

The Evolution of Sex



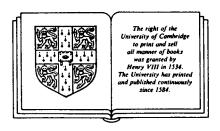
TO THE MEMBERS OF THE SEMINAR ON EVOLUTION THEORY ANN ARBOR, 1976



# The Evolution of Sex

### JOHN MAYNARD SMITH

Professor of Biology University of Sussex



### **CAMBRIDGE UNIVERSITY PRESS**

CAMBRIDGE
NEW YORK · PORT CHESTER
MELBOURNE · SYDNEY



#### CAMBRIDGE UNIVERSITY PRESS

Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore, São Paulo, Delhi

Cambridge University Press
The Edinburgh Building, Cambridge CB2 8RU, UK

Published in the United States of America by Cambridge University Press, New York

www.cambridge.org Information on this title: www.cambridge.org/9780521293020

© Cambridge University Press 1978

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.

First published 1978 Reprinted 1979, 1990 Re-issued in this digitally printed version 2009

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

Library of Congress Cataloguing in Publication data
Smith, John Maynard, 1920—
The evolution of sex
Bibliography: p. 195
Includes index.

1. Sex (Biology) 2. Evolution 3. Population genetics I. Title.
QH481.S64 574.1'66 77-85689

ISBN 978-0-521-21887-0 hardback ISBN 978-0-521-29302-0 paperback



## **Contents**

	Preface	ix
1	The problem	1
2	Some consequences of sex and recombination – I. The rate	
	of evolution	11
	Preamble	11
	A Response to selection based on pre-existing genetic	
	variability	13
	B Response to a sudden change in the environment,	
	based on newly arising mutations	16
	C Continuous evolutionary change	19
	D Genetic load, extinction and the Red Queen	23
	E Transient and steady-state models of evolution	28
	F A review of the models	31
3	Some consequences of sex and recombination – II. Muller's	
	ratchet	33
4	Could sex be maintained by group selection? The compara-	
	tive data	37
	Preamble	37
	A Do parthenogenetic varieties enjoy a twofold advan-	
	tage?	38
	B The nature, genetic consequences and origins of parth-	
	enogenesis in animals	42
	C Parthenogenesis in plants	49
	D The evolutionary potential of parthenogenetic strains	51
	E Cyclical and facultative parthenogenesis - the balance	
	argument	57
	F What is it that goes extinct?	66
	G Conclusions	69



V1	Contents	
5	<ul> <li>Recombination – the problem</li> <li>Preamble</li> <li>A Is there genetic variance for recombination frequency?</li> <li>B Selection against recombination in a uniform environment</li> <li>C Linkage disequilibrium and recombinational load – the observations</li> <li>D Supergenes and inversions</li> </ul>	72 72 73 77 83 85
6	Short-term advantages for sex and recombination – I. An unpredictable environment Preamble A Selection in a varying environment B Spatial variation of the environment C Sib competition D Environmental unpredictability – the evidence from geographical parthenogenesis	89 89 90 96 99
7	Short-term advantages for sex and recombination – II.  Selection in a finite population  Preamble  A Gene selection and hitch-hiking – a digression  B Hitch-hiking and recombination  C Selection for recombination in the presence of recurrent mutations  D Effects of selfing on selection for higher recombination  E Conclusions	111 111 112 114 117 119
8	Hermaphroditism, selfing and outcrossing Preamble A Selection for self-compatibility in hermaphrodites B Resource allocation in hermaphrodites C Other models for hermaphroditism D Hermaphroditism, monoecy, and dioecy in plants E Hermaphroditism in animals F Avoidance of inbreeding in animals G The human incest taboo	124 124 125 130 133 135 138 139 142
9	Anisogamy and the sex ratio  A Methods: evolutionarily stable strategies  B Genetic variance of the sex ratio  C Anisogamy	146 146 148 151



	Contents	vii
	D The sex ratio with random mating	157
	E The sex ratio with local mate competition	160
	F The sex ratio when the value of a male or female varies	
	with circumstances	161
	G Parent-gamete competition: meiotic drive	163
	H Parent-offspring competition	165
	Appendix: The evolution of stable sex ratios	166
10	Sexual selection	168
	A The concept of 'female choice'	168
	B Parental care	175
	C Monogamy, polygamy, and sexual dimorphism	183
11	Mutation	188
	A Are mutation rates optimal or minimal?	188
	B Mutation and hitch-hiking	192
	Appendix: The mutation rate in an infinite asexual population	193
	References	195
	Author Index	211
	Subject Index	215



# **Preface**

The aim of this book is to elucidate the selective forces responsible for the evolution of sex, of recombination rates, of breeding systems, and of mutation rates. I might have called it 'The Evolution of Genetic Systems' were it not that a classic with that title already exists. But whereas Darlington approached these topics from the standpoint of a cytologist with a distrust of mathematical reasoning, my own approach is that of a population geneticist.

It will be obvious that I have been greatly influenced by G. C. Williams's Sex and Evolution. I share with him a distaste for the Panglossian belief that if some characteristic can be seen as benefiting the species, then all is explained. I am under no illusion that I have solved all the problems which I raise. Indeed, on the most fundamental questions – the nature of the forces responsible for the maintenance of sexual reproduction and genetic recombination – my mind is not made up. On sex, the relative importance of group and individual selection is not easy to decide. On recombination, group selection can hardly play a significant role, but it is not clear to me whether the short-term selective forces I discuss are sufficient to account for the facts, or whether models of a qualitatively different kind are needed.

Inevitably, this uncertainty will make the book harder to follow. An author who knows his own mind about everything can present a clear and consistent case. I have felt more that I was carrying on a debate with myself, presenting the arguments first on one side and then on the other. To help the reader, I have provided a 'preamble' to most of the chapters, and I have not been afraid to repeat myself if it seemed to make for clarity.

I have made no attempt to present an exhaustive review of the comparative data on breeding systems. Instead, I have tried to put the theoretical issues as clearly as I can, and to give enough of the



#### x Preface

evidence to show what *kinds* of facts might be relevant. It has struck me, while writing, that the crucial evidence is often missing, simply because the theoretical issues have not been clearly stated, so that the relevance of a particular fact has not been appreciated. If I do no more than encourage experimentalists and field workers to collect the relevant data, I shall be well satisfied.

There are several aspects of the evolution of genetic systems about which I say little. These include chromosome structure, the genetics of sex determination and self-incompatibility, the significance of haplo-diploid life cycles, and parasexual processes in prokaryotes. I have made no attempt to discuss the molecular basis of recombination and mutation. All these topics are relevant to my general theme, but I have preferred to stick to topics about which I have something new to say.

The major part of the writing was done while I was a visitor at the Museum of Zoology at the University of Michigan, Ann Arbor. While there, I ran a seminar at which many of the topics in the book were discussed. I have exploited the graduate students who looked up references, told me of their own work, and suggested ideas; my only excuse is that I warned them that I would do so. I am grateful to them for making my stay at Ann Arbor so stimulating. The book has been read in manuscript by my colleagues Brian and Deborah Charlesworth, by Joe Felsenstein of the University of Washington, and by Eric Charnov and Jim Bull of the University of Utah. I have been helped greatly by their comments, although I have not always taken their advice.

Sussex University
July 1977

J. Maynard Smith