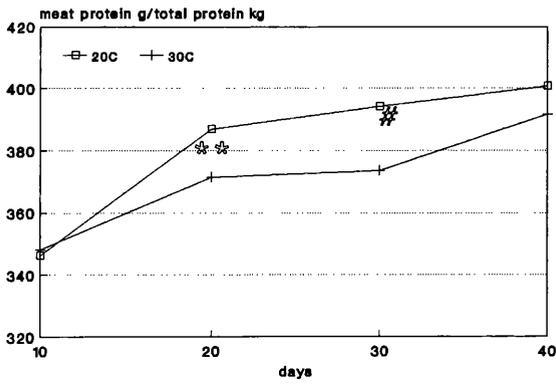


Fig 4.14. Effects of temperature, sex, Na gene and line on whole body protein partition to meat

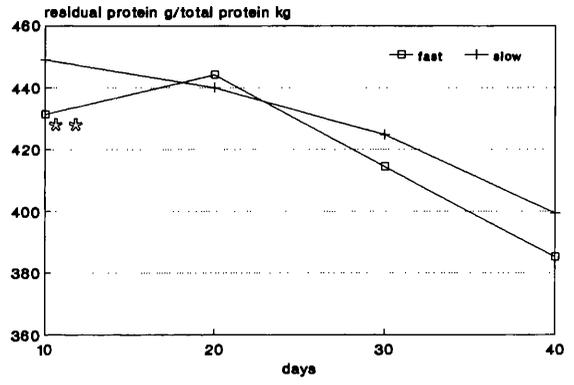
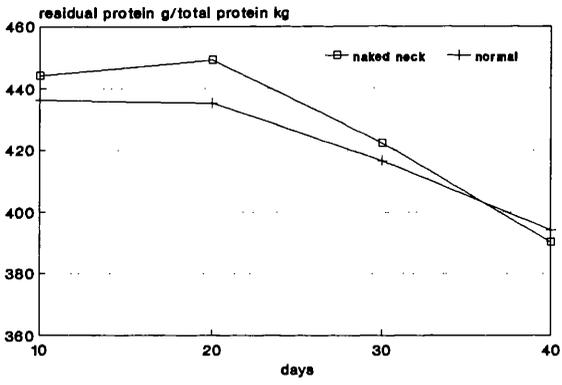
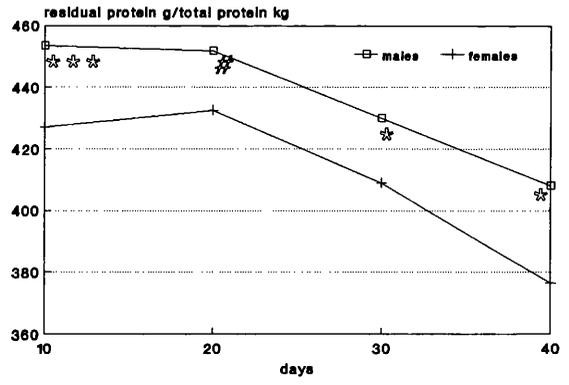
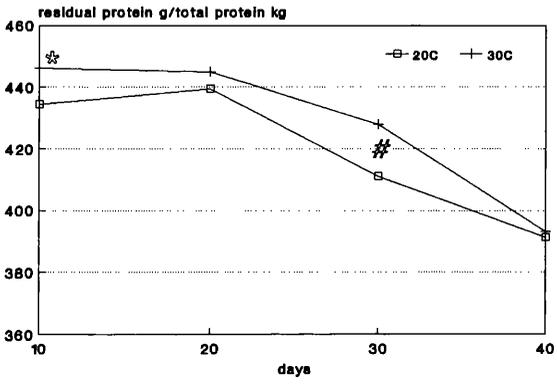


Fig 4.15. Effects of temperature, sex, Na gene and line on whole body protein partition to residuals

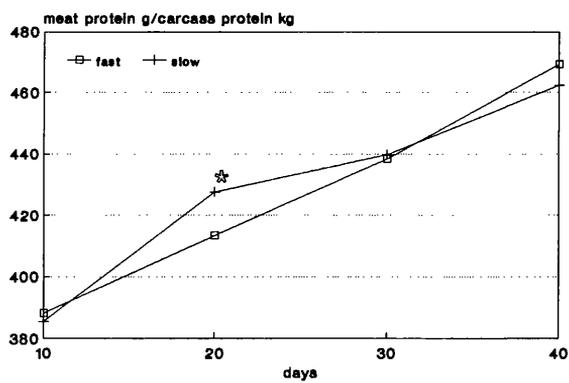
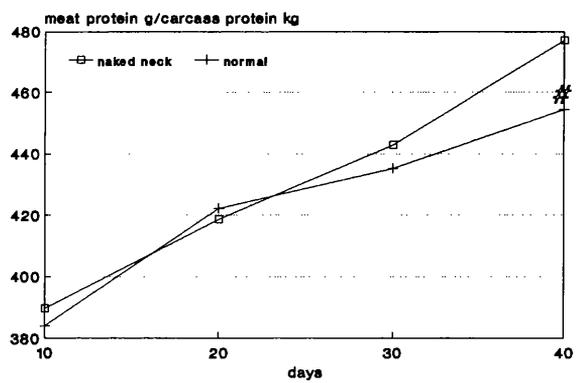
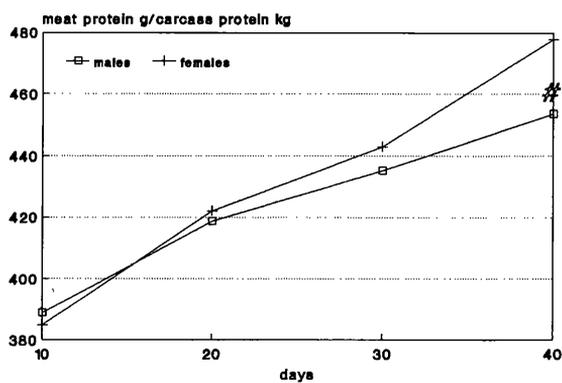
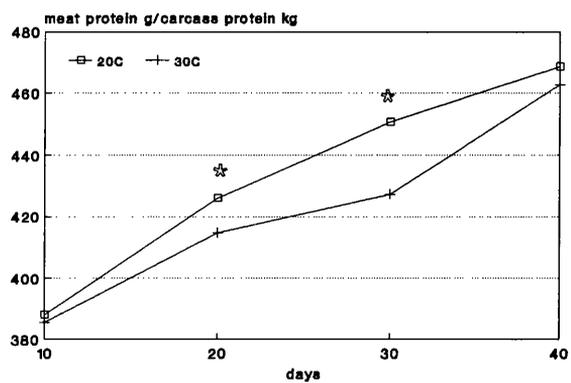


Fig 4.16. Effects of temperature, sex, Na gene and line on plucked carcass protein partition in meat

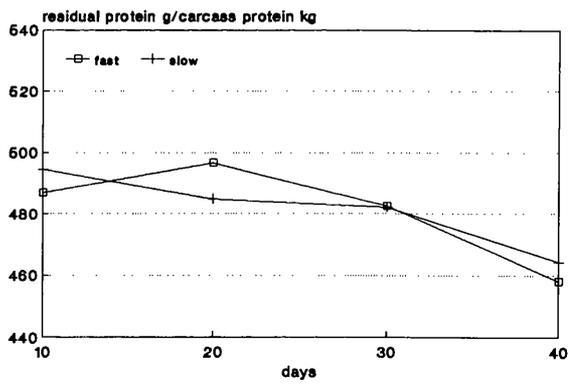
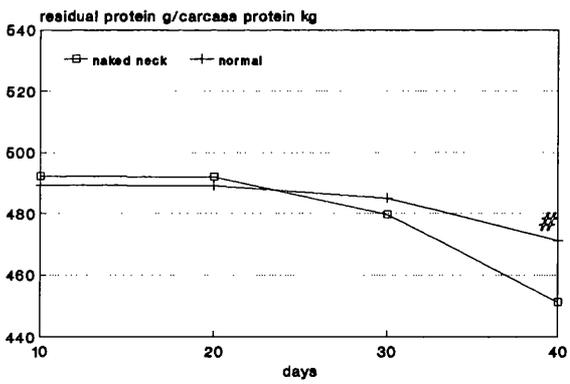
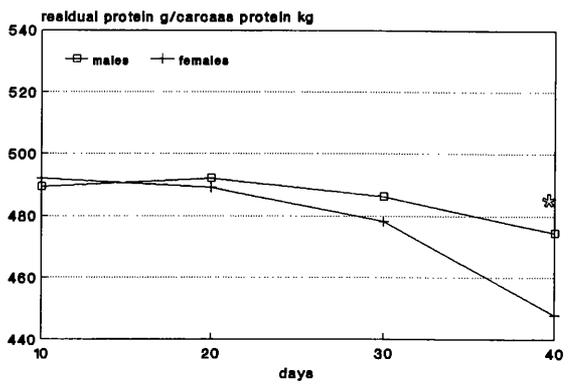
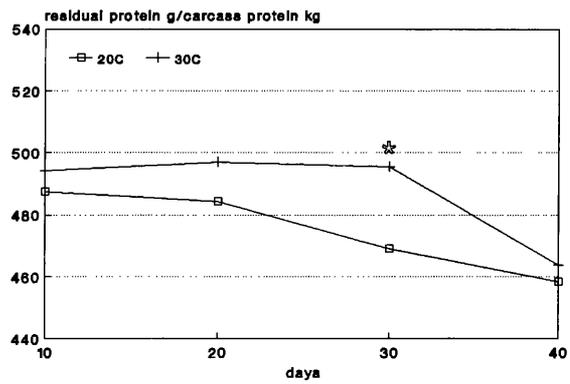


Fig 4.17. Effects of temperature, sex, Na gene and line on plucked carcass protein partition to residual

Table 4.5. Effects of interactions between sex and line on body protein partition in meat and feathers, and plucked carcass protein partition in meat (g/kg)

Age (days)	Males		Females	
	Fast	Slow	Fast	Slow
Body protein in feathers				
*10	100.8	45.4	127.5	135.1
20	91.9	70.0	118.8	112.7
#30	132.4	98.3	141.8	140.2
40	154.5	124.8	164.4	153.6
Body protein in meat				
*10	346.8	373.7	340.1	328.5
**20	368.1	402.0	371.3	374.8
30	377.1	392.5	384.5	381.7
40	384.9	395.5	403.6	400.8
Plucked carcass protein in meat				
10	386.3	391.1	389.8	379.6
*20	404.9	432.2	421.7	422.6
30	434.4	435.8	442.2	443.8
40	455.3	451.8	483.1	472.6

Note: The two way interaction between sex and line was marginally significant (#, $P < 0.1$); significant (*, $P < 0.05$); highly significant (**, $P < 0.01$) or otherwise not significant.

4.4.1.1 Dry matter of the plucked carcass

Fig 4.1 and Table 4.4 indicate that there was no significant effect of the naked neck gene and selection line on the whole carcass DM. At 40 days of age, the fast feathering line (300.8 g/kg) had slightly higher DM than the slow feathering line (292.4 g/kg), and the fully feathered birds also had higher DM (298.9 g/kg) than the naked neck birds (294.3 g/kg). These numerical differences at this age are in agreement with the main conclusions of the earlier reports. Ajang et al. (1993) found that the pure slow feathering line birds (642.9 g/kg in males) at 48 days of age had a higher moisture content (lower DM, $P < 0.01$) than the fast feathering birds (619.7 g/kg in males). In the present experiment, chicks were produced by cross-breeding. Therefore the difference

between the lines had been expected to be smaller than the direct comparison between the two selection lines. As for the effects of the Na gene, Hanzl & Somes Jr. (1983) reported that the carcass moisture content of NaNa birds at 8 weeks was significantly higher (DM lower) than the normal birds.

Carcass dry matter, however, was significantly influenced by temperature and sex, with birds in 30C having higher DM than those in 20C; and females had higher DM than the males (Fig 4.1 and Table 4.5.). The results are supported by several researchers. In an extensive review of broiler growth and body composition experiments, Howliger & Rose (1987) concluded that each degree rise in rearing temperature was accompanied by a 0.15% decrease in moisture content of the as-hatched-broiler carcass. It has been established that females have higher DM than the males (Edwards et al., 1973; Pym & Solvyns, 1979; Broadbent et al., 1981; Chambers et al., 1981; Ajang et al., 1993). However, in the present experiment, the difference between sexes was significant at 10 days of age only, and at later ages, the difference was so small that at 30 days, the DM figure was even higher in the male than in the females. This result was unexpected.

No important interaction effect within age was found for carcass DM content. Therefore, in general, high temperature, being females rather than males, and factors promoting faster or more feather growth tend to have a positive effect on the carcass DM content. More importantly, since carcass DM and fat are positively related with each other, these same factors could have a positive effect on carcass fat content as well.

4.4.1.2. Dry matter in parts

Dry matter contents of various carcass parts are rarely reported in the literature. The effects of single factors on the DM content in meat, viscera and residual are shown in Figs 4.2 , 4.3 and 4.4. The only consistent effect on DM content in the meat was temperature. The meat dry matter content was consistently higher for birds raised in 30C than in 20C (Fig 4.2) (At 10 days, all of the birds were still in the same brooding temperature). Meat produced from the slow feathering line birds was significantly higher ($P < 0.05$) in DM at 30 days. However at 40 days, meat DM was numerically higher in the fast line.

High temperature resulted in higher viscera DM at 30 days of age only. The differences between the two temperatures at other ages were very small.

As in the case of whole carcass, DM in the residual (Fig 4.4) was higher in the females than in the males, and slightly higher in birds raised in 30C. Residual dry matter was not affected by the Na gene and line.

4.4.1.3. Dry matter with age

There were major increases in DM contents of the plucked carcass and the various parts of it between 10 and 20 days of age. After that, there was little further increase in meat DM and residual DM (Fig 4.5a). The small increase in carcass DM at the later ages was mainly caused by a steady increase in the viscera DM.

The relatively small but steady increase in the carcass dry matter content in the duration of the present study was supported by literature. Prescott et al. (1985) showed that the DM content in the eviscerated carcass of broiler cockerels was lowest between 1 and 2 weeks of age, and the DM increase was small up to the age of 9 or 11 weeks. Data presented by Edwards et al. (1973) also showed that the plucked carcass DM increase was steady but small either between 4 and 8 weeks of age (from 27.0% to 28.6% in males and from 27.8% to 30.6% in females) or between 2 and 10 weeks (males from 27.4% to 29.2%, females from 27.8% to 32.2%). The overall means of the plucked carcass DM at different ages in the present experiment (278.1, 292.0, 292.9, 296.6 g/kg for 10, 20, 30 and 40 days of age respectively) were well within the ranges of the above literature.

4.4.2 Protein Contents

The protein contents in the wet, fresh samples are reported here. Although differences in the moisture content (or rather the dry matter content) between the samples, especially for those taken from different ages, tends to have some effect on the protein content on the wet sample basis, expression on this basis is justified since fresh meat is what consumers are buying.

An increase in carcass DM content between 10 and 20 days of age presented in Fig 4.5a coincided with the increase in protein content in meat, viscera and residual samples and of course in the whole body as well. The increase of protein content in the dry feather across age will be discussed later.

4.4.2.1. Protein content in the starved body

The effects of temperature, sex, Na gene and line on the protein contents of the starved body are shown in Fig 4.6.

All of the four factors are occasionally significant for their effects on the whole body protein content. However, the effects of temperature and the Na gene seem to be more consistent than the effects of sex and line. Generally, the higher temperature resulted in higher body protein content (significant at 30 and 40 days). The poorer feathered naked neck birds tend to have lower whole body protein content, and furthermore, the effect of this gene seems to increase with age (not significant at 30 days and before, $P < 0.01$ at 40 days). and the better feathered female chicks had significantly higher ($P < 0.05$) body protein content at 10 days, and slightly so at 30 days ($P < 0.1$) than their male counterparts. The line effect was relatively small, but significant at the end with the fast feathering birds having higher whole body protein content than the slow feathering ones ($P < 0.05$).

Due to the high protein content in feathers, the protein content of the whole starved body is largely influenced by the relative amount of feather covering. The more feather covering, the higher the whole body protein content tends to be.

4.4.2.2. Protein content in the plucked carcass

Because the feathering condition of the birds has a profound effect on the whole body protein content, it could obscure the revealing of effects of the factors on the protein content of the carcass underneath the feathers on the whole body basis.

Fig 4.7 shows that protein content in the plucked carcass was not affected by the Na gene at all. This is in agreement with the result by Hanzl & Somes Jr. (1983). The effect of temperature was nearly negligible in the present experiment because the differences did not reach even the 10% probability level. This result is in accordance with the conclusion reached by Howlinder and Rose (1987), and also with the result obtained by Somes Jr. & Johnson (1983), but against that by Hanzl & Somes Jr. (1983).

In contrast with the situation found in the whole body protein content, male carcasses had a higher protein content at all of the four ages than the female carcasses and the difference was significant ($P < 0.05$) at 20 days. Evidence from the present

experiment suggest that it would be unlikely that the lower carcass protein content in the females is the direct result of more feather growth, for the Na gene which substantially reduces whole body feather synthesis did not enhance the carcass protein content. In the published reports, feathers are usually not included for the carcass composition comparisons, and the protein content of the males is unanimously higher than that of the females (Edwards et al., 1973; Pym & Solvyns, 1979; Broadbent et al., 1981; Chambers, 1981; Ajang et al., 1993).

The line effect was smaller than previously reported by Ajang et al. (1993) at 48 days of age because of the involvement of the non-selected line in the present mating plan. It should be noted that the slow feathering line is higher in carcass protein content than the fast feathering line (Fig 4.7). This is also, as in the case of the sex effect, opposite to the situation with whole body protein.

4.4.2.3. Protein content of carcass parts

4.4.2.3.1. Protein content of the dry feather

The effects of the single factors on the dry feather protein content shown in Fig 4.8 gave a confusing picture. The effect of temperature was small and non-significant at the age of 10, 20 and 40 days, but highly significant ($P < 0.01$) at 30 days of age when the dry feather from 20C had a higher protein content than the dry feather from 30C. The dry feather from the males had higher ($P < 0.05$) protein content than feathers from the females at 10 days of age, but the opposite was true at 20 and 30 days ($P < 0.01$). At 40 days of age, the sex difference diminished ($P > 0.1$).

The effect of the Na gene on dry feather protein content seems to be small and unimportant though the difference in protein content between naked neck feathers and normal feathers was marginally significant ($P < 0.1$) at 20 and significant ($P < 0.05$) at 40 days of age. In the former case, feathers from the naked neck birds had higher protein content, and in the latter, feathers from the fully feathered birds had higher protein content.

The effect of line on the feather protein content was highly significant ($P < 0.001$) at 20 days of age when the fast feathering line had higher feather protein content than the slow feathering line. However the differences at all of the other ages were small and non-significant.

Considering the high value of protein content in dry feathers, and the relatively small effect of all of the factors studied at the end of the experiment (age of 40 days), it can be assumed that the dry feather protein content is uniform under various conditions at the broiler age. Therefore the overall mean of 895g protein/kg dry feather will be used in the later experiments in the calculation of feather protein content at a similar broiler age.

4.4.2.3.2. Protein contents in the meat, viscera and residual

Meat protein content was not affected by temperature, Na gene and line at the four ages studied (Fig 4.9). However meat from the males had a consistently higher protein content than the meat from the females and the sex difference was significant at 20 days of age ($P<0.05$). This sex difference might have reflected the slightly higher fat content in meat from the females.

The viscera protein content shown in Fig. 4.10. was not influenced by temperature and the Na gene (the significant difference between the two temperature groups at 10 days of age was caused by some unknown factors, for the temperature treatment had not started yet at that time). Again the males had slightly higher protein content in the viscera than the females (significant ($P<0.05$) at 20 days of age).

The numerically higher protein content in the residual of the slow feathering line (Fig. 4.11) was in accordance with the trend found in the plucked carcass both in the present experiment and that of Ajang et al. (1993). This line difference was consistent across the ages. Statistically, however, none of the four factors considered had ever reached the 5% significance level for their major effect (Table 4.4).

4.2.4 Age effect on the protein content

A slight increase in the protein content in meat, viscera, residual and whole body with age has been outlined earlier. However the increase of protein content in dry feather with age is much more noticeable than all of the other parts (Fig 4.5.b).

Increasing protein content in dry feather with age was also observed by Fisher et al. (1981) and Prijono (1991) although the increase found in those two reports were not so consistent as in the present experiment. The reasons for this change over the ages have not been previously discussed in any detail. It is possible that the greater amount of

other tissues (other than the keratinised feather structure) around the feather shaft of the younger feather might be responsible. During plucking, a mature feather can be pulled out neat and clean while an immature feather, because the part underneath the skin surface is still being keratinised with a vascular pulp, tends to come off together with the tissues surround it. These contaminant tissues have lower protein content than the feather itself. Therefore the effect of age is actually the effect of degree of feather maturity. This also explains the fact that factors which promote early feather growth (normal rearing temperature, early feathering in the females and fast feathering) all tend to have a positive effect on the feather protein content (Fig 4.6).

4.4.3. Protein Partition

The proportion of whole body protein retained in feathers increased with age (Fig 4.12). This is in agreement with the previous result obtained in the same feather selection lines (Priyono, 1991) and with the fact that feathers are gaining their proportional weight with age in broilers (Edwards et al., 1973; Prescott et al., 1985; Quoi, 1991).

No matter whether feathers are included (whole body) in the calculation of the protein partition or not (plucked carcass), the partition tendency with age among the other three parts are still the same. With increasing age, more protein was found in meat and less in the viscera and residual (Fig 4.12). This result is also in good agreement with the general knowledge that muscles mature later than the digestive organs and the skeleton and with the results obtained by Priyono (1991).

4.4.3.1. Whole body protein partition to feather, meat, viscera and residual

4.4.3.1.1. To feathers

There was great similarity in the patterns of the effects of various factors on the proportional body protein in feathers (Fig 4.13.) and effects of these same factors on the feather weight or even feather length measurements reported earlier (Quoi, 1991; Lou et al., 1992). Considering the small variation in feather protein content and large effect of sex, Na gene and line on dry feather weight, these results were expected. So was the interaction between sex and line (section 4.4.3.3).

4.4.3.1.2. To meat

Fig 4.14. shows that high temperature has an adverse effect on the protein deposition in meat, for the proportion of total body protein found in meat was significantly less ($P<0.05$) at 20 days, slightly less ($P<0.1$) at 30 days and still numerically less at 40 days of age under the high temperature regime than in the normal temperature.

The less feathered naked neck birds and slow feathering birds had more protein deposited in the edible meat. However the effect of the Na gene was more profound at the older age, and the effect of line was largest at about 20 days when it coincided with the time of feather selection in the original lines. These distinct features had not been compared earlier.

The effect of sex (confounded with the effect of hemizygous early and heterozygous late feathering genotypes) was inconsistent with age. At 10 and 20 days, whole body protein partitioned into the total edible meat was highly significantly more ($P<0.01$) in males than in females. At 30 days, the protein found in meat was essentially the same for both sexes. Whereas at 40 days of age, females had more body protein in meat than the males though the difference was not significant statistically (Fig. 4.14).

Protein partitioned in the viscera was not affected by any one of the factors.

4.4.3.1.3. Protein partition to the residual

The most profound and consistent effect on the whole body protein partition to the residual is the effect of sex (Fig 4.15). The males deposited a much larger proportion of protein in this part of mainly bones and skin at all of the ages studied.

The effect of temperature was not significant except 10 days at which age the brooding temperature was the same for both of the groups. The effects of the Na gene and feathering line seem to be not important on the body protein partition to the residual though the line effect was significant at 10 days of age.

4.4.3.2. Protein partition of the plucked carcass to meat, viscera and residual

The protein partition of the plucked carcass is the body protein partition after the direct effect of protein contained in feathers has been eliminated. Therefore the effect of feathering gene(s) found in this way, if any, may include the pleiotropic effect of the gene(s) on the body protein partition.

4.4.3.2.1. To meat

Generally, the pattern of effects of the factors on the carcass protein partition to meat (Fig 4.16) is similar to the partition of the whole body shown in Fig 4.14. The effect of temperature was essentially the same; the effect of the Na gene and feathering line were still evident at 40 days for the former and at 20 days for the latter though both of the effects was reduced to a lesser extent compared with their effects on the whole body basis.

However, the effect of sex on protein partition to meat of the plucked carcass (Fig. 4.16) was profoundly different from that of the whole body protein (Fig. 4.14). The significant effect of sex found on the whole body basis at 10 and 20 days of age was not found on the plucked carcass basis. Female carcasses started to have more protein in meat than the male carcasses from 20 days onward, and the difference between the sexes increased with age (Fig. 4.16). The sex difference was nearly significant ($P < 0.1$) at the end of the experiment. The increasingly higher proportion of carcass protein deposited in the females might mean that the skeleton and / or the digestive organs mature earlier in the females than in the males.

4.4.3.2.2 To the viscera

The viscera share of the total carcass protein was not affected by any of the factors studied.

4.4.3.2.3. To the residual

The plucked carcass protein partition to residual shown in Fig 4.17 had a few important features which were different from the whole body protein partition to residual (Fig 4.15).

First of all, the consistent large difference between the two sexes throughout the duration of the experiment on the whole body basis was evident only at 40 days of age with the males having more protein in residual than the females.

Secondly, on the whole body basis, there was no obvious effect of the Na gene on the amount of protein in the residual, while on the plucked carcass basis, Fig 4.17 shows that the naked neck birds spent slightly less protein ($P < 0.1$) on residual part of the carcass (the bones and skin) towards 40 days of age.

The effect of temperature was similar on both of the two bases. At high temperature, birds spent more protein on the residual than the birds at the normal temperature. No consistent feathering line effect was found on either of the two bases.

4.4.3.3. Effects of interactions on body and carcass protein partition

All of the two way interactions between the four factors considered in the present experiment which were significant at least once were carefully checked for their consistency with age. Most of the significant interactions shown in Table 4.4 lack consistency and therefore might have been caused by some uncontrolled random factors. However, the effect of interaction between sex and line on protein partition to feathers and meat seemed to be reasonably consistent with age. Table 4.5 presented the effect of this interaction on the protein partition to meat and feathers on the whole body basis and to meat on the plucked carcass basis.

The difference between the two lines, in terms of the amount of whole body protein in both feathers and meat, was small and even inconsistent in the early feathering females, while in the males, all of which had a late feathering phenotype, the fast feathering line birds consistently diverted more body protein for feather growth and less protein for meat production than the slow feathering line.

The interaction effect on the amount of feather protein can be looked at as the direct result of the same two way interaction in terms of feather length and feather weight measurements reported earlier by Quoi (1991). This interaction was caused by a lack of response of the early feathering females to the line effect in feathering as explained later by Lou et al. (1992).

The significant but opposite ways of the same two-way interaction of meat protein share and the feather protein share, together with the fact that the residual and viscera protein shares in the plucked carcass were not affected by the interaction, indicated that

much of whole body protein partition difference of the two lines of males was a direct shift of the body protein between meat and feathers, i.e. the more protein in feathers, the less protein in meat, and vice versa. This conclusion was also supported by the fact that the naked neck birds had significantly more protein in meat at 40 days of age, but not in the residual or viscera than the fully feathered birds. However, the meat protein difference in the plucked carcass between the fast and slow feathering males found at 20 days of age was not carried over to the later ages (Table 4.5). Therefore the biological importance of feathering effect on the protein partition underneath the feathers themselves at the broiler age is still to be elucidated.

4.5. CONCLUSIONS

The following can be concluded from the results of the experiment.

1) The DM and protein contents of broiler carcass and its dissected parts were not generally affected by the feathering conditions or the feathering genotypes. High temperature increases the dry matter content in the meat, viscera, residual and whole carcass. The females have higher DM in the residual but lower protein content than the males in the carcass and each of the dissected parts.

2) Protein content of the dried feathers is related to the degree of its maturity. Both increasing age and factors which promote earlier feather growth have positive effects.

3) The reduction in the relative amount of carcass protein diverted to the viscera was not affected by temperature, sex and feathering genotypes. While high temperature reduces the carcass protein diverted to meat and increases it in residual, the naked neck gene has an opposite effect. An increasingly higher proportion of carcass protein was deposited in meat in the females than in the males.

4) The effect of the interaction between K gene genotype (sex) and feathering line on the amount of body protein in feathers followed the pattern of the same interaction effect on the weight or length measurements of feathers.

5) The proportion of meat protein in carcasses increases with age at the expense of both viscera and residual. Feather protein of the whole body also increases with age.

CHAPTER 5.

EFFECTS OF NAKED NECK GENE, Na, EARLY (kk) OR LATE (Kk) FEATHERING AND FAST (F) OR SLOW (S) FEATHERING ON BROILER GROWTH PERFORMANCES AND CARCASS TRAITS

5.1. INTRODUCTION

Growth rate, feed conversion ratio and meat yield of broilers have been the major concerns of the broiler industry, and massive amounts of resources have been put into their improvements. Selection for growth rate in broilers is comparatively straightforward for the ease of individual measurements and a medium to high heritability. By contrast, however, selection for feed conversion and carcass traits is not only expensive but the rate of improvement of these traits may also be slow owing to the difficulties in measuring the traits and the fact that only a limited number of birds can be recorded at a time for the selection purposes. Therefore selection for major genes, like feathering genes, which contribute to the genetic variation of these traits, could be very helpful in a selection programme.

In the past, much effort has been expended in the comparison of the early feathering (kk and k/W) and late feathering (KK, Kk and K/W) phenotypes in terms of growth and carcass traits because of their importance in sexing day-old chicks. However both the body weight and carcass trait responses to the feathering genotypes were inconclusive (Chambers et al., 1993/4).

The naked neck gene, Na, was reported to reduce the amount of skin area covered by feathers (Hutt, 1949; Bordas et al., 1978; Merat, 1986; Horst, 1988) without interfering with feather growth rate (Quoi, 1991). Detrimental effects of the naked neck gene on body weight and feed efficiency were previously reported by Merat (1986) at moderate and low temperatures. A recent report by Eberhart and Washburn (1993b) put the effect of the Na gene on growth into question again. It was found that the heterozygous naked neck birds were heavier at 8-weeks of age than the normally feathered counterparts produced from the same parents both in a light weight population and a heavy weight broiler population at both 21°C and 32°C. FCR of the naked neck birds at 21°C was very close to the normally feathered birds. However, the

naked neck birds were consistently found to be the better meat producers than the normally feathered ones (Zein-el-dein et al., 1981, 1984; El-attar and Merat, 1985; Lou et al., 1992).

The general conclusion that the naked neck gene may have an overall beneficial effect on broiler production at "high ambient temperatures, from 25°C and mainly around 30°C and above" was reached by Merat (1986), mainly based on the data from light body weight birds. There is the possibility, however, that the insufficient feather covering brought about by the naked neck gene might be compensated at the early age by earlier development of the plumage. With the availability of male broiler chicks having a diverse rates of feathering, the present experiment was designed to test this hypothesis at the lower temperature limit of 25°C outlined by Merat (1986) and to seek the best feathering genotype at this temperature for broiler production both in terms of growth traits and carcass traits.

5.2. MATERIALS AND METHODS

5.2.1. Stock

A total of 377 individually wing-banded male chicks with eight different feathering genotypes were created for use following the two step procedures described in Chapter 3. Comparisons were made of naked neck (Nana) vs. normal (nana), early (kk) vs. late (Kk) feathering, and a quarter fast (1/4F) vs. a quarter slow (1/4S) feathering in terms of feather growth, body weight gain, feed efficiency, carcass and meat yields and chemical composition at a post-brooding temperature of 25 °C.

5.2.2. Housing and the Layout of the Experiment

A large room in a controlled environment building was divided into twelve equal sections of 7.4 m² along the two sides with a corridor in the middle. Each section was then sub-divided equally to create 24 pens. The two consecutive sections in one side of the room and the two across the corridor facing them were assigned as one of the three blocks to hold the birds of the four major gene genotypes randomly, and the two pens within a section were used as sub-plots to accommodate the birds from the two different lines differing in polygene genotypes.

Each pen was provided with two new egg trays and a mini drinker for the first five

days and then replaced gradually by a tube feeder and a bell drinker. A space gas heater was installed in the middle of each of the twelve sections. The dry bulb temperature was set at 33°C for the first two days and then reduced by 1°C every two days until 25°C was reached at day 16, after which temperature was kept at 25°C. For other aspects of bird management procedures, see Chapter 3. The experiment ended at 51 days of age.

5.2.3. Diets

Two isoenergetic (12.7MJ/kg) diets, one summit and one protein-free dilution were formulated, as previously used by Ajang et al. (1993) with some minor changes, and were mixed in different proportions to give a series of starter, grower, and finisher /withdrawal feeds, containing 240, 220 and 200 g/kg protein respectively, and each subsequently used in the three 17-day periods. The resultant ingredient compositions and the nutritional values for the diets are shown in Table 5.1. Chemical analysis of diet protein (CP), fibre, starch (STA), soluble sugars (SUG) and ether extract (EE) was carried out with the 500g feed samples taken from each mix at bagging. The metabolisable energy (ME, MJ/kg) was then calculated according to Cooke (1985) as following:

$$ME=0.348 EE\% + 0.159 CP\% + 0.167 STA\% + 0.114 SUG\%$$

5.2.4. Procedure and Measurements

Three birds were randomly selected from each pen at seven days of age for measurements of primary, secondary and tail feather lengths. They were then dyed for the later feather length measurements at ten-day intervals. Individual body weights were taken each time. These same males were also used in the measurements of dry feather weight, carcass and meat yields, and chemical analysis.

At 51 days, feed was withdrawn from the birds for 12 hours before they were stunned and killed at day 52. Just before they were killed, the individual starved live body weight (BW) was recorded to the nearest 10 grams. Following the procedures detailed in Chapter 3, the dry feather weight and various carcass measurements were taken.

After being dissected, the total meat, total skin and the residuals (see section 3.3.3.3, item 9, 12 and 13 respectively) were subjected to chemical analysis for dry matter and protein content. Crude protein content of dry feather at 51 days of age was taken as 895g/kg according to the result from Experiment 1 (Chapter 4).

Table 5.1. Feed composition of the starter, grower and finisher /withdrawal (g/kg) in the second experiment.

Ingredients	starter	grower	finisher/ withdrawal
Wheat	349.70	320.70	291.31
Maize	85.36	78.30	71.11
Maize gluten meal (60%)	60.00	55.02	50.00
Soya bean meal (48.5%)	214.25	196.50	178.50
White fish meal (61%)	56.13	51.50	46.80
Meat and bone meal (50%)	25.71	23.60	21.42
Full-fat-soya bean meal	25.71	23.60	21.42
Maize oil	27.23	28.04	28.90
Dicalphosphate	5.06	7.18	9.32
Limestone	11.06	11.58	12.12
Salt	1.43	1.64	1.86
DL-methionine	1.29	1.18	1.07
L-lysine	1.20	1.10	1.00
Maize starch	100.10	149.80	200.20
Oat hulls	29.17	43.66	58.37
Vitamins and Minerals*	5.00	5.00	5.00
Kemzyme [®] W	1.00	1.00	1.00
Cocciostat**	0.60	0.60	0.60

Calculated (determined) nutrient contents (g/kg as fed)

Crude protein	240(250)	220(234)	200(213)
Methionine	6.76	6.20	5.64
Methionine+cystine	9.69	8.88	8.07
Lysine	12.51	11.47	10.43
Tryptophone	2.55	2.34	2.13
Calcium	10.46(13.54)	9.59(14.23)	8.71(15.35)
Phosphorus	4.71(7.52)	4.32(7.25)	3.93(7.45)
Sodium	1.29	1.18	1.07
AME (MJ/kg)	12.7(11.9)	12.7(12.0)	12.7(11.9)
Ether extract	(59.1)	(56.8)	(53.8)

Note: *Provides (mg/kg feed): retinol 3, cholecalciferol 0.00375, α -tocopherol 30, menaphthone K 4, riboflavin 10, pyridoxine 5, cyanocobalamin 0.02, folic acid 2, biotin 0.1, pantothenic acid 16, nicotinic acid 50, Cu 3.5 I 0.4, Fe 80, Mg 300, Mn 100, Zn 50.

**No cocciostat in the withdrawal.

The total body weight and feed consumption in the pens were recorded at the age of 17, 34 and 51 days. FCR was then calculated as feed : gain.

The Genstat 5 program was used for the variance and covariance analysis. The effects of the genotypes and their interactions on the body weight adjusted feather length and dry feather weight were examined by the following linear model (model 5.1) of covariance analysis:

$$Y = \mu + bI + A + B + AB + e_m + C + CA + CB + CAB + e_p + e_s + r_{bl}X + r_mX + r_pX + r_sX$$

Effects on the average body weight or weight gain, feed intake and FCR were tested with the following variance analysis model (model 5.2):

$$Y = \mu + bI + A + B + AB + e_m + C + CA + CB + CAB + e_p$$

Effects on the carcass and its component weight (relative weight) were tested with the following model (model 5.3):

$$Y = \mu + bI + A + B + AB + e_m + C + CA + CB + CAB + e_p + e_s$$

In all of the three models, Y is the variable to be analysed, μ is the overall mean of the variable, A, B are the major gene effects; C is the line effect; and AB, CB, CA, CAB are the interactions between (among) the factors; the r's are the regression coefficients and X's are the respective deviations in the covariate. Effects of A, B, AB and r_m are tested against e_m , the error term involved in the main plots, and all the rest are tested against e_p , the error term involved in the sub-plots except r_s which is tested against e_s , the sampling error.

5.3. RESULTS

5.3.1. Feather Measurements

The three sets of feather length measurement at different ages and the dry feather weight at the end of the experiment, all adjusted for the individual body weight taken at the same time, are shown in Table 5.2. The back feathers had not yet emerged out of the surface at seven days of age, and no measurement was possible. The statistical significance of the single factors and the interactions between them are shown in Table 5.3.

Table 5.2. Effects of the feathering genotypes on the feather growth(mm) at various ages and dry feather weight (g) at 52 days. All of the means were adjusted for body weight at the measurement.

Age	Naked necks				Normal feathering				Grand mean
	Early (kk)		Late (Kk)		Early (kk)		Late (Kk)		
	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow	
Primary feather									
7d	36.5	37.8	24.2	9.7	38.6	38.9	15.5	10.8	26.5
17d	72.3	73.9	58.4	46.7	77.7	76.7	54.3	42.0	62.9
28d	100.5	99.3	108.5	101.5	103.5	103.4	107.2	100.0	103.0
38d	112.5	115.0	128.6	127.3	121.4	116.9	130.9	125.2	122.2
48d	130.5	132.3	138.6	139.7	133.7	134.0	140.6	143.6	136.6
Tail feather									
7d	9.6	10.3	3.6	0.4	11.5	10.6	1.5	0.4	6.0
17d	39.4	41.6	22.4	9.6	43.7	42.5	17.2	8.9	28.1
28d	68.7	68.2	56.5	27.7	70.2	66.7	47.2	29.9	54.4
38d	87.7	92.5	95.2	57.2	89.7	92.5	85.7	57.1	82.1
48d	113.1	109.9	124.4	80.1	110.1	112.3	112.8	82.9	105.7
Back feather									
7d	(not measured)								
17d	18.6	18.6	12.3	6.8	16.9	17.5	12.5	6.7	13.7
28d	43.0	40.6	37.1	22.0	39.8	39.0	34.8	23.1	34.9
38d	64.7	64.6	63.8	49.3	65.1	65.6	61.3	51.8	60.8
48d	80.0	83.3	80.0	72.5	86.6	81.7	82.9	71.0	80.4
Dry feather weight									
52d	55.2	55.6	55.1	56.0	69.4	68.6	70.3	70.9	62.6

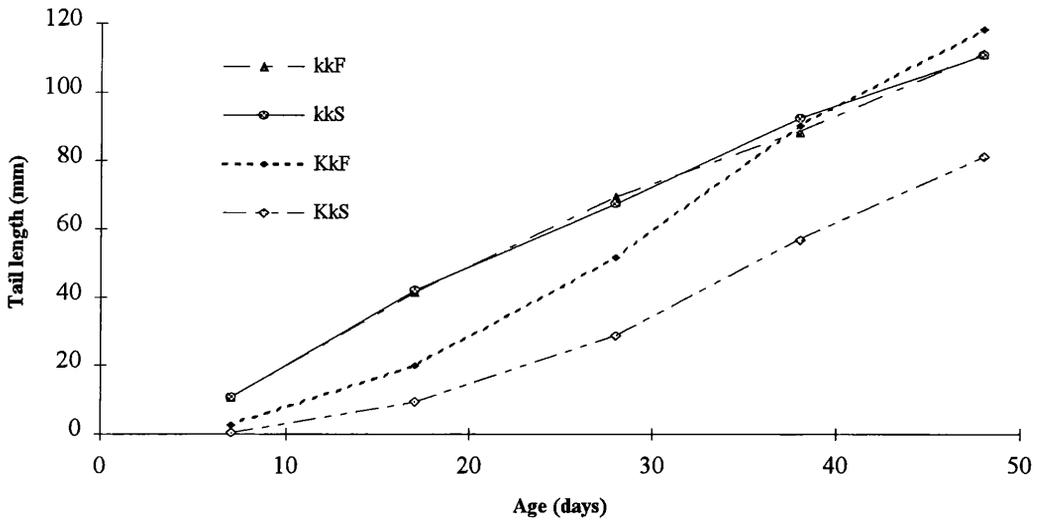
Table 5.3. Test of significance for the effects of the feathering genes and line on feathering traits at various ages (adjusted for body weight).

Source of variation...	Single factors			Interactions			
	Na gene	K gene	Line	Na*L	K*L	Na*K	L*Na*L
Primary feather							
7d	NS	***	***	NS	**	NS	NS
17d	NS	***	***	NS	***	NS	NS
28d	NS	NS	***	NS	**	NS	NS
38d	NS	**	*	NS	NS	NS	NS
48d	NS	**	NS	NS	NS	NS	NS
Tail feather							
7d	NS	***	NS	NS	NS	NS	NS
17d	NS	***	**	NS	**	NS	NS
28d	NS	***	***	NS	***	NS	NS
38d	NS	*	**	NS	***	NS	NS
48d	NS	NS	***	NS	***	NS	NS
Back feather							
7d							
17d	NS	***	***	NS	***	NS	NS
28d	NS	***	***	NS	***	NS	NS
38d	NS	NS	*	NS	*	NS	NS
48d	NS	**	*	NS	NS	NS	NS
Dry feather weight							
52d	**	NS	NS	NS	NS	NS	NS

Note: *, **, and *** stand for $P < 0.05$, $P < 0.01$, and $P < 0.001$ respectively; NS: not significant.

No significant simple effect or any important interaction was found for the naked neck gene. The K genotype showed different patterns in its effects on the different sets of feathers. The tail and back feather length of the kk early feathering males were consistently longer than their Kk late feathering counterparts throughout the experiment, and the difference was significant in most of the cases (Table 5.3). The K effect on the primary feather length was, however, inconsistent: before 28 days of age (the first two measurements), the early feathering males had longer primary feathers ($P < 0.001$), but after that the opposite was true, and at 28 days the two genotypes had nearly equal feather length.

Fig 5.1. Effect of major gene and line on the tail feather length at various ages



With the absence of the dominant K, the effect of line (1/4 fast vs. 1/4 slow) was very small and non-significant ($P>0.10$) in all of the times. However, its effect was evident at the presence of the dominant K, which was inherited from the grandfather of the original selected fast or slow feathering line. These not only made the simple effect of line but also the interaction between K and line become significant at most of the ages (Table 5.3). This interesting manifestation of the interaction between K genotype and line is shown in Figure 5.1 for the tail feather length.

Dry feather weight at 52 days was only significantly affected by the Na gene (Table 5.3). This gene reduced the dry feather weight by 20.5% from 69.8g to 55.5g. No other significant simple effect or interaction was found.

5.3.2. Body Weight and Weight Gain

Body weight is the sum of the hatching weight and the cumulated body weight gain. It was for this relationship, they are presented together here.

Table 5.4 is the three way table for the means for both body weight and weight gain as affected by two sets of major feathering genes and the line. The significance of the individual factors and their interactions can be found in Table 5.5.

Table 5.4. Means of the body weight and weight gain as affected by the feathering genes and the line.

Age or the period	Naked necks				Normal feathering				Grand mean
	Early (kk)		Late (Kk)		Early (kk)		Late (Kk)		
	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow	
Body weight									
17d	349	342	337	352	344	359	343	353	347
34d	1132	1088	1108	1129	1101	1128	1151	1187	1128
51d	2027	1942	1974	2055	1987	1976	1996	2053	2001
Body weight gain in the periods (P)									
P 1	308	302	296	312	304	320	303	313	307
P 2	783	747	772	778	757	769	808	834	781
P 3	895	854	866	926	886	849	845	866	873

Table 5.5. Test of significance for the effects of the feathering genes and line on the body weight and body weight gain at the age or period shown.

Source of variation...	Single factors			Interactions			
	Na gene	K gene	Line	Na*L	K*L	Na*K	L*Na*L
Body weight							
17d	NS	NS	NS	NS	NS	NS	NS
34 d	*	*	NS	NS	NS	0.068	NS
51d	NS	0.070	NS	NS	0.083	NS	NS
Weight gain							
P1	NS	NS	NS	NS	NS	NS	NS
P2	*	**	NS	NS	NS	*	NS
P3	NS	NS	NS	NS	*	NS	NS

Note: * and ** stand for $P < 0.05$ and $P < 0.01$ respectively; actual probabilities are indicated for those between 0.05 and 0.1; NS: not significant.

Body weight at and weight gain to 17 days of age were not significantly affected by any of the factors. Likewise, the two lines did not differ from each other for their body weight and weight gain (Table 5.5).

During the second period (from day 17 to day 34), the late feathering males without the naked neck gene (nanaKk) gained significantly more weight ($P < 0.05$) than all of the other three genotypes in respect of the two loci (Nanakk, NanaKk and nanakk). The higher body weight gain of the nanaKk birds had the following three-fold effects. First of all, significant ($P < 0.05$) effects of both naked neck gene and K genotype on both body weight at 34 days and body weight gain from 17 to 34 days. Secondly, a significant ($P < 0.05$) effect of the interaction between the above mentioned two factors

on the body weight gain in the period. And a nearly significant ($P=0.068$) effect of the same interaction on the body weight at the end of the second period. The effects of the interaction on 34-day body weight and body weight gain in the second period are shown in Table 5.6a and 5.6b.

Table 5.6a The effect of interaction between the naked neck gene and K gene on the body weight at 34 days of age (g)

	Early	Late	Mean
Naked neck	1110	1119	1114
Normal	1115	1169	1142
Mean	1112	1144	1128

Note: The normally feathered birds showing late feathering had a higher body weight than all of the other groups. The interaction was nearly significant ($P=0.068$). This interaction was the direct result of the same two-way interaction on the body weight gain in the second period shown in Table 5.6b below.

Table 5.6b. The effect of interaction between the naked neck gene and K gene on the body weight gain between 17 and 34 days of age (g)

	Early	Late	Mean
Naked neck	765	775	770
Normal	763	821	792
Mean	764	798	781

Note: The much higher body weight gain during the second period of the normally feathered birds showing late feathering made the interaction significant ($P<0.05$).

At 51 days of age, the body weight difference between Kk and kk birds was slightly widened from 32g to 37g in the absolute terms but less significant statistically ($P<0.1$). The naked neck males equalised the body weight with their normal feathering half brothers by gaining 24g more during the third 17-day period. A significant interaction was found between K genotype and line for body weight gain in the third period. Birds tended to gain more when the two series of major- and poly-feathering genes were in 'harmony', i.e. early feathering combined with fast line and late feathering combined with slow line. The body weight gains in the last period for kk1/4F, Kk1/4S were 891g, 896g in contrast with only 852g, 855g for kk1/4S and Kk1/4F. The same kind interaction was found in the final body weight at the 0.10 probability level ($P=0.083$). The average body weights were 2007g, 2054g and 1959g, 1985g for kk1/4F, Kk1/4S and kk1/4S, Kk1/4F, respectively.

5.3.3. Feed Consumption

Feed consumption to different ages and within each of the 17-day periods are shown in Table 5.7 for birds with different feathering genotypes and from different lines. The statistical significance of the single factor effects and their interactions are given in Table 5.8.

Table 5.7. Effects of feathering on the cumulative feed consumption to the days shown or within the period indicated(g)

Age or the period	Naked necks				Normal feathering				Grand mean
	Early (kk)		Late (Kk)		Early (kk)		Late (Kk)		
	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow	
17d	417	396	403	421	412	415	412	423	412
34d	1745	1701	1728	1835	1737	1778	1816	1888	1778
51d	3746	3573	3668	3914	3687	3688	3817	3955	3756
P 2	1328	1305	1325	1414	1325	1363	1404	1465	1366
P 3	2001	1872	1940	2079	1949	1910	2000	2067	1977

Table 5.8. Test of significance for the effects of the feathering genes and line on feed consumption to the age or within the period shown in the table.

Source of variation...	Single factors			Interactions			
	Na gene	K gene	Line	Na*L	K*L	Na*K	L*Na*L
17d	NS	NS	NS	NS	*	NS	NS
34 d	*	*	NS	NS	NS	NS	NS
51d	NS	*	NS	NS	*	NS	NS
P2	*	**	NS	NS	NS	NS	NS
P3	NS	*	NS	NS	*	NS	NS

Note: * and ** stand for $P < 0.05$ and $P < 0.01$ respectively. NS: not significant.

No significant major effect was observed for feed consumption to 17 days of age. After that, the late feathering birds (Kk) had a consistently greater ($P < 0.05$) feed consumption (Table 5. 8). Unexpectedly, the naked neck gene reduced overall feed consumption. The reduction was statistically significant in the second period ($P < 0.05$), which was accompanied by a concomitant reduction in weight gain. Significant interactions ($P < 0.05$) between the K genotype and line were found for the feed consumption. The two way table (Table 5.9) for the significant interactions revealed

that the direction of the interaction effects were the same: males from the fast feathering line did not respond as much as birds from the slow feathering line to the alteration in K genotypes (KkS males consumed much more feed than the kkS ones). Therefore these interactions might be related to the feathering differences among the four groups.

Table 5.9. The effects of interaction between the line and K gene on feed consumption (FC, g) during different periods of time.

	Early	Late	Mean
FC to 17 days			
Fast line	414	408	411
Slow line	406	422	414
Mean	410	415	412
FC to 51 days			
Fast line	3717	3743	3730
Slow line	3631	3935	3783
Mean	3674	3839	3756
FC between 34 and 51 days			
Fast line	1975	1970	1973
Slow line	1891	2073	1982
Mean	1933	2022	1977

Note: While in the fast feathering line, the two genotypes did not differ from each other, the late feathering birds consumed much more feed than the early feathering half brothers in the slow feathering line.

5.3.4. Feed Conversion Ratio (FCR)

Table 5.10 shows the FCR at different ages and periods as affected by the genotypes and lines. The significance of different effects are given in Table 5.11.

Table 5.10. Effects of feathering on the cumulative feed conversion ratio to the days shown or within the period indicated.

Age or the period	Naked necks				Normal feathering				Grand mean
	Early (kk)		Late (Kk)		Early (kk)		Late (Kk)		
	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow	
17d	1.354	1.310	1.364	1.349	1.357	1.298	1.362	1.353	1.343
34d	1.600	1.622	1.619	1.684	1.639	1.633	1.637	1.645	1.635
51d	1.886	1.878	1.897	1.941	1.894	1.904	1.953	1.965	1.915
P 2	1.697	1.748	1.717	1.819	1.752	1.773	1.740	1.755	1.750
P 3	2.234	2.192	2.239	2.250	2.199	2.253	2.370	2.388	2.266

Table 5.11. Test of significance for the effects of the feathering genes and line on the cumulative feed conversion ratio to the age or within the period indicated.

Source of variation...	Single factors			Interactions			
	Na gene	K gene	Line	Na*L	K*L	Na*K	L*Na*L
17d	NS	*	0.090	NS	NS	NS	NS
34 d	NS	NS	NS	NS	NS	NS	NS
51d	0.059	**	NS	NS	NS	NS	NS
P2	NS	NS	*	NS	NS	NS	NS
P3	*	*	NS	NS	NS	0.064	NS

Note: * and ** stand for $P < 0.05$ and $P < 0.01$ respectively. The actual probabilities are given for those between 0.05 and 0.1. NS: not significant.

The fast line had significantly lower ($P < 0.05$) FCR in the second period than the slow line, although the overall FCR difference between the two lines was small and non-significant for a difference in the opposite direction during the first period. A significant ($P < 0.05$) effect of the Na gene in the final 17-day period made the naked neck males superior (lower FCR) to their normal feathering brothers in terms of overall FCR (2.230 vs. 2.303, $P = 0.059$). The kk early feathering males performed significantly ($P < 0.05$) better in the first and third periods, and over the whole duration of the experiment ($P < 0.01$) than the late feathering males (Table 5.10 and 5.11).

5.3.5 Carcass Measurements

The starved live body weight, carcass weight and weight of all dissected parts for the eight combination of feathering genes and feathering lines are provided as references in Table 5.12.

Table 5.12. The starved live body weight (SLBW) dressed carcass weight, and dissected yields of the sampled birds and the weight loss during dissection (grams) at 52 days of age (see text for full explanation of the dissection losses).

Traits	Naked necks				Normal feathering				Grand
	Early (kk)		Late (Kk)		Early (kk)		Late (Kk)		
	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow	mean
SLBW	1959	1867	1929	1984	1926	1969	2046	1946	1953
Dry Feather	55.6	53.3	54.4	56.8	68.7	69.1	72.8	71.1	62.5
NYD	1772.2	1683.4	1738.6	1788.4	1715.3	1744.7	1822.6	1731.0	1749.5
Abd. Fat	40.2	38.6	46.9	42.6	53.5	45.3	49.2	37.1	44.2
EVC	1337.6	1278.4	1307.7	1355.1	1287.8	1320.9	1370.3	1320.3	1322.3
Cutting loss	-1.2	-1.4	-1.9	-1.3	-1.6	-1.3	-.9	-1.2	-1.4
Breast meat	285.2	269.7	282.6	297.4	253.5	283.3	278.4	278.1	278.5
Thighs	278.1	272.3	273.4	279.0	272.1	267.2	281.6	272.8	274.6
--skin	34.3	32.9	31.8	33.5	36.2	30.7	35.2	32.8	33.4
--meat	207.7	205.1	206.0	210.3	200.4	200.4	208.7	204.7	205.4
--bones	35.8	33.8	35.2	34.7	35.0	35.7	37.0	34.8	35.3
--loss	-.3	-.5	-.4	-.5	-.5	-.4	-.7	-.5	-.5
Drums	198.1	195.3	192.7	210.3	191.0	198.5	205.2	202.7	199.2
--skin	17.3	15.8	15.8	17.4	16.1	17.4	18.6	17.0	16.9
--meat	129.3	129.5	125.9	139.4	125.4	129.7	133.5	133.1	130.7
--bones	51.2	49.7	50.6	53.1	49.2	51.0	52.9	52.2	51.2
--loss	-.3	-.3	-.4	-.4	-.3	-.4	-.2	-.4	-.4
Wings	163.0	155.1	158.0	162.1	156.0	161.3	164.4	158.9	159.8
Frame	412.0	384.6	399.1	405.0	413.6	409.3	439.8	406.6	408.7
Total									
--skin	150.6	141.8	147.6	147.7	158.5	155.8	172.0	149.6	153.0
--edible	785.4	759.9	777.3	819.9	741.1	776.5	784.1	778.7	777.8
--residual	811.5	758.0	789.0	798.3	794.1	790.3	841.9	779.7	795.4
--loss	-24.7	-23.7	-24.7	-22.5	-21.6	-22.1	-24.6	-23.0	-23.3

Note: Because body weight differences were not adjusted for the weight of the parts, direct comparison in grams is not meaningful.

Table 5.12. was the basis for further calculations and comparisons, but a direct comparison for the carcass traits (in absolute weight) was hampered by the random fluctuation in body weights of the selected birds. The cutting losses in the different stages of dissection are worthy of comment. There are three items of weight losses in the table. First of all, the cutting loss underlying the EVC was the weight difference between the eviscerated carcass and the sum of the five main items, i.e. breast meat, thighs, drums, wings and the frame. Secondly, the losses under the headings of thighs and drums were the weight losses during deboning of the two parts. Finally, the loss under the heading of total was the weight difference between NYD, the bled-plucked carcass, and the sum of the total skin, total edible and total residuals. It includes all of the cutting losses and the weight loss during the evisceration (the contents of the crop and stomach were discarded), storage and thawing of the carcass. Obviously, the cutting losses were very small compared with the weight loss during the evisceration, storage and thawing of the carcass.

Table 5.13 shows the dissected parts in g/kg of the starved live body weight and Table 5.14 shows the significance of the different effects.

Table 5.13. Feathering genotype effects on the relative carcass and meat yields in g/kg starved live body weight.

Traits	Naked necks				Normal feathering				Grand mean
	Early (kk)		Late (Kk)		Early (kk)		Late (Kk)		
	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow	
Dry f'ther	28.4	28.5	28.2	28.7	35.7	35.1	35.5	36.3	32.0
NYD	904.9	902.1	901.3	901.2	890.7	886.2	891.0	889.9	895.9
Abd. Fat	20.6	20.5	24.3	21.7	27.7	23.0	24.1	19.0	22.6
EVC	682.6	685.0	677.8	683.0	668.4	670.7	669.8	678.6	677.0
Breast meat	145.2	144.7	146.6	149.9	131.6	143.7	136.1	143.1	142.6
Thighs	142.1	146.0	141.5	140.6	141.2	135.7	137.7	140.2	140.6
--skin	17.5	17.6	16.5	16.9	18.8	15.6	17.2	16.9	17.1
--meat	106.2	110.0	106.6	106.0	104.0	101.8	102.1	105.2	105.2
--bones	18.3	18.1	18.2	17.5	18.2	18.2	18.1	17.9	18.1
Drums	101.2	104.5	99.9	106.0	99.1	100.7	100.4	104.2	102.0
--skin	8.8	8.4	8.2	8.8	8.3	8.8	9.1	8.7	8.7
--meat	66.1	69.2	65.2	70.3	65.1	65.7	65.3	68.4	66.9
--bones	26.1	26.6	26.2	26.7	25.6	25.9	25.8	26.8	26.2
Wings	83.2	83.1	81.8	81.6	81.1	81.8	80.4	81.7	81.8
Frame	210.1	206.1	207.0	204.2	214.7	208.1	214.9	208.9	209.2
Total									
--skin	76.7	76.0	76.6	74.5	82.3	79.0	84.2	76.8	78.3
--edible	400.9	407.3	402.6	413.3	384.7	394.0	383.5	400.4	398.3
--residual	414.6	405.8	409.3	402.1	412.3	402.0	411.1	400.4	407.2

Table 5.14. Test of significance for the effects of feathering genotype on the relative carcass and meat yields in g/kg starved live body weight.

Source of variation...	--- Single factors ---			----- Interactions -----			
	Na gene	K gene	Line	Na*L	K*L	Na*K	L*Na*L
Dry feather	***	NS	NS	NS	NS	NS	NS
NYD	**	NS	NS	NS	NS	NS	NS
Abd. Fat	NS	NS	0.078	NS	NS	NS	NS
EVC	**	NS	NS	NS	NS	NS	NS
Breast meat	*	NS	0.067	NS	NS	NS	NS
Thighs	*	NS	NS	NS	NS	NS	NS
--skin	NS	NS	0.099	*	0.088	NS	NS
--meat	**	NS	NS	NS	NS	NS	0.078
--bones	NS	NS	NS	NS	NS	NS	NS
Drums	NS	NS	*	NS	NS	NS	NS
--skin	NS	NS	NS	NS	NS	NS	0.055
--meat	NS	NS	*	NS	NS	NS	NS
--bones	NS	NS	NS	NS	NS	NS	NS
Wings	NS	NS	NS	NS	NS	NS	NS
Frame	NS	NS	*	NS	NS	*	NS
Total							
--skin	*	NS	NS	NS	NS	NS	NS
--edible	**	NS	*	NS	NS	NS	NS
--residual	NS	NS	0.060	NS	NS	NS	NS

Note: *, ** and *** stand for $P < 0.05$, $P < 0.01$ and $P < 0.001$ respectively. The actual probabilities are specified in the table for those which are 0.05 and 0.1; NS: not significant.

No significant effect of the early/late feathering genotypes was found for any of the carcass traits. However, males from the slow feathering line had significantly higher yields of drumsticks, meat of drumsticks, total edible portion, but smaller frame ($P < 0.05$). The statistical analyses also suggest that the slow feathering line birds had slightly lower yields of abdominal fat and the residual, but higher breast meat yield ($P < 0.1$).

A profound effect of the Na gene on carcass yield relative to body weight was found. The Na gene significantly or very significant reduced the yields of dry feather ($P < 0.001$), and skin ($P < 0.05$), and increased the yields of NYD ($P < 0.01$), eviscerated carcass ($P < 0.01$), breast meat ($P < 0.05$), thigh meat ($P < 0.01$), and the total edible meat ($P < 0.01$). Therefore the naked neck gene enhances the value of the starved body.

However, the obvious reduction in feather yield by the naked neck gene will naturally increase the relative yield of NYD (and subsequently yields of its components) because they, together with the yield of blood add up to 1000. In order to overcome the direct part-to-part relationship, Table 5.15 and 5.16 presents the carcass yield and statistical analysis result on the basis of the bled-plucked carcass, i.e. g/kg NYD. Another advantage of using NYD as the calculation basis is that NYD, unlike the live body weight, can be weighed more accurately for research purposes.

Table 5.15. Feathering genotype effects on the relative carcass and meat yields in g/kg NYD.

Traits	----- Naked necks -----				----- Normal feathering -----				Grand mean
	Early (kk)		Late (Kk)		Early (kk)		Late (Kk)		
	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow	
Abd. Fat	22.8	22.7	26.9	24.1	31.1	26.0	27.1	21.4	25.3
EVC	754.3	759.4	751.9	757.9	750.5	756.8	751.7	762.6	755.6
Breast meat	160.5	160.4	162.7	166.4	147.7	162.1	152.8	160.9	159.2
Thighs	157.1	161.8	157.0	156.1	158.6	153.1	154.4	157.5	156.9
--skin	19.4	19.5	18.3	18.7	21.1	17.6	19.3	19.0	19.1
--meat	117.3	122.0	118.2	117.6	116.8	114.9	114.5	118.2	117.4
--bones	20.3	20.1	20.2	19.4	20.5	20.5	20.3	20.1	20.2
Drums	111.8	115.8	110.8	117.6	111.3	113.6	112.6	117.1	113.8
--skin	9.8	9.4	9.1	9.8	9.3	9.9	10.2	9.8	9.7
--meat	73.0	76.8	72.4	78.0	73.0	74.2	73.3	76.9	74.7
--bones	28.9	29.5	29.1	29.6	28.7	29.3	29.0	30.1	29.3
Wings	92.0	92.1	90.8	90.6	91.0	92.3	90.2	91.8	91.4
Frame	232.2	228.4	229.6	226.5	241.0	234.8	241.2	234.7	233.6
Total									
--skin	84.8	84.2	84.9	82.6	92.4	89.1	94.6	86.3	87.4
--edible	443.0	451.6	446.7	458.6	431.9	444.5	430.3	450.0	444.6
--residual	458.2	449.8	454.2	446.2	462.9	453.7	461.6	450.0	454.6

Table 5.16. Test of significance for the effects of feathering genotype on the relative carcass and meat yields in g/kg dressed carcass weight.

Source of variation...	--- Single factors ---			----- Interactions -----			
	Na gene	K gene	Line	Na*L	K*L	Na*K	L*Na*L
Abd. Fat	NS	NS	NS	NS	NS	NS	NS
EVC	NS	NS	*	NS	NS	NS	NS
Breast meat	*	NS	*	NS	NS	NS	NS
Thighs	NS	NS	NS	NS	NS	NS	**
--skin	NS	NS	NS	*	0.099	NS	NS
--meat	*	NS	NS	NS	NS	NS	*
--bones	NS	NS	NS	NS	NS	NS	NS
Drums	NS	NS	***	NS	NS	NS	NS
--skin	NS	NS	NS	NS	NS	NS	0.055
--meat	NS	NS	***	NS	NS	NS	NS
--bones	NS	NS	NS	NS	NS	NS	NS
Wings	NS	NS	NS	NS	NS	NS	NS
Frame	***	NS	*	NS	NS	NS	NS
Total							
--skin	***	NS	0.077	NS	NS	NS	NS
--edible	**	NS	**	NS	NS	NS	NS
--residual	NS	NS	*	NS	NS	NS	NS

Note: *, ** and *** stand for $P < 0.05$, $P < 0.01$ and $P < 0.001$ respectively. The actual probabilities are specified in the table for those which are 0.05 and 0.1; NS: not significant.

Comparing the yields of Table 5.15 in g/kg NYD with those of Table 5.13 in g/kg body weight, the general patterns of the genotypic effects are very much the same. The two ways of expression for the carcass components mainly differ in magnitude of the genotypic effects. The Na gene effects become weaker for the meat yields but still significant ($P < 0.05$), while most of the line effects are unchanged or become slightly stronger. One important difference was that the naked neck gene reduced the yield of frame very highly significantly ($P < 0.001$).

5.3.6. Chemical Analysis and Protein Partition

Results from the chemical analysis for the crude protein and dry matter contents of the meat, skin and residuals at 52 days of age, together with the calculated protein partition among the four parts of the bled-carcass (with feathers) and among the three dissected parts of NYD are presented in Table 5.17. Table 5.18 shows the statistical tests for significance.

Table 5.17. Effects of feathering on the chemical composition (g/kg wet sample) of the carcass parts and the protein partition among the various parts of the bled-carcass with feathers and of the dressed carcass (NYD)

Traits	Naked necks(Nana)				Normal feathering(nana)				Grand
	Early(kk)		Late(Kk)		Early		Late		
	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow	Mean
Protein Content of									
Meat	223.4	220.7	221.1	225.4	219.8	223.6	221.8	224.4	222.5
Skin	164.4	168.0	163.6	156.6	148.9	159.3	152.4	152.4	158.2
Residual	178.2	174.5	179.0	178.6	175.8	176.6	170.4	180.3	176.7
NYD	197.2	195.0	196.7	198.5	192.5	196.2	191.0	198.0	195.6
Dry matter content of									
Meat	282.1	279.8	283.5	287.3	286.0	285.0	286.8	286.7	284.6
Skin	540.2	548.0	560.9	553.8	619.5	578.3	597.6	590.4	573.6
Residual	433.6	424.9	433.2	430.6	456.0	433.3	439.2	430.8	435.2
NYD	375.0	369.0	376.6	374.4	397.1	379.6	388.2	379.0	379.9
Bled-carcass protein partition in									
Meat	444.9	452.1	445.1	460.9	420.3	434.0	425.9	435.8	439.9
Skin	62.15	64.03	62.37	57.73	60.92	61.91	64.05	56.91	61.26
Residual	366.7	355.6	366.2	354.8	359.8	349.5	350.6	349.9	356.7
Feathers	126.3	128.3	126.3	126.6	158.9	154.6	159.5	157.4	142.2
Protein partition of the NYD in									
Meat	509.0	518.6	509.4	527.7	499.8	513.3	506.6	517.2	512.7
Skin	71.16	73.44	71.42	66.13	72.47	73.29	76.21	67.45	71.4
Residual	419.9	408.0	419.2	406.2	427.8	413.4	417.2	415.4	415.9

Table 5.18 Test of significance for the effects of feathering genotype on the chemical composition of the carcass and its parts and on the total bled-carcass protein partition into the four parts and the total dressed carcass protein into the three dissected parts.

Source of variation...	--- Single factors ---			----- Interactions -----			
	Na gene	K gene	Line	Na*L	K*L	Na*K	L*Na*L
Protein content in							
Meat	NS	NS	NS	NS	NS	NS	NS
Skin	0.080	NS	NS	NS	NS	NS	NS
Residual	NS	NS	NS	NS	NS	NS	NS
NYD	NS	NS	NS	NS	NS	NS	NS
Dry matter content of							
Meat	NS	NS	NS	NS	0.073	NS	NS
Skin	***	NS	NS	0.064	NS	NS	*
Residual	*	NS	NS	NS	NS	NS	NS
NYD	**	NS	0.087	NS	NS	NS	NS
Bled-arcass protein partition in							
Meat	***	NS	0.062	NS	NS	NS	NS
Skin	NS	NS	NS	NS	NS	NS	NS
Residual	*	NS	0.090	NS	NS	NS	NS
Feathers	***	NS	NS	NS	NS	NS	NS
NYD protein partition in							
Meat	*	*	*	NS	NS	NS	NS
Skin	NS	NS	NS	NS	NS	NS	NS
Residual	0.078	NS	NS	NS	NS	NS	NS

Note: *, ** and *** stand for $P < 0.05$, $P < 0.01$ and $P < 0.001$ respectively. The actual probabilities are specified in the table for those which are 0.05 and 0.1; NS: not significant.

The protein contents of the dissected samples were not generally affected by feathering except for a slightly higher ($P = 0.080$) skin protein content of the naked neck males than the normally feathered chickens.

Dry matter content in meat was not significantly affected by feathering. For the DM in the skin, residual and the whole carcass, the naked neck gene had the largest effect. The presence of this gene significantly reduced the dry matter content in skin (by 45.8g/kg, $P < 0.001$), in residual (by 9.2g/kg, $P < 0.05$) and the whole carcass (by 12.2g/kg, $P < 0.01$). The slow feathering selected line also had about 1% lower dry matter in the skin, residual and the whole carcass (Table 5.17).

Body protein partition on the basis of bled carcass was significantly affected by the

naked neck gene. Birds carrying this gene distributed very highly significantly less body protein (by -30.7 g/kg, $P<0.001$) to feathers, but significantly more protein in meat (by 21.7g/kg, $P<0.001$) and residuals (by 8.3g/kg, $P<0.05$) than their normally feathered counterparts. The slow feathering line also had slightly more protein in meat (by 11.7g/kg, $P=0.062$) and less in residual (by -8.3g/kg, $P=0.090$). As it was expected from the dry feather yield, the amount of protein in feathers was not affected by the line.

Body protein partition on the basis of the dressed carcass was very different from that on the bled carcass basis for the effect of the naked neck gene. Although the amount of protein in meat was still significantly higher in the naked neck birds than in the normally feathered ones, the difference was much smaller on the bled carcass basis (6.9 vs. 21.7 g/kg). Further more this gene slightly reduced the amount of carcass protein in the residual (by -5.1g/kg, $P=0.078$), instead of an increase as seen on the bled carcass basis. The line differences were very much the same on both of the bases, but slightly larger in magnitude on the NYD basis. The K genotypes also differ from each other in the amount of protein in meat. The late feathering genotype was significantly higher (by 5.1g/kg, $P<0.05$) than the early feathering genotype.

5.4. DISCUSSION

5.4.1. Effects of Feathering Genes on Feather Growth

The results showed that different feathering genes play different genetic roles in controlling feather growth. First of all, the Na gene eliminates the affected feather follicles from initial development at the embryo stage, but has no effect on the subsequent growth of the unaffected feathers, as no major effect or consistent interaction involving this gene on the length of any of the feathers measured was observed. This confirmed our previous observations reported by Quoi (1991).

Secondly, the early feathering males generally have a better feathering condition than the late feathering ones. However, the heterozygous late feathering males can reach the same feathering condition, both in terms of feather length measurements and dry feather mass, as the early feathering ones at the broiler age by means of genetic selection for faster feather growth.

Thirdly, the expression of feathering difference created by divergent selection in the late feathering populations requires a late feathering background (KK or Kk), since this difference was not shown in the early feathering groups. No feathering difference was observed either in the early feathering females resulted from a single cross between the males of the two lines and females of an early feathering population (Lou et al., 1992). The genetic reasons for this phenomenon have not been studied at a molecular level. However, the following two mechanisms might be possible. The first one is that the polygenes themselves are located in the sex-linked part of the Z sex chromosome, so that the bird which does not receive the particular chromosome (indicated by the loss of its resident K) does not show any effect of the selection. The second one is that the polygenes which have been responsible for the divergence in feathering between the lines are scattered throughout the genome, as it is usually assumed for quantitative traits in the genetic analysis, however, the functioning of these genes is mediated through the major genes K or other sex-linked genes.

With the first hypothesis, the difference in feathering will behave like a sex-linked trait controlled by as if a single additive or dominant gene, while with the second hypothesis, this trait would behave analogous to a sex-limited trait (genotype limited here). Furthermore, with the second hypothesis, the effect of the selection will be halved each time when birds from the selected lines or their progeny are crossed to the unselected population; while with the first hypothesis, the line effect will not change (if polygene effect is mostly dominant), or halved once only (if polygene effect is additive). Since the line difference for the tail feather length after a double-cross in the present experiment (19 mm at 21 days of age by regression) equals the difference between the pure line males in both generations 5 and 6 (18 mm), and further the tail length difference between the males of the two lines did not reduce after a single cross to the Mashall (kk) males (12.3 mm) compared to the pureline progeny of the fourth generation (10.3 mm) in the line crossing experiment recorded by Prijono (1991), it seems more likely that most, if not all, of the polygenes responsible for the tail feather length divergence might be located in the Z sex chromosome, and genes selected at both directions seem to be dominant over their corresponding alleles.

The sex-linked feature of the feathering trait indicates that modification of feathering condition of feathering-sexable male commercial chicks (Kk) could be achieved simply by the selection of the female line used, or ultimately by the selection within the male side of the female lines in a three- or four-way crosses.

As far as the inconsistent effect of K on primary feather length is concerned, no literature is available for comparison. The longer flight feather in the late feathering

birds (and maybe some other non-measured feathers as well) may have helped offset the effect of the shorter tail and back feathers on the total feather weight recorded at the end of this experiment.

5.4.2. Effects of Feathering Genes on Growth and Feed Consumption

5.4.2.1. The Na gene

Because the naked neck birds have a poorer insulation, they are usually expected to consume more feed at both low and high temperatures, to maintain their body temperature at the former, and to be less affected by the latter. However, at a moderate temperature condition, the present results show that the heterozygous naked neck males (NaNa birds may be different) need not necessarily consume more feed than the normally feathered birds. In some circumstances, the naked neck birds may even take less feed than the normally feathered ones, as in the second period of the present experiment. Although this phenomenon has no satisfactory explanation and thus has often been ignored, similar results were recorded by several groups of researchers. Equal feed intake for the two genotypes was reported by Hanzel and Somes (1983) and observed in our previous experiment (unpublished data) to 40 days (difference less than one percent). One and half percent less feed consumption for Nana birds than the normal birds was reported both by Monnet et al. (1979) in their uncontrolled environment in females (about 20°C on average) and by Zein-el-dein et al. (1984) at 24°C.

The growth pattern of the naked neck birds was slightly different from that of the normal feathering birds. The reduced body weight gain in the second period and increased gain in the final period may have helped the naked neck birds reduce their cumulative maintenance requirement to 51 days of age.

5.4.2.2. K genotype and line

There was a general trend that favoured the slower or later feathering both in terms of growth and feed consumption, especially in the second period (Tables 5.4 and 5.7). Unlike the effect of K, the main effect of line on growth and FC had never been significant over the three periods, and the final body weight difference was only 11g in favour of the slow feathering line. This line difference was also largely dependent on the major gene background. The final body weight of the late feathering males was in favour of the slow feathering line by 69g over the fast line, which was in agreement

with the result reported by Ajang et al. (1993) using the pure lines. However, the early feathering males was 48g in favour of the fast feathering line. This kind of interaction was not expected. The reason why the bird should seek a harmony in the major- and poly-gene combination (early with fast and slow with late) is still not understood.

A similar interaction effect on feed consumption was observed between K genotype and line. Over the 51 days, the slow line in the late feathering background consumed much more feed than any other groups. Therefore the better growth rate in the late and slow feathering birds were supported by higher feed consumption. Because the naked neck birds did not consume more feed than the normally feathered ones, this might indicate that the genetic consequences of reducing feathering rate and reducing the amount of skin surface covered by feathers might not be the same in terms of feed consumption.

The above interaction effect on body weight and feed consumption caused an interesting phenomenon in the naked neck group: the two extremes in feathering rate achieved a similarly high body weight at 51 days. But the reasons for the high body weight in the two groups were quite different: the *kk1/4F* naked neck birds were mainly for increased efficiency, because the total feed consumption was still less than the overall average, while the *Kk1/4S* naked necks were mainly through the increased feed consumption.

5.4.3. Effects of Feathering Genotype on FCR

The direct effect of feather growth on FCR depends on the balance between the extra nutrients required for feather growth (compared with other body components) and the amount of energy saved from better insulation. However, one important difference between the two has to be taken into consideration. Feather growth requires both energy and protein, while better insulation can only save energy in usual environmental conditions.

Results from the present experiment indicate that the direct effect of nutrient saving from less feather growth, or the nutrient competition between feather growth and body growth, on FCR in the early brooding period (first 17 days in the present experiment), is not as important as it was suggested by early researchers (Sheridan and McDonald, 1963). The reasons are, first of all, the naked neck birds who have at least 20% less feather covering over the body than the normally feathered birds did not show any advantage in FCR in this period. Secondly, the early feathering chicks had significantly ($P < 0.05$) lower FCR (higher feed efficiency) than the late feathering birds. Thirdly, the

slightly higher ($P < 0.10$) FCR of the fast feathering line did not indicate that feathering difference between the lines had contributed much to the FCR difference. The line effect on FCR was observed in both the early feathering birds (1.356 vs. 1.304) and the late feathering ones (1.363 vs. 1.351), while in the early feathering (kk) birds, feathering rate was not affected by line.

The trend of FCR differences in the second and third periods or the cumulative FCR to 34 and 51 days were all in the same direction. They favoured birds with smaller amount of feathers developing earlier or at a higher rate. A correlation analysis between feathering and FCR on the grouped basis (eight genotypes) found that the average cumulative FCR to 51 days was strongly related to the average tail feather length at 28 days ($r = 0.886$, the highest among all of the correlations between FCR and the feathering traits at various ages). When the Na gene effect was further taken into account, the following regression equation (eq.1) was established.

$$\begin{array}{l} \text{FCR} = 2.0163 - 0.00163 * \text{Tail}_{28} - 0.0256 * \text{Na} \quad (\text{eq.1}) \\ \text{SED} \quad 0.0104 \quad 0.00018 \quad 0.0059 \\ \text{P} \quad <0.001 \quad <0.001 \quad 0.007 \end{array}$$

where FCR is the predicted FCR; Tail_{28} is tail length in mm at 28 days; Na is the number of the naked neck genes: 1 for the heterozygous naked neck groups, and 0 for the normal feathering groups. The SED is the standard error of deviation for the coefficients. The total amount of variation in FCR accounted for by eq.1 is $R^2 = 0.937$.

Equation 1 indicates that the length and amount of feathers have distinct effect on FCR. According to Edriss (1989), the tail feather length was the best single predictor of the back feather score or overall feathering condition at three weeks of age. For a better (lower) overall FCR, therefore, this equation calls for a better feathering insulation at the early age, instead of making possible savings from slower feather development. The saving from later or slower feather growth is not permanent anyway, because the total feather weight in the end was no less in the slow or late feathering birds (Table 5.2 and 5.3). Therefore the better insulation at the early age was achieved by the fast or early feathering birds without much extra cost to a typical broiler age. Because the nutrient saving brought about by Na gene is permanent the normally feathered birds need to use extra materials to achieve the better insulation, compared with the naked neck birds. Thus, in the present experimental condition, the two forces in different directions, earlier but less feather development come together to favour FCR in eq.1.

A post brooding temperature of 25 °C was suggested to be the minimum to exploit the naked neck gene for commercial production (Merat, 1986). However, a negative sign for Na in eq. 1 suggests that this temperature has already surpassed the actual

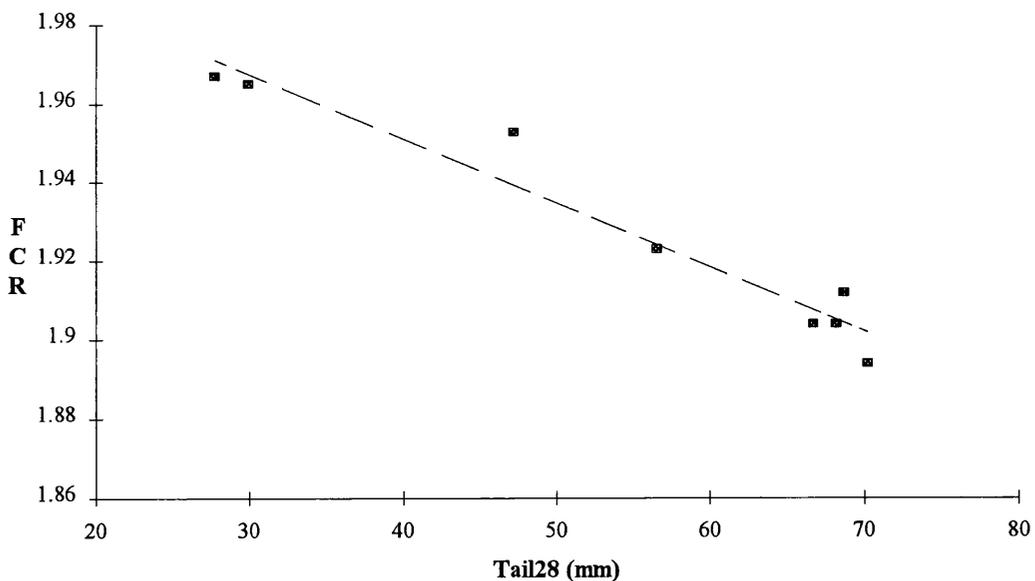
lower limit required for the Na gene to bring no loss in terms of feed efficiency with our stock. In other words, the range of temperature condition to use the naked neck gene for commercial poultry production may be wider than it was originally thought. As broilers achieve fast growth rates in the future and therefore need to lose more heat than at present, the lower temperature limit may reduce further. This conclusion is supported by other researchers. Eberhart and Washburn (1993 b), at 20°C, and Cahaner et al.(1993) at 23°C, observed no detrimental effect of the naked neck gene on FCR.

Because of the independent feature of the Na gene from the feather measurements and because there were only two Na genotypes in the present experiment, the effect of Na gene on FCR can be adjusted by the factor of 0.0256 from eq.1 for all of the naked neck groups. After the adjustment, the relationship between FCR and tail length are presented in Fig.5.2.

In this figure, the four early feathering groups cluster together, since they did not vary so much both in terms of tail length and adjusted FCR as the late feathering groups.

**Figure 5.2. Relationship between tail feather length at 28 days (Tail₂₈) and cumulative feed conversion ratio (FCR) to 51 days adjusted for the effect of Na gene. The full regression equation (see text for detail) is:

$$FCR = 2.0163 - 0.00163 * Tail_{28} - 0.0256 * Na$$**



5.4.4. Interrelationships among BW, FC, FCR and Feathering

FCR is a measurement dependent on the feed consumption and body weight (gain). Therefore it would be worthwhile finding the 'net' effect of the average tail feather length on the total feed consumption and body weight of the eight genotypes at 51 days. The following two regression equations were found to be highly significant ($P < 0.001$) by multiple regression:

$$\begin{array}{l} \text{FC} = 116.7 + 1.919 \cdot \text{BW} - 3.244 \cdot \text{Tail}_{28} - 49.0 \cdot \text{Na} \quad (\text{eq.2. } R^2=0.985) \\ \text{SED} \quad 468.7 \quad 0.224 \quad 0.512 \quad 11.20 \\ \text{P} \quad 0.816 \quad 0.001 \quad 0.003 \quad 0.012 \end{array}$$

$$\begin{array}{l} \text{BW} = 50.2 + 0.494 \cdot \text{FC} + 1.515 \cdot \text{Tail}_{28} + 24.2 \cdot \text{Na} \quad (\text{eq.3. } R^2=0.960) \\ \text{SED} \quad 238.4 \quad 0.0576 \quad 0.414 \quad 6.269 \\ \text{P} \quad 0.844 \quad 0.001 \quad 0.022 \quad 0.019 \end{array}$$

According to eq.2, the estimated overall FCR is 1.919 (the partial regression coefficient of body weight on feed consumption), which is essentially the same as the grand mean of 1.915. Equation 2 also indicates that, to achieve the same body weight at 51 days of age, each mm increase in tail length at 28 days, 3.244g of feed can be saved over the 51-day period, and furthermore the Na gene can bring about an independent feed saving of 49g. Therefore eq.2 not only described the interrelations among FC, BW, Tail₂₈ and Na, but also confirmed the relation between FCR and tail length, and between FCR and Na gene.

Compared with eq.2, eq.3 is less straightforward in explaining the observed results. However it does throw some new insight into the relationships. First of all, the higher feed consumption observed in the slower (later) feathering genotypes is not an advantage in terms of feed efficiency, because the expected return in body weight (0.494, the partial regression coefficient of BW on FC) is lower than the grand mean of feed efficiency (0.524) in the experiment. Secondly, after the effect of FC difference has been removed (FC fixed, or assuming all birds take the same amount of feed), the 'net' effect of tail length on BW (the partial regression coefficient) is positive instead of negative as indicated in the simple regression. The same is true for the Na gene.

5.4.5. Effects of Feathering Genes on the Carcass Traits

5.4.5.1. The Na gene on carcass traits

A reduction in feather weight brought about by the Na gene (Table 5.2) allows for

an equivalent increase in NYD, and consequently the components of the carcass, when they are expressed in relation to body weight. However, if there were no further effect of the gene on the constituent of the carcass, a proportional increase in each of the carcass components according to the average weight would be expected in the naked neck males. This was certainly not the case. A large increase in the residual was not found. Furthermore the increase in the total edible meat yield (15.3g/kg body weight) was over-proportional, and its amount was even larger than the total increase in NYD (13.0g/kg), which was possible for a decrease, instead of increase, in the relative total skin yield (-4.7g/kg). This clarified our previous observations (Lou et al., 1992) in which the positive effect of the naked neck gene on the total edible meat yield was only significant at 20 days of age over the four 10 day-periods of observations up to 40 days of age. The total skin was not separated in that experiment.

The non-significant difference between the naked neck and normally feathered males in total residual indicate that the Na gene does not have much influence on the growth of the gastrointestinal tract and the skeleton. In fact the 4.8 g/kg BW reduction of the frame weight was almost completely caused by the reduced skin weight (about 4.5 g/kg BW) attached to it (all of the skin was left over in the frame except that in the limbs).

The reduction in skin weight brought about by the Na gene is feather-related, because the bared skin lacks of follicles (Hutt, 1949) and the bared skin of the naked neck chickens contains less subcutaneous fat compared with the normal skin (Merat, 1986).

Although amino acid requirements for feather growth may not necessarily have priority over those for the rest of body (carcass) growth, the large amount of protein (amino acids) left over from less feather growth in the naked neck birds could, at least partially, become the extra building material for body, especially muscle growth. A post-brooding temperature of 25°C in the present experiment seemed to have ensured that only a minimum amount of extra protein was catabolized for energy use in the naked neck males compared with the normal feathering ones.

Of the 15.3 g/kg BW increase of the total edible meat yield in the naked neck males, 52% (8.0g/kg) was explained by an increase in the most valuable meat, the breast meat, which was much higher than its proportion in the total edible meat (36%). The remaining part of the increase was explained by the increases in thigh meat (26%), meat of drumsticks (10%), and the other edible portions (12%). The reason for the over-proportional increase in the breast meat is unknown. One explanation might be

that the breast meat is more sensitive to the amino acid supply in the biochemical pool of the body than the other meat components. O'Sullivan et al. (1991a) reported that alternative-day-feeding to 64 days of age in broilers caused significant reduction in weights of pectoralis major and minor relative to body weight, but not in the total weight of the other muscles. This seems to support the above hypothesis. However, results obtained with birds in the third generation of our fast and slow feathering lines (Ajang et al., 1993) did not support the above theory. The breast meat, as a contrast to the leg meat, lacked a significant response to the dietary protein content.

Although the carcass traits calculated on the basis of NYD have been presented in this report for the convenience of different comparisons, it is more proper to discuss naked neck gene effects on carcass traits on the basis of the body weight, because substantial reduction in feather covering is one of the major effect of the gene.

5.4.5.2. K genotype, line and carcass traits

When early (kk) and late (KK) feathering males were compared for carcass traits on the basis of body weight at broiler age, O'Sullivan et al. (1991a) could not find any significant difference between the two genotypes at 64 days of age both under full feeding and restricted feeding between 6 and 27 days. This confirmed the present result that the effect of the K genotype on carcass traits is relatively small and non-significant.

In agreement with the present result, Ajang et al. (1993) reported that birds from the pure slow feathering line had higher meat yield than those from the fast line. These authors tended to explain the higher meat yield in the slow feathering birds as a result of protein (amino acid) repartition in the body, that is between feather growth and muscle growth. This is equivalent to the above interpretation for the mechanism of the naked neck gene effect. However the accumulated evidence suggests that the redistribution of the body protein might be only a minor reason for the line difference in meat yield. First of all, a difference of only 0.55 g feather/kg body weight between the two lines was too small to account for the observed 19.0 g meat/kg NYD difference (meat yield was only provided on the NYD basis) in the report of Ajang et al. (1993). Secondly in the present experiment, meat yield was still significantly higher ($P < 0.05$) in the slow feathering males than the fast feathering males when the line effect had been 'diluted' twice by crossing, and the final feather weight was not different between the two lines. Finally, a consistently significant interaction between K genotype and line on feather length was observed in the present experiment, i.e. the effect of the line

was dependent on the K genotype, and the line effect was only evident in the late feathering (Kk) groups. If the general tendency of 'less feather- more meat' could be extended to explain the line effect, a similar interaction should follow the way of feather measurements in meat yield. However, no evidence for that can be found in the present experiment (Table 5.3 and 5.14 on the live body weight basis and Table 5.15 and 5.16 on the NYD basis) or the experiment reported by Quoi (1991), in which broilers were slaughtered in an age series.

According to Sheridan and McDonald (1963), there might be a critical period early in life when there is a nutrient competition between feather and body growth. Thus what really matters on meat yield might be the early feather growth rate but not the final feather weight difference at broiler age. The fact from the present experiment that the feathering difference was larger between the two feathering genotypes with respect to the K locus at the early ages than the two sources of lines and yet none of the carcass traits differed significantly between the genotypes ruled out the above speculation. Therefore the higher meat yield, including the higher breast meat yield of the slow feathering males is mainly a correlated response due to the selection for slow feathering, as was seen in the response of meat yield to low-fat selection (Cahaner et al., 1986) or feed conversion selection (Leenstra and Pit, 1987). The physiological or biochemical basis for this genetic correlation seems to be more complex than what was suggested previously (Ajang et al., 1993).

5.4.6. Effects of Feathering Genes on Carcass Chemical Composition and Protein Partition

5.4.6.1. Na gene

Although the skin mass (Table 5.12) or the relative weight of skin in the body (Table 5.13) of the naked neck birds is much less than the normally feathered ones, Table 5.17 and 5.18 indicate that the total amount of protein in the skin is just the same for both the naked necks and the normally feathered birds. This is possible because the protein concentration (Table 5.17) was slightly higher in the skin of the naked necks. Thus the extra skin weight of the normally feathered birds is non-protein in its chemical constitution. Because the water content is not higher in the normally feathered skin (actually being significantly lower), this extra mass must be mainly of fat. The protein content of the whole carcass was not affected by the naked neck gene. This is supported by Hanzel and Somes Jr. (1983). The lower dry matter or higher moisture content in the carcass and its components of the naked neck birds (Table 5.17 and 5.18) was also in agreement with the result reported by Hanzel and Somes Jr. (1983). If the

positive relationship between carcass dry matter and fat contents reported by Lewis and Perry (1991) could be extended to the comparison between the normal and naked neck birds, the present result could indicate that the carcasses of the naked neck birds might contain less fat, and therefore be leaner than that of the normally feathered ones.

In an agreement with the results in Experiment 1 (Chapter 4), the naked neck gene caused a redistribution of the body protein mainly between feathers and meat. The naked neck birds deposited more body protein in meat and less in feathers than the normally feathered birds.

5.4.6.2. Effects of K genotypes and line

The present result showed that the early vs. late feathering genotype has little effect on the chemical composition of the carcass or the body protein partition. This is in good agreement with the result obtained by Merkley and Lowe (1988).

Feathering selection did not affect the protein content of the carcass or the dissected parts. However the numerical trend was in the same direction with Ajang et al. (1993) who reported that the carcass protein content was significantly higher in the birds from the slow feathering line than that from the fast line.

The slightly higher dry matter content in the dressed carcass of the fast feathering line is again in line with the result obtained by Ajang et al. (1993) in the earlier generation. The present result indicates that this dry matter difference in the whole carcass was caused by the dry matter differences in residual and skin but not in meat.

The two lines did not differ in the amount of body protein deposited in the skin and feathers at 52 days of age, but they differed in body protein partition between edible portion and the residuals (Table 5.17). The slow feathering line had significantly more carcass protein in meat than the fast line by reducing the amount of protein mainly in the residuals. Therefore again the repartition of the body protein caused by the naked neck gene is different from that caused by the feathering rate selection.

5.5. CONCLUSIONS

In conclusion, the Na gene controls the amount of surface area with feather covering through restricting the feather follicle distribution, but does not control the growth rate of the unaffected feathers. The feathering rate is controlled by both the major gene in the K locus and the polygenes, and also the interaction between them. The polygenes which partially control the feathering rate in the late feathering birds are inactive in the early feathering background.

Body weight to 34 days of age was significantly reduced by both the naked neck gene and by early feathering. The naked neck birds made a complete compensation in weight during the last period of 17 days. The early feathering birds did not. The enhancement in body weight by late feathering genotype was, however, limited to the slow feathering line only.

Reduction in feather coverage area and in feather growth rate had different consequences in terms of feed consumption and FCR. Slower and later feather development was accompanied by an increase in feed consumption which put a penalty on FCR. By contrast, the naked gene reduces feed consumption by about 50 g to reach the same body weight at 51 days, and therefore, it reduces FCR as well.

By considering body weight, feed consumption and feathering together, a combination of fastest feather growth with the Na gene (kkNana1/4F), may provide the best compromise for body weight and efficiency at a temperature of 25°C or even lower.

The naked neck birds are superior to the normally feathered ones for meat production. They have higher yields of the dressed carcass, eviscerated carcass, thigh, thigh meat, breast meat, and the total edible meat, but lower yields of feathers and total skin. The naked neck carcass contains more moisture, possibly less fat, but similar amounts of protein, than the normally feathered counterparts. The influence of the naked neck gene on the body protein partition among the various carcass parts essentially follows the pattern of its effect on the yields of the corresponding parts except for the skin protein, i.e. lower skin yield of the naked neck birds does not result in less amount of protein in the skin.

Meat yield was in favour of the slow feathering line, but neither the early or late feathering genotype.

CHAPTER 6

THE RELATIONSHIP BETWEEN FEATHER GROWTH AND FEED CONVERSION RATIO IN BROILERS

----- A STUDY ON THE INDIVIDUAL BASIS-----

6.1. INTRODUCTION

In the previous experiment (Chapter 5) a negative relationship was revealed between tail feather length at 28 days of age and the overall feed conversion ratio in grouped broilers kept at a post-brooding temperature of 25°C. This relation is, however, dependent on the environmental temperature, and to a certain degree, on the feathering genotypes. Most major breeding companies cage the individual birds for feed efficiency measurement at the 'normal' temperature conditions, and this usually implies a post-brooding temperature of 20-22°C. To make the study more relevant to the poultry breeders, therefore, the present experiment was carried out at a post-brooding temperature of 20°C to evaluate the relationships between feathering and feed efficiency, and between feathering and other important broiler traits. Because this is a more focused study, the naked neck gene was not considered. It was also felt that with the segregation of the early and late feathering genotypes, it might be proper to use only the special males originated from the slow feathering line. In such an experiment with records for each individual, the family relationship between the animals can also be considered. Thus the purposes of the present experiment were, firstly, to elucidate the general relationship between the feathering measurement and feed conversion ratio at a normal temperature condition on the individual basis and the amount of contribution of the variation in feathering to the variation of FCR; and secondly, to evaluate the effect of early vs. late feathering genotype and sire family on broiler growth and carcass traits.

6.2. MATERIALS AND METHODS

6.2.1. Chicks and the Mating Plan

In order to collect more data with the available facilities, the experiment was repeated in time (Trial 1 and Trial 2). The two lots of chicks were hatched at an interval of four weeks. The two-step mating plan to produce the day-old chicks has been detailed in Chapter 3 section 3.1.2. Briefly, eight groups of 7-8 randomly chosen females from the heterozygous naked neck (Nana) line were separately inseminated by the semen from eight special males originated from the slow feathering line with a feathering genotype of *nanaKk*. The resulting fully pedigree-hatched normally feathered male chicks, wing-banded in the hatchery, had the following two feathering genotypes from all of the eight sire families: *nanakk* normal early and *nanaKk* normal late feathering. The same procedure was followed in producing the two crops of chicks. However, the second crop of chicks were produced by rotating the order of the males (sires) to the female groups so that each female group was mated by a different male the second time. Therefore the mating plan was hierarchical within the trials and crossed for the two trials as a whole. In such a plan the effect of sire family can be better evaluated, because the males were mated to larger number of females.

It was expected by the mating procedure that the feather length would be widely and normally distributed in the late feathering group, because the dams were randomly grouped and they had never been selected for feather growth. The inclusion of early feathering genotype would make the range of feather length even wider.

The numbers of day-old chicks recorded were 64 early feathering and 54 late feathering in Trial 1, and the corresponding number in Trial 2 were 52 and 33, respectively. They were group-raised on two floor pens in both of the trials to 21 days of age before being moved to the individual cages.

6.2.2. Diets

The birds were allowed to take an average of 300 g of a commercial starter diet (23% CP) for the first 12 or 13 days. After that, a commercial grower diet containing 22% of crude protein was used up to the age of 21 days before the birds were transferred to the cages.

In the individual cages, chicks were fed *ad libitum* with a purpose-formulated diet (Table 6.1)

**Table 6.1. Composition of feed used during FCR measurements
(from 21 days onwards)**

Ingredients	g/kg
Wheat	450.0
Maize	224.4
Maize gluten meal (60%)	33.0
Soya bean meal (43%)	121.0
White fish meal (61%)	20.0
Meat and bone meal (50%)	37.0
Full-fat-soya bean meal	101.0
Dicalphosphate	3.9
Salt	2.7
DL-methionine	0.4
L-lysine	1.0
Vitamins and minerals*	5.0
Cocciostat	0.6
TOTAL	1000.0
Calculated nutrient contents	
ME (MJ/kg)	12.7
CP	210.0
Methionine	4.1
Meth+cyst	7.9
Lysine	10.5
Arginine	12.9
Calcium	10.2
Phosphorous (av.)	4.5

Note: * Provides (mg/kg feed): retinol 3, cholecalciferol 0.00375, α -tocopherol 30, menaphthone K 4, riboflavin 10, pyridoxine 5, cyanocobalamin 0.02, folic acid 2, biotin 0.1, pantothenic acid 16, nicotinic acid 50, Cu 3.5, I 0.4, Fe 80, Mg 300, Mn 100, Zn 50.

6.2.3. Bird Management

Gas brooders in Trial 1, and spot electrical heaters in Trial 2 were adopted to provide the brooding conditions for the chicks. The two floor pens accommodating the two groups of birds to 21 days were covered with wood shavings.

The six units of single-deck cages available for the present experiment, holding eight individuals each, were arranged into three rows (blocks) within a light and temperature controlled environment room (see Fig. 6.1). At 21 days of age, the six pre-selected chicks (avoiding full brothers being selected, if possible) from each of the eight sire families, three early feathering and three late feathering ones, were transferred to the 48 individual cages. The details of cage allocation for the feathering genotypes and families in trial 1 are shown in Fig. 6.1. Cages were arranged in Trial 2 following the same plan as in Trial 1: a) each of the eight sire families had two random representatives, one early feathering and one late feathering each, in all of the 3 blocks; b) the early and late feathering birds were alternately arranged both within a block and between blocks. c) the family number was randomly arranged within the eight cages assigned for the early or late feathering birds within each of the blocks, and the randomisation was carried out independently for all of the three blocks.

It should be noted that in Trial 2, only two late feathering males were hatched in two of the eight sire families. Therefore the two cages originally assigned to the respective families were filled with the chicks from other families to create the proper neighbourhood for the birds around the otherwise empty cage (data collected from these two birds were omitted in the analyses in the present report except in the REML analysis mentioned in the discussion, 6.4.2.).

Other general management guidelines have already been given in Chapter 3.

Fig 6.1. The cage allocation in the environment controlled room for birds after 21 days in Trial 1

Cage	L8	E6	L4	E4	L6	E8	L7	E2	Cage
Unit 1	E7	L1	E1	L2	E5	L5	E3	L3	Unit 2
- Block 1 -									
Cage	L6	E6	L1	E7	L8	E8	L4	E2	Cage
Unit 3	E4	L5	E1	L3	E5	L7	E3	L2	Unit 3
- Block 2 -									
Cage	L6	E3	L3	E5	L2	E6	L8	E1	Cage
Unit 5	E7	L1	E8	L7	E2	L4	E4	L5	Unit 6
- Block 3 -									
-- Door --									

Note: E and L stand for early (kk) and late (Kk) feathering genotype respectively. The code number followed by E or L is the sire family number.

6.2.4. Records and Procedures

Body weight and feed consumption for the early and late feathering groups were taken at 11 and 21 days of age. Individual measurements of the lengths of the primary, secondary and tail feathers (and body weight at the same time) were taken at an interval of seven days from 21 days of age onwards except for the last one which was taken at the age of 45 days for convenience. The measurement for feed consumption did not start until three days after the birds were transferred to the individual cages to give them a chance to settle down in the new system. The three week measurements therefore were made between 24 and 45 days of age.

After feed being withdrawn at 45 days of age for 12-16 hours, all of the birds were slaughtered for the measurements of carcass traits at day 46. The weights of the following traits were recorded (Chapter 3, section 3.3.3): live body weight, dry feathers, NYD, abdominal fat, eviscerated carcass, breast meat, thighs, drumsticks, wings, frame, and the skin, meat and bones of a thigh and a drumstick separately from the same side of the body (either right or left). The yields of the dissected parts and tissues were calculated as g/kg NYD, because the precision of the starved live body weight taken in the processing plant with a spring scale graduated at 20 g intervals was not high enough.

6.2.5. Models for Data Analysis

The results from the grouped birds before 21 days of age was not statistically analysed because there was no replicate within the trials. The individual measurements at different ages or during various periods of time for feather length, body weight, feed intake, feed conversion ratio, and the carcass traits taken from the two trials separately were subjected to the analysis of variance with the following linear model:

$$Y = \mu + bI + K + F + KF + e \quad (\text{model 1})$$

where Y is the variable to be analysed; μ is the overall mean of the trait; bI is the random effect of the block; K is the fixed effect of the feathering genotype (early vs. late feathering); F is the effect of sire family, which is treated here as fixed; KF is the interaction between the feathering genotype and sire family; and e is the random error term, upon which all of the factors are tested for statistical significance.

The combined data of the overall FCR (from day 24 to day 45) from the two trials together were further analysed with the following variance analysis models:

$$Y = \mu + T + eI + K + e \quad (\text{model 2})$$

$$Y = \mu + T + eI + K + F + KF + e \quad (\text{model 3})$$

where T is the effect of trial; e_t is the error term among blocks within trial, upon which the effect of trial is tested; the rest are the same with those in model 1. In both of the models, the interaction concerned with trial was assumed non-existent (analysis with the full model resulted in F ratios for the interactions less than 1).

Following above, the overall FCR data were subjected to the covariance analyses using the tail feather length at 28 days as a covariate. However, the direct measurements of tail feather length (Tail₂₈) were not independent from the K genotypes, therefore when the fixed effect of K genotype is included in the analysis model, the tail feather length (Tail_k) adjusted for the effects of trial and K genotype was used as the covariate (i.e. the residuals of tail length from the variance analysis without considering the sire family effect). The following three covariance analysis models were compared:

$$Y = \mu + T + r_1 \text{Tail}_{28} + e_t + r_2 \text{Tail}_{28} + e \quad (\text{model 4})$$

$$Y = \mu + T + r_1 \text{Tail}_k + e_t + K + r_2 \text{Tail}_k + e \quad (\text{model 5})$$

$$Y = \mu + T + r_1 \text{Tail}_k + e_t + K + F + KF + r_2 \text{Tail}_k + e \quad (\text{model 6})$$

where r_1 and r_2 are the regression coefficients among the blocks and among the individuals within the block respectively; The tail lengths (Tail) are the corresponding deviations in the models. Model 4 calls the tail feather length to account for both the effects of K genotype and family. Model 5 and 6 seek the extra amount of variation in FCR accounted for by the adjusted feather length after the data have been fitted for the effect of K genotype, and the effects of both K genotype and family.

6.3. RESULTS

6.3.1. The Rearing Period

Table 6.2 contains the hatched weight, and the body weight, feed intake, and feed conversion ratio at 11 and 21 days of age. In Trial 1, the early feathering chicks were slightly heavier and had consumed more feed than the late feathering ones at 21 days of age, while in Trial 2 the opposite was true. The overall FCR was lower in the early feathering groups in both of the trials. The absolute difference was 0.026 in Trial 1 and 0.033 in Trial 2.

Table 6.2. The grouped body weight (BW), body weight gain (BWG), feed intake (FI) and feed conversion ratio (FCR) of the early and late feathering male chicks in the rearing period of 21 days

Age (days)	Traits	----- Trial one -----		----- Trial two -----	
		Early feathering	Late feathering	Early feathering	Late feathering
1	BW(g)	44.1	44.3	44.2	44.2
11	BW(g)	224.8	224.4	212.3	214.8
1 - 11	FI(g)	247.4	258.8	250.7	253.3
1 - 11	FCR	1.369	1.437	1.491	1.485
21	BW(g)	578.5	552.3	581.1	615.4
12-21	FI(g)	394.5	364.6	457.0	516.5
12-21	FCR	1.115	1.112	1.239	1.289
1 - 21	BWG(g)	534.4	508.0	536.9	572.3
1 - 21	FI(g)	741.9	723.4	707.7	769.8
1 - 21	FCR	1.201	1.227	1.218	1.251

Note: The number of chicks in trial 1 were 64 and 54 for the early and late feathering groups. The respective numbers in trial 2 were 52 and 33. No replicate of pens were arranged during the rearing period, and therefore no statistical analysis was possible.

6.3.2. Feathering

The means showing the effects of feathering genotype and family on the feather length measurements at various ages and on the dry feather weight at slaughter in the two trials are presented in Table 6.3.1 and 6.3.2. The statistical tests for various factors are presented in Table 6.3.3 for both of the trials.

The primary feathers were of the same length at 28 days of age for the two feathering genotypes, while before this age, the early feathering birds had significantly longer feathers, and thereafter they had significantly shorter ones than the late feathering half-brothers (Fig 6.2.). The same pattern of the dynamic change between the two feathering genotypes was also true for the secondary feather length measurements. However, the equal length of the two genotypes happened at a later age, between 35 and 45 days instead of around 28 days (Fig 6.2).

The early feathering birds had consistently longer tail and back feathers up to the age of 45 days. The effect of sire family and the interaction between the K genotype and family were also consistently significant for tail feather length in both of the trials and for back feather length in Trial 1. Some family effect on the primary and secondary feather length measurements and the dry feather weight were also evident in both of the trials (Table 6.3.1 and 6.3.2).

Fig.6.2. Growth pattern of the primary and secondary feathers in the early and late feathering males from 21 to 45 days.

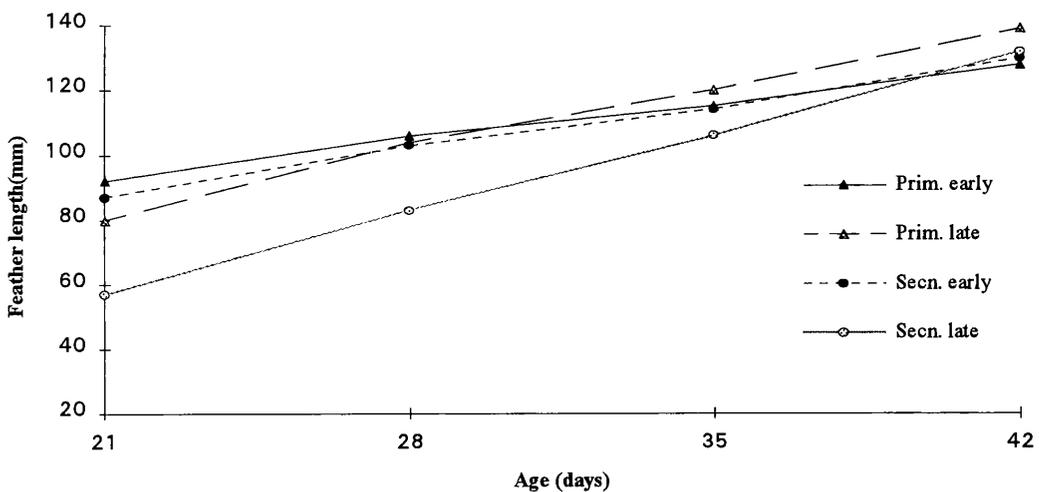


Table 6.3.1. (Trial 1) The effects of feathering genotype (kk early and Kk late) and family (F.No. 1-8) on the primary, secondary, tail and back feather length measurements at the ages of 21, 28, 35 and 45 days in mm, and on the dry weight of flight feathers (in the wings and tail) and other body feathers at 46 days

Age	Early feathering								Late feathering								Mean
F.No.	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	
Primary feather length (mm)																	
21	94	92	94	94	92	94	90	86	84	83	86	77	74	90	78	72	86
28	105	106	108	108	108	108	103	99	109	106	105	102	98	108	106	95	105
35	119	114	115	114	118	121	117	107	127	121	122	118	118	123	123	114	118
45	125	127	129	127	128	129	129	122	145	140	137	136	135	137	141	133	133
Secondary feather length (mm)																	
21	89	87	91	88	86	88	85	82	58	64	67	46	51	71	51	48	72
28	103	105	109	105	107	105	99	94	86	92	93	75	76	99	79	66	93
35	113	116	117	111	120	115	112	109	113	112	115	100	105	109	106	90	110
45	133	129	135	131	133	129	125	128	137	137	135	127	131	133	132	125	131
Tail feather length (mm)																	
21	52	53	52	54	53	49	53	48	12	21	22	9	14	24	10	8	33
28	67	70	70	74	73	68	71	67	24	36	40	19	25	41	21	17	49
35	83	87	82	95	91	83	87	82	34	52	56	30	44	61	33	27	64
45	97	102	92	106	112	101	104	98	63	82	78	54	62	93	59	48	85
Back feather length (mm)																	
21	27	28	29	26	29	26	28	25	13	19	19	3	14	21	9	1	20
28	42	40	44	41	42	39	56	37	25	32	33	15	27	36	20	10	34
35	57	57	56	59	59	53	58	57	41	44	46	26	46	53	32	21	48
45	76	71	72	72	78	73	74	68	61	66	71	47	64	72	56	38	66
Dry feather weight (g)																	
Flight	12.4	10.7	12.5	11.8	12.1	11.2	10.9	10.7	11.7	11.6	13.6	11.2	12.1	12.4	12.0	10.5	11.7
Other	36.8	44.0	38.1	38.3	42.8	38.4	40.6	35.5	42.1	41.7	39.9	39.4	39.9	49.6	34.5	30.9	39.5
Total	49.2	54.6	50.6	50.2	54.9	49.5	51.5	46.2	53.8	53.4	53.5	50.6	51.9	62.0	46.5	41.4	51.2

Table 6.3.2. (Trial 2) The effects of feathering genotype (kk early and Kk late) and family (F.No. 1-8) on the primary, secondary, tail and back feather length measurements at the ages of 21, 28, 35 and 45 days in mm, and on the dried weights of flight feathers (in the wings and tail) and other body feathers at 46 days

Age	Early feathering								Late feathering								Mean
F.No.	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	
Primary feather length (mm)																	
21	91	91	94	95	92	94	95	89	83	85	90	78	78	88	72	79	87
28	101	103	105	104	105	106	105	100	105	104	108	100	100	109	96	105	104
35	111	111	118	119	114	115	115	107	124	119	123	122	115	128	117	124	118
45	124	122	127	123	131	131	128	121	140	136	135	143	135	145	135	147	133
Secondary feather length (mm)																	
21	86	87	89	92	87	89	92	85	57	67	74	48	47	64	36	54	72
28	98	101	103	106	102	104	104	98	86	93	97	77	79	92	64	82	93
35	108	111	115	116	113	115	111	106	109	109	116	102	100	117	90	108	109
45	131	131	124	126	129	130	125	127	137	133	135	134	128	141	120	138	131
Tail feather length (mm)																	
21	50	53	54	53	49	54	59	49	16	22	25	15	17	19	13	12	35
28	63	71	71	74	71	75	78	66	29	35	47	28	36	38	28	27	52
35	79	83	83	89	83	90	94	80	43	58	67	43	52	58	62	44	69
45	91	99	92	108	100	105	105	100	60	84	97	65	73	84	74	66	88
Back feather length (mm)																	
21	25	27	28	27	28	26	32	25	16	19	21	15	17	16	11	11	22
28	38	47	45	44	44	41	47	41	29	39	34	30	28	32	25	24	37
35	61	59	57	56	59	57	62	59	47	53	51	47	46	47	42	39	53
45	76	74	73	79	75	76	78	75	65	78	71	68	68	74	66	60	72
Dry feather weight (g)																	
Flight	11.7	12.4	12.6	14.2	11.8	13.1	14.0	13.5	13.9	12.9	12.7	15.1	11.6	13.6	13.2	13.1	13.1
Other	43.7	44.0	39.9	46.4	44.2	48.8	49.6	41.2	44.7	45.8	36.0	38.8	45.8	50.3	40.3	38.2	43.6
Total	55.4	56.4	52.5	60.5	55.9	61.9	63.6	54.7	58.6	58.7	48.6	53.9	57.4	63.9	53.5	51.3	56.7

Table 6.3.3. Tests for the statistical significance of the effects of the K genotype, family and their interactions on various feathering measurements in trials 1 and 2.

Age (days)	Trial 1			Trial 2		
	----- The effects of ----			----- The effects of ----		
	K gene	Family	K*Family	K gene	Family	K*Family
Primary feather length						
21	***	.053	NS	***	NS	NS
28	NS	NS	NS	NS	NS	NS
35	**	.073	NS	***	NS	NS
45	***	NS	NS	***	NS	.074
Secondary feather length						
21	***	NS	NS	***	.076	*
28	***	***	*	***	.098	*
35	**	.062	NS		.099	NS
45	NS	NS	NS	**	.053	NS
Tail feather length						
21	***	**	**	***	*	*
28	***	**	***	***	**	*
35	***	***	***	***	**	NS
45	***	**	***	***	*	*
Back feather length						
21	***	***	***	***	NS	NS
28	***	**	**	***	.062	NS
35	***	***	***	***	NS	NS
45	***	***	**	***	NS	NS
Dry feather weight						
Flights	NS	NS	NS	NS	*	NS
Other	NS	*	.076	NS	NS	NS
Total	NS	*	NS	NS	NS	NS

Note: *, **, and *** represent a probability less than 0.050, 0.010, and 0.001, respectively; . NS means not significant, i.e. with a probability larger than 0.1. The probability between 0.050 and 0.100 are denoted in actual figures.

6.3.3. Body Weight and Feed Consumption

Table 6.4.1 and 6.4.2. present the effects of feathering genotype and sire family on the body weight, feed consumption, body weight gain and feed conversion ratio at the various ages or different durations of time after 24 days of age in the two trials

respectively. The corresponding results from the analysis of variance of the two trials are shown in Table 6.4.3.

Considering the stressful condition in the single cages for the young chicks and the genetic background of the stocks involved in the present experiment, both of the body weight (2005g and 1949g at 45 days in Trial 1 and Trial 2) and FCR (2.21 and 2.31 between 24 and 45 days for Trial 1 and trial 2) were satisfactory and were not far away from the performance of today's commercial broilers.

The body weight and body weight gain were not significantly affected by the feathering genotypes. In the first trial, the early feathering birds gained 13 g less, while in the second trial, they gained 31 g more than their late feathering half brothers between 24 and 45 days of age. The feed consumption was higher in the late feathering birds than the early feathering ones in both of the trials. The differences were significant ($P < 0.05$) in the first seven-day period and over all of the three periods together in Trial 1, and in the second seven-day period only in Trial 2. The late feathering birds consumed 138 g and 19 g more feed between 24 and 45 days of age in Trial 1 and 2 respectively. Naturally, therefore, these birds had higher feed conversion ratios in both of the trials. The differences in overall FCR were highly significant ($P < 0.01$) in Trial 1 and nearly significant ($P = 0.085$) in Trial 2.

The effect of the sire family was rarely significant on any of the traits considered in the present section in Trial 1, while in Trial 2, it was significant ($P < 0.05$) on the final body weight, the feed intake and body weight gain from the second period onwards, and the cumulative FCR to 38 and 45 days of age. Unlike the feather length measurements, the interaction between the feathering genotypes and the sire family was generally not important for body weight (gain), feed consumption and FCR.

The results of the combined variance and covariance analyses for the FCR data over the two trials are summarised in Table 6.5. Like the results when the two trials were separately analysed, the effects of K genotypes and the family were both highly significant ($P < 0.01$) with all of the models containing them. The two trials were also significantly different from each other with the first trial having a lower FCR than the second. The effect of tail feather length as a covariate was highly significant ($P < 0.01$) when the fixed effect of family was excluded from the model and non-significant otherwise. When the effect of the K genotype was separated in the covariance analysis (with the adjusted tail length as the covariate) in model 5, the regression coefficient of FCR on the tail length was -0.0045 ± 0.00161 ; when the effect of K genotype was not separated in model 4, the regression coefficient was -0.00230 ± 0.000586 .

Table 6.4.1. (Trial 1) Effect of early and late feathering genotype and sire family (F) on body weight, body weight gain, feed consumption and FCR at various ages (24, 31, 38 and 45 days) or during the different periods (P) of time (P1:25-31; P2:32-38; P3:39 -45 days; P1-2: P1+P2; P1-3: P1+P2+P3).

Age	Early feathering								Late feathering										
	F No.	1	2	3	4	5	6	7	8	mean	1	2	3	4	5	6	7	8	mean
Body weight (g)																			
24	664	688	679	730	677	728	716	621	688	724	664	677	659	717	759	729	648	697	
31	986	1031	1027	1072	1028	1086	1070	959	1032	1097	1004	1043	1000	1062	1100	1107	982	1049	
38	1460	1501	1474	1540	1493	1607	1501	1421	1500	1591	1488	1544	1473	1495	1616	1586	1444	1530	
45	1969	1973	1980	2017	1985	2135	1997	1900	1994	2080	1985	2106	1963	1943	2137	1980	1935	2016	
Body weight gain (g)																			
P1	322	343	348	341	351	359	354	338	345	373	340	366	341	345	342	378	335	352	
P2	474	470	447	468	465	521	431	462	467	494	484	501	473	433	516	478	462	480	
P3	509	472	506	477	492	527	496	479	495	489	497	562	490	448	521	395	491	487	
P1-3	1305	1285	1300	1287	1308	1407	1281	1279	1307	1356	1321	1428	1304	1227	1378	1251	1288	1319	
Feed consumption (g)																			
P1	643	687	677	692	690	725	732	656	688	797	713	766	695	733	714	779	654	731	
P2	1012	1017	929	1051	974	1126	964	1016	1011	1136	1033	1100	1020	912	1086	1095	1061	1055	
P3	1189	1111	1099	1108	1140	1250	1106	1075	1135	1258	1178	1253	1181	1073	1245	1069	1221	1185	
P1-3	2844	2815	2705	2851	2804	3101	2802	2747	2834	3190	2923	3119	2896	2719	3045	2943	2936	2971	
FCR																			
P1	2.00	2.02	1.95	2.03	1.97	2.02	2.09	1.95	2.00	2.14	2.10	2.10	2.04	2.13	2.11	2.06	1.95	2.08	
P2	2.13	2.17	2.09	2.24	2.10	2.17	2.23	2.20	2.17	2.31	2.13	2.20	2.16	2.10	2.10	2.29	2.31	2.20	
P3	2.33	2.38	2.17	2.33	2.32	2.39	2.22	2.25	2.30	2.57	2.37	2.23	2.41	2.40	2.40	2.75	2.48	2.45	
P1-2	2.08	2.10	2.02	2.15	2.04	2.11	2.16	2.09	2.09	2.23	2.12	2.15	2.11	2.11	2.10	2.19	2.16	2.15	
P1-3	2.18	2.20	2.08	2.22	2.14	2.21	2.18	2.15	2.17	2.35	2.21	2.19	2.22	2.22	2.21	2.36	2.28	2.26	

Table 6.4.2.2 (Trial 2) Effect of early and late feathering genotype and sire family (F) on body weight, body weight gain, feed consumption and FCR at various ages (24, 31, 38 and 45 days) or during the different periods (P) of time (P1:25-31; P2:32-38; P3:39-45 days; P1-2: P1+P2; P1-3: P1+P2+P3).

Age	Early feathering								Late feathering									
	F No.	1	2	3	4	5	6	7	8	mean	1	2	3	4	5	6	7	8
		Body weight (g)																
24	667	734	625	749	718	688	667	667	669	691	641	599	809	759	765	648	744	707
31	1049	1111	1054	1145	1105	1056	1102	1057	1085	1103	988	914	1146	1111	1210	994	1082	1068
38	1445	1522	1506	1570	1531	1512	1554	1557	1525	1532	1388	1336	1680	1562	1681	1455	1558	1524
45	1835	1887	1949	2030	1951	1934	2027	2031	1955	1889	1735	1751	2201	1991	2111	1894	1965	1942
		Body weight gain (g)																
P1	833	834	757	812	767	784	866	787	395	818	724	644	844	786	884	794	755	362
P2	947	930	965	965	934	1018	1039	1054	440	999	929	885	1120	997	1151	1172	1042	456
P3	1079	937	1067	1094	1036	1155	1181	1133	431	1009	956	968	1245	1037	1085	1162	1114	418
P1-3	2859	2701	2788	2871	2736	2957	3086	2974	1266	2826	2609	2497	3209	2819	3120	3128	2910	1235
		Feed consumption (g)																
P1	382	377	429	396	388	368	435	387	805	413	347	314	338	352	445	346	338	781
P2	397	411	453	426	426	455	451	501	981	429	400	422	534	450	471	461	477	1037
P3	389	365	443	460	419	422	473	474	1085	357	346	415	521	429	430	439	407	1072
P1-3	1168	1153	1324	1281	1233	1246	1359	1362	2872	1199	1094	1151	1392	1232	1346	1246	1221	2890
		FCR																
P1	2.17	2.21	1.78	2.05	1.98	2.13	2.00	2.03	2.05	2.03	2.10	2.06	2.49	2.23	1.99	2.30	2.22	2.18
P2	2.39	2.29	2.13	2.27	2.20	2.23	2.30	2.11	2.24	2.33	2.32	2.10	2.10	2.21	2.48	2.55	2.19	2.29
P3	2.81	2.62	2.52	2.38	2.47	2.77	2.50	2.40	2.56	2.84	2.82	2.35	2.37	2.41	2.58	2.66	2.75	2.60
P1-2	2.28	2.25	1.96	2.16	2.09	2.18	2.15	2.07	2.14	2.18	2.22	2.07	2.25	2.22	2.24	2.44	2.21	2.23
P1-3	2.44	2.35	2.11	2.24	2.22	2.37	2.27	2.18	2.27	2.37	2.40	2.17	2.30	2.28	2.32	2.51	2.39	2.34

Table 6.4.3. Test of significance by analysis of variance for the effects of K genotype, family and their interaction on the broiler performance traits in Trial 1 and Trial 2

Source of variation...	Trial 1			Trial 2		
	----- The effects of ----			----- The effects of ----		
Age	K gene	Family	K*Family	K gene	Family	K*Family
Body weight						
24	NS	*	NS	0.054	NS	NS
31	NS	NS	NS	NS	NS	NS
38	NS	NS	NS	NS	NS	NS
45	NS	NS	NS	NS	**	NS
Body weight gain						
P1	NS	NS	NS	+34*	NS	.094
P2	NS	*	NS	-16	*	NS
P3	NS	.087	NS	+13	**	NS
P1-3	NS	NS	NS	+31	*	NS
Feed consumption						
P1	*	NS	NS	NS	NS	NS
P2	0.067	0.080	NS	*	**	NS
P3	NS	NS	NS	NS	**	NS
P1-3	*	NS	NS	NS	*	NS
FCR						
P1	*	NS	NS	*	.092	*
P2	NS	NS	NS	NS	.056	NS
P3	**	NS	NS	NS	NS	NS
P1-2	.057	NS	NS	*	*	NS
P1-3	**	NS	NS	0.085	*	NS

Note: * and ** represent a probability less than 0.05 and 0.01 respectively. A probability between 0.05 and 0.1 is denoted with the actual figures. NS: not significant, with P>0.1.

Table 6.5. Results from the combined analysis of (co)variance for the overall FCR data (from 24 to 45 days of age) with models 2 - 6

Model No.	Cov ^a	Sources of variation (SS ^b)					Residuals ^c			Regression coefficients
		Trial	K gene	Family	K*F	Cov	SS	DF	MS ^d	
(DF... ^e)		1	1	7	7	1				
2	/	***.2167	** .1456	/	/	/	1.3519	87	.01554	/
3	/	***.2166	***.1455	.3559***	.1196	/	.8788	73	.01204	/
4	Tail28	*.0530	/	/	/	***.2241	1.2699	87	.01460	-.0023±.00059
5	Tailk	** .2169	** .1454	/	/	** .1139	1.2381	86	.01440	-.0045±.00161
6	Tailk	** .2176	***.1410	** .2929	.0924	.0176	.8612	72	.01196	-.0027±.00220

Note: a). Covariance Tail28 is the direct measure of tail length at 28 days of age; Tail_k is the same tail length adjusted for the effect of trial and K genotype.

b). Sum of squares. The total SS was same (1.7120) with all of the models.

c). The residuals in the unit stratum of the analysis. The residuals in the trial.-block stratum, upon which the effect of trial was tested, were omitted in the table.

d). Mean squares

e). The number of the degrees freedom associated with the SS if applicable with the model.

The probabilities from the F test were indicated with the stars (*, ** and *** for P<0.05, 0.01 and 0.001 respectively).

The maximum amount of variance in FCR accounted for by the covariate (tail feather length) was about 13% ($SS_{cov} / (SS_{cov} + SS_{residual})$) in model 4.

6.3.4. Carcass Traits

The carcass traits in the present experiment are all expressed in g/kg NYD, the bled-plucked carcass. The analysis of variance revealed (not shown) that none of the traits studied here are significantly affected by the major effect of the K gene genotype or the interaction involving the factor. The effect of sire family was, however, more important on several carcass traits. Therefore Table 6.6 present the means of the carcass traits according to the sire family only. The yield of the frame was significantly different (P<.05) among the sire families in both of the trials. The differences were also nearly significant for the abdominal fat yield in Trial 1 (P=0.093), and for the breast meat yield in Trial 2 (P=0.076). The effect of family was also significant (P<0.05) on two minor traits, the yields of thigh skin in Trial 1 and the skin of drumsticks in Trial 2.

Table 6.4. Means of the Carcass Traits in different sire families in Trial 1 and Trial 2 in g/kg NYD

--- Trial 1 ---

F.No.	1	2	3	4	5	6	7	8	Mean
Fat	29.2	28.5	22.7	25.4	29.9	27.4	25.5	19.8	26.0
Ev.C.	767.1	767.8	766.3	764.8	768.3	769.0	764.2	769.0	767.1
Breast	150.3	161.9	159.2	166.6	159.0	165.6	166.0	163.6	161.5
Thighs	152.8	155.0	154.0	154.2	155.7	157.3	150.2	155.0	154.3
Drums	112.6	112.5	112.6	110.8	108.4	114.1	111.7	115.3	112.2
Wings	89.8	86.9	90.3	88.5	86.1	87.0	87.9	89.8	88.3
Frame	250.1	250.8	249.5	243.6	258.5	253.5	247.9	243.4	249.7
Th. S	10.7	9.5	10.0	9.2	10.7	10.9	9.3	8.6	9.9
Th. M	56.7	58.0	56.9	58.1	58.3	57.7	57.2	58.8	57.7
Th. B	10.1	9.8	10.3	9.4	9.3	9.4	9.4	9.6	9.7
Dr. S	4.8	4.2	4.3	4.5	4.8	4.8	4.7	4.3	4.6
Dr.M	35.8	36.8	35.7	36.6	35.5	37.0	36.3	38.6	36.6
Dr.B	14.8	14.7	14.9	13.7	13.4	14.3	14.3	14.5	14.3
Leg M	185.0	189.6	185.3	189.3	187.5	189.4	187.0	194.8	188.9
leg+br meat	335.2	351.4	344.5	355.9	346.5	355.0	353.0	358.4	350.0

--- Trial 2 ---

F.No.	1	2	3	4	5	6	7	8	Mean
Fat	26.7	28.1	20.8	24.0	24.7	27.2	25.0	25.1	25.2
Ev.C.	762.8	759.2	762.7	765.8	767.9	763.3	764.0	765.2	763.9
Breast	169.7	154.4	173.9	169.0	173.2	156.3	163.1	172.3	166.5
Thighs	151.5	158.9	156.6	156.4	154.4	157.8	156.5	156.0	156.0
Drums	113.0	110.9	107.2	110.6	109.4	108.7	111.6	105.8	109.6
Wings	87.9	88.4	89.1	86.1	86.3	88.2	87.0	89.5	87.8
Frame	240.0	246.0	235.5	243.4	244.1	252.0	245.2	241.1	243.4
Th. S	9.8	10.2	9.2	9.5	9.6	10.6	9.2	10.2	9.8
Th. M	56.1	58.6	59.2	59.4	57.6	57.6	59.3	58.0	58.2
Th. B	9.8	10.2	9.8	9.4	9.6	10.0	9.9	9.5	9.8
Dr. S	4.5	4.7	4.0	4.2	4.8	5.1	4.3	4.7	4.5
Dr.M	36.4	34.9	35.6	37.3	35.7	34.7	36.4	34.1	35.6
Dr.B	14.9	15.0	14.3	13.6	14.0	14.3	14.3	13.7	14.3
Leg M	185.1	187.0	189.6	193.3	186.7	184.6	191.4	184.2	187.7
leg+br meat	354.7	341.4	363.4	362.3	359.9	341.0	354.5	356.5	354.2

Note: 1) Only one of the two legs was dissected, and the weights of the dissected skin, meat and bones of the thigh and drumstick in the table was therefore of only one side. Leg meat weights were calculated as 2*(Thigh meat + Drum meat).

2) In the table, fat was the abdominal fat + the fat around the gizzard; Ev.C. was the eviscerated carcass; Th. and Dr. stand for thigh and drum; and S, M, and B stand for skin, meat and bones respectively.

6.4. DISCUSSION

6.4.1. Feather Measurements

The present results confirmed the observation made in the previous experiment (Chapter 5) that both of the primary and secondary flight feathers measured (No. 2) grow at a higher rate in the late feathering birds than in the early feathering ones so that the early feathering birds had longer feather measurements at the early ages, while the late feathering ones had longer feathers at the later ages. However, the length differences between the two genotypes in the longest tail feather and the longest back feather are relatively constant across the ages.

The significant effect of interaction between K genotype and family on some of the feather length measurements can be explained in the same way as the interaction between the K genotype and line in the two previous experiments reported in Chapter 4 and 5, when the families were looked as certain forms of sub-lines. The significant effect of the sire family on the feather length measurements in Table 6.2 was not expected as all of the dams were randomly arranged and the sires were originated from the same source (combination of lines). The result indicated that there might be some other major feathering gene or genes segregating among the sire families. It has been suspected (Priyono, 1991) that in the slow feathering line, a mutation from K to K^S might have occurred. Although the mutation has not been established, the implication of this possible mutation on other traits concerned in the present experiment is difficult to speculate at present.

In agreement with the result in the previous experiment (Chapter 5), the total dry feather weight did not differ between the early and late feathering genotypes at the end of the experiment in either of the two trials. The separation of the flight feathers (in the wings and tail) from the rest of the feathers did not seem to give more insight into the possible difference in feather mass distribution between the early and late feathering birds. It was noticed after the removal of the birds from the individual cages at the end of the experiment, however, that while all of the early feathering birds had shed some feathers on the floor underneath the cages, none of the late feathering ones had. Similar differences in feather moulting patterns between the early feathering WL and late feathering RIR and Light Brahmas were noticed by Warren and Gordon (1935). Mueller and Moultrie (1952) further reported that the difference in the moulting pattern between the early and late feathering birds could be used as a criteria to classify the two feathering phenotypes with 100% accuracy at 10 weeks of age. Considering the

FCR data in both of the trials (Table 6.4.1 and 6.4.2), the extra nutritional cost of earlier moulting in the early feathering genotype was not large enough to be a penalty for these birds in terms of feed efficiency.

6.4.2. Body Weight, Body Weight Gain, Feed Consumption and FCR

Body weight and weight gain was generally not affected by the feathering genotypes except for the higher body weight gain of the early feathering birds in the first seven-day period of the second trial. This is in agreement with the previous experiment reported in Chapter 5 and the results of other researchers (Hays, 1951; Godfrey and Farnswarth, 1952; Hurry and Nordskog, 1953; Sheridan and McDonald, 1963). The total feed consumption was significantly increased in Trial 1 and slightly so in Trial 2 by the presence of one copy of the dominant late feathering gene. This reflects the higher energy requirement for maintenance resulted from the poorer feather insulation in birds carrying this gene. Feather insulation is more important in the individually caged birds, especially at a lower temperature, where clustering behaviour, which normally helps the birds reduce the sensible heat loss from the body (Wathes and Clark, 1981), is prevented.

The significant effect of the tail length as a covariate, when family effect was dropped off from the analyses (model 4 and 5), indicates that apart from the major feathering gene effect, FCR is related with the general feathering condition measured by the tail feather length at 28 days of age. The absolute value of the regression coefficient of FCR on the tail feather length (-0.00230 ± 0.00586) or the adjusted tail length (-0.0045 ± 0.00161) was higher than the general regression coefficient across the genotypes found in Experiment 2, Chapter 5 (0.00163 ± 0.00018). The 5°C lower post-brooding temperature and the caging management systems adopted in the present experiment were at least partially responsible for the higher regression (response) coefficient, because both of the two factors tend to make the feather insulation more important for energy saving. The other factors which might have a bearing in the difference of the coefficients are, firstly, FCR in the previous experiment was based on the grouped birds which is less variable than that based on the individuals; secondly, in the previous experiment, the FCR concerned was the accumulated one over the whole 51 days while in the present experiment, the FCR data for the calculation was only available between 24 and 45 days.

The total amount of FCR variation (sum of squares) accounted for by the tail length as a covariate was small (13 % in model 4). At the phenotype level, ignoring the family structure, correlation between FCR and tail feather length at 28 days was not high. It

was calculated as -0.387 ($P < 0.01$) when both traits were adjusted for the effect of trial, and -0.290 ($P < 0.01$) when both were adjusted for the effects of trial and K genotype. Although five models have been compared in the fitting of the overall FCR data, the effect of family and the effect of tail feather length on FCR could still not be separated. In other words, the correlation between FCR and tail length is largely dependent on the family. The significant effect of the covariate in model 4 and 5, and the non-significant effect of the covariate in model 6 showed this difficulty at the phenotypic level. Therefore it is desirable, while taking account of the specific family structure, to analyse the genetic correlation between these two traits.

A preliminary bivariate analysis of all of the 96 individual records on the FCR between 25 and 45 days and tail length at 28 days with the DFREML programme fitting the round of experiment and feathering genotype as the fixed effects and the individual animals as the random effects (see more details about the programme in the next chapter (Chapter 7)) indicate that FCR and the tail length measurement has a reasonably high genetic correlation. The genetic, environmental and phenotypic correlation coefficients were -0.623 , 0.018 and -0.240 (the corresponding h^2 for FCR and the tail length were 0.361 and 0.449). The size of the genetic correlation meant that about 40% of the variation in FCR was explained by the quantitative variation of feathering. Considering the difficulties and the costs of the direct measurements for FCR and the ease (and large number of animals can be measured as well) in measuring the tail feather length, it might be useful to incorporate the tail feather length in breeding programs as an indicator trait for FCR, especially in the late feathering broiler population. However, since the progeny produced for the present experiment had been very variable in feathering (though the major gene effect should have been accounted by the analysis model), furthermore, the individual management in cages tends to make the feathering insulation more important than grouped management as discussed in last section (section 6.4.2), the genetic correlation estimated here might only be used as a top limit for the true correlation under a commercial condition. More data need to be collected before a detailed economic evaluation for the different selection strategies can be properly undertaken.

6.4.3. Carcass and Meat Yields

In agreement with the results of our previous experiment and those of Merkle and Lowe (1988), no important difference in carcass traits was found between the early and late feathering genotypes. In other words, both the early and late feathering birds performed equally well in terms of carcass traits.

The relatively large effect of family on the abdominal fat yield in Trial 1 and on the breast meat yield in Trial 2 might mean that family (sib) selection for these two traits could be effective in the present population. Sib selection procedures have been successfully adopted to establish the divergent high and low fat lines in several research centres (Leclercq et al., 1980; Cahaner et al., 1985; Leenstra and Pit, 1987).

No report concerning the family effect on the yield of frame has been found in the literature, and this might have some important implication on the broiler breeding practice, for the frame is characterised by low value in the carcass. The large family effect means that this trait could be readily modified by effective selection. However, there is a concern that a down-wards selection for the relative weight of frame might undermine the supporting ability of the skeleton.

6.5. Conclusions

During the 21-day brooding period, the early feathering group performed slightly better than the late feathering group in terms of feed efficiency in both of the two trials, though the body weight and feed intake did not show a clear-cut response to the feathering genotypes. In the period from 25 to 45 days in the individual cages, both the early and late feathering birds gained a similar amount of body weight, while the late feathering birds had a higher FCR as a result of their higher feed consumption to support their maintenance than the early feathering half brothers.

The early feathering birds always have longer tail and back feathers up to the broiler age of 45 days than their late feathering half brothers. Differences in the primary and secondary feather length between the two feathering genotypes were inconsistent with age.

The amount of feather mass covering the body at 46 days of age and the carcass traits were not affected by the early or late feathering genotypes.

Consistent and significant differences exist among the sire families not only for the feathering traits, but also for the FCR and the yield of frame. Family variation also exists to a certain extent for the yields of abdominal fat and breast meat. The implication is that these traits might be relatively easily modified by the family selection in a broiler selection program.

Feed conversion ratio was negatively related to the tail feather length phenotypically as well as genetically. More importantly, the genetic correlation between these two traits is stronger than the phenotypic one according to the preliminary REML analysis fitting an individual animal model. The high genetic correlation means that the easily measurable tail feather length not only could be used as a valuable indicator for the general feathering condition but an indicator trait for FCR.

CHAPTER 7

ANIMAL MODEL ANALYSIS OF THE SELECTION EXPERIMENT FOR FEATHERING IN BROILER CHICKENS AT THREE WEEKS OF AGE

7.1. INTRODUCTION

A divergent feathering selection programme with a control population has been conducted for nine generations (years) in the Poultry Science Department. The programme was detailed for the base population and the following two generations by Edriss (1988), and the genetic parameters of the feathering traits and body weight for these generations were estimated with a sire and dam model using Harvey's maximum likelihood computing program. The selection procedures were also outlined by Ajang et al. (1993) to the fifth generation of selection. In this chapter, data abstracted from the selection programme for the two predominant traits, tail feather length and body weight, will be analysed using the restricted maximum likelihood (REML) procedure as suggested by Patterson and Thompson (1971) with a derivative free algorithm of Graser et al. (1987). An animal model has been fitted, and the genetic parameters estimated. The genetic parameters estimated by different methods were compared and the genetic trends over the generations discussed.

7.2. MATERIALS AND METHODS

7.2.1. Data

Data were collected from the divergent feathering selection programme for nine generations (the base population and selection generation 1-8) for the two main traits monitored: tail feather length and body weight at between 21 and 24 days of age. The selection procedures for the fast and slow feathering lines and a control line have been detailed in Chapter 3, section 3.2.1. There were shifts in the selection criteria for the two selection lines in history, reflecting the improving status of our knowledge for the feathering traits of the juvenile chicks. Briefly, all of the three lines were developed from the same base population. The parents of the divergent lines of generation one were selected according to the predicted back feather score at 24 days after the random assignment had been made for the control line. Parents of generation two and three

were selected with the predicted tail feather length as a criteria, a trait not measured in the base population. Parents of generation four and afterwards were selected on the direct measure of the tail feather length. Because only the tail feather length and body weight were measured in the later generations, other traits measured in the early generations (back feather score, primary feather length and secondary feather length) will not be considered in the present analysis.

The data structure showing the number of sires, dams and progeny in each of the lines and generations are presented in Table 7.1. The total number of recorded animals available for the present analyses were 8766. For some historical reasons, it was not possible to trace the parentage of the full- and half-sib groups in generation four birds. After a few discussions with Dr. R. Thompson at the AFRC research centre, Edinburgh, and Dr. R. Crump at SAC, Edinburgh, it was decided that the data collected before and after generation four should be analysed separately. Therefore, two sets of data were constructed with the first set consists of generations one, two and three, and the second set being consisted of generation four, five, six, seven and eight. For the first data set, the pedigree was traced back to the base population, but the records for the base animals were not included in the analysis.

Table 7.1. Number of records in the fast and slow feathering selection lines and the control line for the present analysis from the base population to generation eight

Gener- ation	Fast line			Control line			Slow line		
	Sires	Dams	Records	Sires	Dams	Records	Sires	Dams	Records
Base			(1127)			(1127)			(1127)
Gen. 1	16	82	423	16	79	273	16	81	444
Gen. 2	16	92	603	16	90	577	15	90	542
Gen. 3	8	48	279	8	46	307	8	47	328
Gen. 4	8	41	230	8	33	152	7	26	150
Gen. 5	10	47	248	9	42	235	10	45	283
Gen. 6	10	45	245	10	49	288	10	49	307
Gen. 7	9	45	243	9	50	335	9	43	264
Gen. 8	11	45	248	10	53	350	10	50	285
Total	88	445	2519	86	442	2517	85	431	2603

Another difficulty in analysing these selection data was the fact that the measurements for the selection were made at an inconsistent age in different generations. This might have caused a scale effect, or a heterogeneous variance across the generations. Chicks of generation two and before were measured at about 24 days of age, while birds in generation four and onwards were measured at 21 days. Measurements for birds in generation three were taken at an unknown age to the author. However they were believed to be taken at an older age than the rest of the generations, for the means of both body weight and tail feather length was much higher than those in the other generations.

7.2.2. Data Analysis

7.2.2.1. Outline of the statistical model and analysis procedures

Generally speaking, both the body weight and feather length measurements were subjected to the same fixed and random animal effects in the data sets. The fixed effects considered were the effects of generation, line, hatch within generation, and the sex of the individuals. Therefore, an animal model fitting the additive genetic effect of the individuals as the only random animal effect in a linear form is as follows:

$$Y_{ijklm} = \mu + L_i + G_j + H_{jk} + S_l + a_{ijklm} + e_{ijklm}$$

where Y_{ijklm} is the record of m th individual in i th line j th generation h th hatch in the generation and with l th sex; L_i is the fixed effect of i th line; G_j is the effect of j th generation; H_{jk} is the effect of k th hatch in generation j ; S_l is the effect of l th sex; a_{ijklm} and e_{ijklm} are the random additive genetic effect of the individual and the random error associated with the measurement of the individual.

The above linear model is expressed in the following matrix notation:

$$Y = Xb + Za + e$$

where Y is the vector of N observations; X is the $N \times N_f$ incidence or design matrix for the N_f fixed effects; b is the vector for the N_f fixed effects; Z is the $N \times N_r$ incidence matrix relating the observation to the random animal effects; a is the vector of random additive genetic effect of the N_r animals in the whole pedigree ($N_r = N +$ the number of animals without records) ; and finally, e is the vector of N random residual errors pertaining to the N observations.

The means and variances for the model are assumed to be as follows:

$$E \begin{bmatrix} Y \\ a \\ e \end{bmatrix} = \begin{bmatrix} Xb \\ 0 \\ 0 \end{bmatrix}$$

$$V \begin{bmatrix} Y \\ a \\ e \end{bmatrix} = \begin{bmatrix} ZGZ' + R & ZG & R \\ & GZ' & G & 0 \\ & R & 0 & R \end{bmatrix}$$

Where $G = A\sigma_a^2$, and A is the numerical relationship matrix, σ_a^2 is the additive genetic variance of the trait; $R = I\sigma_e^2$, and I is the identity matrix, σ_e^2 is the residual error variance. In words, the assumptions in the above matrixes are

a). The means of the observations are expected to be Xb , and the expectations of both a and e are 0.

b). Variance of a is $G=A\sigma_a^2$, that is to say that the additive genes effect is the only cause for the random animal effect. In the matrix A , the diagonal elements are $1+f$, where f is the inbreeding coefficient of the animals, and off diagonal elements are determined by the additive relationship of the two animals concerned, e.g. for two unrelated animals, the coefficient is 0, for those between non-inbred full sibs and between parent and offspring are both 0.5; between half-sibs is 0.25. Although the inverse of A , i.e. A^{-1} is required in the evaluation of the likelihood or the estimation of the breeding values of the animals, A itself need not be explicitly established, for the required inverse can be found directly (Henderson, 1976).

c) The variance of e is $V(e)=I\sigma_e^2$. That means that all the errors are independent of each other, and with a uniform variance of σ_e^2 . Further, the errors are not correlated with the random additive genetic effect of the animals, i.e. $Cov(a,e') = 0$.

d) With the above assumptions, the variance of observations are given by the following (see Meyer, 1989): $V(y)=ZGZ' + R$.

According to Henderson (1973), the mixed model equations pertaining to the above model is set up as follows:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ ZR^{-1}X & ZR^{-1}Z'+G^{-1} \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{a} \end{bmatrix} = \begin{bmatrix} X'R^{-1}Y \\ ZR^{-1}Y \end{bmatrix}$$

where \hat{a} and \hat{b} are the solutions to be found for a and b in the mixed model respectively. With REML (Patterson and Thompson, 1971) this linear system is solved by maximising the following likelihood function (see Meyer, 1989):

$$\log L = -1/2[\text{const} + \log|V| + \log|X^*V^{-1}X^*| + (Y-X\hat{b})'V^{-1}(Y-X\hat{b})]$$

where $V=V(y)$, X^* is the full rank submatrix of X , and the two vertical bars mean the determinant of the matrix.

There are several different strategies which can be adopted to deal with the complex process of the maximisation. However, the simplex method was found to be effective in practice, especially with the derivative-free procedure and has been used in the present research with DFREML package as described by Meyer (1989, 1991).

(C.F. With BLUP, σ_a^2 and σ_e^2 are assumed to be known without error, and therefore a unique set of solutions to the a in the model is obtainable).

For a bivariate analysis, after the transformation of data into the canonical scale, the procedure to locate the maximum of the likelihood function is the same as those for the univariate analysis. However the transformation itself cannot usually be fulfilled with only one step, consequently, there has to be an iterative search for the transformation matrix with which the covariances between the traits are below a preset criterion (say $<10^{-6}$). Univariate analyses are conducted on each of the traits and on their sum (Perssaud et al., 1991). Before summing, the two traits are scaled by their respective phenotypic standard deviations. The covariances are estimated as $\text{Cov}(x, y) = [V(x+y) - V(x) - V(y)] / 2$, where $V(x)$, $V(y)$ and $V(x+y)$ are the variances of trait x , trait y and the sum of the two traits, respectively.

7.2.2.2. Analyses of the data sets

7.2.2.2.1. Univariate analyses

Univariate analyses were carried out for both the tail feather length data and body weight data. Generally, a within line analysis was followed by a joint analysis of data combining all of the three lines. The subsets were:

Subset 1: Generation 1-2 and 1-3. The pedigree were traced back to the base population with this data set. However, the records for the base animals themselves were not included. Theoretically the parameters estimated from this subset could have been biased in various ways if any kind of selection corresponding to the trait under consideration had been applied to the parents of Generation 1.

Subset 2: Generation 4-8 and 6-8. The data set ends at Generation 8 but starts at different generations. Therefore parameters estimated from data in Generation 4-8 or 6-8 pertains to the imagined population from which the parents of Generation 4 or Generation 6 were randomly sampled. Compared with the parameters pertaining to the base population, the effects of selection and random drift in the previous generations (G 0-3 or G 0-5) were ignored.

Because a directional feathering selection was started in the base population (the parents of G1) in the two feathering selection lines, and a mild body weight selection was applied to all of the three lines in later generations, selection of parents has been a commonplace instead of exception. In order to account for the effect of selection of the parents in the starting generation within a data set, both data sets were re-analysed treating the parents of G1 for data set 1, and of G4 or G6 for data set 2. For example,

with data for line 1 G1-3, the parents of G1 in this line were treated as animals with fixed effects, while all of the birds in G1, G2, and G3 were treated as random.

The standard errors of the heritability estimations were estimated by a quadratic procedure (see a brief description given by Cameron and Bracken, 1992) whenever possible. With this method, the log likelihoods are calculated for the points of $\alpha \pm \Delta$, where α is the estimated value of heritability where the likelihood was initially maximised and Δ are the increments, 0.05, 0.1 and 0.2. A quadratic equation $a+b\alpha+c\alpha^2$ was fitted to the likelihood and the standard error of α is estimated as $\sqrt{(-1/2c)}$.

7.2.2.2.2. Bivariate analysis

The bivariate analysis is by far more computationally demanding than the univariate analysis. With the same number of records in the analysis, the bivariate analysis usually requires as much as 40 times or more of that for the univariate analysis. Therefore, only a limited number of data sets can be practically analysed. For this reason, the bivariate analyses were carried out for data including G1-G3 and G4-G8 only. Also, the fixed base animal option was not attempted. The standard error of the correlation coefficient is not estimated, as this will be too complex given the method of calculation of the correlations (Perssaud et al., 1991).

7.3. Results

7.3.1. Change of Means by the Selection

7.3.1.1 Change in tail feather length

During the years of direct selection for feathering, the two lines diverged substantially for their tail feather length (Table 7.2). Fig 7.1 and 7.2 show the changes of mean tail feather length in the three lines in males and females, respectively. The consistent differences among the three lines, with the fast feathering selected line having the longest tail feather length and the slow feathering selected line having the shortest tail feather length in both the males and females, is a strong evidence that the selection program had been successful in manipulating the trait under selection.

The divergence in tail feather length of the two selected lines are also shown as the deviations from the control line in Fig 7.3 and 7.4 for the males and females respectively. These two figures show that there was a good response to the feathering selection during the first three or four rounds of selection in both the males and the females. Response in the females was somehow larger than in the males. While the downwards selected line ceased to show any further response in the tail feather length after the third generation in males and the fourth generation in the females, the upwards selected line showed a continued response beyond the fourth generation. This resulted in dramatic asymmetry in selection response between the two lines (Fig 7.3 and 7.4), especially in the males. The 'regression' towards the control line in tail feather length in both of the selected lines between generation four and five was due to a change in the age of the measurement from 25 to 21 days of age in generation five and later.

Table 7.2. The means and standard deviations of tail feather length (mm) in the fast and slow feathering selection lines, and the control line in G1-8.

Gen.	Fast line				Control line				Slow line			
	Males		Females		Males		Females		Males		Females	
	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.
1	20.3	6.5	34.1	10.5	18.7	6.5	30.5	8.3	16.9	5.1	26.8	7.7
2	19.8	8.0	28.2	9.8	14.6	6.6	20.4	8.5	10.9	6.4	15.1	7.1
3	43.0	10.1	55.7	9.5	27.4	7.2	41.6	11.1	18.8	6.6	30.7	10.9
4	34.5	7.8	60.2	8.4	19.3	7.1	39.5	11.6	10.9	5.8	20.9	11.9
5	20.3	7.1	31.9	7.9	8.2	4.3	16.1	7.8	2.8	2.7	7.1	5.0
6	20.8	7.2	32.9	8.1	5.7	3.4	15.0	5.5	2.7	2.5	6.2	4.4
7	35.2	8.6	42.8	8.1	16.2	4.8	23.6	6.8	11.3	4.3	15.4	6.4
8	27.4	9.7	41.7	7.9	10.3	4.8	18.5	7.1	5.4	3.6	10.2	4.8

Note: Means were averaged over the hatches in the generation; and s.d, the standard deviations were the weighed means according to the number of birds in each of the hatches.

Fig 7.1. Tail feather length changes of the males in the three lines during the generations of divergent feathering selection

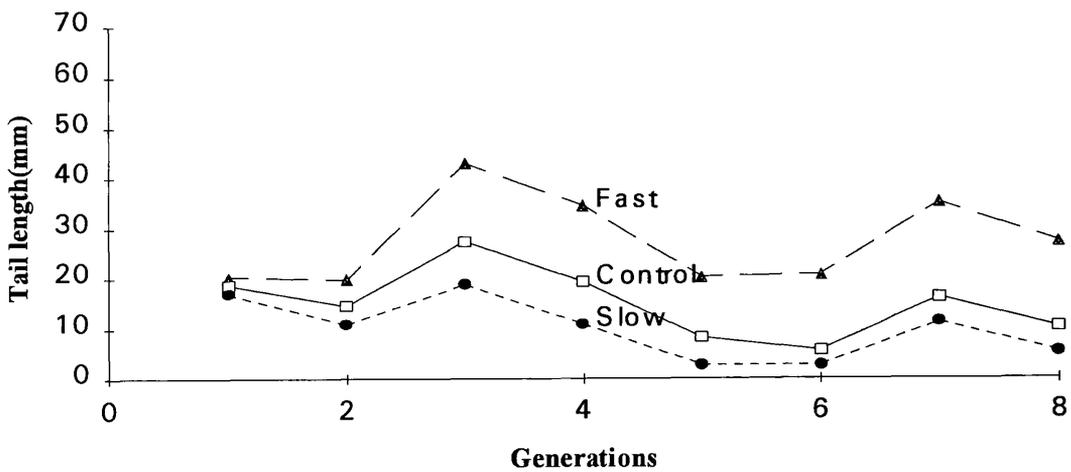


Fig 7.2. Tail feather length changes of the females in the three lines during the generations of divergent feathering selection

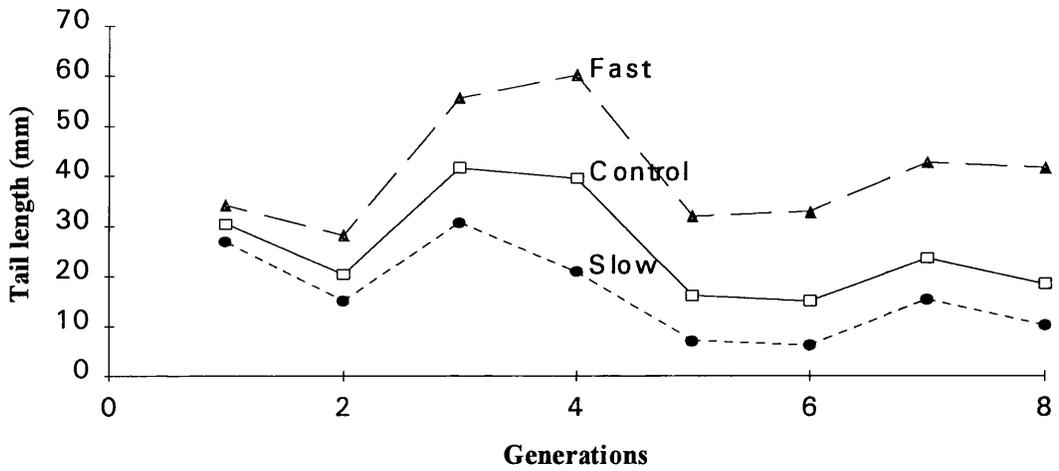


Fig. 7.3. Deviations of tail feather length of the two selected lines from the control line (Males)

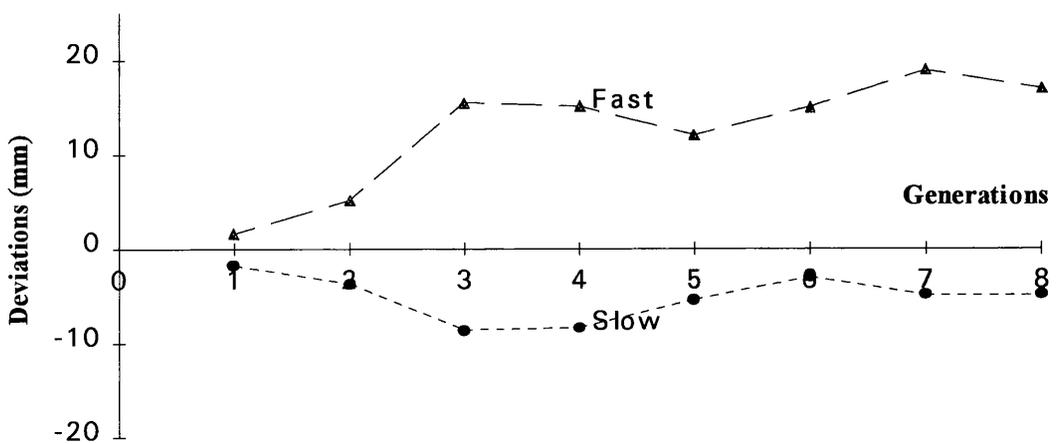


Fig. 7.4. Deviations of tail feather length of the two selected lines from the control line (Females)

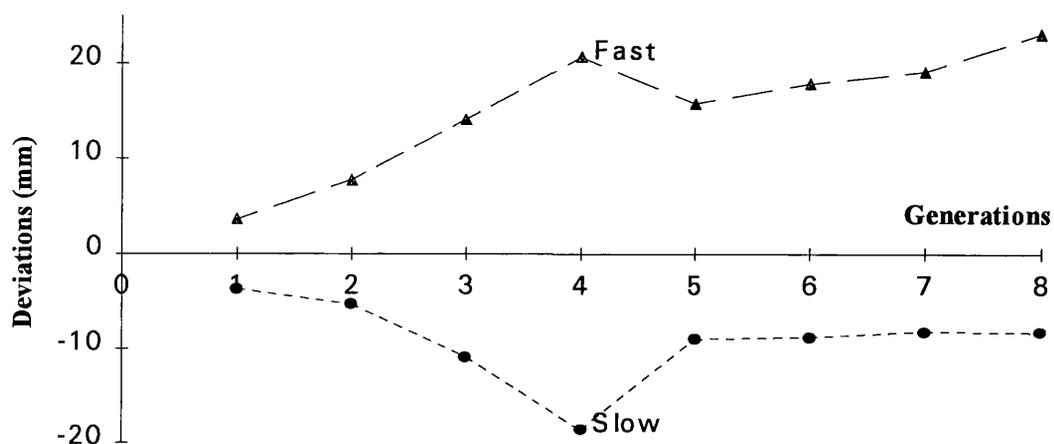


Table 7.3. Realised selection differentials of the tail feather length (mm) weighted according to the contributions of the breeding birds to the next generation (number of progeny) in the fast and slow feathering lines throughout the generations

Gener- ation	Fast feathering line			Slow feathering line		
	Males	Females	mean	Males	Females	mean
1	10.3	4.3	7.3	-5.1	-3.5	-4.3
2	3.6	8.5	6.1	-6.1	-5.7	-5.9
3*	9.4	2.9	6.2	-5.6	-8.3	-7.0
4	5.0	0.7	2.9	-2.4	-1.9	-2.1
5	7.7	3.1	5.4	-0.1	-1.3	-0.7
6	5.6	4.4	5.0	-1.0	-1.2	-1.1
7	2.0	3.5	2.7	+0.9	+0.1	+0.5
Overall			35.6			-20.6

Note: The weighted selection differentials were first calculated within each hatch, and then the selection differential within hatch was weighted again by the total number of progeny produced by the breeding birds selected in that hatch to give the selection differential in the generation. In these calculations, the relationship among the breeding birds from generation to generation was ignored.

*: Because of the loss of the mating sheet, the selection differentials for generation 3 were unweighted and referred to the selection differentials at the time of selection (25 days).

A lack of further response to the selection in the slow feathering line indicate that a plateau had been reached by this line in generation 4. By checking the mean values of this line in generation 5 and later, it seems that the plateau was rather physical at least in generation 5 and 6, as evidenced by the small means of the trait, especially in the males, and therefore, not much selection pressure could be actually practised.

The realised selection differentials through the generations are given in Table 7.3. This table shows that the selection against tail growth in the slow feathering line had been very small from generation five onwards, and the selection differential had even gone positive in generation seven since a higher selection pressure was needed to upgrade the body weight in this line compared with the other two lines.

Fig 7.5 and 7.6 show the direct response in tail feather length (measured as the deviations from the control line in each of the generations) against the cumulative selection differentials for the fast and slow line, respectively, with males and females combined. With these, a regression line can be fitted, and the slope of the regression line, according to the definition, is the realised heritability of the trait under selection. In this way, Table 7.4 presents the realised heritabilities estimated from the males and from the females separately, and also for the different combinations of generations in the two divergently selected lines.

Table 7.4. Realised heritabilities estimated from the regression of selection response to the cumulative selection differential in the fast and slow feathering lines.

Generation	Males + Females		Males*		Females*	
	regr. coef.	probability	regr. coef.	probability	regr. coef.	probability
Fast feathering line						
Gen 1-7	0.379	0.015	0.339	0.04	0.419	0.015
Gen 4-7	0.481	0.001	0.457	0.104	0.504	0.066
Gen 1-3	0.930	0.168	0.811	0.358	1.049	0.006
Slow feathering line						
Gen 1-7	0.052	0.814	0.209	0.237	0.1426	0.639
Gen 4-7	-0.242	0.647	-2.798	0.028	-0.483	0.028
Gen 1-3	0.693	0.092	0.532	0.127	1.033	0.027

Note: The selection differentials used in the calculation of regression coefficients were the means of the two sexes as in the column for Males + Females.

The change in measurement age during the course of the selection program may have caused a biased (downwards) to the estimates with data from generation one to seven in both lines. Moreover, the selection differentials were too small between generation four and seven in the slow feathering line to give a valid estimation. Generally, however, the estimates from the upwards selected (fast) line is slightly higher than those from the downwards selected (slow) line; estimates from the earlier generations are higher than those from the later generations; and furthermore, the females responded to the selection slightly better than the males.

Fig 7.5. Cumulative selection differential and response in tail feather length of the fast feathering line (males+females)

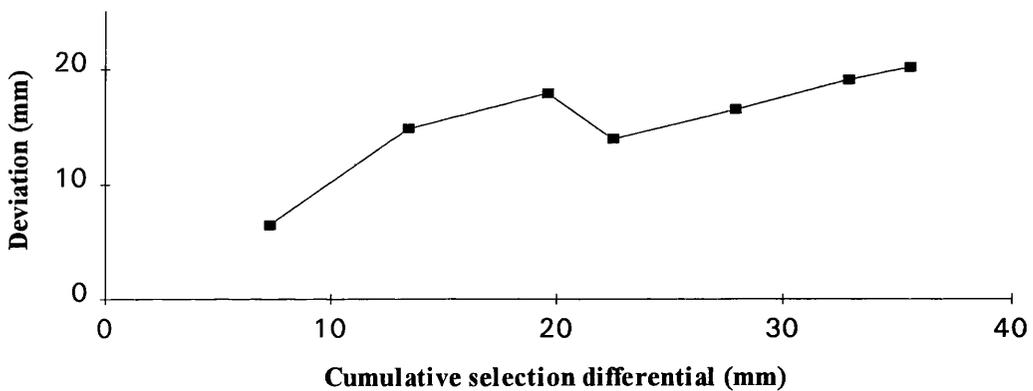
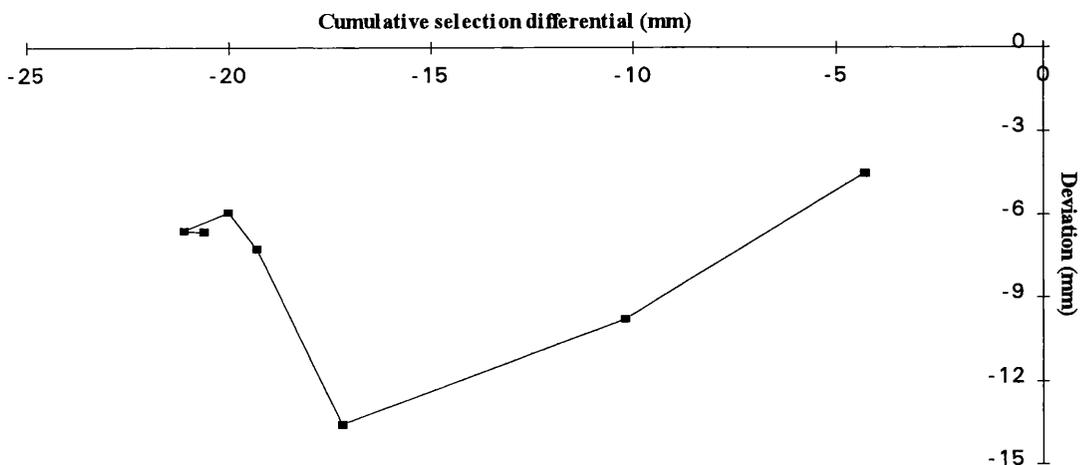


Fig 7.6. Cumulative selection differential and response in tail feather length in the slow feathering line (males+females)



7.3.1.2. Body weight changes

Selection for feathering, notably in the tail feather length, has caused a substantial correlated change in body weight in the selected lines. Changes in body weight are shown in Table 7.5 for the males and females separately, and also in charts from Fig 7.7 through Fig 7.10.

Although there are some fluctuations throughout the generations both in terms of the absolute value of body weight and in terms of the relative body weight of the two selected line expressed in deviations from the control line, the general tendency was clear. That is the body weight is highest in the fast feathering line, and lowest in the slow feathering line. That is to say that the upwards selection for feathering caused an upwards correlated response in body weight, and a downwards selection for feathering also resulted in a downwards response in body weight. Therefore the feathering trait is positively correlated with body weight. However, because of the inconsistency in the correlated response in body weight together with the fact that body weight was subjected to the direct selection as well in the later generations, a calculation of the realised genetic correlation was not attempted. Judged from Fig 7.9 and 7.10, the correlation seemed to be a little more consistent in the slow feathering line than in the fast feathering line. Starting from generation 4, the response in body weight was negative, instead of positive in the fast feathering line, indicating that the genetic correlation had been very small or even negative in sign.

Table 7.5. Means and standard deviations (s.d.) of body weight (g) of the males and females in the three lines from the base population to the eighth generation

Gen.	Fast line				Control line				Slow line			
	Males		Females		Males		Females		Males		Females	
	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.
Base	316	60.2	292	51.7	316	60.2	292	51.7	316	60.2	292	51.7
1	480	98.2	470	90.0	501	81.2	491	71.5	472	75.7	479	70.6
2	438	77.7	392	62.0	417	78.6	383	63.8	399	72.9	363	60.9
3	899	69.4	759	64.0	894	69.3	761	72.4	851	79.8	730	80.5
4	673	55.8	608	58.1	642	67.2	568	70.6	610	73.2	539	60.4
5	444	51.2	490	54.5	457	53.4	463	56.9	407	57.5	423	54.4
6	411	53.9	420	41.2	395	49.6	395	42.3	365	48.4	333	48.7
7	656	60.5	596	47.1	645	66.8	593	46.4	626	50.4	559	44.9
8	508	65.3	494	52.8	514	81.3	477	75.5	434	68.9	441	53.9

Fig 7.7. Body weight changes of males in the three lines during the generations of selection for feathering

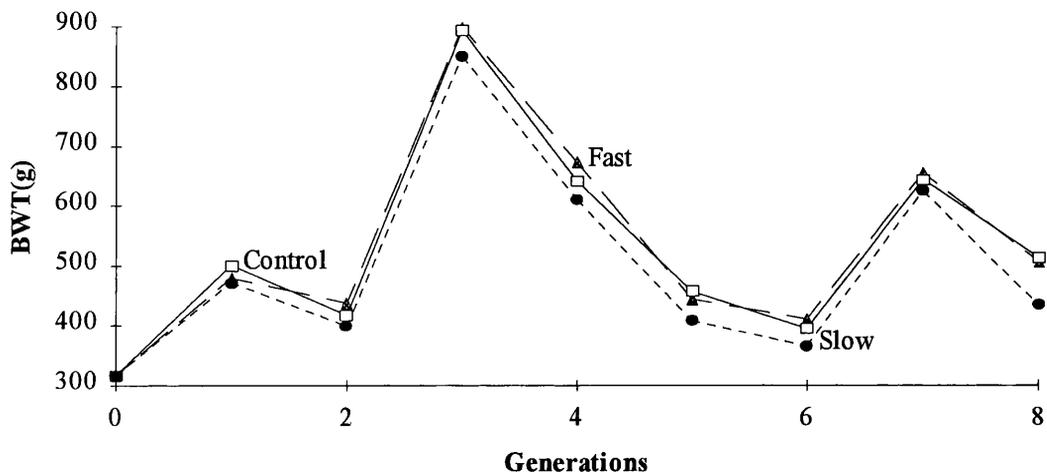


Fig 7.8. Body weight changes of females in the three lines during the generations of selection for feathering

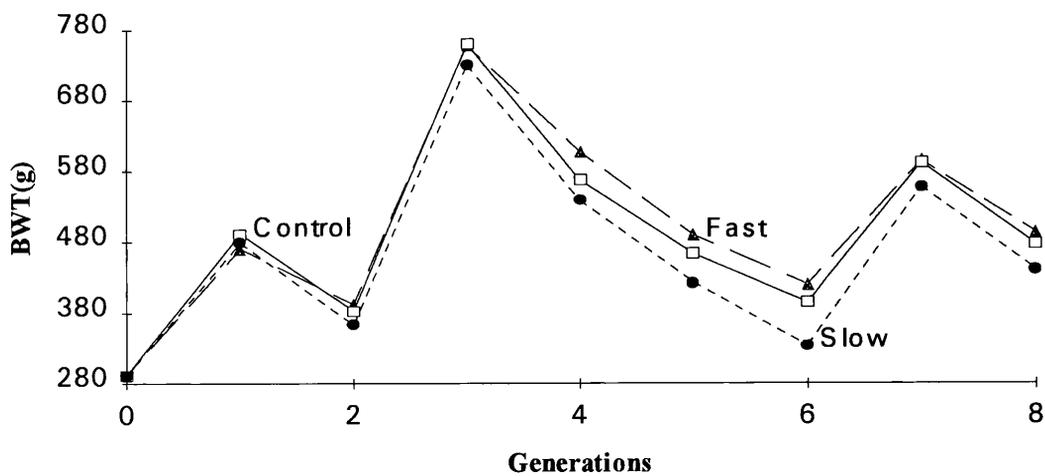


Fig 7.9. Responses of body weight (deviations from the control line) in the two lines to the feathering selection (males)

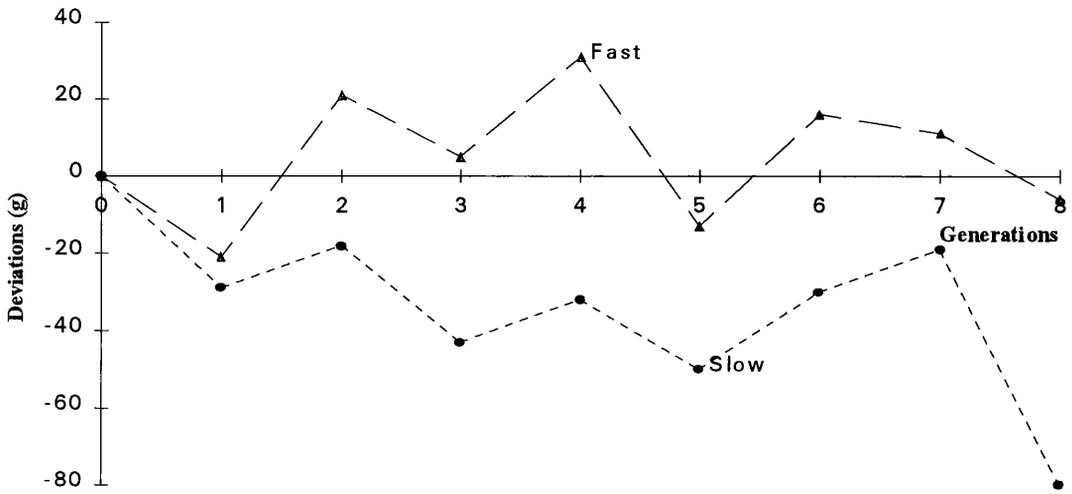
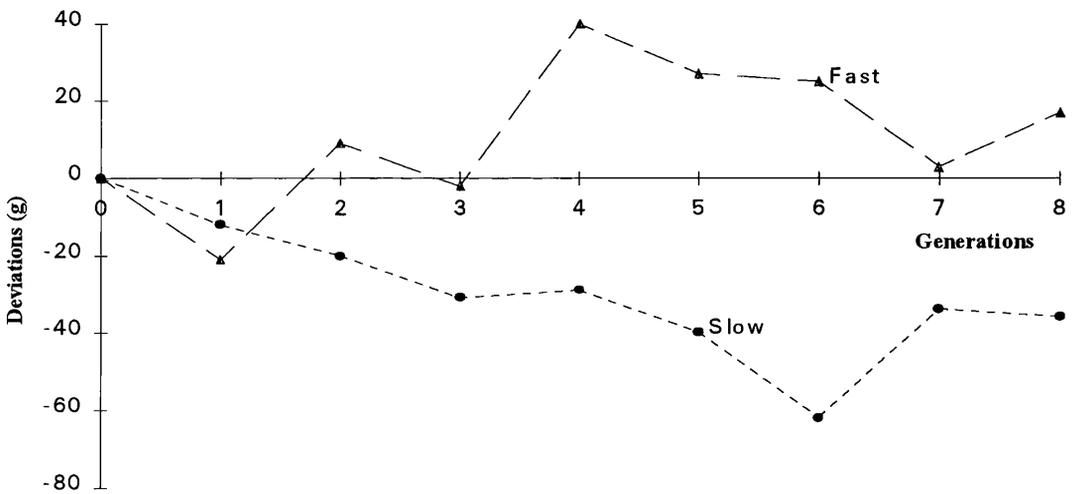


Fig 7.10. Responses of body weight (deviations from the control line) in the two line to the feathering selection (Females)



7.3.2. REML Estimation of the Genetic Parameters

7.3.2.1. Estimation of the heritabilities from the univariate analyses

The REML estimates of the additive genetic (σ_a^2), error or residual (σ_e^2) and phenotypic (σ_p^2) variance components resulted from the univariate analyses for the tail feather length and body weight are presented in Table 7.6 and 7.7, respectively, for the various data sets. Estimates of heritabilities and their approximate standard errors are shown in Table 7.8.

Seven out of the 64 data sets did not converge towards the end of the analysis because some of the diagonals went negative during the equation absorption of Gauss elimination. Therefore, both of the variance components and the parameters could not be found (invalid estimates were given by the program). This was, however, limited to the analyses with the parents without records being fixed and in the slow feathering line or the combined data from all of the three lines only. A similar problem was reported by van der Werf (1992) with the DFREML algorithm when the base animals were treated as fixed. An option which allows for heterogeneous variance across the levels of a fixed factor might help to overcome some of the problems (R. Crump, 1994, personal communication), but not all.

With all of the animals treated as random effects in data set 1, the environmental variances were similar across all of the three lines for both of the traits considered. However, the additive genetic variances were slightly larger in the fast feathering line than in the control line, which in turn were slightly larger than those in the slow feathering line. Therefore, the heritability estimates were in the order of Fast > Control > Slow for both traits. However, the absolute differences among the lines were small. In the later generations with data set 2, the heritability estimates for the feathering trait in the two selected lines were only about one half of those estimated from data set 1. They were similarly lower than or equal to those in the control line in the corresponding generations. However the additive genetic variance in the slow feathering line was only about one third of that in the fast feathering line (Table 7.6). This may partially explain the asymmetry in response of feather length to the similar selection in the two lines.

Treating parents without record as fixed effect resulted in higher heritabilities for the tail feather length in the two feathering selected lines. This had mainly been for slightly higher estimates for the additive genetic variance components. This option did not seem to have a directional effect on the heritability estimates for the tail feather

length in the control line and with the body weight data. However, it did seem to have reduced or even eliminated the declining tendency in heritability estimates over generations within the lines. In other words, it stabilised the heritability estimate within line. Compared with treating all birds as random animal effect, this option also resulted in a higher standard deviation for the heritability estimate, as it was expected from the fact that this option reduces the degrees of freedom for the random variable. With this option, heritability estimates for the feathering trait were highest for the fast feathering line in all of the data sets. In data set 2, the feathering heritability was lowest in the slow feathering line. Body weight heritability was basically in the order of Control > Slow > Fast.

Table 7.6. REML estimates of additive genetic (σ_a^2), error (σ_e^2) and phenotypic (σ_p^2) components for the tail feather length from different lines and sets of data

Data	Fast		Control		Slow		Combined		
	σ_a^2	σ_e^2	σ_a^2	σ_e^2	σ_a^2	σ_e^2	σ_a^2	σ_e^2	
With all birds random									
1-2	51.79	37.02	33.18	24.33	28.18	23.22	51.40	36.32	30.48
1-3	51.06	42.24	34.83	35.71	30.64	32.88	63.51	43.50	35.37
4-8	21.74	63.09	23.73	27.84	7.47	22.49	29.99	44.23	34.92
6-8	25.67	48.94	10.66	23.52	6.70	13.60	20.30	14.20	29.40
With the parents without data being fixed									
1-2	74.21	28.32	102.5	26.48	27.43	53.91	*	*	*
1-3	72.73	33.18	105.9	32.68	37.40	70.08	43.67	27.30	70.97
4-8	47.13	50.52	97.65	20.50	28.75	49.26	5.69	23.04	28.73
6-8	50.59	37.59	88.18	14.86	22.12	36.97	7.69	13.52	21.20
							14.19	29.40	43.59

Note* The variance components were not estimated because the data concerned did not converge for the analysis.

Table 7.7. REML estimates of additive genetic (σ_a^2), error (σ_e^2) and phenotypic (σ_p^2) components for body weight from different lines and sets of data

Data	Fast			Control			Slow			Combined		
	σ_a^2	σ_e^2	σ_p^2									
With all birds random												
1-2	4002.6	2382.4	6385.0	3439.0	2310.7	5749.7	2713.6	2581.3	5294.9	3115.1	2627.0	5742.1
1-3	3839.7	2933.8	6773.5	3058.8	3232.0	6290.8	3024.7	3289.1	6313.9	2995.7	3369.6	6365.3
4-8	1090.5	2201.6	3292.1	2663.0	1993.6	4256.6	1979.6	1912.7	3892.3	2072.8	1988.1	4060.8
6-8	834.9	2315.6	3150.4	1710.0	2531.9	4241.9	955.0	2259.8	3214.8	1272.8	2383.4	3665.3
With the parents without records being fixed												
1-2	2016.6	3255.6	5272.2	3401.9	2364.0	5766.0	*	*	*	*	*	*
1-3	2168.1	3681.7	5849.8	3001.0	3259.2	6260.2	2443.9	3548.8	5992.8	2134.4	3748.5	5882.9
4-8	1202.3	2160.8	3363.2	2617.0	2004.6	4621.7	1791.9	1979.5	3771.5	*	*	*
6-8	1691.2	1926.3	3617.5	2719.2	2115.0	4834.2	1984.6	1751.1	3735.7	2197.1	1977.9	4175.0

Note* The variance components were not estimated because the data concerned did not converge for the analysis.

Table 7.8. REML estimates of heritabilities for the tail feather length and body weight from different sets of data (generations and lines) with various options.

Data	Tail feather length				Body weight			
	Fast	Control	Slow	Combined	Fast	Control	Slow	Combined
With all birds random								
1-2	0.583±0.078	0.577±0.062	0.548±0.079	0.544±0.039	0.627±0.044	0.598±0.068	0.420±0.060	0.543±0.034
1-3	0.547±0.070	0.494±0.066	0.482±0.044	0.559±0.034	0.567±0.054	0.486±0.058	0.479±0.057	0.471±0.032
4-8	0.256±0.091	0.460±0.067	0.250±0.058	0.316±0.038	0.331±0.071	0.572±0.064	0.509±0.080	0.510±0.043
6-8	0.344±0.097	0.312±0.068	0.330±0.076	0.326±0.051	0.265±0.080	0.403±0.078	0.297±0.093	0.348±0.054
With the parents without data being fixed								
1-2	0.724±0.091	0.491±0.108	*	*	0.382±0.116	0.590±0.093	*	*
1-3	0.687±0.084	0.466±0.096	0.615±0.082	*	0.371±0.100	0.479±0.076	0.408±0.076	0.363±0.046
4-8	0.483±0.105	0.416±0.073	0.239±0.061	*	0.358±0.094	0.566±0.076	0.475±0.090	*
6-8	0.574±0.147	0.402±0.090	0.363±0.105	0.435±0.071	0.468±0.111	0.562±0.088	0.531±0.109	0.526±0.072

*Note** These heritabilities were not estimated because the data concerned did not converge for the analysis.

7.3.2.2. Bivariate analysis

Results of the REML estimates from the bivariate analyses for the tail feather length and body weight are presented in Table 7.9 for the individual lines. It was initially attempted to make the estimates for the combined data sets as well as for the individual lines. However, after a lot of effort, it was revealed that none of the combined data sets converged for the bivariate analysis. This might have been caused by the heterogeneous variance among the lines (R. Crump, 1994, personal communication). For this reason, results from the combined analysis were not obtained.

The variance components estimated from the bivariate analyses are similar to those estimated from the corresponding univariate analyses, and therefore the heritabilities are very much the same with the univariate analyses (different only in the third place after the decimal point for most of the data sets).

For the data of generation 1-3, the additive genetic correlation estimated from the slow feathering line (0.35) was slightly smaller than those from the fast and control line (both at about 0.48). The environmental correlation seemed to be smaller in the control line than the two selected lines though the bivariate analysis did not converge well for the control line (after 80 rounds of covariance iterations, the average correlations on the canonical scale was still between 10^{-1} and 10^{-2} and the progression of the calculations did not show any sign of further convergence). The phenotypic correlation was highest in the fast feathering line.

After only a few generations of selection, the phenotypic, environmental and especially the additive genetic correlation between body weight and tail feather length reduced dramatically. For the data from generation 4 to generation 8, the additive genetic correlation was essentially zero for the fast feathering line (-0.017), low but still positive (0.14) for the slow feathering line and moderate (0.38) for the control line. From these correlation estimates, it can be expected that body weight in the fast feathering line would not have any further response to the feathering selection, but that in the slow feathering line could go further down in a response to the down-wards feathering selection though at a lower rate compared with the previous generations. This can serve to explain why it was more difficult to update body weight in the slow feathering line than in the fast feathering line. Both the genetic and phenotypic correlations were much higher in the control line than the two selected lines.

Table 7.9. REML estimates from the bivariate analyses for the tail feather length and body weight: variance (V) and covariance (Cov) components and the resulting heritabilities and the genetic, residual and phenotypic correlations between the two traits.

	Generation 1-3			Generation 4-8		
	Fast	Control	Slow	Fast	Control	Slow
Additive genetic effect						
Cov	213.06	151.72	107.38	-2.73	92.02	17.03
V(tail)	50.67	32.45	30.47	21.94	23.47	7.46
V(bwt)	3802.22	3043.25	3026.56	1104.18	2497.93	1908.45
Residual effect						
Cov	110.95	58.53	102.70	64.24	27.99	46.03
V(tail)	42.40	37.08	32.97	62.98	28.13	22.52
V(bwt)	2955.33	3241.09	3288.12	2193.28	2084.44	1951.93
Phenotypic effect						
Cov	324.01	210.26	210.08	61.51	120.01	63.06
V(tail)	93.08	69.53	63.44	84.93	51.60	29.97
V(bwt)	6757.56	6284.33	6314.68	3297.46	4582.37	3860.38
Correlation coefficients						
Genetic	0.485	0.483	0.354	-0.018	0.380	0.143
Residual	0.313	0.169	0.312	0.173	0.116	0.220
Phenotypic	0.409	0.318	0.332	0.116	0.247	0.185
Heritabilities						
Tail	0.545	0.467	0.480	0.258	0.455	0.249
B. weight	0.563	0.484	0.479	0.335	0.545	0.494

7.4. DISCUSSION

7.4.1. Selection Response

7.4.1.1. Tail feather length

Edriss (1988) discussed the possible reasons for the asymmetry in the response to the direct feathering selection in the two divergently selected lines with the data available at that time. It has become clearer after five more generations of selection that the reasons for the reduction and even cessation of further response in the slow feathering line to the direct selection was mainly threefold. Firstly, the mean of tail feather length in the slow feathering line was approaching the physical limit of zero (especially in the males to which most of the selection pressure is usually applied in a selection program), and therefore, not much selection differential could possibly have been put in this line. Secondly, the phenotypic, as well as the genetic variance, of the tail feather length in this line declined much more rapidly than the other two lines as indicated by both the calculated standard deviation of the tail feather length in Table 7.2 and the REML estimates of the variance components in Table 7.6. Finally, a positive body weight selection might have worked as an indirect upwards selection for feathering to offset some of the efforts being made in the direct selection.

7.4.1.2. Body weight

Although body weight was monitored as a correlated trait only at the beginning of the selection program, this trait has been directly included in the selection decision making in the later generations in all of the three lines. For this reason, any attempt to calculate the realised genetic correlation between the tail feather length and body weight would be improper. Nevertheless, the trends presented in Figs 7.9 and 7.10 strongly suggest that the two traits might be positively correlated. The slow feathering line had the lowest body weight, while the fast feathering line had the highest in most of the generations. Based on the deviations from the control line, however, the slow feathering line seemed to be more consistent in reducing body weight than the fast feathering line in increasing it. This has been supported by the changes in the genetic correlation between body weight and tail feather length in the two lines: with a positive coefficient in the slow feathering line, body weight was expected to continue to decline gradually, while in the fast feathering line, body weight was not expected to change in a response to the feathering selection. In the slow feathering line, selection for slow

feathering rate on the one hand, and selection for higher body weight on the other, is against the direction of the genetic correlation.

7.4.2. Genetic Parameters

Edriss (1988) and Edriss et al. (1988) estimated the genetic parameters for the same lines of chicken in the first two generations with the maximum likelihood methodology. Their estimates of 0.599 and 0.568 for the tail length based on the full-sib variance components were in between the present estimates with and without treating the parents of generation one as fixed effects as far as the two selection lines are concerned. However, the body weight heritability estimates of 0.839 and 0.713 in the first and second generation seemed to be overestimated. Compared with other sources of body weight estimates in broilers (see summary by Chambers, 1990), this might be true.

The small number of the sire family groups within a single generation, as well as the fact that the parents were selected in different directions in respect of feathering and the correlated traits (equivalent to the assorted mating when the three lines were considered together) might be the main reasons for the overestimation. The kind of assortative mating as above has been known to increase the covariance of sibs (Falconer, 1989) and hence increase the heritability estimated by sib analysis.

Theoretically, the univariate analysis, as presented here, might also be biased by several factors. One is the selection on the trait or traits that are not under the direct consideration of the analysis. For example, the heritability estimate for body weight could be biased by the feathering selection, and vice versa. But in practice, this kind of bias seemed to be rather small with the size of a genetic correlation up to 0.5, since the univariate estimates of heritabilities and the variance components were essentially the same as the bivariate estimates with the present data sets.

Secondly, both the univariate and bivariate analyses could have been biased by the selection of the base animals and the selection and drift of their ancestors. In order to account for the effect of selection of the base animals, Meyer and Hill (1991) advocated the option to treat the selected base animals as the fixed effects instead of random. This option was used in the present research in a hope to give more insight into the nature of the bias. However the properties or the consequences of the approach are not yet fully understood (Meyer and Hill, 1991; van der Werf, 1992). The simulation study conducted by van der Werf (1992) showed that when the descendants of the fixed base animals were selected to produce progeny, a new bias could be

introduced to the estimates of genetic parameters. Furthermore, the magnitude as well as the sign of the bias is not general, but was dependent on the population structure, parameters and selection intensity. With the results presented in Table 7.8, this seemed to be the case. With the fixed base animals in generation 1-2 of the fast feathering line, heritability for the tail feather length seemed to be overestimated (0.724 vs. 0.577 for the random control line), while heritability for body weight in the same set of data was likely to be underestimated (0.382 vs. 0.598 in the random controls). A comparison of the results from the more accurate bivariate analyses for the different generations of the control line and for the different lines showed that the random drift in the first three to four generations with the population structure in the present selection program, reduced the heritabilities of both traits little, if any. In the control line, heritabilities for the tail length were 0.467 in generations 1-3 and 0.455 in generations 4-8, and for body weight, the corresponding figures were 0.484 and 0.545. However, drift seemed to have reduced the genetic correlation in the control line from 0.48 to 0.38. The parameter deviations of the selected lines from those of the control line can mainly be attributed to effect the directional feathering selection. Therefore, four rounds of intensive feathering selection in either of the directions had nearly halved the tail length heritability from about 0.5 to 0.25. Selection reduced body weight heritability by 40% from 0.56 to 0.33 in the fast feathering line, but not in the slow line. The lower genetic correlation of the slow line in generations 1-3 (0.354) may explain part of the differences between the lines. Selection in either of the directions also dramatically reduced the genetic correlation between the two traits during the first few generations.

Compared with the present REML estimates, a genetic correlation between the tail feather length and body weight, 0.556 in the first generation and 0.605 in the second, estimated by Edriss (1989) based on the sib analyses seems to be slightly overestimated. A rapid decline in the genetic correlation between body weight and feathering traits was also reported by Siegel (1963b). It reduced from about 0.2 in the first two generations to zero in the fourth generation. The selection, in this case, was made on body weight.

It has been established that directional selection reduces additive genetic variance (Falconer, 1989). However, the high rate of reduction in additive genetic variance for the feathering trait of the selected lines might indicate that the number of segregating quantitative trait loci (QTL) in the base population for the feathering trait might be small. Because the REML analysis implicitly assumes a multivariate normal distribution of data in the bivariate analysis (Meyer and Hill, 1991), or equivalently assumes an infinitesimal model (Bulmer, 1980), this analysis is more prone to the change of gene frequencies. When the actual number of QTL is not large, the

assumption is violated and the gene frequency of the QTL will change rapidly as a result of directional selection. This is likely to be the case while the genetic correlation estimated with data from generation 4-8, in either the fast or slow feathering line was far away from the estimates pertaining to the base population.

The large reduction in phenotypic variance in both of the traits estimated in the later generations might just have been an indication for the change in measurement age in later generations. Strictly speaking, measurements made at 24/25 days in the early generations should be treated as different traits from the measurements made at 21 days in later generations. However, the practical data did allow this kind of data treatment, and the analyses presented here seemed to be satisfactory.

7.5. CONCLUSIONS

There are several important practical implications of the present research.

First of all, the feathering trait, tail length, is an easily measured and readily manipulated trait with a heritability of about 0.5 in the base population. An upward selection for this trait is expected to result a continuous improvement of the trait.

Secondly, the positive genetic correlation between the feathering trait and body weight in the base population means that a selection for improved feathering may not hamper the body weight selection. As indicated in the previous experiment, improved feathering may also help to improve broiler feed efficiency. However, the genetic correlation between the two traits is not very high in the base population, and is changeable for a population undergoing intensive single trait selection. Improvement in feathering cannot be wholly dependent on the indirect selection through body weight selection, and of course, vice versa.

Finally, genetic parameters, especially the genetic correlation, used in a breeding program should be reappraised regularly.

CHAPTER 8

GENERAL DISCUSSIONS AND CONCLUSIONS

8.1 DISCUSSION

The present research program has been focused on the feathering traits and their relationships with important broiler performance traits. The following questions have been asked, and appropriate experiments and analyses were carried out in an endeavour to provide the answers:

1. How the different feathering genes control the feathering traits?
2. What are the consequences of the quantitative feathering selection in terms of the broiler performance traits?
3. What are the effects of different major feathering genes on the broiler performance under the different backgrounds of polygenes?
4. What are the joint effects of the polygenes and the major genes?
5. Has the selection program been successful in manipulating the traits under different directions of selection?
6. Did the body weight respond to the feathering selection?

8.1.1. The Control of Feathering

The involvement of the major genes in the K locus in the control of feathering has long been established (Hutt, 1949). The quantitative selection for feathering was known to alter the initiation of feather development (Priyono, 1991). The present result revealed that the fast feathering selection also speeded up the growth rate of the tail feathers. The fast feathering birds with a late feathering phenotype (Kk) had a much shorter initial feather length than the early feathering birds. These two types of birds had an equal tail length at about 40 days of age. The inability of the selection influencing feathering measurements on an early feathering background was previously reported in the early feathering females (Lou et al., 1992). The present research confirmed that the interaction between K genotype and the polygenes (line effect) on the feathering traits is not limited to the hemizygous females, but is general feature. Results also indicate that the polygenes selected in both the fast and slow feathering lines may have a strong sex-linked feature.

The naked neck gene was known to reduce the amount of feather covering substantially (Merat, 1986). The present research showed that this gene has no effect on

the growth of the unaffected feathers. The naked neck gene, therefore, operates as a "yes or no" switch only for the initial development of the feathers concerned.

8.1.2. The Consequences of the Feathering Selection on the Broiler Traits

The consequences of the feathering selection for three generations has been reported by Ajang et al. (1993) in a study with the progeny produced from the pure lines as follows. The slow feathering line had a higher body weight, higher total meat yield and breast meat yield, more carcass protein, but less carcass fat at 48 days of age than the fast feathering line. The two lines had an equal FCR.

With the cross-bred progeny used in the present research, and in broader major gene backgrounds, the present results agreed with the findings of Ajang et al. (1993) in terms of various carcass traits, including the chemical composition. The line differences, as it was expected, were generally smaller than those between the pure lines.

There might be some interaction between the K genotype and the feathering line for the 51 day body weight in experiment 2 (Chapter 5). With an early feathering genotype (kk), the fast feathering line tended to be the heavier, but in a late feathering background (Kk), the slow feathering line tended to be the larger. This interaction has been traced back to the significant interaction between the two same factors in a similar way for feed consumption.

Feed efficiency difference was small between the lines, but in favour of the fast feathering line. In the following-up experiment (Chapter 6), the relationship between the quantitative difference in feathering and the individual FCR was scrutinised. It confirmed that the tail length was negatively related to FCR, both phenotypically and genetically.

8.1.3. The Roles of Major Feathering Genes in Broiler Production

Two series of major genes, naked neck gene and the early vs. late feathering genes, have been considered in the present research.

Earlier results concerning the effect of Na gene on poultry production was summarised by Merat (1986). Because of the superior growth performance of the naked neck birds under a moderate to high temperature conditions, and superior carcass and meat yields, this gene has been the major subject of several important recent

experiments (Elberhart and Washburn, 1993 a, b; Cahaner et al., 1992, 1993). Based mainly on the growth performance data, earlier results indicated that this gene could be exploited for broiler production at a temperature of 25 °C or higher (Merat, 1986). Recent results showed that the naked neck birds had a better or at least comparable growth performance at 21 °C (Elberhart and Washburn, 1993 a) or 23 °C (Cahaner et al, 1993) either in a genetic population with high growth potential (Elberhart and Washburn, 1993 a; Cahaner et al., 1993) or with a low growth potential (Elberhart and Washburn, 1993 a). The present results agreed with the recent developments: the naked neck males reached 2000g body weight at the same age (51 days) as their normally feathered counterparts at 25 °C, but they consumed 50g less feed/bird.

Superior carcass yield or meat yield in the naked neck birds was universally reported in studies concerning the carcass traits. However, a full balance sheet for the carcass traits has not been found in the literature. Results from the second experiment (Chapter 5) pointed out that the naked neck birds, on the basis of starved body weight, had higher yields of dressed carcass, eviscerated carcass, breast meat, thigh meat, and total meat because they had lower yields of feathers and total skin. And on the dressed carcass basis, they had higher yields of breast meat, thigh meat and total edible portion, because they had a lower yield of the skin. The yield of carcass residuals (mainly bones and other non-edible carcass parts) was not altered by this gene.

The early vs. late feathering genes play the central role in feathering-sexing for many of the commercial day-old chicks. With all the controversies concerning the effects of the K genotypes on broiler growth performance, as reviewed in section 2.2.1.1, the present research showed no significant effect of the genotypes on any of the carcass traits, but repeatedly indicated that the early feathering birds had lower FCR than their late feathering male sibs (Chapters 5 and 6). The interaction between the K genotype and line on feed consumption and also possibly on the body weight meant that the effect of early vs. late feathering genotype on these two important production traits were dependent on the genetic backgrounds of the lines concerned.

8.1.4. The Joint Effects of Feathering Genes on Broiler Production

The effects of different feathering genes were shown to be mostly additive in the present research. That is, the interactions between different feathering genes at different loci were not significant for most of the traits studied. The effects of the same interaction between the line and K genotype on the feather length measurements and on feed consumption and body weight have just been discussed.

8.1.5. Analysis of the Selection Data

A summary of the response in the tail feather length to the direct selection for nine generations and the correlated response in body weight to the feathering selection has been presented in Chapter 7. The upwards selected line showed continuous response in tail feather length. However, the downwards selected line had no further response from generation 4 onwards. Although the heritability in the slow line was similar to that in the fast line, a reduced variance of tail length in this line resulted in a small direct selection differential in the later generations. This, together with an upwards body weight selection in the later generations in the slow line, were given as the explanations for the cessation in tail feather length response.

The mixed model REML analyses gave a moderately high heritability estimates for both the tail length and body weight in the base population. The actual genetic and phenotypic correlation between the two traits in the base population was thought to be lower than it had been indicated earlier by Edriss (1989). A genetic correlation of 0.48 in the base population between the traits may be not enough to result in a consistent prolonged correlated response when selection is operating on one of the traits only. However, when both of the traits are selected, a selection in the direction of genetic correlation, the two traits could reinforce with each other, and a selection against the direction of the genetic correlation (i.e. higher body weight with shorter tail in the slow line) may result in little progress in either of the traits.

The relatively rapid change in the magnitude of the genetic correlation in the selection lines means that a regular reappraisal of this parameter is necessary when selecting the two traits.

8.2. CONCLUSIONS

Based on the results of the experiments and the above discussion, the following general conclusions can be drawn:

1. The rate of feathering in chickens and the amount of the surface area covered with feathers are controlled by independent genes. The K series, the polygenes selected and their interaction are involved in the former, and the Na gene is involved in the latter. The feathering condition of the commercial feathering-sexable male chicks could be manipulated simply by the selection on the females line used, or ultimately by the selection in the male side only of the female lines in a three- or four-way crosses.

2. Rate of feathering in the late feathering background can be easily manipulated by quantitative selection, as it has been indicated by the tail feather length at three weeks of age in the selection program. This trait has a high heritability of between 0.48 and 0.58. While a downwards selected line would respond well for only 3-4 generations, a continuous response in an upwards selected line over many generations would be expected.

3. Selection for shorter tail feather length in the slow line has been accompanied by a reduced body weight owing to a positive genetic correlation in the base population as well as in the later generations in this line. However, a positive response in body weight to the upward feathering selection in the fast feathering line is limited, because the genetic correlation between the two traits reduced to essentially zero after only a few generations of intensive feathering selection.

4. Slow feathering selection results in better carcass traits than the fast feathering selection, as indicated by higher yields of eviscerated carcass, breast meat, total meat, and the amount of carcass protein in meat. However, selection in this direction might increase FCR slightly. Selection for fast feathering has the opposite consequences.

5. Incorporation of the early feathering gene into the fast / slow feathering lines reduces FCR in the males. The K gene series interacts with the fast or slow feathering line effect (controlled by polygenes) in terms of feather growth, feed consumption and 51 day body weight. Feed consumption tends to be especially high in the slow feathering line with the late feathering gene K. Generally, feed efficiency favours earlier or faster juvenile feather development. The advantage of earlier feather development, however, might be unnecessarily magnified in a single cage system. A

genetic correlation of -0.623 has been set as a top limit in absolute value between the feathering and FCR. The K genotype has no effect on carcass traits.

6. Incorporation of the naked neck gene into the broiler lines does not enhance growth rate to 51 days in 25 °C. It does, however, reduce the amount of feed required to reach the same body weight as the normally feathered counterparts. This gene increases the relative yields of dressed carcass, eviscerated carcass, breast meat, thigh meat and total meat to live body weight by reducing the relative yields of feathers and skin. And it increases the relative yields of breast meat, thigh meat and total meat to the dressed carcass by reducing the yield of the skin. Generally, the naked neck gene does not interact with the other feathering genes studied.

7. A combination of Nanakk genotype and fast feathering may give the best compromise in terms of growth, feed efficiency and carcass traits for broiler production in a moderately high temperature of about 25°C and below, while NanaKK slow feathering combination may help improve broiler traits at a higher temperature.

Appendix 2.1. Energy preservation by feathers in chicks

a) The data

The body weight, feed consumption, ambient temperature, dry-plucked feather weight and heat production (AME intake - total energy retention) data are reproduced from the data provided by Prijono (1991, Tables 10.1, 10.2, 10.4, and 10.5) in the table. These data were collected in an energy metabolism experiment at eight different ages from 16 to 44 days in both the males and females of the three feathering selection lines in the fourth generation.

b) Regression analyses

Heat production was first of all regressed on the four factors listed in the table, and the following regression equation was established:

$$\text{Heat (kJ/d)} = 1709 + 0.485\text{BWT(g)} + 3.26\text{FC(g/d)} - 77.8\text{T}^{\circ}\text{C} - 3.88\text{Feather(g)}$$

All of the five parameters in the equation are significant or highly significant. The total amount of variation accounted by the equation is 88.2%.

According to the above equation, each one gram of feather weight can reduce heat production by 3.88 kJ/day (the partial regression coefficient).

Similar regression analyses can be made ignoring feed consumption, or both feed consumption and ambient temperature. The partial regression coefficient of heat production on feather weight are -4.42 and -4.81 respectively for the two cases, either of which is higher than the partial regression coefficient (absolute value) when all data are included. Therefore the coefficient of 3.88 can be looked as the minimum.

c) Calculation of energy cost and balance

The energy cost for each gram of fresh feather growth is calculated according to the assumptions made in section 2. as :

$$24.0\text{kJ/g dry feather} \times 50\%\text{DM} / 60\% \text{ efficiency} = 20.0 \text{ (kJ)}$$

Therefore the energy cost can be recovered by insulation in

$$20.0 \text{ kJ} / 3.88\text{kJ/day} = 5.15 \approx 5 \text{ days.}$$

Table: The body weight, feed consumption, ambient temperature, feather weight and heat production recorded in the energy balance experiment conducted by Prijono (1991)

BWT(g)	FC(g/d)	Temp(°C)	Feather(g)	Heat(kJ/d)
375.0	51.88	21.4	18.3	401
464.0	59.67	20.5	23.0	435
782.5	86.02	20.5	52.0	602
958.5	76.33	20.6	59.0	524
1215.0	87.48	21.0	74.9	556
1342.5	102.52	21.5	79.1	708
1545.0	91.52	21.2	102.2	749
421.5	54.23	21.4	14.6	430
516.0	76.87	20.5	23.4	517
821.0	75.67	20.5	38.2	633
1222.5	99.78	20.4	65.0	800
1455.0	102.77	21.0	87.9	705
1497.5	114.87	21.5	88.6	735
1835.0	125.03	21.2	108.0	912
370.0	48.83	21.4	2.5	362
410.0	54.23	20.5	2.0	450
650.5	77.22	20.5	14.5	607
844.0	74.70	20.6	27.7	486
980.0	86.30	20.4	35.0	804
1295.0	92.97	21.5	77.0	754
1517.5	106.50	21.2	87.2	834
345.0	46.62	21.4	1.5	371
485.5	66.60	20.5	1.9	518
855.5	71.58	20.6	13.9	719
1065.5	93.52	20.4	26.3	928
1231.0	104.42	21.0	44.0	894
1517.0	111.32	21.5	64.0	873
1745.0	138.30	21.2	78.1	997
342.5	49.67	20.5	8.7	367
675.0	79.23	20.5	38.6	553
951.0	79.23	20.6	62.4	570
1034.0	84.52	20.4	61.9	713
1212.5	90.60	21.0	80.7	704
1327.5	96.45	21.5	81.5	627
473.0	68.87	20.5	10.7	461
807.5	86.02	20.5	33.7	666
1083.5	94.48	20.6	50.8	819
1107.5	96.82	20.4	62.1	816
1311.5	101.55	21.0	72.2	631
1735.0	120.27	21.2	95.8	1002

Appendix 4.1. Feed composition of the starter and grower (g/kg) used in experiment 1.

Ingredients	Inclusion level	
	starter	grower
Wheat	310.4	336.0
Maize	300.0	300.0
Maize gluten meal (60%)	100.0	100.0
Soya bean meal (48.5%)	177.9	148.6
White fish meal (61%)	10.0	10.0
Meat and bone meal (50%)	19.7	14.8
Full-fat-soya bean meal	56.5	56.3
Limestone	14.5	22.4
Salt	2.3	3.7
DL-methionine	0.8	0.5
L-lysine	2.3	2.2
Vitamins & Minerals	5.0	5.0
Coccidiostat	0.6	0.6
Calculated (determined within the parentheses) nutrient contents (g/kg as fed)		
Crude protein	244(286)	230(265)
Methionine	5.3	4.9
Lysine	12.2	11.2
Arginine	13.4	12.4
Calcium	10(13.2)	10.5(15.7)
Phosphorus	6.0(5.7)	5.6(5.1)
Sodium	1.5	2.0
AME (MJ/kg)	12.7(11.9)	12.7(12.0)

Appendix 4.2. Body weight and portional weights (g) of the birds used for the chemical analysis at different ages in experiment 1.

Age (days)	Weight of*	Normal Temperature (20°C)						High Temperature(30°C)									
		Males			Females			Males			Females						
		Naked neck	Normal	Naked neck	Normal	Naked neck	Normal	Naked neck	Normal	Naked neck	Normal	Naked neck	Normal				
10	Body	160.1	156.0	163.1	127.5	181.5	157.8	181.7	163.2	181.1	161.9	180.8	145.9	144.9	168.7	162.5	181.2
20		383.1	352.5	442.2	366.9	395.8	365.2	399.7	385.7	384.6	360.4	331.2	359.4	385.0	372.4	383.3	317.1
30		639.4	693.5	696.6	672.4	575.2	699.6	644.1	632.3	793.9	831.8	576.1	604.6	605.8	511.1	549.0	628.3
40		1098.5	1060.4	1173.4	895.7	944.7	1105.1	966.8	980.8	983.4	850.4	1052.3	871.8	940.6	870.9	771.9	768.7
10	Dry	3.7	1.5	4.0	1.3	5.5	4.5	5.6	4.0	2.3	0.4	3.8	2.1	3.9	5.1	3.4	6.1
20	feather	5.4	5.5	9.5	6.3	7.5	7.4	11.3	9.3	7.8	5.2	8.2	5.6	10.0	7.9	10.6	11.0
30		4.1	11.0	21.6	15.0	16.7	19.8	22.2	19.6	21.9	20.9	20.7	13.5	19.7	14.4	24.3	23.1
40		37.8	29.1	44.9	23.1	30.2	27.0	43.5	38.1	31.8	24.0	40.4	29.1	31.5	29.0	33.1	32.6
10	Total	55.1	54.0	50.4	40.6	61.4	49.5	59.9	54.3	63.1	56.2	57.3	47.8	45.5	52.8	54.1	62.3
20	Meat	139.2	138.2	166.1	138.0	139.0	138.7	142.5	142.5	134.0	136.3	105.7	134.1	141.4	137.4	134.3	114.5
30		247.6	260.0	247.0	249.6	239.3	286.4	251.4	250.5	305.3	320.6	210.9	234.5	222.0	187.1	196.6	236.9
40		433.8	457.3	465.6	357.6	386.6	492.5	395.0	376.4	386.0	325.4	387.0	330.7	375.6	356.4	300.5	300.6
10	Viscera	18.0	19.9	24.5	20.7	25.4	20.9	25.4	19.7	23.2	22.0	26.7	21.1	20.6	22.2	25.5	22.0
20		40.3	34.5	40.5	32.8	41.3	35.7	39.9	38.6	37.0	34.2	35.7	39.2	39.8	38.3	38.0	30.1
30		54.7	62.8	72.3	55.3	53.6	60.6	58.2	57.8	67.3	76.6	44.4	55.1	51.6	42.1	53.6	50.4
40		94.4	77.5	88.5	68.6	82.2	93.3	77.7	85.8	79.2	72.6	93.5	85.2	78.6	73.2	71.7	61.3
10	Residual	73.8	74.5	73.5	56.2	80.5	72.7	82.0	76.4	83.1	74.4	83.3	68.3	67.0	81.7	76.9	82.1
20		177.5	157.6	201.3	162.6	184.1	160.5	181.2	172.2	181.0	166.4	158.0	160.7	166.3	167.9	172.2	141.5
30		276.3	317.1	318.3	291.2	236.6	298.4	284.8	265.9	355.8	371.2	266.9	276.5	283.9	242.5	239.8	279.6
40		479.3	447.6	518.6	407.4	401.0	452.6	400.1	423.4	440.2	382.7	469.9	381.5	406.7	365.7	332.1	331.2

*The total meat included all of the dissected muscles and the edible organs (heart, liver and gizzard); Viscera included lungs and G.I.T., and residual include the rest of the carcass, i.e. frame, skin, fat, bones, head and neck (see Section 3.3.3.3 for more detail).

REFERENCES

- ACAR, N., MORAN, E.T.Jr, and BILGILI, Q.S.F.** (1991) Live performance and carcass yield of male broilers from two commercial strains receiving rations containing lysine below and above the established requirement between six and eight weeks of age. *Poultry Science*, 70:2315-2321.
- ACAR, N., MORAN, E.T.Jr. and MULVANEY, D. R.** (1993) Breast muscle development of commercial broilers from hatching to twelve weeks of age. *Poultry Science*, 72:317-325.
- AJANG, O. A., PRIJONO, S. and SMITH, W. K.** (1993) Effect of dietary protein content on growth and body composition of fast and slow feathering broiler chickens. *British Poultry Science*, 34:73-91.
- ANONYMOUS** (1982) The energy cost of activity. in: ARC Poultry Research Centre Report, pp9-10
- ARAFI, A. S., BOOTWALLA, S. M. and HARMS, R. H.** (1985) Influence of dietary energy restriction on yield and quality of broiler parts. *Poultry Science*, 64: 1914-1920.
- ARBOLEDA, C.R., HARRIS, D.L. and NORDSKOG, A.W.** (1976) Efficiency of selection in layer-type chickens by using supplementary information on feed consumption. II. Application to net income. *Theoretical and Applied Genetics*, 48:75-83.
- BACON, L.D., SMITH, E. J., CRITTENDEN, L. B. and HAVEENSTEIN, G. B.** (1988) Association of the slow feathering (K) and an endogenous virous (*ev21*) gene on the Z chromosome of chickens. *Poultry Science*, 67:191-197.
- BARBATO, G.F., CHERRY, J.A., SIEGEL, P.B. and VAN KREY, H.P.** (1980) Quantitative analyses of feeding behaviour in four populations of chickens. *Physiology and Behavior*, 25:885-890.
- BECKER, W.A.** (1984) Manual of quantitative genetics. Academic Enterprises, Pullman, U.S.A.
- BOA-AMPONSEM, K., DUNNINGTON, E.A. and SIEGEL, P.B.** (1991) Genotype, feeding regimen and diet interaction in meat chickens. 2. Feeding behavior. *Poultry Science*, 70: 689-696.
- BORDAS, A., MERAT, P., SERGENT, D. and RICHARD, F.** (1978) Influence du gene Na 'cou nu' sur la croissance, la consommation alimentaire et la composition

corporelle du poulet selon la temperature ambiante. *Annales de Genetique et de Selection Animale*, 10:209-231.

BOUWKAMP, E., BIGBEE, D. and WABECK, C. (1973) Strain influence on broiler parts yields. *Poultry Science*, 52:1517-1523.

BRAOADBENT, L.A., WILSON, B.J. and FISHER, C. (1981) The composition of the broiler chickens at 56 days of age: output, components and chemical composition. *British Poultry Science*, 22: 385-390.

BULMER, M.G. (1980) *The mathematical theory of quantitative genetics*. Oxford University Press, New York.

CAHANER, A. and LEENSTRA, F. (1992) Effects of high temperature on growth and efficiency of male and female broilers from lines selected for high weight gain, favorable feed conversion, and high or low fat content. *Poultry Science*, 71: 8, 1237-1250.

CAHANER, A., DEEB, N. and GUTMAN, M. (1992) Improving broiler growth at high temperatures by the naked neck gene. *Proceedings of 19th World's Poultry Congress, Amsterdam, The Netherlands*. Vol. 2 pp57-60.

CAHANER, A., DEEB, N. and GUTMAN, M. (1993) Effects of the plumage-reducing naked neck (Na) gene on the performance of fast-growing broilers at normal and high ambient temperatures. *Poultry Science*, 72: 767-775.

CAHANER, A., NITSAN, Z. and NIR, I. (1986) Weight and fat content of adipose and nonadipose tissues in broilers selected for or against abdominal adipose tissue. *Poultry Science*, 65:215-222.

CAHANER, A., DUNNINGTON, E.A., JONES, D.E., CHERRY, J.A. and SIGEL, P.B. (1987) Evaluation of two commercial broiler male lines differing in efficiency of feed utilisation. *Poultry Science*, 66:1101-1110.

CAMERON, D. and BRACKEN, J. (1992) Selection for carcass lean content in a terminal sire breed of sheep. *Animal Production*, 54:367-377.

CHAMBERS, J.R. (1987) Response to five generations of multi- trait selection for feed efficiency and abdominal fat in broiler sire strains. *Proceedings of 36th Annual National Breeders Roundtable (St. Louis)*.

CHAMBERS, J.R. (1990) Genetics of growth and meat production in chickens. in: Crawford R.D.(Ed) *Poultry Breeding and Genetics*, pp. 599-643. *Developments in Animal and Veterinary Sciences*, 22. (Amsterdam, Elsevier).

CHAMBERS, R. J. and LIN, C. Y. (1988) Age-constant versus weight-constant feed consumption and efficiency in broiler chickens. *Poultry Science*, 67: 565-576.

- CHAMBERS, J.R., GAVORA, J.S. and FORTIN, A.** (1981) Genetic changes in meat-type chickens in the last twenty years. *Canadian Journal of Animal Science*, 61: 555-563.
- CHAMBERS, J.R., SMITH, E.J., DUNNINGTON, E.A. and SIEGEL, P.B.** (1993/4) Sex-linked feathering (K, k⁺) in chickens: a review. *Poultry Science Review*, 5:97-116.
- CLASSEN, H.L., SMYTH, J.R. Jr.** (1977) The influence of pea comb and naked neck on apteria width in domestic fowl. *Poultry Science*, 56: 1683-1685.
- COOKE, B.C.** (1985) Prediction equations, their potentials for estimating the energy content of compound animal feed. *Feed Compounder*. 5(10):7-9.
- CRAWFORD, R.D.** (1976) Incomplete dominance of the gene for Naked Neck in the domestic fowl. *Poultry Science*, 55: 820-822.
- DARROW, M.I.** (1941) Relations of day-old chick wing feather development to feathering at broiler age. *Poultry Science*, 20: 458(abs).
- DARROW, M.I. and WARREN, D.C.** (1944) The influence of age on expression of genes controlling rate of chick feathering. *Poultry Science*, 23:199-212.
- DAVENPORT, C. B.** (1914) The bare necks. *Journal of Heredity*, 5: 374
- DESCHUTTER, A. and LEESON, S.** (1986) Feather growth and development. *World's Poultry Science Journal*, 42:259-267.
- DUNNINGTON, E. A. and SIEGEL, P. B.** (1986) Sex-linked feathering alleles (K, k⁺) in chicks of diverse genetic backgrounds. 1. Body temperatures and body weights. *Poultry Science*, 65:209- 214.
- EBERHART, D. E. and WASHBURN, K. W.** (1993a) Assessing the effects of the naked neck gene on chronic heat stress resistance in two genetic populations. *Poultry Science*, 72:1391-1399.
- EBERHART, D. E. and WASHBURN, K. W.** (1993b) Variation in body temperature response of naked neck and normally feathered chickens to heat stress. *Poultry Science*, 72: 1385-1390.
- EDRISS, M. A.** (1988) Divergent selection for feather growth in broiler chickens. Ph.D. thesis, University of Glasgow.
- EDRISS, M. A., SMITH, W. K., DUN, P.** (1988) Divergent selection for feather growth in broiler chickens. 18th World Poultry Congress, Japan, pp. 561-562 (Japanese Poultry Science Association).
- EDWARDS, H. M. Jr, DENMAN, F., ABOU-ASHOUR, A. and NUGGARA, D.** (1973) Carcass composition studies 1. Influences of age, sex and type of dietary fat supplementation on total carcass and fatty acid composition. *Poultry Science*, 52:934-948.

- EL-ATTAR, A. and MERAT, P.** (1985) Composition corporelle de poulets 'cou nu' ou normalement emplumes: resultats dans un corisement de type 'chair'. *Genetique, Selection, Evolution*, 17:539-548.
- EMMANS, G.C.** (1987) Growth, body composition and feed intake. *World's Poultry Science Journal*, 208-227.
- FALCONER, D.S.** (1989) Introduction to quantitative genetics. 3rd Edn. Harlow: Longman.
- FISHER, C.** (1984) Fat Deposition in Broilers. in: Wiseman J. (Ed) *Fats in Animal Nutrition*, pp. 437-470 (London, Butterworths).
- FISHER, MARY-LOU; LEESON, S.; MORRISON, W.D. and SUMMERS, J.D.** (1981) Feather growth and feather composition of broiler chickens. *Canadian Journal of Animal Science*, 61: 769-773.
- Genstat 5 Release 2.2**, Copyright 1990, Lawes Agricultural Trust (Rothamsted Experimental Station).
- GLAZENER, E. W. and JULL, M. A.** (1946) Rate of feathering and ten-week body weight observations in strains differing in shank length. *Poultry Science*, 25:433-439.
- GODFREY, G. F. and FARNSWORTH, G. M. Jr.** (1952) Relation of the sex-linked rapid feathering gene to chick growth and mortality. *Poultry Science*, 31:65-68.
- GOODMAN, B. L. and MUIR, F. V.** (1965) The influence of comb and feathering phenotypes on body weight and dressing percentage in broilers. *Poultry Science*, 44:644-648.
- GRASER, H.U., SIMITH, S.P. and TIER, B.** (1987) A derivative-free approach for estimating variance components in animal models by Restricted Maximum Likelihood. *Journal of Animal Sciences*, 64: 1362-1370.
- GREENWOOD, A.W.** (1927) The "hackless" fowl. *Proceedings of the Royal Physical Society (Edinburgh)* 21 (pr. 3): 123-129.
- GREY, T.C., ROBINSON, D. and JONES, J.M.** (1982) Effect of age and sex on the eviscerated yield, muscle and edible offal of a commercial broiler strain. *British Poultry Science*, 23: 289-298
- GUILL, R.A. and K.W. WASHBURN** (1974) Genetic charges in efficiency of feed utilization of chicks maintaining body weight constant. *Poultry Science*, 53: 1146-1154.
- HAMMADE, H., PELITJEAN, M., DOUAIRE, M. and MALLART, J.** (1987) Effect of the Na (naked neck) gene in cocks kept at two temperatures. I. Growth rate, feed consumption and physiological traits. *Genetique, Selection, Evolution*, 19: 249-266.

- HANZEL , C. J. and SOMES, R. G. Jr,** (1983) The effect of the naked neck gene, Na, on growth and carcass composition of broilers raised in two temperatures. *Poultry Science*, 62:934-941.
- HARDY M.E.Jr, FRANCES DENMAN, ATEF ABOU-ASHOUR and DENIS NUGARA** (1973) Carcass composition studies 1. Influences of age, sex and type of dietary fat supplementations on total carcass and fatty acid composition. *Poultry Science*, 52: 934-945.
- HARRIS, D.L., GARWOOD, V.A., LOWE, P.C., HESTER, P.Y. CRITTENDEN, L.B. and FADLY, A.M.** (1984) Influence of sex-linked feathering phenotypes of parents and progeny upon lymphoid leukosis virus infection status and egg production. *Poultry Science*, 63:401-413.
- HATHAWAY, H.E., CHAMPAGNE, G.B., WATTS A.B. and UPP, C.W.** (1953) Meat yield of broilers of different breeds, strains and crosses. *Poultry Science*, 32: 968-977.
- HAVENSTEIN,G.B. and TOELLE, V.D.** (1989) Effects of genetic strain, slow versus rapid-feathering maternal genotype, and cage density on the performance of Single Comb White Leghorns. *Poultry Science*, 68:596-607.
- HAYS, F. A.** (1951) Rate of feathering and growing chick weight in Rhode Island Reds. *Poultry Science*, 30:866-869.
- HAYS, F. A.** (1952) Sex dimorphism in tail length of chicks at ten days of age. *Poultry Science*, 31: 1093.
- HAYSE, P.L. and MARION, W.W.** (1973) Eviscerated yield, component parts, and meat, skin and bone ratios in the chicken broiler. *Poultry Science*, 52: 718-722.
- HEADY, E.O. and BHIDE, S.** (1984), *Livestock Response Functions*. Iowa State University Press.
- HEIL, G. and HARTMANN, W.** (1980) Feed waste in strains of crossbred hens from Leghorn lines selected for egg production and feed efficiency . P 147-155 in *Proceedings of 6th European Poultry Conference*. Vol. II, Hamburg.
- HENDERSSON, C.R.** (1973) Sire evaluation and genetic trends. in: *Proceedings of Animal Breeding and Genetics Symposium in Honor of Dr. J. D. Lush*, pp. 10-41. ADSA and ASAS.
- HENDERSON, C.R.** (1976) A simple method for computing the inverse of a numerator relationship matrix used in prediction of breeding values. *Biometrics*, 32: 69-83.
- HERTWIG, P. and RITTERSHAUS, T.** (1929) Die erb-faktoren der haushühner. I. Beitrag: Die ortsbestimmung von 4 faktoren im X-Chromosom. *Z. ind. Abst. Vererb*, 51: 354-372.

- HESS, C. W., BYERLY, T. C. and JULL, M. A.** (1941) The efficiency of feed utilization by Barred Plymouth Rock and crossbred broilers. *Poultry Science*, 20: 210-216.
- HICKLING, D., GUENTER, W. and JACKSON, M. E.** (1990) The effects of dietary methionine and lysine on broiler chicken performance and breast meat yield. *Canadian Journal of Animal Science*, 70:673-678.
- HILL, W.G. and MEYER, K.** (1988) Developments in methods for breeding value and parameter estimation in livestock. In: *Animal Breeding Opportunities*, pp. 81-98. BSAP Occasional Publication No. 12.
- HOWLIDER, M.A.R. and ROSE, S.P.** (1987) Temperature and the growth of broilers. *World's Poultry Science Journal*, 43: 228-237.
- HURRY, J. F. and NORDSKOG, A. W.** (1953) A genetic analysis of chick feathering and its influence on growth rate. *Poultry Science*, 32: 18-25.
- HUTT, F. B.** (1949) *Genetics of the Fowl*, pp. 117-119 (New York, McGraw-Hill Book Company, Inc.)
- JAAP, R. G. and MORRIS, L.** (1937) Genetical differences in eight week weight and feathering. *Poultry Science*, 16:44-48.
- JAAP, R. G., RENARD, M. M. and BUCKINGHAM, R. D.** (1950) Dressed and eviscerated meat yields from chickens at twelve weeks of age. *Poultry Science*, 29: 874-888.
- JONES, D. G. and HUTT, F. B.** (1946) Multiple alleles affecting feathering in the fowl. *Journal of Heredity* 37: 197-205.
- KEREN-ZVI, S., NIR, I., NITSAN, Z. and CAHANER, A.** (1990) Effect of dietary concentrations of fat and energy on fat deposition in broilers divergently selected for high or low abdominal adipose tissue. *British Poultry Science*, 31:507-516.
- LEENSTRA, F. R.** (1984) Influence of diet and genotype on carcass quality in poultry and their consequences for selection. in: Haresign, W. and Cole, D. J. A. (Eds) *Recent Advances in Animal Nutrition--1984*. pp. 3-16. (London, Butterworths) .
- LEENSTRA, F. R.** (1986) Effect of age, sex genotype and environment on fat deposition in broiler chickens. *World's Poultry Science Journal*, 42:12-25.
- LEENSTRA, F. R. and PIT, R.** (1987) Fat deposition in a broiler sire strain: 2. Compositions among lines selected for less abdominal fat, lower feed conversion ratio, and higher body weight after restricted and *ad libitum* feeding. *Poultry Science*, 66: 193-202.
- LEESON, S., CASTON, L. J. and SUMMERS, J. D.** (1988) Response of male and female broilers to diet protein. *Canadian Journal of Animal Science*, 68: 881-889.
- LEWIS, P.D. and PERRY, G.C.** (1991) Estimation of fat content of poultry carcasses from dry matter data. *Poultry Science*, 70:1386-1389.

- LIN, C. Y.** (1981) Relationship between increased body weight and fat deposition in broilers. *World's Poultry Science Journal*, 37:106-110.
- LOU, M. L., QUOI, O. K. and SMITH, W. K.** (1992) Effect of naked neck gene and feather growth rate on broilers in two temperatures. *Proceedings of 19th World's Poultry Congress, Amsterdam, The Netherlands. Vol. 2* p62.
- LOWE, P. C, and MERKLEY, J. W.** (1986) Association of genotypes for feathering in broilers with production and carcass composition traits. 1. Effect of genotypes, sex and diet on growth and feed conversion. *Poultry Science*, 65:1853-1858.
- LUCAS, A.M. and STETTENHEIM, P.R.** (1972) *Avian Anatomy, Integument. Agriculture Handbook No. 362 (USDA).*
- MAFF, The Standing Committee on Tables of Feed Composition** (1990), UK Tables of Nutritive Value and Chemical Composition of Feedingstuffs. Aberdeen, Rowett Research Services Ltd.
- MARTIN, J. H.** (1929) Rate of feather growth in Barred Plymouth Rock chicks. *Poultry Science*, 8: 167-183.
- MCDUGALD, L. R. and KESHAVARZ, K.** (1984) The effect of polyether, ionophorous anticoccidial drugs on feather growth in genetically slow feathering broilers. *Poultry Science*, 63:1322-1326.
- MCGIBBON, W.H.** (1977) A sex-linked mutation affecting rate of feathering in chickens. *Poultry Science*, 56:872-875.
- MCGIBBON, W.H. and HALPIN, J.G.** (1946) Three alleles affecting completeness of feathering in the chicken. *Poultry Science*, 25:406.
- MENDES, A.A. and CURY, P. R.** (1986) Effects of dietary energy levels and sex on broiler performance and carcass traits. in: Larbier, M. (Ed) *Proceedings of Seventh European Poultry Conference, Paris 1986. Vol. 1, pp. 543-547.*
- MERAT, P.** (1979) Effects associes au gene Na (cou nu) sur le poids corporel et le poids des oeufs chez des poules 'nomales' et 'naines'. *Annales de Genetique et de Selection Animale*, 11:127-131.
- MERAT, P.** (1986) Potential usefulness of the Na gene in poultry production. *World's Poultry Science Journal*, 42:124-142.
- MERKLEY, J.W. and LOWE, P.C.** (1988) Association of rate-of-feathering genotypes in broilers with production and carcass composition traits. 2. Effect of genotypes and diet on processing traits and lipid deposition. *Poultry Science*, 67:914-919.
- MERKLEY, J.W., WEINLAND, B.T., MALONE, G.W. and CHALOUPKA, G.W.** (1980) Evaluation of five commercial broiler crosses. 2. Eviscerated yield and component parts. *Poultry Science*, 59:1755-1760.

- MEYER, K.** (1989) Restricted maximum likelihood to estimate variance components for animal models with several random effects using a derivative-free algorithm. *Genetique, Selection, Evolution*, 21: 317-340.
- MEYER, K.** (1991) Estimating variances and covariances for multivariate animal models by restricted maximum likelihood. *Genetique, Selection, Evolution*, 23: 67-83.
- MEYER, K. and Hill, W.G.** (1991) Mixed model analysis of a selection experiment for food intake in mice. *Genetic Research Cambridge*, 57: 71-81.
- MONNET, L.E., BORDAS, A. and MERAT, P.** (1979) Gène Cou nu et performance de croissance selon la température chez le poulet. *Annales de Genetique et de Selection Animale*, 11:397-412.
- MORAN, E.T., Jr, and BILGLI, S.F.** (1990) Processing losses, carcass quality and meat yield of broiler chickens receiving diets marginally deficient to adequate in lysine prior to marketing. *Poultry Science*, 69:702-710.
- MUELLER, C.D. and MOULTRIE, F.** (1952) Classification of sex-linked early and late feathering in 10-week-old chickens. *Poultry Science*, 31:171-172.
- NITSAN, Z., DVORIN, A. and NIR, I.** (1981) Composition and amino acid content of carcass, skin and feathers of the growing gosling. *British Poultry Science*, 22: 79-84.
- NORDSKOG, A. W., FRENCH, H. L., ARBOLEDA, C. R. and CASEY, D. W.** (1972) Breeding for feed efficiency of egg production. *World's Poultry Science Journal*, 29: 175-188.
- O'SULLIVAN, N.P., DUNNINGTON, E.A. and SIEGEL, P.B.** (1991 a) Growth and carcass characteristics of early-and late-feathering broilers reared under different feeding regimens. *Poultry Science*, 70:1323-1331.
- O'SULLIVAN, N.P., DUNNINGTON, E.A and SMITH, E.J.** (1991 b) Performance of early and late feathering broiler breeder females with different feeding regimens. *British Poultry Science*, 32:981-995.
- ORR, H. L.** (1955) Effect of strain, sex and diet on dressing percentage and on cooked meat yield of 10 week old broilers. *Poultry Science*, 34: 1093-1097.
- ORR, H.L. and HUNT, E.C.** (1984) Yield of carcass, parts, meat, skin, and bone of eight commercial strains of broilers. *Poultry Science*, 63:2197-2200.
- PASTERNAK, H. and SHALEV, B.A.** (1983) Genetic-economic evaluation of traits in a broiler enterprise: reduction of food intake due to increased growth rate. *British Poultry Science*, 24: 531-536.
- PATTERSON, H.D. and THOMPSON, R.** (1971) Recovery of inter-block information when block sizes are unequal. *Biometrika*, 58: 545-554.

- PERSAUD, P., SIMM, G. and HILL, W.G.** (1991) Genetic and phenotypic parameters for yield, food intake and efficiency of dairy cows fed *ad libitum*. 1. Estimates for 'total' lactation measures and their relationship with live-weight traits. *Animal Production*, 52:435-444.
- PRESCOTT, N. J., WATHESC. M., KIRKWOOD, J. K. and PERRY, G. C.** (1985) Growth, food intake and development in broiler cockerels raised to maturity. *Animal Production* 41:239-245.
- PRIJONO, S.N.** (1991) A study of the growth and egg production in lines of meat chickens selected for fast and slow feathering. Ph.D. thesis, University of Glasgow.
- PYM, R. A. E.** (1983) Direct and correlated responses to selection for improved food efficiency. in: Hill, W.G., Manson, J.M. and Hewitt, D. (Eds) *Poultry Genetic and Breeding. Proceedings of the 18th Poultry Science Symposium, in association with the 25th British Poultry Breeders Round Table, 1983.* pp. 97-112 (Edinburgh, British Poultry Science Ltd. (1985)).
- PYM, R. A. E.** (1990) Nutritional Genetics. in: Crawford R.D.(Ed) *Poultry Breeding and Genetics*, pp. 847-876. *Developments in Animal and Veterinary Sciences*, 22. (Amsterdam, Elsevier).
- PYM, A. R. E. and NICHOLLS, P. J.** (1979) Selection for food conversion in broilers: Direct and correlated response to selection for body weight gain food consumption and food conversion ratio. *British Poultry Science*, 20: 73-86.
- PYM, R. A. E. and SOLVYNS, A. J.** (1979) Selection for food conversion in broilers: Body composition of birds selected for increased body-weight gain, food consumption and food conversion ratio. *British Poultry Science*, 20:87-97.
- QUOI, O. K.** (1991) The evaluation of the naked neck gene in broiler lines for meat production. M.Sc. thesis, University of Glasgow.
- RADI, M.H. and WARREN, D.C.** (1938) Studies on the physiology and inheritance of feathering in the growing chicks. *Journal of Agricultural Research*, 56:679-707.
- RENDEN, J.A., BILGILI, S.F. and KINCAID, S.A.** (1992) Effects of photoschedule and strain cross on broiler performance and carcass yield. *Poultry Science*, 71:1417-1426.
- ROBINSON, O.W. and BERRUECOS, J.M.** (1973) Feed efficiency in swine. 1. A comparison of measurement periods and methods of expressing feed efficiency. *Journal of Animal Science*, 37: 643-649.
- SALMON, R. E., CLASSEN, H.L. and MCMILLAN, R. K.** (1983) Effect of starter and finisher protein on performance, carcass grade and meat yield of broilers. *Poultry Science*, 62: 837-845.
- SALMON, R.E., GARDINER, E.E., KLEIN, K. K. and LARMOND, E.** (1981) Effect of Canola (Low Glucosinolate Rapeseed) meal and nutrient density on

performance, carcass grade, and meat yield, and of Canola meal on sensory quality of broilers. *Poultry Science*, 60: 2519-2528.

SCOTT, T. and CRAWFORD, R.D. (1977) Feather number and distribution in the throat tuft of naked neck chicks. *Poultry Science*, 56: 686-688.

SEEMANN, G. (1981) The influence of age, sex and strain on yield and cutting of broilers. in: Mulder, R. W. A. W, Scheele, C. W. and veerkamp, C. H. (Eds) *Quality of Poultry Meat* pp. 21-27 (Beekbergen, Netherlands; Spelderholt Institute for Poultry Research).

SEREBROVSKY, A.S. (1922) Crossing over involving three sex-linked genes in chickens. *American Naturalist*, 56: 571-572.

SHERIDAN, A.K. and MCDONALD, M.W. (1963) The relationship between feathering and body weight in broiler chickens. *Poultry Science*, 42:1468-1471.

SIEGEL, P.B. (1962) Selection for weight at eight weeks of age. I. Short term response and heritabilities. *Poultry Science*, 41:954-962.

SIEGEL, P.B. (1963a) Selection for breast angle at eight weeks of age. 2. Correlated responses of feathering, body weights, and reproductive characteristics. *Poultry Science*, 42: 437-449.

SIEGEL, P.B. (1963b) Selection for body weight at eight weeks of age. 2. Correlated responses of feathering, body weights, and reproductive characteristics. *Poultry Science*, 42:896-905.

SIEGEL, B.P., CHERRY, J.A. and DUNNINGTON E.A. (1984) Feeding behaviour and feed consumption in chickens selected for body weight. *Annales Agriculturae Fenniae*, 23: 247-252

SIEGEL, P.B., CRAIG, J.V. and MUELLER, C.D. (1957 a) Heritabilities, sex differences, and phenotypic correlations for six feathering characteristics. *Poultry Science*, 36:621-628.

SIEGEL, P.B, MUELLER, C.D. and CRAIG, J.V. (1957 b) Some phenotypic differences among homozygous, heterozygous, and hemizygous late feathering chicks. *Poultry Science*, 36:232-239.

SMITH, E.J. and FADLY, A.M. (1988) Influence of congenital transmission of endogenous virus-21 on the immune response to avian leukosis virus infection and the incidence of tumors in chickens. *Poultry Science*, 67: 1674-1679.

SMITH, T. and LEE, R.(1977) A study of the naked neck gene of the fowl. *Poultry Science*, 56: 1758 (abstr.)

SOMES, R. G. Jr, and JOHNSON, S. (1982) The effect of scaleless gene, Sc, on growth performance and carcass composition of broilers. *Poultry Science*, 61: 414-423.

- SOMES, R.G.Jr.** (1990) Mutations and major variants of plumage and skin in chickens. in: Crawford R.D.(Ed) Poultry Breeding and Genetics, pp. 169-208. Developments in Animal and Veterinary Sciences, 22. (Amsterdam, Elsevier).
- SOMES, R. G.Jr. and JOHNSON, S.** (1982) The effect of the scaleless gene on growth performance and carcass composition of broilers. Poultry Science, 61: 414-423.
- SOMES, R.G Jr.** (1969) Delayed feathering, a third allele of the K locus of the domestic fowl. Journal of Heredity, 60:281-286.
- SORENSEN, D.A. and KENNEDY, B.W.** (1984) Estimation of genetic variance from unselected and selected populations. Journal of Animal Sciences, 59: 1213.
- SORENSEN, P.** (1984) Selection for improved feed efficiency in broilers. Annales Agriculturae Fenniae, 23:238-246.
- SPILLANE, R. A.** (1966) Research report analytical service. An Foras Taluntais, pp. 114.
- SUMMERS, J. D., LEESON, S. and SPRATT, D.** (1988) Yield and composition of edible meat from male broilers as influenced by dietary protein level and amino acid supplementation. Canadian Journal of Animal Science, 68: 2441-2448.
- SUMMERS, J. D., SLINGER, S. J. and ASHTON, G. C.** (1965) The effect of dietary energy and protein on carcass composition with a note on a method for estimating carcass composition. Poultry Science, 44: 501-509.
- TAUSON, R.** (1979) Feed waste by caged layers. 1. A method of estimating the technical feed waste in different cages and feeding systems. Swedish Journal of Agricultural Research, 9: 83-93
- TAWFIK, E.S., OSMAN, A.M.A., RISTIC, M., HEBELER, W. and KLEIN, F.W.**(1989) Einfluß der stalltemperatur auf mastleistung, schlachtkörperwert und fleischbeschaffenheit von broilern unterschiedlichen alters und geschlechts. 2. Mitteilung: Schlachtkörperwert. Archiv für Geflügelkunde, 53(6), 235-244.
- ten HAVE, H.G.M. and SCHEELE, C.W.** (1981) A comparison of the effect of different nutritional factors on the carcass composition of three broiler strains at two ages. in: Mulder, R. W. A. W, Scheele, C. W. and veerkamp, C. H. (Eds) Quality of Poultry Meat. pp. 386-396 (Beekbergen, Netherlands; Spelderholt Institute for Poultry Research).
- van der WERF, J.H.J.** (1992) Restricted maximum likelihood estimation of additive genetic variance when selected base animals are considered fixed. Journal of Animal Sciences, 70: 1068-1076.
- van KAMPEN, M.** (1976) Activity and energy expenditure in laying hens. 3. The energy cost of eating and posture. Journal of Agricultural Science (Cambridge), 87: 85-88.

- van VLECK, L.D.** (1985) Including records of daughters of selected bulls in estimation of sire components of variance. *Journal of Dairy Science*, 68: 2396-2402.
- WABECK, C., HEATH, J., MOLONE, G., CHALOUKKA, G. W., MERKEY, J. and HUFF, W.** (1984) Yield evaluations of five broiler crosses. *Poultry Science*, 63 (suppl. 1): 199.
- WARREN, D.C.** (1925) Inheritance of rate of feathering in poultry. *Journal of Heredity*, 16:13-18.
- WARREN, D.C.** (1933) Retarded feathering in the fowl. *Journal of Heredity*, 24:430-434.
- WARREN, D. C. and GORDON,** (1935) The sequence of appearance, molt and replacement of juvenile regimes of some domestic birds. *Journal of Agriculture Research*, 51: 459-470.
- WARREN, D.C. and PAYNE, L.F.** (1945) Influence of the early feathering gene upon a chick's growth rate. *Poultry Science*, 24:191-192.
- WATHES, C.M. and CLARK, J. A.** (1981) Sensible heat transfer from the fowl: Thermal resistance of the pelt. *British Poultry Science*, 22: 175-183.
- WEI, M. and van der WERF, H J.** (1993) Animal model estimation of additive and dominance variances in egg production traits of poultry. *Journal of Animal Science*, 71: 57-65.
- WHITEHEAD, C.C.** (1988) Selection for leanness in broilers using plasma lipoprotein concentration as selection criterion. in: Leclercq, B. and Whitehead, C.C. (Eds) *Leanness in Domestic Birds. Genetic, Metabolic and Hormonal Aspects*, pp. 41-57 (London, Butterworths).
- WHITEHEAD, C.C.** (1990) Responses of body composition, growth and food efficiency to dietary protein in genetically lean and fat broilers up to seven weeks of age. *British Poultry Science*, 31: 163-172.
- WILSON, S.P.** (1969) Genetic aspects of feed efficiency in broilers. *Poultry Science*, 48: 487-495.
- WING, L.T. and NORDSKOG, A.W.** (1982) Use of individual records in a selection programme for egg production efficiency. I. Heritability of the residual component of feed efficiency. *Poultry Science*, 61:226-230.
- ZEIN-EL-DEIN, A., BORDAS, A. and MERAT, P.** (1984) Croissance et efficacite alimentaire de poulets 'cou nu' ou normalement emplues selon la teneur en proteines de la ration. *Genetique, Selection, Evolution*, 16:355-366.
- ZEIN-EL-DEIN, A., ZEING, M. and AYOUB, H.** (1981) Carcass measurements of naked neck and normal chicks. *Annales de Genetique et de Selection Animale*, 13:435-440.