

Contents

1. Darwin and friends	1
2. Primate classification and evolution	7
Evolutionary relationships and time-scales	25
3. Mating systems	28
Primate social organization	28
The concept of 'sexual segregation'	31
Primate mating systems	32
Monogamy in primates	34
Polyandry in primates	38
Polygyny in primates	39
Multimale-multifemale mating systems	48
Evidence that females mate with multiple partners	49
Examples of multimale-multifemale societies	51
Ring-tailed lemur	51
Rhesus monkey	52
Chimpanzees and bonobos	55
Factors determining numbers of males in multimale-multifemale primate groups	58
Dispersed mating systems	59
The mating system of the orang-utan	64
4. Mating tactics and reproductive success	68
Dominance, mating success, and reproductive success	70
Coalitions, alliances, and male mating success	76
Consortship, mate-guarding, and possessiveness	77
Alternative mating tactics—a lifespan view	83
Coercive matings	88
Infanticide: the sexual selection hypothesis	90
Some critical comments regarding the sexual selection hypothesis of male infanticide	95
Harassment and interruption of copulation	98
Genetic assessment of male reproductive success	101
Female dominance, mating success, and reproductive success	109
Female mate 'choice'	115
Sexual preferences: favouritism and friendship	117

Incestuous matings and incest avoidance	120
The major histocompatibility complex and mate choice	122
The problem of skewed birth sex ratios	125
5. Sexual behaviour and sexual response	128
Female sexuality: concepts and definitions	128
The question of oestrus	128
Proceptivity	130
Sexual receptivity	140
Sexual attractiveness	141
Male sexuality: concepts and definitions	142
Pre-copulatory behaviour in male primates	144
Copulatory behaviour in male primates	149
The evolution of copulatory postures	149
The evolution of intromission and ejaculatory patterns	158
Classifying primate copulatory patterns	159
Communication during copulation	170
Facial communication during copulation	170
Vocal communication during copulation	172
Tactile stimulation and the problem of orgasm	175
Post-copulatory genital grooming in primates	184
Some conceptual issues in human sexuality	184
Gender identity and gender role	184
Auto-erotism, including masturbation	187
Abnormal sexual preferences: the human paraphilias	193
6. Socio-sexual, bisexual, and homosexual behaviour	200
Socio-sexual patterns	200
Does socio-sexual behaviour reflect dominance rank?	201
Penile erection and socio-sexual communication	204
Erection in response to the sight or proximity of a female	205
Erection during sleep	205
Erection during play, grooming, or when seeking 'reassurance'	205
Erections during aggression and ritualized penile displays	205
Socio-sexual presentation in New World primates	207
The development of socio-sexual behaviour	208
Social stimuli and socio-sexual development	210
Does socio-sexual behaviour occur during human development?	214
Isosexual mounts and presentations in primates: phylogenetic considerations	216
Hedonic aspects of isosexual behaviour	218
Heterosexuality, bisexuality, and homosexuality	220
Frequencies of homosexuality: cross-cultural perspectives	224
Homosexual patterns and relationships	226
The biological basis of homosexuality	227
Genetic contributions to homosexual development	227
Homosexuality and birth order	229
Experiential contributions to homosexual development	230

7. Sexual selection and sexually dimorphic traits	232
Sexual dimorphism in body weight	233
Sexual dimorphism in canine tooth size	237
Sexual dimorphism in vocal anatomy and display	239
Sexual dimorphism in cutaneous glands and scent-marking displays	249
Sexual skin and other secondary sexual traits in adult males	257
Blue and red sexual skin	257
Capes of hair and facial adornments	264
The problem of fluctuating asymmetry	269
Secondary sexual characters in the adult female	272
The problem of female sexual skin	272
1. The graded signal hypothesis	280
2. The reliable indicator hypothesis	282
Conclusions concerning sexual selection and the evolution of female sexual skin	283
The evolution of sexual skin morphology in various catarrhine lineages	284
Sexual selection and human sexual dimorphism	291
Body composition and shape	291
Facial traits	296
8. Sperm competition	298
Relative testes size and mating systems in primates	298
Relative testis size and mating systems in non-primates	303
Testis size, sperm production, and ejaculate quality	304
The compartments of the testis	304
Rates of sperm production and storage	305
Problems of ejaculate quality	306
Does sexual selection influence sperm morphology?	306
Sperm pleiomorphism in humans and the great apes	311
The male accessory reproductive organs and sperm competition	312
Structure and functions of the vasa deferentia	313
The seminal vesicles and prostate gland	316
The structure and functions of primate copulatory plugs	322
Possible effects of repeated ejaculations	325
Does mating order influence male reproductive success?	329
Do social or sexual stimuli affect sperm counts?	333
9. Sexual selection and genitalic evolution	334
Sexual selection and the evolution of male genitalia	334
1. The lock-and-key hypothesis	334
2. The genitalic recognition hypothesis	337
3. The pleiotropism hypothesis	337
4. Mechanical conflict of interest hypothesis	338
Eberhard's hypothesis: sexual selection by cryptic female choice	339
Penile morphology and mating systems in primates	340
Descriptions of penile morphologies in dispersed and multimale-multifemale species	342

Descriptions of penile morphologies in monogamous and polygynous forms	343
The evolution of the baculum	344
The evolution of penile spines	355
The evolution of distal penile complexity	358
The striated penile muscles and morphological changes in the glans penis during copulation	359
Sexual selection and the evolution of female genitalia	363
Some observations on evolution of the clitoris	363
The vagina	366
The cervix	370
The uterus	371
The uterotubal junction and Fallopian tubes	374
10. The development of sexually dimorphic behaviour	379
The organization hypothesis	379
Sexual differentiation at the genital level	381
The organization hypothesis and primate behavioural development	383
The organization hypothesis and human psychosexual differentiation	388
Congenital adrenal hyperplasia	389
Androgen-insensitivity in males: the testicular feminization syndrome	391
5 α -reductase deficiency and male pseudohermaphroditism	392
Prenatal exposure to exogenous progestagens and oestrogens	396
The postnatal testosterone surge and psychosexual differentiation	397
Hormones and homosexuality	402
The neuroanatomical basis of sexually dimorphic behaviour	407
Sex differences in vocal control systems in the brain	407
Spinal motor neurons innervating penile muscles	412
Sex differences in the primate brain, in comparative perspective	413
Sex differences in the corpus callosum	413
Sex differences in the preoptic area and anterior hypothalamus	415
Sex differences in other hypothalamic nuclei	421
Conclusions: sexual differentiation of the brain and behaviour	422
Neuroendocrine and behavioural changes during puberty	425
Development of the hypothalamic-pituitary-gonadal axis at puberty	426
Behavioural effects of hormones during puberty: organization and activation	427
11. The ovarian cycle and sexual behaviour	430
Ovarian cycles: proceptivity, receptivity, and attractiveness	430
The ovarian cycle and sexual behaviour in prosimians	431
Conclusions: the ovarian cycle and sexual behaviour in prosimians	436
The ovarian cycle and sexual behaviour in New World monkeys	437
Conclusions: the ovarian cycle and sexual behaviour in New World monkeys	450
The menstrual cycle and sexual behaviour in catarrhine primates	451
The rhesus monkey	451
The menstrual cycle and sexual behaviour in other Old World monkeys	457
The menstrual cycle and sexual behaviour in the Hominoidea	464
1. The gibbons	464

2. The great apes	465
3. Sexual behaviour during the human menstrual cycle	472
Some final remarks concerning 'concealed ovulation' and 'oestrus'	477
12. The neuroendocrine regulation of sexual behaviour in the adult female	480
Peripheral effects of hormones upon female sexuality	480
Possible effects upon visual and tactile cues	480
Possible effects upon olfactory cues	481
Central effects of hormones upon female sexuality	484
Some comments on methods of behavioural observation and measurement	484
Central effects of oestrogens upon sexual behaviour	485
Central effects of progestagens upon sexual behaviour	490
Central effects of androgens upon sexual behaviour	491
The adrenal glands and sexual behaviour in female primates	492
The hypothalamic basis of sexual receptivity and proceptivity	495
A neural model of proceptivity in female primates	506
Neurotransmitters and sexual behaviour	512
Monoaminergic neurotransmitters	512
Neuroactive peptides	516
Luteinizing hormone-releasing hormone (LHRH)	517
Oxytocin	519
Opioid peptides	521
13. Hormones and sexual behaviour in the adult male	524
Seasonal changes in hormones and sexual behaviour	524
Effects of castration and testosterone replacement	529
Antiandrogens and sexual behaviour	533
Behavioural effects of metabolites of testosterone	537
Sources of individual variability in sexual behaviour	541
Individual differences in circulating androgen levels	541
Adrenal androgens	543
The role of previous sexual experience	543
The role of the female partner	545
Genetic variability between males	546
Effects of age	547
Peripheral versus central effects of androgens upon male sexuality	551
Androgens and penile morphology	552
The accessory sexual organs	556
Secondary sexual adornments	556
Central effects of androgens upon male sexuality	557
The preoptic area and hypothalamus	561
Influences that impinge upon hypothalamic mechanisms	567
Amygdala and stria terminalis	567
The septum	568
The midbrain	569
Insights gained from brain imaging studies	570

The neural control of pelvic thrusting	570
The neural control of erection and ejaculation	575
The innervation of the penis	575
Neurotransmitters, erection, and detumescence	579
Erectile dysfunction	581
Emission and ejaculation	583
Neurotransmitters and sexual behaviour	584
Neuroactive peptides	585
β -endorphin	585
Luteinizing hormone-releasing hormone	587
Oxytocin	587
Prolactin	587
Other pro-opiomelanocortin-derived peptides	588
Other peptides	589
Monoaminergic neurotransmitters	589
Dopamine	589
Noradrenaline	591
Serotonin (5-HT)	592
14. Socioendocrinology and sexual behaviour	593
Social rank and neuroendocrine function in adult male primates	593
Wingfield's 'challenge hypothesis'	594
Sapolsky's studies of neuroendocrine function in male baboons	596
Social rank and secondary sexual traits in male primates	597
Fatted and non-fatted male mandrills	598
Flanged and non-flanged male orang-utans	599
Female social rank, the ovarian cycle, and fertility	602
Social environment and reproductive synchrony	607
Synchrony between the sexes	607
Synchrony between members of the same sex: the ovarian cycle	613
Does ovarian synchrony or asynchrony occur in primates?	615
Effects of social stimuli upon pubertal development	616
Short-term effects of copulatory stimuli upon gonadal function	620
Male primates	620
Female primates	622
15. Human sexuality in primatological perspective	624
1. Sexual selection and human evolution	624
2. The evolution of human copulatory patterns	631
3. The development of human sexual behaviour	633
4. Homosexuality and bisexuality	637
5. The menstrual cycle and sexual behaviour	638
Epilogue: the shape of things to come	641
References	643
Index	739