

## **Animal Homosexuality**

Homosexuality is an evolutionary paradox in search of a resolution, not a medical condition in search of a cure. Homosexual behaviour is common among social animals, and is mainly expressed within the context of a bisexual sexual orientation. Exclusive homosexuality is less common, but not unique to humans. The author invites the reader to embark on a journey through the evolutionary, biological, psychological and sociological aspects of homosexuality, seeking an understanding of both the proximate and evolutionary causes of homosexual behaviour and orientation in humans, other mammals and in birds. The book also provides a synthesis of what we know about homosexuality into a biosocial model that links recent advances in reproductive skew theory and various selection mechanisms to produce a comprehensive framework that will be useful for anyone teaching or planning future research in this field.



# Animal Homosexuality

A Biosocial Perspective

Aldo Poiani

Monash University, Victoria

with a chapter by Alan Dixson







Shaftesbury Road, Cambridge CB2 8EA, United Kingdom

One Liberty Plaza, 20th Floor, New York, NY 10006, USA

477 Williamstown Road, Port Melbourne, VIC 3207, Australia

314-321, 3rd Floor, Plot 3, Splendor Forum, Jasola District Centre, New Delhi - 110025, India

103 Penang Road, #05-06/07, Visioncrest Commercial, Singapore 238467

Cambridge University Press is part of Cambridge University Press & Assessment, a department of the University of Cambridge.

We share the University's mission to contribute to society through the pursuit of education, learning and research at the highest international levels of excellence.

www.cambridge.org

Information on this title: www.cambridge.org/9780521196758

© A. Poiani 2010

This publication is in copyright. Subject to statutory exception and to the provisions of relevant collective licensing agreements, no reproduction of any part may take place without the written permission of Cambridge University Press & Assessment.

First published 2010

A catalogue record for this publication is available from the British Library

Library of Congress Cataloging-in-Publication data

Poiani, Aldo.

Animal homosexuality: a biosocial perspective / Aldo Poiani; with a chapter on primates by Alan Dixson.

p. cm.

Includes bibliographical references and index.

ISBN 978-0-521-19675-8 (hardback)

 $1.\ Homosexuality\ in\ animals.\ I.\ Dixson,\ A.\ F.\ II.\ Title.$ 

QL761.P65 2010

591.56´2–dc22 2010019223

ISBN 978-0-521-19675-8 Hardback ISBN 978-0-521-14514-5 Paperback

Cambridge University Press & Assessment has no responsibility for the persistence or accuracy of URLs for external or third-party internet websites referred to in this publication and does not guarantee that any content on such websites is, or will remain, accurate or appropriate.



For Marisa, with love



## **Contents**

Contributors pag		
Acknowledgements		
Prefa	ace	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	l
	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 homosexual	ity 58
	Recurrent mutation as a genetic	•
	mechanism underlying homosexual	ity 64
	Candidate genes for homosexual	
	behaviour	65
	The fruitless (fru) gene in Drosophila	a 66
	The genderblind and sphinx genes in	ı
	Drosophila	67
	,	

vii



## viii **Contents**

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



**Contents** ix

Non-steroid hormones	171		Femininity, masculinity and	
Sex hormones and the <i>Lock-in Model</i>			homosexuality	239
for homosexual behaviour in			Behavioural plasticity and sexual	
macaques	172		orientation	243
Bos taurus: hormones, sexual			Brain, emotions and homosexuality	246
behaviour and the buller steer			Aggressiveness, empathy and	
syndrome	178		homosexuality	248
Ovis aries: the case of homosexual			Androgyny and emotional coping	249
rams	179		Homosexuality and cognitive	
Crocuta crocuta: selection of			processes	250
masculinised females	185		Influences of sexual selection on	
Circulating hormones and sexual			homosexuality	255
orientation in adult humans	191		Brain, complex social behaviour and	
Does the use of anabolic androgenic			homosexuality	259
steroids by adults affect sexual			Summary of main conclusions	263
orientation?	191			
Does sexual orientation in men and		6	Immunology and homosexuality	265
women correlate with levels of			Immunity and Fraternal Birth	
circulating hormones?	193		Order effect in the development	
Do orchiectomy and/or			of a homosexual orientation in	
oophorectomy lead to a homosexual			males	266
orientation?	195		Fraternal and Sororal Birth Order	
Effects of endocrine-disrupting			effect in the development of a	
chemicals on the expression of			homosexual orientation in females	270
sexual behaviour in adult mammals			Parental age effects	271
and birds	198		Can immunology explain the	
The neuroendocrine system and			development of homosexuality in	
homosexual behaviour	199		males and/or females?	272
Sexual behaviour and brain			Immunity and the parental age effect	274
plasticity	201		Non-immunological explanations	
Sexual dimorphisms in the adult			for birth order and parental age	
brain	206		effects	275
Homosexual behaviour and the			Family dynamics	276
central nervous system	206		Summary of main conclusions	281
The hypothalamus and			,	
homosexuality	208	7	Sexual segregation effects	283
Beyond the hypothalamus	213	-	List of hypotheses proposed to	
Central nervous system,	210		explain sexual segregation	298
hypersexuality and homosexual			A review of sexual segregation studies	301
behaviour	220		Caprinae	302
Orgasm, sexual arousal and	220		Other bovids	304
homosexuality	224		Cervids	305
Masturbation and homosexuality	232		Giraffids and equids	307
Learning processes in adults and	202		Bears, polecats, marsupials and	307
their role in homosexual behaviour	236		rodents	308
men tote in nomosexual benavioul	230		TOUCHIS	500



## x Contents

	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:	
	Evolutionary models for the			phylogenetic considerations	384
	potential link between sexual			Functions and derivations of	
	segregation and same-sex			homosexual behaviour	388
	mounting	316		Hedonic aspects of sexual behaviour	392
	Birds	317		Human homosexual behaviour and	
	Mammals	319		homosexuality	395
	Summary of main conclusions	321		Summary of main conclusions	399
8	The social, life-history and ecological		10	A Biosocial Model for the evolution and	
	theatres of animal homosexual		10	maintenance of homosexual behaviour	
	behaviour	323		in birds and mammals	401
	Reproductive Skew Theory	323		The long and winding road to the	40
	A historical overview of			Biosocial Model of Homosexuality	403
	Reproductive Skew Theory	324		The Synthetic Reproductive Skew	400
	Queuing to breed	328		Model of Homosexuality	411
	Early-developmental effects	330		The Biosocial Model of Homosexuality	413
	Mate choice and incest avoidance	330			41.
	Tests of Reproductive Skew Theory	331		Bisexuality vs. exclusive homosexuality	416
	The Synthetic Reproductive Skew			Homosexuality  Homosexuality in men and women	417
	Model of Homosexuality	331		What does not seem to work	419
	A comparative test of the <i>Synthetic</i>			Some interesting areas for future	413
	Reproductive Skew Model of			research	420
	Homosexuality	336		Is homosexuality a pathology?	420
	Birds and the Synthetic			One last thought	424
	Reproductive Skew Model of			One last thought	424
	Homosexuality	336			
	Is joint nesting an indication of		App	endix 1: Glossary	427
	homosexuality?	347	Appendix 2: Predictions of the <i>Synthetic</i>		
	Mammals and the Synthetic		Rep	roductive Skew Model of Homosexuality	
	Reproductive Skew Model of		and	results obtained in the comparative tests	
	Homosexuality	348	of tl	ne model carried out in birds and	
	Path analyses	361	mar	nmals	435
	Full correlation matrix	363	App	endix 3: Comments on further results of	
	Direct comparisons between birds		com	parative analyses of independent	
	and mammals	367	con	trasts reported in the full correlation	
	Homosexuality in humans and		mat	rices of birds and mammals	44]
	interest in having children	373	Refe	erences	443
	Same-sex sexual behaviour		Inde	ex	535
	and STD transmission	375	Cole	our plates can be found between	
	Summary of main conclusions	379	pag	es 240 and 241	



## **Contributors**

#### Aldo Poiani

School of Biological Sciences Monash University Victoria 3800 Australia

Aldo Poiani is an evolutionary ecologist at Monash University, Australia. He has studied social behaviour, sexual behaviour and parasitism in birds, having published widely in the fields of avian cooperative breeding and host–parasite interactions, including aspects related to behaviour, endocrinology and comparative biology. He has carried out field research in Australia, Europe and South America and is editor of the book *Floods in an Arid Continent*.

**Alan Dixson** (Chapter 9) School of Biological Sciences Victoria University of Wellington Wellington 6140 New Zealand

Alan Dixson is an internationally renowned primatologist at Victoria University of Wellington, New Zealand. He has made substantial contributions to our understanding of primate reproductive biology and behaviour, having held research and academic positions in four continents. He is the author of the classic book *Primate Sexuality: Comparative Studies of the Prosimians, Monkeys, Apes and Man.* His most recent book is *Sexual Selection and the Origins of Human Mating Systems,* published in 2009.



## **Acknowledgements**

First and foremost I thank Alan Dixson for accepting my invitation to contribute Chapter 9. He was also kind enough to find time, in between the writing of a couple of his own books, to provide constructive feedback on the other chapters. Alan's shrewd comments substantially improved the quality of the text and confronted my ideas with critical challenges that, I believe, finally strengthened the various arguments. Responsibility for what I wrote, however, falls only on my shoulders.

Many thanks to the following colleagues for also providing very valuable and constructive feedback: Prof. Ary Hoffmann (Chapter 3); Prof. Harold Gouzoules (neoteny section of Chapter 4), Dr Andrew Iwaniuk (Chapter 5), Prof. Charles Roselli and Assoc. Prof. Eric Vilain (Ovis aries section of Chapter 5); Prof. Steve Glickman for providing information about F-F mounting in Crocuta crocuta (Chapter 5). Dr Javier Pérez-Barbería (Chapter 7); Assoc. Prof. Mariella Herberstein (Chapter 8), Dr Sonia Altizer (for suggesting examples for the STD section of Chapter 8); Dr Joseph Soltis (for providing information about F-F mounting in Macaca fuscata on Yakushima Island, Chapter 8). A very special thank you to Prof. Douglas Futuyma for commenting on Chapters 1, 2 and 3.

I am especially indebted to Martin Griffiths of Cambridge University Press for believing in this project and to Rachel Eley, Dawn Preston and Lynn Davy for their invaluable assistance during the production process. The project also benefited from the insightful comments and encouragement of three anonymous referees, to whom I am most grateful.

xii



Acknowledgements

XIII

I am thankful to Assoc. Prof. Ian Jamieson for providing the pukeko photograph for the cover that was also used in Figure 2.1, the photograph was taken by Nic Bishop. I thank Prof. Luděk Bartoš for Figure 2.5 of male-male mounting in Dama dama. Figure 3.2 was published in Cell, vol. 121, Demir, E. and Dickson, B.J., fruitless Splicing specifies male courtship behaviour in Drosophila. pp. 785-94, Copyright Elsevier 2005. I am grateful to Elsevier for granting permission to reproduce this figure. Figure 3.3 is reproduced with permission from the National Academy of Sciences, USA from Forger, N.G., Rosen, G.J., Waters, E.M. et al. 2004. Deletion of Bax eliminates sex differences in the mouse forebrain. Proceedings of the National Academy of Sciences, USA 101: 13666-71, copyright (2004) National Academy of Sciences, USA. Figure 3.4 is in the public domain. Figure 4.1 is reproduced from Gahr, M. 2003. Male japanese quails with female brains do not show male sexual behaviors. Proceedings of the National Academy of Sciences, USA 100(13): 7959-64, copyright 2003 National Academy of Sciences, USA, I am grateful to the National Academy of Sciences, USA for granting such permission. Dr Richard Bowen kindly granted permission to reproduce Figure 5.1. Figure 5.3 is published with kind permission from Springer Science + Business Media: Archives of Sexual Behavior, Sexual reward via vulvar, perineal, and anal stimulation: A proximate mechanism for female homosexual mounting in Japanese macaques, vol. 35, 2006, 523-32, Vasey, P. and Duckworth, N., Figure 2, photo by S. Kovacovsky. I am also grateful to Prof. Charles Roselli for Figure 5.4, Dr Christine Drea for Figure 5.5, Prof. Dick Swaab for providing Figure 5.10 and Ms Vanessa Woods for making available the bonobo G-G-rubbing photos used in Figures 2.2 and 5.2; the photos were taken in the Lola ya bonobo sanctuary, Democratic Republic of Congo. I am grateful to the Nature Publishing Group for granting permission to reproduce Figures 5.6 (Figure 1 of Fenstemaker *et al.* 1999), 5.9 (Figure 6 of Lösel and Wehling 2003) and 5.17 (Figure 1 of Thompson et al. 2001). Figure 5.11 is reproduced from Savic, I., Berglund, H. and Linström, P. 2005

Brain response to putative pheromones in homosexual men. Proceedings of the National Academy of Sciences, USA 102: 7356-61, I am grateful to the National Academy of Sciences, USA for granting such permission. Figures 5.12 and 5.13 are published with kind permission of Springer Science + Business Media: full credit Psychopharmacology, The effect of hetero- and homosexual experience and long-term treatment with fluoxetine on homosexual behaviour in male rats, vol. 189, 206, pp. 269-275, Habr-Alencar, S.F., Dias, R.G., Teodorov, E. Bernardi, M.M., Figures 3 and 4. Figure 5.14 is reprinted from Brain Research, Vol. 1024, Komisaruk, B.R., Whipple, B., Crawford, A. et al. Brain activation during vaginocervical self-stimulation and orgasm in women with complete spinal cord injury: fMRI evidence of mediation by the vagus nerves, pp. 77-88, Copyright 2004, with permission from Elsevier. Figures 5.15 and 5.16 are, respectively, Figures 3 and 6 of Holstege et al. (2003) and are reproduced with permission from the Society for Neuroscience. Dr Kathreen Ruckstuhl provided the photos of Capra ibex used in Figure 7.1 A,B, the photos were taken by Dr Peter Neuhaus. Figures included in Chapter 9 have been reproduced courtesy of Oxford University Press (Figures 9.1, 9.4, 9.5, 9.8, 9.9, 9.10 and 9.11); Elmtree Books, Hamish Hamilton Ltd and Edinburgh University Press (Figure 9.2); Edinburgh University Press (Figure 9.3); Zoological Society of London (Figures 9.6 and 9.7); W.B. Saunders and Co. (Figure 9.12) and Harvard University Press (Figure 9.13).

I am also thankful to J. Michael Bailey, Albert Bandura, Michael J. Baum, Sandra L. Bem, Ray Blanchard, Anthony Bogaert, William Byne, Anne Innis Dagg, Lisa Diamond, Milton Diamond, Anke Ehrhardt (photo by Sandra Elkin), Steve Emlen, Richard C. Friedman (photo by Marite Jones), Albert Galaburda, Richard Green, Dean Hamer, Simon LeVay, Eleanor Maccoby, Heino Meyer-Bahlburg (photo by Eve Vagg, from the Audiovisual Department of the New York State Psychiatric Institute), Letitia A. Peplau, Qazi Rahman, Charles Roselli, Joan Roughgarden, Frank Sulloway, Dick Swaab, Robert Trivers, Paul Vasey, Sandra Vehrencamp,



xiv

Cambridge University Press & Assessment 978-0-521-19675-8 — Animal Homosexuality Aldo Poiani Frontmatter More Information

#### Acknowledgements

Martin Weinberg, George C. Williams, Edward O. Wilson and Kenneth Zucker for allowing their photographs to be published as part of Figure 1.1. The images of: Richard von Krafft-Ebing and his wife Marie Louise, Karl-Maria Benkert, Karl-Heinrich Ulrichs, Sigmund Freud and Carl Westphal are all in the public domain. The photos of Vern Bullough, Michel Foucault and Günter Dörner are also published in the understanding that they are in the public domain. Havelock Ellis's photograph is taken from his autobiography My Life (1940, Heinemann, London) and is no longer subject to copyright restrictions. Alan Bell's photograph is published with kind permission from Springer Science + Business Media: Archives of Sexual Behavior, In Memoriam: Alan Bell, 31(5), 2002, 389, Martin S. Weinberg. I am grateful to The Kinsey Institute for Research in Sex, Gender, and Reproduction, Inc. for granting permission to reproduce the images of Alfred Kinsey (photograph by William Dellenback) and John Money (photo graph by José Villarrubia), and to Shawn Wilson in particular for following up on my request. We often forget that the name at the beginning of an article or on the cover of a book is (or was) a real person, deserving of personal homage even though she or he might not always have got it right. After all, knowledge progresses thanks to the collective effort of all who contribute with serious and honest research and we learn from both our successes and our mistakes. I apologise to those whom I did not contact and who, with hindsight, should have been contacted.

The manuscript was completed while I was adjunct researcher in the School of Biological Sciences at Monash University. I thank Prof. Gordon Sanson, Head of School when I joined the University, and Prof. John Beardall, who subsequently replaced Prof. Sanson at the helm of the School, for their hospitality. A big thank you also to Assoc. Prof. Martin Burd in particular for generously sharing his space and computer facilities, not to mention a good friendship and inspiring conversations about evolution, and to Prof. Ralph MacNally for use of his computer facilities.

And in the often last but never least thank you, I also express my gratitude to my wife Marisa and daughter Catiray, for their heroic patience during this intellectual journey of learning and discovery into the depth and breadth of animal homosexuality.



## **Preface**

Sexually reproducing animals are faced with various challenges in order to find, approach and copulate with a mate in reproduction, achieve fertilisation and finally ensure that the offspring survive and in turn reproduce. In social species, this whole process includes additional dimensions involving sometimes intricate relationships of competition and cooperation; further contributing to the overall complexity. Reproduction is central to the survival of the lineage, its suppression leads to extinction. As a consequence of this basic tenet of evolutionary biology we are obviously bound to be puzzled by the emergence of behaviours such as same-sex sexual intercourse, and by the occurrence of exclusively homosexual individuals. Homosexuality is indeed an evolutionary paradox, but one that can be resolved within the broad framework of the theory of evolution itself, after we take into account the many variables and scenarios that make homosexuality likely to be expressed in the first place and then maintained across generations.

In this book the reader will discover that we humans are not the only mammal species that expresses exclusive homosexuality and that some of the evolutionary processes that may explain the emergence of homosexual attraction in humans may be common to other sexually reproducing species as well. More importantly, it will be also shown that across taxa same-sex sexual behaviour is pervasive in the context of bisexuality and its expression takes modalities that can blend in the same individual, whether male or female, characteristics that are both feminine and masculine.

 $\chi V$ 



#### xvi Preface

It is very unlikely that the evolutionary paradox of homosexuality will be resolved by appealing to a single cause or mechanism. On the contrary, this book provides both empirical evidence and theoretical arguments to support a scenario of multicausality for homosexual behaviour. Based on the available comparative evidence, the conclusion is that homosexual behaviour can be broadly understood in the context of adaptive evolution and therefore it is not a malfunction of sexuality. The various dynamics of human homosexuality can be also explained, to a great extent, adaptively, whether as mediator of social cooperative or competitive interactions or as a side effect of selection for traits such as high reproductive rates, high mutation rates and others.

A complex brain produces sexual behaviour that is especially plastic in our species, but we are not the only vertebrate exhibiting plastic sexuality. Other primates, but also rodents, various social mammals and some bird species express intimate sexual contacts between members of the same sex on a regular basis and they do so following complex and dynamic patterns, as part of their normal and evolutionarily adaptive behavioural repertoire.

The aim in this book is to convey not only a sense of wonder when faced with diversity and

complexity, but also a sense of reassurance that such complexity can be integrated in an evolutionary synthesis. The challenge is not only to explore as many as possible of the various dimensions that define the expanse of homosexuality and its levels of causation, but also to cross the boundaries between various disciplines, each contributing unique information on the many specific aspects of sexual orientation. In the process, the limits and barriers imposed by political ideologies, barriers that tend to hinder rather than foster our understanding of sexual orientation, have been intentionally ignored.

This book was written in a somewhat asymmetrical partnership, with Alan Dixson mainly contributing one chapter and many insightful suggestions for the improvement of the other chapters, which were written by Aldo Poiani. The author of each chapter takes personal responsibility for what he writes by using the first-person singular. Finally, during the production of this book I tried to achieve the rather ambitious objective of both ranging wide across the many aspects of same-sex sexuality in various taxa and also digging as deeply as possible into each one of those aspects. I can only hope that the results of this effort may both inform and inspire the reader.