

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

STUDIES ON PUBERTAL DEVELOPMENT IN BOARS AND RAMS:
EFFECTS OF HEMICASTRATION AND ARTIFICIAL
CRYPTORCHIDISM ON HORMONE SECRETORY
PATTERNS AND DEVELOPMENT OF
REPRODUCTIVE ORGANS

A thesis presented in partial fulfilment of
the requirements for the
Degree of Doctor of Philosophy
at Massey University

Vijitha Yasasee Kuruwita

1981

ABSTRACT

STUDIES ON PUBERTAL DEVELOPMENT IN BOARS
AND RAMS: EFFECTS OF HEMICASTRATION AND
ARTIFICIAL CRYPTORCHIDISM ON HORMONE SECRETORY
PATTERNS AND DEVELOPMENT OF REPRODUCTIVE ORGANS

by VIJITHA YASASEE KURUWITA

Experiments described in this thesis were designed to reinvestigate longitudinal patterns of secretion of LH and testosterone in boars and rams; also to determine the effects of hemicastration of boars and the effects of hemicastration and artificially induced cryptorchidism of rams on longitudinal and acute hormone secretion patterns, as well as some parameters of reproductive organ development.

Plasma LH and testosterone levels of spring and autumn born Large White x Landrace boars were relatively high at birth, but declined from about the 4th postnatal week. Autumn born boars showed a distinct prepubertal LH peak, but in spring born animals there was no such peak. LH concentrations of barrows were high throughout the period of study. Plasma testosterone levels were low between 4 and 12 weeks of age then increased progressively until the end of study. Season of birth had little influence on the longitudinal profiles of secretion of either hormone.

Intensive bleeding experiments with entire and hemicastrated boars confirmed that LH and testosterone were secreted in a pulsatile manner; hemicastration had no significant effect on pulsatile secretion, mean hormonal concentrations, nor LH or testosterone responses following injection of GnRH. On the other hand, while LH responses to GnRH administration were not affected by advancing age, the subsequent testosterone output increased with sexual maturation.

Compensatory hypertrophy in testicular and epididymal weights and in seminiferous tubular diameters was noted in organs recovered from hemicastrates. However, qualitative histological analyses of testicular samples revealed that the cellular changes observed in all animals were of maturational nature and entirely age-related. From these observations it was concluded that hemicastration of developing boars did not result in any acceleration of the onset of spermatogenesis nor any advancement of puberty.

In ram lambs LH concentrations were low at birth, increased to peak levels at around 10 weeks of age, then declined to low values between 16 and 30 weeks of age when the experiment ended. In contrast plasma testosterone values were low at birth but increased steadily, particularly from about 18 weeks of age.

Mean LH and testosterone concentrations recorded from longitudinal, acute profile and pre-GnRH plasma samples of hemicastrated ram lambs confirmed the observations recorded from hemicastrated boars that the remaining testes were capable of secreting near normal quantities of testosterone and hence maintaining virtually unchanged plasma LH levels. On the other hand, a transient but significant increase in plasma FSH levels was detected following hemicastration of ram lambs. Conversely, cryptorchidism caused an elevation of LH and FSH secretion throughout the period of study. Neither surgical treatment had any influence on longitudinal or acute prolactin or testosterone secretory patterns. Mean plasma prolactin levels recorded from all animals were high initially then declined steadily throughout the period of study. That decline in prolactin levels coincided with the seasonal decrease in daily photoperiod. Plasma testosterone levels recorded from all three treatment groups increased steadily from birth to reach peak concentrations at 30 weeks of age.

Short term profile studies with entires, hemicastrates and cryptorchids confirmed the episodic mode of secretion of LH, prolactin and testosterone, and to less extent FSH. Hemicastration had no significant effect on episodic secretion of any of these hormones. Cryptorchidism caused a significant increase in number of LH peaks and a decrease in number of testosterone peaks, but had no effect on patterns of prolactin or testosterone secretion.

GnRH administration caused an increase in plasma LH, FSH and testosterone secretion in entires and responses were unaffected by hemicastration. However, exaggerated gonadotrophin responses were noted from cryptorchids, while the testosterone responses recorded from these animals tended to be lower (but not significantly so) than those of entires and hemicastrates. Mean plasma gonadotrophin levels recorded from each group were reduced by testosterone propionate pre-treatment; that result gave support to the concept that hypoandrogenism may have been the major reason for the elevation of plasma LH levels in cryptorchids. While total LH responses declined with age and maximal FSH responses of all three treatment groups were noted at 24 weeks of age, testosterone responses increased with sexual maturation.

Testicular and epididymal weights and seminiferous tubular diameter data obtained from hemicastrate rams confirmed that this treatment resulted in compensatory hypertrophy of the remaining organs. As recorded from hemicastrated boars there was no major alteration in cell populations of the germinal epithelium or Leydig cells. The changes observed were entirely of a maturational nature and age-related. Testes and epididymides obtained from cryptorchids showed no increase in weight during the experiment and thus were smaller than those of age-matched entires. It was apparent that intra-abdominal temperature prevented normal development of these organs. Qualitative histological examination showed that there was complete arrest of all maturational changes, both in the germinal

epithelium and interstitial tissue of cryptorchid testes.

On the basis of hormonal and organ data obtained from experiments described in this thesis it was concluded that LH, FSH and possibly testosterone were responsible for compensatory hypertrophy of the remaining testes of hemicastrates. The transient elevation of plasma FSH levels which occurred following this treatment probably was due to an overall decrease in production of testicular inhibin, the major regulator of FSH secretion. Presumably the remaining testis subsequently produced sufficient inhibin to reduce FSH secretion back to normal levels. These observations add weight to the hypothesis that following hemicastration, the compensatory increase in testicular androgen secretion occurs more rapidly than does the increase in rate of secretion of FSH inhibitory products. In contrast the increased secretion of LH and FSH in the cryptorchids resulted from reduced testicular production of androgens and inhibin, respectively. Those changes in testicular secretion persist throughout the period of cryptorchidism.

ACKNOWLEDGEMENTS

I wish to express grateful appreciation to my supervisor, Dr K.R. Lapwood, for proposing the general area of research and for willing assistance given during all phases of this project.

I also wish to thank Professor R.E. Munford for his role as supervisor and for generously providing facilities within the Department of Physiology and Anatomy.

Massey University sheep farm supervisor, Mr P.H. Whitehead, is thanked for provision and management of sheep used in this study, while Mr J. Carr and Mr T. Rogers of Massey University pig research centre provided and managed the experimental pigs.

I sincerely thank the following for assistance during this project: Mr H.J. Elgar for his enthusiasm and excellent technical assistance with radioimmunoassays and help in thesis preparation; Mr B.A. Vautier for assistance during sample collection; Mr M.J. Birtles for his expertise in histological processing and photomicrography; Mrs A.J. Larsen for help in preparation of figures; Mr T.J. Law for photographic work and Mrs Fae Hewett for typing this thesis.

The following are acknowledged for generously providing materials used in radioimmunoassays: Dr L.E. Reichert, Jr., Emory University, U.S.A.; Dr G.D. Niswender, Colorado State University, U.S.A.; N.I.A.M.D.D., N.I.H., U.S.A.; Professor D.S. Flux, Massey University; Dr H. Papkoff, University of California, U.S.A., and Dr V.W.K. Lee, M.R.C., Unit, Prince Henry's Hospital, Melbourne, Australia.

I am indebted to the Commonwealth Scholarship Committee, New Zealand University Grants Committee, for their financial support, and to the University of Sri Lanka,

Peradeniya for granting me leave to undertake this study.

Finally I appreciate warmly the moral support and encouragement given by my wife Sujatha during the period of this study.

TABLE OF CONTENTS

| | Page |
|--|------|
| CHAPTER I: INTRODUCTION | 1 |
| 1. Neuroendocrine Control of Reproduction | 2 |
| (a) Anatomy of the Hypothalamus | 2 |
| (b) Extra-hypothalamic Influences | 4 |
| (i) Amygdala | 4 |
| (ii) Hippocampus | 5 |
| (iii) Olfactory system | 5 |
| (iv) Pineal gland | 5 |
| (v) Peripheral afferent inputs | 6 |
| (c) Hypothalamic Releasing Hormones | 7 |
| (i) Gonadotrophin releasing hormone | 7 |
| a. Chemistry and structure | 7 |
| b. Synthesis | 7 |
| c. Release from storage sites | 7 |
| d. Metabolism and excretion | 7 |
| e. Distribution of GnRH in the CNS | 8 |
| f. Mechanism of action | 8 |
| g. GnRH analogues and antagonists | 9 |
| h. Clinical applications for GnRH | 9 |
| (ii) Control of prolactin secretion | 10 |
| a. The hypothalamus and prolactin output | 10 |
| b. Prolactin inhibitory factor (PIF) | 11 |
| c. Prolactin-releasing factor (PRF) | 11 |
| (d) Brain Monoamines and Pituitary Hormone Secretion | 12 |
| (i) Gonadotrophins | 12 |
| (ii) Prolactin secretion | 12 |
| (e) Prostaglandins | 13 |
| (i) PGs and gonadotrophin secretion | 13 |
| 2. Anterior Pituitary Hormones | 13 |
| (a) Luteinising Hormone (LH) | 13 |
| (i) Structure and chemistry | 13 |
| (ii) Metabolism | 14 |
| (iii) Site of action | 14 |
| (iv) Mechanisms of action | 14 |
| (v) Actions of LH in males | 15 |
| a. Steroidogenesis | 15 |
| b. Testosterone release | 15 |
| c. Feedback effects | 15 |
| d. Spermatogenesis | 15 |

| | Page |
|---|------|
| (b) Follicle-Stimulating Hormone (FSH) | 16 |
| (i) Structure and chemistry | 16 |
| (ii) Metabolism | 16 |
| (iii) Site of action | 16 |
| (iv) Actions of FSH in the male | 17 |
| a. Spermatogenesis | 17 |
| b. Androgen binding protein production | 17 |
| c. Feedback effects | 18 |
| (c) Prolactin | 18 |
| (i) Structure | 18 |
| (ii) Secretion and metabolism | 18 |
| (iii) Actions | 18 |
| (iv) Prolactin and reproduction in males | 18 |
| | |
| 3. Testicular Steroids | 19 |
| (a) Testosterone | 19 |
| (i) Site of production of testosterone | 19 |
| (ii) Synthesis and metabolism | 20 |
| (iii) Mechanisms of action | 22 |
| (iv) Actions of testosterone | 22 |
| a. Spermatogenesis | 22 |
| b. Accessory reproductive structures | 23 |
| c. Feedback effects | 23 |
| d. Sexual differentiation | 23 |
| e. Sexual behaviour | 24 |
| f. Miscellaneous | 24 |
| | |
| 4. Negative Feedback Control of the Hypothalamo-pituitary-testicular Axis | 24 |
| (a) Testicular Hormones | 25 |
| (b) Pituitary Hormones | 27 |
| (c) Hypothalamic Hormones | 28 |
| | |
| 5. Patterns of Hormone Secretion | 29 |
| (a) Pulsatile Hormone Secretion | 29 |
| (i) LH | 29 |
| (ii) FSH | 29 |
| (iii) Prolactin | 30 |
| (iv) Testosterone | 30 |
| (b) Circadian Rhythms | 30 |
| (c) Seasonal | 32 |
| (d) Stress-induced Changes in Hormone Secretory Patterns | 33 |
| (e) Interrelationships in Patterns of Hormone Secretion | 34 |

| | Page |
|--|------|
| (i) GnRH, LH and FSH | 34 |
| (ii) LH and testosterone | 34 |
| (iii) Gonadotrophins, corticosteroids and prolactin | 35 |
| 6. Physiology of Reproductive Development in Males | 35 |
| (a) Development of Gonads in Rams and Boars | 35 |
| (i) Prenatal | 35 |
| (ii) Postnatal | 36 |
| (iii) Pre-pubertal and pubertal | 37 |
| (b) Development of Other Organs of Reproduction in Males | 40 |
| (i) Prenatal | 40 |
| (ii) Postnatal | 40 |
| a. Epididymis | 40 |
| b. Accessory sex glands | 41 |
| c. External genitalia | 41 |
| (iii) Factors affecting puberty in males | 42 |
| a. Genetic factors | 42 |
| b. Effects of season, light, temperature and stress | 42 |
| c. Nutrition | 43 |
| d. Social and sexual stimuli | 43 |
| 7. Prepubertal Neuroendocrine Mechanisms | 44 |
| (a) Foetal | 44 |
| (i) Rams | 44 |
| (ii) Boars | 45 |
| 8. Postnatal and Pubertal Endocrine Patterns in Rams and Boars | 46 |
| (a) Rams | 46 |
| (i) LH | 46 |
| (ii) FSH | 46 |
| (iii) Prolactin | 47 |
| (iv) Testicular steroids | 48 |
| (v) Responses to GnRH | 48 |
| (b) Boars | 49 |
| (i) LH | 49 |
| (ii) FSH | 50 |
| (iii) Prolactin | 50 |
| (iv) Testicular steroids | 51 |
| (v) Responses to GnRH injection | 52 |
| 9. The Onset and Control of Puberty | 52 |

| | Page |
|---|--------|
| 10. Purpose of the Present Study | 55 |
| CHAPTER II: MATERIALS AND METHODS | |
| 1. Porcine Experiments | 56 |
| (a) Animals | 56 |
| (b) Animal Management | 56 |
| (c) Surgical Techniques | 56 |
| (i) Castration of day old animals | 56 |
| (ii) Castration and hemicastration of animals in experiment 4.1 | 57 |
| (iii) Post-surgical care | 57 |
| (d) Blood Collection | 58 |
| (e) Hormone Assays | 58 |
| (i) LH | 58 |
| (ii) Testosterone | 59 |
| 2. Sheep Experiments | 60 |
| (a) Animals | 60 |
| (b) Animal Management | 60 |
| (c) Surgical Procedures | 61 |
| (i) Hemicastration | 61 |
| (ii) Artificial cryptorchidism | 61 |
| (iii) Castration of animals in experiment 5.2 | 62 |
| (iv) Post-operative care | 62 |
| (d) Blood Collection | 62 |
| (e) Hormone Assays | 62 |
| (i) LH | 62 |
| (ii) FSH | 63 |
| a. Reagents | 63 |
| b. Radioiodination of ovine FSH | 63 |
| c. Radioimmunoassay procedures | 64 |
| d. Validation of ovine FSH radioimmunoassay | 65 |
| (iii) Prolactin | 67 |
| (iv) Testosterone | 68 |
| 3. Histological Procedures | 68 |
| 4. Experimental Design and Analyses | 69 |
| (a) Missing Data | 69 |
| (b) Transformations | 69 |
| (c) Total Responses to GnRH Injection | 69 |
| (d) Statistical Analyses | 69 |

| | Page |
|--|------|
| CHAPTER III: A LONGITUDINAL STUDY OF PLASMA LUTEINIZING HORMONE LEVELS IN BOARS AND BARROWS, AND OF TESTOSTERONE LEVELS IN BOARS, FROM BIRTH TO 180 DAYS OF AGE | |
| 1. Introduction | 71 |
| 2. Materials and Methods | 72 |
| (a) Animals | 72 |
| (i) Experiment 3.1 | 72 |
| (ii) Experiment 3.2 | 72 |
| (b) Sampling | 72 |
| (c) Body Weights | 72 |
| (d) Statistical Analyses | 72 |
| 3. Results | 73 |
| (a) Spring Born Boars and Barrows (Experiment 3.1) | 73 |
| (i) LH levels in boars | 73 |
| (ii) Testosterone levels in boars | 73 |
| (iii) LH levels in castrates | 73 |
| (iv) Body weights | 74 |
| (b) Autumn Born Boars (Experiment 3.2) | 74 |
| (i) LH levels | 74 |
| (ii) Testosterone levels | 74 |
| (iii) Body weights | 82 |
| (c) Informal Comparisons Between Spring and Autumn Born Boars | 82 |
| 4. Discussion | 82 |
| (a) Luteinizing Hormone | 82 |
| (b) Testosterone | 83 |
| (c) Body Weights | 85 |
| (d) Season of Birth | 85 |

| | Page |
|--|------|
| CHAPTER IV: EFFECTS OF HEMICASTRATION AT DIFFERENT AGES ON LUTEINIZING HORMONE AND TESTOSTERONE SECRETORY PATTERNS AND ON COMPENSATORY TESTICULAR HYPERTROPHY IN SEXUALLY MATURING BOARS | |
| 1. Introduction | 87 |
| 2. Materials and Methods | 88 |
| (a) Animals | 88 |
| (b) Surgical Procedures (Experiments 4.1 and 4.2) | 88 |
| (i) Acute profile studies (Experiment 4.1) | 88 |
| (ii) GnRH response study (Experiment 4.2) | 90 |
| (c) Organ Weights and Qualitative Histology | 90 |
| (d) Statistical Analyses | 90 |
| 3. Results | |
| (a) Acute Profile Study (Experiment 4.1) | 90 |
| (i) LH | 90 |
| (ii) Testosterone | 94 |
| (b) GnRH Responses (Experiment 4.2) | 98 |
| (i) LH | 98 |
| (ii) Testosterone | 99 |
| (c) Organ Weights | 99 |
| (d) Qualitative Testicular Histology | 107 |
| (i) 4 and 8 weeks | 107 |
| (ii) 12 and 16 weeks | 111 |
| (iii) 20 and 24 weeks | 111 |
| 4. Discussion | 112 |
| (a) Acute Profile Studies | 112 |
| (b) Hormone Responses to GnRH Injection | 114 |
| (i) Pre-injection hormone levels | 114 |
| (ii) Total hormone responses | 114 |
| (c) Testicular and Epididymal Weights | 115 |
| (d) Qualitative Testicular Histology | 117 |

| | Page |
|---|------|
| CHAPTER V: EFFECTS OF HEMICASTRATION ON SECRETION OF LUTEINIZING HORMONE AND TESTOSTERONE, AND ON COMPENSATORY TESTICULAR HYPERTROPHY IN RAM LAMBS | |
| 1. Introduction | 119 |
| 2. Materials and Methods | 120 |
| (a) Animals | 120 |
| (b) Longitudinal Study (Experiment 5.1) | 120 |
| (i) Sampling procedure | 120 |
| (ii) Body weights | 120 |
| (c) Surgical Treatment Protocol (Experiments 5.2 and 5.3) | 120 |
| (d) Acute Profile Study (Experiment 5.2) | 122 |
| (e) GnRH Response Study (Experiment 5.3) | 122 |
| (f) Organ Weights and Qualitative Histology | 122 |
| (g) Statistical Analyses | 122 |
| 3. Results | 122 |
| (a) Longitudinal Study (Experiment 5.1) | 122 |
| (i) LH | 122 |
| (ii) Testosterone | 126 |
| (iii) Body weights | 126 |
| (b) Acute Profile Study (Experiment 5.2) | 126 |
| (i) LH | 126 |
| (ii) Testosterone | 130 |
| (c) GnRH Responses (Experiment 5.3) | 134 |
| (i) LH | 134 |
| (ii) Testosterone | 141 |
| (d) Organ Weights | 141 |
| (e) Qualitative Testicular Histology | 144 |
| (i) 4 weeks | 144 |
| (ii) 8 weeks | 144 |
| (iii) 12 weeks | 145 |
| (iv) 16 weeks | 145 |
| (v) 20 weeks | 145 |
| (vi) 24 weeks | 145 |
| (vii) 28-32 weeks | 145 |
| 4. Discussion | 146 |
| (a) Longitudinal Study | 146 |

| | Page |
|--|------|
| (i) LH | 146 |
| (ii) Testosterone | 147 |
| (b) Pulsatile Hormone Secretion | 147 |
| (i) LH | 147 |
| (ii) Testosterone | 148 |
| (iii) LH/testosterone interrelationships | 148 |
| (c) Effects of Hemicastration | 148 |
| (i) LH | 148 |
| (ii) Testosterone | 149 |
| (d) Effects of Bilateral Castration | 149 |
| (i) LH | 149 |
| (e) Hormonal Responses to GnRH: Effects of Hemicastration | 150 |
| (i) LH | 150 |
| (ii) Testosterone | 151 |
| (f) Testicular and Epididymal Weights | 151 |
| (g) Qualitative Testicular Histology | 152 |
| CHAPTER VI: EFFECTS OF HEMICASTRATION AND CRYPTORCHIDISM ON HORMONE SECRETION PATTERNS IN MALE LAMBS | |
| 1. Introduction | 155 |
| 2. Materials and Methods | 156 |
| (a) Animals and Surgical Treatments (Experiments 6.1, 6.2 and 6.3) | 156 |
| (b) Longitudinal Hormone Profiles (Experiment 6.1) | 156 |
| (c) Acute Hormone Secretion Study (Experiment 6.2) | 156 |
| (d) Responses to GnRH or Testosterone Propionate (TP) and GnRH (Experiment 6.3) | 157 |
| (e) Organ Weights and Qualitative Histology | 157 |
| (f) Statistical Analyses | 158 |
| 3. Results | 158 |
| (a) Longitudinal Study (Experiment 6.1) | 158 |
| (i) LH | 158 |
| (ii) FSH | 161 |
| (iii) Prolactin | 169 |
| (iv) Testosterone | 169 |

| | Page |
|--|---------|
| (b) Acute Profile Study (Experiment 6.2) | 169 |
| (i) LH | 169 |
| (ii) FSH | 170 |
| (iii) Prolactin | 171 |
| (iv) Testosterone | 172 |
| (c) GnRH Responses (Experiment 6.3) | 178 |
| (i) LH | 178 |
| a. Pre-GnRH | 178 |
| b. Post-GnRH | 178 |
| (ii) FSH | 188 |
| a. Pre-GnRH | 188 |
| b. Post-GnRH | 188 |
| (iii) Testosterone | 199 |
| a. Pre-GnRH | 199 |
| b. Post-GnRH | 206 |
| (d) Organ Weights | 206 |
| (e) Qualitative Histology | 209 |
| 4. Discussion | 214 |
| (a) Basal Hormone Levels | 214 |
| (i) LH and FSH | 214 |
| (ii) Prolactin | 215 |
| (iii) Testosterone | 216 |
| (b) Pulsatile Hormone Release | 217 |
| (c) Pre-GnRH Hormone Levels in Androgenised Lambs | 218 |
| (d) Responses to GnRH | 219 |
| (i) Non-androgenised lambs | 219 |
| a. LH and FSH | 219 |
| b. Testosterone | 221 |
| (ii) Androgenised lambs | 222 |
| (e) Organ Weight Data | 222 |
| (i) Entires | 222 |
| (ii) Hemicastrates | 222 |
| (iii) Cryptorchids | 222 |
| (f) Qualitative Testicular Histology | 223 |
| (g) Endocrine Sequelae to Surgical Treatments | 224 |
| (i) Endocrine basis of compensatory testicular hypertrophy | 224 |
| (ii) Endocrine consequences of cryptorchidism | 225 |

| | Page |
|--|---------|
| CHAPTER VII: GENERAL DISCUSSION AND CONCLUSIONS | |
| (a) Longitudinal Hormone Secretion Patterns | 228 |
| (i) Boars | 228 |
| (ii) Rams | 230 |
| (b) Acute Hormone Profiles | 231 |
| (i) Pulsatile secretion | 231 |
| (ii) Effects of hemicastration on hormone secretion patterns and GnRH responses in boars | 232 |
| (iii) Effects of hemicastration and cryptorchidism on hormone secretion patterns and GnRH responses of ram lambs | 233 |
| (c) Organ Weights and Histological Data | 235 |
| (i) Testicular changes in hemicastrates | 235 |
| (ii) Testicular changes in cryptorchids | 237 |
| (d) Possible Applications of the Present Study and Avenues for Future Research | 237 |
| BIBLIOGRAPHY | 242 |

LIST OF FIGURES

| Figure | | Page |
|--------|--|------|
| 2.1 | Composite standard curve (mean \pm SEM) derived from 8 consecutive ovine FSH radioimmunoassays. | 66 |
| 3.1 | Mean plasma LH levels in boars from 1 to 26 (spring born) or 24 (autumn born) weeks of age (experiments 3.1 and 3.2, respectively, n=10). | 75 |
| 3.2 | Mean plasma testosterone levels in boars from 1 to 26 (spring born) or 24 (autumn born) weeks of age (experiments 3.1 and 3.2, respectively, n=10). | 76 |
| 3.3 | Mean plasma LH levels in spring born barrows from 1 to 26 weeks of age (experiment 3.1, n=10). | 77 |
| 3.4 | Mean body weights of boars and barrows (spring born) (experiment 3.1, n=10) and boars (autumn born) (experiment 3.2, n=8). | 79 |
| 4.1 | Mean (\pm SEM) plasma LH levels recorded from entires (E) and hemicastrate (HC) boars during acute profile studies conducted at the ages indicated (experiment 4.1, n=4). | 91 |
| 4.2 | Mean (\pm SEM) plasma testosterone levels recorded from entires (E) and hemicastrate (HC) boars during acute profile studies conducted at the ages indicated (experiment 4.2, n=4). | 95 |
| 4.3 | Plasma LH and testosterone responses following administration of GnRH (0.5 μ g/kg) to entires and hemicastrate boars at 8 weeks of age (experiment 4.2, n=4). | 100 |
| 4.4 | Plasma LH and testosterone responses following administration of GnRH (0.5 μ g/kg) to entires and hemicastrate boars at 16 weeks of age (experiment 4.2, n=4). | 101 |
| 4.5 | Plasma LH and testosterone responses following administration of GnRH (0.5 μ g/kg) to entire and hemicastrate boars at 24 weeks of age (experiment 4.2, n=4). | 102 |
| 4.6 | Testicular photomicrographs from 4 and 8 week old boars. | 108 |
| 4.7 | Testicular photomicrographs from 12 and 16 week old boars. | 109 |

| Figure | Page |
|--|------|
| 4.8 Testicular photomicrographs from 20 and 24 week old boars. | 110 |
| 5.1 Mean plasma LH and testosterone concentrations in ram lambs between 1 and 30 weeks of age (experiment 5.1, n=8). | 123 |
| 5.2 Mean (\pm SEM) plasma LH levels recorded from entires (E) and hemicastrate (HC) ram lambs during acute profile studies conducted at the ages indicated (experiment 5.2, n=4). | 127 |
| 5.3 Mean (\pm SEM) plasma testosterone levels recorded from entires (E) and hemicastrate (HC) ram lambs during acute profile studies at the ages indicated (experiment 5.2, n=4). | 131 |
| 5.4 Plasma LH and testosterone responses following administration of GnRH (0.5 μ g/kg) to entire and hemicastrate ram lambs at 8 weeks of age (experiment 5.3, n=4). | 135 |
| 5.5 Plasma LH and testosterone responses following administration of GnRH (0.5 μ g/kg) to entire and hemicastrate ram lambs at 16 weeks of age (experiment 5.3, n=4). | 136 |
| 5.6 Plasma LH and testosterone responses following administration of GnRH (0.5 μ g/kg) to entire and hemicastrate ram lambs at 24 weeks of age (experiment 5.3, n=4). | 137 |
| 5.7 Plasma LH and testosterone responses following administration of GnRH (0.5 μ g/kg) to entire and hemicastrate ram lambs at 32 weeks of age (experiment 5.3, n=4). | 138 |
| 6.1 Mean plasma LH levels in entire, hemicastrate and cryptorchid ram lambs from 4 to 32 weeks of age (experiment 6.1, n=6). | 159 |
| 6.2 Mean plasma FSH levels in entire, hemicastrate and cryptorchid ram lambs from 4 to 32 weeks of age (experiment 6.1, n=6). | 162 |
| 6.3 Mean plasma prolactin levels in entire, hemicastrate and cryptorchid ram lambs from 4 to 32 weeks of age (experiment 6.1, n=6). | 164 |
| 6.4 Mean plasma testosterone levels in entire, hemicastrate and cryptorchid ram lambs from 4 to 32 weeks of age (experiment 6.1, n=6). | 166 |

| Figure | Page | |
|--------|--|-----|
| 6.5 | Mean (\pm SEM) plasma LH levels recorded from entire (E), hemicastrate (HC) and cryptorchid (CO) ram lambs during acute profile studies at 8, 16, 24 and 32 weeks of age (experiment 6.2, n=6). | 173 |
| 6.6 | Mean (\pm SEM) plasma FSH levels recorded from entire (E) hemicastrate (HC) and cryptorchid (CO) ram lambs during acute profile studies at 8, 16, 24 and 32 weeks of age (experiment 6.2, n=6). | 174 |
| 6.7 | Mean (\pm SEM) plasma prolactin levels recorded from entire (E) hemicastrate (HC) and cryptorchid (CO) ram lambs during acute profile studies at 8, 16, 24 and 32 weeks of age (experiment 6.2, n=6). | 175 |
| 6.8 | Mean (\pm SEM) plasma testosterone levels recorded from entire (E) hemicastrate (HC) cryptorchid (CO) ram lambs during acute profile studies at 8, 16, 24 and 32 weeks of age (experiment 6.2, n=6). | 176 |
| 6.9 | Plasma LH responses of non-androgenised ram lambs following administration of GnRH (0.5 μ g/kg) at 8 weeks of age (experiment 6.3, n=3). | 179 |
| 6.10 | Plasma LH responses of non-androgenised ram lambs following administration of GnRH (0.5 μ g/kg) at 16 weeks of age (experiment 6.3, n=3). | 180 |
| 6.11 | Plasma LH responses of non-androgenised ram lambs following administration of GnRH (0.5 μ g/kg) at 24 weeks of age (experiment 6.3, n=3). | 181 |
| 6.12 | Plasma LH responses of non-androgenised ram lambs following administration of GnRH (0.5 μ g/kg) at 32 weeks of age (experiment 6.3, n=3). | 182 |
| 6.13 | Plasma LH responses of androgenised (testosterone propionate, 1 mg/kg) ram lambs following administration of GnRH (0.5 μ g/kg) at 8 weeks of age (experiment 6.3, n=3). | 183 |
| 6.14 | Plasma LH responses of androgenised (testosterone propionate, 1 mg/kg) ram lambs following administration of GnRH (0.5 μ g/kg) at 16 weeks of age (experiment 6.3, n=3). | 184 |
| 6.15 | Plasma LH responses of androgenised (testosterone propionate, 1 mg/kg) following administration of GnRH (0.5 μ g/kg) at 24 weeks of age (experiment 6.3, n=3). | 185 |

| Figure | Page |
|---|------|
| 6.16 Plasma LH responses of androgenised (testosterone propionate, 1 mg/kg) ram lambs following administration of GnRH (0.5 µg/kg) at 32 weeks of age (experiment 6.3, n=3). | 186 |
| 6.17 Plasma FSH responses of non-androgenised ram lambs following administration of GnRH (0.5 µg/kg) at 8 weeks of age (experiment 6.3, n=3). | 189 |
| 6.18 Plasma FSH responses of non-androgenised ram lambs following administration of GnRH (0.5 µg/kg) at 16 weeks of age (experiment 6.3, n=3). | 190 |
| 6.19 Plasma FSH responses of non-androgenised ram lambs following administration of GnRH (0.5 µg/kg) at 24 weeks of age (experiment 6.3, n=3). | 191 |
| 6.20 Plasma FSH responses of non-androgenised ram lambs following administration of GnRH (0.5 µg/kg) at 32 weeks of age (experiment 6.3, n=3). | 192 |
| 6.21 Plasma FSH responses of androgenised (testosterone propionate, 1 mg/kg) ram lambs following administration of GnRH (0.5 µg/kg) at 8 weeks of age (experiment 6.3, n=3). | 193 |
| 6.22 Plasma FSH responses of androgenised (testosterone propionate, 1 mg/kg) ram lambs following administration of GnRH (0.5 µg/kg) at 16 weeks of age (experiment 6.3, n=3). | 194 |
| 6.23 Plasma FSH responses of androgenised (testosterone propionate, 1 mg/kg) ram lambs following administration of GnRH (0.5 µg/kg) at 24 weeks of age (experiment 6.3, n=3). | 195 |
| 6.24 Plasma FSH responses of androgenised (testosterone propionate, 1 mg/kg) ram lambs following administration of GnRH (0.5 µg/kg) at 32 weeks of age (experiment 6.3, n=3). | 196 |
| 6.25 Plasma testosterone responses of non-androgenised ram lambs following administration of GnRH (0.5 µg/kg) at 8 weeks of age (experiment 6.3, n=3). | 200 |
| 6.26 Plasma testosterone responses of non-androgenised ram lambs following administration of GnRH (0.5 µg/kg) at 16 weeks of age (experiment 6.3, n=3). | 201 |

| Figure | | Page |
|--------|---|------|
| 6.27 | Plasma testosterone responses of non-androgenised ram lambs following administration of GnRH (0.5 μ g/kg) at 24 weeks of age (experiment 6.3, n=3). | 202 |
| 6.28 | Plasma testosterone responses of non-androgenised ram lambs following administration of GnRH (0.5 μ g/kg) at 32 weeks of age (experiment 6.3, n=3). | 203 |
| 6.29 | Testicular photomicrographs of 8 week old entire, hemicastrate, cryptorchid rams. | 210 |
| 6.30 | Testicular photomicrographs of 16 week old entire, hemicastrate, cryptorchid rams. | 211 |
| 6.31 | Testicular photomicrographs of 24 week old entire, hemicastrate, cryptorchid rams. | 212 |
| 6.32 | Testicular photomicrographs of 32 week old entire, hemicastrate, cryptorchid rams. | 213 |