Reintroduction biology of the eastern quoll (*Dasyurus viverrinus*)

by

Belinda Anne Wilson

Illustration by Madeleine Tranter Creative

Submitted in fulfilment of the requirements for the degree of
Doctor of Philosophy
of the Australian National University
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Candidate declaration

Image by Christine Fernance

I, Belinda Wilson, declare that:

- this thesis contains no material which has been accepted for the award of any other degree or diploma in any university,
- to the best of my knowledge, this thesis contains no material previously published or written by another person, except where due reference is made in the text, and
- the research presented in this thesis represents original work that I carried out during my candidature at The Australian National University, except for contributions to multi-author papers incorporated in the thesis where my contributions are specified in the Statement of Contribution.

Belinda Anne Wilson

Date: 14 October 2023

Preface

Thesis format

This thesis complies with The Australian National University (ANU) College of Science guidelines for a 'thesis by compilation'; a series of connected papers (journal articles) which have either been published (Chapters 2, 3, 5), or submitted (Chapters 4 and 6) at the time of thesis submission, in accordance with ANU policy.

Each of these papers were intended as an independent publication; therefore, there are areas of overlap and repetition between them. The extended context statement (Chapter 1) is not intended to provide a literature review as traditionally included in a 'thesis by dissertation', but rather a framework for understanding the project, and the relationships between different aspects of the research. The Synthesis (Chapter 7) is intended to provide a summary of the key findings from each of my Chapters, and synthesise how these substantially contributed to translocation and conservation science.

Since this thesis includes papers in their original format and these papers were coauthored with my supervisors and other contributors, invariably I have used the term “we” rather than “I”. This writing style has been retained to reflect the authenticity of the original papers as published, however the major contribution of these papers was my own, and I led all aspects of the research reported in this thesis.

Statement of contribution

I conducted the vast majority of the work for each paper included in this thesis, including conceptualisation, methodology, software, validation, formal analysis, investigation, data curation, writing, reviewing, editing, and visualisation.

Professor Adrian D Manning leads the Coexistence Conservation Lab and instigated and designed the Mulligans Flat-Goorooyarroo Woodland Experiment with collaborators, which provided the framework for this project. He also secured the Australian Research Council (ARC) funding for the research and reintroduction (see Funding section) and was the Primary Investigator for the overall eastern quoll reintroduction program as part of the multi-species 'Bringing Back Biodiversity' restoration project.

I was supported by my supervisory panel (Adrian D Manning, Maldwyn J Evans, Iain J Gordon, William G Batson, and Sam C Banks), and other coauthors (Donald B Fletcher, Claire Wimpenny, Jenny Newport, Emily Belton, Annette Rypalski, Tim J Portas, Jennifer C Pierson, Brittany M Brockett, and Shoshana Rapley).

The key areas of input for each collaborator are listed below for the empirical and theoretical papers in this thesis (Chapters 2–6). The CRediT (Contributor Roles Taxonomy) author statements below have been agreed to in writing by all coauthors in the respective papers, and other support is acknowledged as part of each paper.

Chapter 2: Trials and tactics

Title: Adapting reintroduction tactics in successive trials increases the likelihood of establishment for an endangered carnivore in a fenced sanctuary

Authors: Wilson B A, Evans M J, Batson W G, Banks S C, Gordon I J, Fletcher D B, Wimpenny C, Newport J, Belton E, Rypalski A, Portas T J, & Manning A D

Publication outlet: PLOS One (2020), 15(6): e0234455

Current status of paper: Published

Contributions to paper: Conceptualisation: BAW, MJE, WGB, SCB, IJG, ADM; methodology: BAW, MJE, WGB, SCB, IJG, ADM; software: BAW, MJE, SCB; validation: BAW, MJE, SCB; formal analysis: BAW, MJE; investigation: BAW, JN; resources: WGB, CW, JN, ADM; data curation: BAW, MJE, WGB; writing: BAW; review and editing: BAW, MJE, WGB, SCB, IJG, DBF, CW, JN, EB, AR, TJP, ADM; visualisation: BAW, MJE; supervision: MJE, WGB, SCB, IJG, ADM; project administration: WGB, CW, JN, ADM; and funding acquisition: ADM.

Data availability: ANU Data Commons, GitHub.

Chapter 3: Personality and plasticity

Title: Personality and plasticity predict post-release performance in a reintroduced mesopredator

Authors: Wilson B A, Evans M J, Gordon I J, Banks S C, Batson W G, Wimpenny C, Newport J, & Manning A D

Publication outlet: Animal Behaviour (2022), 187: pp 177–189

Current status of paper: Published

Contributions to paper: Conceptualisation: BAW, IJG, SCB, WGB, ADM; methodology: BAW, MJE, IJG, SCB, WGB, ADM; software: BAW, MJE, SCB; validation: BAW, MJE; formal analysis: BAW, MJE, SCB; investigation: BAW, JN; resources: CW, JN, ADM; data curation: BAW, MJE, SCB; writing: BAW; review and editing: BAW, MJE, IJG, CW, JN, ADM; visualisation: BAW; supervision: MJE, IJG, SCB, WGB, ADM; project administration: CW, JN, ADM; and funding acquisition: ADM.

Data availability: GitHub.

Chapter 4: Movement and association

Title: Everybody needs good neighbours: movement, habitat use, and conspecific association in a reintroduced mesopredator

Authors: Wilson B A, Evans M J, Rapley S, Gordon I J, Wimpenny C, Newport J, & Manning A D

Publication outlet: Biodiversity and Conservation

Current status of paper: Under revision

Contributions to paper: Conceptualisation: BAW, IJG, ADM; methodology: BAW, MJE, SR, IJG; software: BAW, MJE, SR; validation: BAW, MJE, SR; formal analysis: BAW, MJE, SR; investigation: BAW, JN; resources: CW, JN, ADM; data curation: BAW; writing: BAW; review and editing: BAW, MJE, SR, IJG, CW, JN, ADM; visualisation: BAW; supervision: MJE, IJG, ADM; project administration: CW, JN, ADM; and funding acquisition: ADM.

Data availability: GitHub.

Chapter 5: Species recovery

Title: Roadmap to recovery revealed through the reintroduction of an IUCN Red List species

Authors: Wilson B A, Evans M J, Gordon I J, Pierson J C, Brockett B M, Wimpenny C, Batson W G, Newport J, & Manning A D

Publication outlet: Biodiversity and Conservation (2023), 32: pp 227–248

Current status of paper: Published

Contributions to paper: Conceptualisation: BAW, MJE, IJG, WGB, ADM; methodology: BAW, MJE, IJG, JCP, WGB, ADM; software: BAW, MJE, JCP; validation: BAW, MJE, JCP; formal analysis: BAW, MJE; investigation: BAW, JN; resources: CW, AR, JN, ADM; data curation: BAW, MJE; writing: BAW; review and editing: BAW, MJE, IJG, JCP, BMB, CW, AR, JN, ADM; visualisation: BAW, MJE; supervision: MJE, IJG, WGB, ADM; project administration: CW, AR, JN, ADM; and funding acquisition: ADM.

Data availability: GitHub.

Chapter 6: Translocation Continuum Framework

Title: The Translocation Continuum Framework for context-specific decision-making

Authors: Wilson B A, Evans M J, Gordon I J, & Manning A D

Publication outlet: Frontiers in Ecology and Evolution (in review)

Current status of paper: Under revision

Contributions to paper: Conceptualisation: BAW, MJE, IJG, ADM; writing: BAW; review and editing: BAW, MJE, IJG, ADM; visualisation: BAW; and supervision: MJE, IJG, ADM.

Endorsements

Senior author for all journal articles: Professor Adrian D Manning, August 7, 2023

AD Manning

Funding

The eastern quoll reintroduction, including translocations, research, and monitoring, was funded through the ARC Linkage Grant "Bringing back Australia's lost woodland biodiversity: towards strategic multi-species reintroductions" secured by Professor Adrian D Manning (LP140100209) in collaboration with ACT Government, CSIRO, and the James Hutton Institute. Equipment and support were provided by the MFGO Woodland Experiment, ACT Government, and WWT. I was supported by an Australian Government Research Training Program Domestic Scholarship and a Postgraduate Research Scholarship.

Equipment

For the benefit of current and future practitioners, I have compiled a list of technical wildlife monitoring equipment used during this project.

Purpose	Equipment	Details
Cage trapping	Wire cage trap	Sheffield Metal Fabrication (31 × 31 × 70 cm), covered in hessian sacks.
Camera trapping	Remote camera	Ltl Acorn LTL-5310a 12MP infrared trail camera.
		SpyPoint BF-10HD 10MP infrared trail camera.
Identification	Microchip	Trovan Microchips Australia.
	Microchip reader	Trovan Microchips Australia compact microreader LID 560 (FDX-A and B).

Release	Wooden den box	Privately-constructed wooden box (50 × 35 × 28.5 cm), including one door at the front for the animal to use, and another on the side to allow researcher access.
Tracking	VHF radiocollar	V6C 163 Zilco (32 g), Sirtrack Ltd, Hawkes Bay, New Zealand.
	GPS collar	LiteTrack 30 RF (38 g), Sirtrack Ltd, Hawkes Bay, New Zealand.
	Yagi antenna	Titley Scientific, Brendale, Australia.
	Receiver	Australis receiver, Titley Scientific, Brendale, Australia.
Transport	Pet carrier	K9 PP30 airline-approved medium pet carrier (62 × 43 × 45 cm).

Risk assessment

A risk assessment, including a disease risk assessment and self-assessment, was undertaken for the eastern quoll reintroduction to the yellow box (*Eucalyptus melliodora*) – Blakely's red gum (*E. blakelyi*) grassy woodland, following the protocols of the *Deputy Prime Minister and Cabinet: guide to preparing implementation plans* (Manning *et al.* 2015). This ecological community is listed as critically endangered under the Environment Protection of Biodiversity Conservation Act (Australian Government 1999).

Ethics statement

Wildlife translocations conducted throughout this project were licensed by the Tasmanian Department of Primary Industries, Parks, Water and Environment (permits TFA 16025 and 17091, export licences 12818/16, 17, 18, 19), Victorian Department of Environment, Land, Water and Planning (permit 14505167), and Australian Capital Territory Government (scientific licence LT2017959, import licence L120161261). Reintroduction and behavioural assay procedures were approved by The Australian National University Animal Experimentation Ethics Committee (protocol A2016/02).

Communications

All research outputs were intended to be published in peer-reviewed journals. The project was also publicised through television, radio, academic presentations and posters, community presentations and discussions, guided tours, podcasts, books, art exhibitions, media releases, and social media, to ensure findings reached local, national, and international audiences. I was directly involved in the following science communications.

Date	Outlet	Communication
Nov 28, 2022	Ecological Society of Australia	Conference presentation as part of 'meaningful targets for biodiversity conservation' symposium.
Nov 20, 2022	Living Arts Canberra, Terroux Peace Garden	'The Quoll Connection' author event, with Nigel Featherstone and Harry Sadler.
Oct 6, 2022	Woodlands and Wetlands Trust	'Science in the sanctuary' community presentation.
	Canberra Times	'Threatened Species Action Plan sets target of no new Australian extinctions' article, with Professor Saul Cunningham and Dr Dejan Stojanovic.
Sep 5, 2022	Quollified Kids podcast	'Eastern quolls with Belinda Wilson' podcast with Lou Hall.
Jul 27, 2021	Affirm Press	'Questions raised by quolls' book by Harry Saddler.
Jul 25, 2021	Woodlands and Wetlands Trust	'Bettong Bungalow' video interview, with Melanie Sim.
Apr 16, 2021	Apple TV+	'Earth at night in colour' docuseries: Kangaroo Valley episode, with Offspring Films.
Mar 11, 2021	Strathnairn Art Gallery	'The precious few: threatened species of Canberra' exhibition, curated by Ceilidh Dalton.
Feb–Jun 2021, 2022	The Australian National University	Demonstrator and research project developer for ANU course BIOL3178: Recovering threatened species and ecosystems
Jul 23, 2020	WIN News Canberra	News interview, with Jason Cummings.
	ANU TV	'Experimental research helping boost the eastern quoll' video interview, with Lannon Harley.
	The Australian National University	'New reintroduction tactics boost eastern quoll survival rate' media release, with Lannon Harley.
Apr 22, 2020	Woodlands and Wetlands Trust	'Bettong Bungalow' video interview, with Andrew O'Meara.
Feb 18, 2020	Institute of Applied Ecology	'Krebs lecture: the effects of Environmental stress on biodiversity' workshop presentation.
Nov 29, 2019	Ecological Society of Australia	Conference presentation as part of 'adaptive management' symposium, and poster.
Jul 10, 2019	Woodlands and Wetlands Trust	'Science in the sanctuary' community presentation.
Jun 4, 2019	The Skeptic Zone	The Skeptic Zone podcast, with Kevin Davies.
May 21, 2019	Pint of Science Australia	'Forget denim, these genes are Australian made' community presentation, with Professor Janine Deakin.
Mar 30, 2019	ABC Science	'Teenage quolls from Australia's 'largest open-air laboratory' set to boost wild population' article, with Dr Ann Jones.

Mar 23, 2019	ABC Radio National	Off Track podcast with Dr Ann Jones and Dr Kate Grarock.
Feb 21, 2019	Rotary Club City of Canberra	Community presentation.
Sep 21, 2018	Goulburn Regional Art Gallery	‘Inhabiting the woodlands: a panel discussion’, with Dr Sue McIntyre and artist Carolyn Young.
Sep 6, 2018	University of Canberra	‘Translocation tactics and captive breeding’ workshop with Dr Jennifer Pierson.
Jul 19, 2018	Woodlands and Wetlands Trust	‘Science in the sanctuary’ community presentation.
Jun 19, 2018	SCI ART CBR	Community presentation.
Mar 9, 2018	Canberra Times	‘Rare photos of baby eastern quolls at play in Mulligans Flat Woodland Sanctuary’ article, with Charles Davis.
	Woodlands and Wetlands Trust	‘And then there were 50’ media release, with Charles Davis.
Oct 15, 2017	Canberra Times	‘Rare video of “extinct” baby quolls born at Mulligans Flat in Canberra’s north’ article, with Dr William Batson.
Aug 30, 2017	ABC Canberra Radio	‘Baby boom: More eastern quoll babies expected at Mulligans Flat Woodland Sanctuary’ radio interview, with Dr William Batson and Greg Bayliss.
Jul 6, 2017	Woodlands and Wetlands Trust	‘Science in the sanctuary’ community presentation.
Apr 2017–Nov 2022	Woodlands and Wetlands Trust	Outreach Officer position delivering conservation and cultural knowledge to all age groups in the form of guided woodland and wetland tours, and outreach at community events.

Appendices

In addition to the core Chapters of the thesis, I list the following published or submitted works as appendices that support the main body of research.

Appendix I: Baseline health in eastern quolls

Portas T J, Evans M J, Spratt D, Vaz P K, Devlin J M, Barbosa A D, **Wilson B A**, Rypalski A, Wimpenny C, Fletcher D, Gordon I J, Newport J, & Manning A D (2020) Baseline health and disease assessment of founder eastern quolls (*Dasyurus viverrinus*) during a conservation translocation to mainland Australia. *Journal of Wildlife Diseases*, 56(3): pp 1–14.

Appendix I presents a study led by the project veterinarian Dr Tim Portas which evaluated baseline health parameters of founder eastern quolls. This study provided insights into baseline health parameters that were previously undescribed for the species. I contributed to data collection and manuscript editing and revisions.

Appendix II: IUCN case study

Wilson B A, Evans M J, Batson W G, Banks S C, Gordon I J, Fletcher D B, Wimpenny C, Newport J, Belton E, Rypalski A, Portas T, & Manning A D (2021) Reintroduction of the eastern quoll to Mulligans Flat Woodland Sanctuary, Australia, using trials, tactics, and adaptive management. *In* book: Soorae (ed. 2021) *Global conservation translocation perspectives 2021: Case studies from around the globe*. IUCN SSC Conservation Translocation Specialist Group, Environment Agency, and Calgary Zoo.

Appendix II presents the eastern quoll reintroduction as a case study in the 2021 edition of the IUCN Global Conservation Translocation Perspectives series. The case study provided a detailed and extensive account of the reintroduction goals, feasibility, implementation, post-release monitoring, difficulties, experience-based learnings, and outcomes. I led the conceptualisation, writing, editing, and revisions.

Appendix III: Coexistence conservation

Evans M J, Weeks A R, Scheele B C, Gordon I J, Neaves E L, Andrewartha T, Brockett B, Rapley S, Smith K J, **Wilson B A**, & Manning A D (2022) Coexistence conservation: reconciling threatened species and invasive predators through adaptive ecological and evolutionary approaches. *Conservation Science and Practice*, 4(7): e12742.

Appendix III presents an essay led by Dr Maldwyn John Evans where we presented the ‘coexistence conservation’ concept for conservation initiatives taking place in the context of threats such as invasive predators. I contributed to manuscript editing and revisions.

Appendix IV: Reintroduction biology research and the IUCN Red List

Evans M J, Gordon I J, Pierson J C, Neaves L, **Wilson B A**, Brockett B M, Ross C E, Smith K J, Rapley S, Andrewartha T A, Humphries N, & Manning A D (2022) Reintroduction biology and the IUCN Red List: The dominance of species of Least Concern in the peer-reviewed literature. *Global Ecology and Conservation*, 38: e02242.

Appendix IV presents a study led by Dr Maldwyn John Evans where we assessed whether reintroduction science has been effectively targeted to threatened taxa using a novel text-analysis tool and by relating the results to the IUCN's Red List and the GDP of relevant countries. I contributed to conceptualisation and manuscript editing and revisions.

Appendix V: Trends in animal translocation research

Evans M J, Gordon I J, Pierson J C, Neaves L, **Wilson B A**, Brockett B M, Ross C E, Smith K J, Rapley S, Andrewartha T, Humphries N, & Manning A D (2023) Trends in animal translocation research. *Ecography*, 2023(3): e06528.

Appendix V presents a study led by Dr Maldwyn John Evans where we explored trends in reintroduction science over time using a novel text-analysis tool. I contributed to conceptualisation and manuscript editing and revisions.

Appendix VI: Havens are a pathway

Read J L, Bradley K, Gordon I J, Manning A D, Neaves L E, Reside A E, Smith K, Southgate R, Wayne A F, Weeks A R, Wilson B A, Moseby K E (2023) Havens are a pathway, not an endpoint, for species recovery: a response to Woinarski *et al*. (2023). Biological Conservation 285: 110212.

Appendix VI presents a letter to the Editor led by Dr John L Read in which we responded to Woinarski *et al.* (2023) that argued that 12 Australian mammals no longer met the criteria for threatened status, based in part on their reintroductions into conservation-fenced havens. We countered that delisting species based on their haven populations alone could have unintended detrimental outcomes due to reduced protection of refugial populations.

Appendix VII: Integration of research and restoration book

Manning A D *et al.* (in prep) The integration of research and restoration: harnessing long-term ecological research.

Appendix VII presents a book prepared by Professor Adrian D Manning, where chapters related to the MFGO Woodland Experiment were contributed by various researchers. I contributed to drafting and editing the eastern bettong, eastern quoll, and teaching chapters.

Acknowledgements

Firstly, I acknowledge and give my respect to the Ngunnawal and Ngambri peoples, on whose land the *murunguny* reintroduction took place and this thesis took form. First Nations peoples were the first scientists, but despite their enduring contributions, colonial structures remain in place that cause them ongoing struggle. Restoration cannot occur without remembering and addressing the need for healing after this continent's recent past. I recognise the atrocities against First Nations peoples, that sovereignty was never ceded, and that the land I have benefited from was founded on genocide and dispossession. This was, and will always be, their land.

This thesis reflects the incredible support provided by my supervisory panel. To Adrian, for your enthusiasm, mentorship, faith in me, and the occasional piece of cake. You instilled some of my now-core values - putting in the effort for 'Rolls-Royce' science, reaching for the stars even if you only get to the moon, and putting your head down and getting on with it. To John, for your remarkable ability to be dropped into the middle of a mess and emerge with clarity. Thank you for your mentorship, for the long hours spent wrangling data and code, for encouraging me to tackle ecological problems with non-ecological tools, and for treating me as an equal. To Iain, for being there to talk about the big things, whether they be my framing thoughts, the overarching narrative, or my internal state of affairs. Your support brought me out of places I didn't think I could dig out of. To Will, for your focus on reality. Thank you for grounding me with your devil's advocacy - challenging me to justify every choice so that future practitioners would see transparent decision-making. In each piece of writing, you were the manager I was writing to. To Sam, for seeing the forest through the trees. You were quick to quell any hints of imposter syndrome, and reminded me that we are all just muddling through it the best we can. I muddled through it a little easier with your help.

To the Mulligans Flat-Goorooyarroo Woodland Experiment team, I cannot thank you all enough for your support. Firstly to Jenny, for being the most dedicated and fierce advocate for ethical science, and being a constant source of knowledge, understanding, and realism. To Catherine, for the motherly care and validation that can only come from having gone through a PhD and come out the other side. To Brittany, for the cups of tea, laughter, and birds - you're nearly there. To Kiarrah, for being a constant source of smiles and helping me slowdown from time to time. To Linda, for your friendship and the opportunity to teach the next generation of ecologists. To Sho, for never letting me forget how capable I am, and for the last-minute road trips to find birds in the rain. To Tim, for being a constant ray of sunshine, even when things were rainy for you. You're nearly there too. To Yaana, for your infectious enthusiasm.

To the Fenner School of Environment and Society, for being my crucible during these formative years as a researcher. To the Research School of Biology, for their support with fieldwork and wildlife care. To the ANU Animal Ethics Committee, for ensuring the best possible care and outcomes for our wildlife. Finally to Researcher Development (shout out to V and Inger), for setting alight the fire that helped me complete this thesis.

This project would not have left the ground without the support and commitment of our partners. To ACT Government, including Claire Wimpenny, Donald Fletcher, Melissa Snape, Renee Brawata, Sam Reid, Simon Stratford, and many more. To the Woodlands and Wetlands Trust, including Emily Belton, Kate Grarock, Kristi Lee, Loren Howell, Millie Sutherland Saines, Jason Cummings, and more. To Mt Rothwell, Odonata, and Annette Rypalski, for your on-ground efforts to support our releases. To Andrew Crane, Annika Everaardt, Claire Hawkins, and Robbie Gaffney of the Tasmanian Department of Primary Industries, Parks, Water and Environment, for your support. To the Eastern Quoll Mainland Recovery Team, if not for your persistence in 2014 this project would never have begun. To the Australian Research Council, ACT Government, and Woodlands and Wetlands Trust, for providing the funding that made this project a reality. For your support, I, and the eastern quolls running around Mulligans Flat, thank you.

While the commitment of the partners lifted this project off the ground, the enormous contributions of the following people kept it in flight. To Andrew O'Meara, Christine Mauger, Daniel Iglesias, Dave Whitfield, David Shorthouse, Dean Heinze, Greg Hosking, Helen Crisp, Joel Patterson, John Lawler, Katherine Jenkins, Katherine Moseby, Lyall Marshall, Madeleine Tranter, Margaret Kitchin, Nick Mooney, Stu Jeffress, and many more. Also a heartfelt thank you to the veterinarians who gave their time and expertise to the project; Tim Portas, Michelle White, Jelena Vukcevic, Suzie Fowler, and more.

To my dear friends (the ‘Mulligang’), every time I’ve turned to you for support you’ve met me with unconditional love and support. I am so thankful to have found you all. To Cat and Maddie, thank you for lending me your vision and expertly capturing the essence of the eastern quoll in your illustrations that appear throughout this thesis. To Ash, for your endless encouragement, excellent eye for detail while reading drafts, and excitement when I passed my milestones - you helped me feel like I was truly capable of finishing this body of work.

To my family, for your unending faith in me. To Mum, for being the wind beneath my wings since the day I was born, and encouraging me to chase my dream of being a biologist. Being the daughter of an incredible force in progressing child and family health in rural and remote settings is one thing, but to be taking the PhD journey alongside you has been an honour. To Dad, for being my rock and being around for to talk about success, struggle, work, life, and the universe. To Peter, for encouraging me to aim for goals that seem just out of reach, and offering your wisdom along my academic journey. To my siblings, Allan, James, Jason, Matt, Rhianna, and Ben, for the laughs and adventures. To Juni, for bringing a little bit of light and love to each day.

Finally to the eastern quolls, thank you for keeping up the fight and saying no to extinction.

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Illustration by Cat Cotsell

Acronyms and abbreviations

ACT	Australian Capital Territory, territory in Australia
AEEC	Animal Experimentation Ethics Committee
ANU	The Australian National University
ARC	Australian Research Council
BOM	Australian Bureau of Meteorology
CMR	Capture-mark-recapture
CRL	Crown rump length
CSIRO	Commonwealth Scientific and Industrial Research Organisation
CTA	Conditioned taste aversion
CWR	Critical weight range
DPIPWE	Tasmanian Department of Primary Industries, Parks, Water and Environment
EPBC Act	Environment Protection of Biodiversity Conservation Act 1999
EQMRT	Eastern Quoll Mainland Recovery Team
GLM	Generalised linear model
GLMM	Generalised linear mixed model
GNR	Goorooyarroo Nature Reserve
GPS	Global positioning system
GUD	Giving-up density
IUCN	International Union for Conservation of Nature
MCP	Minimum convex polygon
MFGO	Mulligans Flat-Goorooyarroo Woodland Experiment
MFWS	Mulligans Flat Woodland Sanctuary
MTR	Mt Rothwell Biodiversity Interpretation Centre
NSW	New South Wales, state in Australia
PCA	Principle components analysis
PRBM	Post-release behavioural modification (Berger-Tal & Saltz 2014)
PVA	Population viability analysis
SEASON	South Eastern Australia Sanctuary Operations Network (Sharp 2021)
TTCS	Translocation Tactics Classification System (Batson *et al.* 2015)
VHF	Very high frequency
VIC	Victoria, state in Australia
WWT	Capital Woodlands and Wetlands Trust

Glossary

Glossary of terms and definitions used throughout this thesis. Where applicable, definitions have been quoted directly from their source(s) to ensure consistency. Bold text indicates terms defined in the glossary.

Adaptive management	A systematic approach for improving management actions by learning from outcomes ('learning by doing', Walters & Holling 1990; Williams *et al*. 2009).
Anthropocene	The global wave of anthropogenically driven biodiversity loss, including species and population extirpations and declines in local species abundance (Dirzo *et al.* 2014).
Area of occupancy	The area within a species' **extent of occurrence** which is occupied by a taxon, excluding cases of vagrancy (IUCN 2021).
Assisted colonisation	The intentional movement and release of a living organism outside its indigenous range to avoid extinction, primarily where protection from threats in the current range is less feasible than at alternative sites (IUCN 2013).
Back-casting	Technique where a desired end point is visualised, and then a pathway to that end point is worked out retrospectively (Manning *et al.* 2006).
Behavioural assay	Standardised experimental test of behaviour.
Behavioural reaction norm	Framework that represents an individual's behavioural responses as a regression line where the intercept corresponds to mean behaviour (**personality**) and the slope corresponds to how rapidly they adjust their behaviour over an environmental gradient (**plasticity**, Dingemanse *et al*. 2010).
Box-gum grassy woodlands	Endangered yellow box (*Eucalyptus melliodora*) - Blakely's red gum (*E. blakelyi*) grassy woodland ecological community in the Australian Capital Territory.
Bringing Back Biodiversity project	Australian Research Council-funded project (LP140100209) aiming to restore locally extinct species to Mulligans Flat Woodland Sanctuary, with collaboration between the ACT Government, ANU, CSIRO, and the James Cook University, as part of the long-term MFGO Woodland Experiment.
Carrying capacity	The threshold of security above which a population becomes insecure, and the surplus animals are vulnerable (Errington 1934).
Conditioned taste aversion	A tactic which can reduce the impact of predation on target species by conditioning an olfactory-reliant predator to associate a specific food source with a negative stimulus (Andrewartha *et al.* 2023).
Conservation introduction	The intentional movement and release of a living organism outside its indigenous range where the primary objective is a conservation benefit (IUCN 2013).
Conservation translocation	The intentional movement and release of a living organism where the primary objective is a conservation benefit: this will usually comprise improving the conservation status of the focal species locally or

	globally, and/or restoring natural ecosystem functions or processes. These can entail releases either within or outside the species' indigenous range (IUCN 2013).
Conspecific	Belonging to the same species.
Core range	Subset of a **home range** that describes the area of most intensive use (e.g., 50% of an estimate's volume contour), excluding excursive locations with the assumption that behaviour differs between core and excursive activities (Hodder *et al.* 1998).
Critical weight range	Australian mammals between 35–5500 g that suffer the greatest attrition, primarily due to predation by **invasive species** (Burbidge & McKenzie 1989).
Dasyurid	Carnivorous marsupial of the family Dasyuridae.
Defaunation	Reduction in population and range of fauna species driven by human-induced environmental change and destruction (Dirzo *et al.* 2014).
Descendent	A descendent of a **founder** (or a **reinforcer**).
Doomed surplus	Excess individuals that will never survive the seasonal bottleneck, primarily for species with high fecundity that trend toward a constant breeding density (i.e., density dependence, Errington 1945; Sibly *et al.* 2002).
Ecological replacement	The intentional movement and release of an organism outside its indigenous range to perform a specific ecological function; aiming to re-establish an ecological function lost through extinction, often involving the most suitable existing sub-species, or a close relative of the extinct species (IUCN 2013).
Evaluation measure	Also known as measure of success; to be monitored and reviewed to determine whether (1) a translocated population has reached the establishment, growth, or regulation phases, and (2) a program has met the criteria to enter the next phase. Evaluation measures should be selected to answer *a priori* questions (Armstrong & Seddon 2008), but are context-specific depending on the phase of the **Translocation Continuum**. Further, evaluation measures may need to be adjusted in light of new knowledge emerging as a **program** progresses along the Translocation Continuum. Examples include survival, dispersal, health, reproduction, recruitment, behavioural and genetic diversity, and ecosystem effects.
Exploration-exploitation dilemma	The trade-off between the need to obtain new knowledge and the need to use that knowledge to improve performance (Berger-Tal *et al.* 2014).
Extent of occupancy	Area contained within the shortest continuous imaginary boundary which can be drawn to encompass all the known, inferred or projected sites of present occurrence of a taxon, excluding cases of vagrancy (IUCN 2021).
Extirpated	No longer exists in the wild but occurs elsewhere (e.g., in captivity).
Founder	Relating to translocation **program**; a translocated individual has "no known genetic relationship to any other animal in the pedigree except for its own descendants: wild-caught animals, animals introduced to

	the pedigreed population from other captive sources for which no information on parentage is available, and other animals with unknown parents" (Lacy 1989).
Goldilocks zone	Where animals are exposed to enough predation that individuals are directionally selected to have traits that increase their likelihood of survival, without threatening their viability (Evans *et al.* 2021).
Harvest	Removal of individuals from a population for **translocation** to other locations.
Haven	Also known as safe haven or sanctuary; islands and conservation-fenced areas where principal threats (e.g., **invasive** predators) is either naturally absent or excluded by management (Ringma *et al.* 2018).
Home range	Broadly represents the interplay between the environment and an animal's understanding of that environment (Powell & Mitchell 2012). Estimates should account for how an animal values space, including places that are important but not necessarily frequented (e.g., 95% of an estimate's volume contour).
Indigenous range	A species' known or inferred distribution generated from historical records, physical evidence of the species' occurrence (IUCN 2013), or Indigenous knowledge.
Introduced species	A non-native species which has been introduced (i.e., translocated) into an environment by humans or other means.
Invasive species	An **introduced species** that has spread beyond the place of introduction and become detrimental to these new environments (e.g., by exerting predation or competition pressure).
Mesopredator	Mid-ranking predator in a food web, regardless of its size or taxonomy (Prugh *et al.* 2009).
Murunguny	Indigenous Ngunnawal language name for the eastern quoll (*Dasyurus viverrinus*).
Overdispersal	Where individuals disperse away from the reintroduction site and do not contribute to population establishment (Richards & Short 2003).
Parsimony	A decision-making approach where the practitioner balances the outcomes of multiple objectives to maximise learning with the least amount of loss (e.g., of **founders**).
Personality	Consistent behavioural differences between individuals that are repeatable over time and across contexts (Svendsen & Armitage 1972; Réale *et al*. 2007).
Phases	Five iterative steps through which a translocation **program** can progress, from high to low uncertainty: **Feasibility Studies**, **Pilot Studies**, **Primary Trials**, **Secondary Experiments**, **Tertiary Reinforcements**. Note that a **program** might not progress linearly through these phases and may need to repeat or regress to a previous phase if a new source of **uncertainty** is revealed.
Feasibility Study	Phase 1 under the Translocation Continuum; translocation planning intended to promote post-release performance using best available knowledge, where the primary **strategies** are identifying and

	designing **tactics**, and developing an **adaptive management** framework. This phase is evaluated using understanding of biological and ecological factors, opportunities and constraints, and a robust translocation plan including management scenarios (IUCN 2013).
Pilot Study	Phase 2 under the Translocation Continuum; limited release into an area with no **conspecifics**, to test the feasibility of a **program** within a defined period, where the primary **strategies** are stress-testing the **adaptive management** framework (developed during **Feasibility Studies**) and maximising learning. This phase is evaluated by survival, dispersal, and health of **founders**.
Primary Trial	Phase 3 under the Translocation Continuum; **parsimonious** release intended to establish a population, where the primary **strategies** are managing short-term survival and maximising learning. This phase is evaluated by survival, dispersal, health, reproduction, and recruitment. Such trials are usually unreplicated and uncontrolled, and used to generate hypotheses relating to persistence through correlation and inductive reasoning (Kemp *et al*. 2015). This phase is synonymous with the establishment phase (where post-release effects drive population dynamics, Sarrazin 2007).
Secondary Experiment	Phase 4 under the Translocation Continuum; **parsimonious** release intended to promote population growth with an opportunity for experimental replication and control, where the primary **strategies** are medium-term growth, and maximising learning across multiple **tactics**. This **phase** is evaluated by survival, dispersal, health, reproduction, recruitment, behavioural and genetic diversity, and ecosystem effects. This phase is synonymous with the growth phase (characterised by high rates of expansion and continuing until the population approaches carrying capacity, Sarrazin 2007).
Tertiary reinforcement	Phase 5 under the Translocation Continuum; appropriate release to reinforce population demographic, behavioural, and/or genetic diversity, where the primary **strategies** are ensuring long-term viability, and maximising learning across multiple **tactics**. This phase is evaluated by survival, dispersal, health, reproduction, recruitment, behavioural and genetic diversity, and ecosystem effects. This phase is synonymous with the regulation phase (where density-dependence limits survival and recruitment, Sarrazin 2007).
Plasticity	The ability to alter behaviour in response to changing conditions (or responsiveness, Komers 1997; Piersma & Drent 2003; Bonte *et al*. 2007).
Post-release behavioural modification	PRBM; the process where an animal will adjust its movement (e.g., foraging, predator avoidance) as it becomes more familiar with its environment (Berger-Tal & Saltz 2014). Translocated individuals are expected to move along the PRBM continuum from exploratory to more knowledge-based movements within an established and familiar **home range**.
Program	A translocation project that aims to establish a population of a target species in an area. Depending on the amount of uncertainty involved,

	a program can begin with a **Feasibility Study** and, if appropriate, progress through the iterative translocation **phases**.
Reinforcement	Also known as supplementation; the intentional movement and release of an organism into an existing population of **conspecifics**, aiming to enhance population viability (e.g., by increasing genetic diversity, IUCN 2013).
Reinforcer	Relating to translocation programs; a type of **founder** that has been translocated to an area with established conspecifics in a subsequent release of a translocation **program** with the aim of reinforcing demographic, behavioural, and genetic diversity in a population.
Reintroduction	The intentional movement and release of an organism inside its **indigenous range** from which it has disappeared, aiming to re-establish a viable population of the species (IUCN 2013).
Resident	**Founders** (and **reinforcers**), their **descendants**, and existing individuals that are established at the recipient site (i.e., are no longer subject to post-release effects).
Risk	Applies to situations where an outcome is unknown, but its probabilities can be quantified (Knight 1921).
Shifting baseline syndrome	The phenomenon where long-term conservation goals are limited by short-term human memory of ecosystems (Pauly 1995; Miller 2005; Manning *et al*. 2006).
Strategy	Clearly defined objective (e.g., minimising dispersal) to be met during a **translocation phase**. Strategies guide **tactics** selection, maximise the probability of positive outcomes, and maintain the **program** efficiency and feasibility (Batson *et al.* 2015).
Stretch goal	Ambitious targets used to inspire creativity and innovation to achieve outcomes that currently seem impossible (Manning *et al.* 2006).
Tactic	Animal- or environment-focussed technique capable of influencing post-release performance or population persistence (Batson *et al.* 2015).
Translocation	The human-mediated movement of living organisms from one area to another (IUCN 2013).
Translocation Continuum	Multi-phased framework which guides the decision-maker through five iterative **phases** along a continuum of **uncertainty**, while being grounded in the context of the three translocation **phases** (Sarrazin 2007). The framework was designed for tetrapod translocations, but can be adapted for other taxa.
Uncertainty	Applies to situations where an outcome is unknown, and its probabilities cannot be quantified (i.e., Knightian uncertainty, Knight 1921).

Abstract

Biodiversity loss in the Anthropocene, driven by human-induced environmental change and destruction, threatens ecosystem function and the health of all living beings. Translocations are a critical tool used to reverse this biodiversity loss, and their outcomes hinge on a population's passage through the establishment (where post-release effects drive population dynamics), growth (characterised by high rates of expansion), and finally, regulation phases (where density dependence limits survival and recruitment). However, management decisions are always made in the face of imperfect knowledge, which have historically led to low levels of translocation success.

In this thesis, I explored tactics, behaviour, movement, and species recovery related to reintroductions (translocation to a species' indigenous range from which it has disappeared), using the model system of eastern quolls (*Dasyurus viverrinus*, 'murunguny' in the Indigenous Ngunnawal language) at a conservation-fenced, 'outdoor laboratory'; Mulligans Flat Woodland Sanctuary (MFWS) in the Australian Capital Territory (ACT). The eastern quoll is an endangered carnivorous marsupial of high conservation priority with an indigenous range that included the ACT, and the potential to fulfil the ecological role of a ground-dwelling mesopredator. I aimed to harness the best available knowledge relating to the eastern quoll's biology and ecology to improve reintroduction outcomes, as well as develop frameworks that could be applied to translocation programs for other species across the globe.

To establish a population of eastern quolls at MFWS, we conducted a reintroduction program in a series of iterative trials from 2016 to 2018, followed by a reinforcement translocation in 2019. We designed each trial to maximise the knowledge we could gain to our inform strategies and tactics for the next trial. Throughout the establishment, growth, and regulation phases of the reintroduction, I assessed eastern quolls using pre-release behavioural assays (Chapter 3), monitored their post-release survival and dispersal using VHF (Chapters 2–4) and GPS collars (Chapter 4), and monitored their population dynamics using capture-mark-recapture methods (Chapter 5).

In Chapter 1, I summarised the literature relating to reintroductions, conservation fencing, and the eastern quoll species. I then presented an overview of the eastern quoll reintroduction to MFWS, to provide the context for understanding the project and the relationships between its different aspects.

In Chapter 2, I demonstrated the value of iterative trials in achieving the reintroduction milestone of establishment. By comparing survival- and dispersal-related measures across three

trial reintroductions of eastern quolls to MFWS, I showed how we can use learnings from such trials to adapt tactics in a way that could lead to positive outcomes in later trials.

In Chapter 3, I investigated whether behavioural measures in reintroduced eastern quolls could predict post-release survival and dispersal using the ‘behavioural reaction norm’ approach. Personality (consistent individual variation in behaviours) and plasticity (ability to adjust behaviour over time) can play a pivotal role in determining post-release performance. By integrating novelty into behavioural assays, I found that they offer significant value as a conservation tool.

In Chapter 4, I investigated how movement, habitat use and preference, and conspecific association differed between eastern quoll residents (established individuals) and reinforcers (individuals translocated to reinforce demographic, behavioural, and genetic diversity of a population) at MFWS. The results revealed movements at a greater spatio-temporal resolution than has ever been achieved for this species. These findings offer important insights into appropriate habitat structure for future reintroduction sites, and highlight the need for intensive post-release monitoring to inform adaptive management interventions to ensure the success of reintroductions and reinforcements.

In the Chapter 5, I demonstrated how demographic parameters can reveal threats to persistence, inform thresholds for management, and create targets for removing species from the IUCN Red List. To avoid the pitfall of long-term restoration goals being limited by short-term human memory of ecosystems (‘shifting baseline syndrome’), I visualised an ambitious end point (‘stretch goal’, i.e., recovery of the eastern quoll species within 10 years), and projected the population size and habitat required to achieve this goal (‘back-casting’). While the targets may appear daunting, our goals must be ambitious to inspire the innovation needed to achieve long-term outcomes that currently seem impossible.

In the penultimate Chapter 6, I took the learnings from this thesis and developed the ‘Translocation Continuum Framework’. The framework creates clarity around translocation ‘phases’, their criteria, strategies, tactics, evaluation measures, and expected outcomes. I discuss the limitations of ‘success’ and ‘failure’ labels in translocation science, and the importance of parsimonious decision making that balances objectives to maximise learning with the least amount of loss. By avoiding ‘short-termism’ and managing expectations of the likelihood of establishment, growth, and regulation throughout a program’s lifetime, we can galvanise trust and investment in translocations so they can contribute meaningfully to long-term restoration.

In the final Chapter 7, I provide a summary of the key findings from each of my Chapters, synthesise how these substantially contributed to the conservation and translocation sciences, and recommend future studies to build on this body of work.

Chapter 1: Extended context statement

“*As I watched [the quolls] in that perfect moment of peacefulness and contentment, I realised that the happiness I feel in any given encounter with wildlife runs parallel with the awareness that such wildlife is a shadow of what it was in my parents' time, or in my grandparents' time. The sorrow is there, but crucially, so is the joy.*”

- Harry Saddler, Questions Raised by Quolls

Illustration by Cat Cotsell

1.1 Biodiversity crisis

Biodiversity loss in the Anthropocene, driven by human-induced environmental change and destruction, threatens ecosystem function and the health of all living beings (Dirzo *et al.* 2014). While restoration presents a major challenge for the next century, our long-term goals can be limited by the short-term human memory of ecosystems, where we begin to accept reduced biodiversity as the new 'normal' (i.e., 'shifting baseline syndrome', Pauly 1995; Miller 2005). This, combined with the radical and complex nature of restoration, can cause decision-makers to limit or postpone their vision before they even begin (Manning *et al.* 2006).

To overcome these barriers, conservationists can capitalise on 'big ideas' by setting highly ambitious, long-term goals ('stretch goals'), and systematically work backwards towards those goals ('back-casting', Manning *et al*. 2006). This pathway "*enables us to think creatively about the society of tomorrow, without being blinded by the obstacles and problems that exist just at the moment*" (Cinq-Mars & Wiken 2002). Indeed, there are some inspiring examples where large-scale restoration has been made possible by this big thinking, such as 'Trees for Life' in the Scottish Highlands (Watson Featherstone 1997), 'Arid Recovery' in South Australia (Moseby *et al.* 2009), and 'Working Lands for Wildlife' in North America (Martinez 2015).

1.2 Reintroductions

Translocations are a critical conservation tool used to reverse biodiversity loss and restore ecosystem function (Armstrong & Seddon 2008). Defined as the intentional movement and release of a living organism, translocations can be of benefit by improving the conservation status of the focal species locally or globally, and/or restoring natural ecosystem functions or processes (IUCN 2013). Further, a translocation can involve the release of organisms into their indigenous range following their local extinction or extirpation. This is known as a reintroduction, and such programs aim to re-establish viable, free-ranging populations.

Reintroduction success hinges on a population's passage through three reintroduction 'phases': establishment (where post-release effects drive population dynamics), growth (high rates of expansion), and finally, regulation (where density dependence limits survival and recruitment, Sarrazin 2007). However, management decisions in the real world are always made in the face of imperfect knowledge about species and ecosystems (Armstrong & Seddon 2008), which have historically led to low levels of reintroduction success (Griffith *et al*. 1989; Kleiman 1989; Armstrong & Craig 1995b; Fischer & Lindenmayer 2000; Seddon *et al*. 2007; Sheean *et al*. 2012). To address this, practitioners are encouraged to incorporate experimental designs into their programs, including defined hypotheses, repetition, and control to facilitate a clearer understanding of the factors that drive outcomes (Armstrong & Seddon 2008).

1.2.1 Monitoring

The success of reintroduction programs inherently relies on the survival, dispersal, and reproduction of founding individuals (henceforth founders); the rates of which are likely to change over time (Støen *et al*. 2009; le Gouar *et al*. 2012; Wilson *et al*. 2020). While survival and reproduction have a clear influence on reintroduction outcomes since high mortality can greatly compromise establishment and genetic diversity (Swaisgood 2010), dispersal can also provide valuable information on habitat quality and indicate the success or failure of restoration actions (Bennett *et al.* 2012; le Gouar *et al.* 2012).

As per the exploration-exploitation dilemma (i.e., the trade-off between learning and using knowledge to improve performance, Berger-Tal *et al*. 2014), an animal will adjust its movement (e.g., foraging, predator avoidance) as it becomes more familiar with its environment (i.e., post-release behavioural modification or PRBM, Berger-Tal & Saltz 2014). Translocated individuals are expected to move along a continuum from exploratory movements to more knowledge-based movements within an established and familiar home range. This sequence of initially high daily movements, followed by home range establishment, has been observed in translocated raccoons (*Procyon lotor*, Mosillo *et al*. 1999), dormice (Bright & Morris 1994), grey wolves (*Canis lupus*, Fritts *et al*. 1984), and swift foxes (*Vulpes velox*, Moehrenschlager & Macdonald 2003). Uncertainty related to translocation outcomes can be addressed by robust monitoring of survival, dispersal, and reproduction; parameters which can indicate population self-sustainability, density-dependence, carrying capacity, and threats to these processes (Manning *et al.* 2019; Parlato *et al.* 2021).

1.2.2 Tactics

Reintroduction outcomes can be actively improved by employing ‘tactics’ (techniques which can influence post-release performance and persistence) guided by well-defined strategies (objectives or goals, Batson *et al*. 2015). Tactics can be animal- or environment-focussed, and include founder selection, pre-conditioning of the release environment, threat mitigation, resource augmentation, and more. Tactics should be informed by well-defined strategies (i.e., objectives), such as maximising survival or minimising post-release dispersal.

To clarify this thinking, Batson *et al*. (2015) developed the Translocation Tactics Classification System (TTCS, Figure 1.1) to provide a framework to improve the ability to identify, select and design tactics which help achieve defined strategies. The TTCS guides practitioners through a logical and ecologically relevant framework. By encouraging a standardised and systematic process for designing translocations, practitioners can use this tool to rapidly learn from less effective tactics and improve outcomes (e.g., Wilson *et al*. 2020).

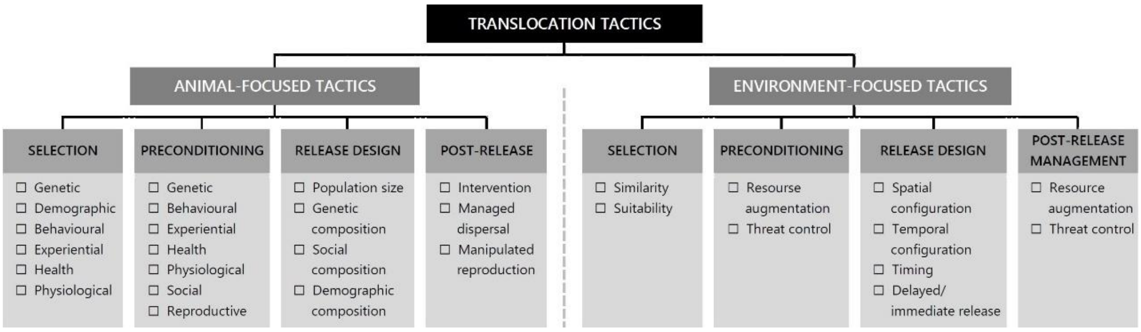

Figure 1.1 Translocation Tactics Classification System, adapted from Batson *et al*. (2015) in Wilson *et al*. (2020).

1.2.3 Adaptive management

Determining which tactics to use can be complex. Translocations are often context-specific, and knowledge of the recipient ecosystem is never complete (Walters & Holling 1990). Adaptive management can address this 'wicked problem' (DeFries & Nagendra 2017) by offering a systematic approach to improve management actions through learning from outcomes (i.e., 'learning by doing', Walters & Holling 1990; Williams *et al*. 2009). Adaptive management is considered the best available approach for managing biological systems where there is considerable uncertainty (Westgate *et al.* 2013). Rather than waiting until enough is known about an ecosystem (Lee 1999), practitioners can implement and adjust their management actions 'on the fly' in response to outcomes observed through robust monitoring (e.g., (Kingsford *et al.* 2021).

1.2.4 Trials and experiments

Translocation practitioners face a plethora of decisions with competing interests, including the need to produce research output (i.e., peer-reviewed publications) to increase their chance of securing future funding. Barriers to publishing in translocation science include limited resources (e.g., funding constraints), lack of scientific novelty (which ignores the value of fundamental studies and repetition) and the required scientific rigour (e.g., sample size) needed to publish in many journals (Batson *et al.* 2015). As such, despite the need for parsimonious decision making, practitioners have been strongly encouraged to design translocations within experimental frameworks to test hypotheses (Armstrong *et al.* 1994; Seddon *et al.* 2007; Armstrong & Seddon 2008; Kemp *et al.* 2015) and control for the effects of demographics, genetics, and the source environment (Jule *et al.* 2008) from the outset.

However, threatened species translocation programs are inherently limited in their ability to source large sample sizes of individuals to use in experimental designs (Kemp *et al.* 2015). Within this context, practitioners need act parsimoniously (i.e., maximising gains while minimising losses) by conducting translocation trials (e.g., Watts *et al.* 2017; West *et al.* 2019b; Wilson *et al.* 2020). Trials are usually unreplicated and uncontrolled, and used to generate hypotheses relating to persistence through correlation and inductive reasoning (Kemp *et al.* 2015), as opposed to strict experimental designs with large sample sizes. Here, a parsimonious number of individuals can be exposed to a single or limited set of tactic designs to answer questions identified *a priori* (Armstrong & Seddon 2008). Only by being parsimonious, even if it is at the expense of scientific rigour, can we minimise unnecessary loss (e.g., of founders). Using this approach, practitioners can address uncertainty, and build the knowledge upon which future releases can be launched.

1.3 Conservation fencing

In the face of rapid biodiversity loss, fences have become an important conservation mitigation tool across the world (Innes *et al*. 2012; Malpas *et al*. 2013; Massey *et al*. 2014; Legge *et al*. 2018). Australia has suffered the highest rate of mammal extinctions of any continent (Woinarski *et al.* 2015), due in large part to predation by invasive species (e.g., European red fox *Vulpes vulpes* and feral cat *Felis catus*, Kinnear *et al*. 2002; Radford *et al*. 2018). To circumvent these threatening processes, substantial efforts have been made to establish fenced reserves across the continent to exclude these invasive predators, as well as destructive herbivores (e.g., European rabbits *Oryctolagus cuniculus*, and European hares *Lepus europaeus*) and livestock. These 'safe havens' (or 'sanctuaries') have enabled the reintroduction of at least 38 species (Hayward & Kerley 2009; Moseby *et al*. 2011; Legge *et al*. 2018). The benefits of conducting long-term, large-scale experiments under such fenced conditions are increasingly being recognised, and offer researchers the opportunity to build an understanding of ecological processes which may otherwise be impossible (Hester *et al.* 2000; Manning *et al.* 2009).

1.3.1 Mulligans Flat-Goorooyarroo Woodland Experiment

Mulligans Flat Woodland Sanctuary (MFWS) is a publicly accessible, 485 ha reserve situated on Ngunnawal and Ngambri Country, on the northern border of the Australian Capital Territory (ACT, -35.166543, 149.157946). Mulligans Flat Nature Reserve (984 ha, within which MFWS is situated) and the adjoining Goorooyarroo Nature Reserve (GNR, 1,138 ha) contain the largest unfragmented patch of yellow box (*Eucalyptus melliodora*) - Blakely's red gum (*E. blakelyi*) grassy woodland in Australia that is under public ownership and is managed primarily for conservation (Figure 1.2, Figure 1.3, McIntyre *et al*. 2010). Since European colonisation, these temperate woodlands have suffered livestock grazing, fertilisation, and removal of coarse woody debris, which has led to soil degradation, weed invasion, and biodiversity loss (McIntyre *et al.* 2010). As a result, this ecological community is listed as endangered in the ACT (ACT

Government 2004) and critically endangered as a component of the federally listed white box (*E. albens*) - yellow box - Blakely's red gum grassy woodland and derived native grassland (Australian Government 1999).

MFWS and GNR act as an 'outdoor laboratory' for the Mulligans Flat-Goorooyarroo Woodland Experiment (MFGO Woodland Experiment), which generates evidence to support conservation decision making aimed at restoring woodlands for biodiversity and ecological function (e.g., supplementing coarse woody debris, controlling grazers, reintroducing species, Manning *et al*. 2011; Shorthouse *et al*. 2012). The MFGO Woodland Experiment represents a long-term partnership between ACT Government managers and researchers, The Australian National University researchers, and the Capital Woodlands and Wetlands Trust members. These partners are committed to conserving woodland and creating a nationally significant, community-led conservation project where research and learning can contribute to the restoration process, as well as act as a catalyst for ambitious conservation thinking that could see similar restoration projects being established elsewhere (Manning *et al.* 2011; Shorthouse *et al.* 2012).

As part of the MFGO Woodland Experiment, MFWS was encircled with an 11.5 km predator-proof fence in 2009 to exclude invasive predators including red foxes and feral cats, destructive herbivores such as European rabbits, European hares, and livestock (Shorthouse *et al.* 2012). While these threatening and destructive species have been eradicated from within the Sanctuary, conditions are otherwise like other unfenced woodlands in the region. The fence design includes an overhang on the outside edge that prevents entry by invasive species (based on successful trials at Arid Recovery, Moseby & Read 2006), but was adapted for local conditions (as per Shorthouse *et al*. 2012). However, this design does not prevent agile species from climbing out of the Sanctuary into the surrounding landscape.

The fencing of MFWS has provided a haven into which locally extinct native species can be reintroduced within an experimental framework (Shorthouse *et al.* 2012). So far, this includes the eastern bettong (*Bettongia gaimardi*, Manning *et al*. 2019), bush stone-curlew (*Burhinus grallarius,* Rapley 2020), and New Holland mouse (*Pseudomys novaehollandiae*, Abicair *et al*. 2020; Smith *et al*. 2022). When the eastern bettong was reintroduced to MFWS in 2012 to restore its role as an ecosystem engineer (Munro *et al.* 2019; Ross *et al.* 2019), the role of a native ground-based predator remained vacant.

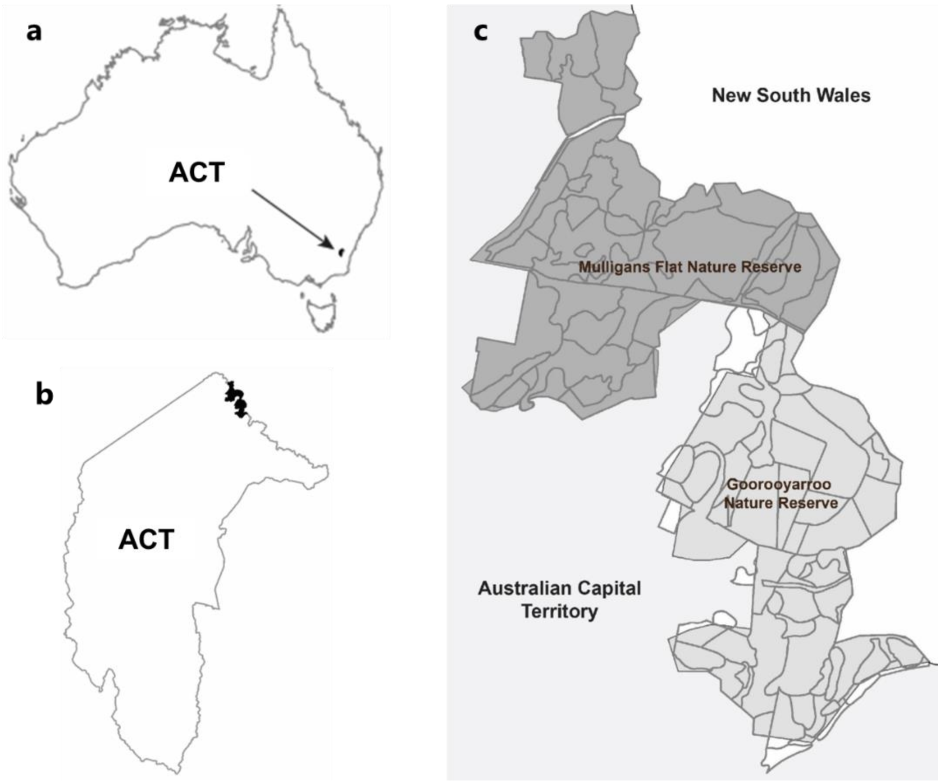

Figure 1.2 Location of the Mulligans Flat-Goorooyarroo Woodland Experiment in south-eastern Australia (**a**), and on the northern border of the Australian Capital Territory (**b**). The Experiment includes Mulligans Flat Nature Reserve (within which Mulligans Flat Woodland Sanctuary resides) and Goorooyarroo Nature Reserve (**c**). Maps by Jenny Newport.

Figure 1.3 Photograph of a typical sclerophyll forest (left), track (centre), and regenerating midstory (right) present in Mulligans Flat Woodland Sanctuary, Australian Capital Territory. Photo commissioned by the Woodlands and Wetlands Trust.

1.4 Eastern quoll

1.4.1 Biology

The eastern quoll (*Dasyurus viverrinus*, ‘murunguny’ in the Indigenous Ngunnawal language) is a carnivorous marsupial (family Dasyuridae, Stannard & Old 2013) of small-to-medium size (700–2000 g). It is in the ‘critical weight range’, where Australian mammals between 35–5500 g suffer the greatest attrition due to invasive predators (Burbidge & McKenzie 1989). They are the only quoll species which exhibit two distinct and non-overlapping colour morphs. Both morphs, fawn (sandy-coloured with white spots) and dark (jet black with white spots, Figure 1.4), can occur in the same litter (Jones *et al.* 2001).

The species is sexually dimorphic, with females (mean 0.7 kg) being two-thirds the size and weight of males (mean 1.1 kg, Bryant 1988). Females breed synchronously in early Austral winter, birth 21 days later, and wean after five months (Jones *et al.* 2001). Populations experience high turnover driven by juveniles (female juvenile annual survival 64.17% ± 19.92, male 64.93% ± 19.87), and fluctuate seasonally with highest densities observed in early summer following the juvenile weaning, and minimum densities in August due to some die-off of males following the breeding season and high juvenile mortality (Godsell 1983; Wilson *et al.* 2023).

Eastern quolls are solitary but tend to form loose neighbourhoods. Individuals may have overlapping home ranges but maintain large interindividual distances (>200m, Godsell 1983), suggesting that they avoid their neighbours. The home ranges of males tend to be larger (mean 44 ha) and more variable in size than those of females (mean 35 ha), though those of the latter increase while weaning their young (Godsell 1983). Home ranges are typically only shared between related females and mothers and their litters, and female aggression is normally only directed to other mothers supporting large young (Godsell 1983).

1.4.2 Ecology

Eastern quolls are nocturnal and become active around dusk for eight hours regardless of season (Jones *et al.* 1997). Due to their generalist and predatory nature, eastern quolls are capable learners (Shettleworth 1984), with olfactory and auditory cues likely to be as important as visual cues because they forage in long grass and thick understory (Blumstein 2000). They are often associated with forest-grassland ecotones that provide open grasslands for foraging during the night, and forest habitat where they can den in hollow logs, rock crevices (Godsell 1983), and abandoned rabbit warrens during the day (B. A. Wilson *pers obs*).

Their diet is dominated by invertebrates, but also comprises small mammals, birds, reptiles, vegetation. Like fellow dasyurids the Tasmanian devil (*Sarcophilus harrisii*) and the

Figure 1.4 Lithograph of a fawn (left) and a dark (right) morph eastern quoll (*Dasyurus viverrinus*) illustrated by Elizabeth Gould (maiden name Coxen) from The Mammals of Australia, written and published by English Ornithologist John Gould, 1863.

spotted-tailed quoll (*Dasyurus maculatus*), they will also scavenge on carrion (Blackhall 1980). As a mesopredator, eastern quolls invest in vigilance behaviour in response to known predators (e.g., masked owls *Tyto novaehollandiae*, Mooney 1993; Frankham *et al.* 2016) and competitors (e.g., Tasmanian devils, Jones & Barmuta 1998).

During the day they den underground or in logs or rocky outcrops, often in areas that are proximal to foraging grounds, with a preference for ecotones between forest and open grassland (Godsell 1983). Den sharing was considered rare (Godsell 1983; Jones *et al.* 2001) until frequently observed between reintroduced females (Wilson *et al.* 2020).

1.4.3 Distribution

Once irruptive and broadly distributed throughout south-eastern mainland Australia (Godsell 1983; Peacock & Abbott 2014), the eastern quoll disappeared from the mainland due to a combination of predation and competition by invasive predators, habitat loss, disease, and human encroachment and persecution (Bryant 1988; Jones *et al.* 2001; Peacock & Abbott 2014). After the 1960s, the eastern quoll became restricted to the island state of Tasmania where it lived in low densities in the drier, eastern half of the island state (Jones & Rose 1996). While there is no robust assessment of population size, spotlighting data indicated sightings in historical hotspots had decreased by 52% from 1999 to 2009 (Fancourt *et al.* 2013), and recent evidence revealed an earlier decline in the north (mid-1990s) and south (~2009) of Tasmania (Cunningham *et al.* 2022). In response, the species was listed as endangered by the International Union for Conservation of Nature (IUCN, Burbidge & Woinarski 2016) and the Environment Protection and Biodiversity Conservation Act 1999 (Australian Government 1999).

1.4.4 Conservation

The loss of a species from an area not only removes it from the ecological community, but also from Country and the connection to Indigenous peoples. This represents a profound loss because of their deep cultural and spiritual obligations to land, water, and their fauna (Taylor-Bragge *et al.* 2021). Likewise, the reintroduction of a species restores it to Country, even if the primary objective is ecological restoration (Ireland *et al.* 2018).

In 2015, the Eastern Quoll Mainland Recovery Team recommended reintroducing eastern quolls to conservation-fenced havens on mainland Australia to safeguard the species should threatening processes drive Tasmanian populations to extinction. There are now two successfully reintroduced populations living ‘as wild’ on mainland Australia: Mt Rothwell Biodiversity Interpretation Centre in Victoria (Mt Rothwell; also a conservation-fenced area) and MFWS in the ACT, where it is now listed as endangered (Nature Conservation Act 2014 s 90C, ACT Parliamentary Counsel 2014). The MFWS reintroduction is detailed below.

1.4.4.1 Reintroduction

The eastern quoll was considered a feasible candidate for a trial reintroduction to MFWS because (1) it is one of 20 mammal species of high conservation priority (Australian Government 2015), 2) it had an indigenous range that included the ACT, and (3) the Sanctuary was depauperate of ground-dwelling predators, and it could therefore fulfil this ecological role.

To reach our stretch goal of re-establishing the eastern quoll in the ACT, we needed to (1) be structured in our selection of tactics, and (2) address uncertainty by adapting our tactics ‘on the fly’ when new knowledge became available. To do this, I used the Translocation Tactics Classification System to clarify my tactical thinking (TTCS, Figure 1.1, Batson *et al.* 2015), and adopted an adaptive management approach where monitoring facilitated rapid learning, and led to interventions that improved the probability of translocation success (Wilson *et al.* 2020). This was achieved by reintroducing founders in a series of trials (Trial 1 in 2016, Trial 2 in 2017, and Trial 3 in 2018) where learnings were used to refine tactics for future trials (Wilson *et al.* 2020, 2021). This staged approach also helped us manage the risk of exceeding the carrying capacity of MFWS, since this was unknown at the start of the program (Manning *et al.* 2015). Since I began my candidature in 2017, I was directly involved in planning, translocations, and monitoring from Trial 2 onward.

Forty-four founding individuals (henceforth founders) were translocated to MFWS across the three trials, with a reinforcement translocation in 2019 to maximise genetic diversity of the population (Wilson *et al*. 2020, 2021). Founders were either captive-bred or wild-caught. Captive founders were sourced from Mount Rothwell, situated 60 km south-west of Melbourne. Wild founders were derived from free-ranging populations across 14 geographic regions in Tasmania, separated by at least 15 km or a significant geographical barrier to eastern quoll dispersal. To minimise impacts on the source population and maximise genetic diversity in the reintroduced population, no more than two animals in each cohort originated from any one site (Manning *et al.* 2015).

We defined our success criteria as ≥67% of founders surviving, maintaining condition, and reproducing after 42 days post-release (the establishment period, Wilson *et al*. 2020). Additional success criteria included population growth and persistence (Chapter 5), and genetic and behavioural diversity, which are being monitored over the long term (as for the eastern bettong, Brockett *et al*. 2022).

1.4.4.1.1 Trial 1 (pilot)

In late February through to early March 2016, the MFGO Woodland Experiment team and the project partners reintroduced fourteen eastern quoll founders (six females and eight males) to MFWS. They selected captive and wild founders that were in fair to excellent body condition (using a subjective assessment of fat and muscle stored between the hips and spine) (Portas *et al.* 2016), weighed more than 640 g, and were estimated to be 1-2 years old (inferred from tooth condition and wear). None of the females were carrying pouch young because mating had yet to occur in late austral Autumn to early Winter (Godsell 1983).

Founders were translocated to the ACT by air and road, where they were anaesthetised and assessed for health and disease (Portas *et al.* 2020). They were microchipped for future identification, fitted with VHF (32g, V6C 163 Zilco, Sirtrack Ltd, Hawkes Bay, New Zealand) or GPS collars (38 g, LiteTrack 30 RF, Sirtrack Ltd, Hawkes Bay, New Zealand), and were sampled for fur, blood, DNA (by ear biopsy), and scats. Releases were carried out as soon as possible (i.e., animals were transported to ACT, underwent health assessments, and were released on the same day) from a cotton bag in randomly allocated locations within MFWS. This was done at night to minimise stress and provide maximum time to explore MFWS and find a den before first light. No supplementary food was provided. Within days of the first release, seven founders escaped over the Sanctuary fence. By the end of the first establishment period, 44% of founders had survived, 38% maintained body condition, and 63% of the remaining females produced young.

The key findings from this pilot reintroduction were that (1) founders that moved between dens on consecutive nights were more likely to escape, and were therefore less likely to survive, and (2) this den movement was lower for females (Wilson *et al*. 2020, 2021). We hypothesised that the greater number of male escapes was exacerbated by the timing of release, because eastern quolls experience elevated breeding hormones in autumn, stimulating mobility and aggression in males (Godsell 1983). We suspect that females may have also struggled to settle because they were being pursued by males and were likely to also have elevated hormones associated with the breeding season.

1.4.4.1.2 Trial 2

After the first trial revealed high male mortality associated with overdispersal (Wilson *et al.* 2020, 2021), we adapted our tactics and selected female founders only for subsequent trials. We hypothesised that maternal females with dependent (i.e., pouch) young (henceforth mothers) would prioritise finding and maintaining a natal den, thereby avoiding the elevated male mortality and dispersal observed in the pilot translocation, and reducing stress and collar fit issues associated with breeding hormones (male eastern quolls put on weight during the breeding season, potentially resulting in collar injury). This 'maternity translocation' tactic has been similarly used in translocations of banded hare-wallabies (*Lagostrophus fasciatus*, Short 1992), black bears (*Ursus americanus*, Eastridge & Clark 2001), black-eared miners (*Manorina melanotis*, Clarke *et al*. 2002), greater sage-grouse (*Centrocercus urophasianus*, (Meyerpeter *et al.* 2021), and crest-tailed mulgara (*Dasycercus cristicauda*, West *et al*. 2022). In our case, by translocating female eastern quolls in winter, several were either pregnant or carrying pouch young, allowing us to reintroduce 'seven for the price of one' (i.e., dependent males and females 'via the pouch'). This also potentially increased genetic diversity because members within each litter can have different sires (e.g., in northern quolls *Dasyurus hallucatus*, Chan *et al*. 2020). However, mothers are likely to have energetic costs associated with parturition and parental care, so their decisions may be driven by an increased trade-off between food intake and offspring safety (Gillingham & Bunnell 1985). This context emphasises the importance of considering life history when selecting founders.

In terms of environmental selection tactics, in the second trial I moved the release site to a central location in MFWS, maximising the distance that would be covered before a founder would encounter the fence. This also allowed them to encounter food resources, den sites, conspecifics, or other features of interest before the fence. In addition, I suspected that the first trial method of releasing founders in bags may have increased stress, so I adapted our animal release design by placing founders *in situ* in a wooden box with the door closed for one to two hours. After last light, I opened the door from behind the den box to allow the founder to leave of its own accord (also adopted for western quolls *Dasyurus geoffroii*, Jensen *et al*. 2021). I hypothesised this would minimise stress and provide maximum time for founders to explore MFWS and find a den before first light.

In the second trial, we translocated thirteen female founders (six captive founders from Mt Rothwell, and seven wild founders from Tasmania), trapping them during the austral winter to capture females carrying pouch young that were fused to the teat (<60 days of age, ~25mm crown rump length, Bryant 1988). Concurrently to employing these tactics, I performed pre-release behavioural assays on the founders to explore whether personality and plasticity could predict post-release performance (Chapter 3, Wilson *et al*. 2022). I achieved this by holding founders in pens for ≥8 nights where, during the assay period, I simulated a risk and measured easily quantifiable behavioural responses including latency to emerge (Fox 1972), time spent vigilant and giving-up density. I then extracted personality and plasticity indices derived from these behavioural responses (using the behavioural reaction norm approach, Dingemanse *et al*. 2010). Finally, I tested associations between these personality and plasticity indices and post-release performance during an initial establishment period.

Due to observed weight loss after assays, I decided to act within an adaptive management framework and supplementarily feed founders in the wild in decreasing amounts over time until their weights stabilised. While supplemental feeding can encourage site fidelity (Doonan & Slade 1995; Doligez *et al*. 2004), dispersal rates between our founders and those of the third trial one year later were comparable despite the latter not requiring supplemental feeding (Wilson *et al.* 2020). By the end of the establishment period in 2017, 92% of founders had survived, 92% maintained body condition, and 85% produced young. From October to December 2017, I trialled harvesting (removing individuals from the population for translocation to another location) juveniles born to female founders. I caught, microchipped, and biopsied nine juveniles.

Of those, I sent four juveniles belonging to Tasmanian mothers to Mt Rothwell as part of metapopulation management for the eastern quoll species. This approach involves managing species through a coordinated and collaborative sanctuary network across multiple sites where decisions regarding management interventions are based on robust monitoring of the populations' demographics and genetic composition (e.g., South Eastern Australia Sanctuary Operations Network or 'SEASON', Sharp 2021). This network will buffer against the demographic and genetic perils facing isolated populations, and limit edge effects associated with small occupancy areas (McGregor *et al.* 2020).

1.4.4.1.3 Trial 3

The third trial took place in 2018, and since conspecifics were established at MFWS, I refer to translocated individuals as 'reinforcers'. I designed this translocation similarly to the second trial, but since no significant differences in survival or dispersal were found between captive and wild founders in the first two trials, I only selected the more genetically diverse wild founders for this trial (preferring those that were mothers, Wilson *et al*. 2020). During this trial, I fitted 38 g (<5% of each animal's body weight) GPS collars (LiteTrack 30 RF, Sirtrack Ltd, Hawkes Bay, New Zealand) on eight reinforcers and eight MFWS-born resident females to compare their movements and conspecific associations at a finer spatio-temporal scale than had ever been achieved for this species (Chapter 4). By the end of the 2018 establishment period, 88% of founders had survived, 100% of those that survived maintained their body condition, and 88% of the survivors also produced young.

Finally, in 2019 I conducted a translocation with the same tactics as the third trial to add genetic diversity to the population, but without intensive post-release monitoring because the knowledge required to ensure positive outcomes had already been gained through previous trials.

1.4.4.2 Monitoring

1.4.4.2.1 Post-release

I monitored the post-release survival and dispersal of founders and reinforcers using several methods. Using VHF collars, I radiotracked founders (Chapter 2), reinforcers (Chapters 3–4), and residents (Chapter 4) to their diurnal dens, and cage-trapped them regularly to monitor their body weight, condition, and collar fit (to ensure the welfare of animals that put on weight, potentially resulting in collar injury). I also used GPS collars to monitor movement at a finer spatio-temporal resolution than had ever been achieved for this species (Chapter 4).

If a founder escaped over the fence, I radiotracked them to their location, and trapped and re-released them at their initial release site at MFWS. If any founder attempted two escapes, we translocated it to Mt Rothwell based on the assumption that it would only escape again if re-released. If a mortality signal was detected, I located the animal immediately and delivered it to the ANU veterinarian for a necropsy. We removed radiocollars from male founders (2016 only) immediately following the establishment period, and from female founders after their young had dispersed from the natal den in Austral spring.

1.4.4.2.2 Long-term

We conducted demographic monitoring of the reintroduced eastern quoll population using a Robust Design capture-mark-recapture (CMR) framework (Pollock 1982; Kendall & Nichols 2002). We conducted eight CMR primary sessions, each consisting of two trap nights (secondary sessions) in Austral summer and autumn each year between 2017 and 2022. Trapping during summer was intended to detect the greatest population density following juvenile dispersal in spring, and trapping during autumn was intended to detect the size of the breeding population. I integrated one night of free-feeding before each trapping night to encourage the capture of more ‘trap-shy’ individuals (Biro 2013). We set traps in a standardised array across 92 sites within MFWS, each placed 25 m from vehicle tracks and approximately 200 m apart. We used wire cage traps (31 × 31 × 70 cm, see Equipment section) that had padded doors, plastic lining (to collect scats), were covered with a hessian sack, and baited with sardines (Manning *et al*. 2019).

We checked traps before first light to minimise stress and allow animals to find shelter before daylight. Health checks included recording body mass, body condition, head and pes length, pouch occupancy, crown rump length of pouch young (CRL), and collection of fur and scat samples (Portas *et al.* 2020). We conducted health checks without sedation but with procedures to minimise handling time (generally <10 mins) and released animals at the point of capture.

1.5 Thesis aims

In this thesis, I aimed to explore reintroduction-related tactics, behaviour, movement, and species recovery using the model system of reintroduced eastern quolls at MFWS. I aimed harness the best available knowledge relating to the eastern quoll’s biology and ecology to demonstrate iterative and adaptive approaches that could be used by other practitioners to improve reintroduction outcomes.

I also aimed to develop a framework for translocation programs using the learnings from this thesis. I aimed to create clarity around translocation ‘phases’, their criteria, strategies, tactics, evaluation measures, and expected outcomes to help practitioners avoid short-term thinking and manage expectations around the likelihood of establishment, growth, and regulation throughout a program’s lifetime.

1.6 Thesis structure

Here, I outline each of the remaining six chapters included in this thesis (conceptualised in Figure 1.5). In Chapter 2, I demonstrated how conducting a reintroduction program as a series of iterative trials within an adaptive management framework can improve the likelihood of success. I present the case study of the eastern quoll reintroduction, where I compared survival and dispersal between three cohorts of eastern quolls reintroduced to MFWS. This study provides the foundation upon which future reintroductions can build.

In Chapter 3, I investigated how behavioural measures in reintroduced eastern quolls could predict post-release survival and dispersal. By integrating novelty into behavioural assays, I found that they offer significant value as a conservation tool.

In Chapter 4, I investigated how movement, habitat use and preference, and conspecific associations differed between eastern quoll residents and reinforcers using GPS collars. My results revealed movements at a greater spatio-temporal resolution than has ever been achieved for this species, and offer important insights into appropriate habitat structure for future reintroduction sites.

In Chapter 5, I demonstrated how demographic parameters can reveal threats to persistence, inform management thresholds, and create targets for removing an endangered species from the IUCN Red List. Using vital rates determined across 6 years of capture-mark-recapture monitoring, I projected the population size and area required to achieve the ‘stretch goal’ of recovering the eastern quoll species within 10 years.

In the penultimate Chapter 6, I took the learnings from this thesis and developed the ‘Translocation Continuum Framework’, a practical planning tool which provides clarity around translocation ‘phases’, their criteria, strategies, tactics, evaluation measures, and expected outcomes. I discussed the limitations of ‘success’ and ‘failure’ labels in translocation science, and the importance of parsimonious decision making that balances objectives to maximise learning with the least amount of loss.

In the final Chapter 7, I provide a summary of the key findings from each of my Chapters, synthesise how these substantially contributed to translocation and conservation science, and propose avenues for expanding this research.

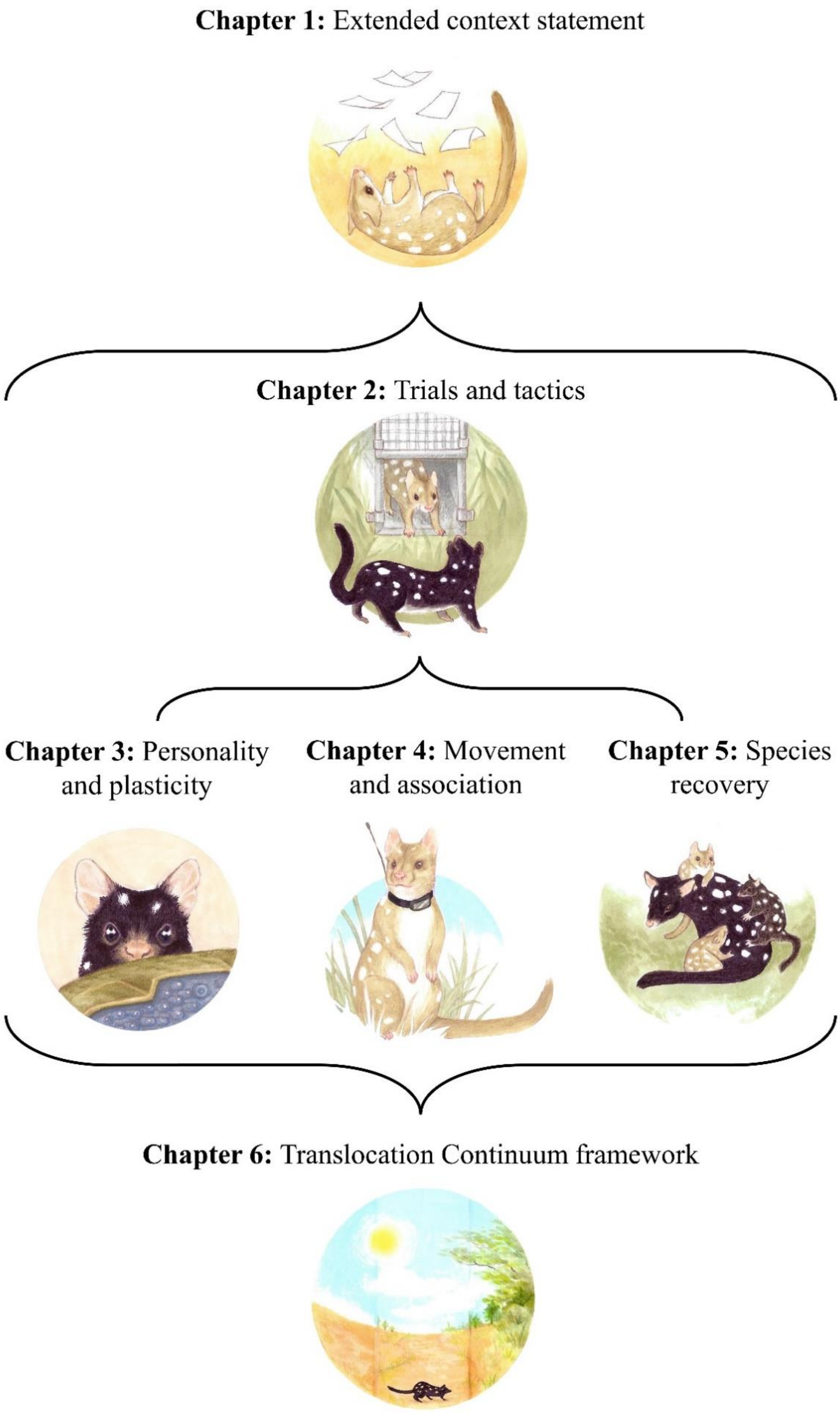

Figure 1.5 A conceptual diagram illustrating how the six Chapters presented in the ‘reintroduction biology of the eastern quoll (*Dasyurus viverrinus*)’ thesis are related. Illustrations by Cat Cotsell.

Chapter 2: Trials and tactics

Where there is imperfect knowledge and uncertainty about a species and its planned recipient ecosystem, reintroduction success in 'one leap' is unlikely (Evans *et al*. 2022). Rather than viewing reintroductions as 'all or nothing' operations, in this Chapter I demonstrate how conducting a reintroduction program as a series of iterative trials within an adaptive management framework can significantly improve the likelihood of success.

I present the case study of the eastern quoll reintroduction, where I compared survival- and dispersal-related measures of success between three cohorts of eastern quolls reintroduced to Mulligans Flat Woodland Sanctuary. By using the learnings from these trials, whether they were 'successful' at first or not, we can better understand the process, build knowledge, and adapt tactics that will lead to success in later trials and, ultimately, full reintroduction. This study provides the foundation upon which future reintroductions can build, and a 'pathway to the wild' for species that are vulnerable to invasive predators (i.e., 'coexistence conservation', Evans *et al*. 2022).

This Chapter was presented at the Ecological Society of Australia conference in November 2019, published in *PLOS One* in June 2020, and has been reformatted for inclusion in this thesis.

Illustration by Cat Cotsell

Adapting reintroduction tactics in successive trials increases the likelihood of establishment for an endangered carnivore in a fenced sanctuary

Wilson B A, Evans M J, Batson W G, Banks S C, Gordon I J, Fletcher D B, Wimpenny C,
Newport J, Belton E, Rypalski A, Portas T J, & Manning A D (2020)
PLOS One, 15(6): e0234455.

2.1 Abstract

Threatened species recovery programs are increasingly turning to reintroductions to reverse biodiversity loss. Here we present a real-world example where tactics (techniques which influence post-release performance and persistence) and an adaptive management framework (which incorporates feedback between monitoring and future actions) improved reintroduction success. Across three successive trials we investigated the influence of tactics on the effective survival and post-release dispersal of endangered eastern quolls (*Dasyurus viverrinus*) reintroduced into Mulligans Flat Woodland Sanctuary, Australian Capital Territory. Founders were monitored for 42 days post-release, and probability of survival and post-release dispersal were tested against trial, origin, sex, den sharing, and presence of pouch young. We adopted an adaptive management framework, using monitoring to facilitate rapid learning and to implement interventions that improved reintroduction success.

Founders released in the first trial were less likely to survive (28.6%, $n = 14$) than those founders released the second (76.9%, $n = 13$) and third trials (87.5%, $n = 8$). We adapted several tactics in the second and third trials, including the selection of female-only founders to avoid elevated male mortality, and post-mating releases to reduce stress. Founders that moved dens between consecutive nights were less likely to survive, suggesting that minimising post-release dispersal can increase the probability of survival. The probability of moving dens was lower in the second and third trials, for females, and when den sharing with another founder. This study demonstrates that, through iterative trials of tactics involving monitoring and learning, adaptive management can be used to significantly improve the success of reintroduction programs.

2.2 Introduction

Reintroduction describes the intentional movement and release of organisms into their indigenous range following their local extinction or extirpation, with the aim to re-establish viable, free-ranging populations (IUCN 2013). Despite their rising popularity as a conservation tool, reintroductions can suffer limited success (Griffith *et al*. 1989; Kleiman 1989; Armstrong & Craig 1995a; Fischer & Lindenmayer 2000; Ewen & Armstrong 2007; Seddon *et al*. 2007; Armstrong & Seddon 2008; Sheean *et al*. 2012). The success of reintroduction programs can be improved by employing 'tactics', defined as techniques which can influence post-release performance and persistence (Batson *et al.* 2015). Tactics may include the selection of founders, release environment and methods (Batson *et al.* 2016, 2017), and the provision of supplementary food and shelter (Armstrong & Seddon 2008). These tactics should be guided by well-defined objectives termed 'strategies', which might include, for example, maximising survival or minimising post-release dispersal (Batson *et al.* 2015). To clarify this thinking, a Translocation Tactics Classification System (TTCS, Figure 2.1, Batson *et al*. 2015) was developed to provide a framework to improve the ability to identify, select and design tactics which help achieve defined strategies. The TTCS divides the diversity of tactics by their focus on either the 'animal' or the 'environment', thereby guiding practitioners through a logical and ecologically relevant framework. By encouraging a standardised and systematic process for designing reintroductions, practitioners can use this tool to rapidly learn from less effective tactics and improve reintroduction success.

Determining which tactics to use can be complex. Reintroductions are often context-specific, and knowledge of the recipient ecosystem is never complete (Walters & Holling 1990). Adaptive management can address this 'wicked problem' (DeFries & Nagendra 2017) by offering a systematic approach to improve management actions through learning from (Walters & Holling 1990; Williams *et al.* 2009). Rather than waiting until enough is known about an ecosystem (Lee 1999), practitioners can implement and adjust management actions 'on the fly' in response to outcomes observed through well-designed monitoring. In reintroductions, this can translate to conducting trials, characterised by low replication and control (Kemp *et al.* 2015), rather than rigid experiments with large sample sizes. This is especially pertinent when dealing with threatened species where inherently small numbers of founding individuals are available. This pragmatic approach can uncover unexpected and valuable results (e.g. Kemp 2010; Norbury *et al*. 2014; and Soorae 2010 case studies), which can inform future trials or feed into full experimental reintroductions. In the face of uncertainty, trial reintroductions can be of greater value than experiments when applied within an adaptive management framework (Kemp *et al.* 2015).

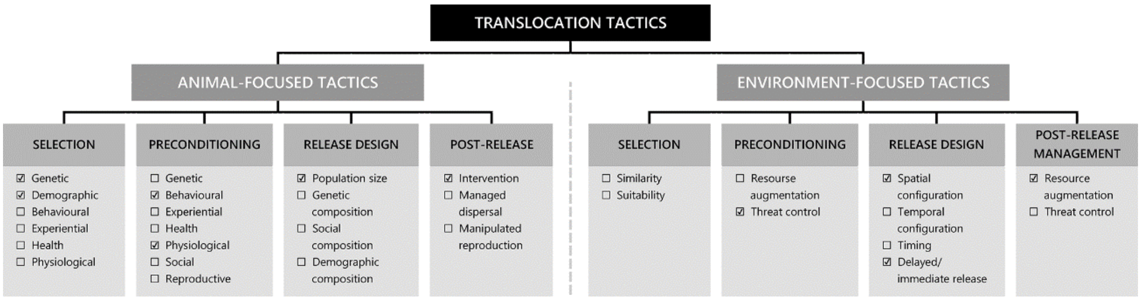

Figure 2.1 Translocation Tactics Classification System, as adapted from Batson *et al*. (2015). Checked boxes indicate tactics which were employed across the three trial reintroductions of the eastern quoll (*Dasyurus viverrinus*) to Mulligans Flat Woodland Sanctuary, Australian Capital Territory from 2016–18.

Here we investigate the effect of tactics employed within an adaptive management framework using a series of three trials for the reintroduction of a locally extinct, marsupial carnivore (the eastern quoll, *Dasyurus viverrinus*) to mainland Australia. Reintroduction success was compared for three cohorts of eastern quolls that were reintroduced to a predator-proof sanctuary in the Australian Capital Territory (ACT) over three years. While survival has a clear influence on reintroduction success because high mortality can greatly compromise establishment and genetic diversity (Swaisgood 2010), post-release dispersal is also a crucial consideration (Clarke & Schedvin 1997; Pierre 1999; Swaisgood 2010). Founders that disperse long distances from the release site often have higher mortality rates and are less likely to contribute to effective population size (Moseby *et al.* 2014), and this dispersal can be impacted by pre-release experience, release method, sex, origin, and sociality (Armstrong & Craig 1995b; a; Maxwell & Jamieson 1997; Wauters *et al*. 1997; Doligez *et al*. 2004; Hardman & Moro 2006; le Gouar *et al*. 2008). Understanding the tactics that influence this process is key to reducing mortality rates, especially in the establishment phase of a reintroduction. Therefore, we employed tactics within the strategy of maximising survival and minimising post-release dispersal, guided by the TTCS (Figure 2.1). We asked two questions: (1) did adapted tactics improve reintroduction outcomes, and (2) what mechanisms drove improvements to reintroduction outcomes?

2.3 Materials and methods

2.3.1 Study area

Mulligans Flat Woodland Sanctuary (MFWS) is a 485 ha reserve containing critically endangered yellow-box *Eucalyptus melliodora* and Blakely's red gum *Eucalyptus blakelyi* grassy woodland (McIntyre *et al.* 2010) and is situated in north-east Canberra, ACT Australia (-35.167, 149.158). MFWS is enclosed by predator-proof fencing to exclude non-native animals such as red foxes (*Vulpes vulpes*), cats (*Felis catus*), European rabbits (*Oryctolagus cuniculus*) and European hares (*Lepus europaeus*), which have been eradicated within the exclosure. The MFWS fence design includes a 'floppy top' which prevents invasive predators from climbing into the Sanctuary but does not prevent animals from climbing out into the surrounding landscape. MFWS, and the adjoining Goorooyarroo Nature Reserve, are used as an 'outdoor laboratory' and form the location of the Mulligans Flat-Goorooyarroo Woodland Experiment (MFGO Woodland Experiment). The experiment aims to restore biodiversity and ecological function to this critically endangered box-gum grassy woodland community (Manning *et al.* 2011; Shorthouse *et al.* 2012).

2.3.2 Study species

The eastern quoll (*murunguny* in the local Ngunnawal language) is a small- to medium-sized marsupial (van Dyck & Strahan 2008) which previously inhabited the south-eastern states of Australia. It was last seen on the mainland in 1967 (Frankham *et al.* 2016); its extinction has been attributed to predation and competition by invasive predators, habitat loss, disease, and human encroachment (Bryant 1988; Jones *et al.* 2001; Peacock & Abbott 2014). It is listed as 'endangered' by the IUCN (Burbidge & Woinarski 2016) and the Commonwealth of Australia (Environment Protection and Biodiversity Conservation Act 1999), and is restricted to Tasmania where it is common in the drier, eastern half of the island State (Jones & Rose 1996; Fancourt 2015). Eastern quolls are often associated with forest-pasture ecotones that provide open grasslands for foraging during the night, and forest habitat where they can den in hollow logs, rocky outcrops, and underground burrows during the day (Godsell 1983). They are nocturnal predators and scavengers, with a diet dominated by invertebrates, as well as occasional birds, small mammals, reptiles, fruit, and carrion (Blackhall 1980; Godsell 1983; Jones & Barmuta 1998). The species is sexually dimorphic with a mean adult body mass of 1250 g (min 900 – max 2000 g) for males and 805 g (min 700 – max 1100 g) for females (Godsell 1983; Jones *et al.* 2001). Males have larger home ranges (mean 44 ha) than do females (mean 35 ha, Godsell 1983; Bryant 1988). Females are seasonally polyoestrous and can carry a single litter of up to six young per year (Godsell 1983). Annual mortality is high, with 20–58% of juveniles surviving to their first breeding season, and life expectancy is 3–4 years (Godsell 1983).

2.3.3 Founders

We reintroduced the eastern quoll into MFWS in a series of three trials over three years (Trial 1 in 2016, Trial 2 in 2017, and Trial 3 in 2018). To maximise genetic diversity, founders in the Trials 1 and 2 were selected from both captive-bred and wild populations, and in Trial 3 only wild founders were selected. Captive founders were sourced from Mount Rothwell Biodiversity

Interpretation Centre (Mt Rothwell), situated 60 km south-west of Melbourne. Wild founders were derived from free-ranging populations across 14 geographic regions in Tasmania, separated by at least 15 km or a significant geographical barrier to eastern quoll dispersal. To minimise impacts on the source population and maximise genetic diversity in the reintroduced population, no more than two animals in each cohort originated from any one site.

2.3.4 Pre-release health assessments

We selected founders that were in fair to excellent body condition (using a subjective assessment of fat and muscle stored between the hips and spine, see Portas *et al*. 2016), weighed more than 640g, and were estimated to be 1–2 years old (inferring from tooth condition and wear). They were translocated to the ACT by air and road, where they were anaesthetised and assessed for health and disease (as described in (Portas *et al.* 2020). Founders were microchipped (each animal was identified using a four-character microchip code, see Table 2.1) and fitted with VHF collars (32g, V6C 163 Zilco, Sirtrack Ltd, Hawkes Bay, New Zealand) or GPS collars (38g, LiteTrack 30 RF, Sirtrack Ltd, Hawkes Bay, New Zealand). Scat, fur, blood, and ear (for DNA extraction) samples were collected.

Translocations were conducted under licenses from the Tasmanian Department of Primary Industries, Parks, Water and Environment (DPIPWE, permits TFA 16025 and 17091, export licences 12818/16 and 13528/17), Victorian Department of Environment, Land, Water and Planning (permit 14505167), and ACT Territory and Municipal Services (import licence L120161261). Reintroduction procedures were approved by The Australian National University Animal Experimentation Ethics Committee (protocol A2016/02).

2.3.5 Post-release monitoring

Founders were monitored using VHF collars in Trials 1 and 2 and VHF-enabled GPS collars in Trial 3. Survival and den location were monitored daily for 42 days post-release (the ‘establishment period’) because survival plateaued after this period in Trial 1. We removed collars from males after this period and from females after their young had dispersed. We located collars immediately if a mortality signal was detected and conducted necropsies on all deceased animals that could be located.

Table 2.1 Reintroduction history of eastern quolls (*Dasyurus viverrinus*) translocated to Mulligans Flat Woodland Sanctuary, Australian Capital Territory in 2016–18.

ID	Sex	Origin	Location	Trial	Release date	Release location	Release method	Release condition	Release weight (kg)	Fate	Escapes (*n*)	Cause of death	Pouch young (*n*)	Fixes (*n*)	Den sharing (%)
8C2B	F	Captive	MTR	1	02/03/16	Pipeline Road	Bag	Good	0.835	Deceased	2	Escaped, retrieved	6	33	6
90FC	M	Captive	MTR	1	29/02/16	Main Mulligans Track	Bag	Excellent	1.215	Deceased	1	Escaped, predated (fox)		1	100
8FC0	F	Captive	MTR	1	29/02/16	Mustering Track	Bag	Good	0.785	Survived	0		7	39	26
0257	M	Captive	MTR	1	01/03/16	Old Coach Road	Bag	Good	1.120	Deceased	1	Escaped, died under observation		29	10
78F7	F	Captive	MTR	1	29/02/16	Dam Paddock	Bag	Good	0.755	Deceased	2	Escaped, died under observation	0	1	0
91DB	M	Captive	MTR	1	02/03/16	Pipeline Road	Bag	Good	1.105	Survived	0			39	5
803C	F	Wild	TAS (Pelverata)	1	29/02/16	Mustering Track	Bag	Good	1.085	Survived	0		0	40	10
8244	M	Wild	TAS (Cygnet)	1	29/02/16	Main Mulligans Track	Bag	Excellent	1.245	Deceased	0	Misadventure within Sanctuary		40	10
F0C7	F	Wild	TAS (Mt River)	1	29/02/16	Main Mulligans Track	Bag	Fair	0.880	Survived	0		5	40	0
8258	M	Wild	TAS (Uxbridge)	1	01/03/16	Old Coach Road	Bag	Good	1.220	Deceased	3	Misadventure within Sanctuary		1	0
81C5	F	Wild	TAS (Geeveston)	1	01/03/16	Dam Paddock	Bag	Excellent	0.875	Deceased	3	Escaped, retrieved	0	1	0
F2F4	M	Wild	TAS (Lonna Vale)	1	01/03/16	Main Mulligans Track	Bag	Excellent	1.430	Deceased	0	Escaped, died under observation		1	0
8DB3	M	Wild	TAS (Pine Tiers)	1	02/03/16	Pipeline Road	Bag	Excellent	1.420	Deceased	0	Transferred, poor condition		40	30
3AA6	M	Wild	TAS (14 Mile Road)	1	02/03/16	Pipeline Road	Bag	Fair	0.825	Deceased	1	Escaped, predated (fox)		8	13
C682	F	Captive	MTR	2	11/07/17	Central MFWS	Den box	Good	0.786	Survived	0		6	42	7
3051	F	Captive	MTR	2	28/06/17	Central MFWS	Den box	Good	0.960	Survived	0		6	42	12

5340	F	Captive	MTR	2	24/06/17	Central MFWS	Den box	Good	0.955	Deceased	1	Escaped, retrieved	0	8	0
1BEF	F	Captive	MTR	2	26/06/17	Central MFWS	Den box	Good	0.830	Survived	0		6	42	31
8849	F	Captive	MTR	2	26/06/17	Central MFWS	Den box	Good	0.880	Survived	0		4	42	43
1801	F	Captive	MTR	2	05/07/17	Central MFWS	Den box	Good	0.750	Survived	0		0	41	80
E384	F	Wild	TAS (Lonna Vale)	2	11/07/17	Central MFWS	Den box	Fair	0.746	Survived	0		6	42	12
DDE1	F	Wild	TAS (Grove)	2	13/07/17	Central MFWS	Den box	Fair	0.890	Survived	0		6	42	50
D6C1	F	Wild	TAS (Grove)	2	13/07/17	Central MFWS	Den box	Good	0.910	Survived	0		6	41	90
F9FC	F	Wild	TAS (Russell Falls)	2	17/07/17	Central MFWS	Den box	Good	0.845	Survived	0		2	42	2
E09E	F	Wild	TAS (Russell Falls)	2	17/07/17	Central MFWS	Den box	Good	0.760	Deceased	2	Escaped, retrieved	6	1	100
D897	F	Wild	TAS (Geeveston)	2	19/07/17	Central MFWS	Den box	Good	0.885	Deceased	1	Escaped, predated (fox)	6	7	0
1715	F	Wild	TAS (Geeveston)	2	19/07/17	Central MFWS	Den box	Good	0.890	Survived	0		5	42	10
3CAB	F	Wild	TAS (Blessington)	3	27/06/18	Central MFWS	Den box	Good	0.960	Survived	0		6	35	11
A98C	F	Wild	TAS (Scamander)	3	27/06/18	Central MFWS	Den box	Excellent	1.070	Deceased	1	Escaped, predated (fox)	5	28	14
414B	F	Wild	TAS (Blessington)	3	27/06/18	Central MFWS	Den box	Good	0.900	Survived	0		4	41	29
4C40	F	Wild	TAS (Scamander)	3	27/06/18	Central MFWS	Den box	Good	0.910	Survived	0		6	29	10
3E0D	F	Wild	TAS (Fingal Forest)	3	28/06/18	Central MFWS	Den box	Excellent	1.100	Survived	0		6	41	5
D0AE	F	Wild	TAS (Gladstone)	3	05/07/18	Central MFWS	Den box	Excellent	1.180	Survived	0		5	42	88
A8AD	F	Wild	TAS (Fingal Forest)	3	05/07/18	Central MFWS	Den box	Good	0.990	Survived	0		6	33	70
A810	F	Wild	TAS (Gladstone)	3	05/07/18	Central MFWS	Den box	Good	1.070	Survived	0		5	42	12

‘MTR’ refers to Mt Rothwell Biodiversity Interpretation Centre, in Victoria, Australia; ‘TAS’ refers to the island state of Tasmania, Australia; ‘Bag’ refers to immediate releases from a cotton bag, and den box releases were delayed; ‘Fixes’ is the number of radiotracking records; ‘Den sharing’ is the percentage of fixes an individual was found den sharing with other tracked individuals; ‘Escapee’ (dispersing outside the exclusion fence) and transferred animals were considered deceased for analyses.

We conducted post-release health checks every two weeks, though timing and frequency varied due to the reproductive stage of females, weight fluctuations (influencing collar fit), logistical constraints, and ability to re-trap the targeted animal. We conducted all trapping with wire cage traps (31 × 31 × 70 cm) that had padded doors, plastic lining (to collect scats), and were covered with a hessian sack. We checked traps before first light to minimise stress and allow animals to find shelter before daylight. Health checks included recording body mass, body condition, head and pes length, pouch occupancy, crown rump length of pouch young (CRL), and collection of fur and scat samples. We conducted health checks without sedation but with procedures to minimise handling time (generally <10 mins) and released animals at the point of capture. When non-target founders were captured, they were either given a health check or were weighed and released, depending on the timing of their next scheduled health check. In total, we recorded 29 founder captures in Trial 1, 50 in Trial 2 and 71 in Trial 3 during the establishment periods.

2.3.6 Trial 1 tactics

In late February through to early March 2016, fourteen eastern quolls (female $n = 6$, male $n = 8$) were translocated to MFWS (Table 2.2). None of the females were carrying pouch young because mating was yet to occur in late austral Autumn to early Winter (Godsell 1983). Releases were conducted immediately (i.e., animals were transported to ACT, underwent health assessments, and were released on the same day) from a cotton bag in randomised locations within MFWS. Releases occurred at night to minimise stress and to provide maximum time to explore MFWS and find a den before first light. No supplementary food was provided.

2.4 Data analysis

To answer our questions, we fitted a series of generalized linear models (GLMs) on five datasets comprising of one record per animal (Table 2.3). Response variables included effective survival (*probability of survival*) and post-release dispersal (*proportion of days moved* between dens and mean *distance moved between dens* (m) and formed our criteria for reintroduction success. Eastern quolls that escaped the Sanctuary or were transferred to another facility were treated as deceased in analyses, so we report here on ‘effective’ survival (henceforth “survival”), which does not include the survival of those escapees that were retrieved from beyond the fence. GLMs were fitted using R version 3.4.0 (Bates *et al*. 2015; R Core Team 2021), model fit was assessed using chi-square tests of significance, and post-hoc Tukey’s tests were used to identify significance differences between groups using the *lsmeans* package in R (Lenth 2016). We logit-transformed the data to satisfy the assumption of normality.

Table 2.2 Tactics employed for three trial reintroductions of the eastern quoll (*Dasyurus viverrinus*) to Mulligans Flat Woodland Sanctuary, Australian Capital Territory. Tactics were organised as per the Translocation Tactics Classification System (Figure 2.1, Batson *et al*. 2015).

Tactic focus	**Tactic group**	**Tactic type**	**Trial 1 (2016)**	**Trial 2 (2017)**	**Trial 3 (2018)**	**Rationale**
Animal	Selection	Genetic	Captive and wild founders	Captive and wild founders	Wild founders	Captive and wild founders were released in Trials 1 and 2 to test the effect of origin on reintroduction success. No significant effect was found, so only genetically unique wild founders were released in Trial 3.
		Demographic	Males and females	Females only, preferably carrying young	Females only, preferably carrying young	Males have larger home ranges than females, which may have resulted in their elevated escapes in Trial 1. Females invest in natal dens, limiting their dispersal (Godsell 1983). Females carrying young were preferred for Trials 2 and 3.
	Pre-conditioning	Behavioural	No behavioural assays	Behavioural assays	No behavioural assays	Behavioural assays were conducted before releases in Trial 2 (*in analysis*).
		Physiological	Pre-mating releases	Post-mating releases	Post-mating releases	Elevated hormones, and associated stress, can be experienced in breeding eastern quolls (Godsell 1983).
	Release design	Population size	14 founders	13 founders	8 founders	Number of founders released was dependant on availability.
	Post-release	Intervention	Limited captures following birth of young	Regular captures	Regular captures	We limited captures of females with pouch young in Trial 1 out of caution. In Trial 2, weight losses necessitated regular captures to ensure weight was regained. In Trial 3 GPS collar issues necessitated regular captures.
Environ-ment	Pre-conditioning	Threat control	Fox control limited	Fox control intensified	Fox control intensified	Fox control was intensified outside the fence to give escapees the best chance of survival until retrieval.
			Hot-wire installed	Hot-wire modified	Hot-wire modified	The voltage of the internal hot-wire was modified following injuries to animals which contacted the wire.
			Baffles installed	Baffles present	Baffles present	Baffles (metal sheets) were installed at ‘weak points’ inside the fence to discourage escapes.
	Release design	Spatial configuration	Randomised release sites	Centralised release sites	Centralised release sites	Release sites were changed to central locations so that founders would be likely to encounter food resources, preferred den sites, other eastern quolls, or other features of interest, before the exclusion fence.
		Delayed/immediate release	Immediate release (bag)	Delayed release (box)	Delayed release (box)	Releases in Trials 2 and 3 were conducted from a box to manage stress (Batson 2015).
	Post-release management	Resource augmentation	No supplement feeding	Supplement feeding	No supplement feeding	Low weights were observed in Trial 2. Supplementary food was deposited into dens until weights stabilised.

Table 2.3 Models, datasets used, and effect sizes for probability of effective survival, den sharing, and proportion of days moved between dens for eastern quolls (*Dasyurus viverrinus*) reintroduced across three trials to Mulligans Flat Woodland Sanctuary, Australian Capital Territory from 2016–18. 'df' refers to residual degrees of freedom.

Response	Predictor	Dataset	Rationale	*n*	df	*p*	Figure
Probability of survival	Trial	1	Included all founders translocated	35	32	0.006	2A
	Origin	1	See 1 above	35	33	0.885	-
	Sex	1	See 1 above	35	33	0.001	2B
	Den sharing	2	Excluded the six founders which did not survive for more than 7 days	29	27	0.133	-
	Presence of pouch young	3	Excluded males	21	19	0.510	-
Den sharing	Trial	2	See 2 above	29	26	0.304	-
	Origin	2	See 2 above	29	27	0.821	-
	Sex	2	See 2 above	29	27	0.363	-
Probability of survival	Proportion of days moved	2	See 2 above	29	27	<0.001	2C
	Mean distance moved between dens (m)	2	See 2 above	29	27	0.182	-
Proportion of days moved	Trial	2	See 2 above	29	26	<0.001	3A
	Origin	2	See 2 above	29	27	0.146	-
	Sex	2	See 2 above	29	27	0.006	3B
	Den sharing	2	See 2 above	29	27	0.049	3C
	Presence of pouch young	4	Excluded males and one female which did not survive for more than 7 days	20	18	0.366	-

We divided the data into four datasets to reflect the number of founders that were appropriate for each analysis (Table 2.3). For example, for analyses involving *probability of survival*, *trial*, *origin*, and *sex*, we included all founders translocated (dataset 1), whereas for analyses involving *presence of pouch young*, males were excluded from analyses (datasets 3 and 4, Table 2.3). Model selection analyses were not appropriate, either because most models were fitted with differing underlying datasets, or because those predictor variables that did use the same datasets (e.g. trial and sex) were confounded (e.g. male founders in the *sex* predictor were nested in Trial 1).

(1) Did adapted tactics improve reintroduction outcomes?

To determine whether survival differed between trials, we fitted a binomial GLM with a logit link function using probability of survival (survived = 1, deceased = 0) as the response variable and trial as the predictor variable (dataset 1, Table 2.3). To determine the factors which influenced survival, we fitted a series of binomial GLMs using probability of survival as the response variable and origin (dataset 1), sex (dataset 1), den sharing (whether a founder was found den sharing with another founder during the establishment period, dataset 2) and presence of pouch young (dataset 3) for females as the predictor variables (Table 2.3). Den sharing in eastern quolls may be a function of sex and sociality (Godsell 1983) and could therefore encourage site fidelity, so we chose to include this behaviour as a predictor variable for post-release survival and dispersal, as well as a response variable for trial, origin, and sex (dataset 2).

(2) What mechanisms drove improvements to reintroduction outcomes?

To determine whether post-release dispersal influenced survival, we fitted a binomial GLM using *probability of survival* as the response variable and *proportion of days moved* between dens and mean *distance moved between dens* (m) as the predictor variables (dataset 2, Table 2.3). For these analyses, only animals which remained alive for 7 days or more (n = 29) were included, and records that did not have a consecutive location from the previous day were discarded from analyses to ensure continuity of data between days post-release. To determine the factors that influenced post-release dispersal, we fitted a series of binomial GLMs with a logit link function using *proportion of days moved* as the response variable and *trial* (dataset 2), *origin* (dataset 2), *sex* (dataset 2), *den sharing* (dataset 2), and *presence of pouch young* (dataset 4) as the predictor variables (Table 2.3).

2.5 Results

2.5.1 Trial 1

To reduce the likelihood of escapes, an 11.5 km electric wire and baffles (metal sheets) were installed on the internal side of the Sanctuary fence (Figure 2.1, Table 2.2). However, four eastern quolls escaped from MFWS within the first two days of Trial 1. Daily radiotracking enabled escaped founders to be located and returned inside the fence if found in good condition. Serial escapees and founders in poor condition were transferred to Mt Rothwell.

Four (28.5%, female n = 3, male n = 1) eastern quolls survived the Trial 1 establishment period. Of the remaining ten founders, two were found dead within MFWS, one was transferred to Mt Rothwell due to poor condition and seven escaped (n = 3 female, 4 male). Of those that escaped, two were found dead, three died under observation from injuries sustained during and after escape, and two were retrieved alive and released back into MFWS. One male was transferred to Mt Rothwell due to poor condition. Following the establishment period, the three surviving females bore an estimated 18 young.

2.5.2 Trials 2 and 3

2.5.2.1 Genetic selection

No significant differences in probability of survival (*p* = 0.546) or proportion of days moved between dens (*p* = 0.577, Table 2.3) were observed between captive and wild founders in Trials 1 and 2. As wild-caught eastern quolls from Tasmania have the potential to contribute unique genetic material which may not be represented within captive populations, we prioritised maximising genetic diversity and translocated only wild-caught female founders in Trial 3 (*n* = 8), all of which had pouch young.

2.5.2.2 Demographic selection

Increased aggression may be responsible for dispersal and mortality of males during the mating season (Godsell 1983). Mortality of male eastern quolls was greater than females in Trial 1. In response, we adopted the tactic of translocating only adult females in Trial 2, preferring those that were carrying pouch young (*n* = 7 out of 13). This tactic allowed us to introduce new male and female juveniles (as pouch young) sired by either captive or wild Tasmanian males, and avoid the elevated male mortality and dispersal observed in Trial 1. Interestingly, this tactic may contribute to greater genetic diversity in founders because members within each litter may be sired by different males, as demonstrated in the closely-related northern quoll (*Dasyurus hallucatus*, Chan *et al*. 2019), and spotted-tailed quoll (*Dasyurus maculatus*, Glen *et al*. 2009).

2.5.2.3 Behavioural pre-conditioning

In Trial 2, we delayed the release of founders so that we could undertake behavioural assays (*in analysis*). Captive founders were translocated 13–22 days prior to the translocation of wild founders (Figure 2.1, Table 2.2). During assays, founders were provided with an individual ‘den box’ with nesting material inside, which also served as their release box. This was intended to encourage habituation with the den boxes by the time of their release to reduce stress. Behavioural assays were not conducted in Trial 3, but we did continue to use the den box tactic.

2.5.2.4 Physiological selection

Greater numbers of male escapes may have been exacerbated by the timing of release because eastern quolls experience elevated reproductive hormones (e.g., luteinising hormone and testosterone) between March and June (Godsell 1983). This stimulates greater mobility and increased aggression in males, which aids in acquiring den sites and food (Godsell 1983). We suspect that females in Trial 1 may have also struggled to settle because they were being pursued by males and were also likely to have elevated reproductive hormones. To avoid these issues, releases in Trials 2 and 3 were conducted in austral Winter after the mating period, which also allowed us to translocate females with fused pouch young. This had the added benefit of reducing stress and collar fit issues (due to changes in neck size) associated with elevated hormones during the mating period.

2.5.2.5 Spatial configuration and delayed release

Founders in Trials 1 and 3 were released within 48 hours of acquisition, while in Trial 2 release was delayed by 11–28 days so that behavioural assays could be undertaken (*in analysis*). Following the assays, we conducted a pre-release health check for founders scheduled for release the following day and released one to three founders every two days.

While releases in Trial 1 were conducted in randomised locations (where some release sites were closer to the predator-proof fence than others), releases in Trials 2 and 3 were conducted from one of four central locations (each separated by 50 m). This tactic aimed to maximise the distance over which a founder needed to travel before encountering the predator-proof fence, while also allowing them to encounter food resources, preferred den sites, conspecifics, or other features of interest, before the fence. Founders were placed *in situ* in their den box with the door closed for one to two hours (delayed release, Parker *et al*. 2012). After last light, the door was opened from behind the den box (so the founder did not see the human) and the founder could leave of its own accord. We employed these tactics to minimise stress and to provide maximum time for founders to explore MFWS and find a den before daylight.

2.5.2.6 Resource augmentation

By 14 days post-release in Trial 2, four captive founders had lost 13–23% of their initial release weight. As an adaptive management intervention, supplementary food was deposited into dens in declining amounts as weights stabilised. All founders were provided with supplementary food because it could not be determined whether the intended animal ate its share due to consistent den sharing. This weight loss was not observed in Trial 3, so no supplementary feeding was provided.

(1) Did adapted tactics improve reintroduction outcomes?

In the female-only cohort of Trial 2, ten eastern quolls (76.92%) survived the establishment period and bore a total of 47 young. Of the remaining three founders, one was retrieved alive following escape, one was preyed upon by a fox following escape, and one was transferred to Mt Rothwell following two escapes. It is worth noting that of the fourteen escapes that occurred in the Trials 1 and 2, four were successfully retrieved at least once and re-released into MFWS and could therefore contribute to the effective population.

In the female-only cohort of Trial 3, seven eastern quolls (87.5%) survived the establishment period and bore a total of 38 young. One founder escaped and was found to have been predated by a fox. Founders translocated in Trials 2 and 3 were significantly more likely to survive than those in Trial 1 ($p = 0.006$, Figure 2.2A, Table 2.3). Females had a significantly greater probability of survival than males ($p = 0.001$, Figure 2.2B).

(2) What mechanisms drove improvements to reintroduction outcomes?

Founders that moved between dens less frequently were more likely to survive the establishment period ($p < 0.001$, Figure 2.2C), suggesting that site fidelity impacts the probability of survival. The proportion of days where founders moved between dens was significantly lower in Trials 2 and 3 than in Trial 1 ($p < 0.001$, Figure 2.3A). Female eastern quolls moved between dens less frequently than males ($p = 0.006$, Figure 2.3B, Table 2.3). The proportion of days where founders moved between dens was significantly lower when an animal was found den sharing with another founder the previous day ($p = 0.049$, Figure 2.3C).

2.6 Discussion

We significantly increased effective survival and limited post-release dispersal in reintroduced eastern quolls at MFWS. This was done by using a series of reintroduction trials within an adaptive management framework (outlined in Table 2.2 which was guided by the TTCS, Figure 2.1, Batson *et al.* 2015)). This adaptive approach is particularly important for threatened species reintroductions, where rapid decisions are often required despite the absence of complete knowledge (Seddon *et al.* 2007), and has been adopted worldwide for reintroductions of threatened birds (Armstrong *et al.* 2007), fish (Bearlin *et al.* 2002), mammals (Varley & Boyce 2006) and reptiles (Canessa *et al.* 2016), as well as ecosystem restorations (Weinstein *et al.* 1997). To maintain our strategies, we needed to employ tactic changes concurrently in Trials 2 and 3 - naturally making a direct comparison between translocations difficult and often confounded. In addition, our inherently small (parsimonious) sample sizes did not allow us to test for potential interactions between predictor variables, reducing inferences we can make as to their combined influence on post-release survival and dispersal. Nevertheless, our results allow us to make some critical inferences about which tactics had the strongest influence on this success.

Females were significantly more likely to survive and less likely to shift to new dens between consecutive days than were males (Figure 2.3B). Only females are known to construct

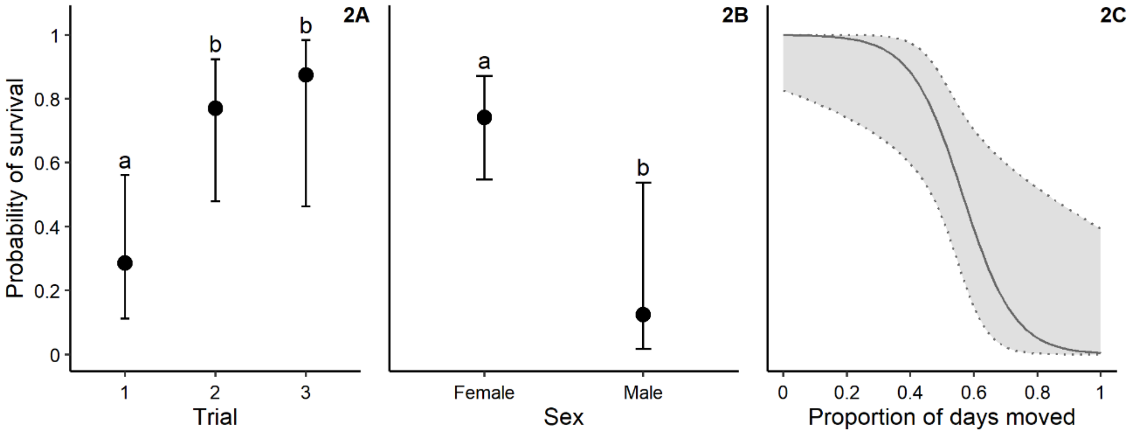

Figure 2.2 Probability of effective survival for eastern quoll (*Dasyurus viverrinus*) founders translocated to Mulligans Flat Woodland Sanctuary, Australian Capital Territory. Survival presented by trial (2A, Trial 1 *n* = 14, Trial 2 *n* = 13, Trial 3 *n* = 8), sex (2B, female *n* = 27, male *n* = 8) and proportion of days moved between dens (2C, *n* = 29). Male animals were translocated in Trial 1 only. Error bars and dotted lines represent 95% confidence intervals for predicted values, and letters indicate significant differences (where *p* < 0.05).

Figure 2.3 Proportion of days moved between dens for eastern quoll (*Dasyurus viverrinus*) founders translocated to Mulligans Flat Woodland Sanctuary, Australian Capital Territory. Proportion of days moved presented by trial (3A, Trial 1 *n* = 9, Trial 2 *n* = 12, Trial 3 *n* = 8), sex (3B, female *n* = 24, male *n* = 5) and whether a founder den shared with another founder (3C). Error bars represent 95% confidence intervals for predicted values, and letters indicate significant differences (where *p* < 0.05).

dens and use grass and sticks as nesting material (Godsell 1983). It is likely that females scout for a suitable natal den, and once selected, put considerable effort into preparing and maintaining it. This would be an energetically costly behaviour, and a female would be unlikely to abandon a den she invested in. This supports our tactic of selecting females as founders in the later trials because it limited their post-release dispersal and, therefore, maximised survival in the establishment phase. This has been similarly observed in reintroductions of maternal black bears (*Ursus americanus*, Clark *et al*. 2002) and elk (*Cervus elaphus*, Bleisch *et al*. 2017), where a combination of parturition and rearing of young increased site fidelity in female founders.

Hyperdispersal, where animals that disperse great distances from the release site are unlikely to contribute to the population (Banks *et al.* 2002; le Gouar *et al.* 2012), can compromise the establishment (Griffith *et al*. 1989; Kleiman 1989; Bright & Morris 1994) and monitoring (Stamps & Swaisgood 2007) of reintroduced populations. Founders that survived the establishment period moved between dens significantly less over consecutive days. Interestingly, our results also indicated that den sharing reduced post-release dispersal by encouraging site fidelity, which could be a function of relatedness, sociality, and den suitability (Godsell 1983). Male eastern quolls are known to avoid sharing dens outside the breeding season (Godsell 1983; Jones *et al.* 2001). Male den sharing in Trial 1, therefore, was likely driven by mating pairs (e.g., microchip codes 8FC0 and 8DB3, Table 2.1), while den sharing between females in Trials 2 and 3 was probably driven by the need to conserve energy during Winter, as observed in smaller dasyurids (fat-tailed dunnart *Sminthopsis crassicaudata*, (Morton 1995), and common planigale *maculatus*, (Andrew & Settle 1982). We do note that den sharing with and between uncollared eastern quolls could not be detected or accounted for, so this behaviour may have been more common than observed.

It is also important to consider that founders in Trial 1 encountered an environment without conspecifics, presenting a different olfactory and social landscape compared to Trials 2 and 3. Presence of conspecifics can act as a cue for habitat quality (as per the conspecific cueing hypothesis, (Stamps 1988), providing indications of foraging conditions or predation risk (Serrano & Tella 2003; Swaisgood 2010; Richardson & Ewen 2016). As such, any mechanism involving conspecific attraction which may have contributed to our observed site fidelity could not be achieved at the initial release (Sarrazin *et al.* 2000). However, manipulation of visual and olfactory conspecific cueing has been used to increase settlement in reintroduced griffon vultures (*Gyps fulvus*, le Gouar *et al*. 2008) and black rhinoceros (*Diceros binornis*, (Linklater & Swaisgood 2008) and should therefore be considered as a tactic when planning initial releases at new sites.

Stress is an unavoidable consequence of reintroductions, and managing its effects is crucial to maximising establishment (Teixeira *et al*. 2007; Batson *et al*. 2017). Increased escapes during the pre-mating period in Trial 1 led us to suspect that stress associated with immediate release may have influenced effective survival and post-release dispersal. Delayed release (where founders are housed *in situ* at the release site temporarily prior to release, Parker *et al*. 2012) can be a useful tactic for managing stress (Batson 2015). Therefore, we delayed releases in Trials 2 and 3 by two hours and made efforts to prevent the founder from seeing the researcher when their release box was opened. Remote cameras showed that some founders left the box immediately, while others explored the area around the box and returned to encounter other conspecifics after their release. This suggests that by delaying release and allowing founders to exit the box of their own accord, we were able to create a low-stress environment.

Supplementary feeding was necessary to offset observed weight losses in Trial 2, possibly due to stress associated with the pre-release behavioural assays or environmental conditions prevalent in that year. In the related yellow-footed antechinus (*Antechinus flavipes*, Cooper *et al*. 2009) and southern brown bandicoot (*Isoodon obesulus*, Cooper 2011), individuals who underwent physiological experiments were found to have comparable survival and reproduction to wild conspecifics. As such, we do not consider behavioural assays contributed greatly to effective survival. While it is worth noting that supplementary feeding can alter behaviour such as migration and dispersal (Doligez *et al.* 2004; Finlayson & Moseby 2004), founders in Trial 3 did not require this resource augmentation, and had similar levels of post-release dispersal to founders in Trial 2 (Figure 2.3A). Future reintroductions for this species should be prepared, therefore, to provide supplementary feed if founder weights drop significantly in response to post-release conditions, though the need for this support should not be assumed (Bannister *et al.* 2018b). Again, this emphasises the importance of an adaptive management approach to reintroductions.

Effective survival and post-release dispersal did not differ between captive and wild founders in the Trials 1 and 2, which is consistent with results found in the reintroduction of the eastern bettong (*Bettongia gaimardi*, Batson *et al*. 2016) and releases of the Tasmanian devil (*Sarcophilus harrisii*, Rogers *et al*. 2016). It is worth noting that there may be inherent differences between captive and wild founders which could impact genetic diversity, as well as performance beyond-the-fence where additional threats are present (e.g., invasive and native predators, roads, human interaction). However, these did not manifest within a predator-proof fence over our establishment period (42 days post-release).

Our study focused on the establishment phase of a reintroduction, which occurs immediately after release and is often associated with elevated mortality (Hamilton *et al.* 2010). This is often due to the behavioural and physiological responses elicited by exposure to a novel environment, which can increase vulnerability to starvation, predation and dispersal (Bennett *et al.* 2013). It is worth recognising that as a founding population transitions from the establishment phase to the regulation phase (IUCN 2013) they are at the mercy of long-term drivers including genetic viability and habitat suitability (Letty *et al*. 2007; Armstrong & Seddon 2008). This emphasises the value of monitoring reintroduced populations over the long term to capture variability over time (Armstrong & Seddon 2008; Jule *et al.* 2008; Robert 2009; Sheean *et al.* 2012).

Reintroduction biologists are being encouraged to adopt experimental frameworks that allow clear testing of hypotheses (Seddon *et al*. 2007; Swaisgood 2010; Sheean *et al*. 2012) and control for the effect of demographics, genetics and source environment (Jule *et al.* 2008). However, threatened species reintroductions are inherently limited in their ability to source large sample sizes of individuals to use in experimental designs (Armstrong & Seddon 2008), and thus trial reintroductions are the most pragmatic and informative option for assessing the efficacy of tactics (Kemp *et al.* 2015). In our study, we observed high mortality and post-release dispersal in male eastern quolls in Trial 1, justifying a change of tactics to female-only founders released in the post-mating period in Trials 2 and 3. Rigid experimental design would dictate that we should have translocated males in each trial for comparability. With an endangered species like the eastern quoll, however, trials need to be parsimonious in the use of founder individuals to yield the maximum learning with the least number of animals (Hume 1995). Further exposure of additional animals to sub-optimal tactics for the sake of replication and control, especially when alternative tactics have shown evidence of greater success based on a multi-trial approach, is unnecessary. Nevertheless, due to these operational constraints, results should always be tested adaptively in other contexts to ensure local applicability. Based on the effectiveness of our approach, we advocate conducting reintroductions strategically within an adaptive management framework, where learnings from early trials inform tactics employed in the next (Sheean *et al*. 2012; Kemp *et al*. 2015). We have demonstrated that each trial had increasing success due to the tactical changes we made.

2.7 Conclusions

Our study demonstrates the value of fenced sanctuaries as ‘outdoor laboratories’. We were able to identify key tactics to improve reintroduction success in the absence of the invasive predators that caused their original extirpation. This provides a strong foundation for future reintroduction trials beyond-the-fence. It is important to view these mainland islands as ‘stepping-stones back to the wild, rather than reservoirs of threatened biota’ (Batson 2015). The fate of eastern quolls that escaped over the fence is a reminder of the barrier that invasive predators (particularly foxes) represent to beyond-the-fence reintroductions. The return of the eastern quoll to mainland Australia is dependent on establishing insurance populations to protect against the threat of extinction (Fancourt 2016), while honing the reintroduction tactics that will ultimately allow the establishment of viable, free-ranging populations. Our results represent the stepping-stones by which future beyond-the-fence releases can progress.

To combat biodiversity declines worldwide, reintroduction biology will continue to develop in its applications and conservation value (Seddon *et al*. 2014a; Batson 2015; Woinarski *et al*. 2015). In contexts where there is imperfect knowledge and uncertainty about a species and its planned recipient ecosystem (for example, where the species has been absent for a long time), reintroduction success in 'one leap' is unlikely. Rather than viewing reintroductions as 'all or nothing' operations, we advocate for multiple reintroduction trials within an adaptive management framework. In this way, as we have done here, we can use our learnings from a series of initial trials, whether they were 'successful' at first or not, to better understand the process, build knowledge and adapt tactics that will lead to success in later trials and, ultimately, full reintroduction.

2.8 Acknowledgements

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Illustration by Cat Cotsell

Chapter 3: Personality and plasticity

Reintroduction success can be influenced by a myriad of factors, including individual variation in behaviours. These ‘personalities’, as well as the ability to adjust behaviour over time (plasticity), can play a pivotal role in determining post-release performance. For example, proactive individuals may dominate by being bolder, exploratory, and more willing to take risks in familiar, stable environments (i.e., the source environment). Reactive personalities, in contrast, may thrive in novel, unstable environments (i.e., the release site) by being vigilant and risk averse.

In this Chapter, I investigated whether behavioural measures in reintroduced eastern quolls could predict post-release survival and dispersal using the ‘behavioural reaction norm’ approach (Dingemanse *et al.* 2010). By integrating novelty into behavioural assays, I found that they offer significant value as a conservation tool to provide the fastest pathway to reintroduction success.

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Illustration by Cat Cotsell

Personality and plasticity predict post-release performance in a reintroduced mesopredator

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3.1 Abstract

Reintroductions involve the relocation of animals into their indigenous range following extinction or extirpation. In this context, individuals with certain personalities may be more successful than others. For example, proactive individuals may dominate by being bolder, exploratory, and more willing to take risks in familiar, stable environments (i.e., the source environment). Reactive personalities, in contrast, may thrive in novel, unstable environments (i.e., the release site) by being vigilant and risk-averse. In addition, an individual's ability to adjust its behaviours over time (plasticity, or responsiveness) can play a pivotal role in determining post-release performance. There is uncertainty, however, surrounding which behavioural measures translate to reintroduction success. We conducted behavioural assays and post-release monitoring for eastern quolls (*Dasyurus viverrinus*) to determine whether behavioural measures (e.g., latency to emerge, time spent vigilant) could predict post-release survival and dispersal in a conservation-fenced sanctuary. Using the 'behavioural reaction norm' approach, we found that personality derived from time spent exposed or vigilant during the assays held significant associations with post-release den sharing and home range, while plasticity derived from latency (i.e., time delay) to reach food held a significant association with mean distance between consecutive dens. We recommend that proactive and rigid founders be preferred for initial trial reintroductions, and that reactive and plastic founders be used to supplement the population in later translocations. Our study demonstrates that by integrating novelty, innovative behavioural assays offer significant value as a conservation tool to provide the fastest pathway to reintroduction success.

3.2 Introduction

Reintroductions aim to re-establish viable populations of species to areas from which they have been previously extirpated (IUCN 2013). When released back into their indigenous range, individuals that will establish the new population (henceforth founders) need to identify resources quickly and establish home ranges to survive (Stamps & Swaisgood 2007). However, the survival strategies that served an individual well in their source environment may not translate to the recipient environment. For example, an individual with a proactive personality may dominate by being bolder, aggressive, exploratory, and taking risks in familiar environments (i.e., the source environment), whereas these traits may make them vulnerable to predation and hyperdispersal in the context of a novel environment (i.e., the release site, (Koolhaas *et al*. 1999; Banks *et al*. 2002; Sih *et al*. 2004). Conversely, a reactive personality that is vigilant and takes fewer risks may outcompete proactive individuals in a novel environment by avoiding these threats (Careau *et al.* 2008).

Practitioners are increasingly recognising the role animal personality plays in conservation, especially for the survival (Smith & Blumstein 2008; Weiss & Adams 2013) and dispersal (Brandt 1992; Fraser *et al*. 2001; Dingemanse *et al*. 2003) of reintroduced species. Personality, defined as consistent behavioural differences between individuals that are repeatable (Svendsen & Armitage 1972; Réale *et al*. 2007), have been demonstrated in several taxa (Wilson *et al*. 1994; van Oers *et al*. 2004; Réale *et al*. 2009). Personality studies tend to explore behavioural traits, including boldness (response to perceived risk), exploration (response toward novelty), activity (tendency to move in a familiar environment), aggressiveness (agonistic behaviour toward conspecifics), and sociality (non-agonistic behaviours toward conspecifics, (Réale *et al.* 2007; Wolf & Weissing 2012). The boldness trait has been of particular conservation interest, because risk-taking by bolder individuals can provide benefit through improved body condition and reproductive success where they outcompete risk-averse individuals (Ward *et al*. 2004; Dammhahn & Almeling 2012). However, boldness is subject to natural selection (Huntingford & Giles 1987), and inappropriate risk-taking behaviour can also result in reduced fitness and shorter lifespans (Smith & Blumstein 2008). For example, Bremner-Harrison *et al*. (2004) found that bold captive-bred swift foxes (*Vulpes velox*) that exhibited less fear in captivity, were also less likely to survive following their release into a novel environment. Management actions, such as reinforcement translocations, supplemental feeding, and placement of physical boundaries (e.g., fences) can also generate different behavioural responses according to personality of an individual (Dunham 2001; Clark *et al*. 2002; Druce *et al*. 2004). In this way, personality may be as important to consider as age, sex, health, and genetics when selecting founders for release (Watters & Meehan 2007).

A critical element of personality is that it is not always constant throughout an individual's lifetime. The ability to alter behaviour in response to changing conditions is referred to as plasticity (or responsiveness, Komers 1997; Piersma & Drent 2003; Bonte *et al*. 2007). Plasticity offers an important measure of behaviour because the mean value of a behaviour (i.e., personality) does not provide insights into behavioural variation over time (Watters & Meehan 2007). Indeed, plasticity can be manipulated to increase anti-predator behaviours by exposing individuals to predators or their cues prior to release (Greggor *et al.* 2019; Rowell *et al.* 2020). Interestingly, some studies have demonstrated that plasticity may be correlated with behavioural traits, such as in chaffinches (Quinn & Cresswell 2005), trout (Frost *et al.* 2007) and weakly-electric fish (Kareklas *et al.* 2016). For example, aggressive mice (*Mus musculus domesticus*) were less plastic in their responses to social and non-social situations than were more timid mice (Benus *et al.* 1990). Dingemanse *et al*. (2010) suggest that plasticity may be as much a trait as boldness, and one that may or may not be adaptive to their environment.

Personality and plasticity can be measured using standardised experimental tests of behaviour (henceforth behavioural assays). Depending on whether conditions are familiar, novel, or risky, certain traits can be targeted and assessed with behavioural assays (Roche *et al.* 2016). For example, emergence (López *et al.* 2005) and trapability assays have been used to measure boldness (Réale *et al.* 2000; Réale & Festa-Bianchet 2003). When behaviours that are relevant to the focal species differ between individuals, and can be easily measured, assays can be used as pre-release screening to inform reintroduction programs (McPhee 2004; Watters & Meehan 2007). For example, wild-caught brushtail possums (*Trichosurus vulpecula*) were shown to have higher chances of post-release survival if they showed fear during handling (May *et al.* 2016).

Here we explore personality and plasticity in the model system of an endangered marsupial carnivore, the eastern quoll (*Dasyurus viverrinus*), which was reintroduced to mainland Australia. We performed pre-release behavioural assays on six captive-bred and seven wild-caught maternal founders by simulating a risk, then measuring easily-quantifiable behavioural responses including latency to emerge (Fox 1972), time spent vigilant, and giving-up density. We then extracted personality and plasticity indices derived from these behavioural responses (using the 'behavioural reaction norm' approach, (Dingemanse *et al.* 2010). Finally, we tested associations between these personality and plasticity indices and founder post-release performance during an initial establishment period. This study took place in a conservation-fenced sanctuary, to remove the ongoing threat posed by the invasive predators that contributed to their extirpation from the mainland (i.e., red fox *Vulpes*, and feral cat *Felis catus*), and to allow us to trial novel tactics in a low-risk 'outdoor laboratory' (Wilson *et al.* 2020, 2021).

While survival is known to have consequences for short-term establishment through to longer-term genetic effects (Swaisgood 2010), hyperdispersal can also influence these processes by exposing founders to threats beyond the release site (where these threats are not typically managed), leading to higher mortality rates (Clarke & Schedvin 1997; Pierre 1999; Swaisgood 2010). This is particularly relevant in the context of havens in Australia, where dispersal over the fence leaves founders vulnerable to predation by invasive predators (Moseby *et al.* 2014; Wilson *et al.* 2020, 2021). Due to proactivity being associated with increased risk-taking (Coppens *et al.* 2010) and plasticity being associated with higher capacity for learning (Snell-Rood & Steck 2019) and therefore identifying critical resources with less exploration, we hypothesised that proactive personalities and rigid (unresponsive) founders would disperse further and, therefore, have lower survival rates than reactive personalities and plastic (responsive) founders.

3.3 Methods

3.3.1 Ethics note

Translocations were conducted under licenses from the Tasmanian Department of Primary Industries, Parks, Water and Environment (permits TFA 16025 and 17091, export licences 12818/16 and 13528/17), Victorian Department of Environment, Land, Water and Planning (permit 14505167), and Australian Capital Territory Municipal Services (import licence L120161261). Reintroduction and behavioural assay procedures were approved by The Australian National University Animal Experimentation Ethics Committee (protocol A2016/02).

3.3.2 Study area

We conducted behavioural assays at The Australian National University (ANU), and released eastern quolls at Mulligans Flat Woodland Sanctuary (MFWS) in the Australian Capital Territory (ACT), Australia (-35.167, 149.158). MFWS is a 485 ha reserve dominated by yellow box (*Eucalyptus melliodora*) - Blakely’s red gum (*E. blakelyi*) grassy woodland, a critically endangered ecological community (McIntyre *et al.* 2010). In 2009, the area was enclosed with an 11.5 km predator-proof fence to allow the reintroduction of locally extinct species in the absence of invasive predators such as the red fox and feral cat, as well as destructive herbivores like European rabbits (*Oryctolagus cuniculus*) and European hares (*Lepus europaeus*, (Shorthouse *et al.* 2012). Aside from the exclusion of invasive species, conditions within the Sanctuary are otherwise like other unfenced woodlands in the region. The fence design includes an overhang that prevents entry by invasive predators (based on successful trials at Arid Recovery, (Moseby & Read 2006), but adapted for local conditions as per Shorthouse *et al*., 2012) but does not prevent eastern quolls from climbing out of the Sanctuary into the surrounding landscape. The site forms a part of the Mulligans Flat-Goorooyarroo Woodland Experiment, which generates evidence to support conservation decision-making aimed at restoring woodlands for biodiversity (Manning *et al.* 2011; Shorthouse *et al.* 2012).

3.3.3 Study species

The eastern quoll (*murunguny* in the local Indigenous Ngunnawal language) is a small-to-medium (0.7–2 kg), critical weight range (Australian mammals between 35–5500 g that suffer the greatest attrition (Burbidge & McKenzie 1989), carnivorous marsupial (family Dasyuridae, (Stannard & Old 2013). As generalist predators they hunt mammals, birds, reptiles, crustaceans, invertebrates, and will also scavenge on carcasses (Blackhall 1980; Godsell 1983). Eastern quolls are nocturnal and become active around dusk for eight hours regardless of season (Jones *et al.* 1997). During the day, they shelter in dens which include fallen logs, rock crevices, or abandoned rabbit warrens (B. A. Wilson, *pers. obs.*). Eastern quolls are usually solitary and territorial, with den sharing considered uncommon apart from mother and young (Jones *et al.* 2001). However, den sharing has been recorded as common in reintroduced females at MFWS (Wilson *et al.* 2020). As a mesopredator, eastern quolls invest in vigilance behaviour in response to known predators (e.g., masked owls *Tyto novaehollandiae castanops*, Mooney 1993) and competitors (e.g., Tasmanian devils *Sarcophilus harrisii*, Jones & Barmuta 1998).

The eastern quoll originally occupied open landscapes throughout the south-east of Australia. These areas have suffered habitat degradation, predator introductions, and due to a combination of these and disease (Peacock & Abbott 2014), the eastern quoll became restricted to Tasmania where it lived in low densities in the drier, eastern half of the island state (Jones & Rose 1996; Fancourt 2015). The species is listed as endangered by the International Union for Conservation of Nature (IUCN, Burbidge & Woinarski 2016) and the Commonwealth of Australia (*Environment Protection and Biodiversity Conservation Act 1999*). There are two successfully reintroduced populations on mainland Australia: Mt Rothwell Biodiversity Interpretation Centre in Victoria (Mt Rothwell) and MFWS in the ACT, where it is now listed as endangered (Nature Conservation Act 2014 s 90C, ACT Parliamentary Counsel 2014).

3.3.4 Founders

In 2015 the Eastern Quoll Mainland Recovery Team recommended reintroducing eastern quolls to predator-proof sanctuaries on mainland Australia to safeguard the species should threatening processes drive Tasmanian populations to extinction. After a trial release in February 2016 revealed high mortality in male founders associated with hyperdispersal (Wilson *et al.* 2020), we adapted within a translocation tactics framework (*sensu* (Batson *et al.* 2015) and selected maternal founders for subsequent trials to maximise survival and minimise mortality (Wilson *et al.* 2020, 2021).

We conducted our study in 2017 during the second trial reintroduction of eastern quolls to MFWS. We sourced six captive founders from a breeding program at Mt Rothwell and seven wild founders from free-ranging populations across four regions in Tasmania (see (Wilson *et al.* 2020). We translocated founders to The Australian National University (ANU) by air and road, where they were anaesthetised and given veterinary health assessments (see (Portas *et al.* 2020). We fitted each animal with a VHF collar (32g, V6C 163 Zilco, Sirtrack Ltd, Hawkes Bay, New Zealand) prior to assays to allow us to monitor the fit. After health assessments, founders recovered in a straw-lined wooden den box (50 × 35 × 28.5 cm) that had one round door at the front for the animal to use, and another larger door on the side to allow researchers to access the animal. This den box functioned as the animal's shelter, a point of reference during assays, and their subsequent release box.

3.3.5 Behavioural assays

We held founders separately in outdoor, steel mesh aviaries (henceforth enclosures) of 6 m length × 2.5 m width × 3 m height at the ANU (Figure 3.1a). Enclosures were standardised with a mulch bottom layer, a food tray near the door, a wooden post for holding the assay stimulus in the centre, a den box, and a water tray beside it at the end furthest from the doors. Due to enclosures being adjacent to one another (i.e., sharing at least one wall with another enclosure), we installed 1 m high shade cloth skirting between them to discourage interaction between adjacent animals.

We installed an array of four remote cameras (Ltl Acorn 5310a) at equal intervals along the centre of the enclosure roof so that each field-of-view was non-overlapping and allowed animals to be viewed in most of the enclosure. Cameras were triggered by body heat and motion using a passive infrared system, and we configured them to record 30 seconds of footage per trigger, with a zero second interval between triggers.

We allowed founders to habituate to captivity in these enclosures for 48 hrs before undergoing assays. In the related Tasmanian devil, stress measured from plasma cortisol concentrations fell to basal levels after this period in captivity (Jones *et al.* 2005), and in the western quoll (*Dasyurus geoffroii*) stress measured from faecal glucocorticoid metabolites peaked at 24 hrs after capture and housing (Jensen *et al.* 2019), suggesting that 48 hrs should be sufficient to allow eastern quolls to adjust to this novel environment. During habituation, we provided their food (40 g kangaroo mince and 30 g chicken neck) at the same time as it would be during their assays (18:00 and 22:00), and provided water *ad libitum*. Contact with researchers was minimised to avoid human habituation. We held founders in these enclosures from their first habituation night to the time of their release.

Due to their generalist nature, quolls are capable learners (Shettleworth 1984), and olfactory and auditory cues are likely to be as important as visual cues because they forage in long grass and thick understory (Blumstein 2000). We employed a set of four experimental treatments (henceforth stimuli, as per Table 3.1), because performing several assays can provide a more comprehensive assessment of personality (e.g., Highfill *et al*. 2010; Carter *et al*. 2013; Andersson *et al*. 2014; Stratton 2015), and would allow us to target multiple senses and maximise our potential to detect behavioural differences between individuals. We considered using handling-bag tests, where docility can be inferred by the amount of time an animal spends static or mobile while suspended in a bag (Martin & Réale 2008; Mella *et al.* 2016). However, we determined that this test was inappropriate because eastern quolls are naturally docile while being handled in a bag and our animals exhibited negligible differences in docility (B. A. Wilson, *pers. obs.*).

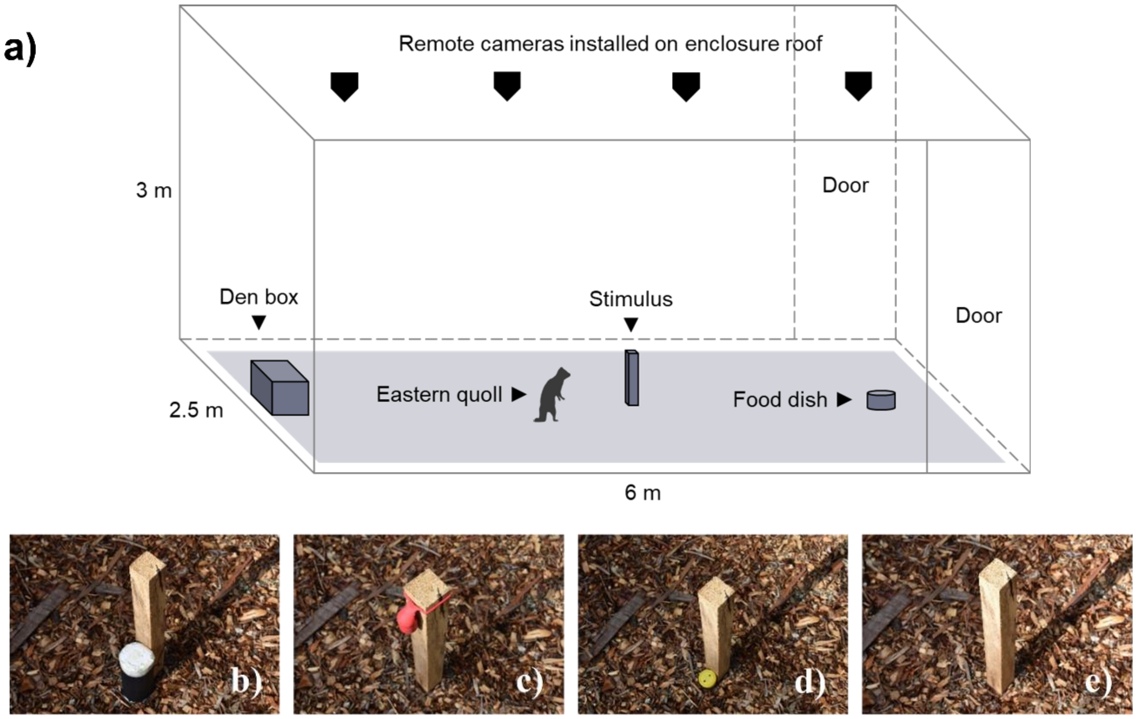

Figure 3.1 Standardised enclosure for the behavioural assay of eastern quolls (*Dasyurus viverrinus*) prior to their reintroduction into Mulligans Flat Woodland Sanctuary, Australian Capital Territory. (**a**) Diagram is to approximate scale, and grey shading indicates the field-of-view of remote cameras installed on the enclosure roof. Stimuli attached to wooden stakes were either (**b**) Ultimate Ears Boom speaker used to play a masked owl (*Tyto novaehollandiae castanops*) calls, **c**) blinking bicycle light, **d**) perforated jar containing the rehydrated faeces of a conspecific (as per Blumstein *et al*. 2002) or (**e**) control.

Each animal underwent 16 assays, defined as a single behavioural test with exposure to a single stimulus (total 208 assays across all animals). The duration of each assay was 120 mins with two assays conducted per night for each animal across eight nights (total 1920 mins observation per animal), with a 2 hr rest period between same-night assays to avoid carryover effects (first assay at 18:00 and second at 22:00, i.e., within the normal hours of eastern quoll activity, (Jones *et al.* 1997). The short intervals between assays were necessitated by the time constraints of the translocation, but a meta-analysis indicated that repeatability tends to be stronger at shorter intervals (Bell *et al.* 2009).

Assays began with a researcher entering the enclosure, providing a prepared amount of food, and attaching the stimulus to the wooden stake (Figure 3.1b–e). We avoided confounding effects by testing animals using the same stimulus at the same time, because the effect of auditory and olfactory stimuli could perforate between adjacent enclosures. We were unable to prevent the animals' vocalisations from perforating to adjacent enclosures, but this rarely occurred. A maximum of eight assays were run concurrently due to availability of enclosures. The order of

Table 3.1 Description and relevance of stimuli used in standardised behavioural assays of eastern quolls (*Dasyurus viverrinus*) prior to their reintroduction to Mulligans Flat Woodland Sanctuary, Australian Capital Territory.

Stimuli	**Description**	**Relevance to reintroductions**
Auditory stimulus to simulate a perceived risk	Exposure to masked owl (*Tyto novaehollandiae castanops*) calls to implicate predation risk. Call recording (27 s, sourced from the (Morcombe 2003) Field Guide to Australian Birds eGuide app) was played every 15 mins during the assay at a standardised volume (50%) to approximate natural sound levels to the human ear (as per (Jones *et al.* 2004) using synchronised Ultimate Ears Boom speakers.	The propensity to take risks can influence predator recognition and avoidance, survival, and reproduction (Coleman & Wilson 1998; McDougall *et al.* 2006; Réale *et al.* 2007).
Visual stimulus to simulate novelty	Exposure to a blinking bicycle light operating continuously.	Exploration or avoidance can predict dispersal which may influence access to resources, survival, and predation (McDougall *et al.* 2006; Réale *et al.* 2007).
Olfactory stimulus to simulate proximity of a conspecific	Exposure to a perforated jar containing the rehydrated faeces of a female conspecific (as per (Blumstein *et al.* 2002)	Sociality to conspecifics may influence dispersal in a novel environment (McDougall *et al.* 2006; Réale *et al.* 2007).
Control	No stimulus but maintaining the same novel environment as with other stimuli (human entering enclosure and replenishing food).	As per visual stimulus.

assays was decided using the Latin square design to ensure that each stimulus was followed by every other stimulus (as per (Jones *et al.* 2004). However, of the total 208 assays conducted, 16 needed to be repeated due to equipment error, which changed the stimulus order for some animals.

Behavioural responses were recorded by a single observer using Behavioral Observation Research Interactive Software (BORIS version 4.1.4, (Friard & Gamba 2016), as follows: (1) latency to emerge: time of first camera trigger following introduction of the novel object to the nearest minute (Fox 1972), 2) latency to reach food: time of first appearance in the quadrat where food was placed (to the nearest minute), 3) time spent active: mobile, eating, or grooming (to nearest 0.001s), 4) time spent vigilant: disrupted behaviour or being in a tensed state (including freezing, looking around slowly with head up, standing on hind legs or sniffing to nearest 0.001s, as per (Jones *et al.* 2004), 5) time spent exposed: sum of time spent active and time spent vigilant, 6) time spent hidden: in the den box or out of the field-of-view (to nearest 0.001s), 7) giving-up density: percentage of available food eaten during the assay (GUD), and (8) number of camera triggers in the furthest half of the enclosure containing the stimulus and food.

These measures were selected based on similar studies (Perals *et al*. 2017; West *et al*. 2019a), and because perceived risk (e.g., of predation) has been demonstrated to increase vigilance, reduce activity, and reduce feeding in open areas (Sih & McCarthy 2002; Eilam 2005; Dammhahn 2012). If there were no camera triggers during an assay, the maximum time available to emerge or reach food was entered (120 mins). When only the animal's tail was in the field-of-view it could not be determined whether it was exhibiting active or vigilant behaviour, so in these instances the animal was considered hidden. This removed the issue of recording activity or vigilance for both the animal's body visible on one camera, and the tail visible on an adjacent camera. It was not possible to make the observer blind to stimulus or morph of individuals because these were visually distinguishable in the footage.

3.3.6 Release

Due to the limited number of enclosures, captive founders underwent translocation, assay, and release 13–22 days prior to the wild founders. All founders underwent a health check one day prior to release, and between one and three founders were released every two nights in a central location in MFWS. To minimise stress, individuals were placed *in situ* in their den box with the doors closed for 1–2 hours, and after last light the door was opened and the quoll was allowed to leave of its own accord (as per Wilson *et al*. 2020, 2021).

3.3.7 Monitoring

We radiotracked founders to their den sites each day for 42 days post-release (the establishment period), because survival plateaued after this period in a previous trial reintroduction involving both male and female founders (see Wilson *et al*. 2020). If a founder escaped over the fence, we radiotracked them to their location, and trapped and re-released them at their initial release site at MFWS (*n* = 1, '5340', Table 3.2). If any founder attempted two escapes, we translocated it to Mt Rothwell based on the assumption that it would only escape again if re-released (*n* = 1, 'E09E'). If a mortality signal was detected, we located the founder immediately and conducted a necropsy (*n* = 1, 'D897'). Due to observed weight losses after assays, we supplementarily fed founders by rolling a ball of beef mince into their den in decreasing amounts over time (100–30 g) until weights stabilised. We removed radiocollars from founders after their young had dispersed from the natal den in Austral spring.

We conducted post-release health checks every two weeks, though the timing and frequency often varied due to reproductive stage, weight fluctuations, logistical constraints, and our ability to trap the targeted animals. We trapped founders with wire cage traps (31 × 31 × 70 cm) before

Table 3.2 Reintroduction history of maternal eastern quolls (*Dasyurus viverrinus*) translocated to Mulligans Flat Woodland Sanctuary, Australian Capital Territory. 'Mt Rothwell' refers to Mt Rothwell Biodiversity Interpretation Centre in Victoria, Australia, 'fixes' refers to the number of radiotracking records, and 'den sharing' is the percentage of fixes found den sharing with another founder. Escaped (dispersing outside the exclusion fence) and transferred animals were considered deceased for analyses.

ID	Origin	Location	Release date	Release condition	Release weight (kg)	Fate	Cause of death	Pouch young (*n*)	Fixes (*n*)	Den sharing (%)
C682	Captive	Mt Rothwell	11/07/2017	Good	0.786	Survived		6	42	7
3051	Captive	Mt Rothwell	28/06/2017	Good	0.960	Survived		6	42	12
5340	Captive	Mt Rothwell	24/06/2017	Good	0.955	Deceased	Escaped, retrieved	0	8	0
1BEF	Captive	Mt Rothwell	26/06/2017	Good	0.830	Survived		6	42	31
8849	Captive	Mt Rothwell	26/06/2017	Good	0.880	Survived		4	42	43
1801	Captive	Mt Rothwell	05/07/2017	Good	0.750	Survived		0	41	80
E384	Wild	Tasmania (Lonna Vale)	11/07/2017	Fair	0.746	Survived		6	42	12
DDE1	Wild	Tasmania (Grove)	13/07/2017	Fair	0.890	Survived		6	42	50
D6C1	Wild	TAS (Grove)	13/07/2017	Good	0.910	Survived		6	41	90
F9FC	Wild	TAS (Russell Falls)	17/07/2017	Good	0.845	Survived		2	42	2
E09E	Wild	TAS (Russell Falls)	17/07/2017	Good	0.760	Deceased	Escaped, retrieved	6	1	100
D897	Wild	TAS (Geeveston)	19/07/2017	Good	0.885	Deceased	Escaped, predated	6	7	0
1715	Wild	TAS (Geeveston)	19/07/2017	Good	0.890	Survived		5	42	10

first light, to minimise stress (as per Wilson *et al*. 2020). In total, we conducted 50 founder captures during the 2017 establishment period.

3.3.8 Analyses

3.3.8.1 Personality and plasticity

We quantified eight behavioural measures during our assays; latency to emerge (min), latency to reach food (min), time spent active (s), time spent vigilant (s), time spent exposed (s), time spent hidden (s), giving-up density (GUD, percent), and number of camera triggers (*N*, Figure 3.2). Firstly, we standardised predictors by scaling their means to zero and standard deviations to one to allow direct comparisons. We then tested for effects originating from assay conditions including stimulus (auditory, olfactory, visual, or control) and session (18:00 or 20:00) using generalised linear models (GLMs). Since environmental conditions influence foraging behaviour in eastern quolls (Linley *et al.* 2020), we also included ambient temperature (˚C), precipitation (mm), humidity (percent), wind (km/hr), pressure (hPa), and moon phase (percent) in these models (Bureau of Meteorology 2022). We found that session, humidity, and moon phase significantly influenced most behavioural measures, so to account for these non-target effects we extracted predicted values from the full model containing each assay and environmental condition as fixed effects, and used these adjusted values for subsequent analyses (Figure 3.2).

We then tested for correlations between behavioural measures, and found that time spent exposed was significantly correlated with time spent active, time spent hidden, and number of camera triggers ($R > 0.7$, Figure 3.2). To avoid redundancy and collinearity issues, we proceeded with time spent exposed in our modelling because it generated the greatest inter-individual variation.

To calculate personality estimates, we analysed our adjusted behavioural measures using the 'behavioural reaction norm' approach (Dingemanse *et al.* 2010). This framework represents an individual's behavioural responses as a regression line where the intercept corresponds to mean behaviour (personality) and the slope corresponds to how rapidly they adjust their behaviour over an environmental gradient, such as time (plasticity). We extracted these personality and plasticity coefficients for each of the remaining five behavioural measures across all assays for each individual. We also created two principal component (PC) measures; one for those where we related greater values to greater proactivity (time spent exposed and GUD, referred to as 'proactive PC') and another for those where we related greater values to greater reactivity (latency to emerge, latency to reach food, and time spent vigilant, referred to as 'reactive PC'). For each group of measures, we conducted a principal components analysis (PCA) on the intercept and slope coefficients and extracted the first-dimension coordinate (Figure 3.2). Finally, we tested for the effects of origin (captive or wild) on all behavioural measures.

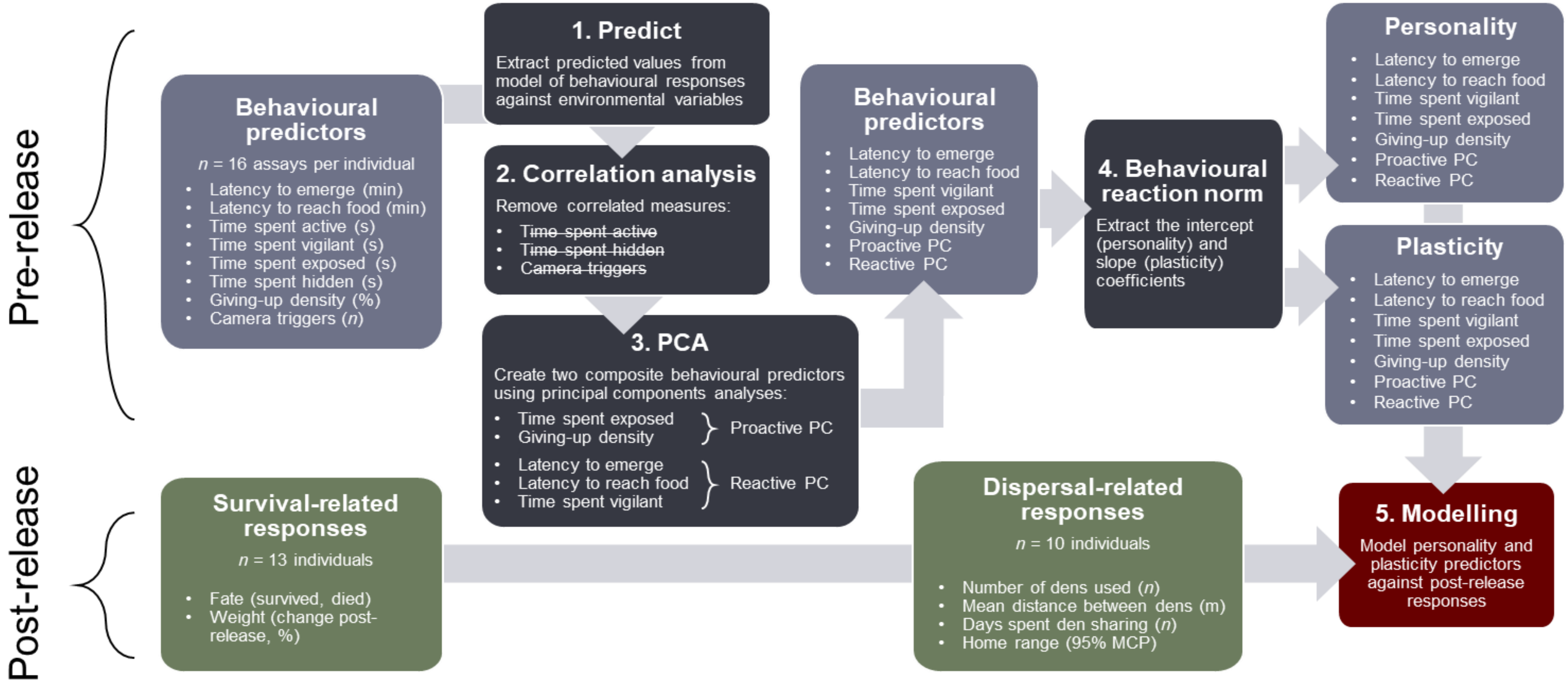

Figure 3.2 Flow diagram illustrating the steps taken to prepare and analyse pre-release behavioural predictors and post-release responses for eastern quolls (*Dasyurus viverrinus*) to be reintroduced to Mulligans Flat Woodland Sanctuary, Australian Capital Territory. Personality and plasticity indices were calculated using the ‘behavioural reaction norm’ (Dingemanse *et al.* 2010). The principal components (PC) predictors were generated from the first dimension coordinate of a principal components analyses combining proactive-related and reactive-related predictors. Post-release responses related to either survival (*n* = 13), and dispersal (included individuals with >10 days post-release survival, *n* = 10). Home range was calculated as the 95% minimum convex polygon (MCP).

3.3.8.2 Post-release performance

Post-release performance responses were related to either survival or dispersal. Survival-related responses included all individuals (*n* = 13) and were quantified as fate (survival or died), and post-release weight (percent change between the pre-release health check and last post-release health check); noting that escapee and transferred animals were considered deceased for analyses. Dispersal-related responses included individuals that survived for >10 days (*n* = 10, (Börger *et al.* 2006) and were quantified as the number of dens used in the establishment period *(n),* mean distance between dens (m), days spent den sharing with another founder (*n*), and home range (95% minimum convex polygon, MCP). MCP was selected because it produces more reliable home range estimations than probabilistic models with small sample sizes (Laver & Kelly 2008). We did not test performance against body weight, condition, or pouch occupancy because these were found to be non-significant in a previous study (Wilson *et al.* 2020).

3.3.8.3 Statistical models

To determine whether personality and plasticity could predict post-release performance, we fitted generalized linear mixed models (GLMMs) for each personality and plasticity coefficient derived from each of the seven behavioural measures (including the two PCs) as predictors and each post-release measure as a response (Figure 3.2). To avoid overfitting with our small sample sizes, we chose to run separate Gaussian error distribution models for each combination of behavioural predictor and post-release response. We interpreted variables as significant if their 95% confidence intervals did not cross the zero-effect line (Du Prel *et al*. 2009; Welsh 2011). Analyses were performed in R version 4.0.2 (R Core Team 2021) using the *adehabitatHR* (Calenge 2006), *brglm* (Kosmidis & Kosmidis 2020), *corrplot* (Wei *et al.* 2017), *ggplot2* (Wickham 2011), *FactoMineR* (Husson *et al.* 2016), *lme4* (Bates *et al.* 2015), and *raster* (Hijmans & van Etten 2015) packages.

3.4 Results

3.4.1 Personality and plasticity

We quantified behaviour using 16 behavioural assays for each of 13 eastern quolls (*n* = 208 assays). We found no significant effect of stimulus (auditory, olfactory, visual, or control) on personality coefficients, and so did not include this factor in subsequent analyses. However, assay number (1–16) significantly influenced latency to emerge ($F = 7.95$, $R^2 = 0.03$, $p < 0.01$), latency to reach food ($F = 6.23$, $R^2 = 0.03$, $p = 0.01$), time spent vigilant ($F = 7.08$, $R^2 = 0.03$, $p < 0.01$), and giving-up density ($F = 10.58$, $R^2 = 0.05$, $P < 0.05$, Figure **3.3**), demonstrating significant ability in our eastern quolls to adjust these responses over time (i.e., plasticity). We also tested whether founder origin (i.e., captive or wild) could predict behavioural measures, and found no significant effects ($p > 0.05$).

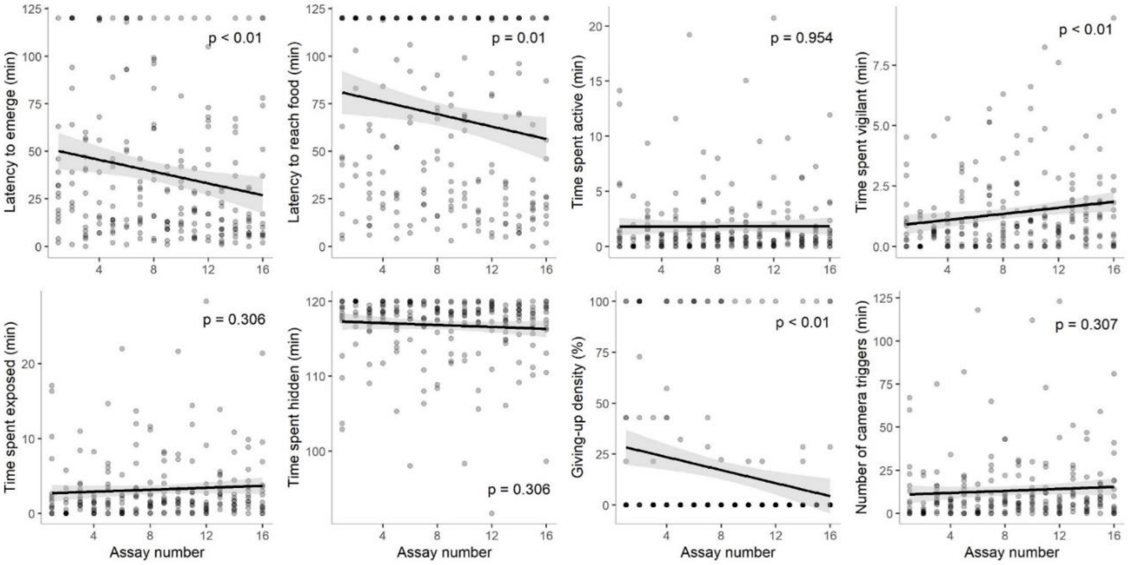

Figure 3.3 Scatter plots with linear regressions and 95% confidence intervals for behavioural measures taken across 16 behavioural assays of 13 eastern quolls (*Dasyurus viverrinus*) prior to their reintroduction to Mulligans Flat Woodland Sanctuary, Australian Capital Territory. 95% confidence intervals are indicated by error bars. Large black icons indicate significant effects ($p < 0.05$, where the confidence interval does not pass the zero line), and small white icons indicate no significant effects.

3.4.2 Post-release performance

For post-release analyses, individuals were represented by a single value for each predictor and response. Personality derived from time spent vigilant achieved a significantly negative association with days spent den sharing (i.e., quolls that were more vigilant during assays spent fewer days den sharing after release, $p = 0.03$), and a significantly positive association with home range (i.e., quolls that were more vigilant during assays had larger post-release home ranges, 95% MCP, $p = 0.03$, Figure 3.4).

Plasticity derived from latency to reach food achieved a significantly positive association with mean distance between dens (i.e., quolls that displayed plasticity in their latency to reach food across assays travelled further between consecutive dens post-release, m, $p = 0.04$), and plasticity derived from time spent exposed was positively associated with days spent den sharing (i.e., quolls that displayed plasticity in their time spent exposed across assays spent more days den sharing post-release, *p* = 0.01, Figure 3.4). No significant relationships were found with the fate (survived, died), post-release weight (percent change), and number of dens used (*n*) post-

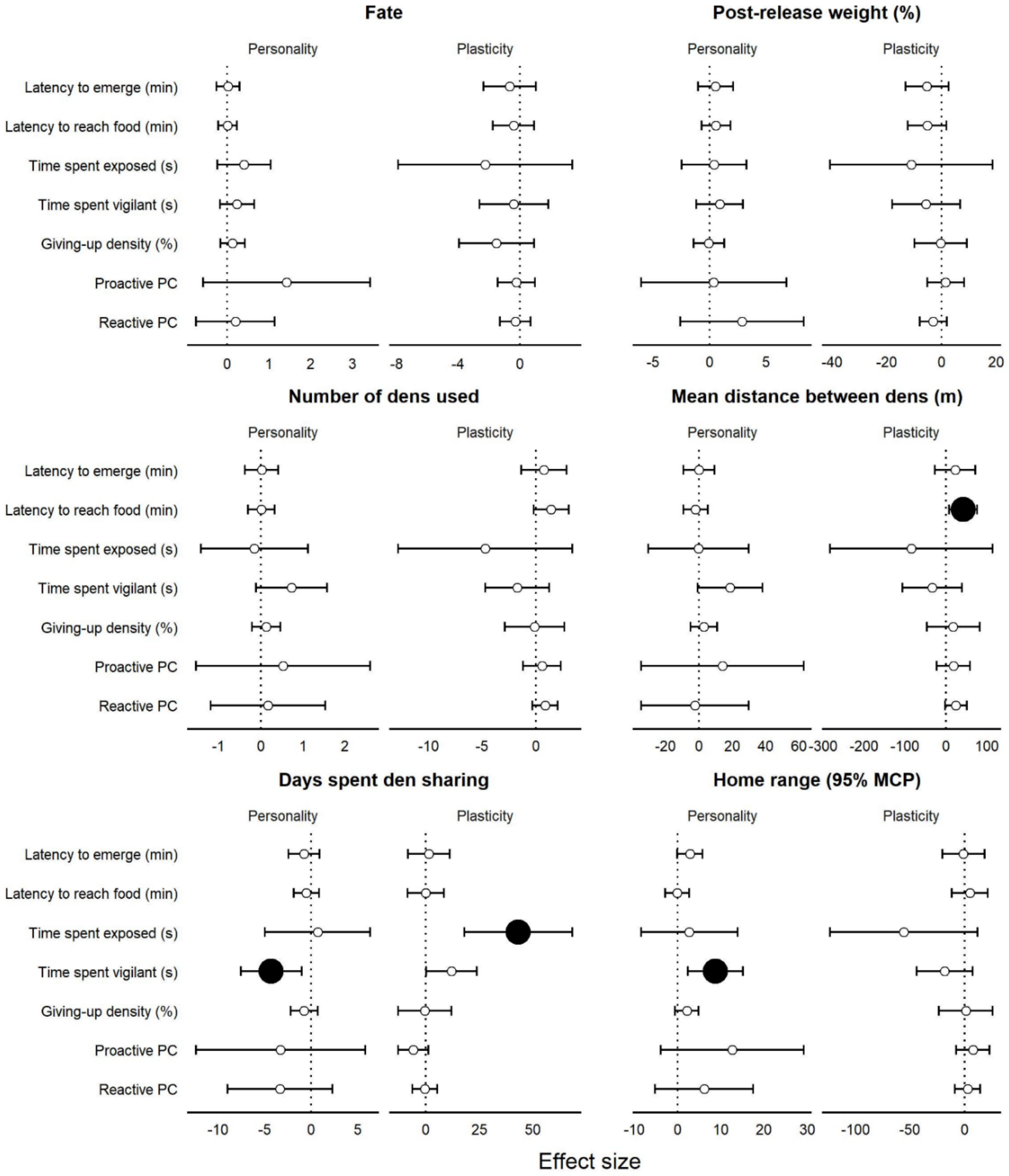

Figure 3.4 Effect sizes of personality and plasticity predictors (calculated using the 'behavioural reaction norm' approach, Dingemanse *et al*. 2010) derived from the latency to emerge (min), latency to reach food (min), time spent exposed (s), time spent vigilant (s), giving-up density (GUD, percent), proactive PC (first dimension coordinate of principal components analysis including time spent exposed and GUD), and reactive PC (as per proactive PC, but including latency to emerge, latency to reach food, and time spent vigilant) by post-release responses relating to survival (fate and post-release weight, *n* = 13), and dispersal (number of dens used, mean distance between dens, days spent den sharing, and home range [95% minimum convex polygon], individuals with >10 days post-release survival, *n* = 10) of assayed eastern quolls (*Dasyurus viverrinus*) reintroduced to Mulligans Flat Woodland Sanctuary, Australian Capital Territory.

Error bars indicate 95% confidence intervals. Large black icons indicate significant effects ($p < 0.05$, where the confidence interval does not pass the zero line).

release responses, or with the latency to emerge (min), giving-up density (percent), proactive PC, and reactive PC behavioural predictors.

3.5 Discussion

By conducting behavioural assays of individual variation, we were able to detect significant relationships between the personality and plasticity of reintroduced eastern quolls and their post-release performance. The limited number of individuals involved and the short interval between repeated assays meant our results may reflect short-term, rather than long-term, differences in personality and plasticity between individuals (Dingemanse *et al.* 2012). Before we discuss the results we will highlight the caveats that accompany our interpretations.

Firstly, founder origin has been shown to affect post-release performance, with wild founders often being more successful than captive founders (Griffith *et al.* 1989; Kleiman 1989). When we cage-trapped wild founders in Tasmania, we unavoidably selected individuals that were susceptible to trapping, which can be considered a personality trait (Wilson *et al*. 1993; Drickamer *et al*. 1995; Réale *et al*. 2000). As a result, our wild founders may not have displayed the breadth of personalities and plasticities that exist in wild Tasmanian eastern quolls, and could explain why we found no significant differences between the captive and wild groups.

Secondly, our tactic of releasing maternal founders meant they had higher energetic costs associated with parturition and parental care, so their decisions were driven by an increased trade-off between food intake and offspring safety (Gillingham & Bunnell 1985). This context emphasises the importance of considering life history when selecting founders and the behaviours to measure.

Thirdly, it can be difficult to distinguish whether founder dispersal and habitat preference is a result of personality, or environmental heterogeneity experienced across the release site (van Overveld & Matthysen 2010; Harrison *et al*. 2015; Haage *et al*. 2017). This problem is further confounded by the necessarily small sample sizes associated with studies of threatened species (discussed below, Rowell *et al*. 2020). Future studies should make use of technological advances (e.g., GPS units) to explore dispersal and social decisions at higher spatio-temporal resolutions.

Fourthly, due to observed weight losses following behavioural assays we decided to act within an adaptive management framework to provide supplemental feed to our founders. While supplemental feeding can encourage site fidelity (Doonan & Slade 1995; Doligez *et al*. 2004), dispersal rates between our founders and those of a release one year later were comparable despite the latter not requiring supplemental feeding (Wilson *et al.* 2020), so it is unlikely that this adaptive action markedly influenced our results.

Finally, we acknowledge the uncertainty driven by our small sample size. This is an inherent challenge for threatened species conservation, because by their nature the available pool of individuals is small and valuable (Hume 1995; Batson *et al*. 2017), and it is near impossible to secure a sample that would be fully representative of the whole population (Garamszegi 2016). Here we maximised our learning from the minimum number of animals (Wilson *et al.* 2020); a deliberately parsimonious approach which can reveal valuable insights despite its uncertainties. These early findings for a threatened species are crucial to the progress of conservation science by informing future management actions (Caro & Sherman 2011; Sinn *et al.* 2013).

In this study, behavioural variation was investigated using quantitative coding of behavioural states (e.g., time spent vigilant) in a novel environment. Behavioural studies often argue for eliminating novelty in their tests because this is required to detect boldness (response to perceived risk, Réale *et al*. 2007), however we could not avoid novelty in our setup because it is an intrinsic part of the translocation process. Rather than inferring a particular trait to each of our measures, for clarity we chose to place our results in the context of the proactive (bolder, more exploratory, social) and reactive (shy, less exploratory, antisocial) syndrome (Koolhaas *et al.* 1999; Sih *et al.* 2004). We characterised proactive individuals as those with low times spent vigilant and latencies to reach food or emerge, and high times spent exposed and GUD, and reactive individuals as those with high times spent vigilant and latencies to reach food or emerge, and low times spent exposed and GUD. These were also reflected in the choice of behavioural measures to be included in each of the two PC measures.

Personality derived from time spent vigilant was negatively associated with days spent den sharing ($p < 0.05$, Figure 3.4), a post-release response that was found to be positively correlated with survival in a related study (Wilson *et al.* 2020). This suggests that reactive founders were more averse to sharing territory with conspecifics, driving them to find unoccupied den sites further afield. This behaviour is not only risky, but energetically costly, especially for maternal eastern quolls (Godsell 1983). In addition, personality derived from time spent vigilant was positively associated with home range (95% MCP, $p < 0.05$, Figure 3.4), supporting the result that reactive individuals ranged further than their proactive counterparts. This was contrary to our hypothesis, where we expected proactive founders to range further due to increased risk-taking (Coppens *et al.* 2010). This result could be explained by competition for territory driving reactive individuals to range further from dominant conspecifics, however, the successful establishment of 76.9% and 87.5% of maternal founders in the second and third trial reintroductions respectively suggests that territory was not limiting (Wilson *et al.* 2020). Regardless of the mechanism, we suggest that proactive founders may be more successful than reactive founders in initial trials, where conspecific attraction could maximise founder settlement.

Personality is typically defined as consistent and repeatable behaviours, but this ignores the value of measuring behavioural change along an environmental or temporal gradient to detect plasticity. Using the ‘behavioural reaction norm’ approach (Dingemanse *et al.* 2010), we found that time significantly affected all behavioural measures, indicating substantial short-term behavioural plasticity in our founder eastern quolls. Interestingly, this is inconsistent with a meta-analysis that found no change in anti-predator behaviour (flight-initiation distances in birds) for short and intermediate time scales (Holtmann *et al.* 2017). This may be driven by differences between taxa, trophic level, or a myriad of other factors, and reinforces the need for selecting species-specific measures of behaviour.

In our study, plasticity derived from latency to reach food increased significantly with mean distance between dens, a dispersal response which positively correlated with mortality in reintroduced eastern quolls across iterative trials (Wilson *et al.* 2020). This is also contrary to our hypothesis, where, because plasticity is associated with a higher capacity for learning (Snell-Rood & Steck 2019), we expected plastic founders would identify optimal resources (e.g., dens) with less exploration and therefore travel shorter distances between dens. Interestingly, plasticity derived from time spent exposed was positively correlated with days spent den sharing, indicating that plastic founders were more tolerant of sharing dens with conspecifics. This combination of results suggests that plastic founders use conspecifics as cues for habitat suitability (i.e., conspecific attraction, (Stamps 1988; Richardson & Ewen 2016), facilitating their increased movement through the landscape.

Plasticity is an emerging area of interest in behavioural ecology (e.g., (Dingemanse & Wolf 2010; Jolles *et al.* 2019), but has rarely been considered in the context of conservation and reintroductions. Overall, our finding that behaviourally plastic eastern quolls were able to adjust their behaviour based on new experiences is encouraging, considering initial responses may not be optimal in a novel environment (Berger-Tal *et al.* 2014). Knowledge of this responsiveness could prove critical to managers when evaluating the progress of founders through their establishment. Here we have demonstrated the value of this under-represented measure in predicting how founders will learn and adapt post-release, and their likelihood of establishing.

Curiously, we found no significant associations between post-release performance and the composite behavioural predictors (proactive PC and reactive PC). Due to the difficulty in interpreting PCA results (Peres-Neto *et al.* 2003) and lack of comparability between studies (Vaughan & Ormerod 2005), this result encourages careful selection of raw behavioural measures, rather than relying on composite methods.

It is critical to recognise the potential genetic consequences of selecting founders with particular personalities or plasticities for reintroduction (Van Oers *et al*. 2005; Haage *et al*. 2017). A key recovery goal for the eastern quoll reintroduction program is to maintain genetic health and diversity, and our results indicate that captive or wild eastern quolls do not have significantly different personalities or plasticities, and can be equally successful as maternal founders to supplement genetic diversity, at least into fenced sanctuaries. However, while a certain personality may be more advantageous in the establishment phase of a reintroduction (initial trial release as compared to when post-release effects are no longer operating), another may be better suited to the growth phase (characterised by high rates of increase and expansion until the population reaches carrying capacity), and another to the regulation phase (where the long-term effects of density dependence and genetic drift are felt, IUCN 2013). For instance, boldness has been linked to greater survival in novel environments, but also exposure to predators and issues with forming stable conspecific associations (Stamps & Swaisgood 2007). This context can cause initial translocations to act like behavioural bottlenecks for certain personality types (May *et al.* 2016). To navigate this, (Bremner-Harrison *et al.* 2013; Lopes *et al.* 2017) suggested that shyer individuals should be released early in a reintroduction program since they have greater capacity for sociality, while bolder individuals should be selected for later reinforcements due to their propensity for exploration. However, (Watters & Meehan 2007; Fogarty *et al*. 2011) recommend releasing a mix of personality types to overcome their inherent trade-offs, resulting in faster colonisation, higher population densities, and greater adaptive potential. This enables managers to ensure a balance of different strategies and 'hedge their bets' against environmental uncertainty (Cote *et al.* 2010). While releasing a mix of personality types may appear to offer the ‘best of both worlds’, when dealing with threatened species practitioners need to be parsimonious with the inherently limited number of founders available, and use best available knowledge to inform translocation tactics (Batson *et al.* 2015).

3.5.1 Management recommendations

We make the following recommendations for reintroductions of eastern quolls and related species based on our results. Firstly, with no significant differences in personality or plasticity (or survival and dispersal, (Wilson *et al.* 2020) between captive or wild founders, eastern quolls of either origin could be used to seed a secondary reintroduction such as ours (while maintaining genetic considerations). Here, established captive-breeding programs and soft-releases provide ideal opportunities to conduct behavioural assays (Dingemanse *et al*. 2012; Baker *et al*. 2016) or anti-predator training to prioritise and prepare individuals for release (Moseby *et al*. 2016; Bannister *et al*. 2018a; Rowell *et al*. 2020).

Secondly, we recommend that easily quantifiable behavioural measures associated with responses to perceived risk and novelty, such as latency to reach food and time spent vigilant, should be prioritised for measurement during behavioural assays.

Thirdly, we recommend selecting proactive and rigid founders for initial trial reintroductions, where reduced dispersal may be most advantageous and few conspecifics could favour these individuals, whereas reactive and plastic founders should be selected for secondary reintroductions or reinforcements, to supplement behavioural diversity. In our case, the broad range of personalities and plasticities detected in our eastern quoll founders demonstrates substantial behavioural diversity, which if heritable, indicates healthy genetic diversity in a growing population.

Finally, we acknowledge that our study took place in a conservation-fenced sanctuary, a setting which provides valuable learning opportunities, but may not reflect the same relationships between personality and post-release performance that may exist ‘beyond-the-fence’ (*sensu* (Evans *et al.* 2021), where founders can encounter invasive predators (particularly red foxes and feral cats). In fact, advantageous behaviours in a sanctuary may prove deleterious in the presence of these predators, and without this selective pressure the population may lose predator-averse behaviours (refuge naïveté, (Jolly *et al.* 2018). To avoid this, low and well-managed levels of predation could be used to drive selection for predator-awareness (the “Goldilocks zone’, (Evans *et al.* 2021). We view predator-proof sanctuaries as “stepping-stones back to the wild, rather than threatened reservoirs of biota” (Batson 2015), and future studies could build on our work by assessing personality and plasticity and their relationships with post-release performance beyond-the-fence.

3.5.2 Conclusions

In this study, we have offered a rare real world example of how practitioners can measure ecologically-relevant and easily quantifiable behaviours that are likely to be divisive between individuals and predict post-release performance. In reintroductions, where founders, funding, and time are limiting, innovative behavioural assays can be used as a conservation tool to select the individuals with appropriate survival and dispersal propensities and provide the fastest pathway to reintroduction success.

3.6 Acknowledgements

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Illustration by Cat Cotsell

3.7 Appendix

Table 3.3 Likelihood ratio chi-square (χ2), residual deviance (RD), and *p*-values (significant values in **bold**) related to generalised linear mixed models of personality (intercept) and plasticity (slope) predictors (calculated using the 'behavioural reaction norm' approach, Dingemanse *et al*. 2010) derived from pre-release latency to emerge (min), latency to reach food (min), time spent exposed (s), time spent vigilant (s), giving-up density (GUD, %), proactive PC (first dimension coordinate of principal components analysis including time spent exposed and GUD), and reactive PC (as per proactive PC, but including latency to emerge, latency to reach food, and time spent vigilant) by post-release responses relating to survival (fate and post-release weight, *n* = 13, *df* = 12), and dispersal (number of dens used, mean distance between dens, days spent den sharing, and home range [95% minimum convex polygon], individuals with >10 days post-release survival, *n* = 10, *df* = 9) of assayed eastern quolls (*Dasyurus viverrinus*) reintroduced to Mulligans Flat Woodland Sanctuary, Australian Capital Territory.

Behavioural response	**Response**	**Fate (survived, died)**			**Post-release weight (%)**			**Number of dens (*n*)**			**Mean distance between dens (m)**			**Days spent den sharing (*n*)**			**Home range (95% MCP)**		
	Coefficient	**χ2**	**RD**	***p***	**χ2**	**RD**	***p***	**χ2**	**RD**	***p***	**χ2**	**RD**	***p***	**χ2**	**RD**	***p***	**χ2**	**RD**	***p***
Latency to emerge (min)	Intercept	0.03	2.30	0.90	0.43	1804.48	0.52	0.01	128.91	0.92	0.05	46883.85	0.99	0.69	1837.36	0.38	3.20	5141.48	0.09
	Slope	0.95	2.12	0.46	1.76	1617.29	0.21	0.01	129.01	0.51	1.08	42512.86	0.40	0.02	1947.91	0.79	0.05	6749.19	0.91
Latency to reach food (min)	Intercept	0.02	2.30	0.94	0.74	1757.73	0.41	0.00	129.08	0.95	0.42	45236.14	0.59	0.72	1831.95	0.47	0.01	6775.67	0.95
	Slope	0.45	2.22	0.56	2.10	1574.53	0.18	0.66	121.74	0.13	6.24	29010.35	**0.04**	0.10	1934.97	0.99	0.27	6604.71	0.58
Time spent exposed (s)	Intercept	5.77	1.51	0.22	0.07	1862.91	0.79	0.99	118.45	0.82	0.33	45624.29	0.99	1.26	1751.44	0.81	1.13	6094.86	0.65
	Slope	0.91	2.13	0.44	0.52	1789.99	0.48	1.29	115.56	0.29	1.23	41971.65	0.43	2.34	1609.34	**0.01**	4.40	4712.58	0.15
Time spent vigilant (s)	Intercept	3.71	1.73	0.25	0.72	1760.39	0.41	3.01	101.37	0.13	2.76	36925.04	0.10	0.04	1944.81	**0.03**	4.70	4616.03	**0.03**
	Slope	0.14	2.28	0.74	0.78	1750.60	0.39	1.09	117.43	0.29	1.34	41533.51	0.39	2.42	1599.90	0.08	3.02	5213.23	0.20
Giving-up-density	Intercept	1.34	2.06	0.40	0.01	1873.74	0.92	1.03	118.00	0.47	0.36	45489.70	0.50	0.18	1920.75	0.33	3.74	4939.11	0.17
	Slope	3.06	1.81	0.23	0.00	1874.69	0.95	0.19	126.87	0.93	0.49	44933.31	0.60	0.70	1835.25	0.93	0.17	6670.96	0.93
Proactive PC	Intercept	5.81	1.51	0.16	0.01	1873.26	0.91	1.77	111.22	0.63	0.58	44551.44	0.59	0.17	1922.20	0.50	4.09	4816.31	0.17
	Slope	0.19	2.27	0.72	0.20	1842.28	0.67	0.19	126.84	0.55	1.64	40484.94	0.41	2.85	1551.05	0.14	0.90	6227.06	0.35
Reactive PC	Intercept	0.12	2.28	0.69	1.06	1711.17	0.33	0.14	127.49	0.82	0.03	46958.55	0.89	0.96	1795.18	0.28	1.44	5933.43	0.32
	Slope	0.58	2.19	0.57	1.45	1656.37	0.25	0.29	125.74	0.19	4.11	33388.49	0.11	0.25	1909.60	0.87	0.19	6657.37	0.65

Chapter 4: Movement and association

As a reintroduction progresses through the establishment, growth, and regulation phases, density-dependent mechanisms increasingly drive population dynamics. This can complicate efforts to reinforce these populations if the translocated individuals (henceforth reinforcers) are excluded, or existing residents become displaced. This is especially pertinent for islands and conservation-fenced havens, where immigration is only possible through translocation. Conspecific associations offer insights into how these density-dependent mechanisms manifest in space and time.

In this Chapter, I investigated how movement, habitat use and preference, and conspecific associations differed between eastern quoll residents and reinforcers using GPS tracking. My results revealed movements at a greater spatio-temporal resolution than has ever been achieved for this species, and offer important insights into appropriate habitat structure for future reintroduction sites. I also highlighted the need for post-release monitoring to inform adaptive management interventions, to give practitioners the best chance of achieving positive outcomes for both trial reintroductions and later reinforcements.

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Illustration by Cat Cotsell

Everybody needs good neighbours: movement, habitat use, and conspecific association in a reintroduced mesopredator

Wilson B A, Evans M J, Rapley S, Gordon I J, Wimpenny C, Newport J, & Manning A D,

in review at *Biodiversity and Conservation*.

4.1 Abstract

As a reintroduction progresses through the establishment, growth, and regulation phases, density-dependent mechanisms increasingly drive population dynamics. This can complicate efforts to reinforce these populations if the translocated individuals (henceforth reinforcers) are excluded, or existing residents become displaced. This is especially pertinent for islands and fenced reserves, where immigration is only possible by translocation. Conspecific associations offer insights into how density-dependent mechanisms manifest in space and time.

We investigated how movement, habitat use, and conspecific associations differed between eastern quoll (*Dasyurus viverrinus*) residents and reinforcers in a 485-ha haven. We used GPS collars to quantify distances travelled per night, home and core ranges, nocturnal (activity) and diurnal (denning) habitat use and preference, and conspecific associations across three periods: baseline (residents only), release (both cohorts), and settlement (reinforcers only).

Eastern quolls travelled greater mean distances (2.15 km > $\bar{x}$ 1.75 km) and had larger home ranges (251 ha > $\bar{x}$ 178 ha) during the release period. Reinforcers had larger home ranges (249 ha) and greater overlap with other collared eastern quolls (115 ha) when compared to residents (range 90 ha, overlap 46 ha). We found a strong preference toward grassland habitat across all animals and periods. During the settlement period, we found a preference for nocturnal activity in greater understory and southwest-facing aspects, a preference for dens with lower overstory and southwest-facing aspects, and lower movement correlation, sociality, and den sharing between collared eastern quolls. We also found lower den sharing in reinforcers (29%) compared to residents (52%), and for fawn- animals compared to dark-morphs.

Our results revealed short-term movements, habitat use, and associations at a greater spatio-temporal resolution than has ever been achieved for this species. Our findings offer insights into the importance of appropriate habitat and conspecific cueing for reintroductions, and highlight the need to monitor density-dependent mechanisms to inform adaptive management to promote positive outcomes for both reintroductions and reinforcements.

4.2 Introduction

Reintroductions are a key weapon in the fight against global defaunation; aiming to re-establish viable, free-ranging populations of target species within their indigenous range following their extirpation (IUCN 2013). Their success hinges on a population's passage through the establishment (where post-release effects drive population dynamics), growth (characterised by high rates of expansion), and regulation (where density dependence limits survival and recruitment) phases (Sarrazin 2007). These mechanisms can have critical demographic (e.g., survival) and genetic consequences (e.g., selection), and so must be monitored closely throughout the reintroduction process (White *et al.* 2018).

Reintroduction establishment initially relies on the survival and dispersal of founders (individuals translocated to an area with no conspecifics), and in later reintroduction stages, reinforcers (individuals translocated to an area with conspecifics, with the aim of reinforcing demographic, behavioural, and genetic diversity in a population); the rates of which are likely to change over time (Støen *et al*. 2009; le Gouar *et al*. 2012; Wilson *et al*. 2020). For species with discrete home ranges and territoriality, movement can provide valuable information on habitat suitability and indicate the success or failure of restoration actions (le Gouar *et al*. 2012; Bennett *et al*. 2013). As per the exploration-exploitation dilemma (trade-off between learning and using knowledge to improve performance, Berger-Tal *et al*. 2014), an animal will adjust its movement (e.g., foraging, predator avoidance) as it becomes more familiar with its environment (i.e., post-release behavioural modification, PRBM, Berger-Tal & Saltz 2014). Translocated individuals are expected to move along the PRBM continuum from exploratory to more knowledge-based movements within an established and familiar home range. This sequence of initially high daily movements, followed by home range establishment, has been observed in several species including translocated raccoons (*Procyon lotor*, Mosillo *et al*. 1999), dormice (Bright & Morris 1994), grey wolves (*Canis lupus*, Fritts *et al*. 1984), and swift foxes (*Vulpes velox*, Moehrenschlager & Macdonald 2003). Monitoring movement can, therefore, indicate an individuals' progression along the PRBM continuum, and alert managers when these movements do not reflect a gradual accumulation of knowledge and acclimatisation to the recipient environment (Berger-Tal & Saltz 2014).

Density-dependent movement patterns emerge when animals assess habitat suitability by direct interaction with the physical environment (Danchin *et al*. 2004), and conspecific cues (presence, density, and health, Danchin *et al*. 2004; Dall *et al*. 2005; Seppänen *et al*. 2007). The well-known ecological mechanisms of conspecific attraction (where animals seek and benefit from associations with conspecifics, Stamps 1988) and conspecific exclusion (where animals are displaced by conspecifics, Muriel *et al*. 2016) are often amplified as a population approaches density-dependence (Armstrong *et al.* 2005). In reintroductions, conspecific attraction can manifest in the social integration of translocated individuals, thereby limiting dispersal, as observed in female yellow-bellied marmots (*Marmota flaviventris*, Snijders *et al*. 2017), however, this may also limit population expansion (Richardson & Ewen 2016). Conversely, conspecific exclusion from territories held by residents can lead to overdispersal and geographic isolation from the intended release site (i.e., priority effects, Fraser *et al*. 2015). Since direct assessment of habitat suitability can be risky and energetically expensive, translocated individuals can use indirect cues from conspecifics that takes advantage of residents' experience or familiarity with the site (Stamps *et al.* 2005; Valone 2007).

Consideration of these behavioural mechanisms is especially crucial for isolated populations such as those on islands or in fenced reserves, where immigration is only possible through reinforcements, and emigration results in permanent removal from the population (Ringma *et al*. 2017; Legge *et al*. 2018). Conspecifics can anchor reinforcers and promote genetic mixing (Richardson & Ewen 2016) or drive reinforcers away from the intended establishment area (Clarke & Schedvin 1997), making monitoring and support difficult.

Here we investigated how movement, habitat use, and conspecific association differed between residents and reinforcers, using the model system of an endangered and solitary mesopredator (the eastern quoll, *Dasyurus viverrinus*) which was reintroduced to a conservation-fenced reserve. We used GPS collars to quantify distances travelled per night, home and core ranges, nocturnal (activity) and diurnal (denning) habitat use and preference (using the National Vegetation Information System and LiDAR), and conspecific associations across three periods: baseline (residents only), release (residents and reinforcers), and settlement (reinforcers only).

We hypothesised that (1) movement (i.e., distance travelled per night and home and core ranges) would be significantly greater for reinforcers as compared to residents, 2) the movement of reinforcers would change between the release and settlement periods as they progressed along the PRBM continuum, 3) habitat use would differ between cohorts but trend towards similarity over time (since resource availability and movement is often inversely related, e.g., Mosnier *et al*. 2015), 4) conspecific associations would be greatest for reinforcers during the release period, where they would make most use of conspecific cueing to determine suitable habitat to establish themselves (e.g., in songbirds, Ahlering *et al*. 2010), and (5) movement and associations between the two distinct pelage colours (fawn- and dark-morphs) would differ, in response to anecdotal differences in their abundance and behaviour (B. A. Wilson *pers obs*).

4.3 Methods

4.3.1 Ethics statement

Translocations were carried out under licenses from the Tasmanian Department of Primary Industries, Parks, Water and Environment (permits TFA 16025 and 17091, export licences 12818/16 and 13528/17), Victorian Department of Environment, Land, Water and Planning (permit 14505167), and Australian Capital Territory (ACT) Government (scientific licence LT2017959, import licence L120161261). Reintroduction (protocol A2016/02) and monitoring procedures (protocol A2020/40) were approved by The Australian National University Animal Experimentation Ethics Committee.

4.3.2 Study area

Our study was conducted at Mulligans Flat Woodland Sanctuary (MFWS), a publicly accessible 485-ha safe haven containing areas of critically endangered box-gum grassy woodland (McIntyre *et al*. 2010; Manning *et al*. 2011; Shorthouse *et al*. 2012) on the northern border of the Australian Capital Territory (-35.167, 149.158). MFWS is surrounded by an 11.5 km conservation fence which excludes invasive species such as the feral cat (*Felis catus*), red fox (*Vulpes vulpes*), European rabbit (*Oryctolagus cuniculus*), and European hare (*Lepus europaeus*). The fence design includes an overhang that prevents entry by invasive species (based on successful trials at Arid Recovery, Moseby & Read 2006, but adapted for local conditions, Shorthouse *et al*., 2012), but it does not prevent climbing animals inside the haven from dispersing over the fence and into the surrounding landscape. While invasive species have been eradicated within the site, environmental conditions are like those of other unfenced woodlands in the region, allowing most terrestrial species (excluding large macropods, which have been excluded from some areas using tall fences to aid restoration) to access all parts of the haven.

MFWS and the neighbouring Goorooyarroo Nature Reserve also form the location of the Mulligans Flat-Goorooyarroo Woodland Experiment, which trials restoration techniques to promote biodiversity in temperate woodlands (e.g., supplementing coarse woody debris, controlling grazers, Manning *et al*. 2011; Shorthouse *et al*. 2012). As part of the Experiment, the fence has enabled reintroductions of locally extinct native species to restore biodiversity and ecosystem function (Shorthouse *et al.* 2012).

4.3.3 Study species

The eastern quoll ('murunguny' in the Indigenous Ngunnawal language) is a critical weight range (0.7–2 kg) dasyurid (carnivorous marsupial, Stannard & Old 2013). It is the only quoll species which exhibits two distinct pelage colours: fawn-morphs (sandy-coloured with white spots) and dark-morphs (black with white spots). The species is sexually dimorphic, with females (mean 0.7 kg) being two-thirds the size and weight of males (mean 1.1 kg, Bryant 1988). Females breed synchronously in early Austral winter, birth 21 days later, and wean after five months (Jones *et al.* 2001). Populations experience high turnover driven by juveniles (female juvenile annual survival 64.17% ± 19.92, male 64.93% ± 19.87), and fluctuate seasonally with highest densities observed in early summer following the juvenile weaning, and minimum densities in August due to some die-off of males following the breeding season and high juvenile mortality (Godsell 1983).

Eastern quolls are nocturnal, becoming active around dusk for eight hours regardless of day length (Jones *et al.* 1997) to hunt invertebrates, small mammals, birds, reptiles, while also eating carcasses and vegetation (Blackhall 1980; Godsell 1983). During the day they den underground or in logs or rocky outcrops, often in areas that are proximal to foraging grounds, with a preference for ecotones between forest and open grassland (Godsell 1983). Den sharing was considered rare (Godsell 1983; Jones *et al.* 2001) until frequently observed between reintroduced females (Wilson *et al.* 2020).

Eastern quolls are solitary but tend to form loose neighbourhoods. Individuals may have overlapping home ranges but maintain large interindividual distances (>200m, Godsell 1983), suggesting that they avoid their neighbours. Males tend to have larger (mean 44 ha) and vary more in size than do the home ranges of females (mean 35 ha), though those of the latter increase while weaning their young (Godsell 1983). Home ranges are typically only shared between related females and mothers and their litters, and female aggression is normally only directed to other mothers supporting large young (Godsell 1983).

Once irruptive and broadly distributed throughout south-eastern mainland Australia (Godsell 1983; Peacock & Abbott 2014), the eastern quoll disappeared from the mainland in the 1960s due to habitat degradation, predation by invasive species, disease, and human persecution (Peacock & Abbott 2014). The species is listed nationally as endangered (Environment Protection and Biodiversity Conservation Act 1999, Australian Government) and was restricted to the drier eastern half of the island state of Tasmania (Rounsevell *et al*. 1991; Jones & Rose 1996) until its successful reintroduction to Mt Rothwell Biodiversity Interpretation Centre in Victoria in 2003 (Mt Rothwell) and MFWS in the ACT in 2016 where it is now listed as endangered (Nature Conservation Act 2014 s 90C, ACT Parliamentary Counsel 2014). After a trial release into MFWS revealed elevated mortality in male reinforcers, only female (preferring maternal) reinforcers were translocated in later trials (Wilson *et al.* 2020, 2021). This tactic, which we adapted using the Translocation Tactics Classification System (Batson 2015), allowed us to reintroduce male and female pups via the mothers' pouches, and since litters can have multiple sires (B. Brockett unpublished data), this could have contributed to increased genetic diversity in the establishing population.

4.3.4 Study design

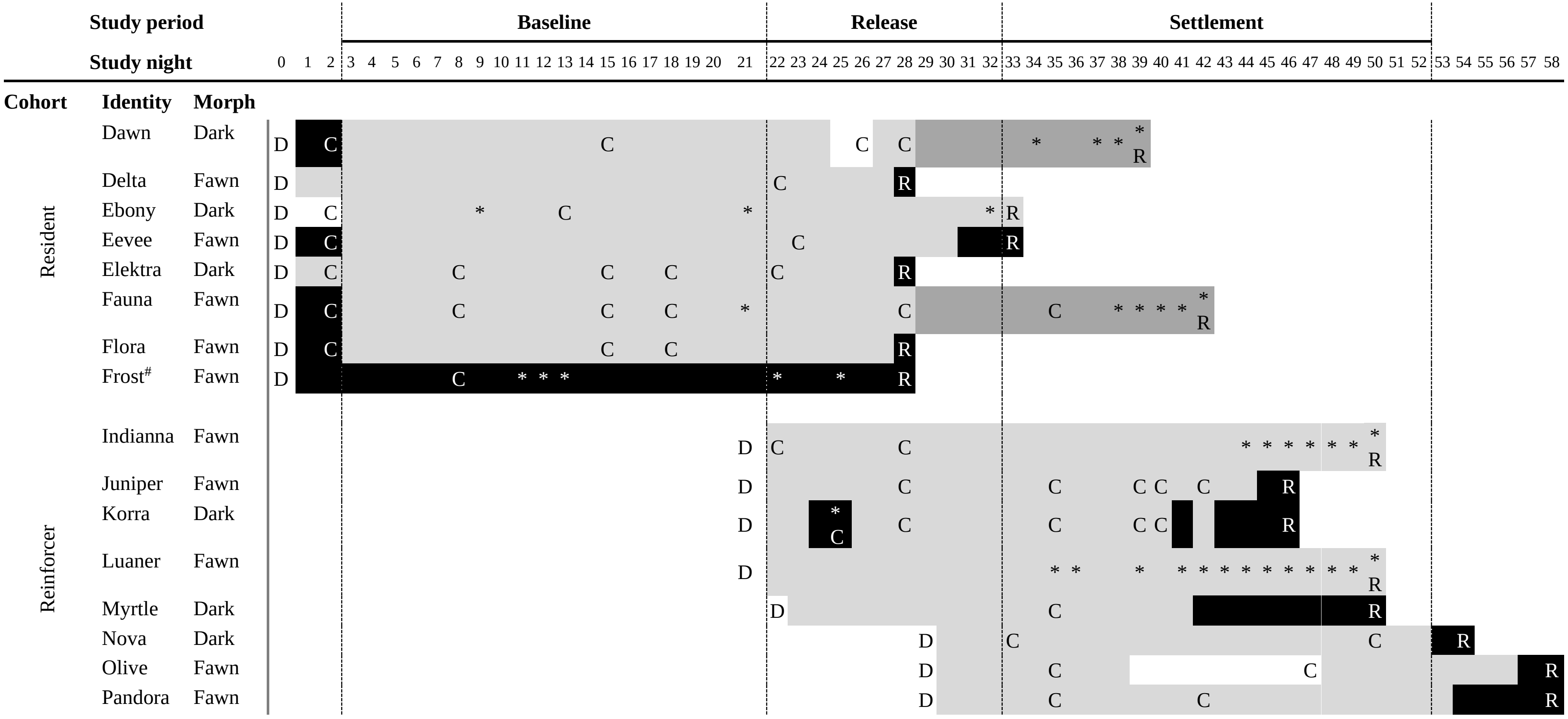
Our study took place in 2018 during the third eastern quoll reintroduction trial at MFWS (Wilson *et al.* 2020). We designed our study to compare the effect of cohort on the movements, habitat use, and conspecific associations of female residents (n = 8) and Tasmanian-born female reinforcers (n = 8). We collected baseline movement data from the residents for 21 nights prior to the reinforcers arriving and followed this with 2–3 months of data collection across all individuals. Due to unforeseen GPS battery performance issues, no unit collected data for more than 31 nights (mean = 25 nights), and one unit deployed on a resident did not collect any locations ("Frost", Table 4.1). This meant that the greatest period of overlap between cohorts (where there were ≥3 individuals per group) was 11 nights. In response, we redesigned our study to compare movements between cohorts (residents n = 7, reinforcers n = 8) in three distinct study periods: baseline (residents only, nights 3–21), release (both cohorts, nights 22–32), and settlement (reinforcers only, nights 33–52), and between pelage colour morphs (fawn n = 9, and dark n = 6, Table 4.1).

4.3.5 Residents and reinforcers

To obtain resident eastern quolls, we first monitored the existing eastern quoll population at MFWS by trapping across 92 sites using wire cage traps (31× 31× 70 cm) in May 2018 (as per Wilson *et al*. 2023). Using the locations of the 17 females caught, in June 2018 we targeted and captured eight first-year females (preferring those that were mothers, i.e., carrying pouch young) and fitted them with 38 g (<5% of each animal's body weight) GPS collars (LiteTrack 30 RF, Sirtrack Ltd, Hawkes Bay, New Zealand). We then released them at their point of capture by 0200 hours, giving them time to adjust to their collar and find their den by first light.

Three weeks later, we captured eight wild-born reinforcers (preferring mothers) from free-ranging populations across Tasmania (Table 4.1). We transported reinforcers by air and road to MFWS in animal carrier crates, and on arrival conducted veterinary checks (as per Portas *et al*. 2020) and fitted them with GPS collars. We allowed reinforcers to recover in a wooden box until their release. Two hours after placing animals in their box in the centre of MFWS, we opened the door and allowed the reinforcers to leave of their own accords to minimise stress (as per Wilson *et al*. 2020).

Table 4.1 Timeline for GPS-deployment and VHF-radiotracking of resident (n = 8) and reinforcer (translocated from Tasmania to reinforce demographic, behavioural, and genetic diversity in the population, n = 8) eastern quolls (*Dasyurus viverrinus*) at Mulligans Flat Woodland Sanctuary, Australian Capital Territory. Study periods were baseline (residents only, nights 3–21), release (both, nights 22–32), and settlement (reinforcers only, nights 33–52) and extended from June to August 2018. Key on next page.



Study period						**Baseline**																			**Release**											**Settlement**																								
Study night			0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58
Cohort	**Identity**	**Morph**																																																											
Resident	Dawn	Dark	D		C													C											C		C						*			*	*	* R																			
	Delta	Fawn	D																						C						R																													
	Ebony	Dark	D		C							*				C								*											*	R																									
	Eevee	Fawn	D		C																					C										R																									
	Elektra	Dark	D		C						C							C			C				C						R																													
	Fauna	Fawn	D		C						C							C			C			*							C							C			*	*	*	*	* R																
	Flora	Fawn	D		C													C			C										R																													
	Frost[#]	Fawn	D								C			*	*	*									*			*			R																													
Reinforcer	Indianna	Fawn																						D	C						C																*	*	*	*	*	*	* R								
	Juniper	Fawn																						D							C							C				C	C		C				R												
	Korra	Dark																						D				* C			C							C				C	C						R												
	Luaner	Fawn																						D														*	*			*		*	*	*	*	*	*	*	*	*	* R								
	Myrtle	Dark																							D													C															R								
	Nova	Dark																														D				C																	C				R				
	Olive	Fawn																														D						C													C										R
	Pandora	Fawn																														D						C							C																R

Light grey indicates when GPS units collected data.

Dark grey indicates when GPS units were collecting data in ‘swift’ mode (GPS accuracy 10 m, rather than 2.5 m).

Black indicates when the GPS unit was not collecting data (recovery mode).

‘**D**’ indicates GPS deployment.

‘**C**’ indicates evenings when an animal was captured (for health checks, GPS download, and/or GPS collar refitting).

‘**R**’ indicates the removal of GPS unit.

***** indicates when an animal could not be located via radiotracking.

[#] The GPS unit deployed on resident “Frost” did not collect GPS locations, but was radiotracked daily.

4.3.6 Monitoring

Since eastern quolls are predominantly nocturnal, we configured GPS units to record a location (henceforth fix) every 15 mins from 1700 to 0700 hours (≤56 fixes within a 14 hr period). To improve accuracy and reduce horizontal dilution of precision (HDOP), we configured GPS units to abandon a fix attempt if they could not detect satellites and compute a location within 75 s (time-out). We also radiotracked each animal to their diurnal den using the VHF beacon for their first 42 days post-release (as per Wilson *et al*. 2020). We captured animals regularly to check their body weight, condition, and collar fit (weight gain can cause collar injury), and were able to retrieve all GPS collars and data at the end of the study period. Overall,

GPS collars were deployed for 25–42 nights (dependent on each unit's functioning) which produced 18,578 raw fixes, and 77 captures were conducted over the study period.

4.3.7 Data analyses

4.3.7.1 Data curation

Errors can be present in GPS data when fixes are missing or when the location of an acquired fix is erroneous, and these must be screened prior to analyses (Frair *et al.* 2010). For example, an eastern quoll denning underground will limit the ability of a GPS unit to communicate with satellites, leading to error (Graves & Waller 2006; Körtner *et al.* 2015). To deal with this, we firstly removed fixes where the GPS unit (1) was not deployed, 2) timed out before recording a location, 3) was not working correctly (i.e., was in 'recovery' mode), and (4) was deployed on a quoll which was caught in a trap, which removed 10,330 fixes (55.6% of total fixes).

Next, we classified fixes according to whether they were inside or outside the conservation fencing. Rather than simply removing outside fixes (which does not account for potentially erroneous fixes inside the fence), we compared generalised linear models (GLMs) using Akaike's Information Criterion corrected for small sample sizes (AICc, Mazerolle 2017) to test whether a fix could be predicted as being inside or outside the fence by GPS variables collected simultaneously with each fix. We used duration (time taken to acquire a fix, <75s), ambient temperature (°C), number of satellites used to calculate the position, and horizontal dilution of precision (HDOP, an index of GPS coordinate precision where lower values considered more precise, D'Eon & Delparte 2005). The GLM including the GPS variables performed significantly better than the null model (>2 △AICc, 343.85 △log-likelihood), and every variable significantly predicted whether a fix was inside the fence (all $p < 0.0001$), so we filtered fixes that were in the first or third quartile of each variable as follows: (1) ≤54 s duration, 2) ≥17°C, 3) ≤2.6 HDOP, and (4) ≤5 satellites, which removed 4,207 fixes. Of the remaining fixes, 21 were outside the fence, which we manually removed to produce a curated dataset of 2,950 fixes for subsequent analyses. We note that since GPS units could not determine locations while eastern quolls were underground, movement measures using these data describe eastern quoll nocturnal 'activity' only.

4.3.7.2 Distance

To calculate the distances each eastern quoll travelled per night, we summed the linear distance between consecutive fixes for each night. In addition, we calculated the distances per fix by standardizing the distance travelled per night by the number of fixes, to account for the varying number of fixes per individual, and the fact that accuracy generally increases with increasing number of fixes (Piedallu & Gégout 2005).

4.3.7.3 Ranges

We used the kernel utilisation distribution (KUD) model, which incorporates distance and time lag (i.e., autocorrelation) between consecutive fixes, to calculate home range (eliminating outlying, exploratory locations, 95% contour) and core range (area used with greater intensity, 50% contour) for each individual in hectares. In addition, we calculated these nightly home and core ranges to determine whether these changed significantly with study night. We also calculated the area of conspecific overlap (or static interaction) in home and core ranges between dyads (pairs of individuals) using methods described by Pebesma (2018).

4.3.7.4 Habitat use

We determined habitat use when eastern quolls were active at night ('nocturnal activity' determined using GPS fixes, animals *n* = 15) and when denning during the day ('diurnal denning' determined using daily VHF locations, animals *n* = 16), and compared these to habitat types and attributes that were available across the site using two data sources.

The first source was the Australian National Vegetation Information System (NVIS version 6.0, NLWRA 2001), which we used to delineate extant native vegetation types in MFWS. Under the NVIS, MFWS contained eight major vegetation groups, but for simplicity we aggregated these into five broad vegetation types (henceforth habitat type) based on similarity: eucalypt woodland (representing 52.5% of the site, Figure 4.1), regrowth (16.1%), eucalypt forest (15.2%), grassland (14.5%), and aquatic (1.74%). We tested for habitat preference in nocturnal activity and diurnal denning compared to a random distribution using the chi-square test for given probabilities, using frequencies of locations in each habitat with the proportional area of each habitat available in MFWS.

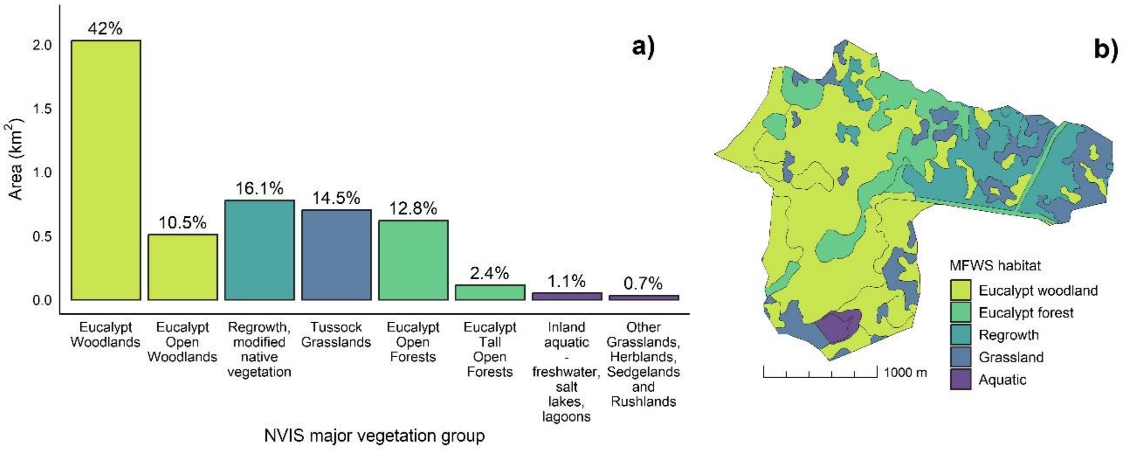


Figure 4.1 (**a**) National Vegetation Information System version 6.0 (NLWRA 2001) major vegetation groups and their percent cover over Mulligans Flat Woodland Sanctuary (MFWS) in the Australian Capital Territory, and (**b**) aggregated vegetation groups representing broad MFWS habitat types.

The second data source for determining habitat use was overstory and understory (cover fraction to 3.2 m resolution), and aspect (orientation in degrees, derived from a digital elevation model) from Terrestrial Ecosystem Research Network (TERN) airborne LiDAR and hyperspectral products (van Dijk *et al.* 2018). We selected these metrics since they predicted appropriate habitat for another mesopredator reintroduced to the site (bush stone-curlew *Burhinus grallarius*, Rapley 2020), and had the potential to contribute to both food availability and foraging success for the eastern quoll. We used generalised linear models (GLMs) to test for significant differences in overstory, understory, and aspect values between nocturnal locations, diurnal dens, and available values across the site.

4.3.7.5 Conspecific associations

To quantify conspecific associations for each individual with any other collared eastern quoll each night, we calculated their (1) proximity index (proportion of simultaneous fixes that are proximal to a conspecific, based on a distance threshold of 50 m, Bertrand *et al*. 1996), 2) movement correlation coefficient (a Pearson product-moment correlation statistic, Shirabe 2006), 3) coefficient of sociality (between two moving objects using a signed significance Wilcoxon-rank test, Kenward *et al*. 1993), and (4) coefficient of association (dynamic interaction comparing the observed with the total number of fixes where two moving objects are observed together, where >0.5 indicates affiliation or fidelity and <0.5 indicates no association, Cole 1949; Bauman 1998). We also quantified the proportion of days each eastern quoll was detected den sharing with another collared eastern quoll while radiotracking them to their diurnal dens as an additional measure of conspecific association. Note that den sharing with and between uncollared eastern quolls could not be detected or accounted for, so this behaviour may have been more common than observed.

4.3.7.6 Modelling

We modelled distance, home and core ranges, habitat use, and conspecific associations using generalised linear mixed models (GLMMs) with cohort, study period, and morph as fixed effects, while incorporating individual as a random effect (to control for variation driven by the individual). For distance, where replication was at the night level, we also incorporated minimum overnight temperature (°C), precipitation (mm), and moon illumination (%) as random effects since these can influence the energetic costs of activity (Linley *et al.* 2020). We fitted models using a gaussian (normal) error distribution based on visual inspection of the data for all tests except den sharing, where we fitted the model using a binomial distribution with a log-link function. We selected the most parsimonious model(s) according to Akaike's Information Criterion corrected for small sample sizes (<2 ΔAICc, Burnham & Anderson 2002). We reported means, standard errors, and *p*-values ($\alpha = 0.05$).

Analyses were performed in R version 4.2.0 (R Core Team 2021) using the following packages: *adehabitatLT* for linear distances and *adehabitatHR* for home and core ranges (Calenge 2006), *ggplot2* (Wickham 2011) and *ggpubr* (Kassambara 2020) for plotting, *lme4* for GLMs and GLMMs (Bates *et al.* 2015), *MuMIn* for model selection (Bartoń 2016), *raster* for loading lidar products (Hijmans & van Etten 2015), *sf* for handling spatial vector data (Pebesma 2018), and *wildlifeDI* for calculating correlation coefficients (Long *et al.* 2014).

4.4 Results

We monitored the nocturnal activity (GPS fixes, $n = 2{,}950$) for 15 eastern quolls, and diurnal denning (VHF fixes, $n = 51$ unique dens) for 16 eastern quolls over a maximum of 31 nights (mean 25 nights).

4.4.1 Distance and ranges

We found study period had a significant effect on the distances travelled per night ($p = 0.008$), with the greatest distances being travelled during the release period (2.15 km ± 0.18, Figure 4.2a). Across the whole study, eastern quolls travelled an average of 1.75 km (±0.08) per night.

We found reinforcer home (249.4 ha ±53.2, $p < 0.0001$) and core (47.3 ha ±11.3, $p = 0.0001$) ranges were significantly larger than those of resident home (89.9 ha ±11.5) and core (19.9 ha ±2.5) ranges (Figure 4.2b, Figure 4.3). Home (251 ha ±58.4, $p = 0.001$) and core (48 ha

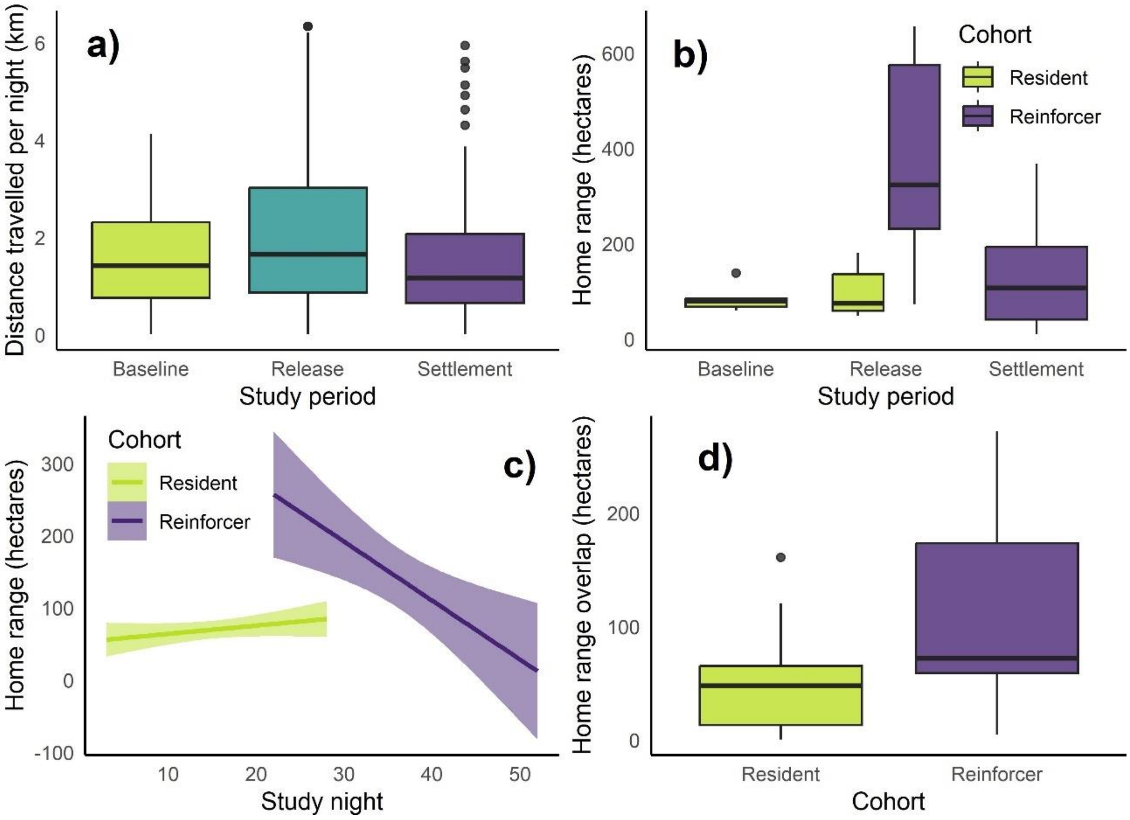


Figure 4.2 (**a**) Distances travelled per night (km) per study period (baseline with residents only, nights 3–21; release with both cohorts, nights 22–32; and settlement with reinforcers only, nights 33–52), **b**) home ranges (95% kernel utilisation distribution, in hectares) per study period and cohort (residents $n = 7$, and reinforcers [translocated from Tasmania to reinforce demographic, behavioural, and genetic diversity in the population, $n = 8$]), **c**) home ranges per study night, and (**d**) home range overlap per cohort, for GPS-tracked female eastern quolls (*Dasyurus viverrinus*) at Mulligans Flat Woodland Sanctuary, Australian Capital Territory. Home ranges were calculated using the *adehabitatHR* package (Calenge 2006) in R version 4.2 (R Core Team 2021).

±12.1, $p = 0.001$) ranges were also significantly larger during the release period (Figure 4.2b, Figure 4.3). In addition, when we assessed nightly home and core ranges, we found the most parsimonious model included both cohort (home range $p = 0.0002$, Figure 4.2c, core range $p < 0.0001$) and study night (home range $p = 0.01$, core range $p = 0.0074$), with residents exhibiting relatively constant ranges (home range $R^2 = 0.02$, core range $R^2 = 0.01$), and reinforcers exhibiting significantly negative trends in ranges (home and core ranges $R^2 = 0.07$) over the study period.

In addition, we found reinforcer home (115.09 ha ±15.28, $p < 0001$) and core (8.54 ha ±1.99, $p = 0.005$) ranges overlapped with those of other collared eastern quolls (i.e., static interaction) significantly more than residents home (45.99 ha ±4.15) and core (3.85 ha ±0.65)

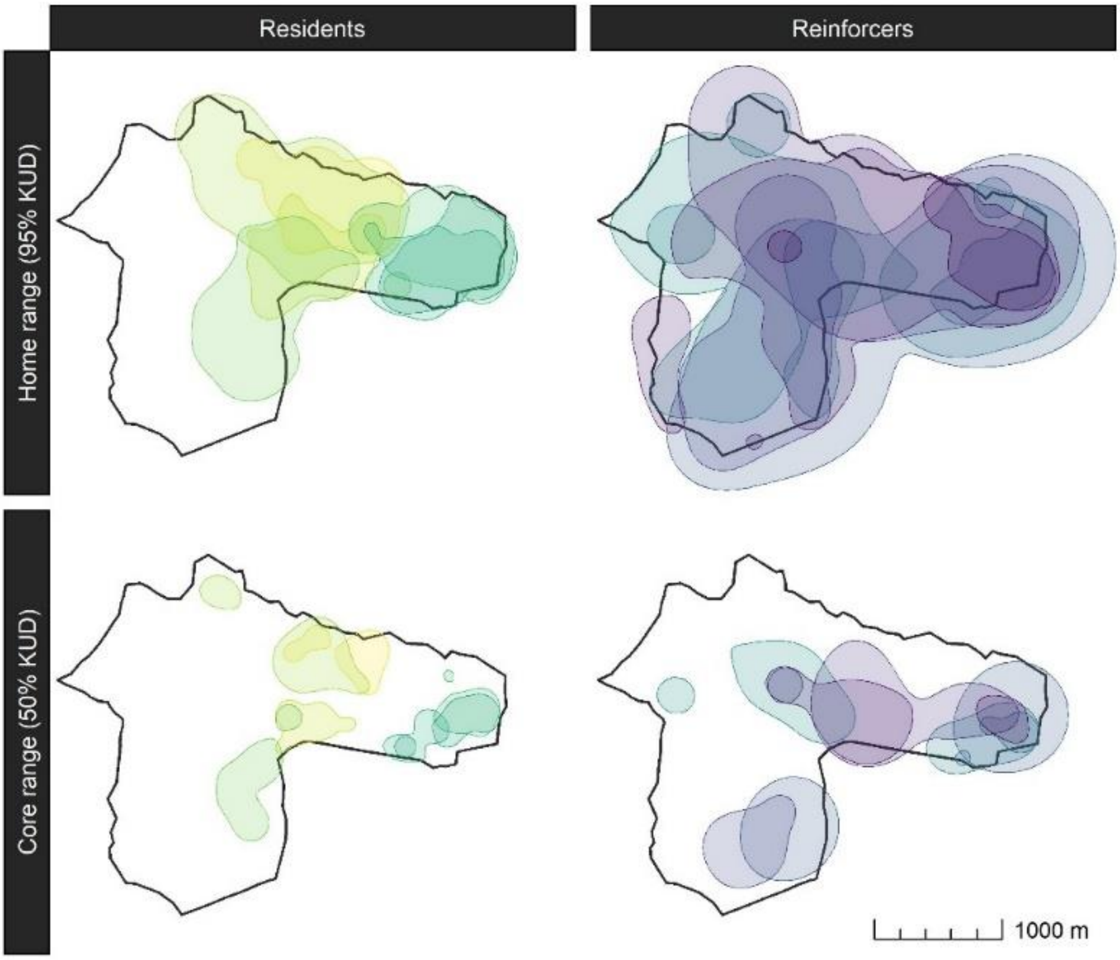


Figure 4.3 Map of home ranges (95% kernel utilisation distribution, KUD) and core ranges (50% KUD) of GPS-tracked resident ($n = 7$) and reinforcer (translocated from Tasmania to reinforce demographic, behavioural, and genetic diversity in the population, $n = 8$) female eastern quolls (*Dasyurus viverrinus*) at Mulligans Flat Woodland Sanctuary, Australian Capital Territory. Home ranges were calculated using the *adehabitatHR* package (Calenge 2006) in R version 4.2 (R Core Team 2021).

ranges (Figure 4.2d, Figure 4.3). Note that we present here minimum percent overlap since we could not account for other uncollared eastern quolls across the site.

4.4.2 Habitat use

4.4.2.1 Nocturnal activity

For habitat types, we found nocturnal activity locations in each habitat type varied significantly from random distribution ($\chi^2 = 1455.8$, df = 3, $p < 0.0001$), with eastern quolls preferring to spend their nocturnal activity in grassland (61.47%, after accounting for habitat

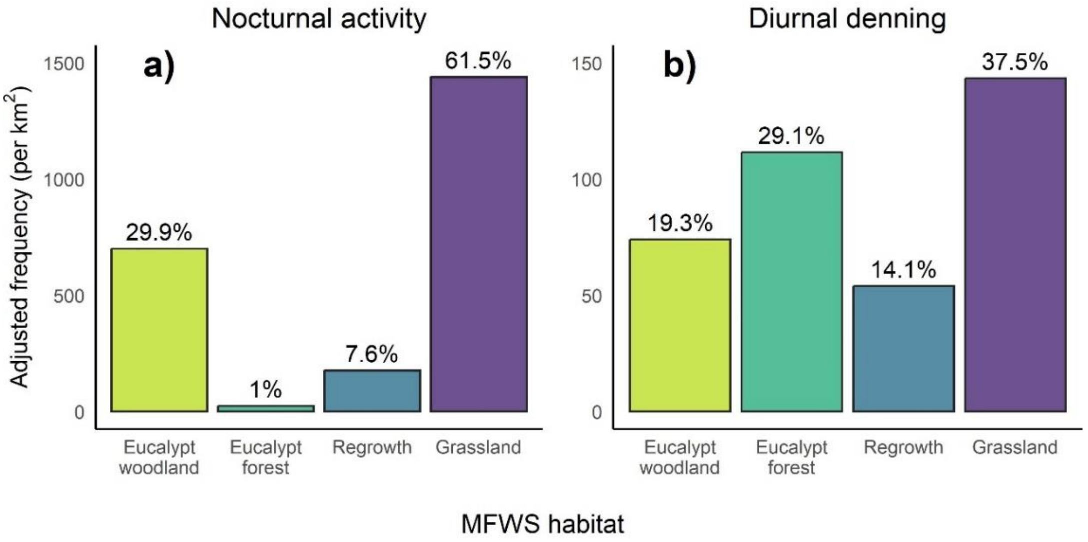


Figure 4.4 Adjusted frequencies (per km^2) and percentage of (**a**) nocturnal activity (GPS locations, *n* = 15), and (**b**) diurnal denning (VHF locations, *n* = 16) spent in Eucalypt woodland, Eucalypt forest, regrowth, and grassland habitat types for resident (*n* = 8) and reinforcers (translocated from Tasmania to reinforce demographic, behavioural, and genetic diversity in the population, *n* = 8) female eastern quolls (*Dasyurus viverrinus*) at Mulligans Flat Woodland Sanctuary (MFWS), Australian Capital Territory. Habitat types were aggregated from eight National Vegetation Information System (version 6.0) major vegetation groups (NLWRA 2001) in R version 4.2.0 (R Core Team 2021).

availability), followed by Eucalypt woodland (29.90%), regrowth (7.58%), and Eucalypt forest (1.05%, Figure 4.4a).

For habitat attributes, we found eastern quolls were active at night in areas with an average overstory cover of 12.65% (±0.27, significantly different to that which was available throughout the site [13.69% ±0.02], $p < 0.0001$, Figure 4.5a), understory cover of 2.23% (± 0.06, significantly greater than that which was available [1.90% ±0.004], $p < 0.0001$, Figure 4.5b), and aspect of 202.98° (±1.27, i.e., south-southwest-facing, not significantly different to that which was available [205.12° ± 0.11], $p = 0.13$, Figure 4.5c).

However, we did find that eastern quolls spent time in a significantly greater understory cover during the release period (2.57% ±0.12, $p < 0.0001$, Figure 4.5d) and more southwest-facing aspects during the settlement period (222° ±2.38, $p < 0.0001$, Figure 4.5e).

4.4.2.2 Diurnal denning

Of the 51 unique den sites, we found that 13 dens were used once, 28 were used on 2–9 occasions, 9 were used on 10–39 occasions, and one den was used on 96 occasions. For three days in a row, this den was used by five collared eastern quolls at once.

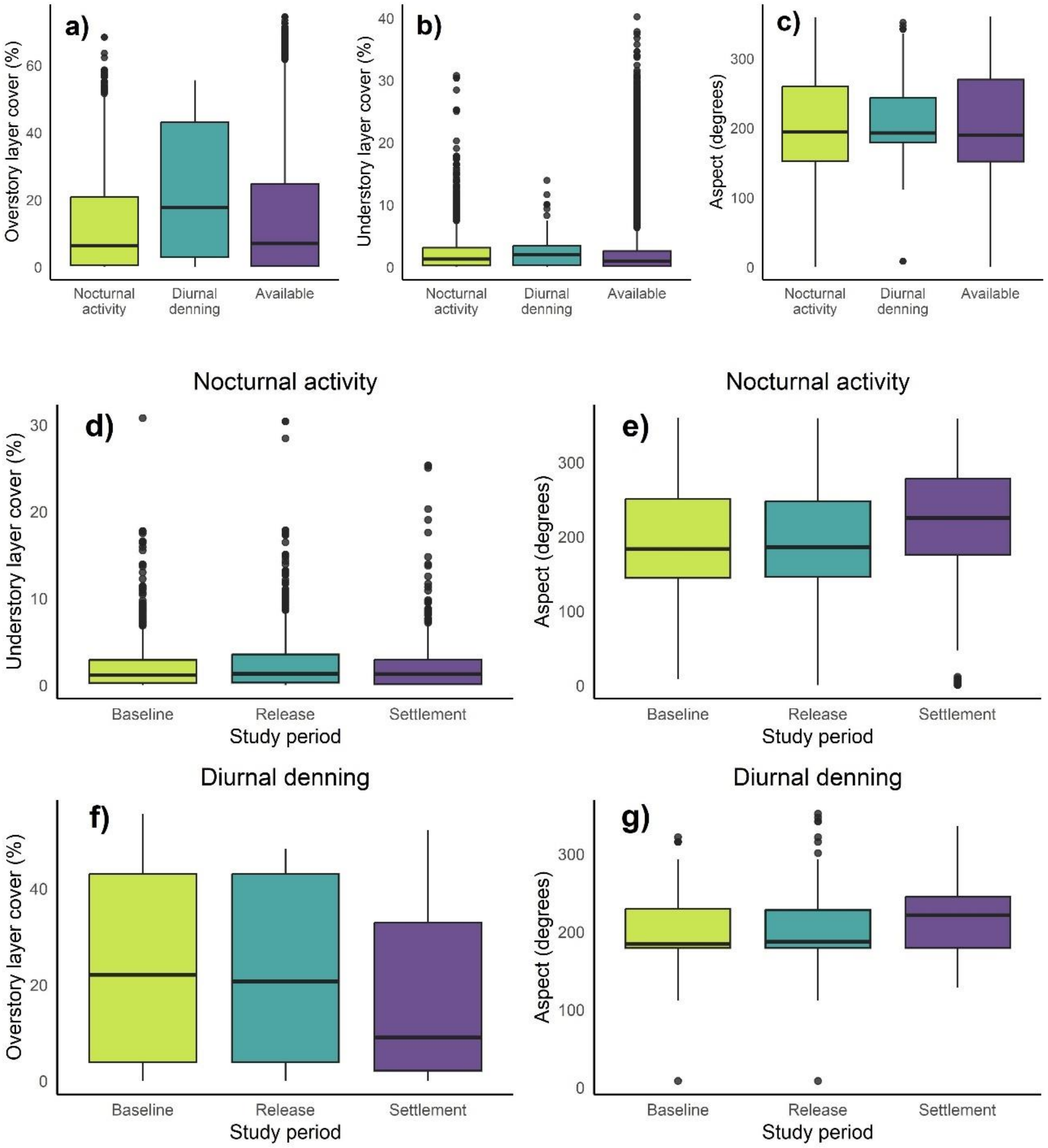


Figure 4.5 Proportion of (**a**) overstory and (**b**) understory (layer cover percent, 3.2 m resolution), and (**c**) aspect (orientation in degrees, derived from a digital elevation model) associated with nocturnal activity (GPS locations, *n* = 15), diurnal denning (VHF locations, *n* = 16), and availability of these variables, **d**) understory associated with nocturnal activity per study period (baseline with residents [*n* = 8] only, nights 3–21; release with both cohorts, nights 22–32; and settlement with reinforcers [translocated from Tasmania to reinforce demographic, behavioural, and genetic diversity in the population, *n* = 8] only, nights 33–52), **e**) aspect associated with nocturnal activity per study period, **f**) overstory associated with diurnal denning per study period, and (**g**) aspect associated with diurnal denning per study period, for female eastern quolls (*Dasyurus viverrinus*) reintroduced to Mulligans Flat Woodland Sanctuary, Australian Capital Territory. Data were sourced from Terrestrial Ecosystem Research Network (TERN) airborne lidar and hyperspectral products (van Dijk *et al.* 2018).

For habitat types, we found diurnal dens in each habitat type varied significantly from random distribution ($\chi^2 = 45.63$, df = 3, $p < 0.0001$), with eastern quolls preferring to den in grassland (37.45%, after accounting for habitat availability), followed by eucalypt forest (29.14%), eucalypt woodland (19.32%), and regrowth (14.11%).

For habitat attributes, we found eastern quolls were active at night in areas with an average overstory cover of 20.88% (± 0.89, significantly different to that which was available throughout the site [13.69% ±0.02], $p < 0.0001$, Figure 4.5a), understory cover of 2.60% (± 0.14, significantly greater than that which was available [1.90% ±0.004], $p < 0.008$, Figure 4.5b), and aspect of 207.27° (± 2.41, i.e., south-southwest-facing, not significantly different to that which was available [205.12° ± 0.11], $p = 0.28$, Figure 4.5c). Similarly, when we compared these attributes between nocturnal locations and diurnal dens, we found these were significantly different for overstory ($p < 0.0001$) and understory cover ($p < 0.02$), but not for aspect ($p = 0.22$). However, we did find that eastern quolls denned in locations with significantly lower overstory cover during the settlement period (17.2% ±1.51, $p = 0.046$, Figure 4.5f) and significantly more southwest-facing aspects during the settlement period (222° ±4.68, $p = 0.042$, Figure 4.5g).

4.4.3 Conspecific associations

For conspecific associations, we found Pearson movement correlation coefficients for each individual each night were significantly lower during the settlement period (-0.11 ±0.03, $p = 0.013$) and for fawn morphs (-0.08 ±0.02) compared to dark morphs (0.03 ±0.03, $p = 0.001$, Figure 4.6a). We also found significantly lower coefficients of sociality during the settlement period (-0.0004 ±0.005, $p = 0.026$, Figure 4.6b).

For den sharing, two collared eastern quolls den shared only once with other collared eastern quolls (both reinforcers), six individuals den shared on 2–6 occasions (five of which were reinforcers), six individuals den shared on 11–20 occasions (four of which were residents), and two individuals den shared on 22 occasions each (both residents). Overall, we found significantly lower probabilities of den sharing during the settlement period (33.4% ±10.1) compared to the baseline period (54.7% ±7.73, $p < 0.0001$) and for reinforcers (28.6% ±7.67) compared to residents (51.7% ±7.26, $p < 0.0001$, Figure 4.6c).

4.5 Discussion

By building an understanding of the movement, habitat use and preference, and associations between members of an endangered species following their reintroduction, we can develop informed strategies for species recovery. To the best of our knowledge, this study

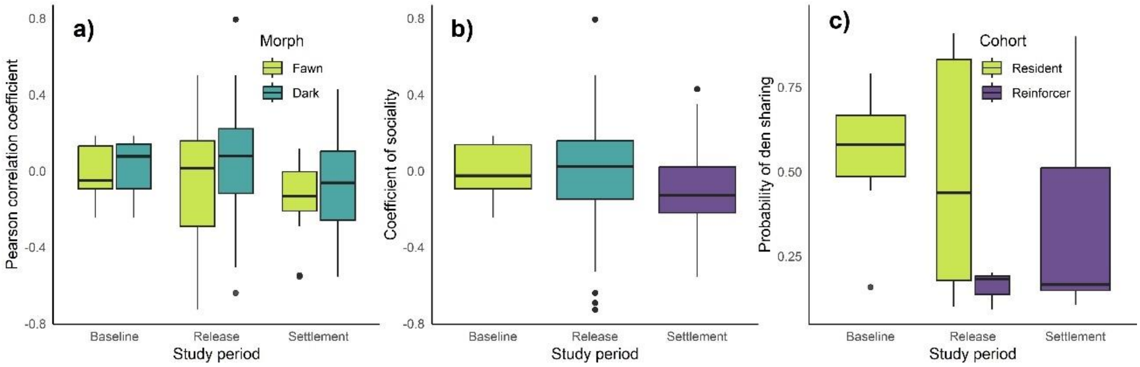


Figure 4.6 Measures of conspecific association derived from nocturnal activity (GPS locations) of female eastern quolls (*Dasyurus viverrinus*) at Mulligans Flat Woodland Sanctuary, Australian Capital Territory: (**a**) Pearson correlation coefficient per study period (baseline with residents only, nights 3–21; release with both cohorts, nights 22–32; and settlement with reinforcers only, nights 33–52) and morph (i.e., pelage colour; fawn *n* = 9, and dark *n* = 6), **b**) coefficient of sociality per study period, and (**c**) probability of den sharing per study period and cohort (residents *n* = 8, reinforcers translocated from Tasmania to reinforce demographic, behavioural, and genetic diversity in the population *n* = 8). Correlation coefficients were quantified using the *wildlifeDI* package (Long *et al.* 2014) in R version 4.2 (R Core Team 2021).

presents the first empirical exploration of eastern quoll spatial behaviour and conspecific associations using GPS-telemetry. While our use of this technology enabled finer temporal resolution than any previous study, we were limited in temporal longitude by rapid battery depletion. While we acknowledge the short-term nature of our results, they nonetheless provide novel information for the species and highlight the value of post-release monitoring during reinforcement translocations to improve decision-making.

4.5.1 Distance and range

We found eastern quolls travelled the greatest distances each night during the release period (2.15 km ±0.2 compared to 1.75 km ±0.1 on average, Figure 4.2a), acknowledging that since GPS units could not determine locations while animals were underground (i.e., denning, described below), this result may not account for distances travelled to and from dens. Indeed, eastern quolls were observed via remote camera visiting multiple dens repeatedly each night (B. A. Wilson *pers obs*).

Despite residents and reinforcers travelling comparable distances each night (rejecting our hypothesis that reinforcers would travel greater distances), reinforcers exhibited significantly greater ranges (home = 249 ha ±53, core = 47 ha ±11) than did residents (home = 90 ha ±12, core = 20 ha ±3, agreeing with our hypotheses, Figure 4.2a, Figure 4.3). Home (251 ha ±58) and core

(48 ha ±12) ranges were also significantly larger during the release period (Figure 4.2b, Figure 4.3), and these ranges decreased significantly across the study period for reinforcers (home and core R^2 = 0.07) when compared to the relatively consistent ranges of the residents (home R^2 = 0.02, core R^2 = 0.01, Figure 4.2b). Decreases in ranging behaviour with time post-release (i.e., post-release behavioural modification, PRBM) has been similarly observed in the related Tasmanian devil (*Sarcophilus harrisii*, Thalmann *et al*. 2016) and other carnivores including grey wolves (Fritts *et al.* 1984) and swift foxes (Moehrenschlager & Macdonald 2003). Our short-term results revealed that reinforcer eastern quolls progressed along the PRBM continuum over two weeks, suggesting an encouraging accumulation of knowledge and acclimatisation to the recipient environment (Berger-Tal & Saltz 2014).

The home ranges of the female eastern quolls in our study (residents 90 ha ± 11, reinforcers 249 ha ± 53) were considerably larger than those of females in a previous study (100% minimum convex polygon 34.7 ha ± 5.9, and AP 95% confidence ellipse 43.3 ha ± 5.6, MAP 95% non-parametric 34.9 ha ± 7.2, Godsell 1983). This is curious, considering our study took place in temporally and spatially limited (by conservation-fencing) area, while Godsell's study took place in unfenced regions across Tasmania (Huon Peninsula, albeit over a similarly short period, 8.58 days ± 4.11). While comparing home ranges determined using different tracking technologies, rates of fixes, and analytical methods should be done with extreme caution, the contrast between our home ranges and those of Godsell (1983) could also be attributed to the dispersion of food resources and productivity of the habitat available (see Oakwood 2002). Tasmania's sclerophyll forests were wetter between 1971 and 2000 (Bureau of Meteorology 2000) and likely to have been more productive when compared to the dry, temperate woodlands of the Australian Capital Territory. In addition, Australia suffered rainfall deficiencies between 2017 and 2020 (Bureau of Meteorology 2022), and these severe climatic conditions likely affected available prey for eastern quolls during our study period (similarly observed in Tasmania by Fancourt *et al*. 2018), thereby necessitating eastern quolls in the latter to range further to meet their energetic needs. Indeed, the eastern quoll population at MFWS underwent a decline in abundance prior to the current study (from N = 32 in Austral summer 2018 to N = 26 in autumn), though this may have been driven by juvenile dispersal between these seasons (Wilson *et al.* 2023).

Considering the larger home ranges of reinforcers, we were unsurprised to find that reinforcer home ranges overlapped significantly more with other collared eastern quolls (home = 115 ha ±15, core = 9 ha ±2) compared to residents (home = 46 ha ±4, core = 4 ha ±1, Figure 4.2c). While we acknowledge that we could not account for other uncollared eastern quolls across the site, this static measure of interaction suggests territoriality among the female residents. Intrasexual territoriality has been observed in other dasyurids including the northern quoll (*Dasyurus hallucatus*, Oakwood 2002), chuditch (*Dasyurus geoffroii*, Serena & Soderquist 1989), and spotted-tailed quoll (*Dasyurus maculatus*, Belcher & Darrant 2006). Most of the female eastern quolls in our study were either pregnant or carrying pouch young (i.e., maternal, B. A. Wilson *pers obs*), so they may have partaken in offspring-defence to prevent infanticide from conspecifics (Wolff & Peterson 1998). While considered rare in marsupials, infanticide has been observed in the MFWS population on one occasion (B. A. Wilson *pers obs* via remote camera).

Despite this evident intrasexual territoriality, none of the reinforcers left the site (as occurred in previous trials, Wilson *et al*. 2020, 2021). With the short-term nature of our results, we cannot differentiate whether the considerable home range overlap by reinforcers was a product of their being at the beginning of PRBM continuum, or being outcompeted for space by residents (as observed in common brushtail possums *Trichosurus vulpecula*, Pietsch 1994). If the latter were true, we would have expected reinforcers to disperse over the conservation fencing in search of territory. Notably, the mean eastern quoll population at MFWS was still growing in 2018 (N = 29 ±4) and reached peak abundance in 2021 (N = 51, Wilson *et al*. 2023). Based on this, it is possible that the population was still in its growth phase, and could absorb reinforcers without displacing residents. However, since the two current mainland populations of the eastern quoll (MFWS at 485 ha and Mt Rothwell at 473 ha) are too small to halt a continued loss of genetic diversity (Weeks *et al.* 2011), these and future populations must be managed as a meta-population with continued reinforcements (Wilson *et al.* 2023). When these populations reach their regulation phase (i.e., maximum carrying capacity), it will be important to monitor the survival of these reinforced reinforcers to ensure they contribute to each population's demographics and genetics.

4.5.2 Habitat use

During nocturnal activity, we found eastern quolls preferred grassland habitats (61%, after accounting for habitat availability), followed by Eucalypt woodland (30%), regrowth (8%), and Eucalypt forest (1%, Figure 4.4a). They were also active in areas of lower overstory (13% ±0.27) and understory (2% ±0.06) than that which was available across the site (overstory 14% ±0.2, understory 2% ±0, Figure 4.5a, b). For diurnal denning, we found eastern quolls preferred to den in grassland (37%) and Eucalypt forest (29%), followed by Eucalypt woodland (19%), and regrowth (14%). Coupled with the preference for significantly greater overstory (21% ± 1, Figure 4.5a) and understory cover (3% ± 0.1, Figure 4.5b) than that which was available throughout the site, we ascertain that both grassland and Eucalypt forest offer preferred foraging and denning conditions for eastern quolls.

Eastern quolls studied in Tasmania were often associated with forest-pasture ecotones that provided open grasslands for foraging (invertebrates, and occasional birds, small mammals, reptiles, fruit, and carrion) during the night, and forest habitat where they can den in hollow logs, rocky outcrops and underground burrows during the day (Godsell 1983). Similarly, a recent dietary study of the eastern quolls at MFWS revealed they also favoured several species of invertebrates and showed opportunistic scavenging of small-medium mammals (S Shippley unpublished data). It is surprising that the eastern quolls at MFWS avoided regrowth for both nocturnal activity and diurnal denning. This could indicate that this mid-succession habitat type offers few resources for the species. However, it may play a role in maintaining functional connectivity (i.e., acting as movement corridors) between patches of appropriate habitat, as observed in European pine martens (*Martes martes*) within agricultural landscapes (Pereboom *et al.* 2008). Since the eastern quoll fills a similar ecological niche to martens (i.e., as mesocarnivores), a mosaic of these habitat types is likely to be important for eastern quolls within fragmented landscapes. It is possible that floristic succession at MFWS may be truncated by its agricultural history (McIntyre *et al.* 2010), so these regrowth and Eucalypt forest habitat types may not progress (without intervention) to more suitable habitat types for eastern quolls in our lifetime. Our results suggest eastern quolls need a mosaic of recently disturbed (e.g., grasslands derived from agricultural clearing) and undisturbed (e.g., remnant woodlands) sites to thrive, and reinforces the need for reintroduction sites to contain suitable habitat from the outset.

We found an effect of study period on habitat use, where eastern quolls preferred to spend their nocturnal activity in areas of greater understory cover during the release period (2.57% ±0.12, Figure 4.5d). This may have been driven by increased competition upon the arrival of the reinforcers, causing all animals to seek open grasslands for increased foraging efficiency (Godsell 1983). Curiously, nocturnal activity and diurnal denning was more frequent on southwest-facing (rather than the average south-facing) aspects during the settlement period (222° ±2.4, Figure 4.5e). For the predominantly north-westerly winds of the ACT, southwest-facing slopes are less sheltered than those to the south (and may be less preferred by eastern quolls). Assuming west-facing aspects are suboptimal, reinforcers may have been forced to select suboptimal foraging grounds and dens. Further, we found denning locations had lower overstory cover during the settlement period (17.2% ±1.5, Figure 4.5f). Since we found a significant preference for greater overstory across all eastern quolls compared to that which was available across the site, this lends weight to the suggestion that reinforcers may have been outcompeted for preferred dens with canopy cover. We posit that the eastern quoll population at MFWS in 2018 may have been approaching density-dependence, given this evidence of conspecific exclusion (Armstrong *et al.* 2005; Muriel *et al.* 2016) and priority effects (Fraser *et al*. 2015).

4.5.3 Conspecific association

We explored conspecific association in eastern quolls using correlation coefficients and den sharing. We found that coefficients of movement correlation and sociality were significantly lower during the settlement period (early July), and this was not significantly driven by cohort as we had hypothesised (Figure 4.6a). We acknowledge the nested nature of the reinforcer cohort within the settlement period, and that we could not account for uncollared eastern quolls within the site and, therefore, present minimum movement correlation. In addition, our results could have been influenced by mothers transitioning from usual associations to territorial defence associated with parturition and offspring growth in mid-winter (Wolff & Peterson 1998).

Den sharing with other collared eastern quolls also occurred less frequently during the settlement period, and for reinforcers (Figure 4.6c). Two reinforcers den shared only once, twelve animals den shared on 2–20 occasions (seven of which were reinforcers), and two residents den shared on 22 occasions each. This behaviour was consistent with den sharing observed during earlier reintroduction trials at MFWS, where the propensity for den sharing had a positive effect on site fidelity (Wilson *et al.* 2020). However, the prevalence of den sharing suggests den sites may be limited across the site, so it is crucial that potential reintroduction sites contain enough of this habitat feature to support eastern quolls. It is worth noting that the majority of dens observed at MFWS were abandoned warrens that had been excavated by European rabbits prior to their eradication (B. A. Wilson *pers obs*). While our results have improved our knowledge of the extrinsic habitat types and attributes eastern quoll prefer, research on the intrinsic characteristics of dens (i.e., structure, soil type) could be used to design artificial dens in sites that are lacking, but otherwise provide appropriate habitat for reintroduction. On a broader scale, incorporating eastern quoll occurrence data from established populations, like MFWS, and habitat attributes into species distribution models (e.g., maximum entropy modelling) could be used to identify appropriate sites for reintroduction across the species' former range.

Interestingly, fawn-morph eastern quolls had significantly lower levels of movement correlation than did dark-morphs (Figure 4.6b). To our knowledge, this is the first evidence of morph affecting eastern quoll movement, and we chose to investigate this effect following anecdotal evidence that abundance and behaviour differed between these morphs (B. A. Wilson *pers obs*). For example, fawn-morphs tended to be more hesitant and agitated during capture and handling, while dark morphs tended to be calmer and more curious, and were more commonly captured during the current study. The lower rates of capture for fawn-morphs may be linked with lower breeding success and survivorship through the 2019–2020 drought years (B Brockett, unpublished data). The significantly lower movement correlation of fawn-morphs suggests they avoid foraging in similar patterns to conspecifics compared to their dark-morph counterparts, which could be beneficial in avoiding competition or aggression, but could be disadvantageous if they fail to perceive habitat suitability using conspecific cueing. While we were unable to discern whether this effect was restricted to fawn-morph reinforcers due to small sample size ($n = 4$), our result lends to the consideration of morph in future species recovery efforts.

4.5.4 Limitations

While we acknowledge that our study only involved maternal eastern quolls, this demographic group was likely to have had higher energetic costs associated with parturition, thereby facing an increased trade-off between resource acquisition and offspring safety. This has been similarly observed in stone martens (*Martes foina*) where females selected more food-rich areas and less disturbed sites than did males (Santos & Santos-Reis 2010), and in jaguars (*Panthera onca*) where female's preference toward intact forest and against roads led to their habitat being more fragmented than those of males (Conde *et al.* 2010). Based on this, we believe site selection that meets the restricted needs of female eastern quolls is likely to meet the needs of males as well. Further, in the absence of information on relatedness between eastern quolls, we could not determine whether this factor influenced their conspecific associations (e.g., home range overlap, den sharing), and will be an important addition to future work. Finally, although our parsimonious experimental approach (maximising learning with the fewest number of individuals) limited our sample size, our findings nevertheless offer valuable insights into the factors influencing movement and associations between reintroduced mesocarnivores in reserves with high levels of threat (i.e., predation) control (as is appropriate for threatened species). However, it is important to view these reserves as "stepping-stones back to the wild, rather than reservoirs of threatened biota" (Batson 2015). We recognise that to prevent the "locking-in" of the current shifted baseline (where native species are accepted as permanently absent from the wild, Manning *et al*. 2006), future research must explore innovative solutions to drive or enable adaptive evolution of threatened species and invasive predators alike (i.e., 'coexistence conservation', Evans *et al*. 2022).

4.5.5 Conclusions

Here we have demonstrated that short-term movements in a reintroduced mesocarnivore can be dynamic in time and shaped both directly by habitat and indirectly through conspecific interactions. While conspecific attraction can encourage reinforcers animals to settle early in a translocation program (as we hypothesised, Stamps *et al*. 2005; Valone 2007), this effect can also be amplified simply by the abundance and ubiquity of conspecifics present in the landscape (Armstrong *et al.* 2005) in later phases (i.e., when the population is in its growth phase, Sarrazin 2007). At some point, however, density dependence may trigger conspecific exclusion, especially for territorial species (e.g., by priority effects, Fraser *et al*. 2015). For the eastern quoll, we found high levels of den sharing across the site and the use of potentially suboptimal habitat by reinforcers, suggesting density dependent mechanisms were active during our study. This juxtaposition reinforces the need to consider a species' life history and monitor reinforcers' progress throughout a translocation program to ensure practitioners can manage these mechanisms adaptively.

Our findings offer important insights into appropriate habitat structure for future reintroduction sites and confirm the need for intensive post-release monitoring to inform adaptive management interventions during the establishment period. We recommend that tactics pertaining to site selection should be made carefully with specific regard to the current population's reintroduction phase, and adaptively within a structured framework to ensure decisions are made with best available knowledge to increase the likelihood of positive reintroduction outcomes.

4.5.6 Acknowledgements

We acknowledge and respect the Ngunnawal and Ngambri (ANU, MFWS) and Palawa (Tasmania) peoples, the traditional custodians of the lands on which this work was undertaken. This study was conducted as part of the Mulligans Flat-Goorooyarroo Woodland Experiment and was part of the Australian Research Council-funded 'Bringing Back Biodiversity' project (LP140100209). We thank our collaborative partners, the ACT Government (Parks and Conservation Service and Conservation Research), Tasmanian Department of Primary Industries, Parks, Water and Environment (DPIPWE), and the Woodlands and Wetlands Trust for their support.

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4.6 Appendix

Table 4.2 Likelihood ratio chi-square (χ2), *F*-statistic, *p*-value (significant values in **bold**), variance (V), *t*-statistic, and residual deviance (RD) values generated through generalised linear mixed models conducted for distances travelled (m), home (95% kernel utilisation distribution, KUD) and core (50% KUD) ranges, proportion of nocturnal activity (GPS locations, n = 15) and diurnal denning (VHF locations, n = 16) spent in habitat types (Eucalypt woodland, Eucalypt forest, regrowth, and grassland), proportion of habitat attributes (overstory and understory [cover percent, 3.2 m resolution] and aspect [orientation in degrees, derived from a digital elevation model] associated with nocturnal activity and diurnal dens, and conspecific association measures (proximity index, Pearson correlation coefficient, coefficient of sociality, coefficient of association, probability of den sharing) derived from the nocturnal activity of female eastern quolls (*Dasyurus viverrinus*) at Mulligans Flat Woodland Sanctuary, Australian Capital Territory.

Depending on the response variable, models included the fixed effects of cohort (residents n = 8, reinforcers translocated from Tasmania to reinforce demographic, behavioural, and genetic diversity in the population n = 8), study period (baseline with residents only, nights 3–21; release with both cohorts, nights 22–32; and settlement with reinforcers only, nights 33–52) and/or morph (i.e., pelage colour; fawn n = 9, and dark n = 6), and the random effects of animal identity, night number, minimum temperature, precipitation, and/or moon phase.

Home ranges were calculated using the *adehabitatHR* package (Calenge 2006) in R version 4.2 (R Core Team 2021). Habitat types were aggregated from eight National Vegetation Information System (version 6.0) major vegetation groups (NLWRA 2001) in R version 4.2.0 (R Core Team 2021). Habitat attributes were sourced from Terrestrial Ecosystem Research Network (TERN) airborne lidar and hyperspectral products (van Dijk *et al.* 2018). Correlation coefficients were quantified using the *wildlifeDI* package (Long *et al.* 2014) in R version 4.2 (R Core Team 2021).

		Fixed effects									**Random effects**					
		Cohort			**Period**			**Morph**			**Identity**	**Night**	**Min temp**	**Precip-itation**	**Moon phase**	**Resid-ual**
Category	**Response**	**$\chi2$**	***F***	***p***	**$\chi2$**	***F***	***p***	**$\chi2$**	***F***	***p***	**V**	**V**	**V**	**V**	**V**	**V**
Distance	Distance travelled	0.28	0.28	0.60	9.61	4.83	**0.01**	2.41	2.41	0.12	0.34	0.00	0.04	0.00	0.00	1.50
Range	Home range	13.27	5.27	**0.00**	13.03	6.50	**0.00**	0.09	0.09	0.77	2495	496	0.00	69.50	680.90	27358
	Core range	14.45	5.46	**0.00**	13.79	6.88	**0.00**	0.07	0.07	0.80	136.34	33.55	0.00	0.00	37.21	1917
Nocturnal activity	Woodland	0.05	0.00	0.82	0.94	0.46	0.63	0.05	0.05	0.82	564.50	-	-	-	-	746.90
	Forest	0.44	0.08	0.50	2.40	1.21	0.30	0.01	0.01	0.91	0.00	-	-	-	-	445.80
	Regrowth	2.22	1.25	0.14	2.03	1.18	0.36	0.02	0.02	0.90	83.02	-	-	-	-	178.45
	Grassland	0.01	0.66	0.93	2.89	1.53	0.24	0.24	0.24	0.63	63.46	-	-	-	-	559.99
	Overstory	0.00	0.03	0.98	0.19	0.09	0.91	0.00	0.00	0.95	0.00	-	-	-	-	0.02
	Understory	4.94	0.86	0.03	27.61	13.72	**0.00**	0.24	0.24	0.62	0.00	-	-	-	-	0.00
	Aspect	0.25	0.94	0.62	18.20	9.11	**0.00**	0.25	0.25	0.62	1512.00	-	-	-	-	3518
Diurnal denning	Woodland	0.05	0.00	0.82	0.94	0.46	0.63	0.05	0.05	0.82	564.50	-	-	-	-	746.90
	Forest	0.44	0.08	0.50	2.40	1.21	0.30	0.01	0.01	0.91	0.00	-	-	-	-	445.80
	Regrowth	2.22	1.25	0.14	2.03	1.18	0.36	0.02	0.02	0.90	83.02	-	-	-	-	178.45
	Grassland	0.01	0.66	0.93	2.89	1.53	0.24	0.24	0.24	0.63	63.46	-	-	-	-	559.99
	Overstory	2.41	1.04	0.12	6.16	3.10	**0.05**	0.85	0.85	0.36	0.02	-	-	-	-	0.01
	Understory	3.40	1.33	0.07	3.99	2.04	0.14	1.06	1.06	0.30	0.00	-	-	-	-	0.00
	Aspect	1.87	2.89	0.17	6.32	3.11	**0.04**	2.04	2.04	0.15	391.60	-	-	-	-	1914
		RD	***t***	***p***	**RD**	***t***	***p***	**RD**	***t***	***p***						**RD**
Conspecific overlap	Home range	225723	5.83	**0.00**	-	-	-	221575	1.29	0.20	-	-	-	-	-	314790
	Core range	4387	2.83	**0.00**	-	-	-	4376	0.46	0.65	-	-	-	-	-	4797

		χ2	**RD**	***p***	**χ2**	**RD**	***p***	**χ2**	**RD**	***p***						**RD**
Conspecific association	Proximity index	0.08	0.93	0.78	2.05	0.92	0.36	0.48	0.92	0.49	-	-	-	-	-	0.94
	Pearson correlation coefficient	3.23	16.23	0.07	8.66	15.73	**0.01**	10.29	15.08	**0.00**	-	-	-	-	-	16.24
	Coefficient of sociality	2.42	0.32	0.12	7.29	0.31	**0.03**	3.07	0.31	0.08	-	-	-	-	-	0.32
	Coefficient of association	0.03	0.04	0.87	1.60	0.04	0.45	0.02	0.04	0.88	-	-	-	-	-	0.04
	Probability of den sharing	31.32	528.85	**0.00**	17.82	510.30	**0.00**	2.96	507.34	0.09	-	-	-	-	-	551.42

Chapter 5: Species recovery

Restoration presents a major challenge for the next century, but to avoid long-term goals being limited by short-term human memory of ecosystems (shifting baseline syndrome) I visualised an ambitious end point (stretch goal): recovery of the eastern quoll species within 10 years.

By projecting the population size and habitat required to achieve this goal (back-casting), in this Chapter I demonstrated how demographic parameters can reveal threats to persistence, inform thresholds for management, and create targets for removing species from the IUCN Red List. While the targets may appear daunting, our goals must be ambitious to inspire the innovation needed to achieve long-term outcomes that currently seem impossible.

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Illustration by Cat Cotsell

Roadmap to recovery revealed through the reintroduction of an IUCN Red List species

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5.1 Abstract

Reintroductions are powerful tools for tackling biodiversity loss, but the resulting populations can be intrinsically small and vulnerable. It is therefore critical to maximise the number of individuals available to contribute to recovery efforts. To address this, we investigated how demographic parameters from a reintroduced population can reveal threats to long-term persistence, inform thresholds for management interventions, and create targets for removing an endangered species from the IUCN Red List.

We calculated capture-mark-recapture population estimates for eastern quolls (*Dasyurus viverrinus*) which had been reintroduced to a fenced reserve in the Australian Capital Territory. We then incorporated the resulting demographic parameters into population viability analyses (PVAs) to estimate probabilities of persistence under several scenarios, including supplementations and harvests (removal of individuals for translocation to other locations). By determining sustainable harvest rates, we could then 'back-cast' the population size and occupancy area required to remove the species from the IUCN Red List within 10 years.

Our demographic results indicated a high mean apparent survival (90% ± 5), and PVAs revealed the probability of persistence over a 50-year time horizon was 50.5% with no interventions, 0% when the population was harvested of >6 individuals, and 100% if harvests ≤54 juveniles were combined with an annual supplementation of ten maternal females (with ≤6 young each). Based on this model, a total harvest area of 413 km^2 and an occupancy area of 437 km^2 would be needed to recover the species within 10 years (i.e., 90 fenced reserves similar to ours, not accounting for edge effects).

Due to the inherent difficulty in securing large areas for species recovery, we see these ambitious targets as a call to create coordinated and collaborative sanctuary networks where species can be managed as a meta-population across multiple sites. By taking advantage of a rapid life history and harvesting the 'doomed surplus', managers can achieve their stretch goals for species recovery in the long term.

5.2 Introduction

Defaunation in the Anthropocene, driven by human-induced environmental change and destruction, threatens biodiversity, ecosystem function, and human health worldwide (Dirzo *et al.* 2014). Restoration presents a major challenge for the next century, but to avoid long-term goals being limited by short-term human memory of ecosystems (i.e., 'shifting baseline syndrome', Pauly 1995; Miller 2005; Manning *et al*. 2006), robust monitoring and species listings are paramount. The International Union for the Conservation of Nature's Red List of Threatened Species (IUCN 2021) provides a powerful tool used by conservationists and researchers to list declining species, and galvanise conservation action and policy change (Rodrigues *et al*. 2006; Betts *et al*. 2020). It provides a repository for information related to species range, population size, threats, and conservation actions, and compares these to broadly applicable and standardised criteria to categorise species from 'Critically endangered' through to 'Least concern'. These criteria enable managers to quantify the targets required to downlist (reclassify from higher risk to lower risk categories) or delist (remove from the IUCN Red List) a species, and encourages small-scale projects to be unified under long-term visions for species recovery.

Reintroductions are a critical tool used to reverse defaunation and restore ecosystem function (Armstrong & Seddon 2008). While aiming to establish a viable and self-sustaining population (IUCN 2013), management decisions must always be made in the face of imperfect knowledge about species and ecosystems (Armstrong & Seddon 2008). This uncertainty can be addressed using robust monitoring of demographic parameters including abundance, survival, and reproduction; which can indicate population self-sustainability, density-dependence, carrying capacity, and threats to these processes (e.g., Manning *et al*. 2019; Parlato *et al*. 2021). This is particularly crucial when a population transitions through the three phases of reintroduction, from 'establishment' (where post-release effects drive population dynamics) to 'growth' (characterised by high rates of expansion) and, finally, to 'regulation' (where density dependence limits survival and recruitment, Sarrazin 2007). However, many reintroduction studies span short timeframes (i.e., <5 years, Parlato *et al*. 2021), limiting their ability to estimate temporal variation in vital rates over the long term (e.g., Leech *et al*. 2007; Cremona *et al*. 2017). From the outset, reintroduction success should be focused on a long-term vision of species recovery, which necessarily requires robust demographic monitoring to ensure the population reaches the regulation phase (Armstrong & Reynolds 2012; McCarthy *et al.* 2012; Nichols & Armstrong 2012).

As part of this long-term approach, demographic parameters from a reintroduced population can be built into stochastic population models (i.e., for population viability analyses [PVAs], Lindenmayer *et al*. 1993). These models can be used to compare alternative management interventions including supplementations (reinforcement of individuals) and harvests (removal of individuals for translocation to other locations), and thus provide crucial insights to guide these management actions. For example, PVAs have revealed that expanding the reintroduction of bearded vultures (*Gypaetus barbatus*) would dangerously deplete the captive source population (Bustamante 1996), and have highlighted the need to establish a second population of Eurasian beavers (*Castor fiber*) to ensure their viability in the Netherlands (Nolet & Baveco 1996). Since population growth is often affected by population size, this can result in a trend toward a constant breeding density (i.e., density-dependence, Sibly *et al*. 2002). Above this density, excess individuals can be considered a 'doomed surplus' (e.g., northern bobwhite *Colinus virginianus*, Errington 1945, but see Williams *et al*. 2004). Harvesting these individuals (especially for species with high fertility) could offer an ideal opportunity to maximise the number of individuals available for translocation to begin or reinforce other populations (e.g., demonstrated in black-footed ferrets *Mustela nigripes*, Biggins *et al*. 2011). Reintroduced populations, however, can be intrinsically small and vulnerable to stochastic effects (Lacy 2000), therefore the impacts of harvesting from these populations should be simulated before any individuals are removed. PVAs can inform thresholds for harvests of the doomed surplus for translocation by indicating the maximum sustainable number of individuals available to contribute to species recovery.

We used a reintroduced population of eastern quolls (*Dasyurus viverrinus*) to investigate how demographic monitoring and PVAs can reveal viable interventions (i.e., supplementations and harvests) that can contribute to removing an endangered species from the IUCN Red List. Specifically, we (1) modelled survival and recruitment rates throughout the establishment, growth, and regulation phases of the eastern quoll reintroduction, 2) incorporated these demographic parameters into stochastic population models to reveal long-term viability under different management scenarios (i.e., no intervention, supplementation, harvest, and combinations of these), and (3) determined the contribution of our program toward species recovery. Since long-term vision is essential for effective restoration, we set an ambitious end point (or 'stretch goal') of eastern quoll species recovery within 10 years, and then retrospectively calculated the area of habitat (henceforth 'area of occupancy') and number of harvests required to achieve this goal (also known as 'back-casting', Manning *et al*. 2006).

Australia has suffered the highest rate of mammal extinctions of any continent (Woinarski *et al.* 2015), due in large part to predation by invasive species (e.g., red fox *Vulpes vulpes*, and feral cat *Felis catus*, Kinnear *et al*. 2002; Radford *et al*. 2018). To circumvent these threatening processes, significant efforts have been made to reintroduce species where invasive predators are absent, such as in fenced sanctuaries (Hayward & Kerley 2009; Moseby *et al*. 2011; Legge *et al*. 2018). The benefits of conducting long-term, large-scale experiments under such fenced conditions are increasingly being recognised, and allow researchers to build an understanding of ecological processes which may otherwise be impossible (Hester *et al.* 2000; Manning *et al.* 2009).

Our eastern quoll reintroduction took place in this fenced context, and presents a unique model for testing the effect of conservation actions on species recovery because (1) the species is categorised as ‘Endangered’ under the IUCN Red List (Burbidge & Woinarski 2016), 2) the founding population was small but within the normal range for mammal reintroductions (*n* = 44), 3) reintroductions to fenced sanctuaries provide an ideal opportunity to undertake ecological experiments, 4) the population has been robustly monitored for over five years, and (5) the program emulates small conservation projects across the globe, creating broad relevance of our outcomes to long-term reintroduction planning.

5.3 Methods

5.3.1 Ethics statement

Translocations were carried out under licenses from the Tasmanian Department of Primary Industries, Parks, Water and Environment (permits TFA 16025 and 17091, export licences 12818/16 and 13528/17), Victorian Department of Environment, Land, Water and Planning (permit 14505167), and Australian Capital Territory Directorate of Territory and Municipal Services (import licence L120161261). Reintroduction (protocol A2016/02) and monitoring procedures (protocol A2020/40) were approved by The Australian National University Animal Experimentation Ethics Committee.

5.3.2 Study area

This study took place at Mulligans Flat Woodland Sanctuary (MFWS), a 485 ha public nature reserve containing critically endangered box-gum grassy woodland (McIntyre *et al.* 2010) situated on Ngunnawal and Ngambri Country in the Australian Capital Territory (-35.167, 149.158). MFWS is part of the Mulligans Flat-Goorooyarroo Woodland Experiment and functions as an ‘outdoor laboratory’ where restoration techniques are trialed (Manning *et al.* 2011; Shorthouse *et al.* 2012). This includes the reintroduction of locally extinct species, such as the eastern bettong (*Bettongia gaimardi*, Manning *et al*. 2019), bush stone-curlew (*Burhinus grallarius*, Rapley 2020), and New Holland mouse (*Pseudomys novaehollandiae*, Abicair *et al*. 2020). To enable these reintroductions, the Sanctuary is enclosed by a 11.5 km fence which excludes invasive species including the red fox, feral cat, European rabbit (*Oryctolagus cuniculus*), and European hare (*Lepus europaeus*, Shorthouse *et al*. 2012). While these threatening and destructive species have been eradicated from within the Sanctuary, conditions are otherwise like other unfenced woodlands in the region. The fence design includes an overhang on the outside which prevents entry by invasive species (Shorthouse *et al.* 2012), but does not prevent agile species from climbing out of the Sanctuary into the surrounding landscape.

5.3.3 Study species

The eastern quoll (‘murunguny’ in the Indigenous Ngunnawal language) is a solitary, small-to-medium (0.7–1.9 kg, Jones *et al*. 2001) marsupial carnivore (family Dasyuridae, Stannard & Old 2013). It is an opportunistic hunter with a diet dominated by invertebrates, but will also depredate birds, reptiles, and mammals, and scavenge on carcasses (Blackhall 1980; Godsell 1983).

The species is promiscuous and facultatively monoestrous, breeding synchronously in early Austral winter (Fletcher 1985), giving birth after 20 days gestation, and weaning ≤6 young in spring when food availability is high (Godsell 1983). Eastern quolls are sexually dimorphic, with males being larger (0.9–2 kg) and having larger home ranges (mean 44 ha) than females (0.7–1.1 kg, mean 35 ha, Godsell 1983). Populations reach their highest densities in early summer when the annual cohort of juveniles disperse from their natal dens, and lowest densities during winter largely due to juvenile mortality (Godsell 1983). The combination of a short lifespan (3–4 years) and these seasonal population fluctuations result in high population turnover (Jones *et al.* 2001).

Originally, eastern quolls were distributed throughout south-eastern Australia until the 1960s. The species disappeared from all but the southern island state of Tasmania due to a combination of habitat destruction, disease, persecution, and predation by invasive species (particularly red foxes, Jones *et al*. 2001; Peacock & Abbott 2014). While there is no robust assessment of population size, state-wide spotlighting surveys revealed a 52% decline in sightings at 150 sites across Tasmania between 1999 and 2009 (i.e., 10,400 decline in population size from a 20,000 estimate, Fancourt *et al*. 2013). In addition, trapping surveys revealed a 61–100% decline at historical ‘hotspots’ (with disproportionately high eastern quoll densities compared with other parts of Tasmania, i.e., Cradoc, Cradle Mountain, and Buckland) compared with trapping conducted 18–31 years earlier. In response, the species was listed as ‘Endangered’ by the IUCN (Burbidge & Woinarski 2016) and the Australian Threatened Species Scientific Committee (2015).

5.3.4 Reintroduction

For the reintroduction of eastern quolls to MFWS, we adopted an adaptive translocation tactics approach (*sensu* Batson *et al*. 2015); involving a series of trials where learnings were used to refine tactics for the following trial. When the first trial in 2016 revealed high male mortality associated with increased conspecific aggression and overdispersal (87.5% mortality, Wilson *et al*. 2020, 2021), we selected only female founders for subsequent trials to maximise survival (12.5–23.1% mortality). By translocating maternal females (henceforth mothers) in winter, several were either pregnant or carrying pouch young, allowing us to reintroduce juvenile males and females ‘via the pouch’. This also potentially increased genetic diversity because multiple sires can be represented in a litter (B. Brockett unpublished data).

Forty-four (female = 36, male = 8) founding individuals (henceforth founders) were translocated to MFWS between 2016 and 2019, with a presumed total of 33 founders surviving the establishment period (42 days post-release, Wilson *et al*. 2020). Founders were either captive-bred (sourced from Mt Rothwell Biodiversity Interpretation Centre, henceforth Mt Rothwell) or wild-caught (sourced from free-ranging populations across four regions in Tasmania, as per Wilson *et al*. 2020).

5.3.5 Monitoring

We used a Robust Design capture-mark-recapture (CMR) framework to conduct demographic monitoring of the reintroduced eastern quoll population (Pollock 1982; Kendall & Nichols 2002). We conducted eight CMR primary sessions, each consisting of two trap nights 2–3 days apart (secondary sessions), in Austral summer and autumn each year between 2017 and 2022. Trapping during summer was intended to detect the greatest population density following juvenile dispersal in spring, and trapping during autumn was intended to detect the size of the breeding population. We integrated one night of free-feeding before each trap night to encourage the capture of more ‘trap-shy’ individuals (Biro 2013).

We standardised an array of 92 trap sites across MFWS, each placed 25 m from vehicle tracks and approximately 200 m apart (Figure 5.1). We used wire cage traps (31 × 31 × 70 cm) baited with sardines, and for each trapped animal we inserted a microchip for identification, sampled fur, scat, and skin (biopsy for genetic material), and recorded sex, weight, and pouch occupancy (Portas *et al*. 2020).

5.3.6 Data analyses

5.3.6.1 Demography

We fitted Robust Design Pradel Recruitment Closed Population Estimation models (Kendall *et al.* 1995, 1997; Pradel 1996) which incorporate closed sampling periods (secondary sessions) within open sampling periods (primary sessions, Pollock 1982; Kendall & Nichols 2002). We assumed emigration and mortality only occurred between primary sessions and that population growth reflected young eastern quolls recruited to adulthood (and not immigration, since

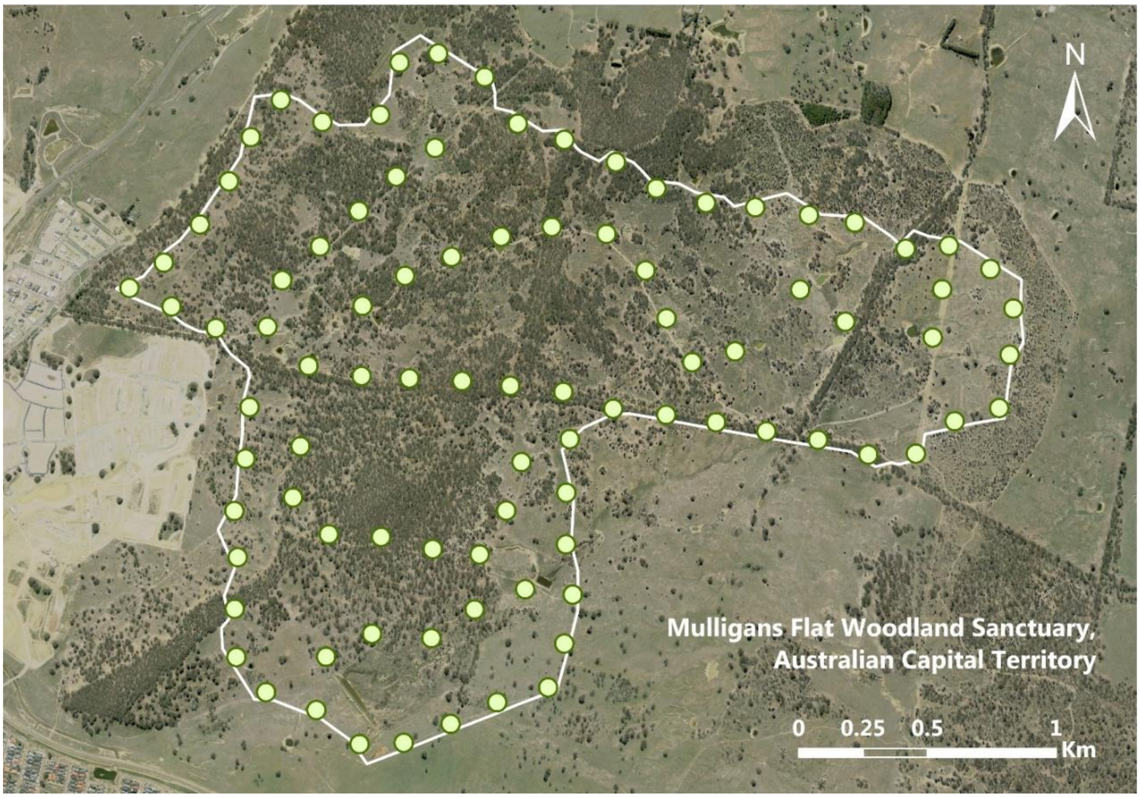

Figure 5.1 Map of 92 standardised trap sites for monitoring the reintroduced population of eastern quolls (*Dasyurus viverrinus*) at Mulligans Flat Woodland Sanctuary, Australian Capital Territory.

secondary sessions varied (either by design or logistical constraints), we ensured the sampling regime was reflected in the models.

We tested 12 candidate models, which included whether *p* was equal to *c* or varied from each other (e.g., due to 'trap shyness'), and whether *p* and *c* were constant over time (null), or varied by session, season, trap night, minimum temperature (°C), maximum temperature (°C), and rainfall on the day of trapping (BOM), and whether there was an additive effect of trap availability (fraction of traps available to eastern quolls after removing traps made unavailable by other species and defective traps), across all individuals and between sexes (Table 5.1). We assessed models based on Akaike's Information Criterion corrected for small sample sizes (AICc) to predict the final parameter estimates (Burnham & Anderson 2002).

We also investigated whether body weight varied by primary session or estimated population size (N) by fitting linear models. Since the eastern quoll is sexually dimorphic, females and males were modelled separately. Finally, we estimated eastern quoll density by dividing the trapped area (485 ha) by the mean female and male estimates (N) across all sessions excluding autumn 2017 (where the population was still establishing). Demographic MFWS is fenced). The Pradel Robust Design allowed us to derive estimates of population size

Table 5.1 Top- and second-ranked predictor models for population estimates (by individual and by sex) based on eight capture-mark-recapture sessions of reintroduced eastern quolls (*Dasyurus viverrinus*) at Mulligans Flat Woodland Sanctuary, Australian Capital Territory. '*p*' indicates initial capture probability, '*c*' recapture probability, 'K' the number of parameters, 'AICc' Akaike's Information Criterion corrected for small sample sizes, and '△AICc' the difference between the top- and second-ranked models.

Population estimate	Best performing model(s)	K	AICc	△AICc	Weight
By individual	$p \neq c$ ~ trap night	34	23.47	0	0.99
	$p = c$ ~ session	27	47.08	23.62	<0.01
By sex	$p \neq c$ ~ trap night	52	310.49	0	0.99
	$p = c$ ~ session	36	359.09	48.59	<0.01

(N) at each primary session from initial capture probability (*p*), recapture probability (*c*), apparent survival (φ), and recruitment (*f*) using a logit link function. Since the length of time between primary and analyses were conducted within the R environment (version 4.1.2, R Core Team 2021) using the packages *AICcmodavg* (Mazerolle 2017), *ggplot2* (Wickham 2011), *lme4* (Bates *et al.* 2015), *lsmeans* (Lenth 2016), *MuMIn* (Barton 2016), and *RMark* (Laake 2013) to interface with the program MARK version 9.0 (White 2016).

5.3.6.2 Viability

We explored the long-term viability of the reintroduced eastern quoll population over a 50-year time horizon using individual-based models simulating a hypothetical, non-spatially explicit population incorporating demographic parameters from our parsimonious model (determined above), and ecological data available for the species (Table 5.2). Due to their rapid life history (3–4 year lifespan), we considered only two life stages where individuals >1 year old were classed as adults, otherwise they were classed as juveniles.

Since eastern quolls, and especially males, have naturally high rates of mortality during the juvenile dispersal (summer) and breeding periods (early winter, Godsell 1983; Wilson *et al.* 2020), we aimed to determine a threshold for sustainably harvesting (i.e., removing individuals for translocation to other locations) this 'doomed surplus' (animals that would never survive the seasonal bottleneck, Errington 1945). In MFWS, this process likely manifests as an exodus over the Sanctuary fence due to limited territory. In addition, supplementing mothers (carrying ≤6 pouch young) allows managers to translocate 'seven for the price of one' (Wilson *et al.* 2020). As such, we ordered the simulated events in a year as: (1) setting of annual rates (EV), 2) aging, 3) carrying capacity (K) truncation, 4) breeding (early winter) with a census, 5) supplementation (mid-winter) with a census, 6) growth rate (*r*) calculation, 7) harvest (late spring) with a census,

Table 5.2 Parameters for population viability analyses of reintroduced eastern quolls (*Dasyurus viverrinus*) at Mulligans Flat Woodland Sanctuary, Australian Capital Territory. 'F' refers to females, and 'M' to males, and 'J' to juveniles. Scenarios were simulated using Vortex 10.5.5 (Lacy & Pollak 2021). 'Current study' refers to parameters computed using the *RMark* package (Laake 2013) in R version 4.1.2 (R Core Team 2021) to interface with program MARK (White 2016).

Category	**Parameter**	**Scenario**					**Reference(s)**
		No intervention	**Harvest (6J)**	**Supplement (1F with 6J)**	**Supplement (1F with 6J) and harvest (4J)**	**Supplement (10F with 60J) and harvest (54J)**	
Scenario settings	Number of iterations	1000	“ ”	“ ”	“ ”	“ ”	
	Number of years	50	“ ”	“ ”	“ ”	“ ”	
	Extinction definition	1 sex remains	“ ”	“ ”	“ ”	“ ”	
Species description	Inbreeding depression lethal equivalent	6.29	6.29	-	-	-	O'Grady *et al*. (2006)
Reproductive system	Reproductive system	Polygynous	“ ”	“ ”	“ ”	“ ”	Godsell (1983)
	Age of first offspring	1	“ ”	“ ”	“ ”	“ ”	Godsell (1983)
	Maximum lifespan	3	“ ”	“ ”	“ ”	“ ”	Godsell (1983)
	Maximum litters per year	1	“ ”	“ ”	“ ”	“ ”	Godsell (1983)
	Maximum progeny per litter	6	“ ”	“ ”	“ ”	“ ”	Godsell (1983)
	Sex ratio at birth[#]	1:1	“ ”	“ ”	“ ”	“ ”	Godsell (1983)
	Maximum female reproduction age	3	“ ”	“ ”	“ ”	“ ”	Godsell (1983)
	Maximum male reproduction age	2	“ ”	“ ”	“ ”	“ ”	Godsell (1983)
Reproductive rates	Adult females breeding	100%	“ ”	“ ”	“ ”	“ ”	Godsell (1983)
Mortality rates	Mortality rate female <age 1	64.17% ± 19.92	“ ”	“ ”	“ ”	“ ”	Godsell (1983)
	Mortality rate male <age 1	64.93% ± 19.87	“ ”	“ ”	“ ”	“ ”	Godsell (1983)
	Mortality rate female >age 1	8.77% ± 6.25	“ ”	“ ”	“ ”	“ ”	Current study
	Mortality rate male >age 1	10.69% ± 5.60	“ ”	“ ”	“ ”	“ ”	Current study
	Carrying capacity	51	“ ”	“ ”	“ ”	“ ”	Current study
Mate monopolisation	Males in breeding pool	25.51%	“ ”	“ ”	“ ”	“ ”	B. Brockett unpublished data
Abundance	Initial population size	47	“ ”	“ ”	“ ”	“ ”	Current study
Harvest	Frequency	-	1 year	-	1 year	1 year	Current study
	Sex ratio	-	1:1	-	1:1	1:1	Wilson *et al*. (2020)
Supplementation	Frequency	-	-	1 year	1 year	1 year	Wilson *et al*. (2020)
	Survival of individuals	-	-	92%	92%	92%	Wilson *et al*. (2020)
	Juvenile sex ratio	-	-	1:1	1:1	1:1	Wilson *et al*. (2020)
Genetics	Maximum female mates	3	“ ”	“ ”	“ ”	“ ”	B. Brockett unpublished data

and (8) mortality (summer) with a census (for definitions see Lacy & Pollak 2021).

We modelled annual scenarios based on a stable stage distribution: (a) no intervention, b) harvest of six (1:1 sex ratio) juveniles (i.e., removed), c) supplementation (i.e., reinforcement) with one mother (carrying six young, effectively n = 7), d) supplementation with one mother (effectively n = 7) and harvest of four juveniles, and (e) supplementation with 10 mothers (effectively n = 70) and harvest of 54 juveniles. We simulated models with 1000 iterations to account for stochasticity in parameter estimates and increase model precision, and did not include catastrophes. Inbreeding depression was included for the 'no interventions' and harvest-only scenarios (lethal equivalent 6.29, as per O'Grady *et al*. 2006), but was not included for scenarios involving supplementations because inbreeding effects would likely be negated (Mills & Allendorf 1996). Parameters derived from the PVAs included population growth rate (λ) and probability of persistence (percent). PVAs were conducted using Vortex 10.5.5 (Lacy & Pollak 2021) and post-simulation visualisations were generated using the *vortexR* package (Pacioni & Mayer 2017) in R version 4.1.2 (R Core Team 2021).

5.3.6.3 Recovery

To reveal a roadmap towards eastern quoll species recovery, we summarised the IUCN Red List criteria for the status of 'Critically endangered', 'Endangered', and 'Vulnerable' (IUCN 2021), and recommended actions that would result in delisting the species based on the eastern quoll assessment (i.e., Burbidge & Woinarski 2016). We then incorporated these targets with our PVA results (i.e., sustainable harvests) to calculate the annual contribution of MFWS towards species recovery (i.e., offsetting the population reductions and increasing geographic range that place the species in the IUCN Red List 'Vulnerable' category). Finally, we back-casted the number of harvests and the area of occupancy that would be required achieve our stretch goal of species recovery within 10 years (as per Manning *et al*. 2006).

5.4 Results

5.4.1 Demography

During 1,472 trapping nights, we made 421 eastern quoll captures (155 unique individuals, 101 females, 54 males) at MFWS over eight trapping sessions between 2017 and 2022. 56.44% of females and 70.37% of males were recaptured at least once. The most parsimonious CMR model included capture probability (p) and recapture probability (c) varying from each other, and trap night (Table 5.1).

In the first monitoring session in autumn 2017, we caught one founder and seven Sanctuary-born eastern quolls (n and N = 8). Between 2018 and 2020 population estimates oscillated, with summer estimates being expectedly greater (coinciding with juvenile dispersal, mean = 37 ± 6.24), and autumn estimates being lower and more variable (between the dispersal and breeding periods, mean = 34.56 ± 14.14, Figure 5.2a). Sex ratios were relatively balanced until summer 2018 (1.12 females: 1 male), but by the following summer 2019 session they skewed heavily toward females (2.24 females: 1 male). The autumn 2021 population estimate deviated from this oscillating trend and reached a new peak (N = 51), with a sex ratio that was also skewed toward females (2.13 females: 1 male). The final autumn 2022 exhibited a similar population estimate (N = 47) and sex ratio (2.35 females: 1 male).

Excluding 2017 where the population was still establishing, mean apparent survival (φ) across all individuals was 90% (± 5) between 2018 and 2022, with females having similar survival rates (91% ± 6) to males (89% ± 6). Estimated recruitment (*f*) was similar between sexes (females 7% ± 5, and males 7% ± 7).

Mean body weights (females 0.84 kg ± 0.13, males 1.13 kg ± 0.15) oscillated between a maximum in autumn and minimum in summer; the opposite to the observed population estimates (Figure 5.2b). However, body weights were unexpectedly lower in autumn 2021 compared to previous autumns (females 0.74 kg ± 0.04, males 1.02 kg ± 0.08), however this was followed by the greatest body weights observed across the study period in autumn 2022 (females 1.02 kg ± 0.04, males 1.35 kg ± 0.08). When fitting a linear model with body weights (kg) against estimated population size (N), we found a significantly negative association ($p = 0.034$), suggesting the population had become density-dependent after 6 years of establishment.

The mean density of eastern quolls across sessions (excluding autumn 2017 where the population was still establishing) was one female per 19.57 ha (± 2.84), one male per 37.51 ha (± 1.06), and for both sexes, one individual per 12.97 ha (± 3.76). The maximum density of eastern quolls at MFWS was one individual per 9.53 ha in autumn 2021, indicating a maximum carrying capacity of 51 adults (34 females: 17 males).

5.4.2 Viability

PVAs revealed that with no interventions, the MFWS population would have a 50.5% probability of persistence over the next 50 years (Figure 5.3). This probability fell to 0% when >6 juveniles were harvested from the population annually, but rose to 100% if the population was supplemented with at least one mother annually (carrying ≤6 young, effectively $n = 7$). Further, four juveniles could be sustainably (100% probability of persistence) harvested from the population annually as long as one mother (effectively $n = 7$) was also supplemented into the population annually. Finally, 54 juveniles could be sustainably harvested if ten mothers (effectively $n = 70$) were supplemented annually. The deterministic annual population growth

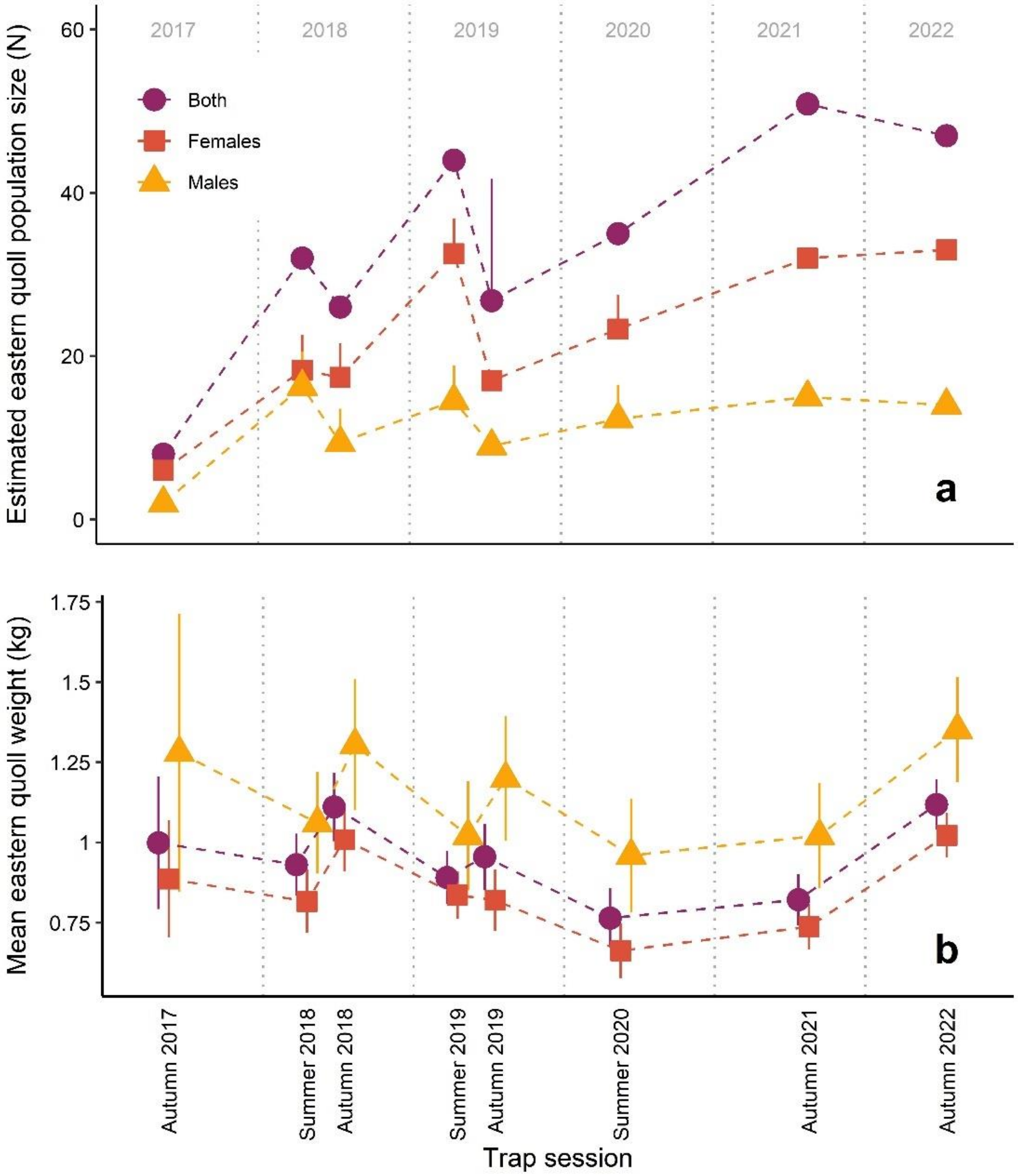

Figure 5.2 Estimated population size (**a**, N, ± 95% CI) and mean body weight (**b**, kg, ± 95% CI) based on eight capture-mark-recapture sessions for female, male, and all ('both') reintroduced eastern quolls (*Dasyurus viverrinus*) at Mulligans Flat Woodland Sanctuary, Australian Capital Territory. Mean body weights were calculated in R version 4.1.2 (R Core Team 2021), and population estimates were calculated using the *RMark* package (Laake 2013) to interface with the program MARK version 9.0 (White 2016).

rate (*r*) was 0.5063 across all scenarios, and probability of persistence was sensitive to carrying capacity (K) and the number of individuals supplemented and/or harvested.

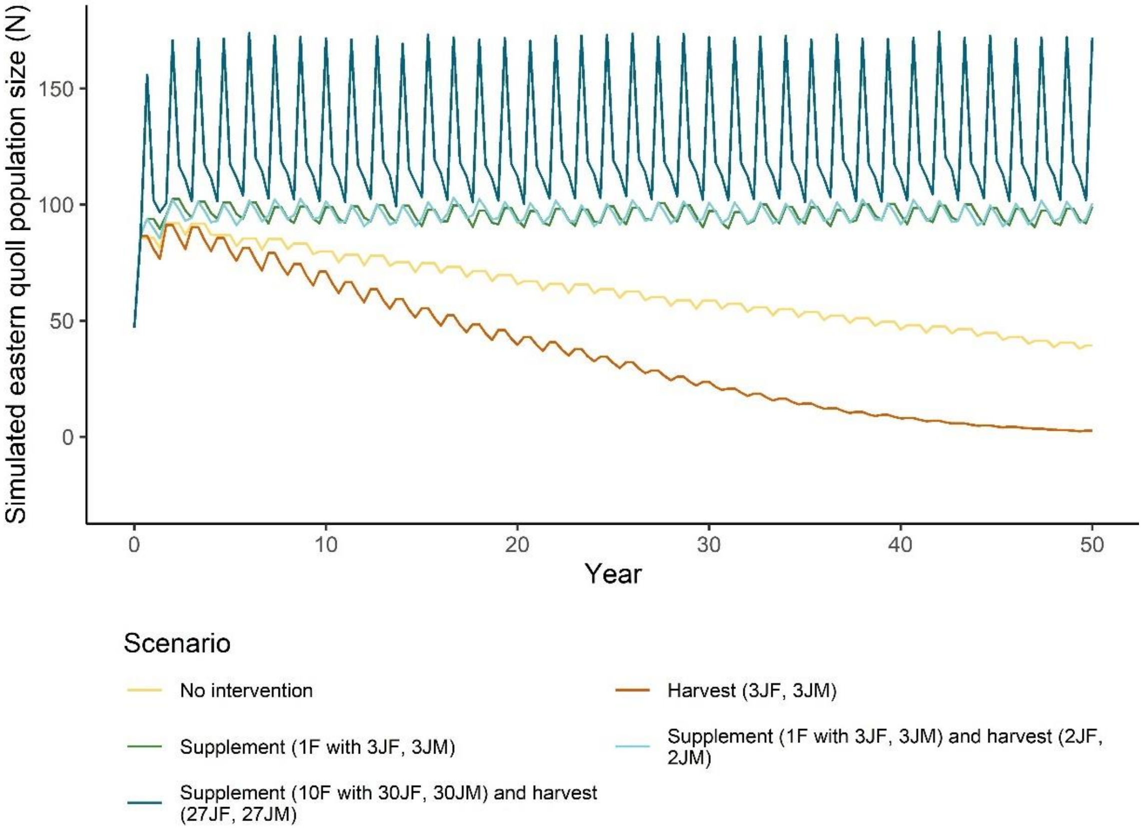

Figure 5.3 Simulated population size (N) for reintroduced eastern quolls (*Dasyurus viverrinus*) at Mulligans Flat Woodland Sanctuary, Australian Capital Territory. 'F' refers to the number of females, 'M' to males, and 'J' to juveniles. Scenarios were simulated using 1000 iterations over a 50-year time horizon with parameters in Table 5.2. Population viability analyses were conducted using Vortex 10.5.5 (Lacy & Pollak 2021) and post-simulation visualisation was generated using the package *vortexR* (Pacioni & Mayer 2017) in R version 4.1.2 (R Core Team 2021).

5.4.3 Recovery

The estimated eastern quoll population size in Tasmania was ~20,000 prior to its 52% decline (Fancourt *et al*. 2013). To avoid meeting the criteria for IUCN Red List 'Vulnerable' category, the current population of ~9,600 would need to be increased to 14,200 (i.e., a <30% decline from the original population size, Table 5.3). This provides us with a stretch goal of producing 4,600 eastern quolls, equivalent to 460 individuals per year for 10 years, to achieve species recovery. Since we can sustainably harvest the MFWS population of 54 individuals per year across its 4.85 km^2 area, this implies that to harvest 460 juveniles, an area of 41.31 km^2 would be needed (this area would need to have conditions comparable to MFWS, i.e., without invasive predators). Finally, a total of 437.45 km^2 (4,600 individuals / MFWS density [10.52 individuals

Table 5.3 Assessment and recommended actions to delist the eastern quoll (*Dasyurus viverrinus*) according to the International Union for the Conservation of Nature Red List Criteria (version 3.1) for the categories of ‘Critically endangered’, ‘Endangered’ (orange), ‘Vulnerable’, and ‘Near-threatened’ or ‘Least concern’ (green). Criteria that were achieved by an “any of” clause are indicated in yellow. * was based on Fancourt *et al*. (2013).

Category	Criteria	Critically endangered	Endangered	Vulnerable	Eastern quoll assessment	Recommended actions to improve assessment
Population reduction	A2) Population reduction observed, estimated, inferred, or suspected in the past where the causes of reduction may not have ceased or may not be understood or may not be reversible.	≥80%	≥50%	≥30%	52%*	Produce ≥4,600 eastern quolls to raise the total number from 9,600 (after 52% decline from 20,000 estimate in Tasmania, Fancourt *et al* 2013) to the 14,200 required to avoid meeting the ‘Vulnerable’ criteria (≥30% decline).
Geographic range	B1) Extent of occurrence (EOO)	<100 km^2	<5,000 km^2	<20 000 km^2	47,000 km^2	
	B2) Area of occupancy (AOO) and at least 2 of the 3 following conditions:	<10 km^2	<500 km^2	<2,000 km^2	2,320 km^2	
	(a) Severely fragmented or number of locations	1	≤5	≤10	2	Assess current reintroduction locations on mainland Australia for inclusion, or establish ≥9 new locations.
	(b) Continuing decline observed, estimated, inferred, or projected in any of:					
	(i) Extent of occurrence	Any of	Any of	Any of	Yes	Reverse decline in Tasmania, and/or offset with ≥ extent of occurrence in new locations.
	(ii) Area of occupancy	“ ”	“ ”	“ ”	Yes	Reverse decline in Tasmania and/or offset with ≥ area of occupancy in new locations.
	(iii) Area, extent and/or quality of habitat	“ ”	“ ”	“ ”	No	
	(iv) Number of locations	“ ”	“ ”	“ ”	No	
	(iv) Number of mature individuals	“ ”	“ ”	“ ”	Yes	See recommended actions for criteria A2.
	(c) Extreme fluctuations in any of:					
	(i) Extent of occurrence	Any of	Any of	Any of	No	
	(ii) Area of occupancy	“ ”	“ ”	“ ”	No	
	(iii) Number of locations or subpopulations	“ ”	“ ”	“ ”	No	
	(iv) Number of mature individuals	“ ”	“ ”	“ ”	No	

per km^2]) would be required to sustain these individuals beyond 10 years (i.e., 90 sanctuaries similar to MFWS, not accounting for edge effects).

In addition, eastern quolls need to occur in >10 'locations' (geographically or ecologically distinct areas in which a single threatening event can rapidly affect all individuals of the taxon present, IUCN 2001) to avoid meeting the criteria for the IUCN Red List 'Vulnerable' category (Table 5.3). We interpreted a 'single threatening event' as being spatially and temporally explicit (e.g., flood, drought, predation) as opposed to a threatening process which is spatially and temporally dynamic (e.g., disease, climate change). Burbidge & Woinarski (2016) indicated there were two locations: Tasmania and Bruny Island. We suggest that MFWS and Mt Rothwell should also be considered locations because they support self-sustaining, density-dependent, and geographically distinct populations since their reintroductions in 2016 and 2003, respectively. Thus, an additional seven locations with similar levels of invasive predator mitigation will be required. Finally, while not quantified, Burbidge & Woinarski (2016) reported a decline in the eastern quoll's extent of occurrence (EOO) and area of occupancy (AOO). These criteria could be addressed by increasing the number of eastern quoll locations on mainland Australia.

5.5 Discussion

We have demonstrated how incorporating a reintroduced population's demographic parameters into PVAs to determine the viability of harvesting a 'doomed surplus' can contribute measurably to species recovery. We also highlighted how back-casting can reveal the pathway to removing an endangered species from the IUCN Red List within 10 years (i.e., by reversing population declines and increasing the number of locations). While our targets may appear daunting, a stretch goal, by definition, must be ambitious enough to inspire the creativity and innovation to achieve long-term outcomes that currently seem impossible (Manning *et al.* 2006). Progress toward large-scale conservation and restoration requires such innovation to prevent the 'locking-in' of the current shifted baseline (Evans *et al.* 2022b).

5.5.1 Demography

The reintroduced eastern quoll population at MFWS grew rapidly in the absence of invasive predators, despite a limited number of founders (n = 44). After autumn 2017, the population oscillated between maximums in summer and minimums in autumn for the next 3 years (Figure 5.2a), depicting a transition from the establishment phase (2017) to the growth phase (2018–2019), and finally, to the regulation phase (2020–2022, *sensu* Sarrazin & Barbault 1996). The combination of a rapid life history (2–3 year lifespan), high reproductive success (100% female breeding, Godsell 1983), and high fertility (≤6 progeny per year) created an ideal scenario for producing an insurance population on mainland Australia.

Mean body weights oscillated between maximums in autumn and minimums in winter (Figure 5.2b) and had a significantly negative association with population estimates ($p = 0.034$). This indicates density-dependence, a fundamental objective of any reintroduction, and mechanistically could have resulted from conspecific competition for prey or territory (e.g., dens). Interestingly, the autumn 2021 and 2022 sessions deviated from the oscillating trends in both population estimates and mean body weights. Australia suffered long-term rainfall deficiencies between 2017 and 2020, with conditions easing in March 2021 (Bureau of Meteorology 2022). The severe climatic conditions likely affected available prey for eastern quolls (similarly observed in Tasmania by Fancourt *et al*. 2018), thereby limiting the carrying capacity of MFWS in these years. In the 2021 session the population estimates reached a new maximum (N = 51), but mean body weights were lower (0.82 kg ± 0.04) than in previous autumn sessions (mean 1.033 kg ± 0.11). This suggests that as population size increased, resources (e.g., prey items) may have become limited, resulting in lower body weights.

Interestingly, mean apparent survival was similar for females (91% ± 6) and males (89% ± 6) at MFWS, whereas historical survival rates in Tasmania differed between the sexes (females 63%, males 25%, Godsell 1983). Sex ratios were relatively balanced until summer 2018 (1.12 females: 1 male), after which it became heavily skewed toward females (2.24 females: 1 male in summer 2019). Our population estimates indicate a maximum carrying capacity of 34 females, each with longer lifespans (2–3 years) than males (1–2 years). While females have smaller and overlapping home ranges (Wilson *et al.* 2020), there may not be enough territory to support all the juveniles produced by these females (34 females produce ≤204 young per year, Godsell 1983); explaining high adult survival but low recruitment. There is no evidence to suggest eastern quolls reduce their fecundity with density-dependence (unlike reintroduced eastern bettongs, Manning *et al*. 2019). Rather, if favourable environmental conditions increased the carrying capacity of MFWS, territory could become limiting by lowering the fecundity of females that cannot secure natal territory (as observed in bobcats, Knick 1990).

Estimated recruitment was low but consistent (females 7% ± 5, males 7% ± 7), suggesting that outcompeted individuals either died in the Sanctuary or emigrated over the fence into the surrounding landscape (note that we estimated apparent, rather than true, survival because we could not distinguish mortality from emigration, Williams *et al*. 2002). Such overdispersal is a problem in reintroductions, where individuals disperse away from the reintroduction site and do not contribute to population establishment (Richards & Short 2003). Serendipitously, some of these migrants have colonised the adjoining Goorooyarroo Nature Reserve which now also has an invasive predator-proof fence (S. Stratford *pers comms*), thereby founding a new population (the MFWS fence only allows one-way passage to Goorooyarroo). Additionally, this spill-over or halo effect (Tanentzap & Lloyd 2017) could be used to colonise the landscape ‘beyond-the-fence' if invasive predators can be maintained below the tolerance levels of eastern quolls (*sensu* Evans *et al*. 2021).

It has been suggested that a population must contain at least 1000 individuals to maintain "*adequate adaptive potential … in the face of environmental change*" (Willi *et al*. 2006; Weeks *et al*. 2011). Due to its limited size this target is not feasible for MFWS, but reinforcement translocations using the one-migrant-per-generation method (Mills & Allendorf 1996) could negate the effects of small population size (i.e., inbreeding depression, Weeks *et al*. 2011). It is encouraging that 100% probability of persistence was achieved by supplementing with one new mother annually, highlighting the need to increase gene flow between isolated populations. As such, we recommend that MFWS and other reintroduction locations be treated as a meta-population; translocating individuals between them to promote *in situ* genetic diversity (Weeks *et al*. 2011; Frankham 2015).

5.5.2 Viability

Despite reaching the regulation phase, the MFWS eastern quoll population is inherently small and vulnerable to demographic stochasticity (Caughley 1994), and self-sustainability does not necessarily translate to long-term persistence (Seddon 1999). There is a 50.5% likelihood of persistence over the next 50 years (Figure 5.3), emphasising the importance of ongoing management interventions. Annual supplementation of one mother could stabilise the population over 50 years, though we note two assumptions: ecological conditions will remain similar to the most recent monitoring sessions (autumn 2021 and 2022), and the population will maintain similar vital rates. Though we assumed high juvenile mortality (females 64.17% ± 19.92, males 64.93% ± 19.87, based on Godsell 1983), similar studies have demonstrated how increases in juvenile mortality can trigger comprehensive mortality and recruitment failure (e.g., in northern quolls *Dasyurus hallucatus*, Cremona *et al*. 2017, and African lions *Panthera leo*, Barthold *et al*. 2016). For example, after persisting for two decades, reintroduced Arabian oryx (*Oryx leucoryx*) suffered a poaching epidemic which rendered the population non-viable (Stanley Price 1989). While we present more than the minimum 5 years of vital rates required to identify temporal parameters driving variation (Gelman & Hill 2006; Parlato *et al.* 2021), each additional year of monitoring will improve our inferences; highlighting the value of long-term datasets informing long-term goals.

5.5.3 Recovery

We explored how our program could contribute measurably to eastern quoll species recovery. For the species to be delisted, we need to produce ≥4,600 eastern quolls to raise the total number from 9,600 (after 52% decline from 20,000 estimate in Tasmania, Fancourt *et al*.

2013) to the 14,200 (≤71% of 20,000 estimate) required to avoid meeting the IUCN Red List criteria for the 'Vulnerable' category (i.e., ≥30% decline). In addition, the eastern quoll must occur in >10 locations (geographically or ecologically distinct areas in which a single threatening event can rapidly affect all individuals of the taxon present, IUCN 2001). While there are currently two recognised locations (Tasmania and Bruny Island, Burbidge & Woinarski 2016), based on the definition for 'location' we suggest that MFWS and Mt Rothwell should also be recognised. Further, we posit that Tasmania (2,320 km^2 occupancy area) may represent more than one location, since significant genetic structure with consistent regional differentiation related to geographic distance has been found between populations (Cardoso *et al.* 2014). This geographical and/or behavioural separation suggests a single threatening event is unlikely to endanger all eastern quolls in Tasmania.

To achieve a stretch goal of species recovery within 10 years, a 41 km^2 harvest area with conditions comparable to MFWS (i.e., without invasive predators) will need to be harvested of 460 individuals annually, and a 437 km^2 occupancy area would be required to sustain these individuals beyond 10 years (i.e., 90 sanctuaries similar to MFWS, not accounting for edge effects). Due to the inherent difficulty in securing large areas for species recovery, we see these ambitious targets as a call to create a coordinated and collaborative sanctuary network where the eastern quoll, and other species, can be managed as a meta-population across multiple sites (e.g., South Eastern Australia Sanctuary Operations Network or 'SEASON', Sharp 2021). In such a network, decisions regarding management interventions should be based on robust monitoring of the populations' demographics and genetic composition. Such a network would buffer against the demographic and genetic perils facing isolated populations, and limit edge effects associated with small occupancy areas (McGregor *et al.* 2020). To identify appropriate areas for future sanctuaries, we recommend incorporating eastern quoll occurrence data from established mainland populations, such as MFWS, into broad-scale habitat modelling across the species' former range (e.g., maximum entropy species distribution modelling).

While fenced sanctuaries have produced insurance populations of 38 species that are susceptible to invasive predators, they are limited in area and capacity to expand, and maintaining them comes at a cost (Ringma *et al*. 2017; Legge *et al*. 2018). Reintroducing species 'beyond-the-fence' where invasive predators are actively managed (and adaptively calibrated) to remain below species' tolerance levels (*sensu* Evans *et al*. 2021) is the next frontier to establish viable, self-sustaining populations and return ecological functions to our increasingly defaunated landscape (James & Eldridge 2007). Maintaining such a 'Goldilocks zone' of tolerance (the 'just right' predation level needed to drive selection for predator-resistant traits, Evans *et al*. 2021) in the area surrounding a conservation-fenced sanctuary could deliver a great return on investment by protecting migrants from the sanctuary and aid in their establishment 'beyond-the-fence' (i.e., spill-over or halo effect, Tanentzap & Lloyd 2017). Finally, to prevent the "locking-in" of the current shifted baseline (where native species vulnerable to invasive predators are accepted as permanently absent from the wild), we must explore innovative solutions to drive or enable adaptive evolution of threatened species and invasive predators alike (i.e., ‘coexistence conservation’, Evans *et al*. 2022).

5.6 Conclusions

Here we demonstrated how demographic parameters from a reintroduced population can inform management interventions and create targets for delisting an endangered species. We also highlighted the value of conducting ecological experiments within fenced sanctuaries. If treated as ‘outdoor laboratories’, they provide unique opportunities to measure vital rates in free-ranging, endangered species when it would otherwise be difficult or impossible (Hester *et al.* 2000; Manning *et al.* 2009). Ironically, these populations may be better understood than the extant populations (e.g., there are no equivalent robust eastern quoll population estimates for Tasmania, Burbidge & Woinarski 2016) for which knowledge of their population dynamics would greatly assist conservation efforts (Ashbrook *et al.* 2016). The current extinction crisis demands that managers use evidence and collaboration to orient decisions and contribute lasting progress towards species recovery.

5.7 Acknowledgements

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Illustration by Cat Cotsell

Chapter 6: Translocation Continuum Framework

"*At first people refuse to believe that a strange new thing can be done. Then they begin to hope it can be done. They see it can be done. Then it is done and all the world wonders why it was not done centuries ago.*" - Francis Hodgson Burnett, The Secret Garden

Translocations are a key tool for reversing biodiversity loss while addressing our shifting baseline syndrome. However, translocations can often suffer from unreasonably high expectations, leading many programs to be brief and cut short before achieving their potential. While guidance has been developed to aid in translocation decision making, there is currently no framework which (1) classifies translocation types in the context of the establishment, growth, and regulation phases, 2) accounts for the uncertainty involved in these phases, and (3) integrates existing guidance on designing strategies, tactics, and evaluation measures.

In this penultimate Chapter 6, I present the 'Translocation Continuum Framework'. This practical planning tool provides clarity around translocation 'phases', their criteria, strategies, tactics, evaluation measures, and expected outcomes. I discussed the limitations of 'success' and 'failure' labels in translocation science, and the importance of parsimonious decision making that balances research and conservation objectives to maximise learning with the least amount of loss. Only by avoiding "short-termism" and managing expectations throughout a program's lifetime can we galvanise trust and investment in translocations so they can contribute meaningfully to long-term restoration.

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Illustration by Cat Cotsell

The Translocation Continuum Framework for context-specific decision-making

Wilson B A, Evans M J, Gordon I J, & Manning A D,
in review at *Frontiers in Ecology and the Environment*.

6.1 Abstract

Translocations are a key tool for reversing biodiversity loss, but often suffer from unreasonably high expectations, leading to many programs being brief and terminated before achieving their full potential. To address these issues, we present the 'Translocation Continuum Framework', an easy-to-use approach which provides clarity around the criteria, strategies, tactics, evaluation measures, and expected outcomes for five key translocation 'phases': Feasibility Studies, Pilot Studies, Primary Trials, Secondary Experiments, and Tertiary Reinforcements. By accounting for uncertainty, the Framework aims to empower practitioners to build translocation programs that suit their specific context. We also discuss the limitations of 'success' and 'failure' labels in translocations, and the importance of parsimonious decision making to maximise learning with the least amount of loss. Only by managing expectations of the likelihood of establishment, growth, and regulation throughout a program's lifetime can we galvanise trust and investment in translocations so they can contribute meaningfully to long-term restoration.

6.2 Translocation science

In response to continuing biodiversity loss, conservation practitioners are increasingly implementing translocations (Seddon 2010). Translocations aim to restore a species to an area after its extirpation (reintroduction), build up existing populations (reinforcement), replace extinct species (ecological replacement), or establish populations beyond the species' indigenous range (assisted colonisation, Seddon 2010). Despite their popularity, translocations have suffered low levels of 'success', often attributed to "poor decision making" (Fischer & Lindenmayer 2000). Another contributing factor may be unreasonably high expectations over short timeframes (for instance, establishing a self-sustaining population from a single translocation). Indeed, translocation programs designed with these expectations can be too brief, often leading them to be terminated before they have reached their full potential (e.g., 79% of 'failed' translocations had a duration of <2 years, Morris *et al*. 2021).

The field of 'translocation science' endeavours to address these issues by increasing our understanding of the ecological processes that influence translocation outcomes (Sarrazin & Barbault 1996). Translocation science has grown prolifically (and unevenly, Evans *et al*. 2022a, 2023) over the last 40 years, leading to the development of several tools to aid in decision making, including how to prioritise de-extinction candidates (Seddon *et al*. 2014b), design translocation tactics (Batson *et al.* 2015), and selecting release sites (Chock *et al.* 2022). Notably, the International Union for Conservation of Nature (IUCN) developed guidelines for reintroductions and other conservation translocations (henceforth 'Guidelines'), which detail considerations for program feasibility, planning, risk assessment, implementation, monitoring, and dissemination (IUCN 1998, 2013). Armstrong & Seddon (2008) extended these Guidelines by proposing key questions to be addressed at the population, metapopulation, and ecosystem levels before proceeding with a translocation. Further, Sarrazin (2007) proposed that a successful translocation enables a population's survival and transition through **establishment**, **growth**, and **regulation phases**, each with unique challenges that require tailored management actions. Despite the increasing recognition that populations undergo genetic, demographic, and behavioural shifts throughout these translocation phases, there is currently no framework which classifies translocations within this context, accounts for the continuum **uncertainty** presents, and integrates existing guidance on selection of **strategies**, **tactics**, and **evaluation measures**.

Here we present the '**Translocation Continuum Framework**', which proposes strategies, tactics, and evaluation measures that account for uncertainty across five iterative translocation **phases**: **Feasibility Studies**, **Pilot Studies**, **Primary Trials**, **Secondary Experiments**, and **Tertiary Reinforcements**. The Framework aims to balance conservation and research objectives, and highlights the need to be both proactive in anticipating and mitigating threats, and reactive within an **adaptive management** framework.

6.3 Glossary

The field of translocation science struggles with inconsistent use of terminology (Armstrong & Seddon 2008). This inconsistency can lead to two types of assumptions: (1) that two different terms are the same because they have the same name ('jingle fallacy', Thorndike 1904) and (2) that two similar terms are different because they have different names ('jangle fallacy', Kelley 1927). Thankfully, overarching definitions related to population restoration (i.e., reintroduction, reinforcement) and conservation introductions (i.e., ecological replacement, assisted colonisation, community construction) have been adequately addressed (Seddon 2010; and with responses from Jørgensen [2011] and Dalrymple & Moehrenschlager [2013]). However, there has been limited discourse relating to terminology within a translocation **program** (e.g., releases, pilots, trials).

Acknowledging that redefining and introducing terms has the potential to hamper communication (Seddon 2010), we believe some terms in translocation science will be helpful in providing more clarity to prevent the ‘jingle-jangle fallacy’ and provide a standard framework for disseminating approaches, processes, and outcomes (see Table 6.1). We have indicated terms that are defined in the Glossary with bold text throughout this article.

Table 6.1 Terms and definitions relevant to the Translocation Continuum Framework for context-specific, and to the field of translocation science more broadly. Bold text indicates terms defined in the glossary.

Term	**Definition**
Adaptive management	A systematic approach for improving management actions by learning from outcomes (‘learning by doing’, Walters & Holling 1990).
Criteria	Standard or **phase** which must be met before a **program** can progress from a higher to a lower **uncertainty** translocation phase.
Descendent	A descendent of a **founder** (or **reinforcer**).
Founder	Relating to translocation **program**; a translocated individual has “no known genetic relationship to any other animal in the pedigree except for its own descendants: wild-caught animals, animals introduced to the pedigreed population from other captive sources for which no information on parentage is available, and other animals with unknown parents” (Lacy 1989).
Evaluation measure	Also known as measure of success; to be monitored and reviewed to determine whether (1) a translocated population has reached the establishment, growth, or regulation phases, and (2) a **program** has met the criteria to enter the next translocation phase. Evaluation measures should be selected to answer a priori questions (Armstrong & Seddon 2008), but are context-specific, depending on the **Translocation Continuum** phase. Further, evaluation measures may need to be adjusted in light of new knowledge emerging as a program progresses. Examples include survival, dispersal, health, reproduction, recruitment, behavioural and genetic diversity, and ecosystem effects.
Parsimony	A decision-making approach where the practitioner balances the outcomes of multiple objectives to maximise learning with the least amount of loss (e.g., of **founders**).
Phases	Five iterative steps through which a translocation **program** can progress, from high to low uncertainty: **Feasibility Studies**, **Pilot Studies**, **Primary Trials**, **Secondary Experiments**, **Tertiary Reinforcements**. Note that a program might not progress linearly through these phases and may need to repeat or regress to a previous phase if a new source of **uncertainty** is revealed.
Feasibility Study	**Phase** 1 under the **Translocation Continuum Framework**; translocation planning intended to promote post-release performance using best available knowledge, where the primary **strategies** are

		identifying and designing **tactics**, and developing an **adaptive management** framework. This phase is evaluated using understanding of biological and ecological factors, opportunities and constraints, and a robust translocation plan including management scenarios (IUCN 2013).
	Pilot Study	**Phase** 2 under the **Translocation Continuum Framework**; limited release into an area with no conspecifics, to test the feasibility of a **program** within a defined period, where the primary **strategies** are stress-testing the **adaptive management** framework (developed during Feasibility Studies) and maximising learning. This phase is evaluated by survival, dispersal, and health of **founders**.
	Primary Trial	**Phase** 3 under the **Translocation Continuum Framework**; parsimonious release intended to establish a population, where the primary **strategies** are managing short-term survival and maximising learning. This phase is evaluated by survival, dispersal, health, reproduction, and recruitment. Such trials are usually unreplicated and uncontrolled, and used to generate hypotheses relating to persistence through correlation and inductive reasoning (Kemp *et al.* 2015). This phase is synonymous with the establishment phase (where post-release effects drive population dynamics, Sarrazin 2007).
	Secondary Experiment	**Phase** 4 under the **Translocation Continuum Framework**; parsimonious release intended to promote population growth with an opportunity for experimental replication and control, where the primary **strategies** are medium-term growth, and maximising learning across multiple **tactics**. This phase is evaluated by survival, dispersal, health, reproduction, recruitment, behavioural and genetic diversity, and ecosystem effects. This phase is synonymous with the growth phase (high rates of expansion and continuing until the population approaches carrying capacity, Sarrazin 2007).
	Tertiary Reinforcement	**Phase** 5 under the **Translocation Continuum Framework**; appropriate release to reinforce population demographic, behavioural, and/or genetic diversity, where the primary **strategies** are ensuring long-term viability, and maximising learning across multiple **tactics**. This phase is evaluated by survival, dispersal, health, reproduction, recruitment, behavioural and genetic diversity, and ecosystem effects. This phase is synonymous with the regulation phase (where density-dependence limits survival and recruitment, Sarrazin 2007).
Program		A translocation project that aims to establish a population of a target species in an area. Depending on the amount of **uncertainty** involved, a program can begin with a **Feasibility Study** and, if appropriate, progress through the iterative translocation **phases**.
Reinforcer		Relating to translocation programs; a type of **founder** that has been translocated to an area with established conspecifics in a subsequent release of a translocation program with the aim of reinforcing demographic, behavioural, and genetic diversity in a population.

Resident	**Founders** (and **reinforcers**), their **descendants**, and existing individuals that are established at the recipient site (i.e., are no longer subject to post-release effects).
Risk	Applies to situations where an outcome is unknown, but its probabilities can be quantified (Knight 1921).
Strategy	Clearly defined objective (e.g., minimising dispersal) to be met during a translocation **phase**. Strategies guide **tactics** selection, maximise the probability of positive outcomes, and maintain the **program** efficiency and feasibility (Batson *et al.* 2015).
Tactic	Animal- or environment-focussed technique capable of influencing post-release performance or population persistence (Batson *et al.* 2015).
Translocation Continuum Framework	Multi-phased framework which guides the decision-maker through five iterative **phases** along a continuum of **uncertainty**, while being grounded in the context of the three translocation phases (Sarrazin 2007). The framework was designed for tetrapod translocations, but can be adapted for other taxa.
Uncertainty	Applies to situations where an outcome is unknown, and its probabilities cannot be quantified (i.e., Knightian uncertainty, Knight 1921).

6.4 The Translocation Continuum Framework

The Translocation Continuum Framework guides decision-makers along a continuum of uncertainty, through five iterative phases: Feasibility Studies, Pilot Studies, Primary Trials, Secondary Experiments, and Tertiary Reinforcements (Figure 1). The Framework is based on decision theory, grounded in the context of the three demographic phases of a translocated population (i.e., establishment, growth, and regulation, Sarrazin 2007), while balancing conservation and research objectives. We note that the Framework is not intended to be restrictive, but to clarify key considerations so that practitioners can build a translocation program that suits their context. While the Framework was designed with animal, and more specifically tetrapod, translocations in mind, we believe this iterative and contextual approach can be adapted for other taxa.

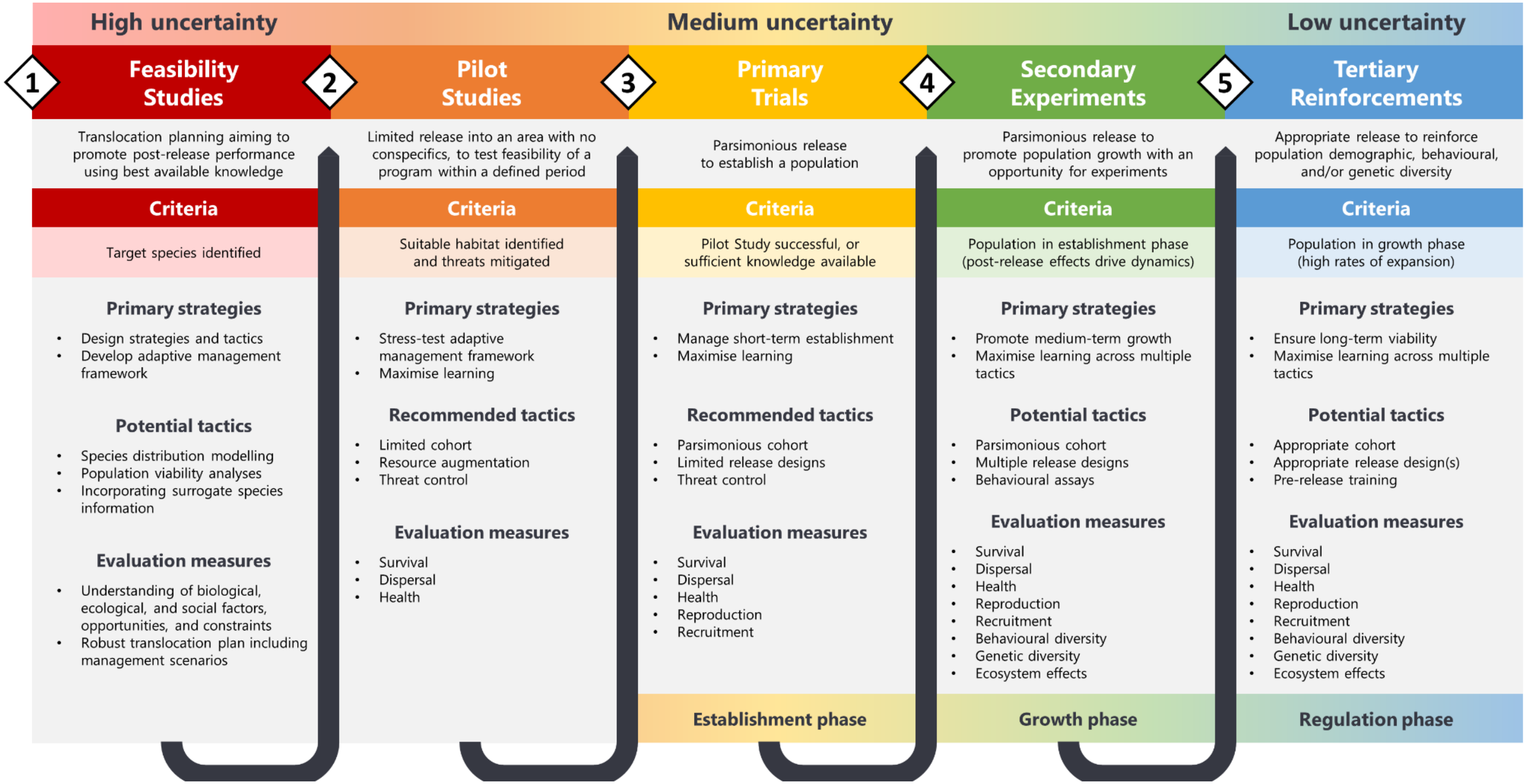

Figure 6.1 The Translocation Continuum Framework, which contextualises decision making along a continuum of uncertainty. It includes five iterative translocation phases, and outlines suggested strategies, tactics (techniques capable of influencing post-release performance or population persistence, Batson *et al*. 2015), and evaluation measures to be monitored and reviewed to determine whether a program meets the criteria to progress to the next phase. The latter three phases are embedded in the translocated population's progression through the establishment, growth, and regulation phases (Sarrazin 2007).

6.4.1 Phase 1 Feasibility Studies

Feasibility Studies involve translocation planning using the best available knowledge to the maximise post-release performance of individuals and populations. Key considerations for Feasibility Studies are outlined in the IUCN 2013 Guidelines (i.e., biological and social feasibility, regulatory compliance, and resource availability, IUCN 2013), and we recommend the two additional primary strategies.

Firstly, all available and relevant tactics should be considered in Feasibility Studies, and a useful tool to guide this process is the Translocation Tactics Classification System (Batson *et al.* 2015). This system offers a standardised process for identifying, selecting, designing, and reviewing animal- and environment-focussed tactics to improve and communicate outcomes. For example, animal selection tactics should consider the genetic, demographic, behavioural, experiential, health, and physiological background of available source individuals (e.g., Wilson *et al*. 2020). Secondly, an adaptive management framework should be explicitly incorporated into a robust translocation plan, where relevant biological and ecological factors, opportunities, constraints, and management scenarios are detailed. For example, monitoring must be feasible so that practitioners can detect (e.g., Moseby *et al*. 2018) and manage (e.g., Butler *et al*. 2019) negative translocation outcomes.

Feasibility Studies should, where possible, include genetic studies to reveal prior gene flow, effective population sizes, and inbreeding severity (Segelbacher *et al.* 2021). In addition, where sufficient data exist (including that of a relevant surrogate, Caro & O'Doherty 1999), computational modelling can provide crucial insights into program feasibility. Such approaches include species distribution modelling to predict habitat suitability at the recipient site (Osborne & Seddon 2012), population viability analyses (ideally integrating genetic measures, e.g., Seaborn & Goldberg 2020) to simulate population trajectories under different management scenarios (at both source and recipient sites, Clark *et al*. 1991), and modelling approaches to predict translocation outcomes (Parlato & Armstrong 2018). Further, knowledge gained from later phases can be used to improve these models iteratively (e.g., evaluating genomic variation to confirm interbreeding between reinforcers from multiple sources, Capel *et al*. 2022) and inform future decisions through adaptive management.

6.4.2 Phase 2 Pilot Studies

For a particular taxon, if (a) no residents exist at the recipient site, b) no translocations have been attempted at the site, c) potentially suitable habitat has been identified (e.g., through a Feasibility Study), and (d) threats have been mitigated, a Pilot Study should be considered (Figure 1). Pilot Studies (i.e., initial translocations) involve releasing a limited cohort of **founders** into an area with no residents with the aim of testing program feasibility within a defined period. Pilot Studies face high **risk** and high **uncertainty**, and when working with threatened species, this risk is compounded by the limited number of individuals available to contribute to a program.

To address this, a Pilot Study's primary strategies should be to stress-test the adaptive management framework created in Feasibility Studies, and maximise learning. This phase will be particularly useful for confirming habitat suitability of the recipient site, and that the initial drivers of decline have been addressed. Given the considerable uncertainty involved in Pilot Studies, we recommend the following tactics: (a) only a limited cohort should be released, b) resource augmentation should be considered (e.g., supplementation of food or shelter), and (c) threat control should be intensive to avoid unnecessary loss of founders. The evaluation measures for Pilot Studies are focussed on short-term indicators of establishment, including founder survival, dispersal, and health. While establishment would be a positive outcome, it will often not be a reasonable expectation for this phase, given the considerable uncertainty present (e.g., Panel 6.1).

The benefits of conducting a Pilot Study before a Primary Trial are in testing modelled habitat suitability (Draper *et al.* 2019), revealing previously unknown threats (Kemp *et al.* 2015), and manipulating the social landscape (e.g., conspecific presence, calls, markings, or scats) which may increase the likelihood of establishment in later phases (e.g., Linklater & Swaisgood 2008).

6.4.3 Phase 3 Primary Trials

In the event that sufficient knowledge is available (e.g., habitat suitability has been confirmed), and/or a Pilot Study has achieved positive outcomes for founder survival, dispersal, and health, Primary Trials can be considered (Figure 1).

While some knowledge will have been gained through earlier stages, Primary Trials still involve considerable uncertainty. Threat control will continue to be crucial, especially if new threats were identified during Pilot Studies. Primary Trials must manage short-term survival while maximising learning. The cohort size (particularly for threatened species) must be **parsimonious** in balancing the risks that are necessary to generate the knowledge upon which subsequent phases can be built (Wilson *et al.* 2020; Evans *et al.* 2022b). As such, Primary Trials need not involve replicated and controlled experiments, but they can be used to generate hypotheses relating to persistence through correlation and inductive reasoning (Kemp *et al.* 2015).

Panel 6.1 Reintroduction of the brown treecreeper: did it fail?

Photograph of a brown treecreeper (*Climacteris picumnus*), by Belinda Wilson Nature Photography.

The first attempt to reintroduce the brown treecreeper (*Climacteris picumnus*) into Mulligans Flat Nature Reserve, Australian Capital Territory, was designed within an experimental framework to test the effect of different social groups (animal selection tactic) and habitat restoration treatments (environmental preconditioning tactic), including controls (Bennett *et al.* 2012). While the program met its *a priori* short-term criterion for success, it failed to meet its medium-term criterion: 40% adult birds surviving after 1-year post-release, and ≥1 surviving fledgling within 2 years. Throughout the program, several previously unknown threats were revealed: (1) translocation stress, 2) lack of habitat familiarity, 3) insufficient effectiveness of restoration treatments, and (4) cooperative harassment by other bird species.

Under the Translocation Continuum Framework, this program would be classified as a Secondary Experiment (since it involved multiple release designs), but with elements of a Pilot Study (since there were no conspecifics in the landscape, Figure 1). In retrospect (with the benefit of resulting learnings), considering the high uncertainty involved, if a follow up translocation were conducted today, it would benefit from being designed as a Pilot Study in the first instance. This would allow practitioners to develop their knowledge on habitat suitability at the recipient site, and explore the previously unknown threats revealed in the study and manipulation of the social landscape to encourage establishment in later phases.

Importantly, the primary strategies for a Pilot Study are to stress-test the adaptive management framework and maximise learning, and the evaluation measures are focussed on short-term indications of establishment. However, establishment itself is not an expected outcome given the considerable uncertainty involved. Were the reintroduction of the brown treecreeper to have been evaluated against the Pilot Study short-term measures of survival, dispersal, and health, it would have been considered a 'success' (i.e., it did not 'fail'). The resulting valuable knowledge can be used to adapt tactics for the next appropriate phase along the Translocation Continuum.

The evaluation measures for Primary Trials build upon the short-term measures for Pilot Studies (survival, dispersal, health) with the medium-term responses of reproduction and recruitment. Intensive monitoring of founders (e.g., sightings, captures, or tracking) must be conducted to detect and deal with negative responses until they plateau (e.g., Wilson *et al*. 2020). The knowledge gained throughout Primary Trials should be rapidly integrated into current management actions (i.e., adaptive management) and inform decision making for subsequent phases.

If the founders display positive responses to the translocation process at the Primary Trials phase, it is likely the population will have established (Sarrazin 2007), and Secondary Experiments can be considered. If the founders display ambiguous or negative responses, another Primary Trial could be undertaken to reduce uncertainty before progressing. The practitioner will need to balance the need to establish a population while maximising learning, and if uncertainty remains considerable (e.g., a new source of uncertainty was revealed) it would not be appropriate to progress to a Secondary Experiment.

6.4.4 Phase 4 Secondary Experiments

If (a) a translocated population has established (per Sarrazin 2007), b) a sufficient number of founders are available (preferably from multiple sources to maximise diversity, Frankham *et al*. 2019), and (c) knowledge from Primary Trials justify it, a Secondary Experiment can be considered (Figure 1). Since this phase requires that residents exist at the recipient site, any individuals released henceforth could be referred to as '**reinforcers**' (Table 6.1 glossary).

Since the knowledge gained from the Pilot Studies and/or Primary Trials will inform tactics for Secondary Experiments, this phase will be accompanied by moderate uncertainty. The primary strategy should be to promote medium-term growth and maximise learning across multiple tactics, so multiple release designs (i.e., treatment and control groups) involving enough replication to achieve scientific objectives (Festing & Altman 2002) can be considered. For example, practitioners may choose to conduct standardised behavioural assays on reinforcers as a method of pre-release screening to inform future tactics (e.g., Bremner-Harrison *et al*. 2004; Wilson *et al*. 2022). Knowledge from Secondary Experiments should be used to adapt tactics to maximise positive outcomes, even if this compromises experimental integrity. Continuing to implement tactics where there is evidence that it leads to sub-optimal outcomes would be unethical, deleterious for threatened species, and waste valuable resources (Wilson *et al.* 2020).

The evaluation measures for Secondary Experiments build upon short- and medium-term measures (i.e., survival, dispersal, health, reproduction, and recruitment) with the long-term responses of genetic and behavioural diversity and ecosystem effects. We note that genetic and behavioural diversity should be considered in tactic design (e.g., animal selection, animal preconditioning, Batson *et al*. 2015) across all five phases, though they may be best considered as evaluation measures once post-release effects are no longer driving population dynamics (i.e., growth and regulation phases, Sarrazin 2007). It is crucial that DNA samples be collected from a program's outset so that robust and generationally specific analyses can be conducted (Brockett *et al.* 2022).

Intensive monitoring of reinforcers should be conducted to detect and adapt to their responses. If the founders, reinforcers, and **residents** (established individuals) display positive responses to the translocation process, it is likely the population will have entered its growth phase (per Sarrazin 2007), and Tertiary Reinforcements can be considered. If the reinforcers display ambiguous or negative responses, another Primary Trial or Secondary Experiment can be considered to reduce uncertainty before progressing.

6.4.5 Phase 5 Tertiary Reinforcements

If (a) a translocated population has entered its growth phase (per Sarrazin 2007), b) sufficient numbers of individuals are available (preferably from new sources to maximise diversity), and (c) knowledge from prior phases justify it, a Tertiary Reinforcement could be considered (Figure 1).

Since tactics will have been optimised from the knowledge gained in previous phases, Tertiary Reinforcements will be associated with low uncertainty. The primary strategy should be to ensure long-term population viability and maximise learning (across multiple tactics if appropriate), so multiple release designs can be considered (keeping in mind that the population may be at, or approaching, carrying capacity). For example, practitioners may choose to conduct pre-release training to restore anti-predator responses (Greggor *et al.* 2019).

It is important to recognise that as a translocated population approaches carrying capacity, density-dependent mechanisms will limit survival and recruitment, which could affect the short-term responses of reinforcers (i.e., survival, dispersal, and health) released into this context. Thus, it continues to be important to adapt tactics to maximise positive outcomes throughout Tertiary Reinforcements, even if these actions compromise experimental integrity. Computational modelling will be useful here to compare the potential outcomes of multiple strategies.

The evaluation measures for Tertiary Experiments include short-, medium-, and long-term measures (i.e., survival, health, reproduction, recruitment, genetic and behavioural diversity, and ecosystem effects). Regular, though not necessarily intensive, monitoring of founders, reinforcers, and residents should be conducted to detect and respond to negative responses. If positive responses are observed, it is likely the population has entered its regulation phase (Sarrazin 2007).

6.4.6 Adapting the Translocation Continuum

We note that a program is unlikely to progress linearly through the Translocation Continuum, and may need to repeat or return to a previous phase if a new source of uncertainty is revealed. For example, if the primary strategy is to determine a site's habitat suitability (perhaps for a future reintroduction), but there are very few founders currently available, and therefore no expectations of establishing a population, the program should begin as a Feasibility Study, followed by a Pilot Study. For a reinforcement translocation, however, residents already exist at the recipient site in sympatry with their threats, and so the program could 'skip' the Pilot Study and Primary Trial phases and be designed as a Secondary Experiment (prioritising population growth) or a Tertiary Reinforcement (prioritising long-term viability). In all cases, a Feasibility Study is necessary to explore the available knowledge before conducting translocations (IUCN 2013).

6.4.7 Importance of monitoring

Monitoring is a fundamental part of any translocation program - it enables practitioners to evaluate their progress along the Translocation Continuum Framework while testing their hypotheses (Seddon *et al.* 2007; Armstrong & Seddon 2008; Berger-Tal & Saltz 2014). While we acknowledge the logistical and financial constraints facing practitioners, we argue that difficulties with, or deprioritisation of, monitoring will risk the entire endeavour (Berger-Tal *et al.* 2020). For instance, lack of fit-for-purpose monitoring may lead to a translocation being erroneously labelled as 'successful' (Fischer & Lindenmayer 2000, discussed below), thereby jeopardising continued support (Bubac *et al.* 2019). By providing clarity around evaluation measures and expected outcomes, the Framework justifies the need for fit-for-purpose, long-term monitoring to achieve a program's full potential.

6.4.8 What comes next?

While the Framework guides the practitioner through a program with the aim of its translocated population reaching the regulation phase, self-sustainability does not necessarily translate to long-term persistence (Seddon 1999). Practitioners should, at this point, prioritise sustainable, long-term monitoring to feed into their adaptive management framework for not only the target species, but the metapopulation and ecosystem it is now a part of (Taylor *et al.* 2017; Armstrong *et al.* 2022). Furthermore, the knowledge gained as part of continued monitoring can be used to iteratively update models to improve their accuracy and validity. For example, long-term monitoring can reveal issues such as overpopulation and associated ecosystem effects (e.g., Moseby *et al*. 2018).

6.5 The limitations of ‘success’ and ‘failure’

A major peril in translocation science is the lack of consistent criteria for defining and assessing ‘success’ and ‘failure’. For example, a translocation can be considered successful if it results in a self-sustaining population (Griffith *et al.* 1989), an unsupported wild population of ≥500 individuals (Olney *et al.* 1994), breeding by the first wild-born generation (Sarrazin & Barbault 1996), recruitment exceeding adult mortality over three years (Sarrazin & Barbault 1996), or an ecological community that will persist without active management (Seddon 1999). These criteria are limited in (a) their usefulness due to variation in life history traits between taxa, and (b) time (i.e., ‘success’ can only be determined at the time of assessment, Seddon 1999).

While labelling a translocation a ‘success’ or ‘failure’ may be useful for comparing programs on a broad scale, we argue that these labels (especially for single translocation phase) do not account for the continuum of uncertainty, how this should affect expectations, and the value of iterative learning, which is not equally distributed throughout a program. This language can be restrictive, and could reduce support for the program, thereby causing it to be terminated before reaching its potential. Lasting population restoration relies on participation by natural resource management agencies, land owners, scientists, citizen scientists, the local community, and other stakeholders. Careful consideration of how translocation outcomes are perceived is paramount for building and maintaining support (Watson & Watson 2015).

Since translocation programs are multi-phased, and often multi-year, endeavours, it is crucial to transparently communicate our expectations of uncertainty, risk, and outcomes, including the level of parsimony behind their designs. For instance, expecting ‘success’ in early translocation phases is unrealistic given the considerable uncertainty they involve, and this label should be avoided, or at least holstered, until later phases. The Translocation Continuum Framework (Figure 1) addresses this by clarifying aims and expected outcomes for each translocation phase. This multi-phased approach encourages a long-term vision (thereby avoiding ‘short-termism’, Evans *et al*. 2022b) where decisions made for each phase are iterative, adaptive, and explicitly account for uncertainty and the likelihood of establishment, growth, and regulation throughout a program’s lifetime.

6.6 Importance of parsimony

By their nature, translocations involve high uncertainty and risk. In response, current guidance has urged practitioners to consider inaction (i.e., hoping a species “might adapt naturally where it is or adjust its range without human intervention”) or alternative conservation solutions (e.g., habitat restoration, improving viability in extant populations, establishing protected areas, changing policy, public education, financial incentives, IUCN 2013). While these alternative solutions are valuable, they do not explicitly address uncertainty and can inadvertently ‘lock in’ a degraded ecological baseline (i.e., due to ‘shifting baseline syndrome’, Manning *et al*. 2006; Evans *et al*. 2022b). They also fail to recognise the value of translocations, including increasing biodiversity, fulfilling ecological roles, creating insurance populations, and building the public and political support needed to galvanise other actions such as species protection and habitat restoration (Seddon 1999).

Translocation practitioners face a plethora of decisions with competing interests, including the need to produce peer-reviewed publications to increase their chance of securing funding. Barriers to publishing in translocation science include limited resources (e.g., funding constraints), lack of ‘novelty’ (which ignores the value of fundamental and repeated studies), the “Gollum Effect” (possessiveness of species, study sites, and research topics by some scientists, Gould & Valdez 2022), and the required scientific rigour (e.g., sample size) needed to publish in many journals (Batson *et al.* 2015). As such, practitioners have been strongly encouraged to design translocations within experimental frameworks to test hypotheses (Armstrong *et al.* 1994; Seddon *et al.* 2007; Armstrong & Seddon 2008; Kemp *et al.* 2015) and control for the effects of genetics, demography, and source environment from the outset. However, threatened species translocation programs are inherently limited in their ability to source large sample sizes of individuals to use in experimental designs (Kemp *et al.* 2015). For example, the number of individuals exposed to habitat of uncertain suitability (e.g., in a Pilot Study) or a tactic of uncertain efficacy (e.g., in a Primary Trial) should be minimised, while balancing the need to develop the very knowledge that can put this uncertainty to rest (e.g., Wilson *et al*. 2020). We suggest that in early translocation phases, a minimum number of individuals should be exposed to a single or limited set of tactic designs to answer questions identified *a priori* (Armstrong & Seddon 2008). Only then can we address uncertainty, and build the knowledge upon which future phases can be launched.

Finally, despite the value of adaptive management in translocation programs (McCarthy *et al.* 2012), the need to maintain experimental integrity can cause a practitioner to hesitate in applying management interventions that could prevent negative outcomes (e.g., supplemental feeding). This hesitation could be especially deleterious in early translocation phases, where the establishing population is small and vulnerable. We recognise the conflicts practitioners face between doing good conservation science (adhering rigidly to experimental design) and doing good conservation (achieving species recovery with as few losses as possible). For the latter, we reinforce that there is immense value and pragmatism in applying adaptive management interventions throughout the Translocation Continuum Framework, as well as designing tactics iteratively through Pilot Studies and Primary Trials before progressing to Secondary Experiments and Tertiary Reinforcements (if appropriate).

6.7 Concluding remarks

The recipe for building and executing a translocation program will change throughout its lifetime, and can never be a ‘set and forget’ affair. Not only do the goal posts (expected outcomes) move over time, but the ground on which a program is built (context) is constantly shifting (revealing additional sources of uncertainty). However, we wish to highlight the opportunities afforded by acting in the face of uncertainty. It gives us the chance to expand our often short-term memory and reverse the shifted baseline where we accept species as being at low densities in, or permanently absent from, their indigenous ranges (Manning *et al.* 2006; Evans *et al.* 2022b).

Restoration presents a major challenge for the next century, and translocations remain a powerful way for humanity to reverse biodiversity loss while addressing the shifting baseline syndrome. Where there is uncertainty and imperfect knowledge, establishing a self-sustaining population in a single ‘leap’ is unlikely (Evans *et al.* 2022b). By promoting parsimony and clarifying phase-appropriate objectives and evaluation measures, the Translocation Continuum Framework offers a multi-phased approach that practitioners can use to guide their decisions to resolve uncertainty and make several ‘steps’ toward their conservation goals.

6.8 Acknowledgements

We acknowledge and respect the Ngunnawal and Ngambri peoples as the Traditional Custodians of the lands on which this thinking and writing was undertaken. This opinion article was written within the Coexistence Conservation Lab as part of the Mulligans Flat-Goorooyarroo Woodland Experiment and the Australian Research Council-funded Bringing Back Biodiversity project (LP140100209). We thank our collaborative partners, the ACT Government (Parks and Conservation Service and Conservation Research), Tasmanian Department of Primary Industries, Parks, Water and Environment (DPIPWE), Mt Rothwell Biodiversity Interpretation Centre, Odonata, and the Woodlands and Wetlands Trust for their support. We also thank Dr Catherine Ross, Brittany Brockett, and Shoshana Rapley for providing comments on an earlier draft of this manuscript.

Chapter 7: Synthesis

Conservation translocations, including reintroductions, offer immense value as tools to reverse biodiversity loss and restore ecosystem function (Armstrong & Seddon 2008). In this thesis, I explored reintroduction-related tactics, behaviour, movement, and species recovery using the model system of reintroduced eastern quolls at Mulligans Flat Woodland Sanctuary (MFWS) in the Australian Capital Territory. I harnessed the best available knowledge relating to the eastern quoll's biology and ecology to develop initial tactics, and then demonstrated an iterative and adaptive management approach that could be used by other practitioners to improve their translocation outcomes. Finally, I proposed a novel framework for designing translocation programs using the knowledge gained across this thesis.

In this Synthesis, I discuss the knowledge gained through the preparation of each Chapter, describe their contributions to translocation and conservation science, and propose avenues for future work that can build on this knowledge.

7.1 The importance of trialling tactics, adopting adaptive management, and considering context

In Chapter 2, I presented a real-world example where adapting tactics through an iterative series of trials improved reintroduction outcomes. For the reintroduction of the eastern quoll to MFWS, I found that founders that (a) were female, b) did not move between dens often, and (c) den-shared frequently with other founders had lower levels of post-release dispersal, and therefore, increased probability of survival (Wilson *et al.* 2020). Rather than viewing our reintroduction as an 'all or nothing' operation, we adapted our tactics iteratively over a series of trials and were able to demonstrate how adaptive management can substantially improve translocation outcomes. This approach is particularly important for threatened species reintroductions, where urgent decisions are often required despite the absence of complete knowledge (Seddon *et al.* 2007).

Since we needed to employ tactic changes concurrently throughout the reintroduction program to maintain our strategies (i.e., maximising survival and minimising dispersal), it was either difficult or impossible to separate the confounding effects of these concurrent tactics - some of which were deliberate, and others which were employed as part of an adaptive management framework (e.g., supplement feeding to offset weight losses in the second trial). This was further complicated by (a) small, but parsimonious, sample sizes, and (b) the presence of conspecifics for those founders released in the second and third trials, thereby reducing the inferences I could make about interactions between predictors of survival and dispersal.

It would be simple to encourage future researchers to test the effect of these tactics using larger sample sizes – indeed, practitioners are often encouraged to adopt experimental frameworks that allow clear testing of hypotheses (Seddon *et al.* 2007; Swaisgood 2010; Sheean *et al.* 2012) and control for the effect of demographics, genetics, and source environment (Jule *et al.* 2008). However, threatened species translocation programs are inherently limited in their ability to source large sample sizes of individuals to use in experimental designs (Kemp *et al.* 2015). The number of individuals exposed to habitat of uncertain suitability, or a tactic of uncertain efficacy, should be minimised, while balancing the need to develop the very knowledge that can put this uncertainty to rest. For this reason, only a small and parsimonious number of individuals (which will change depending on the level of uncertainty) should be exposed to a limited set of tactic designs to answer questions identified *a priori* (Armstrong & Seddon 2008) in early translocation phases - only then can we address uncertainty and build the knowledge upon which future phases can be launched. To aid in translocation planning, in the absence of experimental designs, I encourage practitioners to pre-emptively adopt tactics where they have shown success in the same, and related, species.

That being said, should a translocated population progress to its growth or regulation phases and sufficient uncertainty has been dispelled using the knowledge gained throughout earlier translocation phases, experiments can be incorporated into tactical designs (*sensu* Wilson *et al*. n.d.). For instance, the 'maternal translocation' tactic could be tested for its efficacy using captive-bred animals, where some have been paired and mated with, and others have not. Given the synchronicity of the eastern quoll's breeding system (Godsell 1983), it would be difficult to ensure balanced sample sizes with wild-to-wild translocations, since in the wild, most females will have had a chance to conceive by winter (the recommended temporal configuration tactic, Wilson *et al*. 2020).

Even as uncertainty surrounding strategies and tactics are addressed with the knowledge gained during early translocations (i.e., Pilot Studies and Primary Trials), a successfully translocated population will transition through the establishment, growth, and regulation phases (Sarrazin 2007) or may expand to new environments with a different suite of threats. Each new context will bring with it unique challenges that require tailored management actions. For example, while I found that effective survival and post-release dispersal did not differ between captive and wild founders, there may be inherent genetic differences, or performance differences which may only become apparent in the presence of threats which exist beyond-the-fence (e.g., invasive and native predators, human infrastructure and interactions). For this reason, practitioners should always test their results adaptively in other contexts to ensure local applicability.

7.2 The role of individual behaviour in reintroductions

In Chapter 3, I presented a rare, real-world example of how translocation practitioners can measure ecologically relevant and easily quantifiable behaviours that are likely to vary between individuals and predict post-release performance. I found that personality derived from time spent exposed or vigilant during the assays held significant associations with post-release den sharing and home range, while plasticity derived from latency (i.e., time delay) to reach food held a significant association with distance between consecutive dens (Wilson *et al.* 2022). As a result, I recommended that proactive and rigid founders be selected for initial releases (i.e., Pilot Studies or Primary Trials), and that reactive and plastic founders be used to reinforce the population in later translocations (e.g., Secondary Experiments and Tertiary Reinforcements, as per Chapter 6, Wilson *et al*. n.d.). I demonstrated that by integrating novelty, innovative behavioural assays offer substantial value as a conservation tool to improve reintroduction outcomes.

While I was able to detect significant relationships between the personality and plasticity of reintroduced eastern quolls and their post-release performance, our vigorous approach may not be feasible for every practitioner to replicate for their own programs. To reduce this effort, I recommend that (a) established captive-breeding programs and soft-releases be used as opportunities to conduct pre-release behavioural assays (Dingemanse *et al.* 2012; Baker *et al.* 2016) or anti-predator training to prioritise and prepare individuals for release (Moseby *et al*. 2016; Bannister *et al*. 2018a; Rowell *et al*. 2020), and (b) as highlighted in our study, easily quantifiable behaviours be associated with responses to perceived risk and novelty (e.g., latency to reach food and time spent vigilant) be prioritised for measurement, and (c) repeated behavioural assays be conducted to determine the plasticity of candidate founders, which can indicate how founders will learn and adapt post-release, and their likelihood of establishing.

It is important to acknowledge that certain personalities may be more advantageous in the establishment phase of a reintroduction, when compared to the growth or regulation phases (Sarrazin 2007). For instance, boldness has been linked to greater survival in novel environments, but also exposure to predators and issues with forming stable conspecific associations (Stamps & Swaisgood 2007). While one could recommend releasing a mix of personality types to overcome their inherent trade-offs (Watters & Meehan 2007; Fogarty *et al.* 2011), when dealing with threatened species practitioners should be parsimonious with the inherently limited number of founders available and use best available knowledge to inform translocation tactics (Batson *et al*. 2015, Chapter 6).

I acknowledge that our study took place in a conservation-fenced haven, a setting which provides valuable learning opportunities, but may not reflect the same relationships between personality and post-release performance that may exist 'beyond-the-fence' (*sensu* Evans *et al.* 2021), where founders can encounter invasive predators. In fact, advantageous behaviours in a haven may prove deleterious in the presence of these predators, and without this selective pressure, the population may lose predator-averse behaviours (refuge naïveté, Jolly *et al*. 2018). To avoid this, low and well-managed levels of predation could be used to drive selection for predator-awareness (the “Goldilocks zone’, Evans *et al*. 2021). Future studies could build on our work by assessing personality and plasticity and their relationships with post-release performance beyond-the-fence.

7.3 The role of movement and conspecific associations

In Chapter 4, I used GPS tracking to investigate how movement, habitat use and preference, and conspecific associations differed between eastern quoll residents (born and raised in the recipient environment) and reinforcers (translocated from the wild). I found reinforcers had significantly larger home ranges and greater overlap with other collared eastern quolls when compared to residents, significant preference toward grassland habitat across all animals, significantly more den sharing in residents as compared to reinforcers, and significantly lower movement correlation during the later part of the study period, and fawn-morph eastern quolls compared to dark-morphs. To further investigate the understudied, but potentially crucial role played by conspecific associations (e.g., den sharing) in post-release performance, practitioners should account for den sharing among all individuals (e.g., using observations from remote cameras outside of dens), rather than only other collared individuals.

Crucially, I revealed that reinforcer eastern quolls progressed along the post-release behavioural modification (PRBM) continuum over two weeks, suggesting an encouraging accumulation of knowledge and acclimatisation to the recipient environment (Berger-Tal & Saltz 2014). While I acknowledge the short-term nature of these results, they offer important insights into ideal habitat structure for future reintroductions and highlight the need for intensive post-release monitoring that inform adaptive management interventions to promote positive outcomes for both initial trials and later reinforcements.

This study features movement data at a greater spatio-temporal resolution than has ever been achieved for this species and is the first of its kind to have been conducted since the species’ extinction on mainland Australia. The insight provided by the eastern quolls’ preference for open grassland suggests they need a mosaic of recently disturbed (e.g., grasslands derived from agricultural clearing) and undisturbed (e.g., remnant woodlands) sites to thrive, and reinforces the need for reintroduction sites to contain suitable habitat from the outset. To expand our understanding of these habitat requirements further, I recommend incorporating eastern quoll occurrence (e.g., GPS) data from established populations, like MFWS, and ecologically relevant habitat attributes into species distribution models (e.g., maximum entropy modelling) to identify optimal future reintroduction sites across their former range. Since eastern quolls continue to decline in Tasmania (Cunningham *et al.* 2022), and other reintroduction efforts have been met with mixed outcomes (Hamer *et al.* 2022), the knowledge from this Chapter, and future work as recommended, will prove critical for informing future recovery efforts for this and other similar species.

7.4 How can reintroductions contribute to species recovery?

In Chapter 5, I investigated how demographic parameters from the reintroduced population of eastern quolls could reveal threats to their long-term persistence, inform thresholds for management interventions, and create targets for removing the species from the IUCN Red List. I found the population had a high apparent survival rate, but only a 50% probability of persistence over a 50-year time horizon without intervention, though this rose to 100% if the population was reinforced with at least one maternal female each year (Wilson *et al.* 2023). Further, I found that the population could be sustainably harvested of ≤54 juveniles if reinforced with ten maternal females annually, and by taking advantage of a rapid life history and harvesting the ‘doomed surplus’, I demonstrated how ‘back-casting’ can help managers can achieve their stretch goals for species recovery in the long term (Manning *et al.* 2006).

While I calculated and discussed how reintroductions into fenced havens could contribute measurably to species ‘recovery’, my thoughts on this pathway have evolved to include more nuance. While individuals harvested (ideally from the ‘doomed surplus’) from havens into natural refugia can contribute to species recovery, it could be detrimental to delist a species based on their haven populations alone. Fenced havens, while a crucial conservation tool, are inherently spatially constrained (thereby limiting founder numbers, their genetic diversity, and resilience to environmental stochasticity), can foster maladaptive traits (e.g., predator-naivete, Harrison *et al.* 2023; Moseby *et al.* 2023), are costly to maintain (Ringma *et al.* 2017; Legge *et al.* 2018), and can be rapidly breached by threatening processes (e.g., Short 2016), none of which are currently recognised by Australian legislation (i.e., Environment Protection and Biodiversity Conservation Act, Australian Government 1999). In contrast, natural refugia and the threatened species therein have been inherently protected by their behaviour, geography, and ecology, and shielded from vegetation clearing by their listings (Scheele *et al.* 2017).

In response to Woinarski *et al.* (2023) proposing that 12 Australian mammal species be delisted based in part on their reintroductions to havens, I recently coauthored a letter arguing that doing so would, under current Australian legislation, remove the very support that enables both haven and refugial populations to be maintained (Appendix VI, Read *et al.* 2023). Further, we proposed that threatened species classification requirements should be updated to recognise the particular context of populations within havens (e.g., ‘conservation dependent’) and the inherent resilience and importance of populations within natural refugia to give transparency to policymakers.

The next frontier to returning ecological functions to our increasingly defaunated landscape (James & Eldridge 2007) is reintroducing species to natural refugia and other potential habitat ‘beyond-the-fence’, where invasive predators are actively managed (and adaptively calibrated) to remain below species’ tolerance levels (*sensu* Evans *et al*. 2021). Maintaining this ‘Goldilocks zone’ of tolerance (the ‘just right’ predation level needed to drive selection for predator-resistant traits, Evans *et al*. 2021) in the area surrounding a haven could deliver a great return on investment by protecting migrants from the sanctuary and aid in their establishment ‘beyond-the-fence’ (i.e., spill-over or halo effect, Tanentzap & Lloyd 2017). Indeed, to prevent the “locking-in” of the current shifted baseline (where native species vulnerable to invasive predators are accepted as permanently absent from the wild), we must explore innovative solutions to drive or enable adaptive evolution of threatened species and invasive predators alike (i.e., ‘coexistence conservation’, Evans *et al*. 2022).

7.5 Translocation decision making in the face of uncertainty

Throughout my PhD research, I noticed that unclear translocation planning and infeasible (and sometimes unmanaged) expectations often led to programs to be cut short before achieving their potential. While existing guidance often treats a whole translocation program as a single ‘phase’, no available framework classified translocations within the context of a population’s transition through the establishment, growth, and regulation phases. I identified the need to explicitly account for the uncertainty that each of these phases presents when selecting translocation strategies, tactics, and evaluation measures.

To address this, in Chapter 6 I presented the novel ‘Translocation Continuum Framework’ which enables practitioners to circumvent the common pitfalls of translocation science by offering clarity around the criteria, strategies, tactics, evaluation measures, and expected outcomes for five key ‘phases’ (Feasibility Studies, Pilot Studies, Primary Trials, Secondary Experiments, and Tertiary Reinforcements). Based on decision theory (Dorazio & Johnson 2003), the framework is grounded in the context of the three demographic phases of a translocated population (i.e., establishment, growth, and regulation, Sarrazin 2007), while balancing conservation and research strategies.

I noted that a program is unlikely to progress linearly through the Translocation Continuum and may need to repeat or return to a previous phase if a new source of uncertainty is revealed. For example, if residents (established conspecifics) already exist at the recipient site in sympatry with their threats, a translocation program could 'skip' the Pilot Study and Primary Trial phases and be designed as a Secondary Experiment (prioritising population growth) or a Tertiary Reinforcement (prioritising long-term viability).

I discussed the limitations that can be imposed on translocations when they are prematurely labelled as 'successful' or a 'failure'. While these labels may be useful for comparing programs on a broad scale, they do not account for the continuum of uncertainty, how this should affect expectations, and the value of iterative learning, which is not equally distributed throughout a program. For instance, expecting 'success' in early translocation phases is unrealistic given the considerable uncertainty they involve, and this label should be holstered until later phases. The Translocation Continuum Framework addresses this by clarifying aims and expected outcomes for each translocation phase, thereby encouraging a long-term vision where decisions made for each phase are iterative, adaptive, and explicitly account for uncertainty and the likelihood of establishment, growth, and regulation throughout a program's lifetime.

The recipe for building and executing a translocation program will change throughout its lifetime and can never be a 'set and forget' affair. Not only do the goal posts (expected outcomes) move over time, but the ground on which a program is built (context) is constantly shifting (revealing additional sources of uncertainty). However, I hope to highlight the opportunities afforded by acting in the face of uncertainty. It gives us the chance to expand our often short-term memory and reverse the shifted baseline where we accept species as being at low densities in, or permanently absent from, their indigenous ranges (Manning *et al*. 2006; Evans *et al*. 2022b).

7.6 The need for parsimony

By their nature, translocations involve high uncertainty and risk. In response, current guidance urges practitioners to consider inaction (i.e., hoping a species "might adapt naturally where it is or adjust its range without human intervention") or alternative conservation solutions (e.g., habitat restoration, improving viability in extant populations, establishing protected areas, changing policy, public education, financial incentives, IUCN 2013). While these alternative solutions are valuable, they do not address uncertainty and can inadvertently 'lock in' a degraded ecological baseline (i.e., Manning *et al*. 2006; Evans *et al*. 2022b). They also fail to recognise the value of translocations, including increasing biodiversity, fulfilling ecological roles, creating insurance populations, and building the public and political support needed to galvanise other actions such as species protection and habitat restoration (Seddon 1999).

Translocation practitioners face a plethora of decisions with competing interests, including the need to produce peer-reviewed publications to increase their chance of securing funding. As such, practitioners have been strongly encouraged to design translocations within experimental frameworks that test hypotheses (Armstrong *et al.* 1994; Seddon *et al.* 2007; Armstrong & Seddon

2008; Kemp *et al.* 2015) and control for the effects of genetics, demography, and source environment from the outset. However, threatened species translocation programs are inherently limited in their ability to source large sample sizes of individuals to use in experimental designs (Kemp *et al.* 2015). For example, the number of individuals exposed to habitat of uncertain suitability (e.g., in a Pilot Study) or a tactic of uncertain efficacy (e.g., in a Primary Trial) should be minimised, while balancing the need to develop the very knowledge that can put this uncertainty to rest (e.g., Wilson *et al*. 2020). In early translocation phases, I suggest that a minimum number of individuals be exposed to a single or limited set of tactic designs to answer questions identified *a priori* (Armstrong & Seddon 2008). Only then can we address uncertainty and build the knowledge upon which future phases can be launched.

I recognise the conflicts practitioners face between doing good conservation science (adhering rigidly to experimental design) and doing good conservation (achieving species recovery with as few losses as possible). For this reason, I reinforce that there is immense value and pragmatism in applying adaptive management interventions throughout the Translocation Continuum Framework, as well as designing tactics iteratively through Pilot Studies and Primary Trials before progressing to Secondary Experiments and Tertiary Reinforcements (if appropriate).

7.7 Moving toward coexistence

One of the biggest challenges in Australian conservation is re-establishing critical weight range mammals beyond conservation-fenced havens (i.e., 'beyond-the-fence'). This is challenging because the invasive predators that drove extinction are still present at a broad-scale and are unlikely to be eradicated any time soon (Manning *et al.* 2021). While we have made great strides in reintroducing the eastern quoll to a conservation-fenced haven and demonstrated the value of these landscapes as 'outdoor laboratories', havens like MFWS should be viewed as "stepping-stones back to the wild, rather than reservoirs of threatened biota" (Batson 2015, p. 21). Indeed, the fate of eastern quolls that escaped over the MFWS fence is a reminder of the barrier that invasive predators represent to beyond-the-fence reintroductions. In addition, while havens are crucial for conservation, they could also play a role in 'locking in' our 'shifted baseline' - where we have an entrenched belief that native species vulnerable to invasive predators are accepted as permanently absent from the wild (Manning *et al.* 2006; Soga & Gaston 2016).

Based on our work at MFWS and elsewhere in Australia, our thinking has developed towards exploring how it might be possible to achieve a state of 'coexistence' between native species and invasive predators. To challenge this narrative, we proposed the concept of 'coexistence conservation': "the long-term, iterative, and adaptive process to enable the coexistence of threatened species and invasive predators" (Evans *et al*. 2022b). Coexistence conservation requires that we treat predation (outcome) as the threat, rather than the predator (agent, Evans *et* *al*. 2021). This will drive us to reduce predation levels to a level that is tolerable to a native species population, which provides benefits by driving improved fitness and predator-awareness within the population (Evans *et al*. 2022b).

Currently, invasive species management tends to focus on their removal and exclusion - an approach which does not address the impact of the evasive individuals which can remain at a density that native and reintroduced species cannot tolerate (Moseby *et al.* 2011, 2012; Hayward *et al.* 2012). There is increasing interest in harnessing evolutionary processes to drive adaptation of threatened species to cope. Manning *et al*. (2021) proposed a conceptual framework within which future research and management could shift the survival advantage towards invasive predators that demonstrate behaviours that reduce impact on threatened fauna.

Expanding on this conceptual framework, Andrewartha *et al*. (2021) found that red foxes reduced their interest in novel prey species odours when they were not associated with a reward (e.g., an encounter or kill). In this way, beyond-the-fence reintroductions may benefit from implementing a pre-exposure tactic of 'treating' an area with unrewarded odours prior to releases. This tactic may then translate to a reduction in predation pressure of released animals, or at least a period of relaxed predation pressure during which they could become established in the recipient environment. Most recently, Andrewartha *et al*. (2023) demonstrated that conditioned taste aversion (CTA, which aims to condition an aversion to a target food source) trials reduced consumption of nauseating bait for over 2 months. This shows immense promise as a tactic to allow native prey to persist in the sympatry with invasive predators, thereby helping to achieve the long-term goal of coexistence.

The return of eastern quolls, and many other threatened species, to their indigenous ranges is dependent on establishing insurance populations to protect against the threat of extinction (Fancourt 2016), while honing the tactics that will ultimately allow the establishment of viable, free-ranging populations. My hope is that the work within this thesis can represent the stepping-stones by which future beyond-the-fence programs can progress.

Illustration by Cat Cotsell

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