

Predator-prey interactions through the lens of coevolution and ecological context



Eamonn Wooster

Thesis submitted in fulfilment of the requirements for
the degree of Doctor of Philosophy

under the supervision of Daniel Ramp and Arian Wallach

University of Technology Sydney
Faculty of Science

February 2022

Certificate of Original Authorship

I, Eamonn Ivor Fraser Wooster, declare that this thesis is submitted in fulfilment of the requirements of the award of Doctor of Philosophy, in the School of Life Sciences, Science at the University of Technology Sydney.

This thesis is wholly my own work unless otherwise referenced or acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.

This document has not been submitted for qualifications at any other academic institution.

This research is supported by an Australian Government Research Training Program.

Production Note:
Signature removed prior to publication.

Eamonn Wooster

Date: 4th February, 2022

Acknowledgements

I am deeply thankful for my supervisors, Arian Wallach and Daniel Ramp, who have both been so patient, supportive and inspiring throughout the process of completing my PhD. It is hard to imagine better people to do a PhD with. To Arian, thank you for always believing in me, giving me the opportunity to travel the world, explore and to think deeply. To many more trips to the desert and conversations around the fire. To Dan, for the guidance, the encouragement to chase the things that truly excite me academically, for asking the hard questions and the lessons in analysis. To many more hours spent thinking about how we can explore that new idea. The Centre for Compassionate Conservation has taught and allowed me to think freely and critically about the world I see around me and everyone who lives within it.

I would like to thank Erick Lundgren, for guidance, mentorship, and friendship, doing our PhDs together was a true joy. Thank you for the times travelling the world, being in the middle of nowhere, showing me the beauty of North America. I look forward to many collaborations and, even more so, trips to the middle of nowhere, studying something feral. To Adam O'Neill, for helping me see the beauty of the desert and protected systems. To Charlie Jackson-Martin and all the foxes at Sydney Fox Rescue, thank you Charlie for being inspiring and doing what no one else is willing. To the foxes, thank you for donations to my PhD in the form of your scent, I hope this thesis can one day help make Australia a better place to be a fox. To Erin Rogers, for always being there to listen, proofread and help see reason.

To Gavin Bonsen and Esty Yanco, thank you for being great friends, during field work and travels. To the rest of CfCC and team Freshwater Ecology who made being at UTS a lot of fun.

I would like to thank my family and friends. To my father who was always interested and excited about my work, through the last eight years of study. The many friends who are currently in my life and those who have been but no longer are, thank you.

To the red fox, for being ever inspiring, for being the species that embodies all that I value, adaptability, curiosity and making the most of what you have. In particular the fox that crossed the road that one fateful night, thank you for inspiring me.

Finally, this thesis is dedicated to my late mother. I wish you could have read this. Thank you for being the catalyst to all things animal science in my life.

List of Papers and Statement of Author Contribution

This thesis is a compilation of chapters and 5 published/publishable manuscripts. Each paper is formatted for their destination journals, except for referencing styles which feature as a single list at the end of the thesis.

Chapter 2 – In Preparation

Wooster, E.I.F.; Ramp, D.; Lundgren E.J.; Bonsen, G.T.; O’Neill A.J.; Wallach, A.D. Australian small mammals are fox savvy. In preparation

Contributor	Statement of contribution
Production Note: Signature removed prior to publication. [Wooster, E.I.F.]	Conceptualization (33%) Investigation (50%) Formal analysis (50%) Fieldwork (70%) Visualization (100%) Writing (100%)
Production Note: Signature removed prior to publication. [Ramp, D.]	Conceptualization (33%) Review and editing (50%)
Production Note: Signature removed prior to publication. [Lundgren, E.J.]	Formal analysis (50%) Fieldwork (5%)
Production Note: Signature removed prior to publication. [Bonsen, G.T.]	Fieldwork (5%)
Production Note: Signature removed prior to publication. [O’Neill, A.J.]	Fieldwork (10%)

Production Note: Signature removed prior to publication. [Wallach, A.D.]	Conceptualization (33%) Investigation (50%) Fieldwork (10%) Review and editing (50%)
---	---

Chapter 3 – Published

Wooster, E.; Wallach, A.D.; Ramp, D. 2019, The Wily and Courageous Red Fox: Behavioural Analysis of a Mesopredator at Resource Points Shared by an Apex Predator. *Animals* 9, 907.

Contributor	Statement of contribution
Production Note: Signature removed prior to publication. [Wooster, E.I.F.]	Conceptualization (50%) Investigation (100%) Formal analysis (50%) Visualization (50%) Writing (100%)
Production Note: Signature removed prior to publication. [Ramp, D.]	Conceptualization (25%) Visualization (50%) Review and editing (50%) Formal analysis (50%)
Production Note: Signature removed prior to publication. [Wallach, A.D.]	Conceptualization (25%) Review and editing (50%)

Chapter 4 – Published

Wooster, E.I.F.; Ramp, D.; Lundgren E.J.; O’Neill A.J.; Wallach, A.D. 2019, Red foxes avoid apex predation without increases in fear. *Behavioral Ecology*.

Contributor	Statement of contribution
Production Note: Signature removed prior to publication. [Wooster, E.I.F.]	Conceptualization (50%) Investigation (50%) Formal analysis (60%) Fieldwork (20%) Visualization (50%) Writing (100%)
Production Note: Signature removed prior to publication. [Ramp, D.]	Formal analysis (10%) Visualization (25%) Review and editing (40%)
Production Note: Signature removed prior to publication. [Lundgren, E.J.]	Formal analysis (20%) Fieldwork (20%) Review and editing (10%)
Production Note: Signature removed prior to publication. [O’Neill, A.J.]	Fieldwork (30%)
Production Note: Signature removed prior to publication. [Wallach, A.D.]	Formal analysis (10%) Conceptualization (50%) Fieldwork (30%) Investigation (50%) Visualization (25%) Review and editing (50%)

Chapter 5 – In Review

Wooster, E.I.F.; Ramp, D.; Lundgren E.J.; O’Neill A.J; Yanco E.; Wallach A.D.

Predator protection dampens the landscape of fear. *In Review with Oikos*

Contributor	Statement of contribution
Production Note: Signature removed prior to publication. [Wooster, E.I.F.]	Conceptualization (50%) Investigation (50%) Formal analysis (70%) Visualization (75%) Fieldwork (20%) Writing (100%)
Production Note: Signature removed prior to publication. [Ramp, D.]	Conceptualization (25%) Review and editing (30%) Investigation (25%) Fieldwork (30%) Formal analysis (10%)
Production Note: Signature removed prior to publication. [Lundgren, E.J.]	Fieldwork (10%) Formal analysis (10%) Review and editing (10%)
Production Note: Signature removed prior to publication. [Bonsen, G.T.]	Formal analysis (10%)
Production Note: Signature removed prior to publication. [Yanco, E.]	Fieldwork (10%) Review and editing (10%)
Production Note: Signature removed prior to publication. [O’Neill, A.J.]	Fieldwork (10%)
Production Note: Signature removed prior to publication. [Wallach, A.D.]	Conceptualization (25%) Visualization (25%) Review and editing (50%) Investigation (25%) Fieldwork (30%)

Chapter 6 – In Preparation

Wooster, E.I.F.; Wallach, A.D.; Lundgren E.J.; Ramp, D. Animal cognition has cascading ecological effects. *In preparation for Trends in Ecology and Evolution*

Contributor	Statement of contribution
Production Note: Signature removed prior to publication. [Wooster, E.I.F.]	Conceptualization (50%) Investigation (100%) Visualization (100%) Writing (100%)
Production Note: Signature removed prior to publication. [Ramp, D.]	Conceptualization (25%) Review and editing (50%)
Production Note: Signature removed prior to publication. [Lundgren, E.J.]	Conceptualization (10%) Review and editing (20%)
Production Note: Signature removed prior to publication. [Wallach, A.D.]	Conceptualization (15%) Review and editing (30%)

Ethics Approvals and field work permits

All field work was approved and conducted under a University of Technology Sydney Animal Ethics permit titled: “Do apex predators enable native-non-native coexistence”, permit number ETH16-0237. Israeli Fieldwork was conducted under a permit number “2018/41848” and North American fieldwork was conducted under “DEVA-2019-SCI-0030”.

Table of Contents

<i>Certificate of Original Authorship</i>	<i>i</i>
<i>Acknowledgements</i>	<i>ii</i>
<i>List of Papers and Statement of Author Contribution</i>	<i>iv</i>
<i>Ethics Approvals and field work permits</i>	<i>viii</i>
<i>Table of Contents</i>	<i>ix</i>
<i>List of Figures and Tables</i>	<i>xii</i>
Figures	<i>xi</i>
Tables	<i>xvi</i>
<i>Thesis Abstract</i>	<i>1</i>
<i>Chapter 1: Introduction</i>	<i>3</i>
Biotic globalisation has created novel ecosystems	<i>4</i>
Coevolution and novel ecological interactions	<i>6</i>
The red fox, a globalised mesopredator	<i>7</i>
Thesis overview	<i>8</i>
<i>Chapter 2: Australian Small Mammals are fox savvy</i>	<i>12</i>
Abstract	<i>12</i>
Introduction.....	<i>13</i>
Methods	<i>15</i>
Results.....	<i>21</i>
Discussion.....	<i>24</i>
<i>Chapter 3: The Wily and Courageous Red Fox: Behavioural Analysis of a Mesopredator at Resource Points Shared by an Apex Predator</i>	<i>30</i>
Simple Summary:.....	<i>30</i>
Abstract:.....	<i>31</i>
Introduction.....	<i>31</i>
Methods	<i>36</i>
Results.....	<i>42</i>
Discussion.....	<i>49</i>
Acknowledgements	<i>52</i>
Supplementary material	<i>53</i>

Chapter 4: Red foxes avoid apex predation without increasing fear.....	54
Abstract	54
Introduction.....	55
Methods	57
Results	63
Discussion.....	68
Acknowledgements	70
Supplementary Material	72
Chapter 5: Predator protections dampens the landscape of fear.....	74
Abstract	74
Introduction.....	76
Methods	78
Results	84
Discussion.....	88
Acknowledgements	92
Supplementary Material	93
Chapter 6: Animal cognition has cascading ecological effects	96
Abstract	96
The landscape of fear	97
The landscape of more than fear.....	98
The cascading ecological effects of animal cognition	103
Cognition drives a landscape of knowledge.....	106
Integrating Animal Cognition and Ecology.....	107
Concluding remarks	108

List of Figures and Tables

Figures

Chapter 2

Figure 125
Behavioural responses of small mammals to addition of fox and herbivore scats, outlining changes in a) change in proportion of time small mammals spent vigilant in response to fox and herbivore scats. Positive values (red fill) indicate presumed increase in fear, through proportional increases in time spent vigilant. Horizontal line indicates no change between control days and experimental days (e.g., post scat placement). b) small mammal nut consumption rates in response to the addition of fox and herbivore scats. Negative values (red fill) indicate a decrease in proportional nut consumption (defined as higher fear). Horizontal line indicates no change between control days and experimental days (e.g., post scat placement).

Figure 226
Behavioural responses of small mammal species to addition of fox and herbivore scats, outlining changes in the proportion of time small mammals spent vigilant in response to fox and herbivore scats. Positive values (red fill) indicate presumed increase in fear, through proportional increases in time spent vigilant. Horizontal line indicates no change between control days and experimental days (e.g., post scat placement).

Chapter 3

Figure 147

Behaviours observed in this study and used to classify fox behaviour: (A) confident sniffing and walking, (B) cautious sniffing and walking, (C) confident scavenging, (D) high vigilance, (E) cautious camera investigation, (F) social foraging. See supplementary material 1 for an example of behaviourally scored video.

Figure 2.....50

Confidence and cautiousness of red foxes at key resource points share with dingoes. Proportion of time allocated to each behaviour at each resource type (A). The average amount of time allocated to confident and cautious behaviours at carcasses (B), rabbit warrens (C), and water points (D). F=foraging, S=sniffing, L=locomotion, I=investigating, V=vigilance, D=digging, SM=scent marking). Significant difference indicated by an asterisk

Figure 3.....51

Fox temporal activity patterns at water points, rabbit warrens and carcasses gathered with camera traps in the Painted Desert, South Australia in the winters of 2016-2018. Solid line represents carcass temporal activity patterns, dashed line represents water points and dotted line represents rabbit warrens. Overlap coefficient between the 3 resource points is 0.56.

Chapter 4

Figure 1.....63

Predator-friendly study site in the Painted Desert, South Australia. Together, Evelyn Downs and Mount Willoughby cover 7,900 km², which is large enough to contain several dingo territories. Typical home range sizes of dingoes and foxes in arid areas are shown for scale, based on average home ranges: 17 km² for foxes (Moseby et al., 2009), and 95 km² for dingoes (Thomson, 1992a). Resource points were a minimum of 5 km from poison baiting.

Figure 2.....67

Fox and dingo temporal activity patterns at resource points. The $\Delta 4$ temporal overlap coefficient was 0.43 ($\pm 95\%$ CI: 0.39-0.47).

Figure 3.....69

Proportions of space and time divided into hour-long bins, where predators were exclusively present at resource points or where they overlapped. X-axis indicates resource type: across all, water points, carcasses, and rabbit warrens. Asterisks denote significance ($p < 0.05$).

Figure 4.....70

Predicted relationships from generalized linear mixed models comparing: (a) the proportion of time foxes were cautious to daily dingo activity rate at resource points; (b) the proportion of time foxes were cautious to number of dingo scent-marks counted in surveys across resource points; (c) the proportion of time foxes were vigilant to daily dingo activity rate at resource points; and (d) the proportion of time foxes were vigilant to number of dingo scent-marks counted in surveys across resource points. Grey bands represent 95% confidence intervals. All dingo and fox activity metrics were normalized to be between zero and one. Cautious models can be found in table 2, vigilance models can be found in Supplementary table 2.

Figure 5.....71

Predicted relationships from generalized linear mixed models comparing: (a) the proportion of time foxes were confident to the daily activity rate of foxes at resource points; and (b) daily activity rate of foxes to number of dingo scent-marks counted in surveys across resource points. Grey bands represent 95% confidence intervals. Asterisks denote significance ($p < 0.05$).

Chapter 5

Figure 1.....88

Comparison of fox and dingo weekly occupancy at sites with differing treatments of predators. The probability of (A) foxes and (B) dingoes being present at a camera station (occupancy) at sites of differing treatments of predators. Points and their error bars represent the mean probability of occupancy from weekly bootstrapped single species occupancy models and the 95% confidence intervals. Letters indicate significance groupings.

Figure 2.....89

Comparisons of fox behaviour at sites with differing treatments of predators. The proportion of fox events classified as confident (A) and cautious (B). The frequency (events per day) of fox social (C) and scent-marking behaviour (D). Letters indicate significance groupings.

Figure 3.....90

Fox and dingo temporal overlap at sites with differing treatments of predators. Overlap between the two predators at predator-friendly sites (A) and predator-persecuted sites (B). Ribbons are 95% confidence intervals from bootstrapped temporal activity. Non-overlapping of confidence intervals indicates significance.

Figure 4.....91

Fox temporal overlap between sites with differing treatments of predators. Fox temporal activity comparing dingo-eradicated sites to predator-friendly (A) and predator-persecuted (B) sites. Ribbons are 95% confidence intervals from bootstrapped temporal activity. Non-overlapping of confidence intervals indicates significance.

Chapter 6

Box 1.....103

Examples of cognitively complex interactions and their cascading or potential cascading ecological effects.

Figure 2.....108

Trophic structures of a common mid-west North American ecosystems (i.e., Yellowstone National Park) visualised through two frameworks; a) the landscape of fear, predators inspire fear in small prey and mesopredator species, both directly killing them and altering their behaviour. b) A conceptual model describing the landscape of knowledge, driven by cognitive trophic cascades. Brown bears tolerate fox presence while they hunt, serving to protect foxes from wolf predation (1 - Harris et al. (2008), red foxes, when cohabitating with apex predators develop detailed knowledge of their activity patterns and avoid them (2 - Wooster et al. (2021), elk and other large herbivores increase their vigilance when wolves are present, allowing them to avoid predation (3 - Laundré et al. (2001), coyotes and badgers cooperate, instead of competing to hunt small mammals (4 - Minta et al. (1992). Blue lines represent cognitive trophic cascades. Red lines represent predation

Tables

Chapter 2

Table 1.....20

Descriptions of ecological context of each field site. Columns indicate region and whether each location was in or out of the foxes native range, the locations within each region, the average rainfall within each site, the small mammal study species at each site, reflected by identification from camera trap videos and the predator assemblage present at each of the sites. *indicates the mesopredator scat used to simulate predation risk within the GUD experiment.

Table 2.....27

Outputs from the most parsimonious linear mixed effects models for each small mammal behaviour metric measured. Linear mixed effect models were conducted within the R package lme4 v1.1-23. * denote significance ($P < 0.05$).

Chapter 3

Table 1.....38

Review of fox behaviour literature highlights the most common ecological contexts foxes are studied under. Data gathered for this review comes from a Web of Science search, using “Red fox behaviour” as the search term, the search was refined for “behavioural Sciences”. Reference trails were also included in the review. Unstated was noted if authors did not mention whether the variable in question was present during their study. N/A refers to a variable not being applicable to the study (e.g. Foxes killed is not relevant to a study conducted in captivity).

Table 2.....44

Ethogram for foxes at resource points. Modifiers further describe the behaviour observed. Point events describe instantaneous behaviours (P). State events describe continuous behaviour (S).

Table 3.....48

Descriptions of red fox ethogram modifiers.

Table 4.....52

Descriptive statistics of the time allocated to different behavioural states at the three resource points, depending upon whether the behaviours were expressed cautiously or confidently. Time is represented in seconds (s). Average times that were significantly different are indicated by an asterisk.

Chapter 4

Table 1.....61

Number of resource points monitored across each year. Bracketed numbers represent number of new resource points monitored each year.

Table 2.....67

Output from generalized linear mixed effects model examining the effect of dingo and conspecific predictor variables on fox cautious behavior. Model was constructed using the 'glmer' function within the R package 'lme4'. Asterisks denote significance ($p < 0.05$).

Thesis Abstract

The red fox (*Vulpes vulpes*) is one of the world's most widely distributed mesopredators. They influence ecosystems primarily through the predation of prey species, driving cascading effects on plant and animal communities. In modern times, red foxes have been introduced to new locales, forming part of native and non-native conglomerates. The resulting amalgamation of native and non-native predator communities have been described as producing novel trophic cascades. While some acknowledge the important rewiring of lost functions due to extinction, there remains widespread concern about the negative role introduced species might play as they lack coevolved traits and relationships with native prey. To that end, the introduction of novel predators, like foxes, has been suggested to be a leading cause of decline and extinction of small mammal prey, especially in Australia. Rather than detailed consideration of the niche that introduced predators fit into, and their functional similarities with lost species, foxes and other introduced mesopredators like cats (*Felis catus*) are maligned by conservation values that promote native prey and the prevention of extinction. Negative connotations around alien and invasive species frequently override sound ecological assessment and cloud the establishment of evidence-based environmental policy.

Rather than absorbing narratives of harm, what happens when we suspend our assumptions that introduced species are ecologically damaging? Is it possible that the role of introduced mesopredators in driving extinctions is overstated? Is it also possible that long histories of coevolution are less important than the contextual and functional

roles predators play in trophic cascades? Asking these questions is vital if we are to find transparent and peaceful ecological solutions to improve nature conservation and prevent extinction and harm. Within this thesis, I explore these questions with a desire to understand how the red fox shapes the behaviour and ecology of their prey and how this compares to the foxes native range. Further, I explore how the fox fits into Australian novel ecosystems but exploring their interactions with dingoes and how these are shaped by human hunting.

Red foxes, like any other predator, play important ecological roles, however, assumptions of their harm, have prevented us from fully exploring their ecologies within novel ecosystems. By dropping assumptions that foxes are inherently harmful, I show that the foxes biotic nativeness has very little to do with their ecological interactions, the foxes ecology and behaviour may, instead be better predicted by ecological context.