Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.

Evolutionary interactions of brood parasites and their hosts

Recognition, communication and breeding biology

A thesis presented in partial fulfilment of the requirements for the degree of

Doctor of Philosophy
in
Ecology

at Massey University, Auckland,
New Zealand.

Michael Gareth Anderson

2009

Frontispiece

Photo by Tomáš Grim

Abstract

Obligate brood parasites lay their eggs in nests of other species, relying on these host parents to care for their offspring. This phenomenon has been a curiosity amongst researchers since its first description and has become a model study system for testing such ideas as coevolution and species recognition. This thesis examines a few of the many questions that arise from this breeding system. The New Zealand Grey Warbler (*Gerygone igata*) and its brood parasite, the Shining Cuckoo (*Chrysococcyx lucidus*) are used as the main study species, although research on the eviction behaviour of Common Cuckoos (*Cuculus canorus*) has also been conducted. First, the current state of knowledge and recent discoveries regarding nestling rejection abilities of hosts is reviewed in chapter one. Second, a comparative study of New Zealand passerine begging calls has been conducted to test for begging call similarity between a brood parasite and its host, as well as developing a new technique for detecting the mode of coevolution that may be occurring in the parasite – host relationship. Parent-offspring communication in Grey Warblers is also examined to test for both parental and nestlings Parents use both alarm calls to warn offspring of potential danger, and also parental feeding calls to elicit a begging response from nestlings. By contrast, nestlings are able to signal both age and short term levels of need to parents through the acoustic structure of the begging call. The evolutionary costs and benefits of egg eviction behaviour in the Common Cuckoo are also tested. An experimental approach showed that egg eviction had a growth cost, but this cost was temporary and restricted to during and immediately after the egg eviction phase. A pattern of compensatory growth was observed after the eviction period, so that during the later nestling stages there was no difference in mass,

and no difference in fledging age. Finally, variation in the Grey Warbler breeding biology and Shining Cuckoo parasitism rates are examined through both time and across latitudes. This research has shown a counterintuitive pattern of breeding phenology across latitudes. These patterns have implications for Shining Cuckoos both in terms of timing of available nests and host selection.

Keywords: Begging call, breeding phenology, brood parasitism, coevolution, Common Cuckoo, eviction, Grey Warbler, parent-offspring communication, Shining Cuckoo.

Preface

This study focuses on the evolution and maintenance of key traits that are involved in brood parasitism. Most of the research was conducted within New Zealand on the Grey Warbler (*Gerygone igata*) and its brood parasite, the Shining Cuckoo (*Chrysococcyx lucidus*), although one of the chapters uses the Common Cuckoo (*Cuculus canorus*) and its host the Great Reed Warbler (*Acrocephalus arundinaceus*). Although brood parasitism is the common theme of this thesis, each chapter (chapters 1 – 6) has been modified from manuscripts that have been written as scientific papers, and can therefore be viewed as independent studies. Due to the thesis being in this format, some repetition amongst chapters inevitably occurs. References, acknowledgements and appendices are therefore at the end of each chapter. Supervisors Mark Hauber and Dianne Brunton are co-authors of most manuscripts, as stated at the start of each chapter, and have been important with assistance in experimental design, writing the thesis and advice on statistical analysis procedures. Input from other co-authors is stated specifically below. Chapter one has previously been published as a research focus paper within the journal *Trends in Ecology and Evolution*, of which Mark Hauber is a co-author. This introduces some of the key ideas involved with recognition of brood parasite offspring by host species. Chapter two is in press with the *Biological Journal of the Linnean Society*, and uses comparative and bioinformatic procedures as a new technique of detecting co-evolution within brood parasites. Assistance with the bioinformatic analyses was provided by Howard Ross. Chapter three has been submitted to the journal *Animal Behaviour* and uses an experimental approach to investigate the parent-offspring communication used by the Grey Warbler. Chapter four is research that has been

conducted in Hungary on the Common Cuckoo testing the cost of egg eviction behaviour to cuckoo nestlings' growth rates. For this research, Csaba Moskát and Miklós Bán assisted with fieldwork in Hungary, Tomáš Grim assisted with data analysis and Phillip Cassey provided funding. This research has been submitted to the journal *American Naturalist*. Chapter five investigates the honest information content of begging calls of the Grey Warbler and is being submitted to the journal *Ethology*. Chapter six uses four different data sets on the breeding biology of the Grey Warbler to investigate the changes in breeding phenology with latitude and through time and the ways that this can affect the Shining Cuckoo. Brian Gill and Jim Briskie are both co-authors on this research, as they have provided data on Grey Warbler breeding biology from Kaikoura.

Acknowledgements

When, I completed my Masters thesis, I started off the acknowledgements with a few statistics. Once again, this feels appropriate. At that time, my masters thesis had taken up 822 days, or 8.7% of my life. By contrast, my PhD thesis has taken up (approximately) 1620 days, or 15.04% of my life thus far. Obviously, anyone that has experience such an undertaking knows that it is not possible to spend so much time trying to complete a task, without the help of many people. These people are mentioned below, all of whom I am greatly indebted to for their assistance and support during this time.

First and foremost, my supervisors deserve the biggest thanks, as this work would not have been possible without them. Dianne Brunton, who took me under her wing when I did my masters thesis with her as well, has been supportive, inspirational and a huge help throughout this research. She has been everything from a lab matriarch, counsellor and statistical guru, while also giving me the opportunity to visit extraordinary places and do incredible things. Mark Hauber has been incredibly supportive and involved in this project as well as an amazing supervisor, despite being based at another university. He has done everything from answering emails after midnight, texting advice from Israel and sending me to do research in Hungary. You have both taught me a lot academically and personally as well being fantastic role models. I am greatly indebted to you both.

As with most ecological studies, there have been many aspects of this research that have been impossible to complete without some much appreciated help from others. The following people have helped in various ways, such as mist netting, nest finding and general fieldwork tasks. So a big thanks to Gavin Anderson, Alana Alexander, Shauna Baillie, Marleen Baling, Manuela Barry, Dianne Brunton, Taneal Cope, Mark Delany, Barbara Evans, Brian Gill, Tomas Grim, Charlotte Hardy, Malcolm Harrison, Mark Hauber, Weihong Ji, Mark Low, Luis Ortiz Catedral, Jo Peace, Mark Seabrook-Davidson, John Steemson, Chris Wedding and Birgit Ziesemann. A special thanks is needed for my three field assistants Charlotte Hardy, Alana Alexander and Mark Delaney, all of whom spent many hours in the field looking for nests in what was frequently difficult conditions.

The second chapter of this thesis investigates the begging call similarity of the Grey Warbler and Shining Cuckoo through the use of a comparative framework. In order to do this kind of research, I required begging calls of all New Zealand passerines, which was certainly not an easy task. Many dedicated volunteers, researchers and conservation staff assisted with locating nests of various species from throughout the country. So I am very grateful for the assistance of Alana Alexander, Gavin Anderson, Shauna Baillie, Marleen Baling, Jake Bapty, Manuela Barry, James Briskie, Emily Brugge, Taneal Cope, Mark Delany, Graeme Elliot, Barbara Evans, Morag Fordham, Brian Gill, Tomas Grim, Charlotte Hardy, Malcolm Harrison, Weihong Ji, Stacey Hill, Todd Landers, Barry Lawrence, Nora Leuschner, Tim Lovegrove, Eric Marsden, Luis Ortiz Catedral, Kevin Parker, Jo Peace, Marion Rhodes, Peter Samas, Hazel Speed, Rose Thorogood, Megan Willans (and field assistants) and Sarah Withers.

During the course of this thesis, I was fortunate enough to visit Hungary and do work on the common cuckoo. This trip was facilitated by Mark Hauber and was made possible by the generous assistance of Csaba Moskát who allowed me to work within his study system. Miklós Bán was also very helpful with this research, and taught me a lot about Hungarian culture and the joy of jazz. Rim Lucassen, Lotte van Boheemen and Nicoletta Geltsch were helpful with fieldwork.

Any biology thesis requires a lot of statistical analysis, which is often one of the biggest challenges, so a huge thank you to Marti-Jane Anderson, Allen Rodrigo, Howard Ross, Dianne Brunton, and Mark Hauber for help and discussions.

I have also been lucky enough to have colleagues from several disciplines and countries who have been kind enough to spare their precious time by giving advice, feedback and discussions on research. They are each mentioned within the acknowledgement of specific chapters for clarity of where they have given input. A big debt of gratitude is owed to Marti-Jane Anderson, Dianne Brunton, Brian Gill, Phillip Cassey, Nick Davies, Tomas Grim, Uri Grodzinski, Greg Holwell, Rebecca Kilner, Naomi Langmore, Arnon Lotem, Csaba Moskát, Luis Ortiz Catedral, Kevin Parker, Jo Peace, Allen Rodrigo, Rebecca Safran, Justin Schuetz, Rose Thorogood, David Winkler.

Fieldwork for this research was primarily conducted at Tawharanui Regional Park, with permission of Auckland Regional Council (ARC) and the Department of Conservation. ARC also allowed me to stay at Tawharanui while doing research. The rangers at Tawharanui, particularly Maurice Puckett, Colin Ward and Malcolm Harrison always made it an awesome place to do research.

This research was made possible by funding from a Massey University Doctoral Scholarship, Tertiary Education Commission's Top Achiever Doctoral Scholarship (part of the Bright Futures Scheme) and Massey University. Dianne Brunton also provided funding from a New Zealand Marsden Fund Grant (jointly with Howard Ross) and Massey University. Mark Hauber provided funding from the School of Biological Sciences (University of Auckland), National Geographic Society the New Zealand Marsden Fund Grants and a Human Frontiers Science Program Grant (jointly with Phillip Cassey and Tomas Grim).

The Ecology and Conservation Group in Massey University has always been an interesting and fun group of people to work with. Slowly but steadily we have expanded over the years. A huge thanks for all the laughs and good times are needed for the entire group who are or have been part of this group (sorry if I forget anyone): Shauna Baillie, Marleen Baling, Ben Barr, Rosemary Barraclough, Manuela Barry, Nicolas de la Brosse Dianne Brunton, Taneal Cope, Mark Delany, Barbara Evans, Anna Gsell, David Gudex-Cross, Marta Guemes, Jacqueline Guerts, Jurgen Kolb, Brigit Kreigenhofer, Weihong Ji, Mark Low, Emmanuelle Martinez-Smagghe, Luis Ortiz Catedral, Kevin Parker, Jo Peace, Vincenzo Petrella, David Raubenheimer, Jennifer Ricket, Mark Seabrook-Davidson, Uri Shanas, Idan Shapira, Jodi Smith, Karen Stockin, Monique Van Rensberg, Dylan Van Winkel, Kirsty Verrill, Andy Warneford, Chris Wedding, Sarah Wells, Sarah Whitwell, Cheeho Wong and Birgit Ziesemann.

Last but not least, my family and friends deserve a huge thank you for putting up with my nonsense and gallivanting about doing birdy things. My high school friends, Steve Duval, Steve Ogilvie, Scott Wallace, Bruce Birks, Regan O'Malley and Kit Mollier

have helped to keep me sane (mostly) with much mirth and hilarity. Josh Guilbert and Luis Ortiz Catedral have been incredibly supportive and have helped my through many obstacles and hard times. What more can one ask for? A huge thanks to my lovely Julia, who has brought me a new sense of purpose, and has been incredibly supportive. Finally, a big thanks for my family, my sister, Cushla and my parents, Gavin and Cathy, who have been with me through my thesis experience who have been incredibly supportive throughout my (not so short) time at university.

Table of contents

List of Figures

List of Tables