Genotype-by-Environment Interactions and Sexual Selection

Edited by **John Hunt and David J. Hosken**

with website

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This edition first published 2014 © 2014 by John Wiley & Sons, Ltd

Registered office: John Wiley & Sons, Ltd, The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK

Editorial offices: 9600 Garsington Road, Oxford, OX4 2DQ, UK
The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK
111 River Street, Hoboken, NJ 07030-5774, USA

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Library of Congress Cataloging-in-Publication Data

Genotype-by-environment interactions and sexual selection / edited by John Hunt and David Hosken.
pages cm
Includes bibliographical references and index.
ISBN 978-0-470-67179-5 (cloth)
1. Sexual selection in animals. 2. Genotype-environment interaction. I. Hunt, John, 1974- II. Hosken, David J.
QL761.G46 2014
591.56'2–dc23

2014015268

A catalogue record for this book is available from the British Library.

Wiley also publishes its books in a variety of electronic formats. Some content that appears in print may not be available in electronic books.

Cover image: A female (top) and male (bottom) decorated cricket (*Gryllodes sigillatus*) mating. Photograph courtesy of David Funk.

Typeset in 10.5/12pt Sabon by Laserwords Private Limited, Chennai, India.
Printed and bound in Singapore by Markono Print Media Pte Ltd.

1 2014

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Dedication – To our teachers at the Zoology Department, University of Western Australia.

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Preface

Much of the early history of evolutionary genetics was focused on understanding the relative contribution of genes and the environment to observed levels of phenotypic variation. Chief in this pursuit was Ronald A. Fisher who, amongst his many achievements, developed a statistical framework for partitioning these sources of phenotypic variance in a population. Underlying this framework was the idea that genetic and environmental sources of phenotypic variance in a population could be summed as long as they act independently, providing a simple method to statistically partition the relative effects of these sources of variation in phenotype. This logic is easy to follow if (as Fisher believed) the environment has negligible effects on phenotype and is distributed at random across individuals (and genotypes) in the population. Other researchers at the time (led most notably by Lancelot T. Hogben), however, argued that this framework under-estimated the importance of the environment and also missed a third and important source of phenotypic variation: that which arises from the combination of a particular genetic constitution with a particular kind of environment. Nowadays, we refer to this differential response of genotypes to environmental variation as genotype-by-environment interactions (GEIs) and know that this source of phenotypic variance is almost ubiquitous in most animal and plant populations.

Unfortunately, most researchers in the early part of the twentieth century viewed GEIs as an annoying departure from Fisher's additive framework. This view was particularly evident in agricultural genetics where the presence of GEIs often meant that a good genotype (or crop variety) in one environment may perform poorly in another environment. In such instances, the predictive power of genotypes across environments is greatly reduced, which has obvious consequences for the efficiency of selective breeding programs. It was not until the mid-1980s, however, that the explicit role of GEIs in the evolutionary process was considered. GEIs are now known to play a key role in a number of different evolutionary processes including the maintenance of genetic variation, driving population divergence and speciation, as well as directing the evolutionary response of phenotypes to changing environments.

Over the last decade or so, researchers have started examining the more specific role of GEIs in sexual selection. There is little question that females preferentially

mate with some males in the population but exactly why females are choosing these males is more debatable. "Good genes" models of sexual selection have featured prominently in this debate and assume that females prefer males of high genetic quality to gain genetic benefits for their offspring via enhanced viability. The problem with this logic, however, is that a female can only assess a male's phenotype *not* his genotype. In an ideal world where a male's phenotype maps perfectly onto his genotype, preferentially mating with a male of high genetic quality should be relatively easy for a female to achieve: choose the male with the most elaborate sexual trait or most vigorous sexual display that reliably reflects his underlying genetic quality. However, if the expression of these sexual traits or displays is heavily influenced by GEIs and males disperse freely between environments, the genotype-phenotype map will be considerable weakened making it difficult (if not impossible) for females to assess male genetic quality based on these traits. The operation of sexual selection will be further complicated if GEIs also exist for female mate choice, as appears the case for the few systems where this has been examined. Collectively, this suggests that "good genes" arguments are likely to be overly simplistic when GEIs are present and may go some way to explaining why their effects (although taxonomically widespread) appear to be relatively minor.

Although there is currently an explosion of theoretical and empirical research on the role of GEIs in sexual selection, no single volume has attempted to compile this work or highlight the key findings in this area. Our goal was therefore to produce a volume that provides a clear overview of the importance of GEIs to sexual selection. As many of the leading researchers working on this topic have contributed to this volume, we hope that it will serve as both a primer on the role of GEIs in sexual selection and a guide to help direct future research. We believe this book will be of broad interest to established researchers working on sexual selection, as well as undergraduate and postgraduate students starting their research careers.

We have divided the book into three main sections that we believe cover the key developments on the role of GEIs in sexual selection. Part 1 lays the theoretical foundations outlining the importance of GEIs for sexual selection. Mike Wade (Chapter 1) starts with a general overview of the many problems with "good-genes" models of sexual selection when male genetic quality is correctly viewed as a complex trait that is influenced by GEIs, interactions between genes, as well genes provided by the social environment. Next, Thomas Getty (Chapter 2) examines the role of uncertainty and incomplete information transfer using a simple optimality model that focusses on female choosiness when searching for mates is costly and males of different genotypes are only partially discriminable (due to crossover GEIs and dispersal between environments). Following a similar theme, Luke Holman and Hanna Kokko (Chapter 3) use a genetically explicit individual-based simulation to examine how dispersal, signal reliability and spatial variation affect the evolution of female mate choice for locally adapted genes. Importantly, this simulation does not vary the form of GEIs (whether there is crossover or no crossover) directly. Rather dispersal is varied across a continuous distribution of environments with locally varying phenotypic optima so that dispersing individuals experience weaker

correspondence between environmental conditions at their natal and their breeding sites the further they disperse. They then extend this logic to ask how spatial variation creates differences in local adaptation, and whether female choice can persist when females encounter males from diverse natal environments. Finally, building on some of the key ideas introduced by Mike Wade (Chapter 1), Jason Wolf, Nick Royle, and John Hunt (Chapter 4) use a series of quantitative genetic models to examine how genotype by social environment interactions (GSEIs) influence the operation of sexual selection, when the social environment contains genes. They also provide a guide to measuring GSEIs, as well as an overview of empirical studies measuring this process within the context of sexual selection.

A necessary (and critical) first step for empiricists examining the role of GEIs in sexual selection is to formally demonstrate their existence and quantify their strength. Section 2 therefore provides an overview of the experimental and statistical approaches that can be used to quantify GEIs. Derek Roff and Alastair Wilson (Chapter 5) start by providing an overview of the breeding and statistical methods used to estimate GEIs in laboratory studies where the pedigree structure of the organism being studied is under the control of the experimenter. Matthew Robinson and Anna Qvarnström (Chapter 6) then extend this framework by providing an overview of the numerous of statistical approaches that can be used to quantify GEIs in natural populations when pedigree structure is not controlled by the experimenter. Finally, Jennifer Perry and Judith Mank (Chapter 7) review the application of gene expression approaches to understanding GEIs in sexually selected traits. They place particular emphasis on recent transcriptomic methods and outline some of the methodological concerns with this approach, as well as ways to optimize experimental designs to detect transcriptome by environment interactions (TEIs).

In Part 3 we provide an overview of empirical studies examining the role of GEIs in sexual selection. To start, Michael Greenfield (Chapter 8) provides an overview of his research on GEIs and sexual selection in the lesser waxmoth (*Achroia grisella*). This chapter represents the culmination of over a decade worth of empirical research on the topic and therefore represents one of the best studied systems on how GEIs influence the operation of sexual selection. Next Lawrence Bellamy, Kevin Fowler, and Andrew Pomiankowski (Chapter 9) discuss the potential use of inbreeding to assess GEIs in sexual traits. Inbreeding offers a moderately simple but powerful way to alter the genetic quality of individuals and demonstrating inbreeding by environment interactions (IEIs) is therefore functionally equivalent to GEIs. Reviewing the literature, they then show that sexual traits show clear inbreeding depression but this does not appear any greater than for nonsexual traits and there is little evidence suggesting that inbreeding reveals GEIs. This undoubtedly reflects the current lack of empirical tests. Suzanne Mills, Mikael Mokkonen, Esa Koskela, and Tapio Mappes (Chapter 10) provide an overview of their research on GEIs and signal reliability in bank voles (*Myodes glareolus*). A variety of male signals exhibit GEIs in this species, challenging signal reliability, and potentially disrupting the covariance between male signal and female preference. Mills and colleagues discuss a number of mechanisms that may help mitigate these problems, including parallel reaction norms for male signal and female preference, assortative dispersal and

sexual antagonism. Fiona Ingleby, David Hosken, and John Hunt (Chapter 11) provide an overview of plasticity and GEIs for cuticular hydrocarbons (CHCs) expression in *Drosophila* – a chemical signal that is known to be under strong sexual selection in many *Drosophila* species. They cover the diversity of biotic and abiotic environments influencing CHC expression in *Drosophila*, as well as providing a summary of studies demonstrating GEIs within the context of sexual selection and the likely consequences for CHC evolution in this important genus. Gita Kolluru (Chapter 12) reviews the evidence for GEIs in the sexual traits of guppies (*Peocilia reticulata*). Although there is considerable evidence to suggest that male sexual traits in guppies exhibit substantial genetic variation and plastic responses to the environment, and individuals frequently encounter varying environmental conditions, surprisingly few studies have convincingly demonstrate GEIs for sexual traits in this species. To conclude this section, Scott Sakaluk, Carie Weddle, and John Hunt (Chapter 13) examine the role that GEIs and signal reliability play in chemosensory self-referencing and the maintenance of polyandry in decorated crickets, *Gryllodes sigillatus*. Female crickets in this species mark their male partner with CHCs during mating and use this signal to avoid re-mating with them in favor of a novel male. Thus, there is strong selection for CHCs to reliably signal individual identity in females and the lack of substantial GEIs facilitates this process. No such signaling constraints are likely to exist for males, where strong GEIs for CHCs exist.

Finally, this volume would not have been possible without the help and guidance of our friends, colleagues and mentors. We would like to thank our teachers at the Department of Zoology (University of Western Australia) for sparking our early interest in evolutionary biology, especially sexual selection and genetics. We also thank our friends and colleagues (Rob Brooks, Steve Chenoweth, Mark Blows, Michael Jennions, Luc Bussiere, Jason Wolf, Sasha Dall, Mike Wade, Allen Moore, and Alastair Wilson) for many insightful discussions over the years that have shaped the way we think about GEIs and their consequences for the operation of sexual selection. We are greatly indebted to all of the chapter authors for their excellent contributions and for providing critical feedback on other book chapters. Their hard work and willingness to accommodate changes to their own chapters made the publication of this book a much less painful task. Last but not least, we thank our families for their continued support and patience.

John Hunt and David Hosken
Cornwall, United Kingdom, October 2013

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About the Companion Website

This book is accompanied by a companion website:

www.wiley.com/go/hunt/genotype

This website includes:

- Powerpoints of all figures from the book for downloading
- PDFs of tables from the book

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