
Preface

Parental care is a trait that shows tremendous diversity both within and across different animal taxa, and is an important topic in evolutionary biology and behavioural ecology. Parental care forms an integral part of an organism's reproduction, development, and life-history, and because caring for offspring means that parents have less time, resources, or energy available to search for or attract mates, the evolution of parental care is closely linked with sexual selection. In addition, the evolution of parental care represents an important step in the evolution of sociality as it leads to the formation of family groups, which provides a bridge to more complex forms of social structures. But because parents and offspring share only some of their genes, conflicts emerge in sexually reproducing organisms that shape the evolution of parental care and offspring strategies to demand care. As a consequence, the family also constitutes a model to understand the evolutionary tension between cooperation and conflict.

The importance of parental care in evolutionary biology has only been recognized relatively recently. Darwin did not consider parental care in great detail, except when speculating on the development of a moral sense and the role of selection operating on families in the evolution of more complex sociality: 'With respect to the origin of the parental and filial affections, which apparently lie at the base of the social instincts, we know not the steps by which they have been gained; but we may infer that it has been to a large extent through natural selection' (Page 105; *The Descent of Man*, Darwin 1871). The development of the robust conceptual framework that we have today for understanding the evolution of parental care was dependent on numerous innovations in the wider field of ecology and evolution. In particular: (i) the incorporation

of kin selection to evolutionary thinking (Hamilton 1964), (ii) an appreciation of the relationship between parental care and the ecology and life-history of organisms (Lack 1968), (iii) the recognition that specific ecological conditions can drive the evolution of parental care and sociality (Wilson 1971), (iv) the insight of Trivers (1972) in making the connection between parental care, parental investment, and sexual selection, (v) his application of kin selection logic to derive genetic conflicts between parents and offspring over the amount and duration of parental care (Trivers 1974), and (vi) the introduction of evolutionary game theory to study the evolution of parental care and family conflicts by Maynard-Smith (1977). In particular the concept of parental investment (Trivers 1972) was vital in triggering a large amount of research on sexual selection and mating system evolution. As a result, Tim Clutton-Brock noted in his book *The Evolution of Parental Care*, published in 1991, that 'few areas of evolutionary biology [...] progressed as rapidly over the past two decades as our understanding of animal breeding systems' (p. 3). The underlying rationale for writing a book on the evolution of parental care by Clutton-Brock therefore centred on the importance of parental care in determining the strength of sexual selection. Since then the study of the evolution of parental care has progressed and diversified substantially.

The idea for the present book arose from discussions among the three of us about parental care research, and the realization that more than 20 years had passed since Clutton-Brock's (1991) classic book on this topic. In the intervening years since this book was published there has been growing recognition of the central importance of parental care research in behavioural and evolutionary biology, with an increasing number of papers being

published and new fields of study steadily emerging. For example, there has been notable progress in the study of some aspects of parental care that were newly emerging at the time of the publication of Clutton-Brock's book, such as the physiology of maternal effects or the effect of parentage on parental care. However, there has also been notable progress in other topics that, although they had emerged at the time, had progressed rather slowly, such as within-family conflicts, cooperative breeding, and brood parasite-host co-evolution. More recently new areas of research altogether have emerged, such as the evolutionary and molecular genetics of parental care. It therefore seemed high time to have a go at synthesizing these exciting developments in the study of the evolution of parental care.

The aim of this book is to provide a comprehensive, fresh overview of research on the evolution of parental care in animals. The book integrates the major advances in the field over the last two decades since Clutton-Brock's (1991) book, focusing on establishing key concepts and on drawing general principles whilst emphasizing a broad taxonomic approach throughout. There are three main sections that represent major themes in the evolution of parental care and 18 chapters. The chapters and sections are arranged in a logical order to encourage reading of the book from front to back. Nevertheless, each chapter has been written so that it can easily be read in isolation, too.

Chapter 1: The introductory chapter by Smiseth, Kölliker, and Royle sets the stage for the book by reviewing the diversity of parental care across taxa, providing definitions of key terms and discussing some of the central concepts in the evolution of parental care.

Section I is on the **Origin and evolution of parental care**. This section deals broadly with the factors that promoted the early evolution of parental care. In **Chapter 2**, Klug, Alonzo, and Bonvall review theory and describe under which conditions parental care can evolutionarily originate, and how life-history and ecology interact to determine the favourable conditions for its spread. In **Chapter 3**, Alonso-Alvarez and Velando review the causes of variation in the evolutionary benefits and costs of parental care, especially with respect to

the physiological mechanisms mediating these fitness consequences. Although we have advocated a question-driven approach throughout, any treatment of a biological phenomenon such as parental care also requires appropriate coverage of its natural history and diversity. **Chapter 4** by Balshine covers the diversity and distribution of forms of care among vertebrates, and **Chapter 5** by Trumbo the very diverse and sometimes striking and peculiar forms of care that have evolved among invertebrates. Finally, **Chapter 6** by Kokko and Jennions explains the multiple and complex evolutionary relationships between sexual selection and the sex roles in parental care.

Section II is concerned with **Cooperation and conflict in parental care** and covers the tension between conflict and cooperation that emerges in the context of parental care due to sexual reproduction and the resulting asymmetries in fitness consequences of care and/or genetic relatedness. Kilner and Hinde (**Chapter 7**) discuss how the resolution of parent-offspring conflict affects parent and offspring strategies and review the experimental evidence. **Chapter 8** by Roulin and Dreiss explores conflicts and cooperation between siblings and how these are resolved via mechanisms such as aggression, signalling, and negotiation. Lessells (**Chapter 9**) explores the theoretical underpinning and empirical evidence for conflicts between parents over the provision of care. In **Chapter 10**, Komdeur presents the ecological and social factors that alter the fitness returns of investment in sons versus daughters and the evidence for adaptive sex allocation, and **Chapter 11** by Alonzo and Klug reviews the central importance of parentage in the evolution of parental care. The two extremes of cooperation and conflict in animal families are covered in **Chapter 12** by Cant, on the evolution of cooperative breeding, and **Chapter 13** by Spottiswoode, Kilner, and Davies on the manipulation of parents and exploitation of parental care by brood parasites.

Section III covers the **Evolutionary genetics of parental care**. This section takes a change of perspective from the majority of chapters in sections I and II, which focus on how selection acts on phenotypes, towards establishing how phenotypic variation in parent and offspring traits are generated and maintained by genetic and non-genetic

factors, how this variation is exposed to natural selection, and what the molecular and quantitative genetic trait architecture of parental care are. **Uller (Chapter 14)** describes how parental care can enhance adaptive evolution by generating environmentally induced variation in offspring phenotypes through processes such as phenotypic and genetic accommodation. In **Chapter 15**, Hadfield discusses the mathematical framework of quantitative genetic parental effect models to study the co-evolutionary dynamics of parental effects and offspring phenotypes. **Chapter 16** by Kölliker, Royle, and Smiseth outlines theory and experimental research exploring how the co-evolution of parents and offspring lead to co-adapted strategies individuals use as offspring and as parents. While quantitative genetic results are discussed across the previous chapters, **Chapter 17** by Champagne and Curley presents a comprehensive overview of the current knowledge of the molecular genetics and epigenetics of parental care.

Finally, in the summarizing **Chapter 18** by Royle, Smiseth, and Kölliker we offer a summary of the previous 17 chapters, draw conclusions and discuss promising avenues for future research.

Our main target audiences are new and established researchers and students in behaviour, ecology, genetics, development, and evolution; although we hope the book may also appeal to academics and students in other, related disciplines, such as psychology and sociology.

This project would not have been possible without the contributions of the authors. The editing of this book has been a highly enjoyable process as it has allowed us to interact with some of the most talented researchers working on parental care. We would like to thank all the authors for their hard work, efforts to meet deadlines, and willingness to buy into the project with such enthusiasm. We would also like to extend our gratitude to the many reviewers, some of whom read and commented on several chapters: Kate Arnold, Matt Bell, Jon Blount, Kate Buchanan, Tim Clutton-Brock, James Curley, Sasha Dall, Jeremy Field, Scott Forbes, Simon Griffith, Uri Grodzinski, Reinmar Hager, David Haig, Ian Hardy, Ben Hatchwell, Megan Head, Fabrice Helfenstein, Camilla Hinde, Andy Horn, Clarissa House, Rufus Johnstone, Charlotta Kvarnemo, Tim

Linksvayer, Clauco Machado, Joah Madden, Dario Maestripieri, Joel McGlothlin, John McNamara, Allen Moore, Geoff Parker, Tom Pike, Sarah Pryke, Eivin Røskraft, Andy Russell, Spencer Sealy, Ben Sheldon, Emilie Snell-Rood, Bård Stokke, Tamas Székely, Fritz Trillmich, Tobias Uller, Mary Jane West-Eberhard, and Jon Wright. Finally, we wish to thank the publishers at OUP, especially Helen Eaton and Ian Sherman, who provided invaluable help and advice during the whole process.

Nick Royle: On a professional level I would especially like to thank Ian Hartley and Geoff Parker, my supervisors and mentors during my first postdoc. I never realized research on conflicts could be so much fun, as well as being so educational. Thanks also to Jan Lindström, Neil Metcalfe, Craig Walling, Jason Wolf, Scott Forbes, Maggie Hall, Jon Blount, Josie Orledge, Tom Pike, Sasha Dall, Wiebke Schütt, Allen Moore, Megan Head, Paul Hopwood, Heinz Richner, Philipp Heeb, and Mathias Kölliker, amongst others, for making subsequent collaborations similarly intellectually stimulating and fun. On a personal level I need to thank my parents, John and Sheila, and my brother, Phil, for stimulating and encouraging my interest in parental care and family dynamics throughout my life. Last, but certainly not least, I thank my wife, Marieke, and my two boys, Lachlan and Lucas, for their love and support and for providing daily reminders of the joys of being a parent.

Per Smiseth: I wish to thank Svein-Håkon Lorentsen, Trond Amundsen, and Allen Moore, who acted as supervisors during various stages of my career and who introduced me to various aspects of parental care in organisms as different as grey seals, bluethroats, and burying beetles. I also wish to thank my many collaborators, whose expertise and insights have helped me develop my ideas and thinking about the evolution of parental care, including Andy Gardner, Loeske Kruuk, Mathias Kölliker, Allen Moore, Danny Rozen, Michelle Scott, and Jon Wright. I also wish to thank the members of the burying beetle group at The University of Edinburgh, Clare Andrews, Sarah Matthey, and Roni Mooney, and members of the Institute of Evolutionary Biology, The University of Edinburgh, who helped clear up many of my confusions during coffee; Jarrod Hadfield, Tom Little, and Alastair

Wilson. I also wish to thank the honours students attending the Evolution of Parental Care course at The University of Edinburgh for their contributions to developing my ideas on this subject through discussions and questions. Finally, I wish to thank my partner, Sarah, for a huge amount of patience and understanding during the 18 months of this project.

Mathias Kölliker: I would like to thank particularly Heinz Richner and Butch Brodie for their support as supervisors and mentors, and for introducing me to different perspectives in evolutionary thinking that continue to stimulate my research. I would also like to thank Sabrina Gaba, Ken Haynes, Philipp Heeb, Rufus Johnstone, Allen Moore, Ben Ridenhour, Alexandre Roulin, Nick Royle, Per

Smiseth, Jean-Claude Walser, and Jon Wright for the pleasant and rewarding collaborations. Thanks also to former and current members of the earwig lab at the University of Basel for their enthusiasm and work: especially Stefan Boos, Ralph Dobler, Flore Mas, Joël Meunier, Lilian Rölin, Dimitri Stucki, and Janine Wong. On a personal level, I am grateful to my parents Léonie and Eduard Bühlmann for their parental care and for motivating me early to pursue an academic pathway. My very special thanks are to my wife Geneviève and my children Joachim and Michelle—for their love and support, for travelling with me, for having made me parental, and for having so pleasantly and importantly enriched my social environment that forms our family.

Nick Royle, Per Smiseth, and Mathias Kölliker