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The Genetics and Biology of Sexual Conflict

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The Genetics and Biology of Sexual Conflict

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Contents

Preface, vii

Foreword, ix

The Sexual Cascade and the Rise of Pre-Ejaculatory (Darwinian) Sexual Selection,
Sex Roles, and Sexual Conflict, 1

Geoff A. Parker

The Relationship between Sexual Selection and Sexual Conflict, 23

Hanna Kokko and Michael D. Jennions

Specialists and Generalists: The Sexual Ecology of the Genome, 37

David Haig, Francisco Úbeda, and Manus M. Patten

Sexual Conflict and Seminal Fluid Proteins: A Dynamic Landscape of Sexual Interactions, 49

Laura K. Sirost, Alex Wong, Tracey Chapman, and Mariana F. Wolfner

Paradox of Mother's Curse and the Maternally Provisioned Offspring Microbiome, 73

Michael J. Wade

The Evolution of Sexually Antagonistic Phenotypes, 83

Jennifer C. Perry and Locke Rowe

Sexual Conflict, Life Span, and Aging, 101

Margo I. Adler and Russell Bonduriansky

Copulatory Wounding and Traumatic Insemination, 115

Klaus Reinhardt, Nils Anthes, and Rolanda Lange

Sexual Conflict Arising from Extrapair Matings in Birds, 141

Alexis S. Chaine, Robert Montgomerie, and Bruce E. Lyon

Sexually Antagonistic Zygotic Drive: A New Form of Genetic Conflict between
the Sex Chromosomes, 155

Urban Friberg and William R. Rice

Sex Chromosome Drive, 165

Quentin Helleu, Pierre R. Gérard, and Catherine Montchamp-Moreau

Sex-Biased Gene Expression and Sexual Conflict throughout Development, 181

Fiona C. Ingleby, Ilona Flis, and Edward H. Morrow

Contents

Infanticide as Sexual Conflict: Coevolution of Male Strategies and Female Counterstrategies, 199

Ryne A. Palombit

Human Homosexuality: A Paradigmatic Arena for Sexually Antagonistic Selection?, 229

Andrea Camperio Ciani, Umberto Battaglia, and Giovanni Zanzotto

Sexual Conflict between Parents: Offspring Desertion and Asymmetrical Parental Care, 245

Tamás Székely

Sexual Conflict in Hermaphrodites, 265

Lukas Schärer, Tim Janicke, and Steven A. Ramm

Patterns and Mechanisms of Evolutionary Transitions between Genetic Sex-Determining Systems, 291

G. Sander van Doorn

Reproductive Parasitism: Maternally Inherited Symbionts in a Biparental World, 309

Gregory D.D. Hurst and Crystal L. Frost

Sexual Conflict and Sperm Competition, 329

Dominic A. Edward, Paula Stockley, and David J. Hosken

Conflict on the Sex Chromosomes: Cause, Effect, and Complexity, 341

Judith E. Mank, David J. Hosken, and Nina Wedell

Is Sexual Conflict an “Engine of Speciation”?, 355

Sergey Gavrilets

Sexual Cannibalism as a Manifestation of Sexual Conflict, 369

Jutta M. Schneider

Mechanisms and Evidence of Genital Coevolution: The Roles of Natural Selection, Mate Choice, and Sexual Conflict, 385

Patricia L.R. Brennan and Richard O. Prum

Index, 407

Preface

THE FIELD OF SEXUAL CONFLICT BEGAN in the late 1970s with a seminal book chapter written by Geoff Parker entitled “Sexual Selection and Sexual Conflict.”¹ The field experienced a major burst of activity in the mid-1990s as sexual conflict became more fully integrated into the field of sexual selection. The next decade of studies was then expertly summarized, analyzed, and integrated with earlier work in the highly cited book entitled *Sexual Conflict*, by Göran Arnqvist and Locke Rowe published in 2005.² Now, almost a decade later, we are bringing together the expertise of scientists from a broad cross section of the disciplines that collectively cover the field of genetic sexual conflict. In the Foreword, we describe the breadth of the field of sexual conflict and how essentially all aspects of the discipline derive from a simple reproductive dichotomy: microgametes (sperm) and macrogametes (eggs) that fuse to produce sexual offspring.

We would like to express our appreciation to two people at Cold Spring Harbor Laboratory Press: Richard Sever for inviting us to edit this book and Barbara Acosta for extensive help in the editing and production process. We also are thankful for the welcome response we received from the diverse community of scientists studying sexual conflict—nearly no one declined our request to contribute to this volume. Last, we dedicate this book to our wives, Kathryn Schoenrock and Galia Gavrilets, who have been a constant source of encouragement despite our frequent preoccupation with the development of this book.

BILL RICE
SERGEY GAVRILETS

¹ Parker GA. 1979. Sexual selection and sexual conflict. In *Sexual selection and reproductive competition in insects* (ed. Blum MS, Blum NA), pp. 123–166. Academic, New York.

² Arnqvist G, Rowe L. 2005. *Sexual conflict*. Princeton University Press, Princeton, NJ.

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Foreword

SEXUAL GENETIC CONFLICT OCCURS WHEN genetic variation increases the fitness of one sex at the expense of the other sex. It can occur at many levels—from alleles at a single locus that are selected divergently between the sexes, to different genomic components that are transmitted asymmetrically between the sexes, to alleles at different gene loci that favor opposite sexes during sexual interactions. Some forms of sexual conflict are special cases of intragenomic conflict. The opportunity for sexual genetic conflict originates with the production of two types of interdependent gametes.

Anisogamy. Nearly all multicellular organisms reproduce sexually through anisogamy (aka heterogamy), in which a microgamete (sperm) fuses with a macrogamete (egg) to form an offspring. This fundamental sexual asymmetry in gamete size generates a cascade of secondary asymmetries (like a fundamental tone with its harmonic overtones), which in turn contribute to the diverse forms of sexual genetic conflict that are collectively covered in this volume. Below we describe the major asymmetries and their contribution to sexual genetic conflict.

Unequal meiotic cell division in egg production. In many species, eggs are produced by a pair of unequal meiotic cell divisions that result in one large and functional ovum and three minuscule, dead-end polar bodies. This asymmetry in size and function produces strong selection on heterozygous alleles to cheat on Mendel's law of random segregation and increase their probability of ending up in the functional egg—a process called female meiotic drive. A broad spectrum of both plants and animals has independently evolved female meiotic drive, and indirect evidence indicates that vast stretches of the genome (i.e., the pericentric heterochromatin that can encompass up to 50% of a genome) evolved primarily to influence this process. Female meiotic drive may generate sexual conflict because many lines of evidence indicate that centomeric regions that produce successful drivers in females during oogenesis commonly cause infertility in males during spermatogenesis.

Asymmetrical propagation of genomic components. Meiotic cell division is symmetrical during spermatogenesis, but sperm have evolved to expel most of their cytoplasm during their ontogeny, including nonnuclear genes such as those of the mitochondria and endosymbiotic bacteria. The resulting asymmetry, in which mitochondria and endosymbionts are transmitted only (or predominantly) via the egg, has led (in diverse species) to cytoplasmic genes evolving to kill sons when they compete with their sisters for limiting resources and/or when sibling mating harms daughters via inbreeding depression. Egg-limited genetic transmission has also led to mitochondria in hundreds of species of plants that have evolved to kill developing pollen. Sperm and pollen production leads to sexual conflict (son or pollen killing by female-propagated cytoplasmic genes) because of the asymmetries in transmission that it generates.

Dimorphic sex chromosomes. Separate sexes have commonly led to the evolution of dimorphic sex chromosomes that do not recombine along all or much of their length. The asymmetries in transmission of the X and Y sex chromosomes (X to daughters and Y to sons), and in their genetic relatedness (compared with homologous pairs of autosomes, the X and Y have markedly reduced relatedness), generate many additional opportunities for genomic conflict. In XY males, each sex chromosome is selected to kill or incapacitate the sperm carrying the other type of sex chromosome in order to gain a transmission advantage. Such selection has led to widespread X- and Y-linked segregation distortion (aka male meiotic drive or selective sperm killing) in organisms as diverse as flies, beetles, and mammals. The X and Y are also selected to kill or debilitate the noncarrier sex of offspring

Foreword

when there is sibling competition and/or when brothers harm their sisters via sibling mating (SA-zygotic drive). This phenomenon has recently been documented in flies. Both sex-linked segregation distortion and zygotic drive are forms of sexual conflict because they increase production of one sex at the expense of the other sex.

Another sex chromosome asymmetry occurs because, unlike the autosomes that spend half of their time across generations in each sex, the X spends 67% of its time in females and is always hemizygous when in males. These transmission and expression patterns generate sexual conflict because they facilitate, on the X, the accumulation of dominant female-benefit/male-detriment alleles and recessive male-benefit/female-detriment alleles. This conflict can strongly influence genomic structure in the context of the location of the sex-determining switch. Tight linkage of a new, sex-determining mutation to a sexually antagonistic allele segregating on an autosome can produce a selectively favored supergene that can, in theory, supplant an extant sex-determining locus. This process may explain why it is not uncommon for sex-determining chromosomes to differ between sister taxa.

Intralocus sexual conflict. Male and female function, whether expressed in separate sexes or as separate functions within hermaphrodites, is a fundamental biological dichotomy that generates intrinsically different selective environments and hence sex-specific optimal alleles at many loci scattered across the genome. This selective asymmetry between the sexes generates an inevitable tension within the genome—called intralocus sexual conflict—because different alleles will commonly be favored by male versus female function. As a consequence, adaptive evolution by one sex will be at the expense of the other sex unless gene duplication or sex-specific gene regulation permits each sex to evolve independently. Intralocus sexual conflict can be so widespread that the genome-wide genetic correlation for adult fitness between the sexes was found to be strongly negative in a laboratory populations of flies, and recent studies indicate that gene expression levels underlie much of the observed intralocus sexual conflict.

Interlocus sexual conflict. With the exception of obligately self-fertilizing hermaphrodites, sexual reproduction requires coordinated interactions between different individuals, which we will assume here to be males and females, but the same logic can be applied to male and female function in out-crossing hermaphrodites. These reproductive interactions have both costs and benefits, many of which can differ between the sexes—another form of secondary sexual asymmetry. When there is lifelong monogamy—with no extra-pair reproduction—the costs and benefits of reproductive interactions are symmetrically shared by the pair because they act as a single reproductive unit, and conflict between the sexes is precluded. But most plants and animals are promiscuous to at least some degree, and this deviation from monogamy reduces the correlation in lifetime fitness between mating partners and opens up manifest opportunities for male versus female sexual conflict. The conflict operates through a shared interaction trait, like a prospective pair's decisions: to copulate or not, how many offspring to produce after mating, and how much to invest in each resulting offspring. The genes mediating the shared interaction trait will generally be different in males and females, creating the opportunity for interlocus sexual conflict—for example, a gene in males producing a seminal fluid protein that acts as a pheromone that binds a female receptor and thereby increases her egg-laying rate, and a different gene expressed in females coding for the seminal fluid protein's receptor or other genes influencing its downstream effects on her egg-laying rate. When the optimal egg-laying rate differs between the sexes, this difference sets the stage for interlocus sexual conflict and antagonistic coevolution between the loci in males evolving to increase female fecundity and different loci in females to resist this influence.

There is a surprisingly diverse array of ways for interlocus sexual conflict to be manifest. Some examples in this volume include:

- spiders in which females kill and consume their mates after mating and males that break off their penises during mating to produce plugs that prevent their mates from remating with other males
- many invertebrates in which males have evolved injection-like penises that enable them to fertilize a resisting female through almost any part of her body, and females that have evolved to digest sperm delivered in this way
- outcrossing hermaphrodites that castrate their mates in order to increase the damaged mate's investment in their shared offspring
- females of many bird species that regularly mate with males besides their pair-bonded social mate, causing males of some species to provision and protect a substantial proportion of unrelated offspring
- members of both sexes that have evolved to desert their mates while rearing a family, thereby forcing the deserted partner to rear their shared offspring alone
- males of many mammal species that routinely kill all extant offspring belonging to their newly acquired harem of females
- seminal fluid proteins that collectively increase a male's performance in sperm competition but that are also toxic to their mates
- paternally imprinted genes that modify gene expression in the fetus and thereby increase his mate's resource allocation to fetuses during gestation, and maternally imprinted genes that counterbalance these male-induced changes in gene expression
- spines on the penis that produce a fertilization advantage to males but cause substantial tissue damage to the reproductive tract of females
- genes coding for sperm binding proteins or their receptors on eggs that rapidly and antagonistically coevolve
- homosexuality as a consequence of sexually antagonistic alleles
- chase-away antagonistic coevolution between the sexes that can contribute to speciation and sex chromosome evolution

This volume will explore the diverse kinds and consequences of sexual conflict on the genetics and biology of sexual multicellular organisms. Although we cannot address all of the forms of sexual conflict here, this book brings together perspectives from a broad range of disciplines.

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