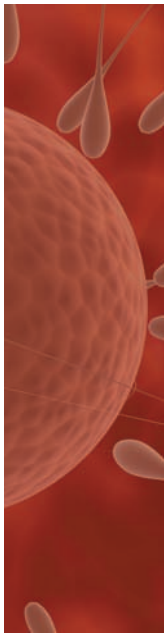
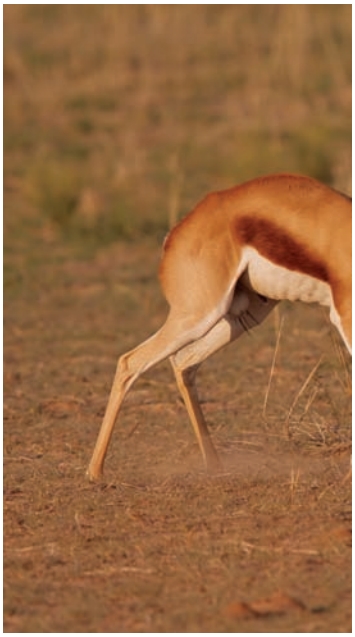
DAVID LOVEJOY | DALIA BARSYTE

SEX STRESS AND REPRODUCTIVE SUCCESS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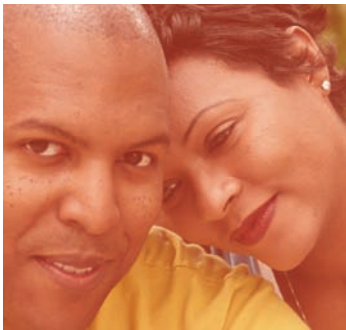

Sex, Stress and Reproductive Success

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By:

David A. Lovejoy
Dalia Barsyte

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To our children:
Sabine and Darius

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About the Authors

David A. Lovejoy is Professor of Neuroendocrinology in the Department of Cell and Systems Biology at the University of Toronto in Toronto, Canada. Previous to taking his appointment at the University of Toronto he was a Lecturer at the University of Manchester in Manchester, England. He is an author of over seventy scientific publications in the field of reproductive and stress-related physiology and is the author of the book *Neuroendocrinology, An Integrated Approach*.

Dalia Barsyte is currently a senior scientist at the Structural Genomics Consortium at the University of Toronto and is an author of numerous publications in the field of the molecular biology of stress, cancer and environmental toxicology.

Preface

This book is intended to provide an understanding of how mechanisms of reproduction and stress-related physiology interact to allow organisms to cope and survive in an all-too-frequently hostile environment. Although it is intended for second- and third-year university students, we have tried to make it accessible to the interested reader outside of an academic setting. We have attempted, wherever possible, to provide a clear and basic understanding of the physiological processes being discussed. However, we realize that many readers will not have the background to understand all of the concepts introduced in this book. For this reason we have provided a comprehensive glossary that includes definitions and descriptions of the topics covered.

Our understanding of the impact of stress on reproduction is changing on an almost month-by-month basis. It is not possible to include every theory and advance that has been published. We have tried to provide a foundation for a basic understanding of the effect of stress on reproduction and have introduced new concepts that will probably have a bearing on future studies.

When we first considered writing this book, many of our colleagues encouraged us to discuss the numerous aspects of stress and reproduction across a wide range of all multicellular animals, not to mention those found in fungi and plants. Undoubtedly, the mechanisms of stress on reproduction on invertebrate animals, plants and fungi are very interesting, and in many cases, exotic and unusual by vertebrate standards, but we had to concentrate on a single group of organisms understandable to most readers in order to maintain a focus. Interested readers are encouraged to read and study the mechanisms of stress and reproduction as they will inspire the imagination and study of those biological mechanisms so different from those we typically understand.

We hope that you will find the material covered in this book compelling, but remember that it is only a very small number of species relative to all forms of life on the planet that have been discussed.

Acknowledgements

No book is, of course, the sole result of the authors, and this book is not an exception. Its production is a result of the combined effort of numerous individuals who contributed their time, ideas and resources over the two years we spent writing.

This volume would not have been possible without the support and encouragement of John Wiley and Sons, and their editorial team. In particular, we wish to thank Nicky McGirr who encouraged us to propose the project and was a tireless cheerleader throughout the project, Fiona Woods who kept us organized and on schedule and Celia Carden who handled contract and review details. In addition, we would like to thank Harriet Stewart-Jones, Sarah Karim and Prakash Naorem, for looking after the final edits, galley proof and production details. It is hard to imagine a better team of editors!

The topics covered in this book were the collective result of discussions with numerous colleagues and friends who suggested many of the concepts covered. Professor Robert Dores at the University of Denver provided considerable insight into the evolution of the stress response, Professor Franco Vaccarino and Dr Susan Rotzinger at the University of Toronto spent many hours discussing the relationship of stress with anxiety and depression with us, and Professors Ted Brown and Denise Belsham in the Department of Medicine at the University of Toronto kept us abreast of the latest developments in reproductive physiology. We owe special thanks to Professor Dr Jackson Bittencourt at the University of Sao Paulo and Dr Jean-Michel Aubry at the University of Geneva Medical School for their ideas and understanding of the neurobiology of stress.

We owe a great debt of gratitude to Dr Ian Dunn at the Roslin Institute and Dr Kevin O'Byrne at King's College, London for critically reviewing an earlier draft of this manuscript. Their experience, insight and suggestions had a huge impact on this book.

Completion of this book would not have been possible without the understanding and hard work of the graduate students and research associates in the

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And we especially thank John, Natalie, Gillian, Rachel, Paul and Tammy at the 'Harbord House' in Toronto, who kept us plied with nutrients while we composed a significant part of these writings. You guys are the best!

1

Reproduction under safe conditions

> When two great forces oppose each other, the victory will go to the one that knows how to yield.
>
> Lao-Tzu, *Tao te Ching* (sixth century BC)

1.1 Introduction

Most of us regard the act of reproduction as a rather private affair. Despite the volumes of books and magazine articles written on sex and reproduction, and its acceptance into public consciousness, we feel uncomfortable discussing sex with a crowd around us. Sex is intensely personal. It's difficult to be romantic with a partner at midday on a crowded city bus, at a football game or when your children are running around the house. No, we prefer those moments of peace when we are alone with our partners. We might put on some music, turn down the lights and unplug the telephone. We create an environment in which we feel calm, relaxed and safe. We don't think about why we do these things, it is intuitive and natural. And we certainly don't consider the results of a few billion years of evolution encouraging us to reproduce under safe conditions.

Reproduction is the primary goal of all forms of life. Without the ability to reproduce, there is no life. This aspect defines all life forms regardless of whether it is a bacterium, protozoan, a plant, fungus or animal. There are a multitude of strategies various life forms have adopted to ensure they reproduce. These include fission of single-celled organisms, the budding of a smaller individual from a larger individual or the fusion of cells, which, in the case of sexual reproduction, leads to the development of a new individual. In

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some cases, a combination of these strategies may be employed. But regardless of the reproductive strategy used, once the new individual is 'born', it must survive in a hostile and unforgiving environment long enough for it to reach a stage of maturity at which it too can reproduce. So, if the primary goal of a species is to reproduce, then a secondary imperative of the individual is to survive long enough until it can itself reproduce. Because the time required to reach reproductive maturity for all organisms is much longer than the time required for the act of reproduction, organisms have evolved a number of strategies and mechanisms that allow them to survive the conditions of a harsh environment.

The environment surrounding an organism is dangerous and constantly challenges its ability to survive. There are seasonal and daily temperature fluctuations, and an atmosphere that allows organisms to respire but is toxic in some ways. There is ionizing radiation from the sun and cosmos. There are mechanical threats in the form of geologic activity, severe weather, wave action, shifting sand and wind. Food sources may be plentiful at some times, but unavailable at other times. And while you, the organism, is trying to survive, other organisms may be interested in attacking you – either larger predators looking for a meal or much smaller ones which cause a variety of diseases. Added to these stressors are the toxins and noxious chemicals that are found in all environments from a variety of sources. We call these aspects that threaten our survival, 'stress' (Figure 1.1).

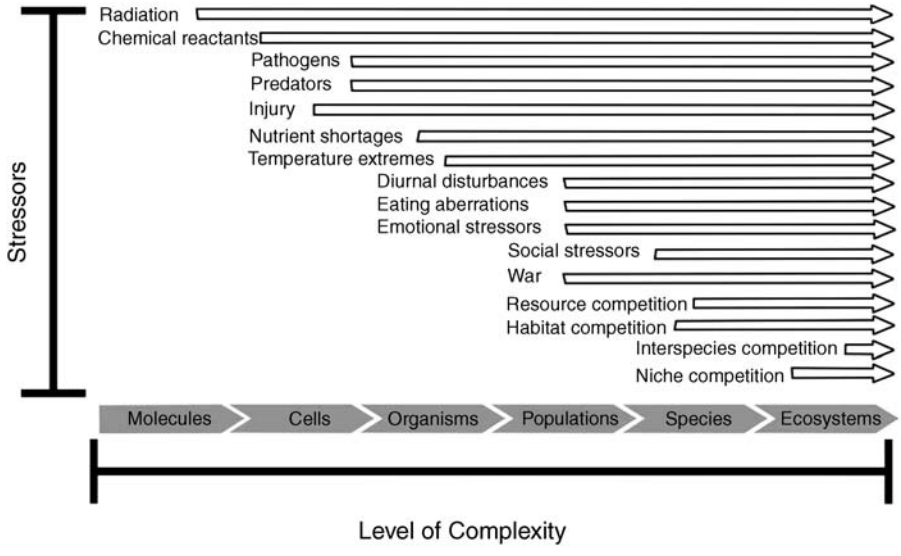

Figure 1.1 Types of stressors that act on various levels of biological complexity. The arrow associated with each stressor indicates the range of complexity that it can affect

One of the fundamental principles of the life history of any organism is that the evolution of fitness-related traits will be constrained by the presence of trade-offs between them. In other words, a beneficial effect on one physiological system can have a negative effect on the expression of another. If we were to consider this with respect to reproduction and stress, an organism could increase its reproductive capacity with a reduced ability to ward off stressful challenges or it could improve its ability to handle stress but with a reduced reproductive capacity. Therefore, for most species there is a compromise that provides a certain level of reproductive capacity with an appropriate level of a stress response that is designed to meet most, but not all, of the challenges for that species.

1.2 What is stress?

Most of us have an intuitive understanding of what constitutes 'stress'. For those of us living in an urbanized civilization, most of what we consider as 'stress', we experience with psychological and social interactions. We face many of the same problems as other animals as well as others that are unique to our species, such as loss of employment, overwork, too many bills and traffic conditions, to name a few. Under normal circumstances, these stressors rarely bother us, but when these events stop us from carrying out our day-to-day activities, we recognize these events as stress. When stress occurs over a long period of time, we might experience anxiety, depression and a variety of other conditions such as post-traumatic stress disorder, panic disorder or various phobias. Then if an additional stressful situation occurs, medical treatment might be required. In our Western style of living, we have a culture based around the stress of living. A quick perusal through newspaper and magazine advertisements will see that the media encourage us to reduce stress by being pampered by spa treatments, take a getaway cruise to a tropical isle or take out golf or gym memberships. The reality is, of course, that we have to indulge in these stress-reducing activities within the confines of the free time allotted to us and within our financial budgets. For the majority of us, both time and money are limited. Excessive indulgence in these commercially related stress-reducing activities can cause debt and reduce our time available for work. This struggle to fit relaxation time into our daily lives might even increase our stress load. We strive for a balance in life, but only a very few actually achieve it.

The concept of stress was originally recognized as a condition associated with humans, but as we came to understand more about the physiology of stress, we could see that it could be applied to all species. What we routinely define as stress, in the biological sense, has a long history. Hans Selye (1907–1982), a