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.

An Australian Abroad: The secret life of the brushtail possum (*Trichosurus vulpecula*)

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

Doctor of Philosophy

in

Veterinary science

at

Massey University, Manawatū,

New Zealand

Kyle Stephen Richardson

2016

Dedication

For Apple Monster

Abstract

The "superspreader" hypothesis relates disease transmission to social contacts and assumes transmission is driven by the frequency, type and distribution of contacts among infected and susceptible individuals. I investigated characteristics of brushtail possum (*Trichosurus vulpecula*) home ranges for six wild free-living subpopulations, (four grids were studied; all of them before possum depopulation and two of them after possum depopulation) constructing social networks relevant to bovine tuberculosis (TB) transmission before and after depopulation. I also experimentally infected possums with a novel strain of TB to monitor secondary case infections in relation to these contact and other factors, including population density and sex ratio.

Before depopulation home range estimates showed adult males had larger home ranges than female and younger possums. Home range overlap and area of overlap differed between subpopulations, and possum sex and age; with adult males having more and larger overlaps with other possums. Possums were fitted with proximity-logging collars and contacts registered between April and October, 2012. The number of connections an individual has with others and the probability of the distribution of contacts it has within the population, or node degree and betweenness, also known as the shortest distance between individuals, were associated with sex, with males having higher values for each. Males also contacted more possums than females. Post-depopulation results showed an influx of male possums, higher population density, and smaller home range sizes than before depopulation. Possums post-depopulation also lacked an apparent 'routine' in contact networks, interacting with other possums haphazardly. The greater level of contact among adult males, than before depopulation, and their effects

Ш

on recovering populations post-depopulation, was likely the cause of more TB infection in adults and males.

This thesis provides empirical evidence that adult male possums have home range and contact network characteristics that are likely to enhance their involvement in the transmission and persistence of TB, relative to female and younger possums. Observations of experimentally infected individuals showed that infected males survived longer than females and that, as a consequence, those males potentially acted as a "supershedding" subgroup. I therefore provide evidence that adult male possums are the most important drivers of TB transmission and persistence of infection in populations, and could be targeted for control measures.

Acknowledgements

First I would like to thank the following individuals for their guidance and support, and for showing me the joy I could find with a carrier in science. Michelle Anderson, Rick Douglass, Bill Good and Amy Kuenzi, you've all been an inspiration to me.

Thank you to my fellow students at the Hopkirk Research Institute in Palmerston North, I think we all found help in helping each other. You made my time in New Zealand a joy.

Thank you to the Royal Society of New Zealand Marsden Fund for making this thesis possible. I wouldn't have completed it without the help of Isa Blasco-Costa, Marcus Bridge, Sam Brown, Dean Clark, Kev Drew, Nyree Fea, Anja Friedrich, Zoe Grange, Steve Hough, Mox, Chris Niebuhr, James Smith, and Cracker. You guys came out and worked harder grids under worse conditions than most scientists ever encounter. You all have my respect and deepest gratitude.

I would like to thank Dr. Nicola Nelson, Dr. Weihong Ji and Dr. Lee Skerratt for taking the time and putting forth the effort to review this thesis. Your recommendations and input are greatly appreciated and have resulted in a better finished product. Thank you.

I've devoted almost four years of my life to this project, but this study had five other men just as dedicated and driven to the task at hand as I was. Nigel French, I know I wasn't easy for you to deal with or the best student for scheduling meetings (or just the best student in general), but I wasn't a bore either. I thank you for that. Most of all, you gave me three years to witness first-hand what it takes to be a true top tier scientist. You definitely set the bar. Chris Jewell, it's always nice to have a stats wiz on board. You sat for hours with me working the data. Thanks for being a part of this project and a valued advisor. Bryce Buddle, it feels like every question we set out to investigate during this study you already knew the answer to. Lots of people know possums and lots of people know disease, but I'd be hard pressed to find anyone who knows more about disease in possums than you. You're a trooper in the bush, a master with a scalpel and a true professional to work with. No one offers better counsel or direction. Dan Tompkins, you've been the most important person in my life these last three years both personally and professionally. To say you went above and beyond the expectations as an advisor would be an enormous understatement. You offered everything you were able from guidance and support to food, drink and a roof over my head. You were the anchor of this study and for the team conducting it. I'm proud to call you my advisor and friend. Thank you to all of you for the opportunity you've given me to learn, and for the important roles you've each contributed to my live. To the last of the five but by no means the least Carlos Rouco, we sure rocked this project didn't we? Possums, TB, earthquakes, wind and rain, no roads, no water, too much water, pigs, the possum pit, there was nothing we couldn't handle. I'm not sure how two guys worked so well for so long out there without killing each other. Sure we had some bumps and bruises; there was a fair amount of pain and blood loss and one a hospital trip, just walk it off right. Along the way you found a way to teach me everything except how to speak Spanish and in the end we got the job done, thanks for everything my friend.

I would also like to thank Scott Carver. You've advised me from my undergrad research through to the end of my PhD. There isn't time to mention the countless times you've supported me. Professionally and personally I hold you in the highest regard, thanks for everything. Melanie Laird, you kept me smiling through the hardest times of this thesis. You encouraged me, supported me and helped me to push through to the finish. From the bottom of my heart, thank you. Finally, I would like to thank my family, Gary and Denise Richardson, my sister Claire and brother Cody. You've loved and supported me all my life. I'm only here now because of you.

Thesis structure and format

This thesis is presented as a series of seven chapters. Encompassed by a general introduction and discussion, five research chapters have been prepared and are presented for future publication in peer reviewed journals.

Chapter one

General introduction and literature review introduces the concepts behind the research contained in this thesis by discussion and reviewing current literature of basic ecology of brushtail possums and disease ecology associated with the aspects of bovine tuberculosis.

Chapter two

Interacting determinants of brushtail possum (*Trichosurus vulpecula*) home range size and implication for possum population management will be submitted to Australian Journal of Ecology

Chapter three

Home range overlaps in the brushtail possum (*Trichosurus vulpecula*): investigating potential intrinsic and extrinsic determinants will be submitted to Australian Journal of Ecology

Chapter four

Construction of brushtail possum (*Trichosurus vulpecula*) contact networks to inform on bovine tuberculosis transmission between individuals, and its persistence in wild populations

Chapter five

Changes in population structure following depopulation; implications for TB transmission and persistence

Chapter six

Relating variation in tuberculosis (TB) transmission in brushtail possums (*Trichosurus vulpecula*) to potential drivers found at the environmental, population and individual level

Chapter seven

General discussion summarises the significant findings of this study. The relevance and implications are discussed and future research directions are suggested.

Chapter eight

Literature cited has been collated at the end of the thesis to reduce repetition. Literature is referred to in the format consistent with the format used for the journal Ecology.

Chapter nine

Appendix: Improving animal welfare standards while reducing disease exposure risk during euthanasia of trapped brushtail possums (*Trichosurus vulpecula*), C. Rouco, K.S. Richardson, D.M. Tompkins. Published Animal Welfare 2015, Vol 24; pg 235-239.

Table of Contents

1.	General introc	luction and literature review	1	
	1.1.Study	aim	1	
	1.2.Study species- the brushtail possums5			
	1.3. <i>M. bovis</i> and its presence in possums			
	1.4.Home range, distribution and behaviour			
	1.5.Contact networks		10	
	1.6.TB tra	nsmission in the brushtail possum	11	
	1.7.Thesis	chapter contents	12	
2.	Interacting de	terminants of brushtail possum (Trichosurus vulpecula) home	range size	
	and implication	on for possum population management	14	
	2.1.Introd	action	14	
	2.2.Metho	ds and materials	17	
	2.2.1.	Study site	17	
	2.2.2.	Data Collection	18	
	2.2.3.	Population-scale density and mean home range estimates	19	
	2.2.4.	Determinants of individual home range size	20	
	2.3.Result	s	20	
	2.3.1.	Population-scale density and mean home range estimates	20	
	2.3.2.	Determinants of individual home range size	24	
	2.4.Discus	sion	27	
3.	Home range o	verlaps in the brushtail possum (Trichosurus vulpecula): inve	stigating	
	potential intri	nsic and extrinsic determinants	29	
	3.1.Introduction2		29	
	3.2.Methods and materials			
	3.2.1.	Study site	31	
	3.2.2.	Data collection		
	3.2.3.	Analysis	32	
	3.3.Results			
	3.3.1.	Number of overlaps		
	3.3.2.	Area of overlaps		
	3.4.Discus	sion	42	

	3.4.1. Implica	ations	44		
4.	. Construction of brushtail possum (Trichosurus vulpecula) contact networks to in for or				
	bovine tuberculosis transmission between individuals, and its persistence in wild				
	populations				
4.1.Introduction					
	4.2.Methods and materials				
4.2.1. Data collection			50		
	4.2.2. Analys	is	51		
	4.2.2.1.	Population-level analysis	52		
	4.2.2.2.	Individual-level analysis	54		
	4.2.2.3.	Contact-level analysis			
	4.3.Results		59		
	4.3.1. Populat	tion-level summaries of network characteristics	59		
	4.3.2. Individ	ual-level analysis	61		
	4.3.3. Contac	t-level analysis	65		
	4.4.Discussion		67		
5.		tail possum (Trichosurus vulpecula) populations to			
5.	The response of brush	tail possum (<i>Trichosurus vulpecula</i>) populations to nsmission and persistence	o control, and		
5.	The response of brush implication for TB tran		o control, and		
5.	The response of brush implication for TB tran 5.1.Introduction	nsmission and persistence	o control, and 72		
5.	The response of brush implication for TB tran 5.1.Introduction 5.2.Methods and n	nsmission and persistence	o control, and 72 72 72		
5.	The response of brush implication for TB tran 5.1.Introduction 5.2.Methods and n 5.2.1. Study s	nsmission and persistence	o control, and 72 72 74 74		
5.	The response of brush implication for TB tran 5.1.Introduction 5.2.Methods and n 5.2.1. Study s 5.2.2. Data co	nsmission and persistence	o control, and 72 72 74 74 74		
5.	The response of brush implication for TB tran 5.1.Introduction 5.2.Methods and n 5.2.1. Study s 5.2.2. Data co 5.2.3. Analys	nsmission and persistence	o control, and 72 72 74 74 74 74 74		
5.	The response of brush implication for TB tran 5.1.Introduction 5.2.Methods and n 5.2.1. Study s 5.2.2. Data co 5.2.3. Analys 5.2.3.1.	nsmission and persistence	o control, and 72 72 74 74 74 74 74 74		
5.	The response of brush implication for TB tran 5.1.Introduction 5.2.Methods and n 5.2.1. Study s 5.2.2. Data co 5.2.3. Analys 5.2.3.1. 5.2.3.2.	nsmission and persistence	o control, and 72 72 74 74 74 74 74 75 75		
5.	The response of brush implication for TB tran 5.1.Introduction 5.2.Methods and n 5.2.1. Study s 5.2.2. Data co 5.2.3. Analys 5.2.3.1. 5.2.3.2. 5.2.3.3.	nsmission and persistence	o control, and 72 72 74 74 74 74 74 75 75 75		
5.	The response of brush implication for TB tran 5.1.Introduction 5.2.Methods and n 5.2.1. Study s 5.2.2. Data co 5.2.3. Analys 5.2.3.1. 5.2.3.2. 5.2.3.3. 5.3.Results	nsmission and persistence	o control, and 72 72 74 74 74 74 74 75 75 75 75		
5.	The response of brush implication for TB tran 5.1.Introduction 5.2.Methods and n 5.2.1. Study s 5.2.2. Data co 5.2.3. Analys 5.2.3.1. 5.2.3.2. 5.2.3.2. 5.2.3.3. 5.3.Results 5.3.1. Home n	nsmission and persistence	o control, and 72 72 74 74 74 74 74 75 75 75 75 75		
5.	The response of brush implication for TB tran 5.1.Introduction 5.2.Methods and n 5.2.1. Study s 5.2.2. Data co 5.2.3. Analys 5.2.3.1. 5.2.3.2. 5.2.3.3. 5.3.Results 5.3.1. Home n 5.3.2. Popular	nsmission and persistence	o control, and 72 72 74 74 74 74 75 75 75 75 75 75 75		
5.	The response of brush implication for TB tran 5.1.Introduction 5.2.Methods and n 5.2.1. Study s 5.2.2. Data co 5.2.3. Analys 5.2.3.1. 5.2.3.2. 5.2.3.3. 5.3.Results 5.3.1. Home n 5.3.2. Populat 5.3.3. Individ	nsmission and persistence	o control, and 72 72 74 74 74 74 74 75 75 75 75 75 75 75 75 		

6.	Relating variation in tuberculosis (TB) transmission in brushtail possums (Trichosurus			
	vulpecula) to potential drivers found at the environmental, population and individual			
	level		93	
	6.1.Introduction			
	6.2.Methods and materials		97	
	6.2.1.	Experimental design	98	
	6.2.2.	Experimental infection methodology		
	6.3.Analysis		101	
	6.3.1.	Survival rates of challenged possums	101	
	6.3.2.	Population-level drivers of transmission	101	
	6.3.3.	Subgroups-level drivers of transmission	101	
	6.3.4.	Individual-level drivers of transmission	102	
	6.4.Results		102	
	6.4.1.	Survival rates of challenged possums in season 2	102	
	6.4.2.	Population-level drivers of transmission	105	
	6.4.3.	Subgroup-level considerations	109	
	6.4.4.	Individual-level drivers	110	
	6.5.Discus	ssion	111	
7.	General discussion		115	
7.1.Possum home range		116		
	7.1.1.	Home range overlaps	117	
	7.2.Possu	m contact networks	119	
	7.3.Post-d	epopulation possum dynamics	120	
	7.4.TB tra	nsmission	122	
	7.5.Implic	ations and management		
8.	Literature cited			
9.	Appendix		147	

List of tables and figures

Tables

2-1
2-2
2-3
2-4
3-1
3-2
3-3
3-4
4-1
4-2
4-3
4-4
4-5
4-6
5-1
5-2
5-3
5-4
5-5
6-1
6-2
6-3
Figures
2-1
2-2
3-1
3-2
3-3
3-4
4-1
4-2

4-3	
4-4	
4-5	
5-1	
5-2	
5-3	
6-1	
6-2	
6-3	
6-4	
6-5	