

Contents

Contributors	page xi
Acknowledgements	xii
Preface	xv
1 Animal homosexuality in evolutionary perspective	1
Historical overview of studies on homosexual behaviour	3
A list of hypotheses	28
2 The comparative study of homosexual behaviour	33
Epistemological caveats	33
Definitions	35
Sources of the datasets and potential biases	38
Comparative analyses	39
Phylogenies	41
Path analysis	44
Meta-analytical methods	45
Is same-sex mounting affected by conditions of captivity?	46
3 Genetics of homosexuality	55
Some genetic models of homosexuality	58
Recurrent mutation as a genetic mechanism underlying homosexuality	64
Candidate genes for homosexual behaviour	65
The <i>fruitless (fru)</i> gene in <i>Drosophila</i>	66
The <i>genderblind</i> and <i>sphinx</i> genes in <i>Drosophila</i>	67

Testicular feminisation mutation (<i>tfm</i>) in mice and rats	68	Stress effects	118
Apoptosis and the <i>Bax</i> gene	69	Stress effects and human homosexuality	124
The <i>c-fos</i> proto-oncogene	70	Adrenarche and the development of homosexuality	128
The <i>trp2</i> and olfactory receptors in mice	71	Fluctuating asymmetry	130
Genes studied in humans	71	Developmental effects of endocrine-disrupting environmental chemicals	131
Genes on the X-chromosome and homosexuality	72	Diethylstilboestrol (DES)	132
Genes on the Y-chromosome and homosexuality	74	Early social experience and learning	134
Other possible genetic markers of homosexuality	76	Juvenile sex play and development of sexual orientation	134
Sex-biased mutation rates	77	Juvenile sex play and homosexuality in humans	138
A study across the human genome	78	Do 'sissy' boys and 'tomboy' girls become adult homosexuals?	140
DNA methylation and X-chromosome inactivation	79	What is the role of learning in the early ontogeny of human homosexual orientation?	145
DNA methylation and genomic imprinting	80	Fetishism and homosexuality	147
Human sex chromosome aneuploidies and homosexuality	81	Contributions of social learning	148
Family analysis	82	Other-sex mimicry: an alternative route to animal homosexuality?	149
Twin studies	85	Evolution and ontogeny: is homosexuality a neotenic trait?	152
Evidence from selection studies	89	Summary of main conclusions	157
Does homosexuality have any link with increased female fecundity?	91		
Kin selection and homosexuality	91	5 The endocrine and nervous systems: a network of causality for homosexual behaviour	159
Summary of main conclusions	95	Human endocrine disorders and homosexuality	159
4 Ontogenetic processes	97	Altered testosterone biosynthesis	160
Hormonal effects during early development	100	5 α -Reductase deficiency	162
The 2nd:4th digit ratio	106	Congenital aromatase deficiency	162
Handedness	111	Complete androgen insensitivity syndrome	163
Dermatoglyphics	112	Congenital adrenal hyperplasia	164
Otoacoustic emissions and auditory evoked potentials	113	Circulating hormones in the adult and homosexual behaviour	166
Tooth crown size and waist-to-hip ratio	113	Hormones and homosexual behaviour in primates	166
Prenatal exposure to steroid hormones and sex-typed toy preferences	114	Hormones and homosexual behaviour in other mammals and in birds	170
Birth order and family size effects	116		
Intrauterine positioning	117		

Non-steroid hormones	171	Femininity, masculinity and homosexuality	239
Sex hormones and the <i>Lock-in Model</i> for homosexual behaviour in macaques	172	Behavioural plasticity and sexual orientation	243
<i>Bos taurus</i> : hormones, sexual behaviour and the buller steer syndrome	178	Brain, emotions and homosexuality	246
<i>Ovis aries</i> : the case of homosexual rams	179	Aggressiveness, empathy and homosexuality	248
<i>Crocota crocuta</i> : selection of masculinised females	185	Androgyny and emotional coping	249
Circulating hormones and sexual orientation in adult humans	191	Homosexuality and cognitive processes	250
Does the use of anabolic androgenic steroids by adults affect sexual orientation?	191	Influences of sexual selection on homosexuality	255
Does sexual orientation in men and women correlate with levels of circulating hormones?	193	Brain, complex social behaviour and homosexuality	259
Do orchietomy and/or oophorectomy lead to a homosexual orientation?	195	Summary of main conclusions	263
Effects of endocrine-disrupting chemicals on the expression of sexual behaviour in adult mammals and birds	198	6 Immunology and homosexuality	265
The neuroendocrine system and homosexual behaviour	199	Immunity and Fraternal Birth Order effect in the development of a homosexual orientation in males	266
Sexual behaviour and brain plasticity	201	Fraternal and Sororal Birth Order effect in the development of a homosexual orientation in females	270
Sexual dimorphisms in the adult brain	206	Parental age effects	271
Homosexual behaviour and the central nervous system	206	Can immunology explain the development of homosexuality in males and/or females?	272
The hypothalamus and homosexuality	208	Immunity and the parental age effect	274
Beyond the hypothalamus	213	Non-immunological explanations for birth order and parental age effects	275
Central nervous system, hypersexuality and homosexual behaviour	220	Family dynamics	276
Orgasm, sexual arousal and homosexuality	224	Summary of main conclusions	281
Masturbation and homosexuality	232	7 Sexual segregation effects	283
Learning processes in adults and their role in homosexual behaviour	236	List of hypotheses proposed to explain sexual segregation	298
		A review of sexual segregation studies	301
		Caprinae	302
		Other bovids	304
		Cervids	305
		Giraffids and equids	307
		Bears, polecats, marsupials and rodents	308

Bats, elephants and pinnipeds	309	9 Homosexual behaviour in primates	381
Cetaceans	310	Alan Dixson	
Birds	311	Primate diversity and evolution	381
Sexual segregation in primates	312	Primate homosexual patterns: phylogenetic considerations	384
Evolutionary models for the potential link between sexual segregation and same-sex mounting	316	Functions and derivations of homosexual behaviour	388
Birds	317	Hedonic aspects of sexual behaviour	392
Mammals	319	Human homosexual behaviour and homosexuality	395
Summary of main conclusions	321	Summary of main conclusions	399
8 The social, life-history and ecological theatres of animal homosexual behaviour	323	10 A Biosocial Model for the evolution and maintenance of homosexual behaviour in birds and mammals	401
<i>Reproductive Skew Theory</i>	323	The long and winding road to the <i>Biosocial Model of Homosexuality</i>	403
A historical overview of <i>Reproductive Skew Theory</i>	324	The <i>Synthetic Reproductive Skew Model of Homosexuality</i>	411
Queuing to breed	328	The <i>Biosocial Model of Homosexuality</i>	413
Early-developmental effects	330	Bisexuality vs. exclusive homosexuality	416
Mate choice and incest avoidance	330	Homosexuality in men and women	417
Tests of <i>Reproductive Skew Theory</i>	331	What does not seem to work	419
The <i>Synthetic Reproductive Skew Model of Homosexuality</i>	331	Some interesting areas for future research	420
A comparative test of the <i>Synthetic Reproductive Skew Model of Homosexuality</i>	336	Is homosexuality a pathology?	421
Birds and the <i>Synthetic Reproductive Skew Model of Homosexuality</i>	336	One last thought	424
Is joint nesting an indication of homosexuality?	347	Appendix 1: Glossary	427
Mammals and the <i>Synthetic Reproductive Skew Model of Homosexuality</i>	348	Appendix 2: Predictions of the <i>Synthetic Reproductive Skew Model of Homosexuality</i> and results obtained in the comparative tests of the model carried out in birds and mammals	435
Path analyses	361	Appendix 3: Comments on further results of comparative analyses of independent contrasts reported in the full correlation matrices of birds and mammals	441
Full correlation matrix	363	References	443
Direct comparisons between birds and mammals	367	Index	535
Homosexuality in humans and interest in having children	373	Colour plates can be found between pages 240 and 241	
Same-sex sexual behaviour and STD transmission	375		
Summary of main conclusions	379		