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.

The Behavioural Ecology of Forced Copulation in the New Zealand Stitchbird (Hihi)

A thesis presented

in

partial fulfilment

of

the requirements for the degree

of

Doctor of Philosophy

in

Zoology

at

Massey University

Palmerston North – New Zealand

Matthew Richard Low 2004

"The breed is guileless and innocent of wile in a peculiar degree; the instinct of deception even in a good cause seems not to enter into their scheme of things...They are careless, too, of stranger birds who may happen to have wandered near the family abode...In October and early November, whilst still engaged in the search for nests, it was disheartening work, after believing we had tracked a male to his lair, to find two males engaged in parley – long, low, chattering, very friendly palavers. It seemed then so improbable that one male would tolerate the presence of another close to his breeding quarters...I have reason to believe, however, that although thus friendly, care is taken not to intrude on one another's domains."

H. Guthrie-Smith (1925) describing the behaviour of the stitchbird in his book *Bird Life on Island and Shore*



The stitchbird female (left) showing her distinctive white wing-bar and the male (right) displaying the characteristic 'cocked' tail position

'Stitchbird' is this species' pakeha name, thus it is also known by the following Maori names:

hihi*, tihi, ihi, tihe, kotihe, tiora, tiheora, tioro, kotihe-wera (male only), hihi-paka (male only), hihi-matakiore (female only), mata-kiore (female only), tihe-kiore (female only)

* This is the most commonly used Maori name today

Abstract

Although many vertebrate species form stable breeding partnerships, extra-pair copulations are often common in these species, potentially leading to intersexual conflict. Forced copulation or rape is an extreme manifestation of this conflict, occurring when a female is forced to copulate with a male despite her resistance. In this thesis, I report research addressing several questions about forced copulation in stitchbirds (Notiomystis *cincta*), a species with frequent forced copulation attempts. I conducted this research over three years on Tiritiri Matangi Island, off New Zealand's northeast coast. Forced copulation was used opportunistically by all males in the population, and male age and morphometrics did not predict forced copulation success or the likelihood of female consent. A newly proposed hypothesis to explain the function of forced copulation in birds, the 'creation of a dangerous environment' hypothesis, was not supported empirically and in its current form appears to be theoretically unworkable. Male stitchbirds seem able to bypass female choice through adopting a face-to-face forced copulation position. This is effective because their cloacae become engorged with sperm, and act similarly to a penile erection to allow cloacal contact when copulating in this species' unique face-to-face position. Forced copulation attempts occurred mainly during females' fertile periods immediately before egg laying, and this was strongly correlated with an increase in female weight, suggesting that males use the weight of the female to judge her fertility status. Resident males also adjusted their behaviour at this time, switching from a territorial site-specific defence to a mate-guarding tactic localising on the position of the female. While costs associated with forced copulation have been previously documented for females, I show that the resident male also suffers a cost as measured by a 5% loss of bodyweight as a result of extra-pair male territorial intrusions on top of a 2.5% weight loss as a result of mate guarding. The resident male's uncertainty of paternity resulting from extra-pair forced copulation had little effect on provisioning by paired males. The key factors affecting male provisioning were brood size (males did not provision one-chick broods) and whether the male was monogamous or polygynous (males only fed the brood of their primary female). Cross-species comparisons can be useful in understanding the function of forced copulation if carefully undertaken, with previous criticism of this approach based on numerous misunderstandings.

Acknowledgements



So many people to thank and so many self-indulgent in-jokes to reminisce about.

Before I thank the people who helped directly with my research, I'd like to thank a few people who helped me get to a point in my life when I could consider tackling something like a PhD and to whom I owe much gratitude. To my mum and dad who have always believed in me and always supported my decisions. They taught me to think critically and not accept anything at face value (even if they quickly learned to regret teaching me that!). They bought me my first pair of binoculars and put up with my incessant raving about birds for years (then they finally broke down and starting birding themselves). Thanks to dad for a comment many years ago that seeded the idea for me to pursue postgraduate studies, and to mum for dealing with all that needed dealing with back in Australia during the past few years. Thanks also to my brothers, Stu and Date, who have been there when needed, to tell me to "pull my head in" when it needs pulling in, and are able to share with me the latest kiwi joke doing the rounds in Australia; and my nieces and nephew, Madeline, Stephanie and Nathan for keeping me young at heart.

To my friends from Australia, Stirling Hinchliffe, Rodger Allen, Graeme Currie, Craig Ruaux, Nimal Fernando and Patrick Burns who for years engaged with me in interesting debates about pretty much everything and thus helped hone my skills in developing a logical argument (so if I haven't convinced you of something in this thesis it is all their fault). They also shaped my perverse sense of humour and taught me how to cheat at cards, two things which allowed me to cope with many extreme situations over the past few years. A big thanks also to Kate McInnes who was there at the beginning and supported my decision to hide from the responsibilities of adult life for just a few more years (but it has finally caught up with me).

Life on the island was simply wonderful and this was more to do with the people that I spent time with out there, rather than the fact that it was warm and had a nice beach (although that helped). Thanks Barbara and Ray for always being there to help out, to organise trips on and off, to let me borrow vehicles when I needed them (or was just too lazy to carry my gear across the island), to bring in my washing, for lemons from your tree on pancake mornings and for being my surrogate parents for the past few years. Thanks also to Ian Price and Ian McLeod who were always available to help out with logistical problems around the island, and would grace us researchers with their fine company for drinks and nibbles in the evening.

The data I collected would have been rather patchy if it wasn't for the help of my long-suffering field assistants, Troy (Poopsoid) Makan and Becky (Randy's obsession) Lewis. They rarely grumbled about being tossed out of bed (as long as it was after midday) and being forced to work in all the "evil" bush patches (*i.e.* bush 21) on the island. I'd also like to thank the other people with whom I shared the "research room" over the years, Jason Taylor, Rosalie Stamp, Ian (Mr Poopsie) Fraser, Sandra Jack, Melinda Habgood, Rose Thorogood, Shaun Coutts, Su Sinclair, Angelique Hoff man and Askia Wittern. It was always fun (especially Ian's narcolepsy and Melinda's propensity to whack her head on the top bunk) and I have forever been converted to the medicinal qualities of a nice Gin & Tonic on a hot afternoon. Thanks also to Barbie TM, a doll with whom we all became obsessed during one Christmas period. This lead not only to us having a Barbie TM advent calendar encouraging us with vignettes of inspiration each day (and some pretty dodgy chocolate), but also to the renaming of a patch of bush on Tiri – "Barbie TM Bush" which was followed up soon after with "Ken TM Bush" (I can guarantee that any jokes combining the words "Barbie" TM and "bush" were well aired, but unfortunately the Barbie TM pink nest box didn't get beyond the drawing board).

I was also fortunate to have the help of numerous volunteers over the years, without whose help many things could not have been accomplished. Thanks to Clare and Colin (the original volunteers), Rainer, Petra, Sophie and Georgie. Deb Anthony, Karen Robertson-Hynes, Isabel Castro, Petrina Duncan, Sally Jones, Su Sinclair, Clare Miller, Kirsty Chalmers all took time off work or out of their spare time to spend weeks taking orders from me (and let's face it, who wouldn't?). Little did they know that I'd have them perving at the nether regions of poor defenceless birds for hours on end while I said things like "Check out the willy on this one!" Thanks also to a number of the supporters who helped me in the field or with other more general things; Morag, Simon, Val, Elizabeth, Sally, Yvonne, Mike, Anne and Carl; it was always nice to have you around and your assistance was always appreciated. Thanks also to Department of Conservation staff; Rosalie Stamp, Shaarina Taylor, Shaun Dunning, Richard Griffiths, Rory Renwick and the staff of the Mt Bruce National Wildlife Centre; especially Rose Collen, Bryan Welch and Glen Holland.

The logistics of my life on the island would have been made significantly more difficult without the generous friendship of Thomas (Helmig) Christensen and Rachel Curtis. For over 3 years they put up with me arriving on their doorstep in Auckland every couple of weeks unshaven, with a bag of dirty laundry demanding to watch TV, eat chips and make ice-cream spiders (and listen to lilting Danish ballads from Helmig and Nags Underbogen – music so bad that it's great!). They never grumbled about my free-loading (at least not within earshot) and were good humoured when I won at Ludo (Hoongerdoonger up Mt Roehold – it's Danish for "I win" or something like that). Thanks also to their daughter, Maya, who was born during my first season on the island and their son, Jonas, who was born during my last season (honestly, nothing to do with me!). The kids treat me as a member of the family and make it feel like I'm coming home when I arrive on their doorstep.

The ecology group at Massey University has been an enjoyable place to do science. A big thanks to my supervisors Ed Minot, Isabel Castro, Doug Armstrong and Brian Springett who have always been there with advice, ideas and comments and I have always appreciated the time you have spent keeping me on track. I have been lucky to enjoy the friendship of many people in or associated with the department, and I thank them for keeping me sane during the 11 month winters that are Palmerston North. Thanks to Mike Joy, Allison Hewitt, Viv Nicholls, Tony McGlynn, Wayne Linklater, Elissa Cameron, Halema Flannagan, Suzanne Bassett, Grant Blackwell, Russell and Fiona Death, Alastair Robertson, Masha Minor, Maurice Alley, Jay McCartney, Cath Morrison, Becky Lewis, Troy Makan, Carol Nicholson, Robin Fordham, Angus Fordham and Scott Carver. Thanks also to Barbara Just and Erica Reid for always having time to help me sort out administrative things and for making it almost fun in dealing with financial matters associated with the project. To Ian and Heather (the Palmerston North Low family connection!), thanks for the fab food and company and for making me feel at home.

Thanks to Jennie Hay for making the DNA buffer that I used to collect the hundreds of blood samples that are sitting in a fridge waiting for money to be thrown at them to unlock their mysteries. Thanks also to Amy Roeder at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany who offered to throw some of their money at my blood samples (unfortunately the money ran out). And to fellow forced copulation researchers (yes there is more than one of us): Clint Kelly, Sharon Birks and Ellen Davis for answering my questions and sending me reprints of articles. Thanks especially to Clint for his insightful perspectives on the importance of meat, not only in haute cuisine but also haute couture (the meat dress…what sublime creation!). Thanks also to Staffan Roos for sending me articles when I asked for them and for admitting to being as much of a titelbög as I am. And just for Leigh and Brent, the 'challenge word' made it into the thesis!

This project would not have been possible without the generous funding contributions of the New Zealand Lotteries Board (Environment and Heritage), the Supporters of Tiritiri Matangi Inc. and the Massey University Institute of Natural Resources (especially Russ Tillman for granting funding to attend the Australasian Ornithological Conference 2003).

Of course there wouldn't be a study without the birds. They did what they did in a spectacular fashion and allowed me to follow behind them while taking notes and describing their sex lives. Many of these birds I started to see as friends (this is what happens when you are stuck on an island for months at a time) and would enjoy coming back the next season to see if how they were going. They would come and say "hi" at the beginning of each observation session and didn't grumble too much when I had to catch and handle them for measurements (except BM/RY who was always a real bastard). I will miss spending my summers watching these amazing little birds and their dirty little ways.

I would like to express my deep gratitude to Åsa Berggren who has helped and had to put up with more than anyone else during the past few years. Not only has she assisted in the field, joined with me in "bird rescue " missions, patiently listened to my latest ideas and then helped me communicate these to other people, but she has provided support and encouragement when I needed it most. Thank you. It would have been much harder without you by my side.

One final thanks goes to my examination committee; Jim Briskie, Robin Fordham and Andrew Cockburn. I appreciated the time you put in to read and critically review the thesis. I especially appreciated you awarding me my doctorate and the end of it all!

If you are the person who I failed to mention because I only remembered you 5 minutes after I sent this to the printers, I am sorry, but thanks for whatever it was you did – it was great and I couldn't have done it without you.

.

Table of Contents

page

Title Page		i
Abstract		v
Acknowledgements		vii
Introduction		xiii
Chapter One	Female resistance and male force: context and patterns of copulation in the New Zealand stitchbird	1
Chapter Two	Intimidate or inseminate? Modelling the CODE hypothesis	29
Chapter Three	Cloacal erection in the stitchbird: functional convergence with mammalian genitalia promotes stiff competition	45
Chapter Four	Female weight predicts the timing of forced copulation attempts in stitchbirds	57
Chapter Five	Behavioural tactics and energetic costs of mate guarding in a species with high levels of forced extra- pair copulation	79
Chapter Six	A hierarchical model predicts male provisioning of offspring in the stitchbird	103
Discussion		127
Appendix One	Can non-human animals rape?	137
Appendix Two	<i>Ten misunderstandings of forced copulation / rape in non-human animals</i>	155
Thesis Statements		177

Note on text:

Each chapter is set out in the style of the journal to which it has been submitted. Consequently there is some repetition, particularly in the Methods sections and there are minor stylistic differences between chapters. For the two submitted chapters that include other authors (Chapters 3 and 6), while my input was the greatest, I received assistance from my co-authors. I designed the research, undertook or coordinated the field work, analysed the data and wrote the manuscripts.