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.

# Behavioural Ecology of New Zealand Invasive Rodents (*Rattus norvegicus* and *Mus musculus*): Implications for Rodent Control

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

Doctor of Philosophy in Ecology

at Massey University, Auckland, New Zealand

Idan Shapira

2013

#### FRONTISPIECE



- Walter: And let's also not forget... let's not forget, Dude... that keeping wildlife, an amphibious rodent, for uh, domestic, you know, within the city... that isn't legal either.
- Dude: What're you, a fucking park ranger now?

(Ethan and Joel Coen, "The Big Lebowski")

#### ABSTRACT

Biological invasions are natural phenomena that have occurred throughout the natural history of earth. The highly negative context of the term biological invasion is associated with the fact that many modern invasive processes are anthropogenically driven. Indeed, human affiliated invasions are among the primary drivers of the current biodiversity crises. Murid rodents (Rodentia: Muridea) of the genus *Rattus* and *Mus* have become among the worst vertebrate invasive species and apart from man are the most widespread mammals on earth. Invasive rodents have severe and negative effects on human health, agricultural systems, and natural environments. The practice of rodent control is extensive and substantial attempts are made to decrease rodents' severe impacts on the environment. However, although these attempts are largely successful, there are still issues in the control of invasive rodents and new methodologies, whether at a macro or micro scale are actively pursued.

Behavioural conservation attempts to understand and improve conservation processes and practices through the study of animal behaviour. Indeed, it is becoming increasingly apparent that the behaviour of animals can be a strong tool for conservation. The control of invasive species has the goal of reducing predatory or competition pressure on species of conservation concern and advocates for behavioural conservation acknowledge the importance of behavioural studies of invasive species that can directly benefit or inform control measures. In this thesis, I explore several aspects of behavioural ecology in the Norway rat *R. norvegicus* and the house mouse, *M. musculus*, with the overarching aim of informing and improving rodent control.

I conducted a series of laboratory and field experiments focused on rodent behaviour and pest control. 1) I tested whether laboratory rats can act as effective lures for wild Norway rats and hence overcome the problem of rats avoiding food baits. This field experiment was based on the highly social behaviour exhibited by this species. I found that live traps containing live lures were significantly more effective than those with food baits at capturing wild Norway rats. In a second series of tests, I found that live lures were more efficient than food baits at attracting rats to kill traps. A study of radio-collared rats released onto a rat-free island produced inconclusive but promising results on the potential of live lures to be used to control incursions. I suggest that the use of laboratory rats as lures should be considered as an additional tool for use in future pest control management plans for invasive Norway rats. 2) I used Y-maze laboratory experiments to examine the attractiveness of urine from mice fed high and low protein diets to male and female wild mice, whether the protein content of the diet of mice affected their response and the strength of attraction of wild mice towards wild and laboratory live lure conspecifics of the opposite sex. I found that mice preferred to spend more time close to urine from donors that had eaten a high protein diet, that mouse strain did not affected conspecific attraction and that males were more active than females toward the urine of the opposite sex. These results may have implications for improving mouse capture and control. 3) I assessed the impacts of mammalian odours (specific direct cues of predation or competition) and illumination intensity (a general indirect cue of predation) on the foraging of free-ranging mice that are naïve to mammalian predators, using feeding trials in the field. Here I found that phases of the moon, but not odour, had significant effects on mouse foraging behaviour. I suggest that repeating the study over multiple lunar cycles is required to confirm this influence and, if confirmed, recommend coordinating management efforts according to the phases of the moon to improve mouse bait take and reduce bait wastage. 4) I tested for the responces of rat-naïve mice to scent cues from rats, which are competitors and potential predators in laboratory experiments, in a Y-maze apparatus. Mice behaviours revealed unexpected differences in male and female responces to rat scent. Male mice showed preference to control over rat scented food trays, while females were indiference in their preferation or even prefered rat scented food trays over control ones. These sex-based differences can suggest that males and females might be under different evolutionary pressures in regard to novel scents. 5) I looked at macronutrient selection in wild caught mice, under controlled laboratory conditions. I found that mice consumed more of diets with a high carbohydrate/protein ratio, but were highly generalist and opportunistic feeders, in general prioritising energy over macronutrients. These results demonstrate that the pattern of macronutrient selection is sensitive to ecological circumstances, and associates an opportunistic strategy with successful invasion by a small mammal in a temperate environment.

The understanding and improvement of conservation practices directly through the study of animal behavioural processes is an emerging and rapidly growing science, but relatively little attention is given to the benefits that we can draw from incorporating and understanding of invasive species behaviour into their control. To maintain an effective and continuous control of invasive species, managers need comprehensive knowledge of the behaviour of the species they target. This can be achieved only through targeted behavioural research of invasive species that is directed at improving pest control. In this thesis I have attempted to do just this.

#### ACKNOWLEDGMENTS

"One of the symptoms of an approaching nervous breakdown is the belief that one's work is terribly important".

(Bertrand Russell)

I had my semi nervous breakdown at the end of the first year of my PhD. Luckily, my children Omer and Alma, who were born during this PhD have knocked me back to my senses. This thesis is dedicated to them with love.

First and foremost I would like to thank my supervisors. To Dianne Brunton, the principle supervisor, who told me to come over from Israel after one email correspondence, and always made sure I had everything I needed. Hopefully she doesn't regret placing my desk just next to her office, an act that resulted in countless knocks upon her door... Nonetheless, all my visits were met with a smile! To the one and only Uri Shanas, who after supervising my MSc in Israel, (understandably) had to send me to the most far away place possible, but still provided professional and emotional support. And to David Raubenheimer, who was last to jump aboard but nevertheless delivered significant scientific perspectives and new research directions. Not to mention the mutual respect we share for the Dude... I have learned much from you all!

During the four years of this immense project, many people were involved in my research and in my life. Their contribution varies from crucial help to a friendly word. Here I wish to thank all these people, named in a random order. Shauna Billie, Michael Anderson, Mark Delaney, Kevin Parker, Marleen Barling, Jenny Laycock, Achyut Aryal, Alice Tait, Elizabeth Laman-Trip, Andy Warneford, Debbie Chesterfield, Brigitte Kreigenhofer, Anne Sophie Boyer, Birgit Ziesemann, Cheeho Wong, Chris Wedding, David Gudex-Cross, Dylan van Winkel, Emmanuelle Martinez, Gabriel Machovsky-Capusca, Jennifer Ricket, James Dale and Laura Redfern, Jo Peace, Jurgen Kolb, Luis Ortiz Cathedral, Karen Stockin, Manuella barry, Ben Barr, Mark Seabrook-Davidson, Anna Gsell, Monique Van Rensberg, Sarah Dwyer, Sarah Wells, Ravit and Reuben Hass, Natalie and Ra'anan Neuman, Shanee and Moses Sheleg, Gavin Martin, Anna Drijver and Terry Chee, Joshua Thoresen, Craig Knapp, Rebecca Greenop, Rodney Bowden, Christophe Amiot, James Russell, Ian Fraser, Tineke Joustra, Samantha Kudwe, Adrian Peterson, Megan Young, Miriam Ludbrook, Kelsey Nichols, Frederica Jordan, John Innes, Susan Alberts, Keith Hawks, John Cope, Jim & Eddie (Massey Albany facilities), Pablo Stevenson, Tony Lawson, Cheridan Mathers, Fiona McKenzie, Virginia Moreno, John Steenman.

Amorita Petzer from the University of Auckland kindly provided most of the laboratory animals, always willingly and with a smile.

The following organizations have been extremely helpful and their cooperation and support is highly appreciated. Auckland Council provided permits to work on council land as well as help with field assistance and funds. I am especially grateful to Matt Maitland, Steve Burgess, Bruce Harvey, Tim Lovegrove and Maurice Puckett. The Department of Conservation (DOC) provided permits to work in their reserves, technical support and aid in running experiments. Special thanks should go to Phil Brown, Fin Buchanan and Pie (the super rat dog) for their grate support - you guys rock! I also thank all the DOC Auckland area office Skippers, Tawharanui Open Sanctuary Society (TOSSI) and Shakespear Open Sanctuary Society (SOSSI), Forest and Bird, especially John Staniland, Honda Marine for contributing a research boat, and of course Massey University for supporting this project.

I thank my good friends and broader family in Israel for moral support: Avia and Amos Nevo, Ynon, Nitzan and Alon Nevo, Tamar and Elisha Shapira, Haim Dovrovni, Neta and Einat Shapira, Orna and Gili Salomon, Greg Golomb, Nurit and Gilad Ben-Ziv, Shani and Tomer Lavi, Tsur Kramer, Batya Reznick, Noam Evron, Gal and Shacham Mittler, Inbar and Yali Dagan, Elya and Alon Lotan, Ohad Fleiderman, Gadi Katzir, Ran Dreilich, Ayelet Ben-Nahum, Amir (Chatuka) Arnon, and Idit Brill.

I thank with love my close family, my brothers and their families, Liron, Sigalit and Carmel, Gal and Matan Shapira, Oran Shapira, Delphine Vann and Scott Roe Vann. Special thanks should go to my parents Shoshana and Gideon Shapira - I couldn't have accomplished this PhD without your support!

Thanks should also go to my partner's close family, bobe Berta Waitzman, brothers David Lischinky and Doron and Lital Lischinsky and a huge muchas gracias to my partner's parents Sofia and Julio Lischinsky who have greatly supported our family in New Zealand. I wish to thank my partner Dana Lischinsky, who travelled with me all the way to the far end of the world, and supported me in more than one way throughout many good times as well as numerous hard moments. I love you very much!

Special thanks should go to Ed Minot, Kay Clapperton and Peter Banks for reviewing the thesis and for making usefull comments that have improved the outcome of the thesis greatly.

I would like to further dedicate this PhD to my grandmother Zehava Teper (passed away 2013), my aunt Chava Dovrovni (passed away 2011) and my friend Einav Brill (passed away 2011). My they rest in peace.

# TABLE OF CONTENTS

Frontispiece		II
Abstract		III
Acknowledgm	ents	VI
Table of Cont	ents	X
List of Tables		XV
List of Figure	8	XVI
Apendices		XVIII
Chapter 1: In	troduction	1
1.1	. Biological invasions	1
1.2	. Invasive rodents	2
1.3	. Invasive rodents in New Zealand	4
1.4	. Ecology of the Norway rat <i>Rattus norvegicus</i> with emphases to	
	New Zealand	5
1.5	. Ecology of the house mouse Mus musculus with emphases to	
	New Zealand	7
1.6	. Rodent control for conservation	8
1.7	Animal behaviour and the control of invasive species	10
1.8	. Objectives	12
1.9	References	17
Chapter 2: Laboratory rats as trap lures for invasive Norway rats: field trial		32
an	l recommendations	
2.1	Abstract	32

	2.2.	Introduction	32
	2.3.	Methods	35
	2.3.1.	Data Analysis	38
	2.4.	Results	39
	2.5.	Discussion	41
	2.6.	Acknowledgments	45
	2.7.	References	46
Chapter 3:	Labo	ratory rats as conspecific biocontrol agents for invasive	
	Norw	ay rats <i>Rattus norvegicus</i>	52
	3.1.	Abstract	52
	3.2.	Introduction	52
	3.3.	Methods	56
	3.3.1.	Experiment 1(E1): Conspecific attraction at low rat population	
		densities	57
	3.3.2.	Experiment 2 (E2): Conspecific attraction in areas of high food	
		abundance	59
	3.3.3.	Experiment 3 (E3): Conspecific Attraction in island rat	
		incursions	61
	3.3.4.	Data analysis	64
	3.4.	Results	65
	3.5.	Discussion	72
	3.6.	Acknowledgments	76
	3.7.	References	76

XI

Chapter 4: Conspecific attraction in wild house mice: effects of strain, sex	
and diet	86
4.1. Abstract	86
4.2. Introduction	87
4.3. Methods	90
4.3.1. Effect of mouse diet on conspecific attraction to scent	91
4.3.2. Data analysis	94
4.3.3. Effect of mouse strain on conspecific attraction to live lures	94
4.3.4. Data analysis	96
4.4. Results	97
4.5. Discussion	100
4.6. Acknowledgments	103
4.7. References	104
Chapter 5: Responses to direct versus indirect cues of predation and	
competition in naïve invasive mice: implications for management	113
5.1. Abstract	113
5.2. Introduction	114
5.3. Methods	117
5.3.1. Data analysis	120
5.4. Results	122
5.5. Discussion	127
5.6. Acknowledgments	131
5.7. References	131

Chapter 6: First en	acounters of wild house mice with novel rat scent: risk-	
taking f	females and cautious males?	138
6.1. A	bstract	138
6.2. In	ntroduction	139
6.3. M	fethods	142
6.3.1. D	Data analysis	145
6.4. R	esults	147
6.5. D	Discussion	152
6.6. A	cknowledgments	156
6.7. R	eferences	156
Chapter 7: Prioriti	izing energy over macronutrient balance in wild <i>Mus</i>	
musculi	us: implications for mouse domestication and invasiveness	162
7.1. A	bstract	162
7.2. In	ntroduction	163
7.3. M	Iethods	165
7.3.1. D	Data analysis	168
7.4. R	esults	170
7.5. D	Discussion	176
7.6. A	cknowledgments	181
7.7. R	eferences	181
Chapter 8: discussi	ion	186
8.1. B	ehavioural conservation	186
8.2. C	onspecific attraction using live lures	189

	8.2.1.	Issues concerning Animal Ethics	191
	8.3.	Predatory and competitive cues and vigilance behaviour	194
	8.4.	Macronutrient selection and invasiveness	196
	8.5.	Epilogue	197
	8.6.	References	198
Appendices		205	
	Apper	ndix 1	205
	Apper	ndix 2	206
	Apper	ndix 3	207
	Apper	ndix 4	208

# LIST OF TABLES

Table 1.5.1. Reference list.	12
Table 2.4.1. Number of unique Norway rats caught.	40
Table 3.3.1. Type of trapping devices and effort.	61
Table 3.3.2 Trapping frequencies of R. norvegicus.	65
Table 3.4.1. First and last animals to be caught and total captures at each site.	67
Table 3.4.2. Calculations of adjusted standardized residuals.	67
Table 3.4.3. Capture frequencies of R. norvegicus as a function of the gender.	67
Table 7.3.1. Nutritional profile of purified isocaloric foods.	168
Table 7.3.2. Experimental timeline.	

# LIST OF FIGURES

Figure 2.3.1. Live lure enclosure, and map of the study site and trap locations.	38
Figure 2.4.1. Trap efficacy for Norway rats.	41
Figure 3.3.1. Three trapping devices used during the experiments.	63
Figure 3.3.2. Arrangement of traps lay around a rat rest site.	64
Figure 3.4.1. Wild invasive Norway rats caught at four mainland sites.	68
Figure 3.4.2. Norway rats trapped with live lures and food-baited controls.	69
Figure 3.4.3. Map of Browns Island showing two release events.	69
Figure 4.3.1. Experimental apparatus.	96
Figure 4.4.1. Activity near hp and lp urine samples.	99
Figure 4.4.2. Cumulative time spent by wild mice near the stimulus cages.	99
Figure 4.4.3. Cumulative visits made by wild mice to the stimulus cages.	100
Figure 5.4.1. Effect of odour treatments on mouse selectivity.	124
Figure 5.4.2. Effect of moon phase on mouse giving-up densities.	125
Figure 5.4.3. Effects of scent and moon phase on the proportions of foraged trays.	126
Figure 5.4.4. Effect of full and new moons on the proportion of foraged trays.	127
Figure 6.4.1. Selectivity of all mice, and separately for females and males.	149
Figure 6.4.2. Time in test cages: all mice and separately for females and males.	150
Figure 6.4.3. Visits to test cages: all mice and separately for females and males.	151
Figure 6.4.4. Mass of seeds harvested by mice as a function foraging time.	152
Figure 7.4.1. Geometric representation of macronutrient energy selection by mice.	173
Figure 7.4.2. Total energy intake by mice confined to a single food.	174

Figure 7.4.3. Geometrical representation of protein and carbohydrates intake.	175
Figure 7.4.4. Relative body fat composition of male and female mice.	176
Figure 8.1.1. Schematic presentation of the behavioural conservation framework.	187

### APPENDICES

Appendix 1: Shapira I, Shanas U, Raubenheimer D, Brunton D 2013a. Laboratory	
rats as trap lures for invasive Norway rats: field trial and recommendations. New	
Zealand Journal of Ecology 37: 240-245. (Abstract).	205
Appendix 2: Shapira I, Shanas U, Raubenheimer D, Knapp C, Alberts S, Brunton	
D 2013d. Laboratory rats as conspecific biocontrol agents for invasive Norway	
rats Rattus norvegicus. Biological Control 66: 83-91. (Abstract).	206
Appendix 3: Shapira I, Shanas U, Raubenheimer D, Brunton D 2013b.	
Conspecific attraction in invasive wild house mice: effects of strain, sex and diet.	
Applied Animal Behaviour Science 147: 186-193. (Abstract).	207
Appendix 4: Shapira I, Walker E, Brunton D, Raubenheimer D 2013c. Responses	
to direct versus indirect cues of predation and competition in naïve invasive mice:	
implications for management. New Zealand Journal of Ecology 37: 33-40.	
(Abstract).	208