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Understanding Reproduction

Our understanding of reproduction and reproductive processes is often biased towards the behaviour of organisms most familiar to us. As a consequence, the amazing diversity in the phenomena of reproduction and sex is often overlooked.

Understanding Reproduction addresses all the main facets of this large chapter of the life sciences, including discussions of asexual reproduction, parthenogenesis, sex determination, reproductive effort and much more. The book features an abundance of examples from across the tree of life, including animals, plants, fungi, protists and bacteria.

Written in an accessible and easy-to-digest style, overcoming the intimidating diversity of the technical terminology, this book will appeal to interested general readers, biologists, science educators, philosophers and medical doctors.

Giuseppe Fusco is Associate Professor of Zoology in the Department of Biology of the University of Padova. His research is in the area of evolutionary biology, with a focus on the variation produced in each generation through reproduction and development, the 'raw material' on which natural selection and other mechanisms of evolutionary change operate. He is editor of the volumes *Evolving Pathways: Key Themes in Evolutionary Developmental Biology* (2008), *From Polyphenism to Complex Metazoan Life Cycles* (2010), *Arthropod Biology and Evolution: Molecules, Development, Morphology* (2013), *Perspectives on Evolutionary and Developmental Biology* (2019) and author, with Alessandro Minelli, of *The Biology of Reproduction* (2019).

Alessandro Minelli was Professor of Zoology at the University of Padova until his retirement in 2011. He previously served as the Speciality Chief Editor for evolutionary developmental biology for the journal *Frontiers in Ecology and Evolutionary Biology*. He was previously Vice-President of the European Society for Evolutionary Biology. Having studied animals for the majority of his career, on retirement he decided to study plant evolutionary development.

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He is the author of *Biological Systematics* (1993), *The Development of Animal Form* (2003), *Forms of Becoming* (2009), *Perspectives in Animal Phylogeny and Evolution* (2009), *Plant Evolutionary Developmental Biology* (2018), *The Biology of Reproduction* (2019, with Giuseppe Fusco) and *Understanding Development* (2021).

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Understanding Reproduction

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> 'Fusco and Minelli provide a very clear and accessible overview of the strange and wonderful diversity of reproductive strategies and mechanisms in animals, plants and other organisms. They explain key concepts, define important terms, and place reproductive modes within an ecological and evolutionary context. This book will be a useful reference for biologists, students and even curious non-specialists.'

> > Russell Bonduriansky, University of New South Wales, Australia

'As a plant biologist, I often find myself trying to explain reproduction in plants as though they are somehow an anomaly rather than just another way of reaching the same goal following first principles. This perception of anomaly comes from a pedagogical bias of teaching reproduction as "sex in mammals". This book ties together concepts regardless of organism, drawing clear lines between a complex diversity of patterns and their underlying reproductive processes.'

Chelsea D. Specht, Barbara McClintock Professor in Plant Biology, Cornell University, USA

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Foreword

Everybody has heard of reproduction; it has to do with sex and sexes, but not always. When it comes to humans, it is at the same time both an interesting and a taboo topic. Teachers may find it easier to teach about reproduction in plants rather than animals, and students may be puzzled when they are told that the beautiful flowers they have in that vase in their living room are in fact reproductive organs - I do not think that anyone would like the idea of having the reproductive organs of animals exposed in a vase in the living room! But this also shows the biased way in which we think about reproduction, taking ourselves and other animals - particularly mammals - as the starting point of any such discussion. But as Giuseppe Fusco and Alessandro Minelli show in this marvellous and informative book, there is a lot more to sex and reproduction than what we are usually familiar with. The present book is a real journey during which the authors masterfully describe and explain the diversity of forms of sex and reproduction across the whole tree of life. Reading this book will make you perceive sex and reproduction in a new way, far removed from the anthropocentricism that usually characterizes our perceptions of the subiect. One message of the book is that we cannot draw on nature in order to make decisions about what is normal or abnormal when it comes to human sex and reproduction. What happens regularly in some groups may never happen in others; what could be considered as ordinary in some cases might be exceptional for others. Life has evolved a variety of ways for reproduction to occur, and Fusco and Minelli are to be commended for bringing us such a rich view of this complex topic in a single concise volume.

Kostas Kampourakis, Series Editor

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Preface

We all have an intuitive idea of what reproduction is and how it occurs in the living world. Images that might come to mind are those of a lioness licking her cubs, a puffball mushroom that explodes releasing spores, two damselflies copulating on a reed leaf, a bumble bee that brings the pollen collected from the stamens of a snapdragon to the pistils of another and possibly many others. All of this is right, but there is so much more than that. Common understanding of reproduction and reproductive processes is biased towards the behaviour of organisms (especially animals) more familiar to us. At variance with other fields of biology such as development or evolution, in this area of biology there are no widespread 'misconceptions', but rather a lack of appreciation of the amazing diversity of the phenomena of reproduction and sex. These are often unexpectedly different from what everybody knows from humans or other vertebrates. The variation lies not only in the way parents provide care for offspring, but in whether or not they do; not only in how males court females, but in who courts whom. There is variation in the number of sexes, the number of parents, what eggs do with sperm, whether offspring are the same kind of animal, or plant, as their parents.

Inspired by a graduate textbook we published in 2019, *The Biology of Reproduction*, to which this book owes most of its field-specific contents, we will address all the main facets of this large chapter of the life sciences – asexual reproduction, parthenogenesis, sex determination, reproductive effort and much more – with a coverage across the tree of life that extends across all the main groups: animals, plants (including 'algae'), fungi, protists

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and bacteria. While dealing with subjects as varied as the binary division of unicellular algae, the splitting of a strawberry's stolon from the mother plant, the mating of squid, the production of spores by boletus mushrooms, or the paternal care of Darwin's frog, we will try to present all these phenomena using a common language for all living beings, at least for the most general aspects of their reproductive biology, thus overcoming the diversity of the technical terminology still alive in different disciplinary traditions, such as in botany, zoology, microbiology and transmission genetics.

This is not a book of curiosities. How do porcupines do it? (in some way). How long is a baleen whale's penis? (very long). How many times can a lion copulate in a single day? (several). What we propose here is a planned journey through what we may call a 'phenomenology of reproduction'. The first chapter will prepare the ground with some preliminary concepts. There, we will also explain the difference between investigating sex and reproduction across the whole tree of life and in relation to our own species, where psychology and social sciences get involved. After an exploration of the great diversity of life cycles (Chapter 2), we will start with reproduction that does not involve sex (Chapter 3), before moving on in Chapter 4 to sexual reproduction, then to sexual reproduction in its most canonical form, where the parents are two (Chapter 5), and then to other, less well-known forms of sexual reproduction, where the parent is one, or nearly so (Chapter 6). In the last two chapters we will have a look at how sexual traits develop (Chapter 7), before closing with the broad subject of reproductive strategies (Chapter 8).

We will not systematically discuss the evolution and the adaptive value of different reproductive modes or strategies, but our classification of reproductive phenomena largely reflects the way these are relevant in evolutionary ecology and evolutionary developmental biology. During the journey we will encounter, along with more 'regular' reproductive modes, offspring produced solely for the purpose of nourishing their siblings, plants that entrust their pollen to bats, animals that have not known sex for tens of millions of years, insects with very many X and Y sex chromosomes, apparently immortal trees and bugs that are generated by mothers that are still to be delivered by their own mother. In the very last part of the book, we will see cases where there are doubts on how many individuals, either parents or

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offspring, have to be counted and cases at the border of what we can call reproduction, bearing a closer resemblance to the development or the growth of an individual.

Let's start our exploration of this overwhelming variety of forms through which reproduction has evolved along the larger and smaller branches of the great tree of life.

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Mariagiulia Sottoriva produced all the final artwork, and significantly contributed to designing its adaptation for the present book from more technical sources. We thank her for her patience in dealing with our not always clear ideas on what the final artwork should be.