Wildlife in mining landscapes: a case study of the endangered northern quoll (*Dasyurus hallucatus*)

Mitchell Alec Cowan

BSc (Hons)

Submitted to Charles Sturt University in fulfilment of the requirements
for the degree of Doctor of Philosophy

Gulbali Institute
School of Agricultural, Environmental and Veterinary Sciences
Faculty of Science

November, 2024

Table of contents

Certificate of authorship

I declare that this submission is my own work and to the best of my knowledge and belief, understand that it contains no material previously published or written by another person except where due acknowledgement is made in this submission, as appropriate. Any contribution made to this submission by any person at Charles Sturt University or elsewhere is fully acknowledged.

I declare that this submission contains no material which to a substantial extent has been accepted for the award of any other qualification at Charles Sturt University or any other educational institution.

I declare that I have made all reasonable efforts to obtain copyright permission for any third-party content included in this submission and I have not included such content in this submission without the copyright owner's permission.

I agree that this submission be accessible for the purpose of study and research in accordance with normal conditions established by Charles Sturt University for the care, loan and reproduction of submissions subject to confidentiality provisions as approved by the University.

I certify that appropriate ethics and other compliance approvals have been sought where required and the ethics approval number is A21062.

The thesis complies with University requirements for a thesis as set out in the related University policies and procedures.

Mitchell Alec Cowan
4/11/2024

[redacted]

Preface

I have structured this thesis into six chapters, comprising of an introductory chapter, four data chapters, and a summary chapter. **Chapter one** provides relevant background information and introduces the following chapters of this thesis. **Chapters two, three, four, and five** are manuscripts that are either under review (**chapters two and five**) or published (**chapters three and four**) in peer-reviewed scientific journals. As a result, there is some unavoidable repetition and formatting differences between chapters. **Chapter six** synthesises the previous chapters and discusses broader lessons and future directions. I am the principal contributor for all chapters in this thesis, and they are all co-authored by a minimum of three of my supervisors. **Appendices E–I** are relevant manuscripts completed during my PhD where I am the principal author or a co-author, that are published in peer-reviewed scientific journals. Published appendices have been included as formatted by their respective journal.

Approvals and funding

The Charles Sturt University (CSU) Animal Ethics Committee provided ethics approval (A21062) for all fieldwork involving animals. A Ministerial Authorisation to Take or Disturb Threatened Species (TFA 2021-0078) was issued by the Western Australian Department of Biodiversity, Conservation and Attractions, and a Scientific Use Licence (U218/2021-2023) was issued by the Western Australian Department of Primary Industries and Regional Development. Permission from appropriate landowners and managers was received prior to any work being conducted on private properties or leaseholds, as well as in consultation with Traditional Owners. My PhD was supported by an Australian Government Research Training Program scholarship from Charles Sturt University. Project funding was provided by Charles Sturt University, the Department of Biodiversity, Conservation and Attractions, Consolidated Minerals, the Holsworth Wildlife Research Endowment – Equity Trustees Charitable Foundation & the Ecological Society of Australia, the Gulbali Accelerated Publication scheme from the Gulbali Institute, and the AusIMM and BHP Social and Environment Student Award. In-kind support was provided by the National Environmental Science Program Resilient Landscapes Hub, the University of Western Australia, Consolidated Minerals, Fortescue Metals Group, Spectrum Ecology, Atlas Iron, Roy Hill, De Grey Mining, and the Nyamal Aboriginal Corporation.

Acknowledgements

First and foremost, I would like to acknowledge the Nyamal people upon whose land most of my research was conducted. It was a pleasure to undertake fieldwork with you on Country and thank you for supporting this project. I also acknowledge the Kariyarra, Eastern Guruma, Palyku, Nyiyaparli, Yindjibarndi, and Puutu Kunti Kurrama and Pinikura (PKKP) people as the Traditional Owners of the land upon which the remainder of my fieldwork was conducted.

To my primary supervisor Dale Nimmo, I am extremely grateful for your guidance and support over the past six years, from my Honours until now. You have not only helped me become a better scientist, but you have been the exemplar of a kind, honest, constructive, and supportive person. Through the trials and tribulations of my PhD your support has been unwavering, and your dedication to your students was recently recognised with the CSU Supervisor of the Year Award. This is testament to the environment you create and promote within our lab group. Thanks for believing in me and pushing me to be my best.

To Judy Dunlop, thank you for your guidance and support over the past six years as well. Early on in my PhD when Covid caused a roadblock, you gave me an opportunity to work for six months while we figured out what was next—I must also thank Harriet Davie and Lesley Gibson for their parts in this. At the same time, you along with Dale worked extremely hard to find me a new project, which we built from the ground up and I am very proud of now. Your expertise in the field and vast knowledge of quolls and the Pilbara held me in good stead, and I really appreciate you being out there with me in the formative, early field trips of my research.

To Lesley Gibson, thank you for your support during my PhD. Your contributions and feedback early on in my project helped to build the foundations of my research and it has been great to continually pick your brain throughout the journey. Thank you for the opportunities you have given me, as well as access to the equipment which allowed me to undertake my fieldwork. Thank you also to John Angus for helping to facilitate the logistics of accessing and sending gear to and from the Pilbara.

To Sam Setterfield, thank you for giving me a community to be a part of at UWA. I am very grateful to you, Dougo and the entire NESP collective for your support throughout my PhD. Your positivity, encouragement, and frequent footy/sports chats have kept me on track and in a good frame of mind. I have also appreciated greater insight into the plant world, which I think was much needed for my mammal-centric brain. To the rest of my NESP colleagues; Michael Douglas (Dougo), Thiaggo, Leah, Caroline, Fi, Kate, Owen, Deb, Erika, Ollie T, Mark, Haylee, Stephen, Michelle, and Angela, and my awesome fellow office PhD students; Ollie P, Lenore, and Aidan, thank you for your advice, motivation, cakes, and general support over the course of my project. It has been great to be part of such a supportive group of people.

To Harry Moore, you have been there over the course of my Honours and PhD as well, and I am privileged to call you a mentor and mate. Thanks for leading the way and showing me how to approach research with enthusiasm and rigour, as well as for always being a sounding board and reliable encourager. The scientific community is lucky to have a young researcher like you among its ranks.

Thank you to Consolidated Minerals (ConsMin) for supporting my project, particularly Kaylee Prince and Sarah Thomas, who helped to develop the ideas and basis for my research at the beginning. Kaylee, your steadfast support and commitment to my project was fantastic and I am very thankful for that. I am glad you got to come out and see a quoll on our last trip, a small reward for your hard work behind the scenes. To the on-site team during my project, particularly the enviros, Luke Barrett, Rory Embleton, Jacqui Roberts, Kerryn Forster, and Sam Covich-Lindsay, thank you for all the hard work and support during the project—I hope you all enjoyed it as much as me. Particularly to Luke and Rory who were with me in the field for the entire journey, we shared many ups and downs, and I am extremely grateful for your help over the past few years. I am looking forward to The Rock 2000 countdown this year! To the other organisations and people within that supported my research, thank you very much. This included FMG, Todd Edwards, Jared Nelson, Zena Harman, and Damien Cancilla; Spectrum Ecology, Astrid Heidrich; Roy Hill, Harriet Davie; Atlas Iron, Kate Stanbury and Riley Pattinson; De Grey, Sarah Thomas, Lorinda Hunt, and Theda Morrissey; and Biologic, Chris Knuckey. Thank you also to all my co-authors and those who contributed time and expertise to my research. I have gained valuable skills and knowledge because of your contributions to my PhD, so thanks to Scott Forrest, Eamonn Wooster, Bronwyn Hradsky, Michael Wysong, Lorna Hernandez-Santin, Chris Jolly, Rob Davis, Diana Fisher, Damian Michael, James Turner, Chris Knuckey, Melinda Henderson, Astrid Heidrich, Michael Callan, Carl Tippler, and the Nyamal Rangers.

To my fellow Conservation in Human Landscapes Lab members; Grant, Dylan, Eamonn, Chris, Leanne, Harry, Hannah, Ben, Chloe, Amy, and all others that have been there for part of the journey, thanks for creating such a comfortable environment to share and learn, as well as for being such exemplary academics and people. Thank you also to Cathy Garbuio, Debra Noy, Paul Humphries, Kylee Imlach, and Sandra Savocchia, for their academic and administration support throughout this project. Thanks to Jodi Price for helping to initiate my path into research with Dale way back in 2018, and thank you to Teigan Cremona and Tom Newsome for reviewing my PhD project proposal and offering great advice in the early stages of my project.

A tremendous thank you to my friends and family for their unwavering support of me and my PhD journey. I am very lucky to have a village spread from Wodonga to Perth and everywhere in between, and I love every one of you. To my Mum and Dad (Anthony and Jo), you fuelled my love of the outdoors and inquisitive nature. To have two role models like you to look up to and lean on has been the greatest gift and I wouldn't be here without either of you. Thank you for your unconditional love and encouraging me to follow my dreams. To my brother and sister, Lachy and Caity, thank you for keeping me grounded over the past few years. I can't wait to keep sharing future adventures with you both, along with Grace, Mila, and Ollie. Thank you also to Darren and Lee, and Gary, Jess, Henry, and Elijah for your consistent support and encouragement.

Lastly, a monumental thank you to my extraordinary wife Alyse. You moved across the country with me to pursue this whirlwind journey and have supported me fiercely through all the highs and lows. You are one in a million and your resolute encouragement and love has been the catalyst for me to push forward on many occasions. I am eternally grateful for you and the ride we've been on. I cannot wait for what we have in store next.

"We don't own the planet Earth, we belong to it. And we must share it with our wildlife."

– Steve Irwin

From: The Crocodile Hunter: The incredible life and adventures of Steve and Terri Irwin (2002)

Publications resulting from the research

Chapter 2

Cowan, M.A., Wooster, E.I.F., Gibson, L.A., Setterfield, S.A., Dunlop, J.A., Nimmo, D.G. **Mining reshapes animal communities at a local and landscape-scale.**

Under review in *Biological Conservation* in April 2024.

Cowan, M.A. Conceived and designed the study, collected data, performed statistical analysis, and wrote the manuscript.
Wooster, E.I.F. Contributed to statistical analysis and manuscript preparation.
Gibson, L.A. Contributed to manuscript preparation.
Setterfield, S.A. Contributed to manuscript preparation.
Dunlop, J.A. Contributed to manuscript preparation.
Nimmo, D. G. Conceived and designed the study, and contributed to statistical analysis and manuscript preparation**.**

Senior author: Dale Nimmo

[redacted]

Chapter 3

Cowan M.A., Moore H.A., Hradsky B.A., Jolly C. J., Dunlop J.A., Wysong M.L., Hernandez-Santin L., Davis R.A., Fisher D.O., Michael D.R., Turner J.M., Gibson L.A., Knuckey C.G., Henderson M., Nimmo D.G. (2023). **Non-preferred habitat increases the activity area of the endangered northern quoll (*Dasyurus hallucatus*) in a semi-arid landscape.**

Published in *Australian Mammalogy* in September 2022.

Cowan, M.A. Conceived and designed the study, collected data, collated external data, performed statistical analysis, and wrote the manuscript.
Moore H.A. Collected data, and contributed to statistical analysis and manuscript preparation.
Hradsky B.A. Contributed to statistical analysis and manuscript preparation.
Jolly C.J. Contributed to manuscript preparation.
Dunlop, J.A. Contributed to data collection and manuscript preparation.
Wysong M.L. Contributed to statistical analysis and manuscript preparation.
Hernandez-Santin L. Collected data and contributed to manuscript preparation.
Davis R.A. Contributed to manuscript preparation.
Fisher D.O. Contributed to manuscript preparation.
Michael D.R. Contributed to manuscript preparation.
Turner J.M. Contributed to manuscript preparation.
Gibson L.A. Contributed to manuscript preparation.
Knuckey C.G. Collected data and contributed to manuscript preparation.
Henderson M. Collected data and contributed to manuscript preparation.
Nimmo, D.G. Conceived and designed the study, and contributed to statistical analysis and manuscript preparation**.**

Senior author: Dale Nimmo

[redacted]

Chapter 4

Cowan, M.A., Dunlop, J.A., Gibson, L.A. Moore, H.A., Setterfield, S. A., Nimmo, D.G. (2024). **Movement ecology of an endangered mesopredator in a mining landscape.**

Published in *Movement Ecology* in January 2024.

Cowan, M.A. Conceived and designed the study, collected data, performed statistical analysis, and wrote the manuscript.
Dunlop, J.A. Conceived and designed the study, and contributed to data collection and manuscript preparation.
Gibson, L.A. Contributed to manuscript preparation.
Moore, H.A. Contributed to manuscript preparation.
Setterfield, S.A. Contributed to manuscript preparation.
Nimmo, D.G. Conceived and designed the study, and contributed to statistical analysis and manuscript preparation.

Senior author: Dale Nimmo

[redacted]

Chapter 5

Cowan, M.A., Forrest, S.W., Setterfield, S.A., Dunlop, J.A., Gibson, L.A., Nimmo, D.G.
The impact of mining on animal movement and landscape connectivity revealed through simulations and scenarios.

Under review in *Ecological Applications* in September 2024.

Cowan, M.A. Conceived and designed the study, collected data, performed statistical analysis, and wrote the manuscript.
Forrest S.W. Contributed to statistical analysis and manuscript preparation.
Setterfield, S.A. Contributed to manuscript preparation.
Dunlop, J.A. Contributed to data collection and manuscript preparation.
Gibson, L.A. Contributed to manuscript preparation.
Nimmo, D.G. Conceived and designed the study, and contributed to statistical analysis and manuscript preparation.

Senior author: Dale Nimmo

[redacted]

Appendix E

Cowan, M.A., Dunlop, J.A., Hernandez-Santin, L., Heidrich, A., Knuckey, C.G., Nimmo, D.G. **High post-sex survival of the world's largest semelparous species.**

Published in *Austral Ecology* in September 2024

Cowan, M.A. Conceived the study, collected data, collated external data, performed statistical analysis, and wrote the manuscript.
Dunlop, J.A. Conceived the study, collected data and contributed to manuscript preparation.
Hernandez-Santin, L. Collected data and contributed to manuscript preparation.
Heidrich, A. Collected data and contributed to manuscript preparation.
Knuckey, C.G. Collected data and contributed to manuscript preparation.
Nimmo D.G. Conceived the study, and contributed to manuscript preparation.

Senior author: Dale Nimmo

[redacted]

Appendix F

Gibson L.A., Moore H.A., Cowan M.A., Craig M.D., Nimmo D.G., Dunlop J.A. (2023). **A review of progress of a research program for the endangered northern quoll (*Dasyurus hallucatus*) in the multi-use landscapes of the Pilbara.**

Published in *Australian Mammalogy* in June 2023.

Gibson L.A. Conceived and wrote the manuscript.
Moore H.A. Contributed to research program and manuscript preparation.
Cowan, M.A. Contributed to research program and manuscript preparation.
Craig M.D. Contributed to manuscript preparation.
Nimmo D.G. Contributed to research program and manuscript preparation.
Dunlop J.A. Managed research program and contributed to manuscript preparation.

Lead author: Lesley Gibson

[redacted]

Appendix G

Moore, H.A., Dunlop, J.A., Jolly, C.J., Kelly, E., Woinarski, J.C.Z., Ritchie, E.G., Burnett, S., van Leeuwen, S., Valentine, L.E., Cowan, M.A., Nimmo, D. G. (2022). **A brief history of the northern quoll (*Dasyurus hallucatus*): a systematic review.**

Published in *Australian Mammalogy* in August 2021.

Moore, H.A. Conceived and designed the study, collected the data, and wrote the manuscript.
Dunlop, J.A. Conceived and designed the study, and contributed to manuscript preparation.
Jolly, C.J. Contributed to manuscript preparation.
Kelly, E. Contributed to manuscript preparation.
Woinarski, J.C.Z. Contributed to manuscript preparation.
Ritchie, E.G. Contributed to manuscript preparation.
Burnett, S. Contributed to manuscript preparation.
van Leeuwen, S. Contributed to manuscript preparation.
Valentine, L.E. Contributed to manuscript preparation.
Cowan, M.A. Contributed to manuscript preparation.
Nimmo, D.G. Conceived and designed the study, and contributed to manuscript preparation.

Senior author: Dale Nimmo

[redacted]

Appendix H

Cowan, M.A., Callan, M.N., Tippler, C., Nimmo, D.G. (2023). **A technological advancement in artificial refuges for an endangered marsupial predator.**

Published in *Conservation Science and Practice* in June 2023.

Cowan, M.A. Conceived and designed the study, and wrote the manuscript.
Callan, M.N. Conceived and designed the study, and contributed to manuscript preparation.
Tippler, C. Conceived and designed the study, and contributed to manuscript preparation.
Nimmo, D.G. Conceived and designed the study, and contributed to manuscript preparation.

Senior author: Dale Nimmo

[redacted]

Appendix I

Cowan, M. A., Nyamal Rangers, Dunlop, J. A., Moore, H. A., Nimmo, D. G. **Movement patterns of two northern quolls after a large wildfire.**

Published in *Austral Ecology* in July 2024.

Cowan, M.A. Conceived and designed the study, collected data, performed statistical analysis, and wrote the manuscript.
Nyamal Rangers. Contributed to data collection and manuscript preparation.
Dunlop, J.A. Contributed to data collection and manuscript preparation.
Moore, H. A. Contributed to manuscript preparation.
Nimmo D.G. Conceived and designed the study, and contributed to manuscript preparation.

Senior author: Dale Nimmo

[redacted]

Abstract

Mining causes significant landscape modification and overlaps with many areas of high biodiversity value. Therefore, some species must persist in mining-disturbed landscapes, likely influencing broader community dynamics and species-specific behaviours, such as movement. One species impacted by mining is the endangered marsupial mesopredator, the northern quoll (*Dasyurus hallucatus*). The northern quoll exists across northern Australia and has suffered range contractions in all populations except for in the Pilbara region of Western Australia—likely due to the absence of the invasive, poisonous cane toad (*Rhinella marina*). However, mining is prominent in this region, often targeting the rugged, rocky outcrops that northern quolls rely on for denning and food resources. Rocky habitats are naturally fragmented by wide expanses of spinifex (*Triodia* spp.) grasslands and riparian habitats, which northern quolls are required to move through to access rocky habitats. The addition of mining alters this habitat structure and likely influences northern quoll movement. Indeed, determining the impacts of mining on northern quoll movement has been listed as a priority for the species. In this thesis, I sought to contextualise mining impacts on animal communities in the Pilbara, build on our understanding of northern quoll movement in undisturbed landscapes, and explore the impacts of mining on fine-scale northern quoll movement and landscape-scale connectivity.

Chapter one provides a brief introduction to the thesis. In **chapter two**, I explored the impact of mining infrastructure on fauna species, ecosystem processes, and predator-prey networks in the Pilbara. Mining landscapes facilitated novel species assemblages and reduced mammal richness and the variation of ecological roles. Some species altered their temporal activity in mining landscapes, shifting predator-prey pressures for some animal groups. However, predator-prey networks remained broadly stable, likely due to the resilience of some species to mining.

In **chapter three**, I investigated the movement of northern quolls in undisturbed landscapes. Northern quolls preferred rugged, rocky habitats and dry riverbeds, and avoided spinifex grasslands relative to the availability of each habitat. Northern quolls had larger home ranges when they used higher proportions of non-preferred spinifex grassland, suggesting that using more unfavourable habitat increased the area needed to obtain resources.

In **chapter four**, I examined the movement and energy expenditure of northern quolls in a mining landscape. Northern quoll habitat use shifted seasonally: during the breeding season when quolls use more energy, they avoided mining habitats, but in the non-breeding season when quolls use less energy, they used mining habitats similarly to rocky and riparian habitats. Moving through mining habitats increased energy expenditure, likely driving avoidance during the energy-costly breeding season, and potentially affecting breeding dispersal.

In **chapter five**, I built on the findings of **chapter four** to simulate northern quoll movement across landscape scenarios with various mining configurations, and without mining, to assess impacts on quoll movement and landscape connectivity. Mining landscapes significantly altered movement corridors and had reduced rocky habitat connectivity compared to the landscape without mining, driven by reduced availability of and longer distances between rocky habitat patches.

Broadly, my findings highlight the complex impacts of mining on wildlife and the need to consider community-level effects when undertaking management in mining landscapes. I have also enhanced our understanding of fine-scale northern quoll movement and habitat selection, particularly in mining landscapes. Mining has negative impacts on northern quoll fine-scale movement and energy expenditure, and is likely to have broader impacts on population-level dispersal and breeding success. The retention and conservation of rocky habitats and existing movement corridors will be important to allow northern quolls to persist efficiently in mining landscapes. Further my findings support the incorporation of animal movement and landscape connectivity into future development planning. **Chapter six** places my findings in the broader context and discusses some future directions identified in this thesis.

Chapter 1: Introduction

1.1. Mining and its threat to wildlife

Mining is a global disturbance that alters and reshapes landscapes of all types, stretching over 135 countries (Tang and Werner, 2023), and affecting at least 75,000 large-scale sites across 50 million km^2 of land (Sonter et al., 2020). There is also rapidly expanding illegal and small-scale mining that is harder to quantify but has equally devastating effects on landscapes (Siqueira-Gay and Sánchez, 2021, Suglo et al., 2021). Mining involves the extraction of minerals and is deemed critical for the financial stability of several countries (Schulz et al., 2017, Suglo et al., 2021). In this sense, mining contributes significantly to the global economy, contributing more than 60% of the gross domestic product of at least 81 countries (IPBES, 2019).

There are many forms of terrestrial mining, including several types of underground mining (Martino et al., 2021). However, the method with the largest impact on Earth’s terrestrial surface is open-pit mining, accounting for almost 60% of all terrestrial mines and nearly 90% of total ore extraction globally (Martino et al., 2021). Open-pit mining consists of surface clearing and the creation of large pits in the Earths’ crust, which are commonly drilled and blasted with explosives, before being dug out to form horizontal benches from the top down (Figure 1.1; Blom et al., 2019). Extracted material is then separated into ore (for processing), or waste, which is stacked in piles, creating waste rock dumps (Figure 1.1; Blom et al., 2019). The surface area required to accommodate these activities results in vast clearing of native vegetation, soil, and rock (Sonter et al., 2017).

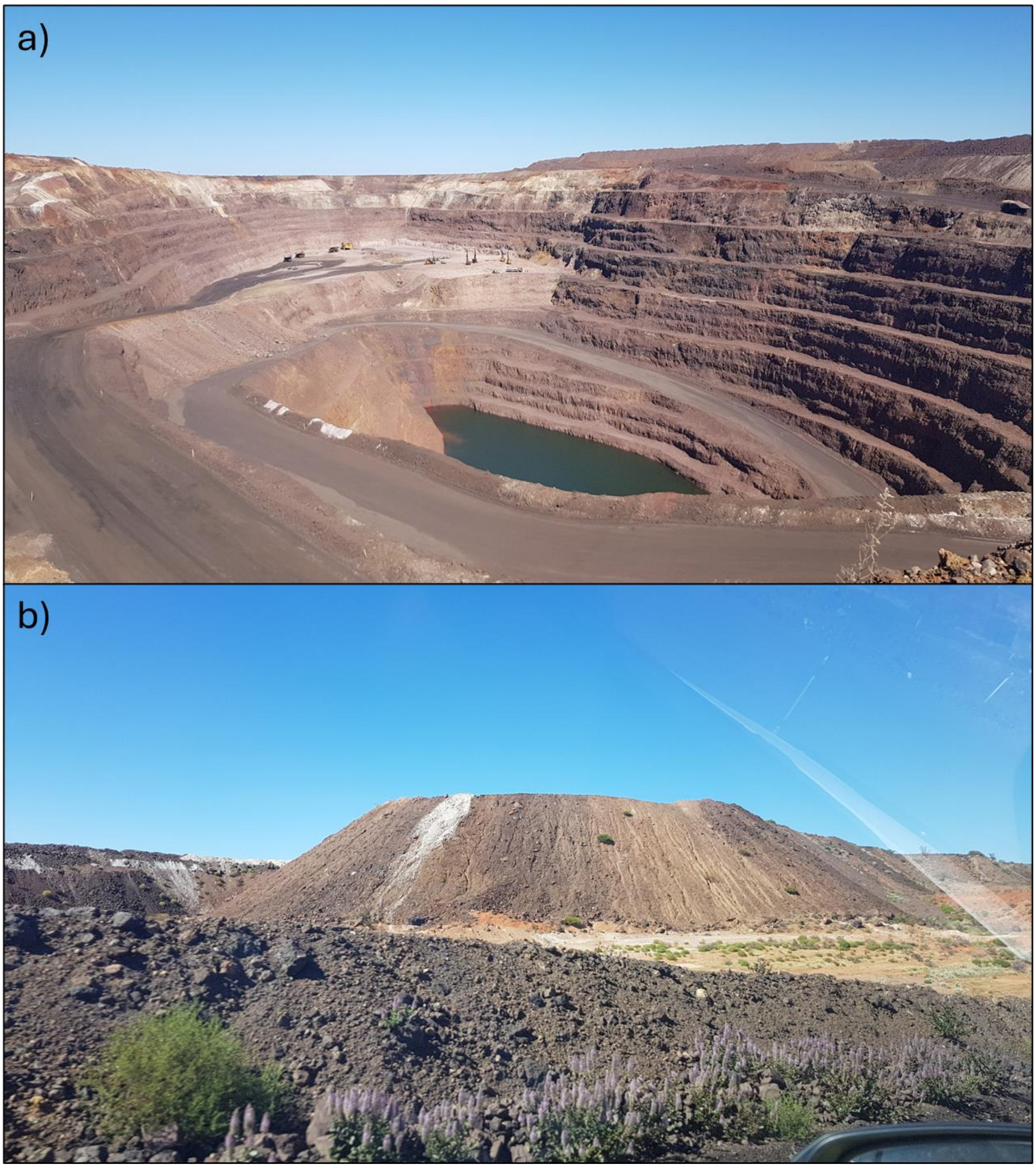


Figure 1.1: Images of a) a mine pit and b) a rocky waste dump, from the mining landscape in the Pilbara where my PhD was focused.

As of 2016, mining threatened at least 900 animal species globally (Maxwell et al. 2016). The anticipated increase in mining, coupled with the high conservation value of many mineral-rich regions (Butt et al., 2013, Durán et al., 2013, Aska et al., 2024), means that threats to biodiversity are expected to grow (Sonter et al., 2020). Future changes in mining activities are also likely to shift threats for species, increasing the need for conservation (Sonter et al., 2018). Indeed, current trends in mineral extraction suggest a future threat of mining for over 24,000 animal and plant species (Torres et al., 2022). Of all terrestrial mammals, 136 species have >30% of their habitat within 10 km of a mine or exploration site (Sonter et al., 2022), with one third of these species being threatened with extinction according to the International Union for Conservation of Nature (IUCN) (Sonter et al., 2022). This suggests that many species—including several threatened species—will be forced to persist in mining-dominated landscapes in the future.

For species currently threatened by mining, some already live within or close to mining landscapes (e.g., up to one-third of Africa's great ape population; Junker et al., 2024). Living in close proximity to disturbance can introduce novel stressors for wildlife, such as artificial light and noise pollution (Herbert-Read et al., 2017), and anthropogenic structures (e.g., waste rock dumps; Schulz et al., 2012). Some species can thrive in mining habitats, aided by resource subsidies like food from human waste scraps (Newsome et al., 2013a, Newsome et al., 2014a), or increased hunting efficiency. For example, wolves (*Canis lupus*) prey on moose (*Alces alces*) more often in mining habitats due to reduced habitat complexity reducing protection for moose (Neilson and Boutin, 2017). Other species, such as those more specialised or reliant on certain habitats, are more likely to be negatively impacted by altered habitat conditions (Lindenmayer et al., 2023), such as mining. These contrasting responses to disturbance can result in complex effects on the ecological function of ecosystems, predator-prey interactions, and the makeup of animal communities in mining or other disturbed landscapes (Hobbs et al., 2018, Tscharntke et al., 2012). It is therefore important to consider how landscape modification from mining affects animal communities, as well as the behavioural responses of the species within.

1.2. Animal movement in modified landscapes

Movement is a fundamental requirement for animals to find resources, breed, and maintain gene flow among populations (Nathan et al., 2008). The ability of animals to move efficiently (i.e., in a way that minimises energy expenditure) to access favoured habitats and resources contributes to animal survival, foraging efficiency, and overall health (Nathan et al., 2008, McNab, 1963). Efficient movement allows animals to disperse and forage with minimal energetic costs, contributing to their fitness and reproductive success (Emlen, 1966, Doherty et al., 2019). In this sense, animals often favour particular habitats, based on their ability to move efficiently while balancing foraging requirements and predation risk (Stokes et al., 2004). Understanding the relationship between movement, energy use, and resource availability is vital for optimising conservation efforts to promote the long-term viability of animal populations (Nathan et al., 2008, Avgar et al., 2016).

The impacts of landscape modification, such as mining, on animal movement are vast, although responses to disturbance often vary between species (Doherty et al., 2021). When landscapes introduce unfavourable habitats or resources are scarce, animals must allocate more energy to obtain resources, which can impact their health and increase vulnerability to predation (Rus et al., 2020, Gardiner et al., 2019, Stobo-Wilson et al., 2021). The addition of novel infrastructure during open pit mining—such as waste rock dumps, pits, and buildings—in turn alters the configuration of habitats, likely influencing animal movement and habitat use (Newsome et al., 2013b). Indeed, migrating mule deer (*Odocoileus hemionus*) avoid mining habitats and use more energy when moving through areas of large-scale gold mining in the Ruby Mountains of the USA (Blum et al., 2015). Many mining companies globally have conservation requirements to maintain species populations in impacted areas (zu Ermgassen et al., 2019). Therefore, understanding how species interact with mining landscapes could lead to conservation interventions that enhance the persistence of native wildlife within mining footprints. While there are some examples of studies investigating the effects of historic and active mining disturbance on large animal movement (Newsome et al., 2013b, Newsome et al., 2013a, Cristescu et al., 2016a, Cristescu et al., 2016b, Oehler et al., 2005, Zoellick et al., 2002, Webb et al., 2011), there is little information for critical-weight-range (CWR; 35–5500 g) species, particularly in active mining landscapes (Martins-Oliveira et al., 2021). Critical weight range species in Australia are particularly susceptible to extinction compared to larger species (Chisholm and Taylor, 2007).

1.3. The northern quoll

One CWR species impacted by mining is the endangered marsupial mesopredator, the northern quoll (*Dasyurus hallucatus*) (Gould, 1842) (Figure 1.2). The northern quolls is the smallest of the four Australian *Dasyurus* species, and displays sexual dimorphism, with females weighing between 350–700g and males larger at 500–1000g (Oakwood, 1997). Male northern quolls engage in an uncommon reproductive behaviour for mammals known as semelparity, where they breed only once in their lifetime, experience a surge in testosterone and energetic requirements (Gaschk et al., 2023), before rapidly declining in condition, typically not surviving beyond 11 months (Oakwood et al., 2001). However, there has been evidence of up to 5% of males in an *in situ* population surviving to a second year (Hernandez-Santin et al., 2019), and up to six years in captivity (Oakwood, 1997, Jackson, 2007). This significant annual mortality in adult male northern quolls places a heavy reliance on the survival of offspring for population persistence (Moro et al., 2019). To facilitate this annual die-off and promote genetic diversity, female quolls can have up to eight young, with multiple paternity allowing each of them to be sired by a different male quoll (Chan et al., 2020). Breeding season is variable across the quoll's range, usually occurring prior to the wet season (Oakwood, 2000). During this time, males disperse over large distances, establishing much larger home ranges than female quolls (Oakwood, 2000, Hernandez-Santin et al., 2020). The diet of the northern quoll is opportunistic and omnivorous, and the proportion of vertebrates, invertebrates, and flora eaten varies across its range (Dunlop et al., 2017).

Prior to European colonisation of Australia in 1788, the geographic range of the northern quoll incorporated much of northern Australia, across Queensland, the Northern Territory, and the Kimberley and Pilbara regions of Western Australia (Moore et al., 2019). Average annual rainfall across these regions varies significantly, ranging from 220 mm in the eastern extent of the Pilbara bioregion, to nearly 4500 mm in northern Queensland (Bureau of Meteorology, 2020, Moore et al., 2019). Similarly, average maximum temperatures exceed 40°C in the Pilbara bioregion and fall below 30°C in southern Queensland (Australian Bureau of Meteorology 2020). Habitat differences are common across these regions, with the vast semi-arid savannas of the Kimberley and Pilbara contrasting the tropical savannas, open woodlands, and monsoonal rainforests of the Northern Territory and northern Queensland (Moore et al., 2019).

Since European colonisation, the geographic range of the northern quoll has reduced significantly, largely constrained to areas of high topographic ruggedness and rainfall near the coast line (Moore et al., 2019). Consequently, the northern quoll is classified as Endangered nationally and by the IUCN, as well as in Western Australia under the *Biodiversity Conservation Act 2016* (Department of the Environment, 2024, Oakwood et al., 2016). In the Northern Territory, northern quolls are listed as Critically Endangered under the Territory Parks and Wildlife Conservation Act 1976 (Department of the Environment, 2024). Threats implicated in the decline of the northern quoll include altered and inappropriate fire regimes (Griffiths and Brook, 2015), over-grazing by introduced herbivores (Braithwaite and Griffiths, 1994), and predation pressures from the introduced feral cat (*Felis catus*) and red fox (*Vulpes*

vulpes) (Oakwood, 1997, Hernandez-Santin et al., 2016). However, the introduction of cane toads (*Rhinella marina*) in 1935 to control sugar cane pests in northeastern Queensland (Shine, 2010)—and their subsequent range expansion from Queensland to the Kimberley (Kearney et al., 2008)—is attributed as the biggest contributor to the decline of northern quolls in many parts of their range (Braithwaite and Griffiths, 1994, Moore et al., 2019). The cane toad poisons animals that eat it, resulting in population declines for many native predators across northern Australia (Shine, 2010).

1.4. The Pilbara context

The Pilbara population of northern quolls has suffered the least dramatic decline of all regions in northern Australia, likely due to the absence of cane toads in the region (Moore et al., 2019). Hence, the Pilbara is the last stronghold for northern quolls on mainland Australia. Yet, this population is far from secure. Over 90% of the Pilbara bioregion is under mining lease (Environmental Protection Authority, 2014), and in 2022/23, the region's onshore mineral extraction was valued at over $130 billion AUD (Department of Mines, Industry Regulation and Safety, 2023). The Pilbara also hosts the largest amount of rock pile habitat outside the Kimberley (Burbidge and McKenzie, 1989). These rocky habitats serve as critical refuges for northern quolls, providing protection against predators (Hernandez-Santin et al., 2016), fire, and extreme weather (Begg, 1981, Molloy et al., 2017), as well as providing important breeding dens (Cowan et al., 2020b, Hernandez-Santin et al., 2022). However, these rocky outcrops are often targeted by mining, due to their rich mineral deposits (Ramanaidou and Morris, 2010, Cramer et al., 2016). Most of the activities that remove rocky habitat in the Pilbara involve open-pit mining that removes large areas of complex rocky habitat to access minerals, including iron ore, lithium, gold, and manganese (Department of Mines, Industry Regulation and Safety, 2023). Most mining activities in the Pilbara are in remote areas, relying on short-term shift workers accommodated on-site in ‘mining camps’ (Goodfield et al., 2011). Therefore, Pilbara mines are often made up of large areas of infrastructure and modified habitats.

Figure 1.2: A northern quoll at a Pilbara mine site. Adam Brice/Shutterstock.

The rocky outcrops of the Pilbara are naturally-fragmented, scattered amongst vast spinifex grasslands and stands of *Acacia* and *Eucalyptus* species (Moore et al., 2021b). Despite this, northern quoll populations are genetically connected across the Pilbara (Shaw et al., 2022), meaning quolls often disperse between these critical rocky habitats using other available habitats. However, it is not known exactly how quolls use available habitats at a fine-scale, and what impacts these habitats have on northern quoll movement and energy requirements (Cramer et al., 2016). Further, while northern quolls have been recorded within active (Figure 1.2., Figure 1.3., Henderson, 2015, Dunlop et al., 2015), and post-mining landscapes in the Pilbara (Cowan et al., 2020b), the influence of mining on northern quoll movement and habitat connectivity is relatively unknown. At the beginning of the Pilbara Northern Quoll Research Program managed by Western Australia’s Department of Biodiversity, Conservation and Attractions (DBCA), Cramer et al. (2016) identified several priorities for northern quoll research. These included i) investigating how disturbance and infrastructure development (e.g., roads, mining) impacts northern quoll habitat quality and connectivity, and ii) investigating how northern quolls interact with infrastructure.

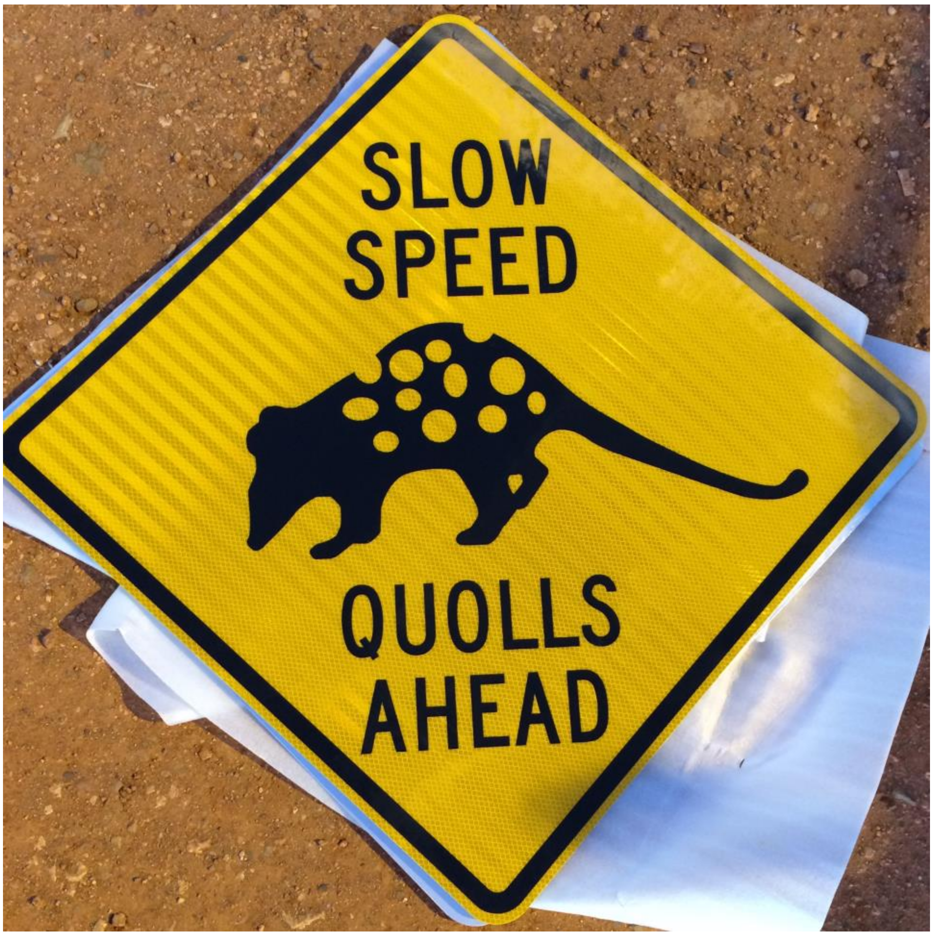


Figure 1.3: A road sign for a mine site to enforce slow driving speeds around potential quoll habitat.

1.5. Thesis objectives

This PhD was designed in collaboration with DBCA and Consolidated Minerals (ConsMin) to address impacts of mining on northern quoll movement and habitat connectivity. The results of this PhD are outlined in chapters 2–6. In **chapter two**, I assess the broader effects of mining on Pilbara wildlife using a distributed control-impact camera trapping design across eight mining landscapes and eight ecologically similar, but undisturbed, reference landscapes. I investigate how mining shapes the composition, diversity, and temporal activity of animal communities, as well as how it influences ecosystem function and predator-prey networks. For this chapter, quolls were initially of highest interest but could not be sampled sufficiently, so this chapter took a more generalised approach.

In **chapter three**, I assess the habitat selection of northern quolls in undisturbed landscapes of the Pilbara bioregion, using four existing GPS tracking datasets collected between 2014 and 2018—including my own. I investigate the influence of each habitat on the space use requirements of northern quolls. This serves to act as a baseline as to how quolls interact with different habitats in the absence of disturbance. In **chapter four**, I assess the fine-scale habitat selection of northern quolls in a mining-disturbed landscape, evaluating how the use of mining habitats influences movement and energy expenditure in the breeding and non-breeding seasons. In **chapter five**, I use findings from **chapter four** to inform landscape-scale movement simulations that imitate movements from observed northern quolls. This allowed me to scale up movements to compare broader landscape connectivity and movement across landscapes with varying compositions of mining disturbance (i.e., the current mining footprint, more dispersed mining, more aggregated mining, and no mining). In **chapter six**, I summarise the findings from each of my four data chapters and briefly discuss broader lessons and future directions. Images from undisturbed and mining landscapes in the Pilbara are shown below to better visualise this multi-use region (Figures 1.4–1.7).

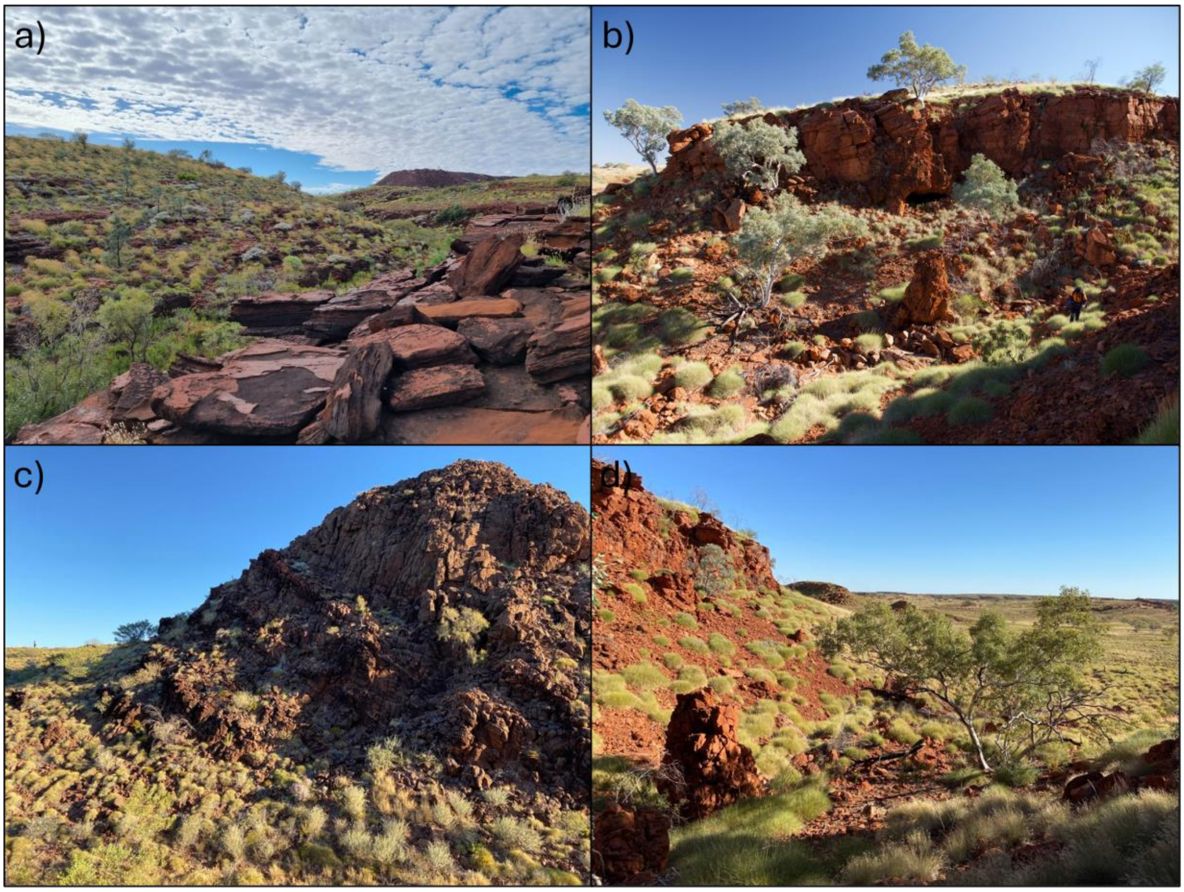


Figure 1.4: Examples of rocky outcrops and ridges used by quolls for denning, just outside the mining footprint where my PhD was focused in the Pilbara region.

Figure 1.5: Examples of a–b) spinifex grasslands surrounding rocky features and scattered *Eucalyptus* trees, c) radio-tracking for northern quolls towards mining-disturbed areas of the landscape, and d) another spinifex grassland.

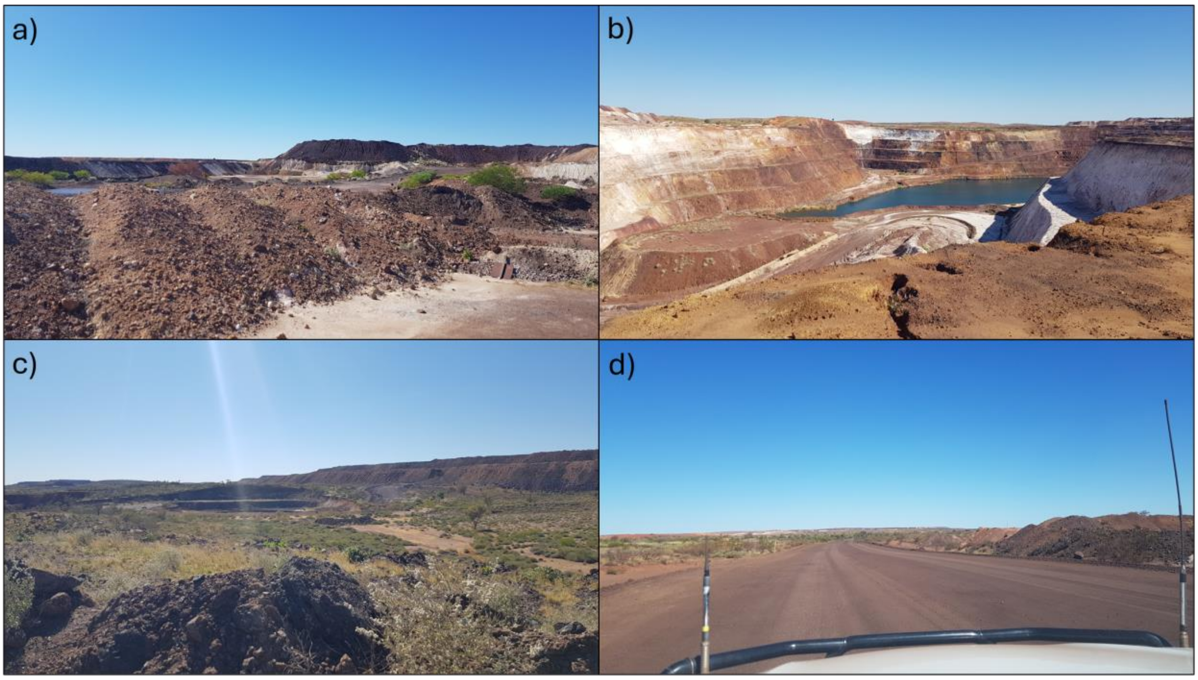


Figure 1.6: Parts of the mining landscape including a) small waste rock piles, b) a large mine pit, c) remnant vegetation within the mining footprint with waste rock dumps in the distance, and d) a road.

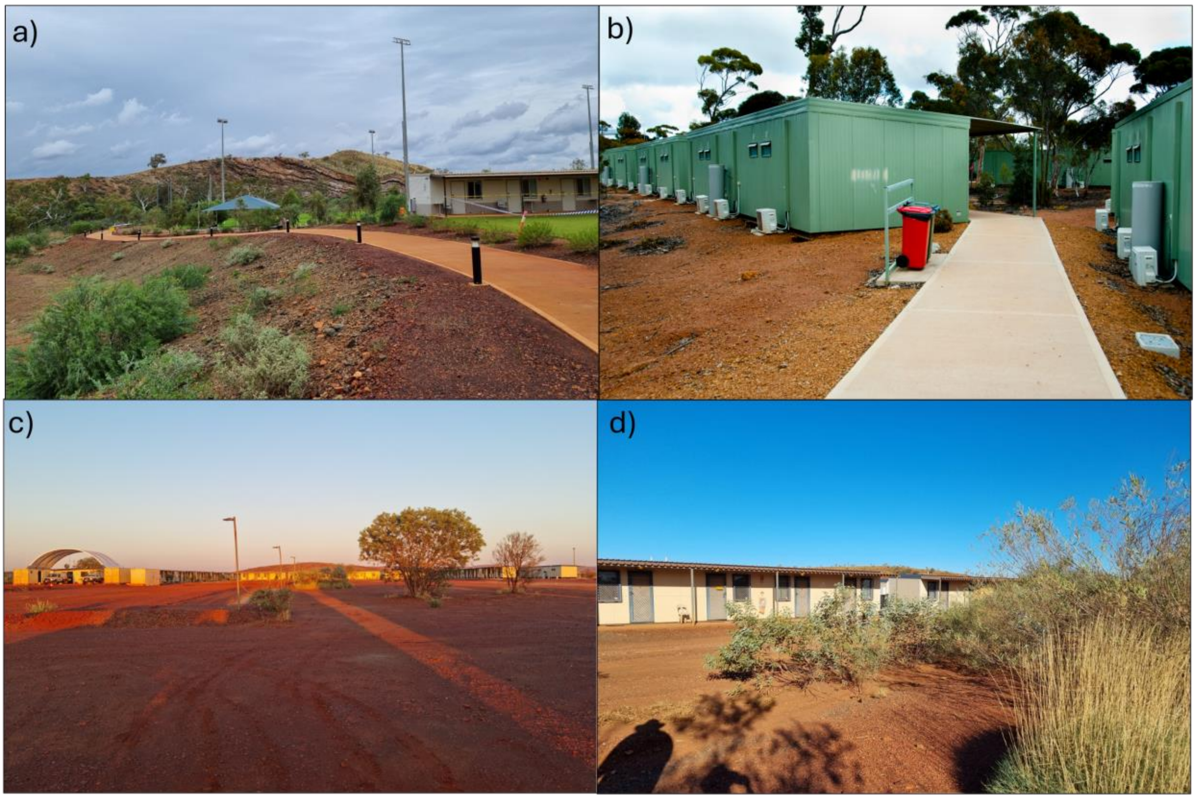


Figure 1.7: Parts of the mining landscape at mining camps, which accommodate staff, including a) remnant habitats and landscaped areas, b) buildings, bins, and footpaths, c) a large cleared area for vehicles, and d) remnant vegetation nearby buildings.

Chapter 2: Mining reshapes animal communities at a local and landscape-scale

Manuscript under review in Biological Conservation.

Cowan, M.A.[1,2], Wooster, E.I.F.[1], Gibson, L.A.[3,4], Setterfield, S.A.[2], Dunlop, J.A.[1,2], Nimmo, D.G.[1]

[1]Gulbali Institute, School of Agricultural, Environmental and Veterinary Sciences, Charles Sturt University, Thurgoona, NSW, 2640, Australia.

[2]School of Agriculture and Environment, The University of Western Australia, Crawley, WA, 6009, Australia

[3]Department of Biodiversity, Conservation and Attractions, Kensington, WA, 6151, Australia.

[4]School of Biological Sciences, The University of Western Australia, Crawley, WA, 6009, Australia

2.1. Abstract

Anthropogenic disturbances, such as mining, significantly modify landscapes which can have negative effects on ecosystems and the wildlife therein. Here, we investigate the ecological impacts of mining camps (semi-urban accommodation areas in mining landscapes) on wildlife communities, including species composition and diversity, ecosystem function, predator-prey networks, and temporal activity. Using a distributed control-impact design, we deployed camera traps at mining camps and ecologically similar reference landscapes across Western Australia's Pilbara region. We found a marked difference in species composition at mining camps, suggesting the formation of novel assemblages. Lower functional dispersion at mining camps suggests that the ecological functions being performed by species here are less varied, although ecosystems at mining camps have high functional redundancy, likely buffering the effects of future disturbance. Predator-prey networks at mining camps had similar overall structure to reference landscapes despite major differences in species composition. However, lower network connectance at mining camps suggests that food webs are more vulnerable to future disturbance or species loss. Behavioural animal responses included altered temporal activity by some animal groups, shifting predator and competition pressures at mining camps. Some animal groups though (e.g., dingoes, feral herbivores), were resilient to disturbance, with no clear relationships between landscape types. These results demonstrate the complex impacts of human disturbance on ecosystems, and the need to consider community-wide approaches when undertaking management in modified landscapes.

2.2. Introduction

Landscape modification alters ecosystems across the globe by modifying biological, chemical, and physical processes (Lindenmayer et al., 2023). These changes reconfigure ecological communities, as some species decline and others increase, resulting in novel assemblages (Hobbs et al., 2006). A common consequence of landscape modification is a decline in species diversity (Owusu et al., 2018) and the range of ecological functions performed by species—sometimes termed ‘functional diversity’ (Tilman et al., 1997). Functional diversity enhances resilience in the face of disturbance (Chillo et al., 2011), and reduced functional diversity can trap ecosystems in degraded states (Chillo and Ojeda, 2012). Landscape modification also changes species’ temporal niches (Gaynor et al., 2018, Gilbert et al., 2023), altering interactions between species, and modifying predator-prey networks (Gilbert et al., 2022). Such changes can destabilise food webs, leaving them more vulnerable to future disturbances (Tylianakis et al., 2010).

Mining affects up to 50 million km^2 of land globally (Sonter et al., 2020), and threatens > 900 animal species (Maxwell et al., 2016). Mining modifies landscapes through the clearing of vegetation, and the creation of mining pits, rock dumps, and infrastructure for workers (i.e., mining camps). Some species persist in mining landscapes (Cowan et al., 2024), particularly within mining camps, due to the provision of resources such as water and food waste (Newsome et al., 2013a, Newsome et al., 2013b). Mining camps can attract top predators (Newsome et al., 2013a), and changes to habitat structure (Neilson and Boutin, 2017), and resource subsidies provided by mining camps can affect predator-prey interactions (Newsome et al., 2014a, Newsome et al., 2019). Mining camps introduce novel disturbances, such as artificial light, noise pollution, and traffic that can affect species spatial and temporal niches, resulting in altered species interactions (Francis et al., 2009). Mining camps are also often targeted for animal management (e.g., culling of feral species or fencing), due to a higher chance of human-wildlife conflict. However, the impacts of mining on ecological communities are poorly understood (Gibson et al., 2023). The anticipated increase in threats to biodiversity from mining (Sonter et al., 2020), coupled with the high conservation value of many mineral-rich regions (Durán et al., 2013), highlights the need for a better understanding of the ecological ramifications of mining globally.

We employed a distributed control-impact design to examine the impacts of mining infrastructure—specifically mining camps—on animal communities, with a focus on species composition, functional diversity, and predator-prey interactions. We monitored mining camps (n = 8) and ecologically similar but largely unmodified reference areas (n = 8) at sixteen landscapes within the Pilbara region of Western Australia (Figure 2.1)—a region in which mining tenements cover 90% of land. We hypothesised that the presence of mining camps would lead to a decrease in species richness and diversity, while benefiting larger more mobile predators such as feral cats (*Felis catus*) and dingoes (*Canis lupus dingo*), which are better able to exploit resource subsidies (Newsome et al., 2014b). Consequently, this would result in changes to community structure and modifications in the temporal activity patterns of species, potentially leading to more interactions between predators and their prey. Such dynamics would likely result in alterations to the functional makeup of animal communities and modify the networks of species interactions.

2.3. Methods

Study area

Our study area spanned > 51,000 km^2 of the 179,000 km^2 Pilbara bioregion, a semi-arid region in north-western Australia (Figure 2.1), with maximum temperatures averaging 37°C during summer and 25°C during winter (McKenzie et al., 2009). Annual rainfall varies from 250–500 mm, and falls mostly between December and February (Bureau of Meteorology, 2020). The region features ancient, rugged terrain with deep gorges, rocky escarpments and outcrops, alongside extensive hummock grasslands, primarily composed of *Triodia* spp. and sparse stands of *Acacia* and *Eucalyptus* spp. (Van Vreeswyk et al., 2004). Mining tenements cover > 90% of the Pilbara bioregion (Environmental Protection Authority, 2014), and open pit mining is common, which often requires the establishment of a mining camp for workers. Mining camps do not contain areas of active mining or large waste landfills, but include infrastructure for accommodation, recreation, and catering. Lethal control of wildlife at mining camps is common, mostly focused on feral cats, dingoes, and rodents (*Rodentia* spp.), although no feral animal control was undertaken during monitoring. More details on mining camps are provided in Table A1 and Appendix A1.

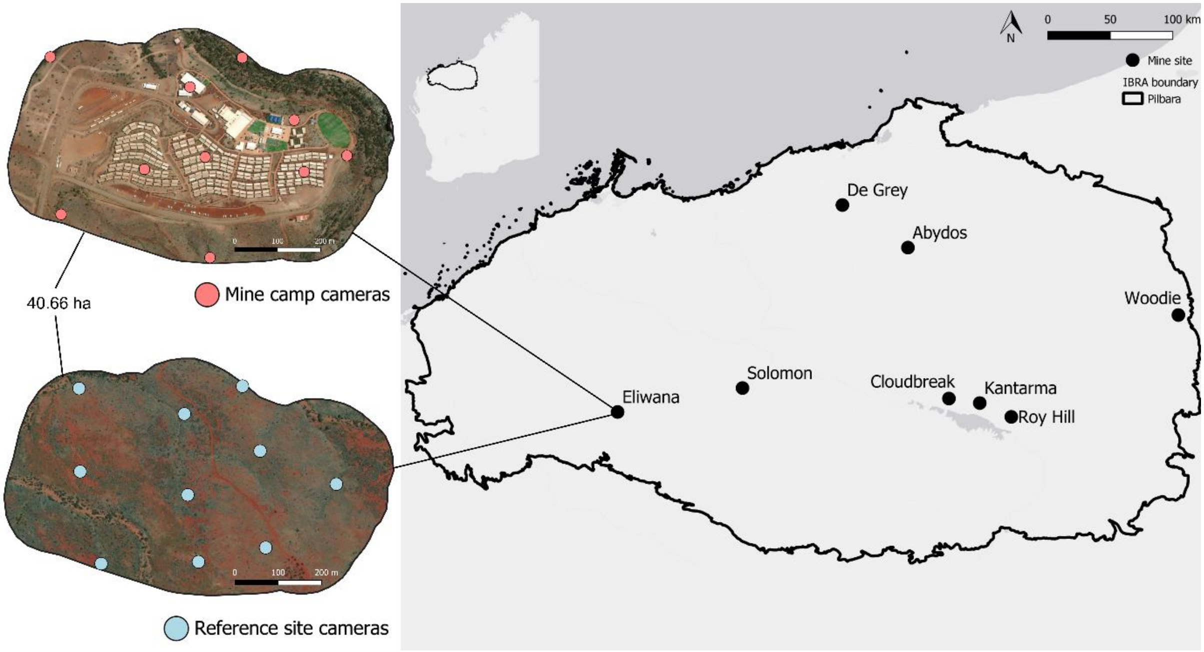


Figure 2.1: Mining camps monitored as part of this study across the Pilbara bioregion and an aerial view of the Eliwana mining camp and reference landscape showing camera trap placement (ESRI, 2021). Further describing information on mining camps is available in Table A1.

Landscape and site selection

We selected sixteen landscapes comprised of eight pairs, with each pair consisting of a mining camp and an ecologically similar but largely unmodified 'reference' landscape (Figure A1, Figure A2). The survey area of each mining camp was determined by digitising the camp boundary and adding a 100 m buffer using QGIS version 3.12.2-București (QGIS Development Team, 2020; Figure A3). Nearby reference landscapes were equal in area and chosen to be within the same major vegetation subgroup as the mining camp (pre-construction), while also meeting other environmental criteria (Appendix A2, Table A1). Ten survey sites were positioned within each mining and reference landscape > 100 m apart (16 landscapes x 10 sites = 160 survey sites in total). Within mining camps, five sites were positioned < 5 m from infrastructure (henceforth referred to as *inside* the mining camp), and five were randomly positioned > 50 m but < 100 m from infrastructure (henceforth referred to as *outside*; Figure A3). At the eight reference landscapes, ten sites were randomly placed >100 m apart.

Data collection

At each site, we deployed a Swift Enduro camera trap (Outdoor Cameras Australia, QLD), for ≥30 nights. Camera traps were mounted on stakes ~ 30 cm above the ground facing outward and south (Moore et al., 2020). A tuna and fish oil lure (in a cannister) was placed ~ 1.5 m in front of each camera (Heinlein et al., 2020). We note that using a lure can bias detectivity for some species, so there is a likelihood that some species were not detected in the landscape but the lure helps to attract animals in the immediate area. Camera arrays were standardised across landscapes, and results relate to species detectable by camera traps. Cameras were programmed to take five images per trigger at high sensitivity with no delay between triggers. Camera images were classified using Wildlife Insights (Cowan, 2023, Ahumada et al., 2020). We calculated the number of individual detections for each species, defined as those separated by at least 15 minutes (henceforth detection events) (Diete et al., 2016). Where there were many individuals of one species in a detection event, we included the highest count (Dundas et al., 2019). Where species-level identification was not possible, images were excluded from analysis (*n* = 35; except for rodents). Rodent species were pooled due to difficulty in identification (Potter et al., 2019), except for the spinifex hopping mouse (*Notomys alexis*), which has unique characteristics. We removed all detections of humans and domestic animals.

Data analysis

All analyses compare data at two levels. First, we compare responses between landscape types: mining camps and reference landscapes. In these analyses, data are pooled for each of the ten sites within each landscape (‘landscape treatment') to compare wildlife within mining (n=8) and reference (n=8) landscapes. Second, we compare response variables between locations within the mining camps, either inside or outside (‘location treatment’). In these comparisons, data are pooled across each of the five sites inside and outside of the mining camp, and data from the reference landscapes are not included. All analyses were performed in R version 4.3.1 (R Core Team, 2023b).

Species diversity, richness, and composition

We calculated the number of detection events within each landscape and location for 10 animal groups: dingoes, feral cats, varanids (*Varanidae* spp.), other reptiles (*Reptilia* spp.), ground-nesting birds (*Aves* spp.), arboreal-nesting birds, macropods (*Macropodidae* spp.), critical-weight-range (CWR) mammals (*Mammalia* spp.) (35–5500 g; Burbidge and McKenzie, 1989), small mammals (< 35 g), and feral herbivores (Figure A4). Dingoes and feral cats were modelled separately because they are top predators, and hence are both ecologically important and often controlled at mining camps. European rabbits (*Oryctolagus cuniculus*) were included in the feral herbivores group despite also being CWR mammals. We calculated Shannon’s diversity index for all native species, mammals, birds, and reptiles, respectively, at each landscape and location using the following formula:

$$H' = -\sum_{i=1}^{R} p_i \ln(p_i)$$

Where H' is Shannon's diversity index, p_i is the proportion of species i relative to the total number of species (i.e., $p_i = \frac{n_i}{N}$, where n_i is the detections of species i, and N is the total detections across all species), and R is the total number of species (Oksanen et al., 2007).

We used generalised linear mixed models (GLMMs) with the 'glmmTMB' package (Magnusson et al., 2017) to model the number of animal detections, species richness and Shannon's diversity in relation to landscape type (mining or reference) and location (inside versus outside), respectively. Animal detections and species richness were modelled assuming a Poisson distribution and Shannon's diversity assuming a Gaussian distribution. Random effects were included to account for the pairing of landscapes and the non-independence of sites within mining camps. An offset for trap nights was included to account for differing camera effort across landscapes and locations (i.e., due to occasional camera failure; Kotze et al., 2012). An observational random effect was included to account for overdispersion where needed (Harrison, 2014). We considered there to be a clear relationship between response and predictor variables when 95% confidence intervals do not overlap zero (Senior et al., 2023).

We compared species composition using permutational multivariate analysis of variance (PERMANOVA), fit using the "adonis2" function from the 'vegan' package (Oksanen et al., 2007). We used the Bray–Curtis distance metric to calculate dissimilarities following a square root transformation of detection events (standardised by camera trapping effort) to account for overdispersion (Bray and Curtis, 1957). We included a strata term to account for the pairing of landscapes and the non-independence of sites within mining camps. Community composition was visualised using non-metric multidimensional scaling (NMDS; Table A2) (Legendre and Legendre, 1998). Multivariate homogeneity of group dispersion tests (Gallé et al., 2021) were undertaken to assess dispersion within treatments using the "betadisper" function in the 'vegan' package (Oksanen et al., 2007).

Functional richness and dispersion

Functional traits are morphological, physiological, or behavioural characteristics of organisms that influence fitness and allow the organism to perform their ecological functions (Nock et al., 2016). Functional richness describes the trait composition diversity within an ecological community and functional dispersion describes the average trait dissimilarity (Cooke et al., 2019). We collated functional traits for all species from published trait databases and filled remaining gaps using published literature. We calculated the pairwise Gower's distance between species trait composition to measure the dissimilarity in functional traits among species (Gower, 1971). Species traits were weighted equally, except for categorical traits (e.g., leg development), which were individual binary traits weighted by a proportion of the number of categories (e.g. biped/quadruped/limbless each weighted by 1/3) (Lundgren et al., 2020). We calculated functional richness and functional dispersion for each landscape using the 'FD' package (Laliberté et al., 2014). We modelled functional richness and dispersion using GLMMs with the same model structure as above, specifying a Gaussian distribution with a log-link function for functional richness and a gamma distribution with a log-link function for functional dispersion using the "glmer" function from the 'lme4' package to fit these GLMMs (Bates et al., 2020).

Predator-prey networks

We collated dietary information for all predators from published diet databases and literature and identified all potential predatory links between co-occurring predators and prey across all landscapes and locations (Appendix A3). To test the impact of landscape type and location on predator-prey networks, we estimated four network metrics for each landscape and location using the 'omnivor' package (Violet and Gravel, 2019). Networks included the number of species interactions (analogous to species richness), network connectance, link density, and nestedness (Tylianakis et al., 2010). We only considered landscapes and location pairs that had networks with more than three interactions. This resulted in the removal of the Cloudbreak pairs. Networks were created using the 'igraph' package (Csardi, 2013). We performed a PERMANOVA following the same method for species composition, but replaced species detections with the four network metrics, after rescaling them to range from 0–1. We also fit a GLMM for each metric following the same model structure as above. The number of interactions was specified as having a Poisson distribution, link density a Gaussian distribution, and connectance and nestedness were modelled assuming beta distributions. Network metrics were visualised with a principal component analysis (PCA), using the 'stats' package (R Core Team, 2023a).

Temporal activity

To investigate how mining camps influence the temporal activity overlap of and between animal groups, we compared kernel density curves of activity between landscape types and locations using the ‘overlapEst’ function from the ‘overlap’ package (Meredith et al., 2014). This produces a coefficient of overlap that ranges from 0 (no overlap in activity) to 1 (complete overlap; Meredith and Ridout, 2018). We used the Dhat 1 ($\Delta 1$) estimator when the smallest group sample size was lower than 75, and the Dhat 4 ($\Delta 4$) estimator when the smallest group sample size was higher than 75 (Ridout and Linkie, 2009). We used Watson’s U^2 tests to test for significant differences in activity between treatments (Lund et al., 2017). Finally, we estimated the temporal overlap between all potential pairings of animal groups for each treatment. This analysis compared 83% confidence intervals of each animal group between landscape types and inside and outside mining camps, with overlapping confidence intervals suggesting no change in temporal overlap groups (Austin and Hux, 2002).

2.4. Results

Camera traps recorded 30,417 wildlife images over 5,266 trap nights (e.g., Figure A5). Images comprised 3,250 detection events of 3,561 animals (Table A3). Seventy-two species were identified (rodents, excl. spinifex hopping mice, were treated as one ‘species’): 15 mammal, 44 bird, and 13 reptile species. (Figure A4).

Species diversity, richness, and composition

Varanids and arboreal-nesting birds were detected at mining camps more than reference landscapes, with no clear relationships between landscape type and other animal groups (Figure 2.2, Table A4). Feral cats, ground-nesting birds, and macropods were detected less often inside mining camps than outside, while varanids were detected more inside than outside (Figure 2.2, Table A4). There were no clear relationships between location and other animal groups. Mammal diversity was lower at mining camps than reference landscapes (Figure 2.2, Table A5), whereas there was no clear relationship between landscape type and the diversity of all native species and other groups. The diversity of all native species, mammals, and birds was lower inside mining camps than outside, while reptile diversity was higher inside (Figure 2.2, Table A5). Species composition varied between landscape type (PERMANOVA, $F_{1,14} = 3.630$, $P = 0.008$; Figure A6), and location (PERMANOVA, $F_{1,14} = 2.062$, $P = 0.008$; Figure A6), and within-treatment dispersion was homogenous for both (landscape type: $F_{1,14}$ = 3.551, P = 0.084; location: $F_{1,14}$ = 0.090, P = 0.783).

Functional richness and dispersion

Functional richness had no clear relationship with landscape type but was lower inside mining camps than outside (Figure 2.2, Table A5). Functional dispersion was lower at mining camps than reference landscapes but had no clear relationship with location (Figure 2.2, Table A5). The mean body mass of species was roughly 2.5 kg at mining camps while it was almost 9 kg at reference landscapes (Table A6). This size dimorphism was also evident at the location scale with smaller species inside mining camps (~ 1.5 *cf.* ~ 3.5 kg). The mean number of offspring per breeding event was similar across landscape types but was slightly higher for species detected inside mining camps (Table A6). Four functional traits were absent from mining camps (limbless, ambulatory, undulatory, and cathemeral species), while all but two traits (arboreal and nectarivorous species) were present at reference landscapes (Table A7). Invertivores and omnivores dominated all landscapes and locations. Species with volant locomotion were present in higher proportions at mining camps than in reference sites (59% *cf.* 55%), as were diurnal species (71% *cf.* 68%), while nocturnal species were in present similar proportions across landscape types (20% of species; Table A6).

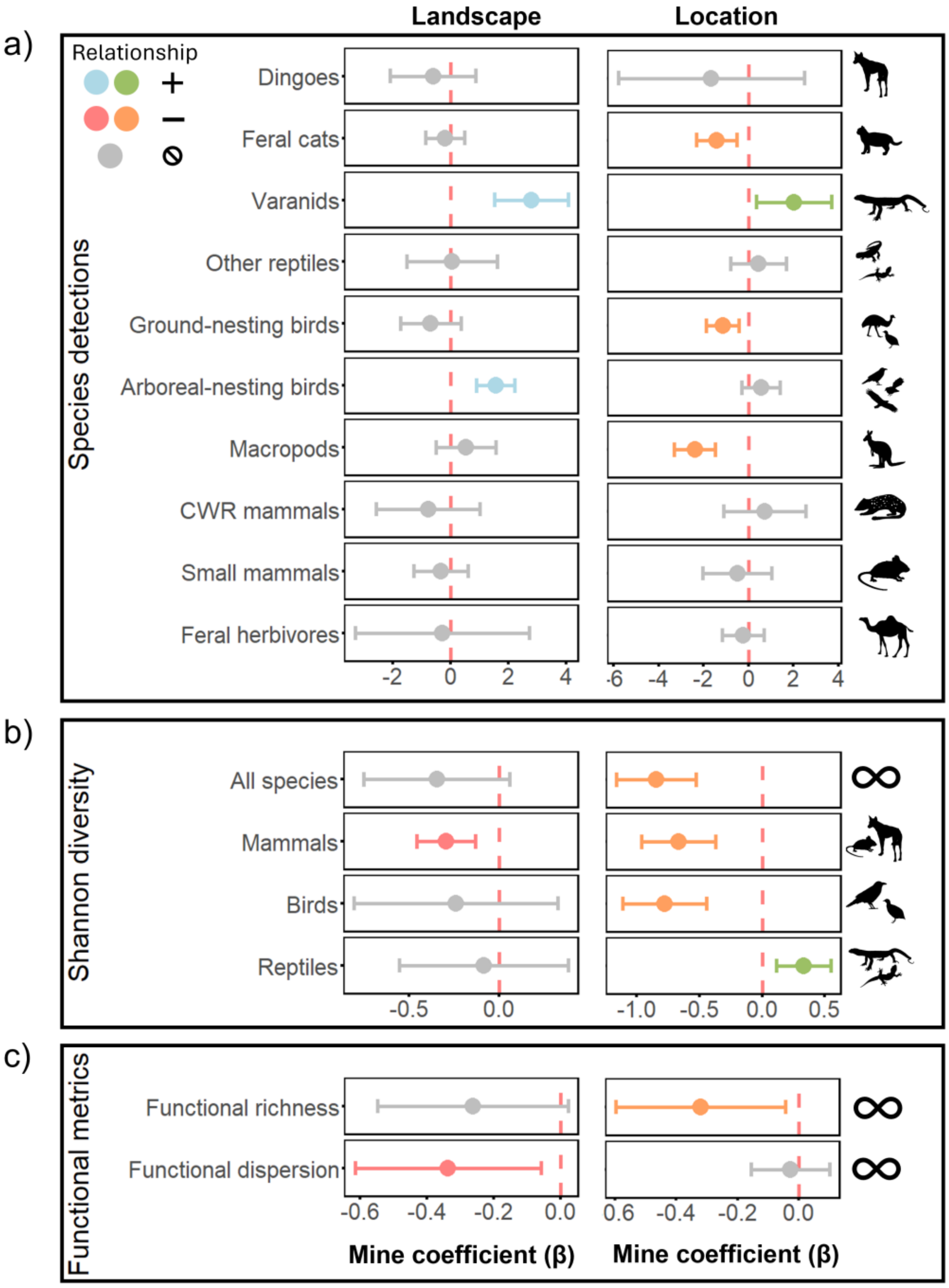


Figure 2.2: Coefficient plots from GLMMs investigating a) species detections, b) Shannon diversity and c) functional richness and dispersion, between landscape types and locations. Points reflect model coefficients for mining camps (landscape treatment) and inside mining camps (location treatment). Error bars represent 95% confidence intervals, with those in grey overlapping zero and showing no clear relationship. Positive relationships (i.e., no overlap with zero) are shown in blue (landscape treatment) and green (location treatment). Negative relationships are shown in red (landscape treatment) and orange (location treatment).

Predator-prey networks

Predator-prey networks showed no clear differences between landscape types (PERMANOVA, $F_{1,12}$ = 0.321, P = 0.719; Figure 2.3), or locations (PERMANOVA, $F_{1,12}$ = 1.414, P = 0.234; Figure 2.3), while within-treatment dispersion was homogenous for both (landscape type: $F_{1,12}$ = 3.743, P = 0.079; location: $F_{1,12}$ = 4.075, P = 0.070). However, GLMMs investigating specific network structures revealed that network connectance was lower at mining camps than reference landscapes (Figure 2.3, Table A8), and the number of interactions between predators and prey was lower inside compared to outside mining camps (Figure 2.3, Table A8).

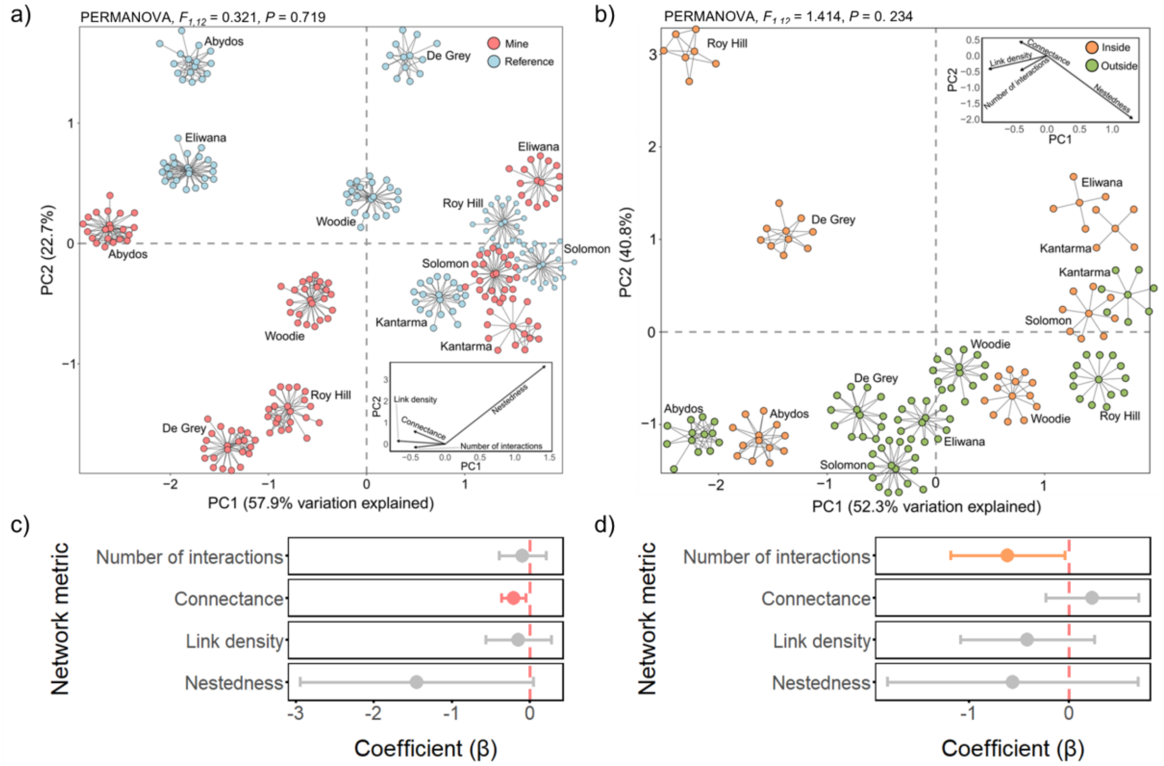


Figure 2.3: PCA plots presenting predator-prey networks at a) landscape types, and b) locations (excluding Cloudbreak). Networks are colour-coded by treatment type and labels indicate mine site name. The inset plot displays network metric importance on the first two principal components, determining the plotting of each landscape or location network. Arrows indicate the direction and strength of influence by each metric on PC1 and PC2. The results of PERMANOVA analyses are displayed above PCA plots and coefficient plots from GLMMs compare network metrics between c) landscape types and d) locations. Points reflect model coefficients for mining camps (landscape treatment) and inside mining camps (location treatment). Error bars represent 95% confidence intervals, with those in grey overlapping zero and showing no clear relationship. Negative relationships are shown in red (landscape treatment) and orange (location treatment).

Temporal activity

Temporal activity differed between mining camps and reference landscapes for three animal groups: ground-nesting birds, arboreal-nesting birds, and CWR mammals (Figure 2.4; Table A9). Birds were more active during the middle of the day at mining camps, while activity at reference landscapes followed a more diurnal-crepuscular pattern. CWR mammal activity was consistent across both diel periods at reference landscapes, but their activity narrowed at mining camps, being primarily nocturnal (Figure 2.4). Seven animal groups had no clear changes to their own temporal activity between landscape types. Two species (CWR and small mammals) narrowed their temporal activity inside mining camps to be primarily nocturnal—like the trend at the landscape scale—with more crepuscular activity observed outside (Figure 2.4; Table A9). Eight other animal groups had no clear changes to their own temporal activity between locations.

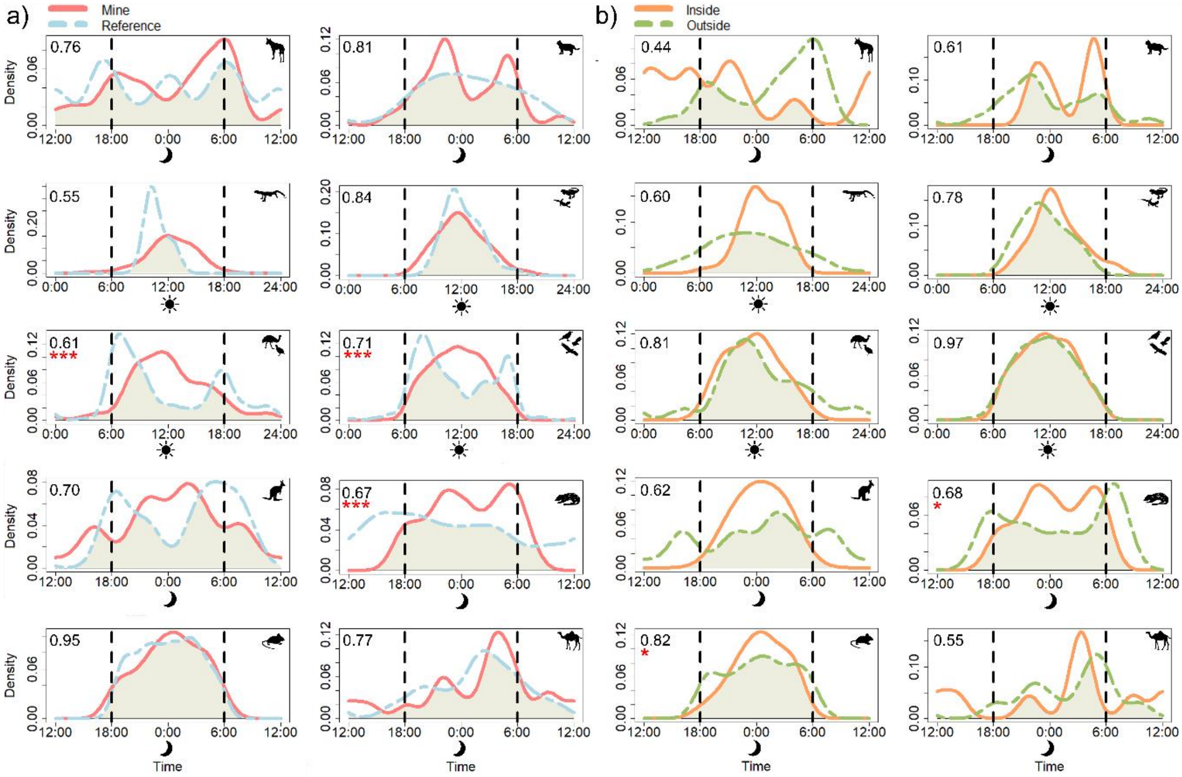


Figure 2.4: Activity patterns and temporal overlap plotted against time of day for animal groups at a) mining camps (red solid line) and reference landscapes (blue dashed line), and b) inside (orange dashed line) and outside (green dashed line) mining camps. Shaded areas represent the activity overlap between treatments, with the overlap value in the top left corner of each plot. Significant differences ($P < 0.05$) in temporal activity between treatments, as tested by Watson's U^2 tests, are represented by red asterisks under overlap values. Vertical black dashed lines indicate 6 am and 6 pm, the transition points in the diel cycle, and sun and moon symbols indicate if the plot is centred on noon (sun) or midnight (moon).

Differences in temporal overlap between animal groups at mining camps and reference landscapes were found for 16 pairs (Figure 2.5; Table A10). Nine of these pairs had higher temporal overlap at mining camps, with varanids particularly having higher overlap with small mammals, macropods, and birds at mining camps (Figure 2.5; Table A10). CWR and small mammals mirrored this relationship. Conversely, birds had lower temporal overlap at mining camps with potential mammalian predators, including dingoes, feral cats, and CWR mammals (Figure 2.5; Table A10). Feral herbivores had no clear changes in temporal overlap with other animal groups between landscape types.

Differences in temporal overlap between animal groups inside and outside mining camps were found for 16 pairs (Figure 2.5; Table A11). All pairs had lower overlap inside mining camps than outside. This included lower temporal overlap inside mining camps between feral cats and other predators—dingoes and varanids—and higher overlap between some predators and potential prey outside mining camps: including dingoes with macropods and small mammals, feral cats with birds, and varanids with small and CWR mammals (Figure 2.5; Table A11). Feral herbivores had no clear changes in temporal overlap with other animal groups between locations.

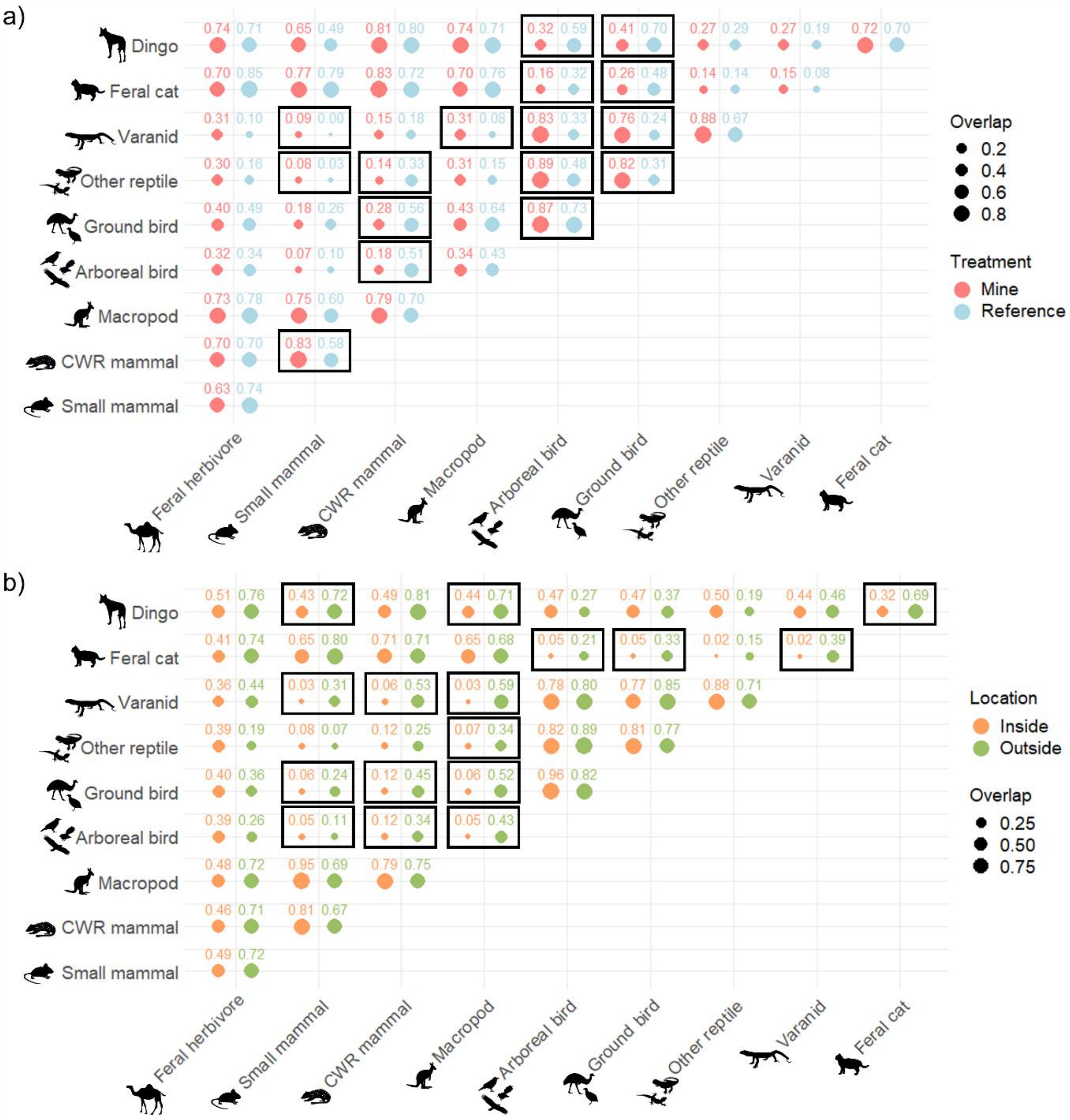


Figure 2.5: The temporal overlap between each animal group at a) mining camps (red circles) and reference landscapes (blue circles), as well as b) inside (orange circles) and outside (green circles) mining camps. Larger circles indicate higher overlap between animal groups, with overlap values written above their respective circles. Black bounding boxes surround animal group interactions where 83% confidence intervals do not overlap between treatments (suggesting a significant difference in temporal overlap).

2.5. Discussion

The establishment of mining camps—which are common features of mining landscapes across the globe—involves radical landscape change, yet we have little understanding of how their presence affects wildlife (Gibson et al., 2023). We show that mining camps have lower mammal diversity, functional dispersion, and connectance of predator-prey networks than unmodified reference landscapes, as well as altered species compositions. Species within mining landscapes also shift their temporal niches, sometimes leading to increased overlap with competitors and predators. Despite these differences, some community measures remained resilient to the landscape change. Total species diversity was similar across landscape types, as was functional richness. Predator-prey networks at mining camps also mirrored those at reference landscapes, albeit with an increased risk of collapse due to lower connectance.

Ecological function in mining camps

Our findings offer support for the 'landscape-divergence hypothesis' (Laurance et al., 2007), which postulates that unique disturbance pressures in spatially-separated landscapes (e.g., mining camps and reference landscapes here) aid the divergence of species compositions, despite initial similarities (Tscharntke et al., 2012). Landscape modification does not affect all species equally: in modified landscapes, adaptive, mobile species often have an advantage (Newsome et al., 2013a), with specialised, less mobile species, less able to adjust to modified conditions (Lindenmayer et al., 2023). For example, we detected more arboreal-nesting birds at mining camps—a functional group commonly associated with humans due to their ability to fly and their adaptive, opportunistic feeding strategies (Møller, 2009). Differences in species responses to disturbance act as a biotic filter (i.e., excluding some species not well adapted), shifting communities from historic species compositions, to those better adapted to disturbance (Tscharntke et al., 2012), thus forming novel assemblages (Higgs, 2017). Restoring these systems to their former condition could be highly challenging, expensive, or impossible (Hobbs et al., 2006).

Despite differences in species composition, mining camps and reference landscapes had similar functional richness, indicating a comparable breadth of ecological traits. By contrast, mining camps exhibited lower functional dispersion, indicating an unequal distribution of functional traits and a redundancy in ecological functions (i.e., multiple species with similar traits performing fewer ecological roles). For example, there was an increased proportion of cursorial, scansorial, and volant species at mining camps, with less representation by species with other locomotion methods (e.g., undulatory, saltatorial). Increased functional redundancy at mining camps suggests that mining camp ecosystems are somewhat resilient to species loss, given the presence of several other species with similar traits that can fill the same role (Carmona et al., 2016). However, lower functional dispersion at mining camps has the potential to destabilise ecosystem function, with a lack of diversity in functional roles reducing the chance of at least some species being able to adapt to future disturbances (Mori et al., 2013). It is important to balance functional richness and dispersion, to combat negative impacts of disturbance events and species loss (Cooke et al., 2019). Our results suggest that this is not the case for mining camp ecosystems. Threats to ecosystem function are exacerbated inside mining camps, where functional richness was much lower than outside, highlighting that there are fewer functional roles being filled here and likely reduced capacity for ecosystem function (Petchey, 2003).

Do mining camps impact predator-prey interactions?

Contrary to predictions, detections of top predators (i.e., dingoes, feral cats) were similar at mining camps and reference landscapes. This result was unexpected given that mining camps attract predators by providing resource subsidies (Newsome et al., 2013a, Newsome et al., 2014b). It is possible that past control programs at mining camps have reduced dingo and feral cat numbers. Conversely, varanid species were detected more at mining camps than reference landscapes. Varanids fill top and middle-order trophic positions across the Pilbara (Shine, 1986), and some large varanids can outcompete and predate upon feral cats (Doody et al., 2023), which may also explain the lower-than-expected activity of feral cats at mining camps. Newsome et al. (2014a) showed that increased consumption of food waste by dingoes at a mining camp in the Tanami Desert led to decreased predation of varanids. Such prey-shifting could explain the heightened varanid activity detected at mining camps, given varanids also likely make use of resource subsidies here.

Despite differences in species composition and functional dispersion, the structure of predator-prey networks was similar in mining camps and reference landscapes. Similar detections of high-trophic predators like dingoes and feral cats, and increased detections of varanids at mining camps offsetting reduced mammal diversity, likely help stabilise predator-prey networks across landscape types. Large predators are important for food web stabilisation, but in this case, the average species body mass at mining camps was more than three times less than reference sites—highlighting potential reductions in the trophic levels of species (Barnes et al., 2010). The stability of predator-prey networks across landscape types despite differences in species body mass could be explained by universal dynamics (i.e., consistent patterns governing dynamics across diverse systems and scales; McGill, 2003). This would suggest that fundamental predator-prey interactions (e.g., the Lotka-Volterra model; Lotka, 1920), underlie the structure of ecological networks across landscape types, regardless of disturbance pressures or the level of trophic relationships (Bashan et al., 2016). Hatton et al. (2015) studied thousands of animal communities of varying trophic levels in different environments and found that food webs scaled with changes to predator-prey biomass (i.e., the predator-prey power law). This indicates that a common pattern stabilises predator-prey interactions despite variation in species composition, trophic level, and environmental disturbance (Perkins et al., 2022).

Nonetheless, we identified differences in specific network metrics. Network connectance was lower at mining camps, suggesting a simplified predator-prey structure (Dunne et al., 2002a). At mining camps, we found a lower proportion of vertivores (i.e., meat eating animals) compared to reference landscapes, and higher proportions of invertivores, nectarivores, and granivores—likely due to increased resources for these animals—suggesting a reduction in top or middle-order predators relative to the number of lower trophic species. Low network connectance can reduce food web robustness and increase vulnerability to species loss and secondary extinctions (Dunne et al., 2002b, Baumgartner, 2020). Predator-prey networks had fewer links inside mining camps than outside—likely driven by lower total species diversity reducing the number of trophic relationships. Predator-prey networks with a low number of links can destabilise ecosystem processes to the detriment of overall ecosystem function (Tylianakis et al., 2010). This means that, despite a similar overall function of predator-prey networks across landscape types, the presence of top-down and bottom-up pressures from humans in mining camps likely makes them fragile to the effects of future disturbances or management changes (McCann, 2007, Dorresteijn et al., 2015).

Behavioural responses to disturbance

Thirty percent of animal groups shifted their temporal activity at mining camps compared to reference landscapes, narrowing their temporal niches in all cases—a common trend for animals in response to human disturbance (Lewis et al., 2021). One animal group, CWR mammals, despite having similar detections across landscape types, became exclusively nocturnal at mining camps, while birds became exclusively diurnal, showing more crepuscular activity at reference landscapes. These activity shifts drove changes in overlap between some animal groups, suggesting shifts in species interactions (e.g., predator-prey relationships, competition). For example, temporal overlap between CWR and small mammals increased at mining camps, raising competition and predation risk for small mammals. Meanwhile, birds had higher temporal overlap with varanids at mining camps, and lower overlap with dingoes, feral cats, and CWR mammals. As a result of this shift, birds likely encounter different predators in mining camps compared to reference landscapes. Feral cats had lower overlap with dingoes and varanids inside mining camps, supporting the notion that predators segregate their activity in high-disturbance, low-resource habitats (Vilella et al., 2020).

We found 16 changes in temporal overlap between animal groups at mining camps, increasing, and decreasing in roughly even numbers. Reasons for this relate to differing animal responses to disturbance; if some animals have stable temporal niches in modified landscapes, others with altered activity may cause changes in overlap between those species (Lewis et al., 2021). For example, arboreal-nesting birds had altered temporal overlap with six other animal groups, and ground-nesting birds with five. They were also two of the few animal groups with altered temporal activity at mining camps. This may also explain the lack of a clear trend in overlap differences between landscape types, which may be due to niche differences between animal groups (i.e., diurnal or nocturnal *cf.* crepuscular) and the nature of the change. Emphatically however, at the location scale, all 16 changes in temporal overlap between animal groups were lower inside mining camps. Species likely concentrate their activity outside mining camps at similar times due to habitat preferences or to avoid disturbance inside mining camps such as artificial light or humans (Ciach and Fröhlich, 2019). This higher overlap potentially increases pressure on resources or species interactions here, while lower overlapping activity inside mining camps reinforces the segregation of temporal niches by animals in modified landscapes (Vilella et al., 2020).

Are impacts of disturbance localised?

In many cases, we found varying responses at the landscape and location scales for the same animal group. For example, feral cats, ground-nesting birds, and macropods were detected similarly across landscape types, but were detected less inside mining camps. Total species diversity was also lower inside mining camps, despite being similar across landscape types. Highly disturbed habitats, like those inside mining camps, broadly evoke negative responses for many species (Doherty et al., 2021). This indicates that the impacts of disturbance at mining camps are sometimes quite localised (i.e., communities respond differently to variable disturbance at sites within the landscape; Sepúlveda and Valdivia, 2016). Communities are likely not completely separate at this scale, linked by the dispersal of some species, forming metacommunity dynamics (Leibold et al., 2004). The fact that we identified differences in animal responses at this scale indicates that disturbance variability at mining camps should be considered during animal management here (Gallo et al., 2017).

2.6. Conclusion

The observed impacts on wildlife at mining camps underscore the distinct ecological footprint of this disturbance. While there are some species that benefit—the apparent release of varanids for instance—localised effects of disturbance at mining camps suggest that areas of high disturbance reduce species diversity and functional richness. Importantly, predator-prey networks at mining camps seem to somewhat replicate those in reference landscapes, despite considerable differences in species composition and species mass. However, low connectance of predator-prey networks at mining camps puts food webs at risk of potential future disturbances, such as the removal of keystone species. High functional redundancy somewhat buffers mining camp ecosystems from the same threat, but the lack of functional diversity among ecological roles suggests that ecosystems here do not function similarly to those in unmodified landscapes. Identifying species that are influenced by disturbance aids their management in human landscapes, but it is also important to consider species which are less affected and may offer links between novel and unmodified ecosystems, allowing important ecosystem dynamics to occur. As mining landscapes continue to expand globally, the implications of our findings extend to other similarly modified landscapes. Current conservation approaches often prioritise individual species for conservation or management, yet our study advocates for an ecosystem-wide, community level approach. Recognising the importance of species roles, interactions, and structures within ecosystems is essential for effective conservation (Tylianakis et al., 2010). These insights are important to help inform sustainable land management practices that appropriately balance environmental and economic needs in human-dominated ecosystems.

2.7. Acknowledgements

We acknowledge the Nyamal, Kariyarra, Eastern Guruma, Palyku, Nyiyaparli, Yindjibarndi, and Puutu Kunti Kurrama and Pinikura (PKKP) people as the traditional owners of the land on which fieldwork was conducted. This research was supported by Fortescue Metals Group, Consolidated Minerals, Spectrum Ecology, Atlas Iron, Roy Hill, De Grey Mining, and the Department of Biodiversity, Conservation and Attractions for their support. Thanks to Todd Edwards, Damian Cancilla, Astrid Heidrich, Harriet Davie, Stewart O'Brien, Jarred Di Marco, Kate Stanbury, Riley Pattinson, Luke Barrett, Kaylee Prince, Jacqui Roberts, Theda Morrissey, Sarah Thomas, and Alyse Burns. All research was undertaken under ethics approval, granted by Charles Sturt University (A21062), an 'Authorisation to Take or Disturb Threatened Species', granted by DBCA (TFA 2021-0078), and a 'Scientific Use Licence', granted by DPIRD (U218/2021-2023).

Chapter 3: Non-preferred habitat increases the activity area of the endangered northern quoll (*Dasyurus hallucatus*) in a semi-arid landscape

Manuscript published: Cowan, M. A., Moore, H. A., Hradsky, B. A., Jolly, C. J., Dunlop, J. A., Wysong, M. L., Hernandez-Santin, L., Davis, R. A., Fisher, D. O., Michael, D. R., Turner, J. M., Gibson, L. A., Knuckey, C. G., Henderson, M. & Nimmo, D. G. 2022. Non-preferred habitat increases the activity area of the endangered northern quoll (*Dasyurus hallucatus*) in a semi-arid landscape. *Australian Mammalogy,* 45**,** 138–150.

Cowan, M. A.[1,2,*], Moore, H. A.[3], Hradsky, B. A.[4], Jolly, C. J.[1,5], Dunlop, J. A.[1,2,6], Wysong, M. L.[7], Hernandez-Santin, L.[8], Davis, R. A.[9], Fisher, D. O.[10], Michael, D. R.[1], Turner, J. M.[11], Gibson, L. A.[3,12], Knuckey, C. G.[13], Henderson, M.[9], Nimmo, D. G.[1]

[1]Gulbali Institute, School of Agricultural, Environmental and Veterinary Sciences, Charles Sturt University, Thurgoona, NSW, 2640, Australia.

[2]School of Agriculture and Environment, University of Western Australia, Crawley, WA, 6009, Australia.

[3]Department of Biodiversity, Conservation and Attractions, Kensington, WA, 6151, Australia.

[4]School of Ecosystem and Forest Sciences, University of Melbourne, Parkville, VIC, 3010 Australia.

[5]School of Natural Sciences, Macquarie University, Macquarie Park, NSW, 2109, Australia

[6]Western Australian Feral Cat Working Group, Mandurah, WA, 6210, Australia.

[7]Research Institute of Environment and Livelihoods, Charles Darwin University. Casuarina, NT, 0810, Australia.

[8]Centre for Mined Land Rehabilitation, Sustainable Minerals Institute, University of Queensland, St Lucia, QLD, 4067, Australia.

[9]School of Science, Edith Cowan University, Joondalup, WA, 6027, Australia.

[10]School of Biological Sciences, University of Queensland, St Lucia, QLD, 4072, Australia.

[11]Institute of Biomedical and Environmental Health Research, School of Health and Life Sciences, University of the West of Scotland, South Lanarkshire, G72 0LH, United Kingdom

[12]School of Biological Sciences, University of Western Australia, Crawley, WA, 6009, Australia.

[13]Biologic Environmental Survey, East Perth, WA, 6004, Australia.

3.1. Abstract

Animal conservation requires a sound understanding of the movement ecology and habitat selection of the species in question. A key component of this is identifying habitats that animals actively seek or avoid. We quantified habitat selection and investigated the drivers of variability in the short-term activity area of a small, endangered mesopredator, the northern quoll (*Dasyurus hallucatus*), in the Pilbara region of Western Australia. We collated, standardised, and analysed 14 northern quoll GPS tracking events from four studies conducted between 2014 and 2018. Northern quolls selected activity areas in locations that were more topographically rugged than the broader landscape, characterised by higher percentage cover of rocky habitat and riverbed, and lower percentage cover of spinifex sandplain. The size of their activity area also increased with higher percentage cover of non-preferred spinifex sandplain. Therefore, the destruction of habitats preferred by northern quolls—such as mining of rocky habitat—and introduction of structurally simple habitat like spinifex sandplain, is likely to negatively impact resource availability and lead to altered movement patterns that could decrease survival. Future conservation planning should place emphasis on the protection of rugged rocky habitat for northern quolls, as well as efficient movement pathways between patches of this critical habitat.

3.2. Introduction

Effective conservation requires knowledge of the spatial and temporal use of preferred habitats by target species (Dellinger et al., 2020). Animal space use reflects resource availability in the landscape (Michel et al., 2020, Wysong et al., 2020a). If landscapes are resource-rich, animals travel shorter distances (Doherty et al., 2019, Martin and Martin, 2007, Viana et al., 2018). Conversely, where resources are limited, animals travel further to access food, shelter, or mates (Gardiner et al., 2019, Rus et al., 2020, Stobo-Wilson et al., 2021). In fragmented landscapes, where an animal's preferred habitat is interspersed among non-preferred habitat, animals may need to acquire resources from multiple patches of the preferred habitat type (Dunning et al., 1992). The spatial extent and configuration of non-preferred habitat can affect the capacity of animals to move between preferred habitat (Nimmo et al., 2019): large areas of non-preferred habitat can lead to increased travel time (Beasley and Rhodes, 2010) and reduced foraging efficiency while increasing predation risk and energy expenditure (Brown, 1988, Haapakoski et al., 2013). These behaviours are often influenced by predator interactions and the 'landscape of fear', where animals perceive certain habitats and resources as riskier than others (Bleicher, 2017, Brown, 1988).

One species which lacks information about its movement and habitat use is the northern quoll (*Dasyurus hallucatus*)—an endangered, nocturnal mesopredator native to northern Australia (Moore et al., 2019). Over the past century, northern quolls have suffered substantial range declines (Moore et al., 2019, Braithwaite and Griffiths, 1994), presumably due to habitat loss, introduced predators (namely the feral cat, *Felis catus*), altered fire regimes, and cane toads (*Rhinella marina*) (Ibbett et al., 2018, Moore et al., 2019, Woinarski et al., 2010). The Pilbara region of Western Australia contains the last cane toad-free populations of northern quolls (Moore et al., 2019, Woinarski et al., 2014). Yet quolls in the Pilbara are far from secure (Cramer et al., 2016, Moore et al., 2021a). Drill and blast mining operations often target the rocky habitat that also provides crucial denning sites for northern quolls (Ramanaidou and Morris, 2010), because of their rich deposits of minerals such as iron ore, resulting in a structurally simplified landscape (Cramer et al., 2016, Henderson, 2015). Based on previous research, we know northern quolls are most likely to be found in rugged rocky outcrops but are less common in spinifex sandplain habitats (Moore et al., 2021b, Hernandez-Santin et al., 2016, Shaw et al., 2022).

While this research has informed much conservation work (Moore et al., 2021a), we know very little about how rocky habitat and spinifex sandplain influence northern quoll movement and space use, and even less about how northern quolls interact with other habitat types (Cramer et al., 2016). Understanding how northern quolls use different habitats, and how these habitats influence their movements, will allow greater protection of critical habitat and better inform rehabilitation projects which seek to reconnect remnant habitat or replicate northern quoll habitat that has been disturbed or destroyed (e.g., Cowan et al., 2020b).

In this study, we investigate the space use and habitat selection of northern quolls in a naturally fragmented landscape of rocky outcrops, spinifex sandplains, *Acacia* stands, and dry riverbeds in the Pilbara, Western Australia. Riverbed in the Pilbara is often associated with rocky habitat, while *Acacia* stands are patchily distributed amongst spinifex sandplain and rocky habitat (Van Vreeswyk et al., 2004). Previous estimates of northern quoll movement are mostly derived from Very High Frequency (VHF) tracking (e.g., Cook, 2010, King, 1989, Oakwood, 2002)—a technology now largely superseded by Global Positioning System (GPS) tracking (e.g., Heiniger et al., 2020, Hernandez-Santin et al., 2020). We collated, standardised, and analysed GPS data from four studies to investigate habitat selection, and the influence of habitat type on movement, by northern quolls. We developed two predictions based on existing knowledge of northern quoll behaviour and ecology:

First, we predicted that northern quolls would select for habitats which are topographically rugged, such as rocky habitat and riverbed—which likely offer many resources required for survival—and due to the potential increased exposure to predators, would avoid simpler habitats like spinifex sandplain and *Acacia* stands. Rocky habitat is likely perceived as less risky by northern quolls, as feral cats—an agent of northern quoll decline and a threat to other quoll species (Fancourt et al., 2015)—are more common and more successful hunters in less complex habitats such as spinifex sandplain (McGregor et al., 2015, Williamson et al., 2021).

Second, we predicted that northern quoll activity areas (i.e., the movement footprint of northern quolls over seven nights) would be larger when containing higher percentages of presumably non-preferred habitat, such as spinifex sandplain, due to a lack of necessary resources for quolls, requiring them to travel further to access preferred habitat (e.g., rocky habitat).

3.3. Methods

Study area

The Pilbara bioregion covers 179,000 km^2 of Western Australia and experiences a semi-arid climate, with average maximum temperatures of 37°C during summer and 25°C during winter (McKenzie et al., 2009). Annual rainfall is variable (250–500 mm), and falls predominately between December and February (Bureau of Meteorology, 2020). The Pilbara is characterised by patches of rocky habitat with rugged hills, deep gorges, rough escarpments, and sandy plains (Carwardine et al., 2014, Van Vreeswyk et al., 2004). The flora is diverse but is predominately composed of *Acacia*, *Triodia* (spinifex), and *Eucalyptus* species, the composition of which is largely influenced by local geology and fire history (Maslin and van Leeuwen, 2008, Van Vreeswyk et al., 2004).

We studied habitat selection of northern quolls at four sites in the Pilbara, using data from four different studies conducted between 2014 and 2018 (Cowan et al., 2020b, Hernandez-Santin et al., 2020; Moore, unpubl. data; Figure 3.1; Table B1 & B2, Biologic, 2016). Studies occurred primarily on Karriyarra, Ngarluma, and Nyamal country, and occupied a mixture of pastoral leases, national parks, and mining tenements (Table B1). Study sites were broadly similar in that they all contained rocky habitat, spinifex sandplain, and scattered *Acacia* stands. One site, Red Rock, also contained a sandy riverbed which flows seasonally and is closely associated with rock (Van Vreeswyk et al., 2004; Figure 3.2).

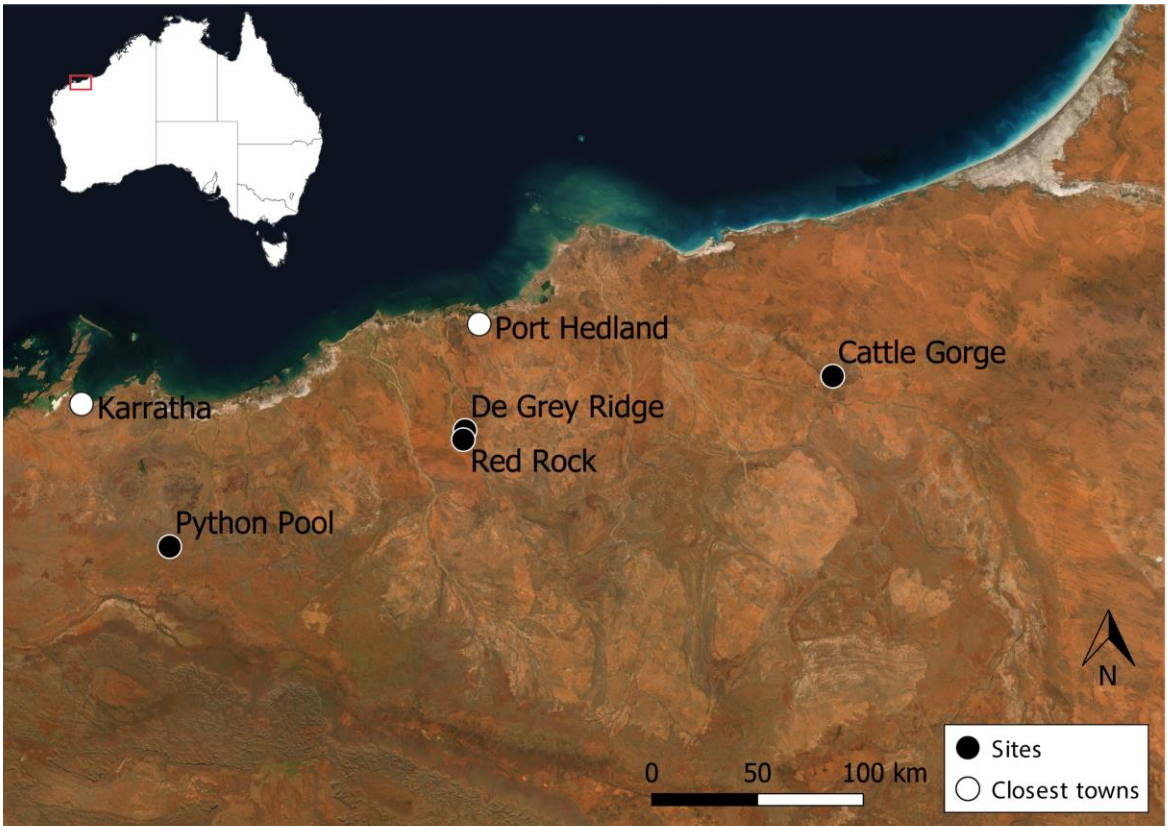


Figure 3.1: A map of the locations of the four sites in the Pilbara region of Western Australia where northern quolls were tracked between 2014 and 2018. Black points represent study sites and white points represent major towns close to study sites. The satellite base map was sourced from ESRI (2021).

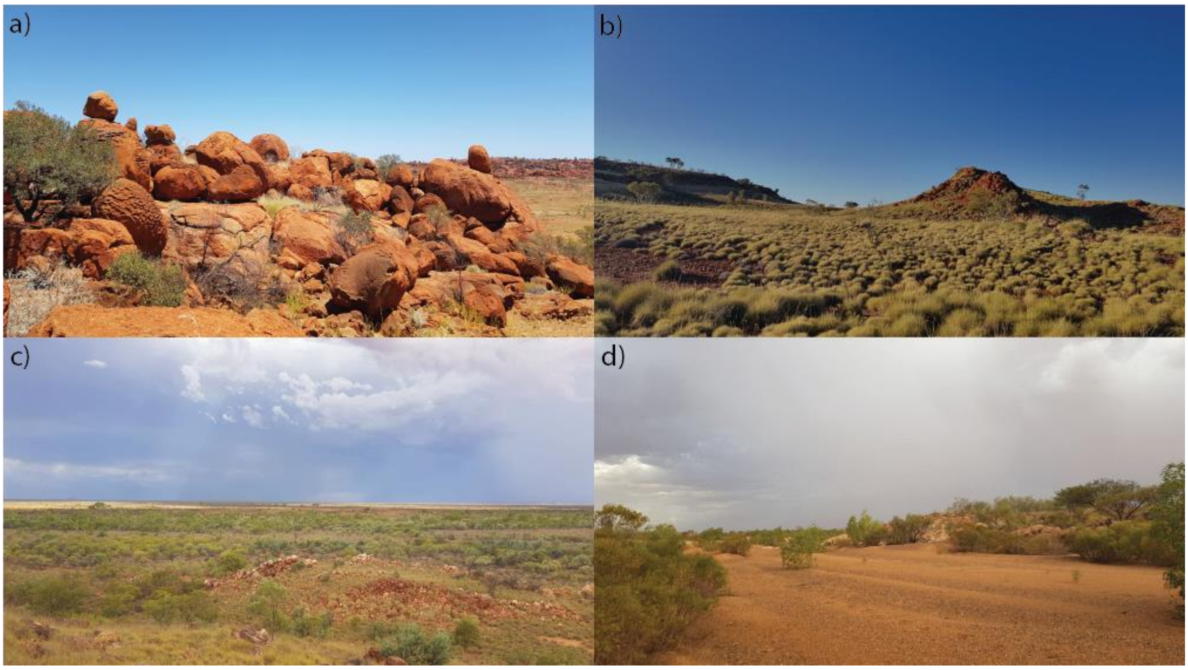


Figure 3.2: Examples of the dominant habitat types at our study sites in the Pilbara region of Western Australia: a) rocky habitat, which often rises above the landscape to form outcrops; b) spinifex sandplain, which fragments rocky habitat and can stretch for kilometres; c) *Acacia* stands, which can form thick patches throughout the rocky spinifex matrix; and d) riverbed, which consists of a sandy base between rocky habitat and vegetation. Photographs: Cowan, M.

Maps of habitat features

We used QGIS v3.12 (QGIS Development Team, 2020) to create a map of habitat features for each site. We applied semi-supervised classification of normalised difference vegetation index (NDVI) layers (Pandey and Kulhari, 2018), derived from Sentinel-2 imagery (USGS, 2023), to map the six habitat types we considered likely to influence the spatial ecology of northern quolls: rocky habitat, spinifex sandplain, *Acacia* midstory over spinifex understory (henceforth *Acacia* stands), sandy dry riverbeds (henceforth riverbed), water, and disturbed ground (e.g., a road or cleared land). This was done using the semi-automatic classification plugin (SCP) in QGIS (Congedo, 2016). Feature layers for the habitat maps were captured at a scale of 10 m for each site during the year tracking took place and as close to the month as possible (depending on cloud cover limitations)—except for at Red Rock where we used a consistent layer (2014) for each year. Red Rock had no fires between 2014 and 2018 and habitat features remained relatively consistent across years. Habitat feature maps were cross-examined with the corresponding satellite imagery to ensure the accuracy of habitat feature classification and to train the classification of habitats (as per Tilahun and Teferie, 2015). All landscapes were classified independently to account for differences in seasonal or temporal variation in NDVI. During analysis, we did not investigate northern quoll selection of water or disturbed ground due to a lack of representation among sites.

Animal capture and data acquisition

Trapping effort varied slightly between the studies, however, the same broad method was applied, and all live animal research was approved by the respective institutional animal ethics committees (see Acknowledgements). Wire cage traps (45 cm × 17 cm × 17 cm, Sheffield Wire Co., Welshpool, WA) were deployed in transects during autumn, winter, or spring between 2014 and 2018 (see Biologic, 2016, Cowan et al., 2020b, Hernandez-Santin et al., 2019). Trapping did not occur during summer to avoid trapping females raising young during this time (Dunlop et al., 2014). Traps were placed in rocky and riparian habitats because these are the areas in which northern quolls locate their dens in the Pilbara (Hernandez-Santin *et al.* 2022), resulting in an increased likelihood of trap success. Traps were baited with universal bait (oats and peanut butter) or a mixture of the universal bait and sardines (as per Dunlop et al., 2014). Traps were opened in the evening and checked the following morning. All individuals were processed at the site of trapping, which involved taking a series of morphological measurements, recording sex and weight, and attaching a GPS unit (provided the unit did not exceed five percent of the animal’s bodyweight). GPS units were deployed on 25 individuals for up to 37 days before animals were re-trapped and the GPS unit was removed. GPS units were fitted as collars or backpacks; brands and tracking methods differed slightly between studies due to limitations of battery life, data storage, and study time (Table B2).

Data screening and processing

To eliminate errors and reduce bias due to variation in study methods, data were screened prior to being included in analysis. Data contributed by Biologic (2016) had been pre-screened by the authors to discard all locations not recording elevation, as well as those with low GPS accuracy (horizontal dilution of precision greater than 5). We screened all datasets further by discarding GPS points before 12:00 pm on the day of collaring, as well as all those after 12:00 pm on the date before collar retrieval, as GPS fixes may have been affected by quolls being in a trap. Unrealistic GPS fixes were removed based on the average sprinting speed of northern quolls (4.5 m s^{-1}) (Wynn et al., 2015), where points too far to be reached in the time between fixes were excluded (Bjørneraas et al., 2010).

To ensure that GPS locations reflected the times when northern quolls were active, we only included GPS locations recorded between 6:00 pm and 6:00 am. Individuals with fewer than 30 fixes, as well as individuals whose GPS units failed within the first day, were removed because there was unlikely sufficient data to accurately measure activity areas (Girard et al., 2002, Seaman et al., 1999). We did not standardise fix rates among datasets because doing so resulted in many unusable individuals with too few GPS locations, and differences in fix rate are often negligible when applying kernel density estimation (Huck et al., 2008, Mitchell et al., 2019, Peris et al., 2020).

Activity area size

Many tracking events did not represent complete home ranges of each individual and instead represented a sample of each individual's home range. This is because they did not reach an asymptote with fixes added sequentially (i.e., over time) at 10-fix intervals. An asymptote is calculated by plotting activity area with the number of fixes—with 10 sequential fixes added in each iteration in this case—and is reached when adding additional fixes has little to no effect on the size of the activity area, thus representing a true home range (Harris et al., 1990). Instead, to account for differing tracking durations among individuals, we standardised each dataset to a total period of seven nights (one week) and refer to the area used by northern quolls during this time as their 'short-term activity area' (henceforth activity area) (Doherty et al., 2019).

Some individuals were tracked for one week, but GPS tracking ceased before seven nights of data could be reached (likely due to battery failure or memory limitations). Therefore, six individuals were tracked for less than seven nights, and six individuals were tracked for seven nights (*n* = 12). The shorter tracking duration for these individuals is accounted for in further analyses (see below). For one individual (E6CA67) tracked for 29 nights, we isolated each seven-night period (hereafter referred to as a 'tracking event'), separated by a buffer of one night between each. Each tracking event was treated as an individual event, and therefore the individual quoll appears in the data three times. We accounted for this by including 'individual' as a random effect in all analyses (Bates et al., 2015).

We estimated northern quoll activity area from utilisation distributions (UDs) at the 95% isopleth using fixed kernel density estimation (KDE). Kernel density estimation uses a smoothing parameter or bandwidth (*h*) to smooth GPS points, creating a probability density estimate which reflects the intensity of use within an animal's activity area (Signer et al., 2015). We used the *ad hoc* method ($h_{ad\ hoc}$) (referred to as 'reference scaled' in the R package; see below) to determine h because $h_{ad\ hoc}$ is robust to sample size, accurately reflects the true activity area, and is consistent and repeatable (Kie, 2013). We used fixed KDE (where the kernel width remains the same regardless of the distance between points) instead of adaptive KDE (where the kernel width increases with increasing distance between points) because adaptive KDE can sometimes over-estimate activity area size (Powell, 2000, Kernohan et al., 2001, Blundell et al., 2001). We used the package "rhr" (Table B3, Signer and Balkenhol, 2015) in R version 1.3.959 to estimate activity area (R Core Team, 2023b).

Habitat selection

To analyse northern quoll habitat selection, we quantified the percentage of habitat types in each "used" short-term activity area (*n* = 14) and 10 randomly placed circular "available" activity areas per individual (*n* = 140), equal in size to the activity area of the individual being measured and randomly placed within the available landscape (Squires et al., 2013, Wysong et al., 2020a). Due to the fragmented nature of northern quoll habitat in the Pilbara (Moore et al., 2021b), available activity areas for each individual were sampled within habitat considered accessible by that individual (Hazen et al., 2021). To define the boundaries for the available landscape for each individual, we followed a similar method to Wysong et al. (2020a). We fitted a 100% minimum convex polygon (MCP) to the GPS data of each individual tracking event. We then placed a buffer around each MCP equal to the radius of the largest northern quoll activity area if assumed to be circular (897 m). We then subtracted the radius of the activity area being measured. We used the "extract" function in the "raster" package to determine the proportion cover of each habitat type within each "used" and "available" activity area in R (Hijmans et al., 2015).

To test our predictions about selection and avoidance of the four habitat types, we used Beta-Binomial Mixed Models (BBMMs) to evaluate if the proportion cover of each habitat type differed between "used" and "available" activity areas. BBMMs allow for the analysis of proportion data—including over-dispersed proportion data—and random effects (Douma and Weedon, 2019). We did not account for tracking duration in BBMMs because the data were proportion data which was relative to each individual tracking event. A separate BBMM was fitted for each habitat type. The response variable was the proportional cover of the habitat type (rocky habitat, riverbed, spinifex sandplain, *Acacia* stands) within an activity area, and the predictor variable was the "used" or "available" activity area. The reference category (intercept) was the "available" activity area category. Selection (or avoidance) was evaluated using a *p*-value statistical significance approach. We included 'individual' and 'site' as random effects (Muff et al., 2020). BBMMs were fitted using the package "PROreg" in R (Najera-Zuloaga et al., 2020).

We also investigated whether northern quolls selected for highly topographically rugged areas. The topographic ruggedness index (TRI) is defined as the difference in elevation between a cell and the eight cells surrounding it (Riley et al., 1999). To create topographic ruggedness index maps for each site, we sourced Digital Elevation Models (30 m scale) (Gallant et al., 2009), and used the "Terrain Ruggedness Index" function in QGIS (QGIS Development Team, 2020). We overlaid the "used" and "available" northern quoll activity areas onto topographic ruggedness maps and identified the median topographic ruggedness index for each activity area. To evaluate if northern quolls used activity areas with a higher median topographic ruggedness index compared to the broader landscape, we fitted a Generalised Linear Mixed Model (GLMM) with 'individual' as a random effect, and median topographic ruggedness as a continuous response variable (Bates et al., 2015). We could not include site as a random effect due to small sample size. The categorical predictor variable was either the "used" or "available" (intercept) activity area. GLMMs were fitted using the package "lmerTest" in R (Kuznetsova et al., 2015).

Determinants of activity area

To test our prediction that northern quoll activity areas would increase in size with an increasing percentage cover of spinifex sandplain, we developed Linear Mixed Models (LMMs) in which the response variable was the "used" activity area size, and the predictor variable was one of: median topographic ruggedness index (median TRI), sex, weight, or the proportional cover of rocky habitat, spinifex sandplain, or riverbed. We included only univariate models to simplify model selection and preclude overfitting, due to our small sample size. We also only considered habitat variables that northern quolls either selected or avoided disproportionately more than what was available in the broader landscape (i.e., rocky habitat, spinifex sandplain, and riverbed), therefore, *Acacia* stands were excluded. The response variable was $\log_{10}$ transformed because predictor variables had non-linear relationships, and 'individual' was included as a random effect to account for the repeat sampling of the same individual (Bates, 2010). We could not include 'site' as a random effect due to small sample size (Bates et al., 2015, Stratmann et al., 2021). To account for some individuals having less than seven nights of data, we included 'nights' as an offset in the model, which was the number of nights each individual was tracked (Stobo-Wilson et al., 2021). This variable was also $\log_{10}$ transformed. GLMs were fitted using the package "lme4" in R (Bates et al., 2020).

We applied second order Akaike's Information Criterion (AICc) ranking to determine the best model explaining variation in activity area size. We determined the goodness of fit (r^2) for all models and acknowledged models as having substantial support when Δ AICc <2 (Mac Nally et al., 2018, Burnham and Anderson, 2001). We used the "AICcmodavg" package in R to conduct model selection (Mazerolle and Mazerolle, 2017).

3.4. Results

Of the 25 northern quolls collared in the four studies, data for eight female and four male northern quolls met our study criteria (n = 12), resulting in 14 tracking events (Figure B1). Three of these tracking events occurred during autumn, seven during winter, and four during spring (Table B4). Nine tracking events occurred at Red Rock, three at Cattle Gorge, and one each at De Grey Ridge and Python Pool. After data were trimmed to the relevant diel period, five location errors were removed from the datasets of three northern quolls in total. The mean number of GPS fixes for all weekly (seven-night) short-term activity areas was 267 ± 57 fixes (mean ± SE) while the minimum was 69 fixes, and the maximum was 418 fixes (Table 3.1; Table B4).

Activity area size

For weekly short-term tracking events, the mean activity area for females and males combined was 153.42 ± 38.69 ha (Table 3.1). The mean weekly activity area for females was 91.24 ± 24.39 ha (min = 22.96 ha, max = 128.62 ha), while the mean weekly activity area for males was 215.61 ± 61.75 ha (min = 53.84 ha, max = 340.54 ha) (Table 3.1; Table B4).

Table 3.1: The mean and standard error (SE) of short-term activity area size and percentage cover of each habitat type for all northern quolls, female northern quolls, and male northern quolls. Means and SE for habitat cover (%) reflect all short-term activity areas (i.e., including those tracked for less than seven nights). However, short-term activity area size (ha) marked with an asterisk (*) reflects only activity areas which reached seven nights. Individual characteristics for each tracking event can be found in Table B4.

Measure	Sex	Short-term activity area size (ha)*	Rocky habitat (%)	Spinifex sandplain (%)	*Acacia* stands (%)	Riverbed (%)
Mean	All	153.42	23.14	57.09	12.68	4.86
	Female	91.24	27.07	50.95	13.89	4.98
	Male	215.61	13.33	72.44	9.66	4.57
SE	All	38.69	3.12	3.86	3.94	1.27
	Female	24.39	0.03	0.04	0.05	0.02
	Male	61.75	5.97	4.55	2.74	1.78

Habitat selection

Northern quolls selected activity areas in locations with significantly higher percentage cover of rocky habitat and riverbed, and significantly lower percentage cover of spinifex sandplain, compared to the available landscape (Figure 3.3, Table 3.2). Their activity areas had a similar percentage of *Acacia* stands compared to the available landscape (Figure B2; Table 3.2). Finally, northern quolls selected activity areas in locations with significantly higher topographic ruggedness compared to the available landscape (Figure 3.3, Table 3.2).

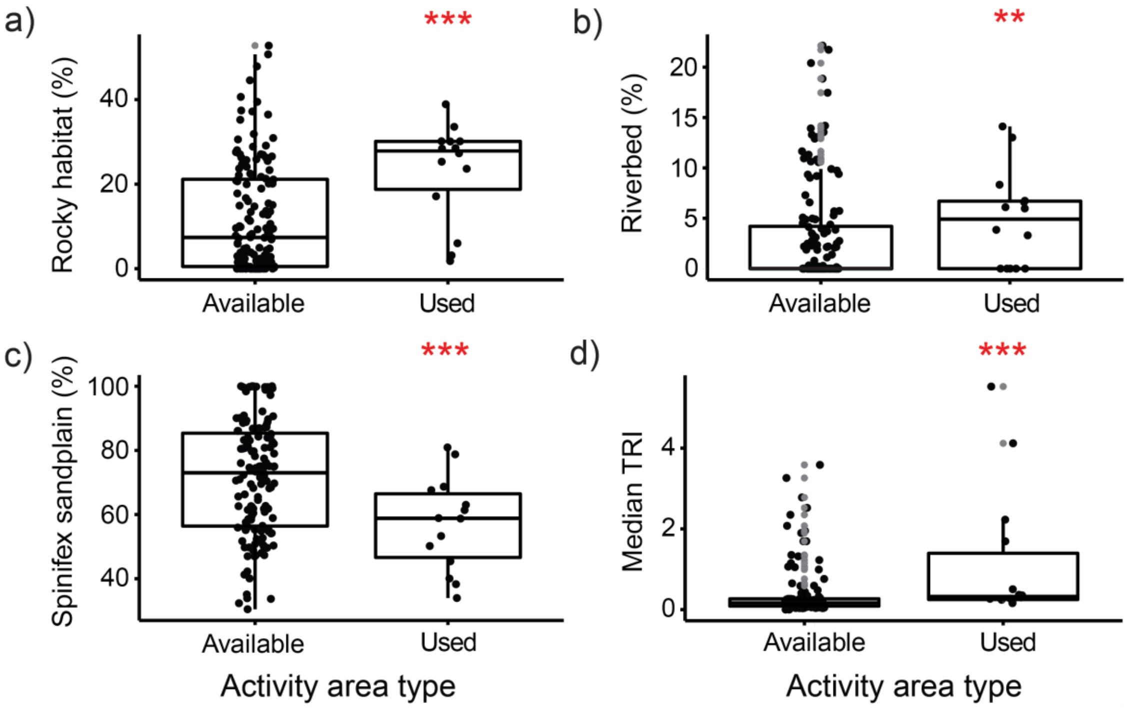


Figure 3.3: Habitat variables significantly selected or avoided by northern quolls were: the proportional cover of a) rocky habitat, b) riverbed, and c) spinifex sandplain, and d) the median topographic ruggedness index (median TRI), Black points represent data values within ‘available’ and ‘used’ northern quoll activity areas, grey points represent outliers, and red asterisks signify a significant difference between ‘used’ and ‘available’ activity areas. Boxplots show the distribution of the data for available and used activity areas.

Table 3.2: Outputs from BBMMs and GLMMs for northern quoll habitat selection. Habitat types in bold denote that used activity areas differed significantly to the intercept (available activity areas). SE represents the standard error.

Habitat variable	Activity area type	Coefficient	SE	*t* value	*p* value
Rocky habitat	Intercept	-2.48	0.09	-27.88	<0.001
	Used	**1.08**	**0.25**	**4.32**	**<0.001**
Riverbed	Intercept	-9.55	0.12	-81.62	<0.001
	Used	**0.92**	**0.31**	**2.92**	**0.004**
Spinifex sandplain	Intercept	0.87	0.07	11.69	<0.001
	Used	**-0.79**	**0.23**	**-3.41**	**<0.001**
Acacia stands	Intercept	-2.44	0.06	-41.68	<0.001
	Used	0.19	0.18	1.03	0.302
Median TRI	Intercept	0.63	0.31	2.00	0.140
	Used	**0.79**	**0.18**	**4.48**	**<0.001**

Some northern quolls primarily used rocky habitat connected by riverbed and spinifex sandplain; riverbed was often associated with rocky habitat at Red Rock (Figure 3.4a). One male northern quoll used an activity area covering large areas of spinifex sandplain at Python Pool to access patches of rocky habitat (Figure 3.4b). Others used mainly rocky habitat like at Cattle Gorge (Figure 3.4c), while one female had an activity area with high cover of *Acacia* stands at De Grey Ridge (Figure 3.4d, Table B4).

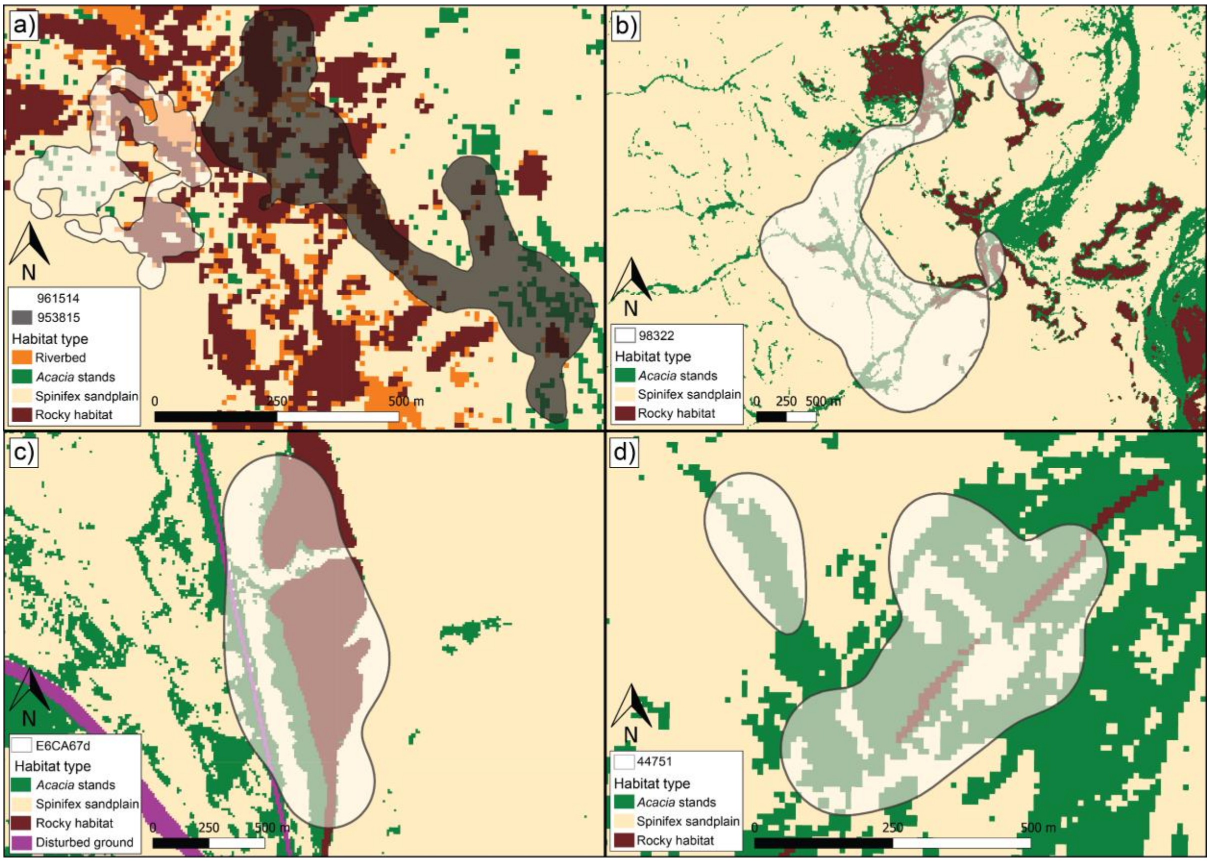


Figure 3.4: Habitat maps of the four sites in the Pilbara region of Western Australia with examples of a) two female northern quoll activity areas at Red Rock showing use of rocky habitat, riverbed, and spinifex sandplain; b) a male northern quoll activity area at Python Pool covering rocky habitat and *Acacia* stands but also large amounts of spinifex sandplain; c) a female northern quoll activity area at Cattle Gorge primarily using rocky habitat; and d) a female northern quoll activity area at De Grey Ridge using primarily rocky habitat and *Acacia* stands. Habitat maps were derived from Sentinel-2 imagery (USGS, 2023).

Determinants of activity area size

The model "spinifex sandplain" was the top-ranked model ($_{wi}$ AICc = 0.56) and explained 20% of the variability in activity area size (Table 3.3). This model showed that northern quoll activity area increased in size when the percentage cover of spinifex sandplain was higher (Figure 3.5).

Table 3.3: Model selection outputs for possible determinants of northern quoll activity area size, offset for the number of nights tracked. Rocky habitat, riverbed, and spinifex sandplain are the proportion of the activity area comprising that habitat type, median TRI is the median topographic ruggedness index of the activity area, sex is whether the quoll was male or female, and weight is the body weight of the individual. Models are ranked in descending order from best to least supported. K represents the number of estimated parameters for each model, AICc represents the Akaike's Information Criterion, Δ AICc indicates the delta AIC value, and $_{wi}$ AICc indicates the level of support for each model. Log-likelihood and model fit are also provided for each model. Models in bold are those which had substantial support (Δ AICc <2, Burnham and Anderson, 2001, Mac Nally et al., 2018).

Rank	Model	K	AICc	Δ AICc	$_{wi}$ AICc	Log-likelihood	r^2
1	**spinifex sandplain**	**4**	**43.05**	**0**	**0.56**	**-15.3**	**0.20**
2	median TRI	4	45.84	2.79	0.14	-16.7	0.02
3	riverbed	4	46.5	3.45	0.1	-17.03	0.13
4	rocky habitat	4	46.98	3.93	0.08	-17.27	0.03
5	weight	4	47.47	4.42	0.06	-17.51	0.04
6	sex	4	47.74	4.7	0.05	-17.65	0.01

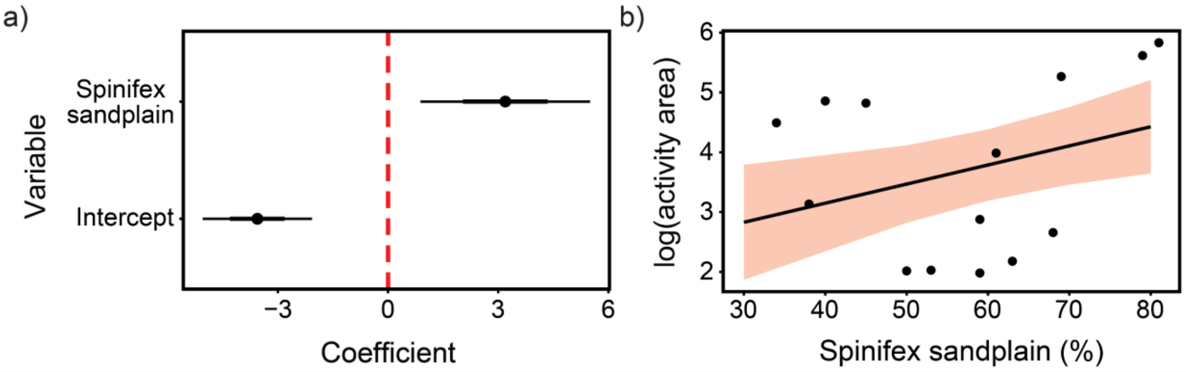


Figure 3.5: The a) coefficients, and b) predicted effects of the top-ranked model (spinifex sandplain) determining northern quoll activity area. Northern quoll activity area was $\log_{10}$ transformed to increase normality. In plot a), black points reflect coefficients, thick bars represent the standard error, thin bars represent 95% confidence intervals, and the red dashed line represents the zero line (zero difference from the intercept). All bars which do not touch the zero line are significant. The intercept reflects the reference level: 0% cover of spinifex sandplain. In plot b), the black line represents the predicted effects, black points represent the raw data, and the red band represents the 95% confidence interval.

3.5. Discussion

We investigated the movement ecology of the endangered northern quoll in an arid landscape to identify their preferred habitat and drivers of activity area size. As predicted, northern quolls located their short-term activity areas in habitats that were more rugged, characterised by higher percentage cover of rocky habitat and riverbed than the available landscape. Northern quolls also selected activity areas in locations with a lower percentage cover of spinifex sandplain than the available landscape, and activity areas increased in size when they contained a higher percentage cover of spinifex sandplain. Our findings support those of previous studies which suggest rugged rocky areas provide critical habitat for the Pilbara northern quoll (Moore et al., 2021a), and are likely rich in key resources compared to spinifex sandplain. Together these results have important implications for the conservation of this species, particularly in terms of the loss of rugged rocky habitat.

As predicted, northern quolls selected activity areas in locations with higher percentage cover of rocky habitat and in areas which were more topographically rugged than the available landscape. This supports findings from other studies and confirms that northern quolls and many other critical weight range mammals (CWR, 35–5500 g) (Murphy and Davies, 2014) persist in rugged, rocky habitat at a landscape scale (Burbidge and McKenzie, 1989, Hernandez-Santin et al., 2022, McDonald et al., 2017, Molloy et al., 2017, Moore et al., 2019, Oakwood, 2002, Shaw et al., 2022). Structurally complex rocky habitats in the Pilbara provide several resources and functions to northern quolls which are critical for survival. These include thermally stable denning habitat (Cowan et al., 2020b), protection from predators (Hernandez-Santin et al., 2016), and abundant prey (Dunlop et al., 2017). Rocky habitat also protects CWR mammals from fire, grazing, and extreme temperatures (Fitzsimons and Michael, 2017, McDonald et al., 2017). The availability of rugged rocky habitat therefore appears critical for northern quoll persistence, and potential removal of rugged rocky habitat due to human disturbance (e.g., mining) is likely to heavily impact their persistence (Cramer et al., 2016).

Some habitat types may be avoided because they lack crucial resources or contain risks which animals prefer to avoid (Aldridge and Boyce, 2007, Polfus et al., 2011). Here, the apparent avoidance of spinifex sandplain by northern quolls is likely explained by increased predation risk in this habitat type, which suggests that individuals move between resource patches more regularly in areas close to shelter, due to greater perceived safety (Bleicher and Dickman, 2020, Laundré et al., 2001). For example, feral cats are most successful at hunting in open habitats, where prey is more exposed (McGregor et al., 2015, Moseby et al., 2021), such as spinifex sandplain. Hernandez-Santin et al. (2016) showed that feral cats frequently used flat, open spinifex sandplain in their Pilbara ranges and northern quolls avoided areas used by cats spatially and temporally. Moving through spinifex sandplain is likely risky for the smaller quoll, due to the increased chance of intraguild predation (Virgós et al., 2020). Reducing the predation risk by feral cats through control programs could benefit quolls by enabling them to make greater use of spinifex sandplains and reducing their reliance on fragmented rocky habitat. For example, after feral cat baiting in the Pilbara, northern quolls were detected using lowland habitats most frequently used by feral cats, likely due to reduced predation pressure

(Palmer et al., 2021). Similarly, on Groote Eylandt—an island in the Northern Territory with a low abundance of northern quoll predators—northern quolls occupied, had better body condition, and fed within a broader dietary niche within savanna woodland compared to rocky habitat (Thomas et al., 2021).

The rocky habitat preferred by northern quolls [in the presence of feral cats] in the Pilbara is naturally fragmented by spinifex sandplain and (sometimes) by riverbed (Moore et al., 2021b, Van Vreeswyk et al., 2004). Therefore, northern quolls must travel through these habitats to reach isolated rocky habitat patches. When present, northern quolls selected activity areas in locations with higher percentage cover of riverbed. Conversely, activity areas were larger when they contained higher percentage cover of spinifex sandplain. Spinifex sandplain covers great expanses between rocky habitat and does not offer much protection to northern quolls, with a lack of denning structures or shelter due to low habitat complexity (Hernandez-Santin et al., 2022, Moore et al., 2021b). The increased travel time caused by having large amounts of spinifex sandplain within their activity areas likely exacerbates the already increased risk of predation for northern quolls in this habitat, and may negatively affect their foraging efficiency or fitness (Perry and Pianka, 1997). This is supported by the fact that northern quolls in the Pilbara are less abundant in landscapes where rocky habitat is more fragmented (Moore et al., 2022b). A return to landscape management techniques, such as traditional mosaic burning, may reduce the large-scale burning of spinifex sandplain, creating increased habitat complexity (Greenwood et al., 2022). When coupled with effective feral cat management (Cowan et al., 2020a), this may decrease feral cat success in spinifex sandplain and increase the usability of this habitat by northern quolls (Doherty et al., 2015b)—like mosaic burning has done for other small Australian species (Bliege Bird et al., 2013, Holland and Bennett, 2007, McDonald et al., 2016).

The selection of areas with increased cover of riverbed by northern quolls is likely because riverbed is often associated with rocky habitat and may facilitate movement and foraging opportunities (Ruprecht, 1996). Hernandez-Santin et al. (2016) found that the distribution of northern quolls in the Pilbara was positively associated with creek lines, but the distribution of feral cats was not, highlighting potential benefits of using this habitat for quolls, as for many small terrestrial vertebrates (Sánchez-Montoya et al., 2016). However, this habitat is also likely important for the dispersal of larger predators of the northern quoll in some instances, including feral cats and dingoes (*Canis lupus dingo*) (Williamson et al., 2021, Wysong et al., 2020a).

Riverbeds may also offer food for northern quolls. Here, riverbeds were dry, but often hold surface water in the form of puddles for much longer than the surrounding landscape (Smit and Grant, 2009). In a mesic environment in Queensland, Pollock (1999) found that ~60% of northern quoll locations were less than 200 m from permanent water, while Hill and Ward (2010) noted that in the Northern Territory there was higher prey availability for northern quolls near water sources. In the Pilbara, northern quoll occurrence decreased with increasing distance from water (Shaw et al., 2022). Therefore, riverbeds may facilitate a form of landscape complementation for northern quolls, where quolls benefit from the resources available within two key habitats (i.e., rocky habitat and riverbed) (Dunning et al., 1992, Nimmo et al., 2019). Previously, emphasis has been placed on protecting or attempting to replicate only rocky habitat for northern quolls (Cowan et al., 2020b). However, this emphasises the importance of considering potential dispersal routes and supplemental foraging habitats when planning for northern quoll conservation and management (Bennett, 1990, Doherty and Driscoll, 2018).

Our study adds to the growing body of knowledge that suggests that northern quolls require rugged, rocky habitat for survival in the Pilbara, and that their space use is driven by selection for habitats which provide shelter from larger predators such as feral cats. This study also provides a baseline for future studies to investigate how human disturbances such as fire, mining, and agriculture influence northern quoll movement and space use (Moore et al., 2021a). The destruction of complex rugged habitat or efficient movement corridors, and replacement with simple habitat—such as cleared land or spinifex sandplain—will likely have dramatically negative effects on northern quolls, including expulsing local populations, or having cumulative impacts on the broader population by limiting movement or causing populations to become isolated. Alternatively, it may force northern quolls to travel longer distances to gain the resources needed for survival, potentially decreasing individual body condition and leaving quolls exposed to increased predation, risk of fire, and grazing pressures. The conservation of northern quolls in the Pilbara should value existing rugged, rocky habitat which provides important food resources and protection from predation (Oakwood, 1997), as well as efficient movement pathways such as riverbeds that facilitate dispersal. Spinifex sandplain may also offer foraging resources for northern quolls in the Pilbara, but currently, predation risk is likely driving its' avoidance. Management actions to increase complexity of spinifex sandplain may drive higher use of this habitat by northern quolls, and all conservation actions should be coupled with effective management of invasive predators such as feral cats.

3.6. Acknowledgements

We acknowledge the Karriyarra, Ngarluma, and Nyamal people as the Traditional Owners of the land where northern quolls were trapped and tracked. We also thank the Department of Biodiversity, Conservation and Attractions (DBCA), Biologic Environmental, Roy Hill, BHP, De Grey Mining, and Colin and Betty Brierly of Indee Station for access to field sites and data. Thank you to Harriet Davie for assisting with and facilitating much of this fieldwork. All animal capture and handling was undertaken with ethics approval from Charles Sturt University (A18034), the University of Queensland (SBS/348/12/ARC), the Department of Environment and Conservation (AEC2011/14, AEC 2014/19), and DBCA (AEC 2017/23, AEC 2020/21D). Relevant research permits were also obtained from DBCA (SF009747, 08-002376-1).

Chapter 4: Movement ecology of an endangered mesopredator in a mining landscape

Manuscript published: Cowan, M. A., Dunlop, J. A., Gibson, L. A., Moore, H. A., Setterfield, S. A., & Nimmo, D. G. (2024). Movement ecology of an endangered mesopredator in a mining landscape. *Movement Ecology,* 12, 5.

Cowan, M. A.[1, 2], Dunlop, J. A. [1, 2], Gibson, L. A.[3], Moore, H. A.[2, 3], Setterfield, S.A.[2], Nimmo, D. G.[1]

[1]Gulbali Institute, School of Agricultural, Environmental and Veterinary Sciences, Charles Sturt University, Thurgoona, NSW, 2640, Australia.
[2]School of Agriculture and Environment, The University of Western Australia, Crawley, WA, 6009, Australia.
[3]Department of Biodiversity, Conservation and Attractions, Kensington, WA, 6151, Australia.

4.1. Abstract

Introduction

Efficient movement and energy expenditure are vital for animal survival. Human disturbance can alter animal movement due to changes in resource availability and threats. Some animals can exploit anthropogenic disturbances for more efficient movement, while others face restricted or inefficient movement due to fragmentation of high-resource habitats and risks associated with disturbed habitats. Mining, a major anthropogenic disturbance, removes natural habitats, introduces new landscape features, and alters resource distribution in the landscape. This study investigates the effect of mining on the movement of an endangered mesopredator, the northern quoll (*Dasyurus hallucatus*). Using GPS collars and accelerometers, we investigate habitat selection and energy expenditure in an active mining landscape, to determine the effects of this disturbance on northern quolls.

Methods

We fit northern quolls with GPS collars and accelerometers during breeding and non-breeding seasons at an active mine site in the Pilbara region of Western Australia. We calculated the movement ranges of quolls using utilisation distributions at the 95% isopleth, and compared habitat types and environmental characteristics within observed movement ranges to the available landscape. We investigated fine-scale movement by quolls with integrated step selection functions, assessing the relative selection strength for each habitat type and environmental characteristic. Finally, we used piecewise structural equation modelling to analyse the influence of each habitat type and environmental characteristics on energy expenditure, integrating spatial and movement data.

Results

At the broad scale, northern quolls predominantly used rugged, rocky habitats, and used mining habitats in proportion to their availability. However, at the fine scale, habitat use varied between breeding and non-breeding seasons. During the breeding season, quolls notably avoided mining habitats, whereas in the non-breeding season, they frequented mining habitats equally to rocky and riparian habitats, albeit at a higher energetic cost.

Conclusion

Mining impacts northern quolls by fragmenting favoured rocky habitats, increasing energy expenditure, and potentially impacting breeding dispersal. While mining habitats might offer limited resource opportunities in the non-breeding season, conservation efforts during active mining, including the creation of movement corridors, progressive clearing and habitat restoration would likely be useful. However, prioritising the preservation of natural rocky and riparian habitats in mining landscapes is vital for northern quoll conservation.

4.2. Introduction

Movement and energy expenditure play a critical role in animal survival (Nathan et al., 2008, McNab, 1963). Efficient movement, that is, the ability of animals to disperse and access resources (e.g. food, shelter) with minimal energetic cost, is a key factor determining their fitness and reproductive success (Emlen, 1966, Doherty et al., 2019). When resources are scarce, animals allocate more energy to obtain resources, which can reduce their fitness and increase mortality risk (Rus et al., 2020, Gardiner et al., 2019, Stobo-Wilson et al., 2021). Hence, understanding the relationship between movement, energy use, and resource availability is important for informing conservation management (Nathan et al., 2008, Avgar et al., 2016).

When anthropogenic disturbance is introduced into the landscape, it can influence animal movement (Tucker et al., 2018, Doherty et al., 2021, Tucker et al., 2023). Currently, between 75% and 95% of terrestrial land has been disturbed by humans globally (Ellis et al., 2021, Ellis et al., 2010, Williams et al., 2020a). The influence of disturbance on animal movement depends on how it alters the availability and distribution of threats and resources (Tuomainen and Candolin, 2011). Animal movement efficiency can sometimes be improved in human-disturbed landscapes, due to the availability of anthropogenic food or shelter subsidies (Catlin et al., 2016), reducing the distance required to access resources (Newsome, 1971, Dawson et al., 2023, Adams, 1994, Main et al., 2020). For example, grey wolves (*Canis lupus*) use linear human infrastructure—like roads and seismic survey lines—to move faster and enhance their ability to search for prey (Dickie et al., 2017, Finnegan et al., 2018). Other species may be negatively impacted by human disturbance, restricting movement by limiting access to natural habitat and reducing resource availability (Ricketts, 2001, Richardson et al., 2000, Tucker et al., 2018). For some animals, decreased resources can actually increase animal movement, as the area required to gain sufficient resources is larger (Rus et al., 2020, Stobo-Wilson et al., 2021, Doherty et al., 2021), requiring animals to move through low quality habitat to access areas where resources are high (Dunning et al., 1992).

The spatial extent and configuration of low quality habitats can have flow on effects to movement (Nimmo et al., 2019): moving through low quality habitats can lead to reduced foraging efficiency while increasing mortality risk (Haapakoski et al., 2013). For example, the Amur tiger (*Panthera tigris altaica*), whose habitat has been severely fragmented by human activities, must cross busy roads and populated areas to reach favoured habitat patches, increasing their energy expenditure and risking human-wildlife conflict (Kerley et al., 2002). Disturbance can also introduce sublethal effects for animals, disrupting or altering other processes such as predator-prey interactions, genetic connectivity, and disease transmission (Trakhtenbrot et al., 2005, Tucker et al., 2018, Doherty et al., 2020). Changes in movement patterns due to disturbance can also negatively affect fitness or breeding success, sometimes requiring more energy than in natural habitats to avoid increased threats or to search for scarce resources (Wang et al., 2017, Perona et al., 2019, Doherty et al., 2021). The presence of habitats which are attractive (e.g., offer shelter), but do not offer all required resources—or increase other threats to the animal—may lead to what has been termed an 'ecological trap' (Battin, 2004, Penteriani et al., 2018, Hale and Swearer, 2016). For example, African wild dogs (*Lycaon pictus*) can be attracted from protected areas into surrounding areas which are less safe, due to increased hunting success and lower competition with larger predators, but suffer higher mortality risks due to anthropogenic causes (van der Meer et al., 2014).

Mining is an anthropogenic disturbance responsible for large-scale habitat modification around the world (Sonter et al., 2014, Meira et al., 2016). Globally, mining threatens more than 900 animal species (Maxwell et al., 2016), and threats to biodiversity from mining are expected to increase, with many mineral-rich regions also having high conservation value (Durán et al., 2013, Sonter et al., 2018). Mining destroys and fragments natural habitats, introduces novel landscape elements such as pits, roads, large clearings and waste rock dumps, and changes the distribution and abundance of resources such as shelter, water, and food (Newsome et al., 2013c). With the increasing pressure of mining on natural habitats, it is important to understand how it affects animals and their movement and energy requirements (Newsome et al., 2013b, Martins-Oliveira et al., 2021, Cross et al., 2019).

We examined the effects of mining disturbance on the movement ecology and behaviour of an endangered marsupial mesopredator, the northern quoll (*Dasyurus hallucatus*)—*marlarlparra* in Nyamal language—in an extremely modified, active mining landscape. Drill and blast mining operations often target the rocky habitat that provides crucial denning sites for northern quolls (Ramanaidou and Morris, 2010, Cowan et al., 2020b, Hernandez-Santin et al., 2022), because of their rich deposits of minerals such as iron ore—removing complex rocky denning habitat and vegetation cover (Cramer et al., 2016, Gibson et al., 2023). While quolls do use structurally simple habitats (e.g., spinifex (*Spinifex* spp.) grassland; Figure 4.1) in natural landscapes when moving between patches of favoured rocky habitat (Moore et al., 2021b), they tend to be avoided where possible given the increased risk of encountering predators such as feral cats (*Felis catus*) and dingoes (*Canis lupus dingo*) (McDonald et al., 2020, Hernandez-Santin et al., 2016).

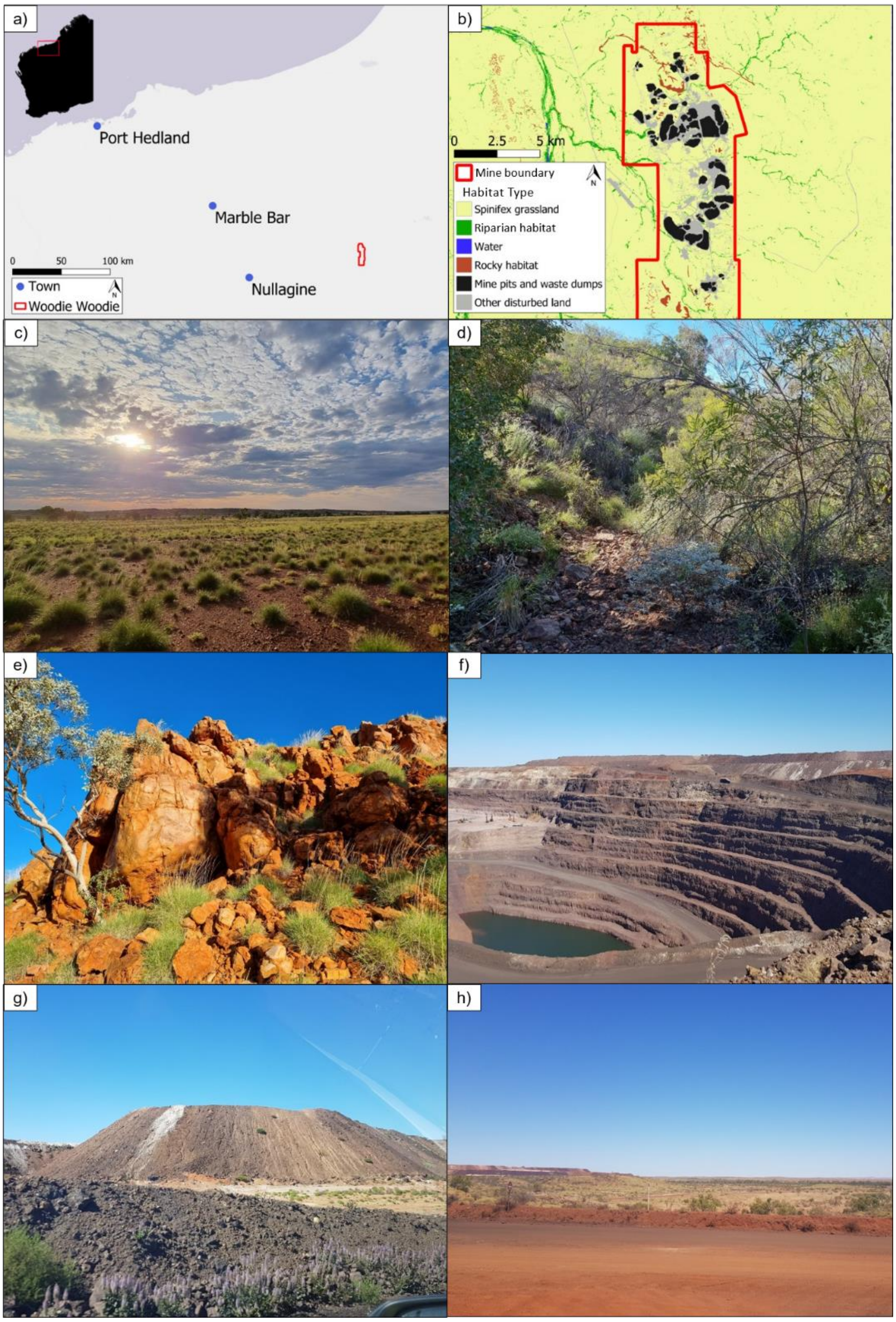


Figure 4.1: Maps of the a) location of Woodie Woodie in the Pilbara landscape, and b) habitat types at the site, including spinifex grassland, riparian habitat, water, rocky habitat, mine pits and waste dumps, and other disturbed land. The red line is the mine tenement boundary. Also included are photographs of the common habitats within the mining landscape: c) spinifex grassland, d) riparian habitat, e) rocky habitat, f) mine pits, g) waste dumps, and h) other disturbed land (e.g., roads, buildings, cleared areas).

Active mine sites are expected to be similarly attractive to northern quolls as spinifex grassland, given the similar predator risk (Hamilton and Algar, 2004, Bradley et al., 2022), and presumed lack of denning resources compared to rocky habitat (Hernandez-Santin et al., 2022). While there are some known instances of northern quolls interacting with human features such as rail infrastructure (Henderson, 2015, Creese, 2012) and rehabilitated habitats (Cowan et al., 2020b), our understanding of their movement and energy requirements in active mining landscapes remains poor (Gibson et al., 2023). We used GPS collars and accelerometers to investigate broad and fine-scale habitat selection, and energy expenditure, of northern quolls living in an active mining landscape (Nathan et al., 2022). Based on existing knowledge of northern quoll movement and habitat use in natural landscapes, we predicted that:

1. At the broad scale, northern quolls will use areas with lower proportions of disturbed mining habitat and higher proportions of rugged, rocky habitat than what is available in the landscape, likely due to a lack of resources (e.g., dens, vegetation) in mining compared to rocky habitats.
2. At the fine scale, quolls will avoid mining habitats (e.g., cleared areas, roads) and select for rocky habitats and areas close to rocky habitat, due to an expected higher risk of predation and lack of key resources (e.g., dens, food) in mining compared to rocky habitats.
3. When quolls do traverse mining disturbed habitats in the landscape, the energetic costs will be higher than in natural habitats—where food and den availability is likely to be higher—because it will take longer to gain resources.

We use our results to provide management recommendations for the conservation of northern quolls in areas of active mining and make suggestions more broadly about the use of disturbed landscapes by small-medium sized mammals.

4.3. Methods

Study species

The northern quoll is a small-medium sized (~300-600 g) marsupial mesopredator native to northern Australia (Moore et al., 2021a). The northern quoll is an opportunistic omnivore, eating a range of vertebrate, invertebrate, and flora species (Moore et al., 2021a). Over the past century, northern quolls have suffered substantial range declines, largely due to a combination of habitat loss, introduced predators, altered fire regimes, and invasive cane toads (*Rhinella marina*)—a toxic species of toad that is lethal to quolls when consumed (Moore et al., 2019, Braithwaite and Griffiths, 1994). Except for the cane toad, all of these threats are present in the Pilbara region of Western Australia, yet there has been relatively little range contraction compared to other regions of northern Australia (Moore et al., 2019). Nonetheless, northern quolls are listed as Endangered under IUCN, national EPBC, and Western Australian state listings (Oakwood et al., 2016, Department of the Environment, 2016).

Study area

This study was undertaken in the Pilbara bioregion of northern Western Australia. The region experiences a semi-arid climate, with average maximum temperatures of 37°C during summer and 25°C during winter (McKenzie et al., 2009). Annual rainfall is variable (250–500 mm), with most falling between December and February (Bureau of Meteorology, 2020). The region is characterized by ancient, topographically rugged rocky terrain, deep gorges, and rough escarpments, interspersed with expansive hummock grasslands (Carwardine et al., 2014, Van Vreeswyk et al., 2004). The grasslands are dominated by a *Triodia* (spinifex) ground layer (to < 1 m), with a sparse *Acacia* and *Eucalyptus* spp. upper story. Plant species composition is largely influenced by the local fire history and geology. The rocky habitat contains a mixture of grass, *Eucalyptus*, and *Ficus* species scattered amongst embedded and scattered rock (Maslin and van Leeuwen, 2008, Van Vreeswyk et al., 2004). Drainage lines (e.g., creeks) typically have a narrow riparian zone, with a dense layer of grass species, shrubs, and trees (e.g., *Acacia* and *Eucalyptus* spp.), while they are often associated with rocky features (Van Vreeswyk et al., 2004).

Quolls were monitored at the Woodie Woodie mine, located on Nyamal Country in the eastern Pilbara region, bordering the Great Sandy Desert and close to the eastern edge of the northern quoll's Pilbara range (Moore et al., 2019; Figure 4.1). Woodie Woodie is an active manganese mine managed by Consolidated Minerals (ConsMin), which has been in operation since the early 1950's and has historic and active mining disturbance. Active mining occurs 24/7 with night operations aided by spot lights. The mine site is situated within Warrawagine station and cattle grazing occurs on and around the mine. Woodie Woodie employs an open pit mining strategy and is surrounded by natural habitat encompassing spinifex grassland, hills, and rocky habitat (Figure 4.1). The mine site is made up of open pits, waste rock dumps (henceforth waste dumps), buildings, roads, flat cleared areas, and patches of natural habitat. All areas of disturbed and undisturbed habitats, including mine pits and waste rock dumps are accessible to northern quolls. The mining footprint is approximately 127 km^2 (12,700 ha). The Oakover River runs south to north ~6 kms east of the mine with many non-perennial tributaries feeding this river from around and through the mine site (Figure 4.1). The mine site also contains patches of permanent water within historic mine pits, storage ponds, and pools in sections of creeks. All data included in this study were collected from individuals caught within the mine tenement boundary (Figure 4.1).

Data Collection

We completed two data collection periods at Woodie Woodie, one during part of the northern quoll breeding season when females begin to have pouch young (September – October 2021) and another during part of the non-breeding season the following year, before mating began (June – July 2022) (Shaw et al., 2022). Northern quolls were trapped using wire cage traps (45 cm × 17 cm × 17 cm, Sheffield Wire Co., Welshpool, WA). We set a maximum of 50 cage traps per night, in different parts of the mine, targeting areas where northern quolls had been sighted previously or areas that were likely to contain northern quolls based on the availability of den sites and food (e.g., native *Ficus* spp.). Initial trapping was undertaken for 14 nights in each season. Traps were moved around the mine tenement to avoid capturing the same individuals and to ensure we captured quolls from a range of areas and habitats. Traps were placed in transects ~50–100 m apart in rocky and riparian habitats where northern quolls den (Hernandez-Santin et al., 2022). These areas were often close to mining disturbance (Figure 4.1). Traps were baited with a mixture of oats, peanut butter, and sardines (as per Dunlop et al., 2014). Traps were opened in the evening and checked and closed the following morning.

All individuals were processed at the site of trapping. A series of morphological measurements were recorded, including sex, weight, testes size (for males), hindfoot length, and tail base circumference. Animal ethics permits required collar weight to not exceed 5% of the animal’s body weight, so we attached a 20 g LiteTrack 20 RF GPS Collar (Lotek, Havelock North) to animals weighing 400 g and above. Twelve GPS collars were deployed for ~30 days, although all stopped recording data before retrieval due to memory and battery limitations (mean ± SE; 20 ± 1.5 nights after cleaning). To retrieve GPS collars, we set targeted traps around daytime den locations, located using very-high frequency (VHF) transmitters inside each collar. Upon successful overnight trapping, the GPS collar was removed the following morning, and a general health check was undertaken in the field, including repeating the morphological measurements taken in the initial trapping. The quoll was then released.

GPS collars were set to record GPS locations between 6 pm and 6 am to target the time when northern quolls are most active (Cowan et al., 2020b, Gaschk et al., 2023), and to avoid unsuccessful fixes draining the battery while quolls were denning. GPS collars were set to record locations every 30 minutes, resulting in a possible 24 fixes per night. This fix rate enabled frequent recordings to investigate fine-scale habitat use, but also enabled a longer monitoring period given battery limitations with a small GPS tracker. GPS collars also contained accelerometers and temperature loggers. Accelerometers were set to record raw acceleration (*g*) and temperature (°C) at 5 s intervals, 24 hours a day. Accelerometers measured acceleration at a range of ± 4G and temperature monitoring was accurate to ± 0.5°C. Raw acceleration was recorded on 3 axes—X, Y, and Z—representing surge (forward-backwards movement), heave (upwards-downwards movement), and sway (sideways movement). Accelerometers were positioned at the bottom of the collars, sitting under the chin of the quoll. However, because collars were circular, we could not guarantee that they would always remain in perfect orientation due to the collars' rotational ability. We accounted for this during analyses (see below).

To quantify northern quoll movement in relation to landscape variables, we used QGIS v3.12 (QGIS Development Team, 2020) and RStudio version 2022.07.2 (R Core Team, 2023b) to create four maps of landscape features: 1) habitat type, 2) topographic ruggedness index (TRI), 3) distance from disturbance, and 4) distance from rocky habitat. Habitat type, distance from disturbance, and distance from rocky habitat were mapped at a 10 m scale, while topographic ruggedness index was mapped at a 12.5 m scale. Habitat types on the habitat map included spinifex grassland, riparian habitat (dense vegetation associated with drainage lines), rocky habitat, and mining disturbed land. During breeding season, quolls were often tracked to dens within rocky waste dumps and mine pits, therefore, we split mining disturbed land into two types: 1) mine pits and waste dumps, and 2) other disturbed land (e.g., roads, buildings, and large cleared areas). To compare the environmental characteristics of each habitat type, we extracted the mean NDVI values (10 m scale) and the median topographic ruggedness for each habitat type from the *observed* and *available* landscapes. For detailed methods of map creation and layer details, see Appendix C1.

Data Processing and Preparation

To eliminate GPS errors, we cleaned and processed all data before analyses. All data processing and analyses were performed in RStudio version 2022.07.2, unless stated otherwise (R Core Team, 2023b). We removed all GPS points with a horizontal dilution of precision (HDOP) >10, due to the decreased accuracy of these GPS points (D'eon and Delparte, 2005, Coulon et al., 2008, Cargnelutti et al., 2007). This resulted in the removal of 59 GPS points. Fix error often increases with increasing HDOP, but the suitability of using HDOP as a filtering method is debated (Forrest et al., 2022). Some fixes with a high HDOP can also have low error, meaning that the removal of high HDOP fixes can remove some accurate locations (Recio et al., 2011, Adams et al., 2013). However, the effective use of a HDOP limit can remove major outliers from data—important for fine scale movement analysis—while limiting data loss (D'eon and Delparte, 2005, Poessel et al., 2018), with only a 3% data reduction seen here. Four trial GPS collars in fixed locations had a mean ± SE locational error of 8.3 ± 0.46 m when HDOP was <10. After this, any remaining unrealistic GPS fixes were removed based on the average maximum speed of northern quolls (4.5 m s^{-1}) (Wynn et al., 2015), where points too far to be reached in the time between fixes were excluded (Bjørneraas et al., 2010). This resulted in one location being excluded. We screened data further by discarding all GPS points on the night prior (6 pm – 12 am) and morning of (12 am – 6 am) any captures, to avoid locations when an individual was in a trap. One individual was discarded from all analyses, as fix success was extremely low and there were too few fixes to undertake movement analyses (24 GPS fixes; Girard et al., 2002, Seaman et al., 1999). For one collared individual which was predated upon by a feral cat after 20 nights (confirmed by DNA analysis), we removed all GPS points from 6 pm onwards on the night of the predation event (time of event ~7:30 pm).

To investigate the habitat selection of northern quolls, we converted all GPS points to movement steps (henceforth ‘observed steps’) using the R package ‘amt’ (Signer et al., 2019). To ensure movement was standardised by time, we removed all locations that were separated by more than 30 minutes, as longer time periods would likely miss finer movements between GPS fixes (Thurfjell et al., 2014). This resulted in the creation of several bursts (isolated groups of steps with a 30-minute sampling rate). We removed all bursts with less than three movement locations, the minimum required to calculate turning angles (Signer et al., 2019). Further data processing is outlined in the Data Analysis – Fine Scale Habitat Selection section when describing the fitting of integrated step selection functions (iSSFs).

Raw acceleration data (g) measured by accelerometers were converted from raw acceleration (X, Y, Z) to the vector of the dynamic body acceleration (VeDBA)—which has been used for northern quolls previously (Gaschk et al., 2023). VeDBA is adept as a proxy for energy expenditure and deals with variation in accelerometer orientation (caused by potentially rotating collars) better than other measures such as overall dynamic body acceleration (ODBA) (Qasem et al., 2012, Wilson et al., 2020). Raw accelerometer data were first converted to dynamic body acceleration (DBA) by smoothing each axis to obtain the static acceleration using a running mean over 10 s (encompassing two consecutive values), then subtracting the static acceleration from the raw values for each 5 s measurement (Qasem et al., 2012). The dynamic body acceleration values were then converted to positive values, and we calculated VeDBA using:

$$VeDBA = \sqrt{A_X^2 + A_Y^2 + A_Z^2}$$

Where A is the dynamic body acceleration corresponding to the X, Y, and Z axes of the accelerometer (Qasem et al., 2012). We then calculated the mean VeDBA for each 30-minute *observed* movement step for each individual quoll. This meant that all mean VeDBA values recorded between 6 am and 6 pm when GPS collars were not recording, were discarded for this analysis.

Only one female was captured that was large enough to be collared, therefore all individuals were pooled regardless of sex. In non-breeding season, when the female quoll was collared, home ranges are relatively similar between sexes and habitat selection is not likely to differ substantially (Moore et al., 2021a, Oakwood, 2002).

Data Analysis – Broad Scale Habitat Selection

To identify the broad scale habitat selection of northern quolls, we estimated northern quoll movement ranges. Movement ranges represent the broad-scale space which animals use, and encompass all habitats that they may access during movement (Burt, 1943). GPS tracking time was not long enough for quolls to cover their complete home range; thus, none reached an asymptote when fixes were added sequentially (i.e. over time) at 10-fix intervals (Harris et al., 1990). We therefore refer to the broad areas used by quolls during tracking as ‘movement ranges’, which were estimated from utilisation distributions (UDs) at the 95% isopleth using fixed kernel density estimation (KDE) (Signer et al., 2015, Blundell et al., 2001). The UD represents a probabilistic density function that estimates how frequently an animal is expected to be found in a particular area (Fieberg and Kochanny, 2005). The 95% isopleth refers to the area where the animal has a 95% probability of being found, excluding potential outliers (Mitchell et al., 2019). We used the *ad hoc* method ($h_{ad\ hoc}$) to determine *h*—which is the bandwidth (smoothing) parameter that dictates the width of the kernel function used to estimate the probability density function (Silverman, 1986)—because $h_{ad\ hoc}$ is robust to sample size, accurately reflects the observed movement range, and is consistent and repeatable (Cowan et al., 2022, Kie, 2013; Table C1). We used the package "rhr" in R to estimate movement ranges (Signer and Balkenhol, 2015).

To compare the composition of landscapes within '*observed'* quoll movement ranges with what was available in the landscape, we identified the area of the landscape considered accessible but not visited by an individual (Hazen et al., 2021). To define the boundaries for the available landscape for each quoll, we followed methods described in Cowan et al. (2022) and Wysong et al. (2020a). We fit a 100% minimum convex polygon (MCP) to the GPS data of each quoll. We then placed a buffer around each MCP equal to the radius of the largest *observed* movement range (5220 m) and subtracted the radius of the activity area being measured (Cowan et al., 2022). Within the available area, we randomly generated five circular '*available*' movement ranges per individual, which were equal in size to the movement range of the individual being measured (Squires et al., 2013, Wysong et al., 2020a, Cowan et al., 2022). We overlaid the *observed* (n = 9) and *available* (n = 45) movement ranges on habitat maps (see Appendix C1), then used the 'extract' function in the "raster" package to determine the proportion cover of each habitat type (spinifex grassland, riparian habitat, rocky habitat, mine pits and waste dumps, other disturbed land), as well as the median topographic ruggedness, mean distance from disturbance, and mean distance from rocky habitat for each *observed* and *available* movement range (Hijmans et al., 2015).

Next, to determine if northern quolls preferred to locate their *observed* movement ranges in areas with certain environmental characteristics compared to what was *available*, we fit zero-inflated beta regression models for proportion data and we fit generalised linear mixed regression models (GLMMs) with a Gaussian distribution for continuous data in R. We did not have enough data to accurately model seasons separately, so data were combined for breeding and non-breeding season. For zero-inflated beta regression models to determine selection for different habitat types, we fit separate models for each habitat type, where the response variable was the proportion of that habitat within the movement range, and the predictor variable was the movement range type (*observed* or *available*) (Brooks et al., 2017). We allowed the zero-inflation component to vary for each movement range type, which models the excess zeros in the response variable—that can occur when the habitat type is not present for some observations and helps to deal with overdispersion (Brooks et al., 2017). We included a random effect of individual to account for the non-independence of multiple *available* movement ranges for the same individual, and to capture the variability in the intercepts across different individuals (Muff et al., 2020). Second, to determine if northern quolls selected movement ranges with differing topographic ruggedness, distance from disturbance, or distance from rocky habitat compared to the available landscape, we fit GLMMs where the response variable was the environmental variable (i.e., median topographic ruggedness, mean distance from disturbance, or mean distance from rocky habitat) and the predictor variable was the movement range type (*observed* or *available*) (Bürkner, 2017). We classified a Gaussian distribution as data were continuous and again included a random effect of individual (Muff et al., 2020, Oberpriller et al., 2022). Significant differences between *observed* and *available* movement ranges were identified if 95% confidence intervals did not cross zero. Zero-inflated beta regression models and GLMMs were fit using the 'brm' function from the "brms" package in R (Bürkner, 2017).

Data Analysis – Fine Scale Habitat Selection

To investigate how northern quolls interact with mining disturbance, as well as with other environmental variables at the fine scale, we used integrated step selection functions (iSSFs) (Avgar et al., 2016). Step selection functions involve a form of conditional logistic regression where each '*observed* step' (path connecting two consecutive observed locations of the individual) is compared with a set of '*available* steps' with a strata term (step ID) which pairs *observed* steps with their respective *available* steps (Thurfjell et al., 2014, Fortin et al., 2005, Duchesne et al., 2010). Integrated step selection functions take this further, by including animal movement and resource selection parameters in the model, reducing bias, and allowing further estimation and simulation of habitat selection (Forester et al., 2009, Signer et al., 2019, Mercker et al., 2021). For each *observed* step, we generated five random *available* steps with turning angles drawn from a von Mises distribution and step lengths drawn from a gamma distribution (Thurfjell et al., 2014, Ganz et al., 2022, Avgar et al., 2016, Duchesne et al., 2015). For each *observed* and *random* step, we extracted covariates from the four landscape maps at the end of the step. We constructed separate models for the breeding and non-breeding seasons due to differences in northern quoll behaviour during these periods (Oakwood, 2002).

When including multiple individuals in an iSSF model, it is common to account for individual variation in selection (Muff et al., 2020). However, individual-specific random slopes are extremely difficult to fit in conditional logistic regression (Muff et al., 2020, Fieberg et al., 2021, Thurfjell et al., 2014). There are other options, including mixed effects modelling of step-selection functions (Muff et al., 2020), however, we did not have enough strata per individual to fit these (Iverson et al., 2023). Therefore, to allow inference of population effects and further analysis of relative selection strength (RSS), we assumed homogeneity across individuals and pooled data by season for iSSF analyses (Iverson et al., 2023, Signer et al., 2019). We fit iSSFs using the 'fit_issf' function in the "amt" package in R (Signer et al., 2019).

For our global model, the case (i.e., an *observed* or *random* step) was the response variable (Signer et al., 2019, Fortin et al., 2005). Predictor variables included the four landscape variables extracted from the end of each *observed* and *random* quoll step (i.e., the habitat type, topographic ruggedness, distance from disturbance, and distance from rocky habitat). Rocky habitat was set as the reference category (i.e., the intercept) for habitat type. Habitat selection depends on the scale at which resources are distributed throughout the landscape and how animals move between them, so we included the $\log_{10}$ of the step length and the cosine of the turning angle as covariates in iSSF analyses (Forester et al., 2009). Unexpectedly, there was a high survival rate of males living into their second year (three males)—males often die off after their first breeding season (Oakwood, 2004)—therefore, for quolls tracked during the non-breeding season, we included an interaction of age with the $\log_{10}$ of the step length and the cosine of the turning angle to determine if second year quolls moved differently to first year individuals. We included 'step ID' as a strata term in both models to ensure *observed* steps were paired with their respective *random* steps (Signer et al., 2019). We checked categorical and continuous variables for correlation using Pearson‘s *r*, ANOVA, and chi-square tests. Water was excluded from analyses due to a lack of representation.

We compared the global model with simplified variations of the model separately for each season (Iverson et al., 2023; see Table C2, for simplified model structures, Burnham and Anderson, 2004, Arnold, 2010). We undertook model selection using Akaike's Information Criterion corrected for small sample bias (AICc) using the 'aictabCustom' function in the "AICcmodavg" package in R (Mazerolle and Mazerolle, 2017). Models were regarded as having substantial support when ΔAICc <2 (Mac Nally et al., 2018, Burnham and Anderson, 2001).

The global model had substantial support in both seasons (see Results). Therefore, we undertook relative selection strength (RSS) analysis using this model, so we could investigate the potential influence of all environmental variables on northern quoll fine-scale habitat selection (Signer et al., 2019, Iverson et al., 2023, Avgar et al., 2017). For categorical covariates, the RSS estimates the probability of an animal selecting a particular habitat relative to another, and for continuous covariates, it measures the probability of selection across differing values, while holding all other covariates constant (Avgar et al., 2017). This approach is appropriate for "observed-available" designs such as this (Avgar et al., 2017, Iverson et al., 2023). To determine northern quoll RSS for each covariate, we first updated the selection-free movement kernel with the habitat selection coefficients of the global models to be able to estimate the RSS using both the movement (e.g., the $\log_{10}$ of the step length) and habitat selection parameters—which reduces bias (Signer et al., 2019, Fieberg et al., 2021). This was done separately for each season. RSS was calculated using the 'log_rss' function in the "amt" package (Signer et al., 2019). We present the RSS for all habitat types, distance from disturbance, and distance from rocky habitat, and present the log(RSS) for topographical ruggedness to better visualise the relationships between seasons.

Data Analysis – Energy Expenditure

To examine the influence of mining disturbance and other landscape features on mean VeDBA (i.e., energy expenditure), by combining spatial and movement data (Northrup et al., 2022, Nathan et al., 2012, Williams et al., 2020b), we used a piecewise structural equation modelling (PSEM) approach using the 'psem' function from the "piecewiseSEM" package in R (Lefcheck, 2016). PSEMs are a statistical approach used to analyse multiple complex interacting variables by uniting them into a single model (Lefcheck, 2016). They are useful for investigating direct and indirect effects of multiple predictor variables on response variables, and for examining causal relationships in ecological systems (Lefcheck, 2016, Grace et al., 2012). Unlike classical SEMs, where global estimation is used to construct a model, the piecewise approach allows each response variable to be modelled separately as simultaneous generalised linear mixed-effects models (GLMMs) (Grace et al., 2012, Geary et al., 2018). We fit a separate PSEM for each environmental variable, which were; the proportions of each habitat type, the median topographic ruggedness index (TRI), the mean distance from disturbance, and the mean distance from rocky habitat for each *observed* step (Fortin et al., 2005, Thurfjell et al., 2014). The first GLMM in each PSEM included step length as the response variable and both the environmental variable as well as mean temperature (C°) as predictor variables—mean temperature was controlled for in all PSEMs. The second GLMM within each PSEM included mean VeDBA as the response variable and the environmental variable, mean temperature, and step length as predictor variables. Both models included a random effect of individual to account for repeated measurements by the same individual (Zuur et al., 2009). We calculated the conditional R^2 for each GLMM to determine the variance explained by the predictor variables (Nakagawa and Schielzeth, 2013, Geary et al., 2018). For each GLMM within the PSEM, we calculated the relevant range coefficients—which represent the standardised effects of the predictor variables on the response variables for each model, and are useful for comparing the relative effects of predictors (Lefcheck, 2016, Grace and Bollen, 2005). We also calculated the total effect of each environmental variable on mean VeDBA both directly and indirectly as mediated through step length. This was done by calculating the partial correlation between the environmental variable and mean VeDBA while controlling for step length (direct effect), calculating the partial correlation between step length and mean VeDBA while controlling for the environmental variable (indirect effect), and then summing both the direct and indirect effects (Muthén, 2011). Finally, we fit a single PSEM with the inclusion of season as a predictor variable, to test its effect on mean temperature, step length, and mean VeDBA.

4.4. Results

In total, we tracked 12 northern quolls across two seasons at Woodie Woodie. Of these individuals, two collars were not recovered. Of the remaining 10 individuals, one was excluded from analysis due to a lack of data. This left us with nine individuals for analysis: four from the breeding season and five from the non-breeding season (Figure C1; Figure C2; Figure C3; Figure C4). Only one female was collared (in non-breeding season; Table 4.1), and one collared male was predated by a feral cat on a waste rock dump in the mining landscape. Individuals were heavier and had larger tail circumference in non-breeding season compared to breeding season, whereas foot length was similar, and testes were larger in breeding season (Table 4.1). Following data cleaning, the average number of days with GPS locations for the nine individuals was 20.50 ± 0.50 days in breeding season, and 21.20 ± 2.97 days in non-breeding season. The average number of total fixes after data cleaning was 257 ± 10 fixes for breeding season. Fix success was lower in non-breeding season with an average of 186 ± 49 fixes per individual (Table 4.1).

Table 4.1: The body condition and tracking details of the nine northern quolls used in analyses.

Season	ID	Sex	Age (years)	Fixes	Days	Weight (g)	Foot length (mm)	Tail circ. (mm)	Testes diameter (mm)	Movement range (ha)
Breeding	33421	M	1	274	22	640	34.80	45	23.20	6584.67
	33427	M	1	260	20	540	37.90	55	24.50	6331.69
	33411	M	1	227	20	545	36.60	42	21.20	3115.55
	33425	M	1	266	20	640	38.20	50	24	8576.21
	Average		*1*	*257*	*20.50*	*591*	*36.90*	*48*	*23.20*	*6152.03*
	SE		*0*	*10*	*0.50*	*28.16*	*0.77*	*2.86*	*0.73*	*66.79*
Non-breeding	33415	F	2	99	17	450	31.30	60	*NA*	157.87
	33413	M	1	92	13	855	37.50	69	16.30	1169.05
	33423	M	2	226	25	805	34.30	65	14.90	723.78
	33412	M	1	356	30	760	38.20	71	20.10	85.99
	33422	M	2	158	21	700	35.20	55	21.60	387.46
	Average		*1.6*	*186*	*21.20*	*714*	*35.30*	*64*	*18.20*	*504.83*
	SE		*0.24*	*49*	*2.97*	*70.77*	*1.23*	*2.93*	*1.57*	*199.84*

On average, northern quolls had movement ranges which were more than 12 times larger in breeding season compared to non-breeding season (Table 4.1; Figure C1; Figure C2). Northern quoll observed movement ranges had a higher proportion cover of rocky habitat compared to the available landscape, and all other habitats were used in proportion to their availability (Figure 4.2; Table C3). Northern quoll movement ranges were located in the most topographically rugged areas of the landscape, and were, on average, closer to rocky habitat and disturbed mining habitats relative to the available landscape (Figure 4.2; Table C3). Quolls did not use movement ranges based on distance from disturbance (Figure 4.2; Table C3).

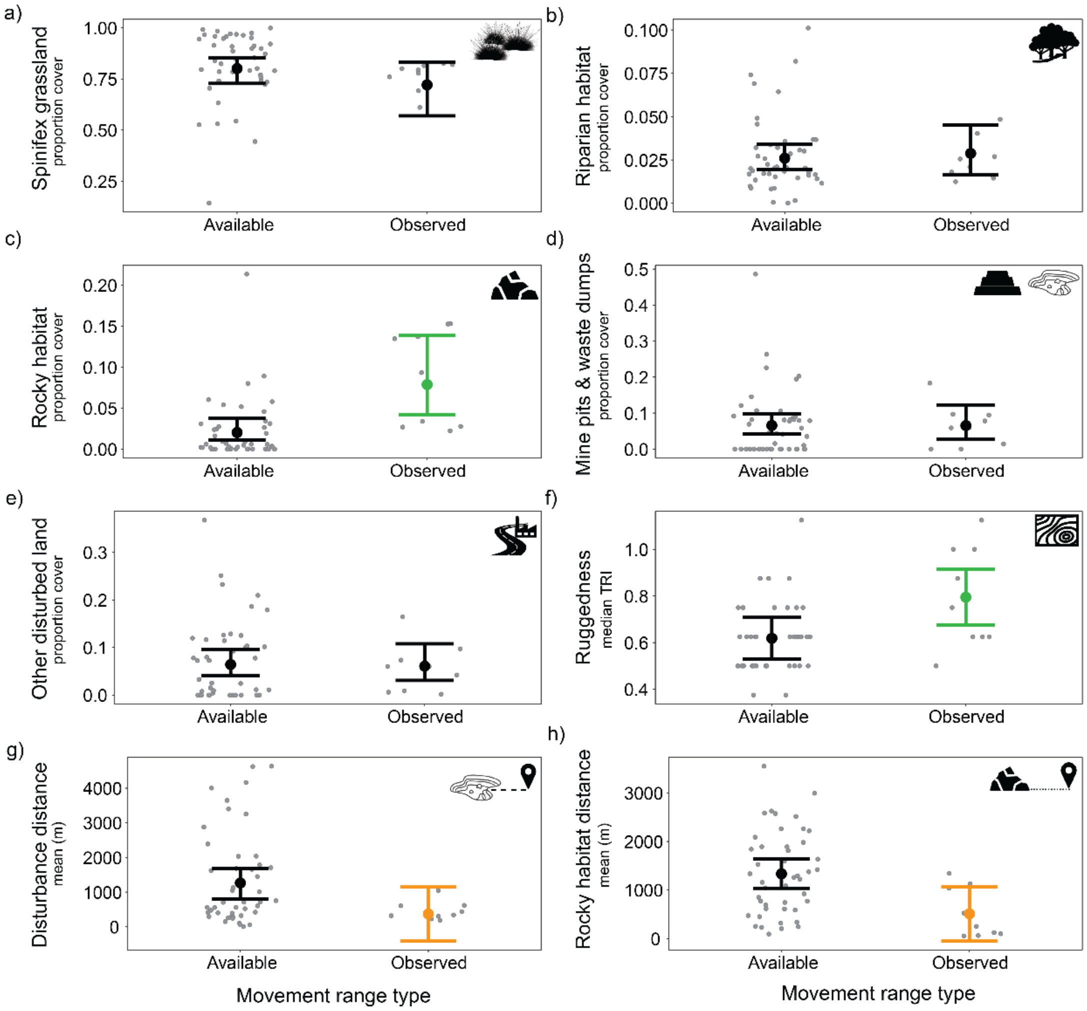


Figure 4.2*:* Conditional effects plots for all models analysing the influence on broad scale northern quoll movement ranges by the proportional cover of a) spinifex grassland, b) riparian habitat, c) rocky habitat, d) mine pits and waste dumps, and e) other disturbed land, as well as the f) median topographic ruggedness index, g) mean distance from disturbance, and h) mean distance from rocky habitat. Grey points indicate raw data, large points indicate the conditional effect for each model, and bars indicate the 95% confidence intervals. Green bars indicate a positive significant relationship for *observed* compared to *available* movement ranges, and orange bars indicate a significant negative relationship for *observed* compared to *available* movement ranges.

In terms of fine-scale habitat selection, which refers to night-time movements, the global iSSF model had substantial support in both seasons (Table C2). The global iSSF model for breeding season suggests that, within their movement range, northern quolls were significantly less likely to select mining habitats, spinifex grassland, and riparian habitat compared to rocky habitat. However, the global iSSF model for non-breeding season suggests that, within their movement range, northern quolls used both mining habitats and riparian habitat at a similar rate to rocky habitat, but used spinifex grassland significantly less (Figure 4.3; Table C4). Northern quolls selected for areas with higher topographic ruggedness relative to the landscape median in breeding season but did not show significant selection preferences for topographic ruggedness in non-breeding season (Figure 4.4). Distance from disturbance had no effect on northern quoll fine scale habitat selection during either season, while quolls selected for areas which were further from rocky habitat relative to the landscape mean in breeding season, with no selection preference in non-breeding season (Figure 4.4). Age had no influence on northern quoll step length or turning angle (Table C4). When undertaking VHF tracking of northern quolls during the day, we observed northern quolls denning within a mixture of rocky habitat, mine pits, and waste dumps.

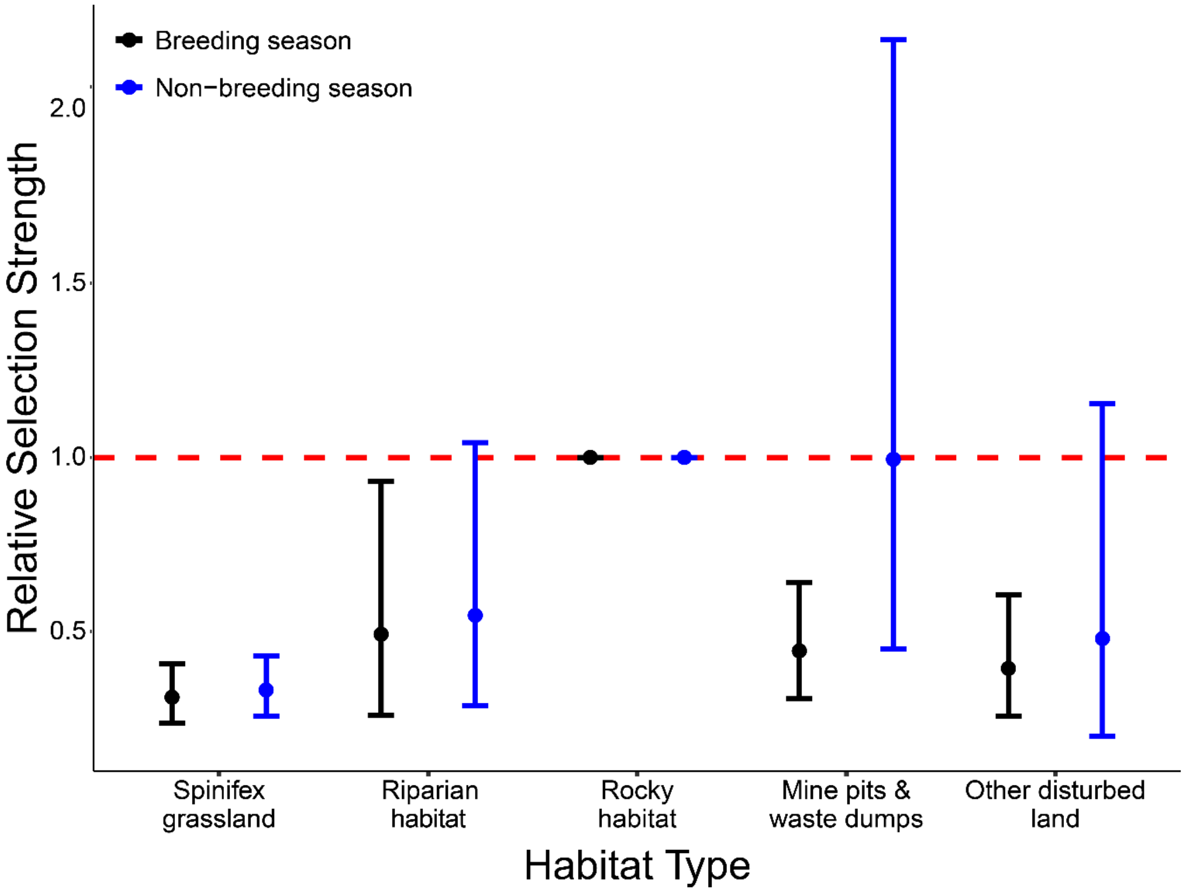


Figure 4.3: The relative selection strength (RSS) for northern quolls in breeding and non-breeding season, where the selection of spinifex grassland, Riparian habitat, mine pits and waste dumps, and other disturbed land is compared relative to selection for rocky habitat. Points reflect the RSS and bars reflect the 95% confidence intervals. Black points and bars reflect selection in breeding season while blue points and bars reflect selection in non-breeding season. The red dashed line for this plot reflects the relative selection strength for rocky habitat and a significant difference is observed if error bars do not cross this line.

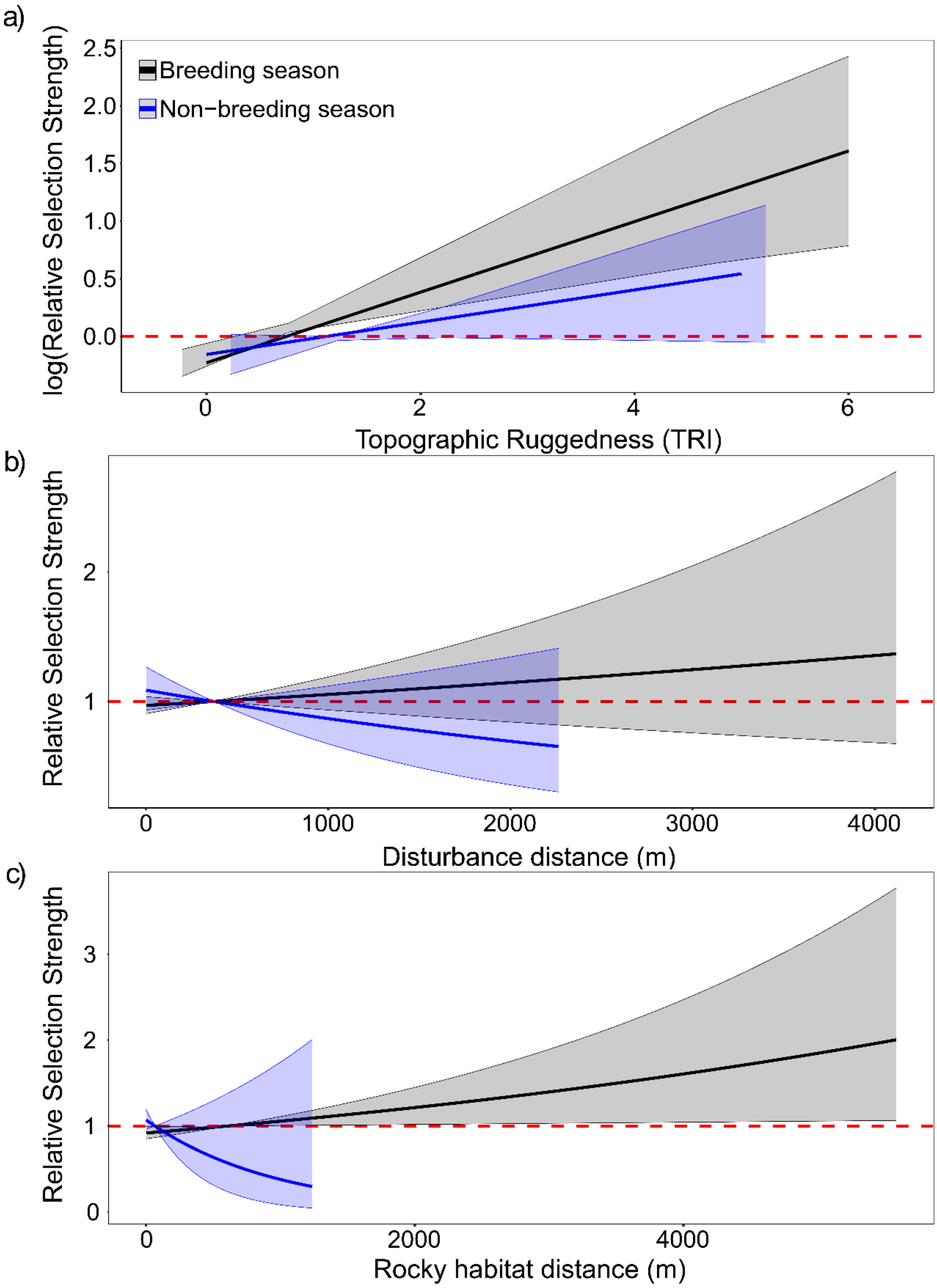


Figure 4.4: The a) log relative selection strength (RSS) for topographic ruggedness is compared for topographic ruggedness as well as the RSS for distance from b) disturbance and c) rocky habitat. The black line reflects breeding season while the blue line reflects non-breeding season. Shaded areas reflect the 95% confidence intervals. The red dashed line for these plots reflects the median topographic ruggedness, the mean distance from disturbance, and the mean distance from rocky habitat respectively. Selection above or below this line reflects the relative selection strength being higher or lower than the median or mean.

Among all habitat types, riparian habitat had the highest mean NDVI value ± SD (0.36 ± 0.11), followed by rocky habitat (0.19 ± 0.05), spinifex grassland (0.16 ± 0.04), other disturbed land (0.11 ± 0.04), and mine pits and waste dumps (0.09 ± 0.04; Table C5). Rocky habitat had the highest median topographic ruggedness ± IQR (1.25 ± 1), followed by spinifex grassland, mine pits and waste dumps, and other disturbed land which all had a median TRI of 0.5 ± 0.375. Riparian habitat had the lowest median topographic ruggedness (0.375 ± 0.375). Mine pits and waste dumps had the highest maximum topographic ruggedness (6.875).

PSEMs demonstrated that using higher proportions of spinifex grassland increased northern quoll step length, with a total effect of 0.086, effectively raising mean VeDBA by 8.6% per unit increase despite its negative direct effect (Figure 4.5). Riparian habitat had a similar, though less pronounced total effect, with an increase of 1.7%. Conversely, higher proportions of rocky habitat led to shorter step lengths, decreasing mean VeDBA by 28% per unit increase (Figure 4.5). Mine pits and waste dumps had the highest positive total effect on mean VeDBA raising VeDBA by 16.2% per unit increase. Using higher proportions of other disturbed land also resulted in longer step lengths, contributing to a 19.5% increase in mean VeDBA per unit increase (Figure 4.5).

Median ruggedness, similar to rocky habitat, had a negative total effect on VeDBA, mainly due to shorter step lengths with increased ruggedness, resulting in a 33.1% decrease in mean VeDBA with every unit increase in median ruggedness (Figure 4.5). Increasing distance from mining disturbance had a negative total effect on mean VeDBA (7.7%), whereas increasing distance from rocky habitat had a positive total effect on mean VeDBA (24.3%), showing contrasting total effects despite both resulting in higher step lengths and lower direct effects on mean VeDBA (Figure 4.5).

In all cases, rising mean temperatures decreased step lengths and mean VeDBA, while longer step lengths resulted in higher mean VeDBA (Figure 4.5). Breeding season had a positive total effect of 0.282 on mean VeDBA, indicating that quolls used more energy in breeding season than in non-breeding season (Figure C5).

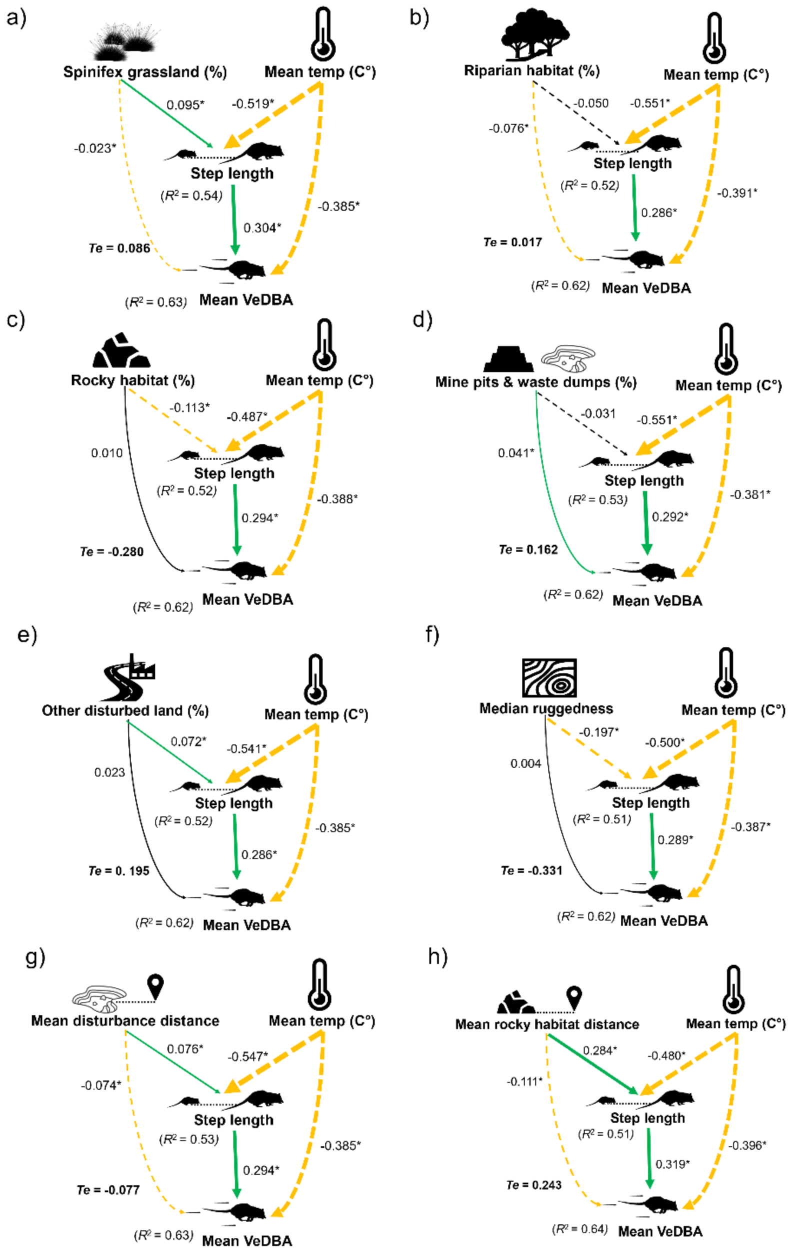


Figure 4.5: Relevant range coefficients for step length and mean VeDBA (a proxy for energy expenditure) related to the influence of mean temperature and the proportion used of a) spinifex grassland, b) riparian habitat, c) rocky habitat, d) mine pits and waste dumps, e) other disturbed land, as well as f) median ruggedness, g) mean distance from disturbed land, and h) mean distance from rocky habitat. Dashed arrows represent a negative relationship and solid arrows represent a positive relationship. Arrow colour represents significance (p = <0.05) with green representing significant positive relationships, orange representing significant negative relationships, and black representing a non-significant relationship. Arrow width reflects the size of the effect, with wider arrows representing a larger effect. An asterisk also signifies that the relationship is significant and the conditional R^2 value for step length and mean VeDBA is listed for each model, outlining the variance explained by the predictor variables. *Te* represents the total effect coefficient of each environmental variable on mean VeDBA, both directly and mediated through step length. Icons were adapted from Microsoft PowerPoint, NESP Hub, Flaticon.com, Pinterest, and Iconfinder.

4.5. Discussion

Our study evaluated the habitat selection and energy use of the endangered northern quoll in an active mining landscape. As predicted, we found that at the broad scale, quolls preferred rugged, rocky habitats, and used spinifex grassland, riparian habitat, and disturbed mining habitats in proportion to their availability. At the fine scale, quolls used all habitats less than rocky habitat during breeding season, but used mining and riparian habitats at similar amounts during non-breeding season. Moving through mining habitat increased energy expenditure (mean VeDBA), suggesting that these areas may impose higher energetic costs than natural habitats. This supports existing concerns for quolls regarding the continued expansion of large-scale mining disturbance in the Pilbara and highlights the sub-lethal threats to species living in human-altered landscapes.

Northern quoll broad-scale movement ranges had higher proportions of, and were closer to, rocky habitat compared to the broader landscape—consistent with previous findings (Cowan et al., 2022, Gibson et al., 2023, Moore et al., 2022a). By contrast, quolls used mining habitats in proportion to their availability. This suggests that the quolls here were accessing mining habitats and did not avoid mining habitats on a broad scale. In the Pilbara, mining often targets rocky habitat given they are typically rich in mineral reserves (Ramanaidou and Morris, 2010), and it is likely that the mined area in this study, was once rocky habitat used by northern quolls (Gibson et al., 2023, Henderson, 2015). It is therefore likely that quolls did not move into this landscape post-disturbance, but that they were already there before mining began. Living in or near to mining disturbance may inflate quoll movement ranges—with larger ranges observed here than in natural landscapes (Moore et al., 2022a)—which could suggest that quolls are required to move more in mining landscapes (Beasley and Rhodes, 2010).

During the breeding season, fine-scale integrated step-selection analysis suggested that quolls avoided mine pits and waste dumps, as well as other disturbed land, spinifex grassland, and riparian habitat, relative to rocky habitat. Mining habitats had lower perceived vegetation cover (i.e., NDVI) and topographic ruggedness than rocky habitat, and for these two criteria, was more similar to spinifex grassland (Paruelo et al., 1997, Pettorelli, 2013, Wang et al., 2004). Avoidance of spinifex grassland by quolls in natural landscapes has been previously documented (Cowan et al., 2022, Hernandez-Santin et al., 2016), and the avoidance of mining habitats in breeding season suggests a potential lack of resources like food (e.g., *Ficus* species—which only occur in rocky habitats) or dens during breeding. All quolls tracked in breeding season were male, and in general male northern quolls travel long distances when breeding, seeking females and food (Moore et al., 2022a, Oakwood, 2002)—as they did here. Anthropogenic landscape disturbances like mining can reduce the abundance of potential prey species such as reptiles (Doherty et al., 2020, Macdonald et al., 2023, Craig et al., 2012), mammals (Ardente et al., 2016, Andrén, 1994), birds (Nichols and Nichols, 2003), invertebrates (Hendrychová et al., 2008, Hoffmann and Andersen, 2003), and vegetation (Gould, 2011), meaning that disturbed mining habitats may not satisfy the high resource requirements of quolls during breeding season (Wang et al., 2017).

The avoidance of mining habitats by male quolls may also be driven by a reduced chance of breeding success for several reasons. Female animal abundance is often lower in human-disturbed landscapes compared to males (Berger, 2007, Lasky and Bombaci, 2023). Further, female northern quolls require specific denning and environmental conditions (e.g., deep, cool dens) to protect their young during breeding season (Cowan et al., 2020b), which mining landscapes may not satisfy. This is supported by the fact that we were only able to collar one female northern quoll here. In highly fragmented landscapes—like mining habitats—northern quolls are often less abundant (Moore et al., 2022b), and vast areas of non-rocky habitat can reduce genetic connectivity in the species (Shaw et al., 2022, Hohnen et al., 2016, von Takach et al., 2022). To persist in fragmented landscapes like this, it often requires increased long distance dispersal by animals (Trakhtenbrot et al., 2005), which may be exacerbated in mining landscapes where naturally-fragmented habitats are broken up further. Considering that male northern quolls typically perish after their first breeding season (Oakwood, 2004, Oakwood et al., 2001), successful annual reproduction is vital for population success (Moro et al., 2019). Reduced breeding opportunities in mining habitats could decrease the likelihood of males using this habitat and breeding successfully, decreasing the amount of viable breeding habitat in the landscape.

Another potential explanation for the observed avoidance of mining habitats may be due to risk avoidance, or the landscape of fear (Bleicher, 2017, Laundré et al., 2010). Similar to natural landscapes where quolls avoid predators that thrive in spinifex grassland (Hernandez-Santin et al., 2016, McGregor et al., 2015), mining habitats often present comparable or greater threats from feral cats and dingoes (Cowen et al., 2019, Bradley et al., 2022, Hamilton and Algar, 2004, Newsome et al., 2013b). Built infrastructure such as roads and waste dumps, can attract predators and increase predation risk (Wysong et al., 2020a, Doherty et al., 2015a, Wysong et al., 2020b). Animals often use habitats based on their perception of what is low and high risk, with areas of high predation risk often avoided (Bleicher and Dickman, 2020). Disturbances such as artificial light and noise pollution (such as that associated with machinery, spotlights, and ore processing within the mine) can also interfere with foraging and mating, and force unnecessary movements for animals (Linley et al., 2020, Robert et al., 2015, Kight and Swaddle, 2011, Doherty et al., 2021). These risks coupled with reduced body condition in the breeding season may make mining habitats appear more dangerous (Brown et al., 1999, Laundré et al., 2001), deterring quolls during this period.

In contrast, in non-breeding season at the fine scale, quolls used mine pits and waste dumps, and other disturbed land in similar amounts to rocky habitat. This also applied to riparian habitat (e.g., densely vegetated drainage lines). During this time, northern quoll body condition was improved compared to breeding season and movement ranges were considerably smaller. Small movement ranges and healthy body condition often reflect the use of resource-rich habitats (Viana et al., 2018, Moore et al., 2023). However, for quolls, the lack of breeding-driven movement for males in non-breeding season likely requires fewer resources generally (Oakwood, 2002), potentially contributing to better body condition (Gardiner et al., 2019). It is possible that quolls during this time obtain sufficient food resources from natural rocky and riparian habitats (similar to natural landscapes; Cowan et al., 2022)—but take advantage of limited resources in mining habitats due to lower energy demands in this season. Optimal foraging theory (Emlen, 1966, MacArthur and Pianka, 1966)—which postulates that foraging animals seek to maximise energy intake in the minimum time needed to gain nourishment (Perry and Pianka, 1997, Schoener, 1971)—would suggest that quolls would avoid mining habitats regardless of season, due to decreased food resources in these areas. However, mining structures like waste rock piles have some evidence of short-term denning by quolls (Cowan et al., 2020b, Dunlop et al., 2015), including by males in this study. Therefore, this increased use may be explained by a game-theoretical approach (Fudenberg and Tirole, 1991, Osborne and Rubinstein, 1994), where animals might settle for a lower-quality habitat above a certain threshold in a fragmented landscape, to avoid moving towards known high-quality sites which may be lost to competitors or increase predation risk (Lima and Zollner, 1996).

Long term population maintenance requires effective energy use. However, the increased use of mining habitats here comes with an energetic cost. Accelerometers revealed that northern quolls expended the most energy when mostly using other disturbed land, and mine pits and waste dumps, likely driven by faster movement and high-cost behaviours such as bounding, jumping, and galloping (Gaschk et al., 2023). This supports the suggestion that mine sites contain fewer resources or are riskier than favoured rocky habitat, where energy expenditure was lower—probably due to more resting or foraging behaviours there. Other small mammals show similar negative behavioural responses to anthropogenic habitats, by increasing speed (Bista et al., 2021) or tortuous movements (Tucker et al., 2018). Lower resources in mining habitats may force quolls to either traverse these areas quickly or use more energy to find food and shelter, increasing their overall food requirements (van Donk et al., 2019). For example, cougars living in anthropogenically-disturbed landscapes use more energy and are required to consume more deer annually to meet their energy requirements (Wang et al., 2017). In non-breeding season, quolls used riparian habitat similarly to rocky habitat, which is expected to allow efficient movement between rocky habitats (Cowan et al., 2022, Shaw et al., 2022, Hernandez-Santin et al., 2016). The use of this habitat slightly increased energy expenditure, but not as much as mining habitats or spinifex grassland. This suggests that in non-breeding season, despite using habitats that were more energetically costly, quolls may be able take advantage of mining and riparian habitats due to lower energy requirements overall. However, in breeding season when efficient dispersal is vital and energy requirements are already high, rocky habitats are likely favoured given the higher chance of breeding and increased resource availability.

4.6. Conclusion

Anthropogenic disturbance can significantly influence animal movement and energy expenditure (Doherty et al., 2021), as evidenced by our study on northern quolls. Rocky habitat is the most important habitat for quolls, despite the presence of disturbance in the landscape. The replacement of favoured natural habitats such as this with energetically-costly mining habitats may exacerbate risks for quolls and negatively impact movement—more than if less-favoured habitats such as spinifex grassland were disturbed (Lindenmayer et al., 2023). Conservation strategies such as establishing or retaining movement corridors (e.g., rocky and riparian habitats; Bennett, 1990, Hodgson et al., 2011, Krishna et al., 2016), creating artificial refuges (Cowan et al., 2021, Watchorn et al., 2022), revegetation or restoration (Erickson et al., 2019, Erickson et al., 2017, McGregor et al., 2014b), and invasive predator control (Palmer et al., 2021), could enhance disturbed habitats for animal movement in disturbed landscapes

(Gibson et al., 2023, Goldingay, 2023). However, restoring disturbed mining habitats can be difficult (Cross et al., 2022, Cross et al., 2020) and offsetting habitat destruction is problematic, with few demonstrable successes (Bull et al., 2013, zu Ermgassen et al., 2019, Maron et al., 2018). So, to conserve northern quolls, the preservation and protection of favoured habitats and movement corridors like rocky and riparian habitats, should be prioritised in areas with active mining. More emphasis should also shift from focusing only on the impacts of habitat destruction before or after disturbance, to also managing potential negative impacts on animals during disturbance (Cross et al., 2021).

4.7. Acknowledgements

We would like to acknowledge the Nyamal people as the traditional owners of the land on which this project took place. We would also like to thank ConsMin and all staff for supporting this project, with special thanks to, in no certain order; Kaylee Prince, Luke Barrett, Ying Li, Kirsten Cadle, Rory Embleton, Jacqui Roberts, Kerryn Forster, Sam Covich-Lindsay, Matt Holt, Dan Bull, Mark Menzies, Sarah Thomas, Liz Wadham, Zoe Demidjuk, Richard Darcey, Aaron Kelly, Brendan Dunell, Ben Barker, Greg Reed, and Matt Jones. We would also like to acknowledge support for this project by the Nyamal Rangers and the Nyamal Aboriginal Corporation, as well as Abbey Ernst, Marc Wohling, John Angus, Alyse Burns, Donell Hole, Kylee Imlach, Michael Douglas, the NESP Resilient Landscapes Hub, and Warrawagine Station staff. We also thank Charles Sturt University, the Gulbali Institute, the Department of Biodiversity, Conservation and Attractions, ConsMin, BHP, AusIMM, and the Ecological Society of Australia for project support.

Chapter 5: The impact of mining on animal movement and landscape connectivity revealed through simulations and scenarios

Manuscript under review in Ecological Applications.

Cowan, M. A.[1,2], Forrest, S. W.[3,4], Setterfield, S. A.[2], Dunlop, J. A.[5], Gibson, L. A.[6,7], Nimmo, D. G.[1]

[1]Gulbali Institute, School of Agricultural, Environmental and Veterinary Sciences, Charles Sturt University, Thurgoona, NSW, 2640, Australia.
[2]School of Agriculture and Environment, The University of Western Australia, Crawley, WA, 6009, Australia
[3]School of Mathematical Sciences, Queensland University of Technology, Brisbane, QLD, 4000, Australia
[4]Environment, CSIRO, Dutton Park, QLD, 4102, Australia
[5]School of Molecular and Life Sciences, Curtin University, Bentley, WA, 6102, Australia.
[6]Department of Biodiversity, Conservation and Attractions, Kensington, WA, 6151, Australia.
[7]School of Biological Sciences, The University of Western Australia, Crawley, WA, 6009, Australia

5.1. Abstract

Movement is essential for animal life and significantly influences community dynamics. Landscape-scale disturbances, such as mining, alter habitat structure, introducing new stressors that can severely disrupt animal movement. Understanding how landscape modification impacts animal movement and landscape connectivity is vital for effective conservation in the Anthropocene. Here, we use movement simulations and 'landscape scenarios' to evaluate how mining influences movement, using an endangered mesopredator as a focal species. We aim to determine the effects of different configurations of mining on the movement costs, habitat accessibility, and landscape connectivity of this species. We used GPS data collected from a mining landscape in the Pilbara region of Western Australia to assess temporally dynamic habitat selection. This then informed movement simulations across four landscape scenarios: current mining, dispersed mining, aggregated mining, and non-mining. We compared animal movements, energetic costs, and landscape connectivity across all landscape scenarios. The presence of mining habitats increased energetic movement costs through unfavourable habitats and led to significant changes in landscape connectivity. For example, simulated movements visited fewer favourable habitat patches in mining landscapes and took more steps between them. Mining configuration affected movement differently, with current mining conditions having the greatest impact on movement, increasing simulated home ranges and funnelling movement through unfavourable habitats more than the other mining and non-mining landscapes. Our study highlights the influence of disturbance configuration and altered habitat structure on animal movement. It also emphasises that effective management and development planning must consider impacts on animal movement and landscape connectivity.

5.2. Introduction

Movement is a fundamental part of animal life and community dynamics (Nathan et al., 2008). The ability of an animal to move through a landscape determines dispersal success, gene flow, population demographics, and predator-prey interactions (Tucker et al., 2018, Leigh et al., 2012). Changes to landscape configuration and resource availability from anthropogenic disturbance can disrupt natural movement (Doherty et al., 2019)—often requiring animals to move through or around disturbances when dispersing between favoured habitats (Webb et al., 2011). Therefore, the ability of animals to move effectively and efficiently in disturbed landscapes depends on adequate landscape connectivity (Fahrig, 2003)—which is the degree to which a landscape facilitates movement among resource patches (Baguette et al., 2013, Taylor et al., 1993). Understanding how disturbance influences connectivity and animal movement is critical for conservation in anthropogenic landscapes and requires high quantities of fine-scale data (Nathan et al., 2022).

Mining affects more than 50 million km^2 of land globally (Sonter et al., 2020), with broad-scale impacts for terrestrial habitats (Sonter et al., 2022), and animal behaviour (Newsome et al., 2013b). Altered habitat structure by mining can alter animal movement, resulting in avoidance of disturbed habitats, larger movements, and higher energetic costs (Cowan et al., 2024). For example, migrating mule deer (*Odocoileus hemionus*) avoid mining-disturbed habitats and have higher energetic costs when travelling through areas of large-scale gold mining in the USA (Blum et al., 2015). Similar avoidance of mining habitats were observed in a resident population of American pronghorn (*Antilocapra americana*) in gold-mining areas of the USA (Osterhout et al., 2024). Mining can also reduce the availability of favoured habitats, decreasing landscape connectivity and increasing reliance on suboptimal habitats (Zhuo et al., 2022). This can alter animal survival and population distributions. For example, vicuña (*Vicugna vicugna*) are struck by vehicles more in mining habitats (Mata et al., 2016), and large areas of mining act as barriers to bat (*Chiroptera* spp.) movement, reducing species richness in disturbed habitats (Theobald et al., 2020).

Northern quolls (*Dasyurus hallucatus*)—*marlarlparra* in Nyamal language—are an endangered mesopredator threatened by mining (Moore et al., 2022a). In the Pilbara region of Western Australia, northern quolls persist in highly rugged, rocky habitats (Moore et al., 2019, Hernandez-Santin et al., 2022), which provide denning and food resources (Cowan et al., 2020b). Rocky habitats are generally embedded within a matrix of other habitat types that northern quolls must move through to access their favoured habitat, including spinifex (*Triodia*) grasslands and riparian habitats (Moore et al., 2021b). This is particularly important during the breeding season, when male northern quolls make long-distance movements in search of mates (Oakwood, 2002). Drill and blast mining operations remove complex rocky denning habitat and simplify vegetation cover (Gibson et al., 2023). Hence, mining changes the amount and spatial configuration of rocky habitats, as well as altering the matrix in between. Northern quolls can persist within mining landscapes, but tend to avoid direct mining disturbance (e.g., roads, mine pits) at a fine-scale, probably because moving through it is risky and energetically expensive (Cowan et al., 2024). While recent work has helped understand the implications of mining disturbance on northern quoll movement at a fine scale, we are yet to understand how mining affects landscape-scale northern quoll movement and habitat connectivity.

Recently, approaches have been developed to ‘scale up’ fine-scale movement data using simulated movement trajectories (Potts and Börger, 2023). Simulations are informed by tracking data and allow predictions to be made about animal movement under various scenarios (e.g., Forrest et al., 2024, Hofmann et al., 2023, Sells et al., 2023). These include ecological questions pertaining to animal dispersal (Sells et al., 2023) or landscape connectivity (Hooker et al., 2021, Hofmann et al., 2023, Osipova et al., 2019). For example, Aiello et al. (2023) used habitat selection information from nine desert bighorn sheep (*Ovis canadensis nelsoni*) populations to simulate their movement in landscapes with and without highways. Aiello et al. (2023) found that the removal of highways increased accessible habitats for all but one population. Globally, plans for future development (e.g., mining) often lack assessments of impacts on animal movement and landscape connectivity (Bergès et al., 2020). Excluding such information is risky given the scale of negative impacts driven by landscape modification, and understanding these impacts in disturbed landscapes can lead to better biodiversity outcomes (Bergès et al., 2020, Tarabon et al., 2019).

Using similar analyses to those described by Aiello et al. (2023) and Whittington et al. (2022), we investigate how the presence and configuration of mining influences animal movement and landscape connectivity using the northern quoll as our focal species. We follow a simulation-approach that allows us to investigate how disturbance affects movement in the absence of before/after data (e.g., Whittington et al., 2022). First, we assess the habitat selection of northern quolls to inform movement simulations that replicate observed movements in the current mining landscape. Second, because mines have many shapes and forms, and different disturbance configurations might have varying consequences, we introduce several different scenarios. We do this by artificially modifying the landscape to create different configurations of mining disturbance (i.e., more dispersed, more aggregated), as well as removing mining completely to reflect pre-mining conditions. We then simulate northern quoll movements in these landscapes. Third, we compare measures of movement, including home range size, habitat revisitation, and the energetic cost of movement—using a cost surface—among landscape scenarios. Lastly, we apply the three-step approach for assessing landscape connectivity as developed by Hofmann et al. (2023), to compare landscape connectivity among the different mining scenarios.

5.3. Methods

Study area

This study takes place in the Pilbara bioregion of Western Australia. The Pilbara is characterised by topographically rugged rocky outcrops, gorges, and mesas, interspersed with expansive hummock grasslands dominated by *Triodia*, with a scattered overstory of *Acacia* and *Eucalyptus* species (Carwardine et al., 2014, Van Vreeswyk et al., 2004). Rocky habitats contain a varying mixture of grass, *Eucalyptus*, and *Ficus* species amongst embedded and scattered rock (Maslin and van Leeuwen, 2008, Van Vreeswyk et al., 2004). Drainage lines (e.g., creeks) are often rocky and typically riparian—with a dense combination of grasses, shrubs, and trees (Van Vreeswyk et al., 2004).

Northern quolls were tracked at the Woodie Woodie mine (Cowan et al., 2024), located on Nyamal Country in the eastern Pilbara region—close to the eastern edge of the northern quoll’s Pilbara range (Moore et al., 2019). Woodie Woodie is an active manganese mine with historic (since 1950’s) and active mining disturbance covering > 30 km^2. Mining activities have resulted in several open pits, waste rock dumps, buildings, roads, cleared areas, and patches of remnant natural habitat encompassing spinifex grassland, riparian habitat, and rocky habitat (Cowan et al., 2024). All areas of the mine are accessible to northern quolls. The Oakover River runs south to north ~6 kms east of the mine with many non-perennial tributaries feeding this river from around and through the mine site.

Data collection

We used movement data (observed and random steps) from Cowan et al. (2024), of four male northern quolls tracked at Woodie Woodie during part of their breeding season (September–October 2021). Observed steps connect each subsequent GPS fix while five random steps were created for each observed step, with step lengths drawn from a Gamma distribution and turning angles drawn from a von Mises distribution (Avgar et al., 2016). See Cowan et al. (2024) for details on individuals, trapping, GPS collaring, and data processing and cleaning. Data was collected during the northern quolls' primary activity period (6 pm – 6 am; Moore et al., 2024) over an average of 20.50 ± 0.50 (mean ± S.E.) nights with a fix rate of one fix per 30 minutes (Cowan et al., 2024). To assess northern quoll habitat selection, we created three environmental variable maps for the current mining landscape: 1) a habitat type map consisting of: riparian habitat, spinifex grassland, rocky habitat, mine pits and waste dumps, and other disturbed land, 2) a distance from rocky habitat map, and 3) a distance from mining disturbance map (all at a 10 m scale). See Cowan et al. (2024) for details on the creation of environmental variable maps.

Habitat selection models

We extracted covariates from the environmental variable maps at the end of each observed and random step. To determine northern quoll habitat selection and inform movement simulations, we fit integrated step-selection functions (iSSFs) (Avgar et al., 2016). The response variable for the model was the step type (i.e., observed or random). We included 'habitat type' as a categorical predictor with rocky habitat set as the reference category, as well as several other variables (see below).

Northern quolls den predominantly in rocky habitats in the Pilbara (Hernandez-Santin et al., 2022, Cowan et al., 2020b), but were occasionally found denning in rocky mine pits and waste dumps at Woodie Woodie (Cowan et al., 2024). It is expected that northern quolls emerge from dens at around dusk to forage and find mates, and return to them to rest around dawn each morning (Moore et al., 2024). To determine if observed northern quolls followed this pattern, and to create simulations that mirrored this behaviour, we explored habitat selection across time. To assess the temporally dynamic selection of potential denning habitats, we included 'distance from rocky habitat' and 'distance from mining disturbance' as linear predictors, as well as interacting with pairs of harmonics relating to each 30-minute time step over the 12-hour data collection period (n = 24) (Forrest et al., 2024). Harmonics are pairs of sine and cosine terms that have cyclic periods of varying frequency that often align with the temporal changes that animals respond to (Forrest et al., 2024). Interacting harmonics with distance values allowed an assessment of selection for areas near or further from potential denning habitats at each time step. The set of harmonics used were $s1 = \sin(2\pi\tau/24)$, $s2 = \sin(4\pi\tau/24)$, $s3 = \sin(6\pi\tau/24)$, $c1 = \cos(2\pi\tau/24)$, $c2 = \cos(4\pi\tau/24)$, and $c3 = \cos(6\pi\tau/24)$, where τ was indexed by 30-minute periods. Given the extremely high values of the distance covariates relative to other predictors, we log-transformed their values prior to fitting the iSSF models to dampen their effects in the simulations.

Northern quolls have distinct home ranges (Heiniger et al., 2020, Hernandez-Santin et al., 2020), so we included a memory parameter in our model that was also temporally dynamic (Forrest et al., 2024). The memory parameter allows for a tendency to return to previously visited locations, constraining simulations much like real animal home ranges (Van Moorter et al., 2009, Riotte-Lambert et al., 2015, Ranc et al., 2022). Prior to fitting the iSSF models, we estimated home ranges for all individuals using kernel density estimation (KDE). We used the reference bandwidth (h_{ref}) and took the mean of the h_{ref} values (Kie, 2013, Signer and Fieberg, 2021). For each observed and random step, we used the mean h_{ref} value to estimate the kernel density of previous observed locations, which approximates space use up to that point. We also log-transformed previous space use density prior to fitting the iSSF models. We excluded locations from the previous 24 hours when estimating the previous space use density as they are likely to reflect the autocorrelation in the movement process rather than resulting from a memory process (Forrest et al., 2024, Rheault et al., 2021).

Habitat selection depends on the scale at which resources are distributed throughout the landscape and how animals move between them, so we included the step length, the log-transformed step length, and the cosine of the turning angle as covariates in iSSF analyses (Forester et al., 2009). We included ‘step ID’ as a strata term in models to ensure observed steps were paired with their respective random steps (Signer et al., 2019). We included a cluster term of ‘individual’, to account for repeated observations by individuals. We fit four population-level iSSFs with differing pairs of harmonics ranging from 0, to 1, 2 and 3 pairs (Forrest et al., 2024). We fit models using the ‘TwoStep’ approach in the ‘TwoStepCLogit’ package (Craiu et al., 2011, Muff et al., 2020).

Simulation validation and model selection

To determine the optimum number of harmonics to include in our final model, we used each model to construct simulations by replicating the step-selection process (Duchesne et al., 2015), then compared simulations to the observed data (Forrest et al., 2024). We began simulations at the starting locations of the four observed northern quolls. Simulations at each starting point were replicated 10 times for models fit with 0, 1, 2, and 3 pairs of harmonics respectively (n = 40 total simulations). Step lengths and turning angles of simulated movements were sampled independently from the Gamma and von Mises distributions of the observed data, while habitat selection was informed by the temporally dynamic iSSF coefficients, resulting in a selection probability for habitat type, distance from rocky habitat/mining disturbance, and space (memory) for each proposed movement step at each time step. Each movement step had 50 proposed new locations from which probabilities were drawn and the next step was chosen. We ran simulations for 480 steps—equal to 20 nights (the mode of the observed data)—resulting in 4,800 simulated steps for each model with different pairs of harmonics. The landscape was set to have a hard boundary, and any proposed steps that fell outside of the landscape extent were not considered.

To select the final model from which to inform simulations and build our analyses, we calculated a range of summary statistics for all simulated and observed movements (Appendix D1; Forrest et al., 2024, Abrahms et al., 2017, Kays et al., 2023). We performed a principal component analysis (PCA) on these statistics using the 'stats' package (R Core Team, 2023a), to visualise how closely each model's simulations mirrored the observed data (Figure D1; Figure D2; Forrest et al., 2024, Kays et al., 2023, Abrahms et al., 2017). We selected the final model that created simulations which most closely resembled the observed movement (as shown by the PCA).

Creating multiple landscape scenarios

To compare how different mining configurations influence simulated northern quoll movement and habitat connectivity, we created three hypothetical landscape scenarios in addition to the current mining landscape at Woodie Woodie (similar to Whittington et al., 2022). These were 1) a non-mining landscape, which represents the likely landscape structure prior to the establishment of Woodie Woodie, 2) a dispersed mining landscape (with fragmented mining disturbance across the landscape), and 3) an aggregated mining landscape (with consolidated mining disturbance in a localised area; Figure 5.1). Exploring non-mining, dispersed mining, and aggregated mining scenarios allows for a comprehensive impact assessment, which is critical for developing effective land management and restoration strategies. See Appendix D2 for details on the creation of habitat maps associated with each landscape scenario. The composition of each habitat was kept within 0.09% across the mining-disturbed landscapes despite differing configurations.

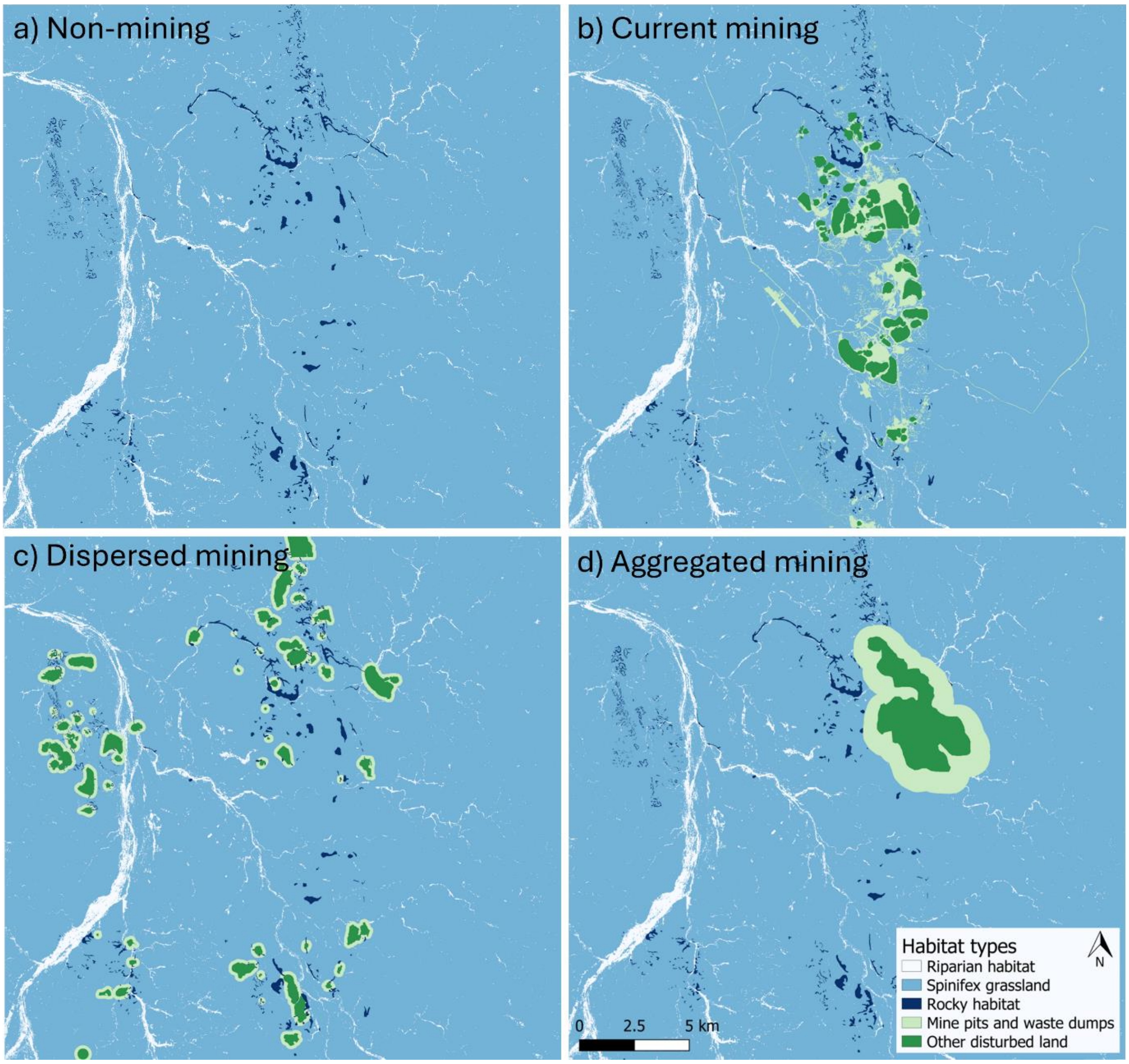


Figure 5.1: The four landscape scenarios compared in analyses: a) the non-mining landscape, b) the current mining landscape, c) the dispersed mining landscape, and d) the aggregated mining landscape.

Simulating movement and energetic costs in each landscape scenario

To compare simulated movement differences among landscape scenarios, we generated 100 random starting locations from observed northern quoll GPS data (Hooker et al., 2021). These locations were kept the same across all landscape scenarios. Simulations were replicated 5 times at each starting location, resulting in 500 total movement simulations with 480 steps each for a total of 240,000 steps in each landscape scenario.

To determine if space use was influenced by mining configuration, we calculated 100% minimum convex polygons (MCPs; henceforth home ranges) for each of the 500 simulations using the “st_convex_hull” function from the ‘sf’ package in R (Pebesma, 2018). MCPs are a basic measure of measuring home range but are standardised and useful when comparing across landscape scenarios. We compared simulated home range size across landscape scenarios using generalised linear mixed models (GLMMs). The response variable for models was home range size, and the predictor variable was the landscape scenario. We fit two GLMMs: 1) the ‘non-mining vs. mining model’, where the non-mining landscape was used as the reference category, and 2) the ‘mining configuration model’, where we excluded the non-mining landscape, and the current mining landscape was used as the reference category. This allowed us to compare a) simulated movements in the non-mining landscape with those in each mining landscape, and b) simulated movements in the current mining landscape with those in scenarios with different mining configurations. We included a random effect that was unique for each starting location to account for replicated simulations at each starting location, as well as simulations starting from the same location across landscape scenarios. Home range values were fitted using a Gamma distribution with a log link function. GLMMs were fit in the ‘glmmTMB’ package in R (Magnusson et al., 2017). We considered coefficient plots for all GLMMs and denoted clear relationships when 95% confidence intervals did not cross zero (Senior et al., 2023).

We assessed the energetic costs of simulated movement across landscape scenarios by creating a cost surface that assigns energetic costs to each habitat (Etherington, 2016, Etherington et al., 2014). Energetic costs were informed using total effects from piecewise structural equation models (PSEMs) from Cowan et al. (2024). Total effects calculated the effects of each habitat type on northern quoll vectorial dynamic body acceleration (VeDBA)—an energy use proxy (Qasem et al., 2012)—directly and mediated through step length. We normalised total effects between zero (lowest cost) and one (highest cost) (Etherington, 2016), with cost values assigned to each habitat type: rocky habitat (0), riparian habitat (0.63), spinifex grassland (0.77), mine pits and waste dumps (0.93), and other disturbed land (1). We overlaid the movement simulations for each landscape scenario and sampled the mean energetic cost along each step. We then fit the two GLMMs following the same model structure as above (i.e., the non-mining vs. mining model, and the mining configuration model), with the mean energetic cost for each step as the response variable and landscape scenario as the predictor. We included a random effect which was unique for each starting location and modelled energetic costs using an ordered beta distribution, given the distribution was continuous with upper and lower bounds (0, 1; Kubinec, 2023).

To determine how often movement simulations returned to the same habitat patches in each landscape scenario (Bracis et al., 2018), we calculated the number of revisitations (simulated steps) to areas within 20 m of previously visited points. We did this using the "getRecursions" function from the 'recurse' package in R (Bracis, 2019). We categorised revisitations by the habitat type at the end of each step and fit the two GLMMs separately for each habitat type following the same model structure as above. Although, the number of revisitations for each habitat type were used as the response variable. Revisitations were identified as having a Poisson distribution and we included an observation-level random effect to account for overdispersion (Harrison, 2014).

Simulating habitat connectivity in each landscape scenario

To compare habitat connectivity among landscape scenarios, we constructed a new set of simulations where we omitted the memory process to allow simulations to cover the entire landscape without being restricted to a home range (Figure D2; Hofmann et al., 2023). We randomly generated 50 starting locations (not restricted to observed northern quoll locations) and ran one simulation per location for 8760 steps each (equal to one year of movement), resulting in 50 total movement simulations for a total of 438,000 steps per landscape scenario. This was replicated in each landscape scenario using the same starting locations. All other simulation parameters were kept the same as previously. Using memory-free movement simulations that cover the entire landscape is important to sample the entire landscape consistently, allowing accurate connectivity results (Hofmann et al., 2023). To confirm that landscape connectivity reached a steady state (i.e., simulations covered the entire landscape reliably), we randomly distributed 100 checkpoints (500 x 500 m squares) across the current mining landscape and measured the traversal frequency for increasing numbers of simulations (one to 50), with 10 random subsamples at each increment (Hofmann et al., 2023). A steady state was considered reached when the traversal frequency across all subsamples reached 100%.

To determine the connectivity of rocky habitat patches in each landscape scenario, we calculated the average number of steps required for landscape-scale simulations to travel between rocky habitat patches (Hofmann et al., 2023). When a rocky habitat patch was successfully reached by a simulation, it became the next starting patch and so on until all successful connections between subsequently accessed rocky habitat patches were identified. We fit the two GLMMs described above (i.e., the non-mining vs. mining model, and the mining configuration model), where the response variable was the average number of steps, and the predictor variable was the landscape scenario. Average steps were fit using a Gamma distribution with a log link function.

To visualise hotspots of movement for each landscape scenario, we created heatmaps by rasterizing all 50 landscape-scale simulations onto a 10 x 10 m raster and counting the number of simulations (*n* = 50) that overlapped each cell (as per Hofmann et al., 2023). We counted each simulation only once, which reduces bias by avoiding simulations that become focused in a specific area and repeatedly enter the same cells (Hofmann et al., 2023).

To locate movement corridors in each landscape scenario, we converted simulations into networks and calculated landscape betweenness (as per Hofmann et al., 2023). Betweenness (i.e., betweenness centrality) is defined as the number of steps entering a node (raster cell) relative to the total number of steps in the landscape—reflecting the importance of the node for connectivity in the landscape network (Bastille-Rousseau et al., 2018). To calculate betweenness, we overlaid the study area with a grid containing 257 x 257 m cells (median observed northern quoll step length), where the centre of each cell served as a node for the network. To identify edges between nodes, we overlaid landscape-scale simulations and interpolated points every 10 m. This detects cell-transitions at a greater resolution than using just the end of each step (Hofmann et al., 2023). We determined all transitions occurring from one cell to another, as well as the frequency at which those transitions occurred (Hofmann et al., 2023). The resultant edge-list was converted into a weighted network using the ‘igraph’ package in R (Csardi, 2013), that was used to calculate betweenness scores for all cells (Hofmann et al., 2023).

5.4. Results

The iSSF with one pair of harmonics created simulations that most closely resembled observed northern quoll movement, and thus was selected as the final model to simulate northern quoll movement from (Figure D1; Figure D2; Figure D3). Riparian habitat, spinifex grassland, mine pits and waste dumps, and other disturbed land were all avoided relative to rocky habitat (Figure 5.2). The temporally dynamic coefficients for previous space use (the memory process), and distance to rocky habitat and mining disturbance, showed modes at roughly 9 pm and 3 am. As expected, at 9 pm, there was strong attraction to previously used areas and rocky habitat, and repulsion from mining disturbance, resulting in restricted movement close to rocky habitat (Figure 5.2). At 3 am, there was a repulsion from previously used areas, little preference for mining disturbance (close to 0) and a weaker preference for rocky habitat, resulting in wider and more exploratory movements which may suggest foraging (Figure 5.2). At 6 am—around sunrise—there was again strong attraction to previous space use and rocky habitat, and repulsion from mining disturbance, suggesting a return to known rocky habitats for denning (Figure 5.2).

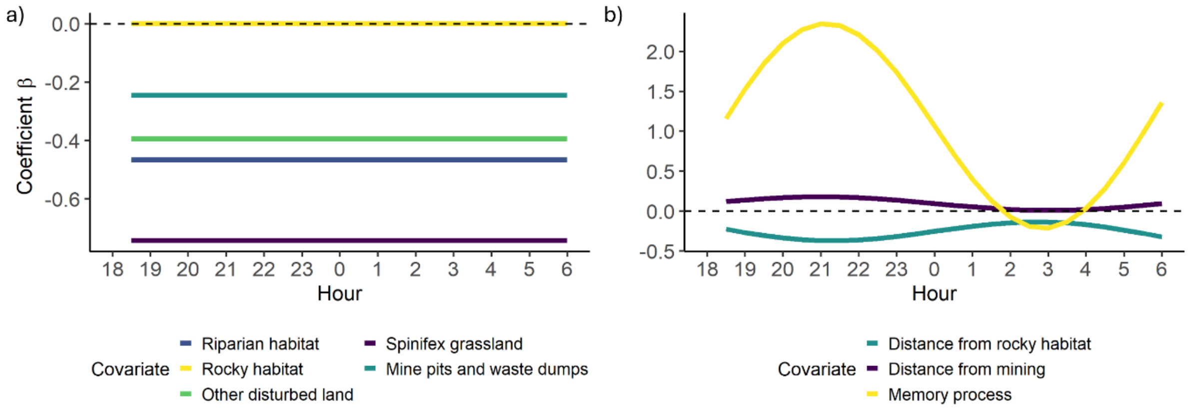


Figure 5.2: Selection coefficients from iSSFs with one pair of harmonics (interacting with distance from rocky habitat, distance from mining disturbance, and the memory process), for a) non-temporally dynamic habitat types (where rocky habitat is the reference category), and b) temporally dynamic distance from rocky habitat, distance from mining disturbance, and the memory process. Positive coefficients for the memory process indicates attraction to previous space use, and positive coefficients for the distance variable indicate an attraction to further distances, with northern quolls repelled from those habitats.

Simulated home ranges were larger in the current mining landscape than the non-mining landscape, and similar among the non-mining, dispersed mining, and aggregated mining landscapes (Figure 5.3; Table D1). Home range sizes were similar between the current mining landscape and the dispersed mining landscape but were smaller in the aggregated mining landscape than the current mining landscape (Figure 5.3; Table D1). Mean energetic movement costs were lower along steps in the non-mining landscape than in all mining landscape scenarios, being highest in the current mining landscape (Figure 5.3; Table D1). Rocky habitat patches were revisited more often in all mining landscape scenarios compared to the non-mining landscape, and most often in the aggregated mining landscape compared to the current mining landscape (Figure 5.3; Table D1). All other habitat patches were revisited at similar rates across all landscape scenarios. The average number of steps required to move between rocky patches was higher in all mining landscape scenarios compared to the non-mining landscape, being highest in the current mining landscape (Figure 5.3; Table D2).

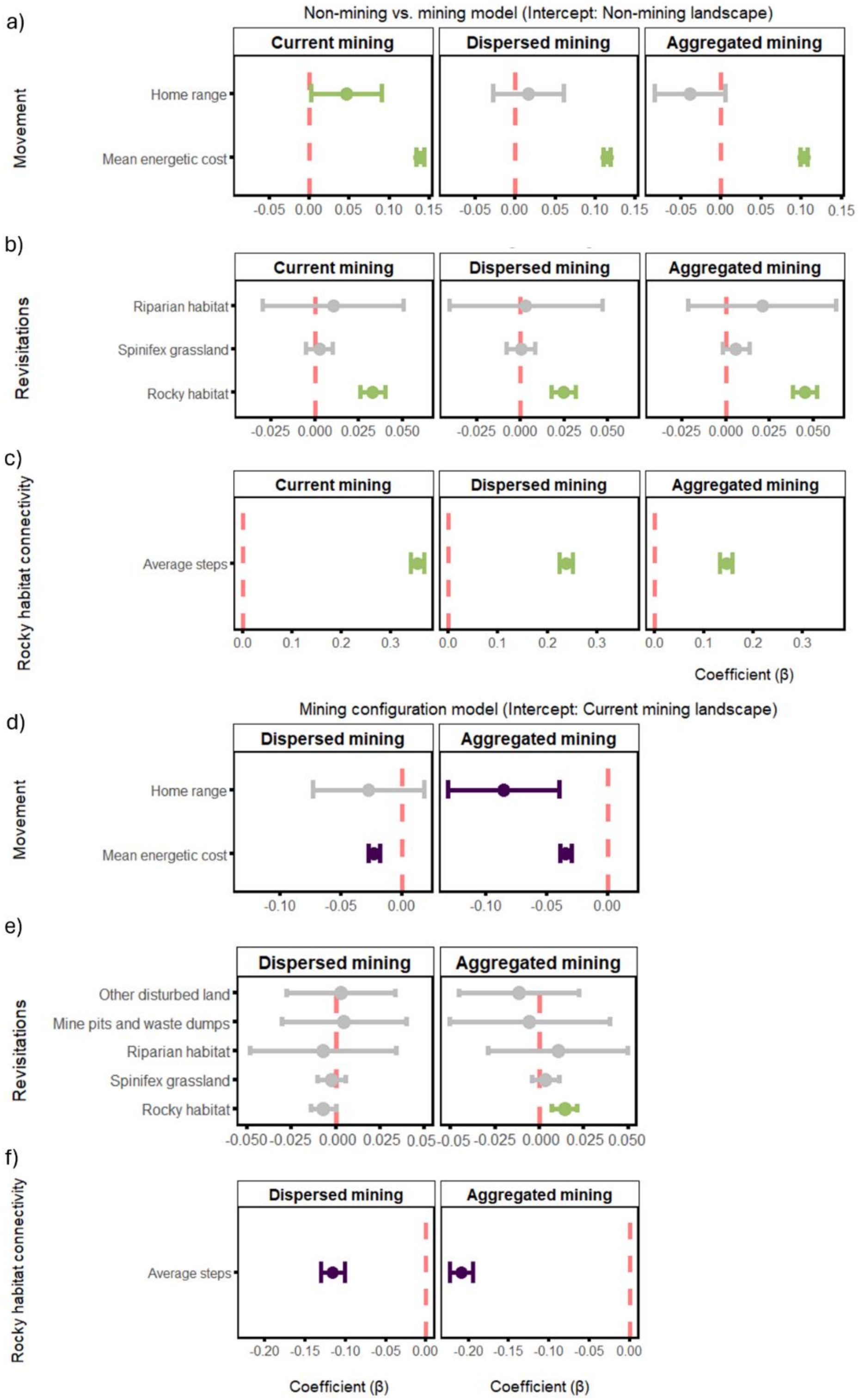


Figure 5.3: Coefficients and 95% CIs of GLMMs comparing movement simulations among landscape scenarios. The non-mining vs. mining model is compared for a) home range and energetic movement costs, b) habitat revisitations, and c) average steps between rocky habitats, with the non-mining landscape as the reference category. The mining configuration model is compared for d) home range and energetic movement costs, e) habitat revisitations, and f) average steps between rocky habitats, with the current mining landscape as the reference category, and the non-mining landscape excluded. Clear relationships are considered when 95% CIs do not overlap zero (red dashed line). Positive relationships are shown in green, and negative relationships are shown in purple.

Landscape connectivity reached a steady state after six landscape-scale simulations (Figure D4). Heat maps showed high frequency of use around rocky habitats, with lower frequency in mining habitats and spinifex grasslands (Figure 5.4). By visual assessment, the heat map of the dispersed mining landscape most closely resembled the non-mining landscape, while the aggregated mining landscape showed reduced use of rocky habitat patches in the north, which were used more often in other landscape scenarios (Figure 5.4).

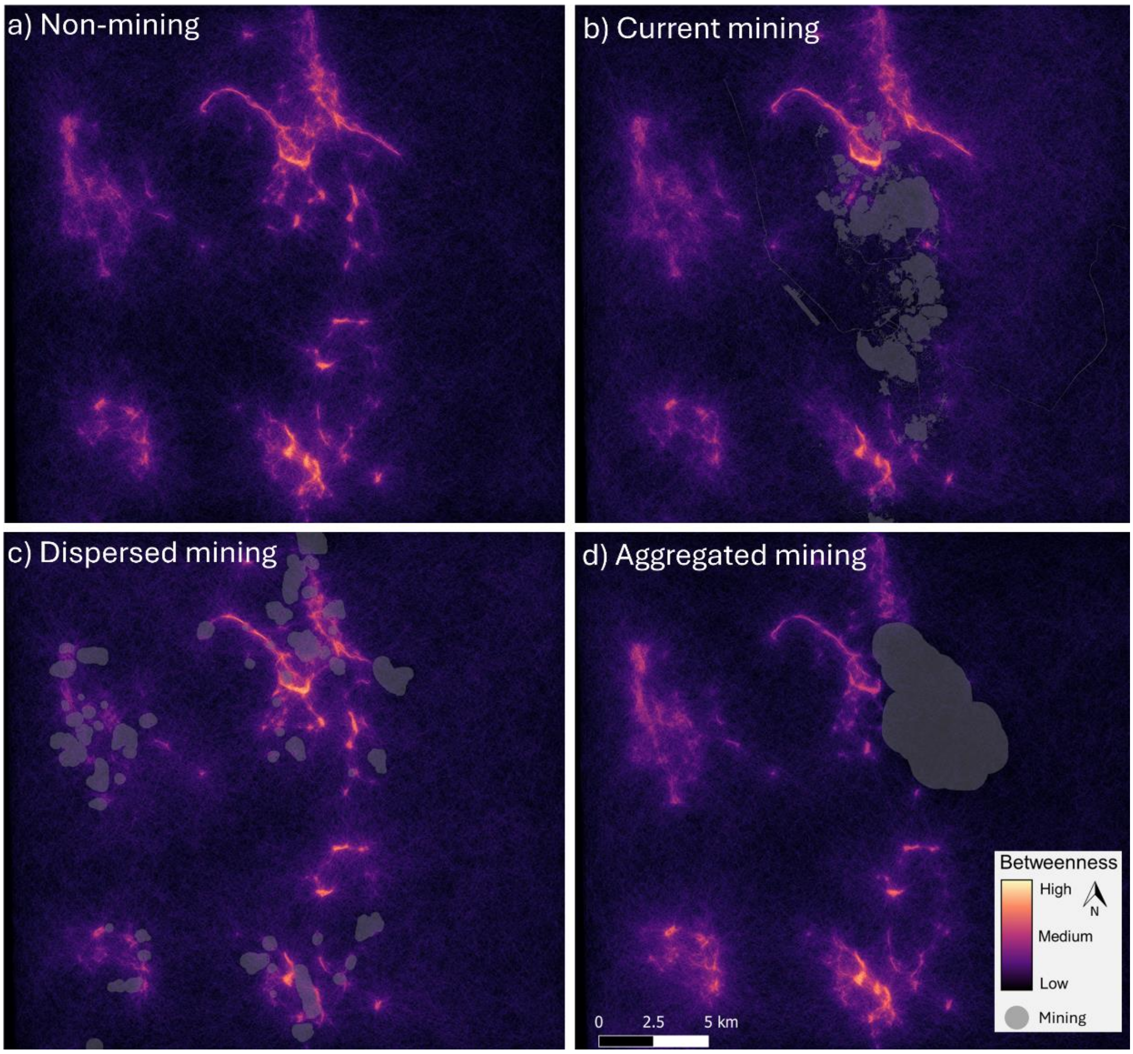


Figure 5.4: Heatmaps showing the trajectory traversal frequency of 50 movement simulations for each cell (10 x 10 m) in the a) non-mining landscape, b) current mining landscape, c) dispersed mining landscape, and d) aggregated mining landscape. Lighter colours highlight areas which were traversed more often, while darker areas highlight areas that were traversed less. Transparent grey patches depict mining disturbance.

Landscape betweenness (and thus the distribution of movement corridors) differed considerably in each mining landscape scenario compared to the non-mining landscape. Movement corridors in the non-mining landscape had strong connections in the central west of the landscape, while movement corridors in the current mining landscape travelled through mining disturbance more heavily than any other mining landscape scenario (Figure 5.5). Conversely, movement corridors in the dispersed mining landscape showed high avoidance of mining disturbance, using gaps in the disturbance, which resulted in higher landscape coverage and a network of corridors (Figure 5.5). Movement corridors in the aggregated mining landscape avoided a large area of the landscape close to the localised mining disturbance, with most movement concentrated away from mining (Figure 5.5).

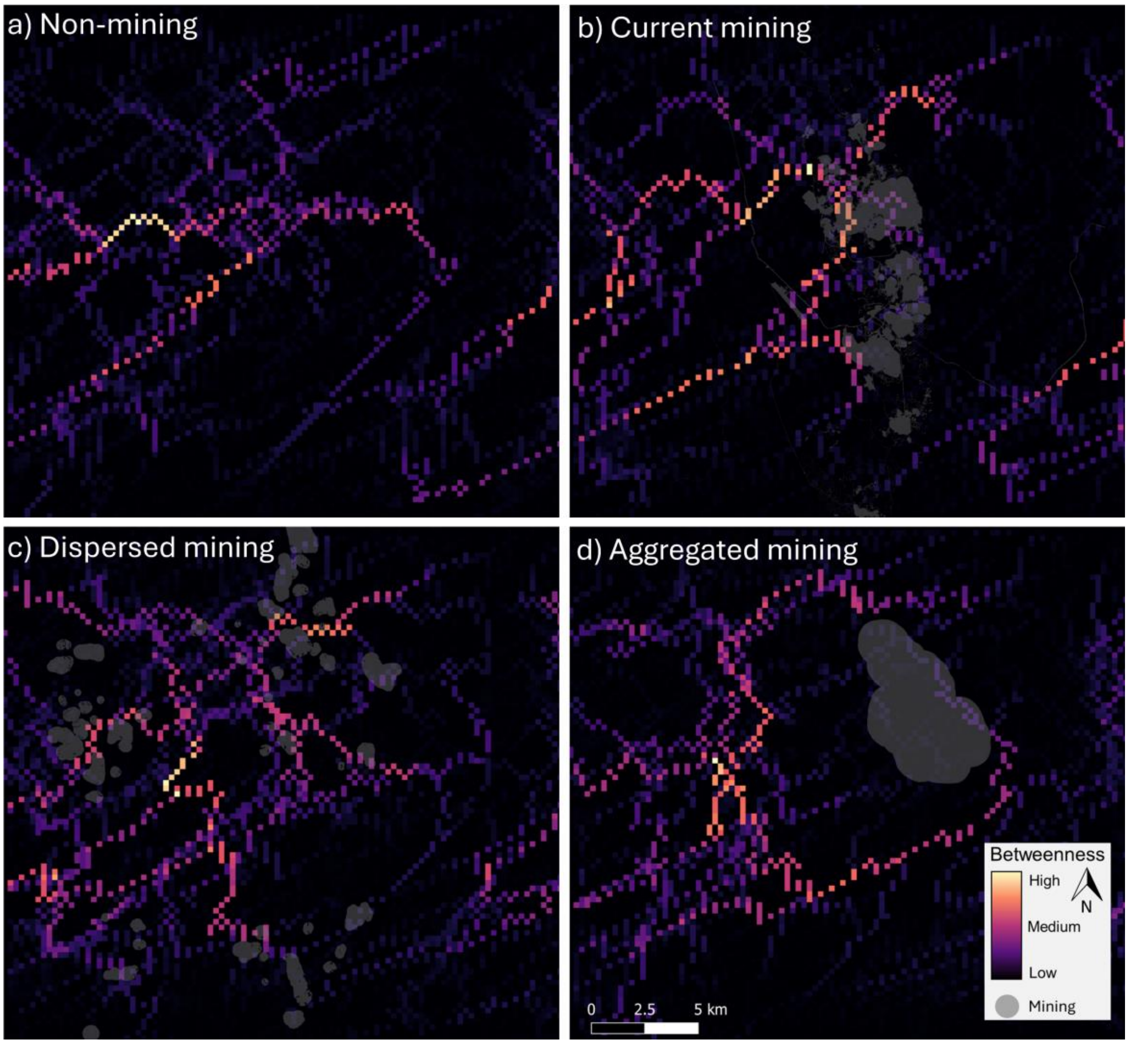


Figure 5.5: Maps of landscape betweenness scores for each cell (257 x 257 m) in the a) non-mining landscape, b) current mining landscape, c) dispersed mining landscape, and d) aggregated mining landscape. A high betweenness score suggests high importance of that area in maintaining landscape connectivity. Transparent grey patches depict mining disturbance.

5.5. Discussion

We integrated animal movement simulations with altered landscape structure to evaluate the landscape-scale effects of mining configuration on simulated northern quoll movement and habitat connectivity. Mining created barriers to movement leading to greater distances and larger home ranges required to access preferred rocky habitat. The availability and connectivity of rocky habitats was also lower in mining landscapes as suggested by higher revisitations of the same rocky habitat patches. As a result, simulated movements in mining landscapes travelled through larger amounts of energetically costly mining habitat. The configuration of mining influenced simulated movement and habitat connectivity differently, diverting movement corridors in each mining landscape from paths used in the non-mining landscape. These findings support existing concerns for northern quolls regarding the continued expansion of large-scale mining disturbance in the Pilbara (Moore et al., 2022a), and highlight the influence of altered habitat structure on the movement and habitat connectivity of animals in disturbed landscapes.

Previous GPS tracking studies have shown that northern quolls prefer rocky habitat and avoid spinifex grasslands and mining disturbance (Cowan et al., 2022, Cowan et al., 2024). We expanded on this by examining temporal variation in habitat selection for the first time. Northern quolls selected areas closer to rocky habitats and further from mining habitats early in the night—likely when they emerged from their dens. This was followed by more exploratory behaviours further from rocky habitats later in the night, before returning to rocky habitats closer to known areas at the end of the night. This reflects what we would expect from Pilbara northern quolls, due to their reliance on rocky habitats for refuge (Hernandez-Santin et al., 2022). Exploratory movements away from rocky habitats are energetically-costly and increase predation risk (Cowan et al., 2024), taking place after midnight likely following a period of rest and digestion (Moore et al., 2024). Such movements might be motivated by the search for mates or potential new resources. Simulations with one pair of harmonics closely mirrored observed northern quoll movement, but did not quite overlap completely, meaning there is scope for future work to assess which other covariates might be important to drive northern quoll fine scale movement. However, including temporally dynamic behaviour in our model allowed more robust and ecologically accurate simulations of northern quoll movement (Forrest et al., 2024).

In a naturally fragmented landscape like the Pilbara, northern quolls require access to multiple rocky habitat patches to gain the resources needed for survival (Moore et al., 2022b). In disturbed or fragmented landscapes, the ability to access these multiple refuge patches becomes more important (Nimmo et al., 2019, Andrén, 1994). Despite this, northern quoll simulations revisited the same rocky habitats more often in mining landscapes compared to the non-mining landscape, suggesting reduced access to multiple patches of rocky habitat. This is likely a result of direct habitat loss (i.e., the replacement of rocky habitat with mining) and decreased habitat connectivity between rocky patches. When habitat connectivity is reduced, it can negatively impact population persistence (Morelli et al., 2017). For example, low habitat connectivity driven by habitat fragmentation of the southern tiger cat (*Leopardus guttulus*) led to reduced population viability in some areas (Sartor et al., 2024). An over-reliance on fewer high-resource patches may also increase competition for dens and mates—or exhaust finite resources like food—negatively impacting population dynamics (Mänd et al., 2005, Murray and Illius, 2000). Further, northern quoll simulations required more steps to connect rocky habitats in mining landscapes, suggesting that the limited rocky habitats were more difficult to reach than in the non-mining landscape. This will likely reduce breeding success, with fewer opportunities for males to reach females in high-quality denning habitats (Shaw et al., 2022). It may also increase predation risk for individuals by extending their time away from safer refuge habitat (Bleicher and Dickman, 2020, Johnson et al., 2009).

High habitat connectivity and resource abundance decreases the area required by animals to gain resources (Viana et al., 2018, Doherty et al., 2019), while low connectivity and resource scarcity increase it (Rus et al., 2020, Cowan et al., 2022). Energetic movement costs for simulated northern quolls were higher in all mining landscape scenarios compared to the non-mining landscape. This was likely driven by the need to traverse more mining habitats to reach rocky habitats, compared to less costly spinifex grasslands or riparian habitats (Cowan et al., 2024). Energetic costs were highest in the current mining landscape, reflected in simulated home ranges being larger here than in the non-mining landscape. This may relate to the sprawled configuration of the current mining landscape forcing movement corridors through mining habitats more than any other mining landscape scenario—as reflected in betweenness maps. Movement corridors in mining habitats likely lead to negative impacts, such as human-wildlife conflict and increased mortality (e.g., vehicle strikes; Mata et al., 2016). Sprawled areas of landscape modification like that seen in the current mining landscape can also create barriers to movement, reducing genetic connectivity and population size (Bishop et al., 2017).

Localised disturbances, where impacts are confined to discrete areas, generally have larger impacts on individuals restricted to that area, but less direct impacts for individuals using non-disturbed parts of the landscape (König et al., 2019, Fahrig, 2003). Heat and betweenness maps showed that simulated hotspots and habitat corridors in the aggregated mining landscape generally avoided mining disturbance in the northeast and focused movement in the undisturbed southwestern areas. This suggests that aggregated mining largely excludes northern quolls from benefitting from large parts of the landscape and likely contributed to the higher revisitations of rocky habitats in this scenario than in the current mining landscape. Increased use of a smaller area of the landscape also likely drove smaller simulated home ranges in this landscape compared to the current mining landscape. If animals are restricted to few favourable patches due to habitat degradation it can increase competition for resources and mates, and reduce carrying capacity (Calizza et al., 2017). In turn, this can force some individuals to use unfavourable habitats (such as mining habitats) to avoid high competition in favourable habitats (Lima and Zollner, 1996)—creating ecological traps (Battin, 2004).

In the dispersed mining landscape, simulated movement corridors—as evidenced by betweenness maps—also avoided the scattered mining disturbance more than the current mining landscape. This increased the number of corridors required to access rocky habitats, funnelling movement into areas that were avoided in the non-mining landscape. The addition of disturbance to favoured habitats which are already fragmented can restrict dispersal for species reliant on them—such as for species trying to access their preferred successional vegetation stage after fire (Driscoll et al., 2021). Large networks of corridors into ‘sub-optimal’ areas could also lead to an increased reliance on unfavourable natural habitats (e.g., spinifex grassland). This can result in lethal and sublethal effects. For example, increased use of unsuitable artificially afforested habitat patches increased predation of a critically endangered lizard in an arid scrubland, resulting in local extirpation (Hawlena et al., 2010). Increased use of sub-optimal habitats have been shown to have detrimental effects on the body condition of northern quolls in the Pilbara (Moore et al., 2023). Therefore, the effects of avoiding dispersed mining disturbance would likely lead to similar results.

5.6. Conclusion

Our study demonstrates the significant influence of altered habitat structure on animal movement and landscape connectivity, highlighting the negative ecological impacts associated with mining disturbance. Management strategies for active mines should prioritise the preservation and restoration of pre-disturbance habitat corridors, to enhance connectivity between rocky habitat patches and reduce the need for northern quolls to engage in energetically costly movements. Mining development that minimises sprawled contiguous disturbances which disconnect the landscape—such as that seen in the current mining landscape—could mitigate some effects on northern quoll movement and habitat connectivity. Although, dispersed and aggregated disturbances will still negatively affect landscape connectivity, and likely population persistence, in different ways. Including measures of animal movement and landscape connectivity in ecological impact assessments before disturbance is uncommon, but it is likely to lead to more positive biodiversity outcomes in mining landscapes (Sales Rosa et al., 2023, Dalloz et al., 2017, Tarabon et al., 2019). Habitat restoration during active mining (e.g., revegetation and the retention and deployment of large rock piles) may also mitigate some of the negative effects on movement in mining landscapes (Zhuo et al., 2022). Given our small sample size being all male northern quolls, studies including female northern quolls would be useful. Future research may include applying the methods used here to consider animal movement for mining rehabilitation and closure, as well as for other landscape-scale disturbances such as fire and urbanisation.

5.7. Acknowledgements

We would like to acknowledge the Nyamal people as the traditional owners of the land on which data was collected. We would like to thank ConsMin and all staff for supporting this project, particularly Kaylee Prince, Luke Barrett, Rory Embleton, and Jacqui Roberts for assisting with fieldwork. Thank you also to Charles Sturt University, the Gulbali Institute, the Department of Biodiversity, Conservation and Attractions, and the NESP Resilient Landscapes Hub for project support.

Chapter 6: Summary

Many terrestrial mammal species live in close proximity to mining disturbance (Sonter et al., 2022). This number is expected to grow into the thousands (Torres et al., 2022), due to future increases in mining (Sonter et al., 2018, Sonter et al., 2020), and high mining overlap with biodiverse regions (Aska et al., 2024). For the northern quoll (*Dasyurus hallucatus*), the importance of movement to disperse and breed is only heightened due to their semelparous life history and low survival of males into a second year (Oakwood, 2000, Hernandez-Santin et al., 2019). Any interruptions to movement from mining are likely to be detrimental, due to the need for new recruits annually (Moro et al., 2019).

In the previous chapters, I have increased our understanding of the impacts of mining on fauna communities and ecosystems. I have also explored the habitat use of northern quolls and highlighted the influence of mining on northern quoll movement and landscape connectivity—which was raised as a priority by Cramer et al. (2016). Here, I summarise the results of each chapter and discuss some broader lessons and future directions related to this study.

In **chapter two**, to contextualise mining impacts on wildlife, I deployed camera traps using a distributed control-impact design to monitor fauna in eight mining camps—semi-urban areas in mining landscapes—and eight ecologically similar reference landscapes across the Pilbara. Using the collected data, I investigated species composition, species diversity, functional richness, predator-prey networks, and temporal activity. I then compared these measures between treatments. I found variable responses for different animal groups: some thrived in mining camps (e.g., *Varanidae* spp.); some were adaptable to mining with no clear changes in detections or temporal activity between treatments (e.g., feral herbivores); and some animal groups were negatively affected by mining disturbance, evidenced by lower mammal species richness and increased nocturnality of critical weight range mammals. Broadly, I found support for the novel assemblage hypothesis in mining camps, suggesting that future wildlife management here will affect ecosystems differently to reference landscapes (Hobbs et al., 2018, Higgs, 2017). Effects of mining disturbance were localised, indicating that wildlife management and conservation should incorporate some consideration of spatial scale in mining landscapes. Based on the findings of this study, ecosystem-level planning is crucial when developing and implementing management in and around mining camps.

In **chapter three**, to define northern quoll movements in undisturbed landscapes, I collated four datasets of northern quoll GPS data from undisturbed landscapes across the Pilbara—including my own—and calculated home ranges. I compared habitat use within home ranges to what was available in the broader landscape. I found that quolls preferred using areas with higher proportions of rugged, rocky habitat and dry riverbeds, and lower proportions of spinifex grasslands than what was available. This supports much of the literature on quoll habitat use and reinforces the importance of highly rugged, rocky habitat in the Pilbara (Moore et al., 2021b, Moore et al., 2022a). The key takeaway from this study was that using increased proportions of unfavourable spinifex grassland increased the home range size of the northern quoll, requiring them to move further to access the resources needed for survival.

In **chapter four**, I further investigated the movement of northern quolls, this time in a mining landscape—which involved tracking nine individuals in the breeding and non-breeding seasons. I used integrated step-selection functions to assess fine-scale habitat selection and explored energy use in each habitat using accelerometers. Quolls showed seasonal differences in their habitat use: they avoided mining habitats, riparian habitats, and spinifex grassland, and preferred rocky habitats in the breeding season, but preferred mining habitats similarly to rocky habitats in the non-breeding season. Energy expenditure was highest in mining habitats and lowest in rocky habitats. Overall, the results from this study suggest that mining impacts northern quolls by fragmenting rocky habitats, increasing energy expenditure, and potentially affecting breeding dispersal. Although, mining habitats might provide some resources during the non-breeding season. Conservation efforts such as preserving complex rocky habitats, creating movement corridors, and progressive habitat restoration would be beneficial for northern quolls. Interestingly, 50% of male northern quolls survived into a second year in the mining landscape (Appendix E), a much higher percentage than the previous maximum of 5% observed within the northern quolls' range (Hernandez-Santin et al., 2019). Reasons for this high survival may be related to reduced breeding opportunities for males, likely driven by low female densities in the mining landscape and mining habitats impacting breeding dispersal. Lower breeding opportunities would decrease the hormonal-related stress of breeding for males (Fisher et al., 2013), increasing survival. For example, in a captive setting where male northern quolls have lower breeding-related costs and reduced energy requirements, they have lived for up to six years (Jackson, 2007). High survival may allow males a second chance to contribute to the next breeding season, but this is unconfirmed in free-living northern quolls.

In **chapter five**, I used the northern quoll habitat selection information gathered in **chapter four** to inform temporally dynamic movement simulations. I artificially altered the configuration of the current mining landscape to create four potential scenarios (i.e., landscapes with current mining conditions, dispersed mining, aggregated mining, and no mining). This allowed me to infer the impacts of mining presence and configuration on simulated northern quoll movement and landscape connectivity. Simulated northern quolls in mining landscapes revisited the same rocky habitat patches more often, and required more steps to move between rocky habitats compared to the non-mining landscape. The configuration of mining also had clear effects on the shape and structure of simulated movement corridors, with the current mining landscape having the greatest impact on movement—driving larger home ranges, increased energetic costs, and more mining-impacted habitat corridors compared to landscapes with more dispersed or aggregated mining disturbance. This emphasises the need to consider animal movement and landscape connectivity in future development planning (Bergès et al., 2020, Tarabon et al., 2019).

6.1. Broader lessons

Collectively, my research has enhanced our understanding of northern quoll movement ecology, particularly in mining landscapes. It has also helped to contextualise the animal community and ecosystem changes that mining brings about. Specific management implications derived from my findings are discussed throughout my chapters, however, broader lessons from this research may have relevance for other species globally—given mining impacts 50 million km^2 of land (Sonter et al., 2020), and the IUCN lists 2821 mammal, bird, reptile, and amphibian species as threatened by energy production and mining (IUCN, 2024). In the Pilbara alone, there are many other species that rely on rocky habitats and therefore have some relationship with mining, including the vulnerable Pilbara olive python (*Liasis olivaceus barroni*), ghost bat (*Macroderma gigas*), and Pilbara leaf-nosed bat (*Rhinonicteris aurantia*). For example, mining increases habitat loss and vehicle strikes for Pilbara olive pythons, while dams can attract the species in mining landscapes (Pearson, 2003). Both bat species roost in caves, but mining can remove these roosts as well as reduce the amount of foraging habitat available. Determining their movement, landscape connectivity, and impacts of mining are listed as priorities for both bat species (Cramer et al., 2023, Bradley et al., 2024). In the United States of America, the flat-tailed horned lizard (*Phrynosoma mcallii*) lives in rocky habitats that often overlap with sources of natural gas, oil, and minerals (Turner and Medica, 1982).

While in China, the snow leopard (*Panthera uncia*) inhabits rocky mountainous areas affected by mining and is known to use mining habitats in some capacity (Alexander et al., 2016, Heiner et al., 2024). For all these species, active mining is likely to influence movement and resource availability in some way.

My research identified that impacts from mining are often species-specific and localised, with varying responses to disturbance by species within mining landscapes. This is supported by the broader literature. For example, while northern quoll movement was negatively impacted by mining, a top predator, the dingo (*Canis lupus dingo*) has reduced movement requirements in mining landscapes, suggesting increased resources (Newsome et al., 2013a, Newsome et al., 2013b). Indeed, most of the dingoes' movement is focused around areas of human waste (e.g., rubbish dumps) (Smith et al., 2020, Meek et al., 2024). Responses to mining can also be sex specific. For example, males of another top predator, the grizzly bear (*Ursus arctos*), avoid active mining habitat, but females with cubs often select for mining habitats (Cristescu et al., 2016b, Cristescu et al., 2016a). Further, other quoll species such as the spotted-tailed quoll (*Dasyurus maculatus*) and chuditch (*Dasyurus geoffroii*) have shown positive responses to post-mining landscapes in forested landscapes (Henderson et al., 2023, McGregor et al., 2014b). However, these species rely more on renewable denning substrates such as tree hollows, logs, and burrows that can eventually return following restoration. The northern quolls' reliance on non-renewable rocky habitats—which once destroyed cannot return without active intervention—means that such restoration goals in Pilbara mining landscapes will be more difficult. The variability in species responses to mining highlights the importance of creating species-specific and landscape-specific plans to conserve wildlife in mining landscapes—much like in fire-affected landscapes (Geary et al., 2020).

Werner et al. (2020) identified 95,320 active and inactive mines across Australia with 28% of these existing in Western Australia. Most of the mines (89%) are inactive and 68% are classified as neglected (Werner et al., 2020). Only 4% of mines in Australia have undergone rehabilitation, highlighting the urgent need for increased national rehabilitation efforts. Of the remaining inactive mines, 75% are classified as terminated, with minimal likelihood of rehabilitation (Werner et al., 2020). Overall, Werner et al. (2020) suggests that approximately 82% of existing Australian mines may require rehabilitation, posing significant economic, environmental, and social challenges for the future. When coupled with expected increases in mining activity, due to large deposits of precious minerals such as lithium, iron ore, and gold

(Sonter et al., 2020), mining disturbance is likely to continue to expand across Australia, and particularly the Pilbara. This study did not have the scope to consider effects of mining rehabilitation on animal communities, nor or northern quoll movement and habitat connectivity. However, continued destruction of important habitat features in the absence of effective restoration of disturbed landscapes, such as rocky outcrops and riparian habitats, will likely have greater broad-scale impacts on populations of northern quolls and other animals in the Pilbara and beyond.

6.2. Future directions

In Appendix F, we reviewed the progress of Pilbara northern quoll research since the first priorities were published by Cramer et al. (2016), highlighting the outcomes and defining future directions. These future directions relate to several aspects of the original priorities which were: (i) assessing and refining survey and monitoring protocols; (ii) improving our understanding of fine-scale habitat use to identify areas of critical habitat; (iii) improving our understanding of population dynamics and structure; (iv) assessing the impacts of introduced predators; (vi) understanding the spread and impacts of cane toads; (vii) understanding interactions with infrastructure and built environments; and (viii) understanding the influence of interacting threats.

In Appendix G, we reviewed all literature from across the entire northern quoll range (the Pilbara, the Kimberley, the Northern Territory, and Queensland) and outlined ten priorities related to all northern quoll populations, not restricted to the Pilbara. These were: (i) resolving taxonomy, (ii) clarifying the status of the Queensland northern quolls; (iii) understanding mechanisms allowing the persistence and resistance of northern quoll populations during cane toad invasions; (iv) quantifying the impacts of mining; (v) investigating the threat of population isolation and the feasibility of genetic rescue; (vi) unwinding interacting threats; (vii) predicting the impact of climate change; (viii) further incorporating Indigenous knowledge; (ix) harnessing the heritability of toad avoidance behaviour; and (x) investigating the role of artificial refuges as a conservation tool.

Here, I summarise three future directions identified during my PhD which align with the current priorities defined in Appendix F and Appendix G.

Artificial refuges to conserve northern quolls in post-mining landscapes

This thesis was primarily focused on the influence of active mining on wildlife. However, it is also important to understand how post-mining landscapes influence species such as the northern quoll. One potential tool which has been proposed for post-mining landscapes is the use of artificial refuges (Cramer et al., 2016). Artificial refuges are “purposefully designed habitats meant as human-made substitutes for (or supplements to) natural habitat structures, and are usually deployed in degraded, disturbed, or modified environments” (Watchorn et al., 2022). However, existing artificial refuges in Pilbara mining landscapes—often consisting of piles of rock, concrete, and rubble formed using machinery to mimic the rocky crevices that quolls den within—have fallen short (Cowan et al., 2020b). While these structures buffer temperatures similarly to natural dens, they are much shallower and often have decreased vegetation and rock structure in the surrounding area (Cowan et al., 2020b). This likely contributes to decreased mammal prey and increased visitations of larger, predatory feral cats (*Felis catus*) (Cowan et al., 2020b). Most global studies of artificial refuges are focused on non-ground dwelling species (e.g., birds and bats) and many have not monitored the success of artificial refuges with effective experimental designs (Cowan et al., 2021). This means that there is limited guidance in this space to create functional and safe refuges (Cowan et al., 2021). Therefore, I outline a new artificial refuge design targeted at northern quolls in mining landscapes (Appendix H). This design uses rotational moulding to form standardised refuges that consider the internal denning requirements of northern quolls as well as environmental extremes such as fire, hot temperatures, and flooding. They are constructed using linear low-density polyethylene with a flame-retardant additive and an air-circulating vent to reduce internal temperatures at the hottest parts of the day. The use of artificial refuges may help to increase connectivity or provide shelter for northern quolls moving through disturbed mining landscapes, much like artificial refuges have done in post-fire landscapes (Watchorn et al., 2024)—although this design has yet to be tested in the field for this species. There are also risks with relying on artificial refuges and they should never be used to greenwash or enable further habitat destruction (Watchorn et al., 2022, Watchorn et al., 2023). In mining, or other disturbed landscapes, artificial refuges may increase habitat connectivity for northern quolls where rocky features have been removed, but they should be strictly monitored following best practices, with adaptive co-management techniques (e.g., feral predator control, revegetation) (Cowan et al., 2021). When done successfully, mine restoration can contribute to restoring ecological processes at the animal population or community level (McGregor et al., 2014b).

Northern quoll interactions with fire

The effects of fire on northern quoll habitat use, movement, and abundance are understudied in the Pilbara. Moore et al. (2022b) found no strong effects of burnt habitat on northern quoll abundance or occupancy three years post-fire. It is thus likely that northern quolls respond to fire in the time frame much closer to the disturbance—like other mesopredators in Australia (e.g., feral cats and red foxes [*Vulpes vulpes*]; Doherty et al., 2023). In fact, northern quolls in the Northern Territory declined the year following fire (Kerle and Burgman, 1984), and modelled northern quoll recruitment decreased by 20% following fire (Griffiths and Brook, 2015). Post-fire landscapes share similarities to mining landscapes, with similar vegetation structure (Fox et al., 1996), potentially leading to similar predation pressure. Indeed, feral cats have been found moving towards fire scars, presumably to hunt (McGregor et al., 2014a). Despite this, the interactions of northern quolls in the Pilbara with recent (< 1 year) fires are not well known (Appendix F).

I observed the movement responses of two northern quolls to fire at Ripon Hills, a rugged landscape close to Woodie Woodie, where fieldwork for **chapter four** took place (Appendix I). Here, a male and female northern quoll were tracked with GPS collars and accelerometers in a landscape that was burnt seven months prior, resulting in a ~5000 ha fire scar. Movement responses in burnt habitats reflected those in mining habitats: energy expenditure was higher when moving through burnt habitats. The male northern quoll avoided recently burnt habitats during the breeding season, while the female northern quoll showed no clear preference for burnt habitats but favoured rocky habitats. This suggests sex-specific responses to fire among quolls and the potential for large patches of burnt habitat to have similar negative impacts on northern quoll dispersal and landscape connectivity as mining. Further research into the effects of fire on quolls will better allow us to conserve them in a landscape where fires are expected to become larger and more frequent. This observation was discovered with the help of Nyamal Rangers, and I advocate for the continued incorporation of Indigenous knowledge in future research of the northern quoll, as prioritised in Appendix G. Further, unwinding the interacting threats of fire (or mining) with other threats, such as predation and grazing on northern quolls is likely to be particularly important to their conservation, given these threats occur together across their entire range (Appendix G).

Further applications of movement simulation approaches

The combination of big data (e.g., fine-scale GPS tracking; Nathan et al., 2022) and simulation approaches can enhance our understanding of animal movement and landscape connectivity across various undisturbed and disturbed landscapes (Tang and Bennett, 2010). The simulation methods I applied in **chapter five** to compare northern quoll movement and landscape connectivity among different mining configurations—including the three step approach for assessing landscape connectivity developed by Hofmann et al. (2023)—would also be effective for assessing movement and landscape connectivity in landscapes with other disturbances, such as urbanisation, agriculture, or fire. They would also be useful for assessing mining restoration options, given the appropriate data. For instance, Aiello et al. (2023) simulated the movement of desert bighorn sheep (*Ovis canadensis nelsoni*) in landscapes with and without highways (which act as barriers to movement). This allowed comparisons of habitat selection and conservation options to enhance gene flow between different areas. Whittington et al. (2022) simulated the movements of grizzly bears and gray wolves (*Canis lupus*) in landscapes with existing urbanisation conditions, reference conditions, and expected future conditions. This allowed investigations of how current and proposed development or restoration actions would influence movement, habitat use, and landscape connectivity. Similar methods could be applied to any species and environment where movement and habitat data can be collected—including for marine or flying species (Mortensen et al., 2021, Aurbach et al., 2020). The continued development of movement simulations that better replicate animal movement (e.g., using memory and temporally-dynamic habitat selection; Forrest et al., 2024), will likely promote more applications of movement simulations in the future. Future studies of northern quolls at mine sites that are able to investigate female northern quoll responses would also make this method more robust. The ability to artificially configure landscapes as required, like in **chapter five** will also allow several disturbance scenarios to be considered. Given the assessment of animal movement and landscape connectivity is often lacking in development plans for large-scale disturbances (Bergès et al., 2020), methods such as this would likely contribute much needed information before development begins.

References

Abrahms, B., Seidel, D. P., Dougherty, E., Hazen, E. L., Bograd, S. J., Wilson, A. M., Weldon McNutt, J., Costa, D. P., Blake, S., Brashares, J. S. & Getz, W. M. 2017. Suite of simple metrics reveals common movement syndromes across vertebrate taxa. *Movement Ecology,* 5**,** 12.

Adams, A. L., Dickinson, K. J. M., Robertson, B. C. & van Heezik, Y. 2013. An Evaluation of the Accuracy and Performance of Lightweight GPS Collars in a Suburban Environment. *PLOS ONE,* 8**,** e68496.

Adams, L. W. 1994. *Urban wildlife habitats: a landscape perspective,* U of Minnesota Press.

Ahumada, J. A., Fegraus, E., Birch, T., Flores, N., Kays, R., O'Brien, T. G., Palmer, J., Schuttler, S., Zhao, J. Y., Jetz, W., Kinnaird, M., Kulkarni, S., Lyet, A., Thau, D., Duong, M., Oliver, R. & Dancer, A. 2020. Wildlife Insights: A Platform to Maximize the Potential of Camera Trap and Other Passive Sensor Wildlife Data for the Planet. *Environmental Conservation,* 47**,** 1-6.

Aiello, C. M., Galloway, N. L., Prentice, P. R., Darby, N. W., Hughson, D. & Epps, C. W. 2023. Movement models and simulation reveal highway impacts and mitigation opportunities for a metapopulation-distributed species. *Landscape Ecology,* 38**,** 1085-1103.

Aldridge, C. L. & Boyce, M. S. 2007. Linking occurrence and fitness to persistence: Habitat-based approach for endangered greater sage-grouse. *Ecological Applications,* 17**,** 508–526.

Alexander, J. S., Gopalaswamy, A. M., Shi, K., Hughes, J. & Riordan, P. 2016. Patterns of Snow Leopard Site Use in an Increasingly Human-Dominated Landscape. *Plos One,* 11**,** 15.

Andrén, H. 1994. Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat: A Review. *Oikos,* 71**,** 355–366.

Ardente, N. C., Ferreguetti, Á. C., Gettinger, D., Leal, P., Mendes-Oliveira, A. C., Martins-Hatano, F. & Bergallo, H. G. 2016. Diversity and Impacts of Mining on the Non-Volant Small Mammal Communities of Two Vegetation Types in the Brazilian Amazon. *PLOS ONE,* 11**,** e0167266.

Arnold, T. W. 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. *The Journal of Wildlife Management,* 74**,** 1175–1178.

Aska, B., Franks, D. M., Stringer, M. & Sonter, L. J. 2024. Biodiversity conservation threatened by global mining wastes. *Nature Sustainability,* 7**,** 23-30.

Aurbach, A., Schmid, B., Liechti, F., Chokani, N. & Abhari, R. 2020. Simulation of broad front bird migration across Western Europe. *Ecological Modelling,* 415**,** 108879.

Austin, P. C. & Hux, J. E. 2002. A brief note on overlapping confidence intervals. *Journal of Vascular Surgery,* 36**,** 194-195.

Avgar, T., Lele, S. R., Keim, J. L. & Boyce, M. S. 2017. Relative Selection Strength: Quantifying effect size in habitat- and step-selection inference. *Ecology and Evolution,* 7**,** 5322–5330.

Avgar, T., Potts, J. R., Lewis, M. A. & Boyce, M. S. 2016. Integrated step selection analysis: bridging the gap between resource selection and animal movement. *Methods in Ecology and Evolution,* 7**,** 619–630.

Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M. & Turlure, C. 2013. Individual dispersal, landscape connectivity and ecological networks. *Biological Reviews,* 88**,** 310-326.

Barnes, C., Maxwell, D., Reuman, D. C. & Jennings, S. 2010. Global patterns in predator–prey size relationships reveal size dependency of trophic transfer efficiency. *Ecology,* 91**,** 222-232.

Bashan, A., Gibson, T. E., Friedman, J., Carey, V. J., Weiss, S. T., Hohmann, E. L. & Liu, Y.-Y. 2016. Universality of human microbial dynamics. *Nature,* 534**,** 259-262.

Bastille-Rousseau, G., Douglas-Hamilton, I., Blake, S., Northrup, J. M. & Wittemyer, G. 2018. Applying network theory to animal movements to identify properties of landscape space use. *Ecological Applications,* 28**,** 854-864.

Bates, D., Maechler, M., Bolker, B. & Walker, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software,* 67**,** 1–48.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., Dai, B. & Scheipl, F. 2020. Package 'lme4'.

Bates, D. M. 2010. *lme4: Mixed-effects modeling with R,* Madison, Wisconsin, USA, Springer New York.

Battin, J. 2004. When Good Animals Love Bad Habitats: Ecological Traps and the Conservation of Animal Populations. *Conservation Biology,* 18**,** 1482–1491.

Baumgartner, M. T. 2020. Connectance and nestedness as stabilizing factors in response to pulse disturbances in adaptive antagonistic networks. *Journal of Theoretical Biology,* 486**,** 110073.

Beasley, J. C. & Rhodes, O. E. 2010. Influence of patch- and landscape-level attributes on the movement behavior of raccoons in agriculturally fragmented landscapes. *Canadian Journal of Zoology,* 88**,** 161–169.

Begg, R. J. 1981. The Small Mammals of Little Nourlangie Rock, N.T III. Ecology of Dasyurus hallucatus, the Northern Quoll (Marsupialia : Dasyuridae). *Wildlife Research,* 8**,** 73-85.

Bennett, A. F. 1990. Habitat corridors and the conservation of small mammals in a fragmented forest environment. *Landscape Ecology,* 4**,** 109–122.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. *Biology letters,* 3**,** 620-623.

Bergès, L., Avon, C., Bezombes, L., Clauzel, C., Duflot, R., Foltête, J.-C., Gaucherand, S., Girardet, X. & Spiegelberger, T. 2020. Environmental mitigation hierarchy and biodiversity offsets revisited through habitat connectivity modelling. *Journal of Environmental Management,* 256**,** 109950.

Biologic 2016. Cattle Gorge and Callawa West Vertebrate Fauna Studies. Perth: Report prepared for BHP Billiton Iron Ore Pty Ltd: Biologic.

Bishop, M. J., Mayer-Pinto, M., Airoldi, L., Firth, L. B., Morris, R. L., Loke, L. H. L., Hawkins, S. J., Naylor, L. A., Coleman, R. A., Chee, S. Y. & Dafforn, K. A. 2017. Effects of ocean sprawl on ecological connectivity: impacts and solutions. *Journal of Experimental Marine Biology and Ecology,* 492**,** 7-30.

Bista, D., Baxter, G. S., Hudson, N. J., Lama, S. T., Weerman, J. & Murray, P. J. 2021. Movement and dispersal of a habitat specialist in human-dominated landscapes: a case study of the red panda. *Movement Ecology,* 9**,** 62.

Bjørneraas, K., Van Moorter, B., Rolandsen, C. M. & Herfindal, I. 2010. Screening Global Positioning System Location Data for Errors Using Animal Movement Characteristics. *The Journal of Wildlife Management,* 74**,** 1361–1366.

Bleicher, S. S. 2017. The landscape of fear conceptual framework: definition and review of current applications and misuses. *PeerJ,* 5**,** e3772.

Bleicher, S. S. & Dickman, C. R. 2020. On the landscape of fear: shelters affect foraging by dunnarts (*Marsupialia, Sminthopsis* spp.) in a sandridge desert environment. *Journal of Mammalogy,* 101**,** 281-290.

Bliege Bird, R., Tayor, N., Codding, B. F. & Bird, D. W. 2013. Niche construction and Dreaming logic: aboriginal patch mosaic burning and varanid lizards (*Varanus gouldii*) in Australia. *Proceedings. Biological sciences,* 280**,** 20132297-20132297.

Blom, M., Pearce, A. R. & Stuckey, P. J. 2019. Short-term planning for open pit mines: a review. *International Journal of Mining, Reclamation and Environment,* 33**,** 318-339.

Blum, M. E., Stewart, K. M. & Schroeder, C. 2015. Effects of large-scale gold mining on migratory behavior of a large herbivore. *Ecosphere,* 6**,** art74.

Blundell, G. M., Maier, J. A. K. & Debevec, E. M. 2001. Linear home ranges: Effects of smoothing, sample size, and autocorrelation on kernel estimates. *Ecological Monographs,* 71**,** 469–489.

Bracis, C. 2019. Package 'recurse'. *Computes Revisitation Metrics for Trajectory Data*.

Bracis, C., Bildstein, K. L. & Mueller, T. 2018. Revisitation analysis uncovers spatio-temporal patterns in animal movement data. *Ecography,* 41**,** 1801-1811.

Bradley, H. S., Armstrong, K. N., Bullen, R. D., Ellis, R., Knuckey, C. G., Ottewell, K., Reiffer, S., Somaweera, R., Umbrello, L. & van Leeuwen, S. 2024. Conserving the Pilbara leaf-nosed bat: directions for future research and management. *Pacific Conservation Biology,* 30**,** PC23031.

Bradley, H. S., Craig, M. D., Tomlinson, S., Cross, A. T., Bamford, M. J. & Bateman, P. W. 2022. Predators in a mining landscape: Threats to a behaviourally unique, endangered lizard. *Austral Ecology,* 47**,** 1077-1090.

Braithwaite, R. W. & Griffiths, A. D. 1994. Demographic variation and range contraction in the northern quoll*, Dasyurus hallucatus* (*Marsupialia : Dasyuridae*). *Wildlife Research,* 21**,** 203–217.

Bray, J. R. & Curtis, J. T. 1957. An Ordination of the Upland Forest Communities of Southern Wisconsin. *Ecological Monographs,* 27**,** 326-349.

Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, M. & Bolker, B. M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R journal,* 9**,** 378-400.

Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology,* 22**,** 37-47.

Brown, J. S., Laundré, J. W. & Gurung, M. 1999. The Ecology of Fear: Optimal Foraging, Game Theory, and Trophic Interactions. *Journal of Mammalogy,* 80**,** 385-399.

Bull, J. W., Suttle, K. B., Gordon, A., Singh, N. J. & Milner-Gulland, E. J. 2013. Biodiversity offsets in theory and practice. *Oryx,* 47**,** 369-380.

Burbidge, A. A. & McKenzie, N. L. 1989. Patterns in the modern decline of western Australia's vertebrate fauna: Causes and conservation implications. *Biological Conservation,* 50**,** 143-198.

Bureau of Meteorology. 2020. *Climate Data Online* [Online]. Available: http://www.bom.gov.au/climate/averages/tables/cw_004032.shtml [Accessed 30 July 2020].

Bürkner, P.-C. 2017. brms: An R package for Bayesian multilevel models using Stan. *Journal of statistical software,* 80**,** 1-28.

Burnham, K. & Anderson, D. 2004. Model selection and multi-model inference. *Second. NY: Springer-Verlag,* 63**,** 10.

Burnham, K. P. & Anderson, D. R. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research,* 28**,** 111-119.

Burt, W. H. 1943. Territoriality and Home Range Concepts as Applied to Mammals. *Journal of Mammalogy,* 24**,** 346-352.

Butt, N., Beyer, H. L., Bennett, J. R., Biggs, D., Maggini, R., Mills, M., Renwick, A. R., Seabrook, L. M. & Possingham, H. P. 2013. Biodiversity risks from fossil fuel extraction. *Science,* 342**,** 425-426.

Calizza, E., Costantini, M. L., Careddu, G. & Rossi, L. 2017. Effect of habitat degradation on competition, carrying capacity, and species assemblage stability. *Ecology and Evolution,* 7**,** 5784-5796.

Cargnelutti, B., Coulon, A., Hewison, A. J. M., Goulard, M., Angibault, J.-M. & Morellet, N. 2007. Testing Global Positioning System Performance for Wildlife Monitoring Using Mobile Collars and Known Reference Points. *Journal of Wildlife Management,* 71**,** 1380-1387, 8.

Carmona, C. P., de Bello, F., Mason, N. W. H. & Lepš, J. 2016. Traits Without Borders: Integrating Functional Diversity Across Scales. *Trends in Ecology & Evolution,* 31**,** 382-394.

Carwardine, J., Nicol, S., Van Leeuwen, S., Walters, B., Firn, J., Reeson, A., Martin, T. G. & Chades, I. 2014. Priority threat management for Pilbara species of conservation significance. Brisbane: CSIRO Ecosystems Sciences.

Catlin, D. H., Zeigler, S. L., Brown, M. B., Dinan, L. R., Fraser, J. D., Hunt, K. L. & Jorgensen, J. G. 2016. Metapopulation viability of an endangered shorebird depends on dispersal and human-created habitats: piping plovers (Charadrius melodus) and prairie rivers. *Movement Ecology,* 4**,** 6.

Chan, R., Dunlop, J. & Spencer, P. B. S. 2020. Highly promiscuous paternity in mainland and island populations of the endangered Northern Quoll. *Journal of Zoology,* 310**,** 210-220.

Chillo, V., Anand, M. & Ojeda, R. A. 2011. Assessing the Use of Functional Diversity as a Measure of Ecological Resilience in Arid Rangelands. *Ecosystems,* 14**,** 1168-1177.

Chillo, V. & Ojeda, R. A. 2012. Mammal functional diversity loss under human-induced disturbances in arid lands. *Journal of Arid Environments,* 87**,** 95-102.

Chisholm, R. & Taylor, R. 2007. Null-Hypothesis Significance Testing and the Critical Weight Range for Australian Mammals. *Conservation Biology,* 21**,** 1641-1645.

Ciach, M. & Fröhlich, A. 2019. Ungulates in the city: light pollution and open habitats predict the probability of roe deer occurring in an urban environment. *Urban Ecosystems,* 22**,** 513-523.

Cook, A. 2010. *Habitat use and home-range of the northern quoll, Dasyurus hallucatus: effects of fire.* Master's thesis, The University of Western Australia.

Cooke, R. S. C., Bates, A. E. & Eigenbrod, F. 2019. Global trade-offs of functional redundancy and functional dispersion for birds and mammals. *Global Ecology and Biogeography,* 28**,** 484-495.

Coulon, A., Morellet, N., Goulard, M., Cargnelutti, B., Angibault, J.-M. & Hewison, A. J. M. 2008. Inferring the effects of landscape structure on roe deer (Capreolus capreolus) movements using a step selection function. *Landscape Ecology,* 23**,** 603-614.

Cowan, M. 2023. *Last updated July 2023. Pilbara mine camp fauna monitoring.* [Online]. Available: http://n2t.net/ark:/63614/w12004109 [Accessed 20 September 2023].

Cowan, M., Moro, D., Anderson, H., Angus, J., Garretson, S. & Morris, K. 2020a. Aerial baiting for feral cats is unlikely to affect survivorship of northern quolls in the Pilbara region of Western Australia. *Wildlife Research,* 47**,** 589-598.

Cowan, M. A., Callan, M. N., Watson, M. J., Watson, D. M., Doherty, T. S., Michael, D. R., Dunlop, J. A., Turner, J. M., Moore, H. A., Watchorn, D. J. & Nimmo, D. G. 2021. Artificial refuges for wildlife conservation: what is the state of the science? *Biological Reviews,* 96**,** 2735–2754.

Cowan, M. A., Dunlop, J. A., Gibson, L. A., Moore, H. A., Setterfield, S. A. & Nimmo, D. G. 2024. Movement ecology of an endangered mesopredator in a mining landscape. *Movement Ecology,* 12**,** 5.

Cowan, M. A., Dunlop, J. A., Turner, J. M., Moore, H. A. & Nimmo, D. G. 2020b. Artificial refuges to combat habitat loss for an endangered marsupial predator: How do they measure up? *Conservation Science and Practice,* 2**,** e204.

Cowan, M. A., Moore, H. A., Hradsky, B. A., Jolly, C. J., Dunlop, J. A., Wysong, M. L., Hernandez-Santin, L., Davis, R. A., Fisher, D. O., Michael, D. R., Turner, J. M., Gibson, L. A., Knuckey, C. G., Henderson, M. & Nimmo, D. G. 2022. Non-preferred habitat increases the activity area of the endangered northern quoll (*Dasyurus hallucatus*) in a semi-arid landscape. *Australian Mammalogy,* 45**,** 138–150.

Cowen, S., Clausen, L., Algar, D. & Comer, S. 2019. Using Genetics to Evaluate the Success of a Feral Cat (*Felis catus*) Control Program in North-Western Australia. *Animals,* 9**,** 1050.

Craig, M. D., Hardy, G. E. S. J., Fontaine, J. B., Garkakalis, M. J., Grigg, A. H., Grant, C. D., Fleming, P. A. & Hobbs, R. J. 2012. Identifying unidirectional and dynamic habitat filters to faunal recolonisation in restored mine-pits. *Journal of Applied Ecology,* 49**,** 919-928.

Craiu, R. V., Duchesne, T., Fortin, D. & Baillargeon, S. 2011. Conditional Logistic Regression With Longitudinal Follow-up and Individual-Level Random Coefficients: A Stable and Efficient Two-Step Estimation Method. *Journal of Computational and Graphical Statistics,* 20**,** 767-784.

Cramer, V. A., Armstrong, K. N., Bullen, R. D., Cross, S. L., Gibson, L., Hanrahan, N., Knuckey, C. G., Ottewell, K., Reiffer, S., Ruykys, L., Shaw, R. E., Thavornkanlapachai, R., Thompson, S. A., Wild, S. & van Leeuwen, S. 2023. Research priorities for the ghost bat (*Macroderma gigas*) in the Pilbara region of Western Australia. *Australian Mammalogy,* 45**,** 1-12.

Cramer, V. A., Dunlop, J., Davis, R. A., Ellis, R., Barnett, B., Cook, A., Morris, K. & van Leeuwen, S. 2016. Research priorities for the northern quoll (*Dasyurus hallucatus*) in the Pilbara region of Western Australia. *Australian Mammalogy,* 38**,** 135–148.

Creese, S. 2012. *The use of rail culverts to facilitate the movement of fauna.* Masters thesis, University of Queensland, Brisbane.

Cristescu, B., Stenhouse, G. B. & Boyce, M. S. 2016a. Large Omnivore Movements in Response to Surface Mining and Mine Reclamation. *Scientific Reports,* 6**,** 19177.

Cristescu, B., Stenhouse, G. B., Symbaluk, M., Nielsen, S. E. & Boyce, M. S. 2016b. Wildlife habitat selection on landscapes with industrial disturbance. *Environmental Conservation,* 43**,** 327-336.

Cross, S., Tomlinson, S., Craig, M. & Bateman, P. 2022. Build it and some may come: early stage habitat restoration may initially favour herbivore return. *Pacific Conservation Biology,* 29**,** 300-311.

Cross, S. L., Bateman, P. W. & Cross, A. T. 2020. Restoration goals: Why are fauna still overlooked in the process of recovering functioning ecosystems and what can be done about it? *Ecological Management & Restoration,* 21**,** 4-8.

Cross, S. L., Cross, A. T., Tomlinson, S., Clark-Ioannou, S. M., Nevill, P. G. & Bateman, P. W. 2021. Mitigation and management plans should consider all anthropogenic disturbances to fauna. *Global Ecology and Conservation,* 26**,** e01500.

Cross, S. L., Tomlinson, S., Craig, M. D., Dixon, K. W. & Bateman, P. W. 2019. Overlooked and undervalued: the neglected role of fauna and a global bias in ecological restoration assessments. *Pacific Conservation Biology,* 25**,** 331-341.

Csardi, M. G. 2013. Package ‘igraph’.

D'eon, R. G. & Delparte, D. 2005. Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. *Journal of Applied Ecology,* 42**,** 383-388.

Dalloz, M. F., Crouzeilles, R., Almeida-Gomes, M., Papi, B. & Prevedello, J. A. 2017. Incorporating landscape ecology metrics into environmental impact assessment in the Brazilian Atlantic Forest. *Perspectives in Ecology and Conservation,* 15**,** 216-220.

Dawson, S. J., Kreplins, T. L., Kennedy, M. S., Renwick, J., Cowan, M. A. & Fleming, P. A. 2023. Land use and dingo baiting are correlated with the density of kangaroos in rangeland systems. *Integrative Zoology,* 18**,** 299-315.

Dellinger, J. A., Cristescu, B., Ewanyk, J., Gammons, D. J., Garcelon, D., Johnston, P., Martins, Q., Thompson, C., Vickers, T. W., Wilmers, C. C., Wittmer, H. U. & Torres, S. G. 2020. Using Mountain Lion Habitat Selection in Management. *The Journal of Wildlife Management,* 84**,** 359–371.

Department of Mines, Industry Regulation and Safety 2023. Western Australian Mineral and Petroleum Statistics Digest 2022-23 [government statistical document].

Department of the Environment 2016. EPBC Act referral guideline for the endangered northern quoll *Dasyurus hallucatus*. Canberra: EPBC Act Policy Statement: Commonwealth of Australia.

Department of the Environment 2024. *Dasyurus hallucatus* in Species Profile and Threats Database. Canberra: Department of the Environment.

Dickie, M., Serrouya, R., McNay, R. S. & Boutin, S. 2017. Faster and farther: wolf movement on linear features and implications for hunting behaviour. *Journal of Applied Ecology,* 54**,** 253-263.

Diete, R. L., Meek, P. D., Dixon, K. M., Dickman, C. R. & Leung, L. K. P. 2016. Best bait for your buck: bait preference for camera trapping north Australian mammals. *Australian Journal of Zoology,* 63**,** 376-382.

Doherty, T. S., Balouch, S., Bell, K., Burns, T. J., Feldman, A., Fist, C., Garvey, T. F., Jessop, T. S., Meiri, S. & Driscoll, D. A. 2020. Reptile responses to anthropogenic habitat modification: A global meta-analysis. *Global Ecology and Biogeography,* 29**,** 1265-1279.

Doherty, T. S., Bengsen, A. J. & Davis, R. A. 2015a. A critical review of habitat use by feral cats and key directions for future research and management. *Wildlife Research,* 41**,** 435-446.

Doherty, T. S., Dickman, C. R., Nimmo, D. G. & Ritchie, E. G. 2015b. Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. *Biological Conservation,* 190**,** 60-68.

Doherty, T. S. & Driscoll, D. A. 2018. Coupling movement and landscape ecology for animal conservation in production landscapes. *Proceedings of the Royal Society B: Biological Sciences,* 285**,** 20172272.

Doherty, T. S., Fist, C. N. & Driscoll, D. A. 2019. Animal movement varies with resource availability, landscape configuration and body size: a conceptual model and empirical example. *Landscape Ecology,* 34**,** 603–614.

Doherty, T. S., Hays, G. C. & Driscoll, D. A. 2021. Human disturbance causes widespread disruption of animal movement. *Nature Ecology & Evolution,* 5**,** 513–519.

Doherty, T. S., Watchorn, D. J., Miritis, V., Pestell, A. J. L. & Geary, W. L. 2023. Cats, foxes and fire: quantitative review reveals that invasive predator activity is most likely to increase shortly after fire. *Fire Ecology,* 19**,** 22.

Doody, J. S., Rhind, D., McHenry, C. M. & Clulow, S. 2023. Invasional meltdown-under? Toads facilitate cats by removing a naïve top predator. *Wildlife Research,* 51**,** WR22177.

Dorresteijn, I., Schultner, J., Nimmo, D. G., Fischer, J., Hanspach, J., Kuemmerle, T., Kehoe, L. & Ritchie, E. G. 2015. Incorporating anthropogenic effects into trophic ecology: predator–prey interactions in a human-dominated landscape. *Proceedings of the Royal Society B: Biological Sciences,* 282**,** 20151602.

Douma, J. C. & Weedon, J. T. 2019. Analysing continuous proportions in ecology and evolution: A practical introduction to beta and Dirichlet regression. *Methods in Ecology and Evolution,* 10**,** 1412–1430.

Driscoll, D. A., Armenteras, D., Bennett, A. F., Brotons, L., Clarke, M. F., Doherty, T. S., Haslem, A., Kelly, L. T., Sato, C. F., Sitters, H., Aquilué, N., Bell, K., Chadid, M., Duane, A., Meza-Elizalde, M. C., Giljohann, K. M., González, T. M., Jambhekar, R., Lazzari, J., Morán-Ordóñez, A. & Wevill, T. 2021. How fire interacts with habitat loss and fragmentation. *Biological Reviews,* 96**,** 976–998.

Duchesne, T., Fortin, D. & Courbin, N. 2010. Mixed conditional logistic regression for habitat selection studies. *Journal of Animal Ecology,* 79**,** 548-555.

Duchesne, T., Fortin, D. & Rivest, L.-P. 2015. Equivalence between Step Selection Functions and Biased Correlated Random Walks for Statistical Inference on Animal Movement. *PLOS ONE,* 10**,** e0122947.

Dundas, S. J., Ruthrof, K. X., Hardy, G. E. S. J. & Fleming, P. A. 2019. Pits or pictures: a comparative study of camera traps and pitfall trapping to survey small mammals and reptiles. *Wildlife Research,* 46**,** 104-113.

Dunlop, J., Cook, A. & Morris, K. 2014. Pilbara northern quoll project: surveying and monitoring *Dasyurus hallucatus* in the Pilbara, Western Australia. Perth: Department of Parks and Wildlife.

Dunlop, J., Rayner, K. & Doherty, T. S. 2017. Dietary flexibility in small carnivores: a case study on the endangered northern quoll, *Dasyurus hallucatus. Journal of Mammalogy,* 98**,** 858–866.

Dunlop, J. A., Cook, A. & Lees, J. 2015. Use of quarry infrastructure by the Pilbara northern quoll, *Dasyurus hallucatus*. Woodvale, Western Australia: Department of Parks and Wildlife.

Dunne, J. A., Williams, R. J. & Martinez, N. D. 2002a. Food-web structure and network theory: The role of connectance and size. *Proceedings of the National Academy of Sciences,* 99**,** 12917-12922.

Dunne, J. A., Williams, R. J. & Martinez, N. D. 2002b. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters,* 5**,** 558-567.

Dunning, J. B., Danielson, B. J. & Pulliam, H. R. 1992. Ecological processes that affect populations in complex landscapes. *Oikos,* 65**,** 169–175.

Durán, A. P., Rauch, J. & Gaston, K. J. 2013. Global spatial coincidence between protected areas and metal mining activities. *Biological Conservation,* 160**,** 272-278.

Ellis, E. C., Gauthier, N., Klein Goldewijk, K., Bliege Bird, R., Boivin, N., Díaz, S., Fuller, D. Q., Gill, J. L., Kaplan, J. O., Kingston, N., Locke, H., McMichael, C. N. H., Ranco, D., Rick, T. C., Shaw, M. R., Stephens, L., Svenning, J.-C. & Watson, J. E. M. 2021. People have shaped most of terrestrial nature for at least 12,000 years. *Proceedings of the National Academy of Sciences,* 118**,** e2023483118.

Ellis, E. C., Klein Goldewijk, K., Siebert, S., Lightman, D. & Ramankutty, N. 2010. Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography,* 19**,** 589-606.

Emlen, J. M. 1966. The role of time and energy in food preference. *The American Naturalist,* 100**,** 611-617.

Environmental Protection Authority 2014. Cumulative environmental impacts of development in the Pilbara region. Perth: The Government of Western Australia.

Erickson, T. E., Munoz-Rojas, M., Guzzomi, A. L., Masarei, M., Ling, E., Bateman, A. M., Kildisheva, O. A., Ritchie, A. L., Turner, S. R., Parsons, B., Chester, P., Webster, T., Wishart, S., James, J. J., Madsen, M. D., Abella, S. R. & Merritt, D. J. 2019. A case study of seed-use technology development for Pilbara mine site rehabilitation. *In:* FOURIE, A. B. & TIBBETT, M. (eds.) *13th International Conference on Mine Closure.* Perth: Australian Centre for Geomechanics.

Erickson, T. E., Muñoz-Rojas, M., Kildisheva, O. A., Stokes, B. A., White, S. A., Heyes, J. L., Dalziell, E. L., Lewandrowski, W., James, J. J., Madsen, M. D., Turner, S. R. & Merritt, D. J. 2017. Benefits of adopting seed-based technologies for rehabilitation in the mining sector: a Pilbara perspective. *Australian Journal of Botany,* 65**,** 646-660.

ESRI 2021. World Imagery, (Featuring Earthstar Geographics (TerraColor NextGen) imagery).

Etherington, T. R. 2016. Least-Cost Modelling and Landscape Ecology: Concepts, Applications, and Opportunities. *Current Landscape Ecology Reports,* 1**,** 40-53.

Etherington, T. R., Perry, G. L. W., Cowan, P. E. & Clout, M. N. 2014. Quantifying the Direct Transfer Costs of Common Brushtail Possum Dispersal using Least-Cost Modelling: A Combined Cost-Surface and Accumulated-Cost Dispersal Kernel Approach. *PLOS ONE,* 9**,** e88293.

Fahrig, L. 2003. Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution and Systematics,* 34**,** 487-515.

Fancourt, B. A., Hawkins, C. E., Cameron, E. Z., Jones, M. E. & Nicol, S. C. 2015. Devil Declines and Catastrophic Cascades: Is Mesopredator Release of Feral Cats Inhibiting Recovery of the Eastern Quoll? *PLOS ONE,* 10.

Fieberg, J. & Kochanny, C. O. 2005. Quantifying Home-Range Overlap: The Importance of the Utilization Distribution. *The Journal of Wildlife Management,* 69**,** 1346-1359.

Fieberg, J., Signer, J., Smith, B. & Avgar, T. 2021. A ‘How-to’ Guide for Interpreting Parameters in Habitat-Selection Analyses. *Journal of Animal Ecology,* 90**,** 1027–1043.

Finnegan, L., Pigeon, K. E., Cranston, J., Hebblewhite, M., Musiani, M., Neufeld, L., Schmiegelow, F., Duval, J. & Stenhouse, G. B. 2018. Natural regeneration on seismic lines influences movement behaviour of wolves and grizzly bears. *PLOS ONE,* 13**,** e0195480.

Fisher, D. O., Dickman, C. R., Jones, M. E. & Blomberg, S. P. 2013. Sperm competition drives the evolution of suicidal reproduction in mammals. *Proceedings of the National Academy of Sciences,* 110**,** 17910-17914.

Fitzsimons, J. A. & Michael, D. R. 2017. Rocky outcrops: A hard road in the conservation of critical habitats. *Biological Conservation,* 211**,** 36-44.

Forester, J. D., Im, H. K. & Rathouz, P. J. 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. *Ecology,* 90**,** 3554-3565.

Forrest, S. W., Pagendam, D., Bode, M., Drovandi, C., Potts, J. R., Perry, J., Vanderduys, E. & Hoskins, A. J. 2024. Simulating animal movement trajectories from temporally dynamic step selection functions. *bioRxiv***,** 2024.03.19.585696.

Forrest, S. W., Recio, M. R. & Seddon, P. J. 2022. Moving wildlife tracking forward under forested conditions with the SWIFT GPS algorithm. *Animal Biotelemetry,* 10**,** 19.

Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T. & Mao, J. S. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology,* 86**,** 1320-1330.

Fox, B. J., Fox, M. D., Taylor, J. E., Jackson, G. P., Simpson, J., Higgs, P., Rebec, L. & Avery, R. 1996. Comparison of regeneration following burning, clearing or mineral sand mining at Tomago, NSW: I. Structure and growth of the vegetation. *Australian Journal of Ecology,* 21**,** 184-199.

Francis, C. D., Ortega, C. P. & Cruz, A. 2009. Noise pollution changes avian communities and species interactions. *Current biology,* 19**,** 1415-1419.

Fudenberg, D. & Tirole, J. 1991. *Game theory,* MIT press.

Gallant, J., Dowling, T. & Read, A. 2009. 1 second SRTM Level 2 Derived Digital Elevation Model v1.0. Canberra: Geoscience Australia.

Gallé, R., Gallé-Szpisjak, N., Zsigmond, A.-R., Könczey, B. & Urák, I. 2021. Tree species and microhabitat affect forest bog spider fauna. *European Journal of Forest Research,* 140**,** 691-702.

Gallo, T., Fidino, M., Lehrer, E. W. & Magle, S. B. 2017. Mammal diversity and metacommunity dynamics in urban green spaces: implications for urban wildlife conservation. *Ecological Applications,* 27**,** 2330-2341.

Ganz, T. R., DeVivo, M. T., Kertson, B. N., Roussin, T., Satterfield, L., Wirsing, A. J. & Prugh, L. R. 2022. Interactive effects of wildfires, season and predator activity shape mule deer movements. *Journal of Animal Ecology,* 91**,** 2273-2288.

Gardiner, R., Proft, K., Comte, S., Jones, M. & Johnson, C. N. 2019. Home range size scales to habitat amount and increasing fragmentation in a mobile woodland specialist. *Ecology and Evolution,* 9**,** 14005–14014.

Gaschk, J. L., Del Simone, K., Wilson, R. S. & Clemente, C. J. 2023. Resting disparity in quoll semelparity: examining the sex-linked behaviours of wild roaming northern quolls (Dasyurus hallucatus) during breeding season. *Royal Society Open Science,* 10**,** 221180.

Gaynor, K. M., Hojnowski, C. E., Carter, N. H. & Brashares, J. S. 2018. The influence of human disturbance on wildlife nocturnality. *Science,* 360**,** 1232-1235.

Geary, W. L., Doherty, T. S., Nimmo, D. G., Tulloch, A. I. T. & Ritchie, E. G. 2020. Predator responses to fire: A global systematic review and meta-analysis. *Journal of Animal Ecology,* 89**,** 955-971.

Geary, W. L., Ritchie, E. G., Lawton, J. A., Healey, T. R. & Nimmo, D. G. 2018. Incorporating disturbance into trophic ecology: Fire history shapes mesopredator suppression by an apex predator. *Journal of Applied Ecology,* 55**,** 1594-1603.

Gibson, L. A., Moore, H. A., Cowan, M. A., Craig, M. D., Nimmo, D. G. & Dunlop, J. A. 2023. A review of progress of a research program for the endangered northern quoll (*Dasyurus hallucatus*) in the multi-use landscapes of the Pilbara. *Australian Mammalogy,* 45**,** 251-263.

Gilbert, N. A., McGinn, K. A., Nunes, L. A., Shipley, A. A., Bernath-Plaisted, J., Clare, J. D. J., Murphy, P. W., Keyser, S. R., Thompson, K. L., Maresh Nelson, S. B., Cohen, J. M., Widick, I. V., Bartel, S. L., Orrock, J. L. & Zuckerberg, B. 2023. Daily activity timing in the Anthropocene. *Trends in Ecology & Evolution,* 38**,** 324-336.

Gilbert, N. A., Stenglein, J. L., Pauli, J. N. & Zuckerberg, B. 2022. Human disturbance compresses the spatiotemporal niche. *Proc Natl Acad Sci U S A,* 119**,** e2206339119.

Girard, I., Ouellet, J.-P., Courtois, R., Dussault, C. & Breton, L. 2002. Effects of Sampling Effort Based on GPS Telemetry on Home-Range Size Estimations. *The Journal of Wildlife Management,* 66**,** 1290–1300.

Goldingay, R. L. 2023. Movement Patterns, Home Range and Habitat Selection of Australasian Marsupials. *American and Australasian Marsupials: An Evolutionary, Biogeographical, and Ecological Approach.* Springer.

Goodfield, D., Anda, M. & Ho, G. 2011. Carbon neutral mine site accommodation village: Developing the model. *19th International Congress on Modelling and Simulation-Sustaining Our Future: Understanding and Living with Uncertainty, MODSIM2011.* Perth, Western Australia Murdoch University.

Gould, J. Characters of a new species of *Perameles*, and a new species of *Dasyurus*. Proceedings of the Zoological Society of London, 1842. 41-42.

Gould, S. F. 2011. Does post-mining rehabilitation restore habitat equivalent to that removed by mining? A case study from the monsoonal tropics of northern Australia. *Wildlife Research,* 38**,** 482-490.

Gower, J. C. 1971. A General Coefficient of Similarity and Some of Its Properties. *Biometrics,* 27**,** 857-871.

Grace, J. B. & Bollen, K. A. 2005. Interpreting the Results from Multiple Regression and Structural Equation Models. *The Bulletin of the Ecological Society of America,* 86**,** 283-295.

Grace, J. B., Schoolmaster Jr., D. R., Guntenspergen, G. R., Little, A. M., Mitchell, B. R., Miller, K. M. & Schweiger, E. W. 2012. Guidelines for a graph-theoretic implementation of structural equation modeling. *Ecosphere,* 3**,** art73.

Greenwood, L., Bliege Bird, R. & Nimmo, D. 2022. Indigenous burning shapes the structure of visible and invisible fire mosaics. *Landscape Ecology,* 37**,** 811–827.

Griffiths, A. D. & Brook, B. W. 2015. Fire impacts recruitment more than survival of small-mammals in a tropical savanna. *Ecosphere,* 6**,** art99.

Haapakoski, M., Sundell, J. & Ylönen, H. 2013. Mammalian predator–prey interaction in a fragmented landscape: weasels and voles. *Oecologia,* 173**,** 1227–1235.

Hale, R. & Swearer, S. E. 2016. Ecological traps: current evidence and future directions. *Proceedings of the Royal Society B: Biological Sciences,* 283**,** 20152647.

Hamilton, N. A. & Algar, D. 2004. Further Assessment of Feral Cat Abundance and Control Options at Plutonic Gold Mine: A Report to Barrick Gold of Australia Limited. Woodvale, Western Australia: Department of Conservation and Land Management, Western Australia.

Harris, S., Cresswell, W., Forde, P., Trewhella, W., Woollard, T. & Wray, S. 1990. Home-range analysis using radio-tracking data - a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review,* 20**,** 97–123.

Harrison, X. A. 2014. Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ,* 2**,** e616.

Hatton, I. A., McCann, K. S., Fryxell, J. M., Davies, T. J., Smerlak, M., Sinclair, A. R. E. & Loreau, M. 2015. The predator-prey power law: Biomass scaling across terrestrial and aquatic biomes. *Science,* 349**,** aac6284.

Hawlena, D., Saltz, D., Abramsky, Z. & Bouskila, A. 2010. Ecological Trap for Desert Lizards Caused by Anthropogenic Changes in Habitat Structure that Favor Predator Activity. *Conservation Biology,* 24**,** 803-809.

Hazen, E. L., Abrahms, B., Brodie, S., Carroll, G., Welch, H. & Bograd, S. J. 2021. Where did they not go? Considerations for generating pseudo-absences for telemetry-based habitat models. *Movement Ecology,* 9**,** 5.

Heiner, M., Oakleaf, J., Davaa, G. & Kiesecker, J. 2024. Chapter 10 - Emerging threats to snow leopards from energy and mineral development. *In:* MALLON, D. & MCCARTHY, T. (eds.) *Snow Leopards (Second Edition).* Academic Press.

Heiniger, J., Cameron, S. F., Madsen, T., Niehaus, A. C. & Wilson, R. S. 2020. Demography and spatial requirements of the endangered northern quoll on Groote Eylandt. *Wildlife Research,* 47**,** 224–238.

Heinlein, B. W., Urbanek, R. E., Olfenbuttel, C. & Dukes, C. G. 2020. Effects of different attractants and human scent on mesocarnivore detection at camera traps. *Wildlife Research,* 47**,** 338-348.

Henderson, M. 2015. *The Effects of Mining Infrastructure on Northern quoll Movement and Habitat.* Honours Thesis, Edith Cowan University.

Henderson, T., Fancourt, B. A., Rajaratnam, R., Vernes, K. & Ballard, G. 2023. Habitat use by the endangered spotted-tailed quoll in a fragmented landscape. *Mammal Research,* 68**,** 93-103.

Hendrychová, M., Šálek, M. & Červenková, A. 2008. Invertebrate communities in man-made and spontaneously developed forests on spoil heaps after coal mining. *Journal of Landscape Studies,* 1**,** 169-187.

Herbert-Read, J. E., Kremer, L., Bruintjes, R., Radford, A. N. & Ioannou, C. C. 2017. Anthropogenic noise pollution from pile-driving disrupts the structure and dynamics of fish shoals. *Proceedings of the Royal Society B: Biological Sciences,* 284**,** 20171627.

Hernandez-Santin, L., Dunlop, J. A., Goldizen, A. W. & Fisher, D. O. 2019. Demography of the northern quoll (*Dasyurus hallucatus*) in the most arid part of its range. *Journal of Mammalogy,* 100**,** 1191–1198.

Hernandez-Santin, L., Goldizen, A. W. & Fisher, D. O. 2016. Introduced predators and habitat structure influence range contraction of an endangered native predator, the northern quoll. *Biological Conservation,* 203**,** 160–167.

Hernandez-Santin, L., Goldizen, A. W. & Fisher, D. O. 2022. Northern quolls in the Pilbara persist in high-quality habitat, despite a decline trajectory consistent with range eclipse by feral cats. *Conservation Science and Practice***,** e12733.

Hernandez-Santin, L., Henderson, M., Molloy, S. W., Dunlop, J. A. & Davis, R. A. 2020. Spatial ecology of an endangered carnivore, the Pilbara northern quoll. *Australian Mammalogy,* 43**,** 235–242.

Higgs, E. 2017. Novel and designed ecosystems. *Restoration Ecology,* 25**,** 8-13.

Hijmans, R. J., Van Etten, J., Cheng, J., Mattiuzzi, M., Sumner, M., Greenberg, J. A., Lamigueiro, O. P., Bevan, A., Racine, E. B. & Shortridge, A. 2015. Package 'raster'.

Hill, B. M. & Ward, S. J. 2010. National recovery plan for the northern quoll *Dasyurus hallucatus*. *Department of Natural Resources, Environment, The Arts and Sport, Darwin*.

Hobbs, R. J., Arico, S., Aronson, J., Baron, J. S., Bridgewater, P., Cramer, V. A., Epstein, P. R., Ewel, J. J., Klink, C. A., Lugo, A. E., Norton, D., Ojima, D., Richardson, D. M., Sanderson, E. W., Valladares, F., Vilà, M., Zamora, R. & Zobel, M. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography,* 15**,** 1-7.

Hobbs, R. J., Valentine, L. E., Standish, R. J. & Jackson, S. T. 2018. Movers and Stayers: Novel Assemblages in Changing Environments. *Trends in Ecology & Evolution,* 33**,** 116-128.

Hodgson, J. A., Thomas, C. D., Cinderby, S., Cambridge, H., Evans, P. & Hill, J. K. 2011. Habitat re-creation strategies for promoting adaptation of species to climate change. *Conservation Letters,* 4**,** 289-297.

Hoffmann, B. D. & Andersen, A. N. 2003. Responses of ants to disturbance in Australia, with particular reference to functional groups. *Austral Ecology,* 28**,** 444-464.

Hofmann, D. D., Cozzi, G., McNutt, J. W., Ozgul, A. & Behr, D. M. 2023. A three-step approach for assessing landscape connectivity via simulated dispersal: African wild dog case study. *Landsc Ecol,* 38**,** 981-998.

Hohnen, R., D. Tuft, K., Legge, S., Hillyer, M., Spencer, P. B. S., J. Radford, I., Johnson, C. N. & Burridge, C. P. 2016. Rainfall and topography predict gene flow among populations of the declining northern quoll (Dasyurus hallucatus). *Conservation Genetics,* 17**,** 1213-1228.

Holland, G. J. & Bennett, A. F. 2007. Occurrence of small mammals in a fragmented landscape: the role of vegetation heterogeneity. *Wildlife Research,* 34**,** 387-397.

Hooker, M. J., Clark, J. D., Bond, B. T. & Chamberlain, M. J. 2021. Evaluation of connectivity among American black bear populations in Georgia. *The Journal of Wildlife Management*, 85**,** 979-988.

Huck, M., Davison, J. & Roper, T. J. 2008. Comparison of two sampling protocols and four home-range estimators using radio-tracking data from urban badgers *Meles meles*. *Wildlife Biology,* 14**,** 467–477.

Ibbett, M., Woinarski, J. C. Z. & Oakwood, M. 2018. Declines in the mammal assemblage of a rugged sandstone environment in Kakadu National Park, Northern Territory, Australia. *Australian Mammalogy,* 40**,** 181–187.

IPBES 2019. Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. *In:* E. S. BRONDIZIO, J. S., S. DÍAZ, AND H. T. NGO (ed.). Bonn, Germany: IPBES secretariat.

IUCN. 2024. *The IUCN Red List of Threatened Species. Version 2023-1* [Online]. Available: https://www.iucnredlist.org/ [Accessed 8th July 2024].

Iverson, A. R., Humple, D. L., Cormier, R. L. & Hull, J. 2023. Land cover and NDVI are important predictors in habitat selection along migration for the Golden-crowned Sparrow, a temperate-zone migrating songbird. *Movement Ecology,* 11**,** 2.

Jackson, S. 2007. *Australian mammals: biology and captive management*, CSIRO Publishing.

Johnson, C. A., Fryxell, J. M., Thompson, I. D. & Baker, J. A. 2009. Mortality risk increases with natal dispersal distance in American martens. *Proceedings of the Royal Society B: Biological Sciences,* 276**,** 3361-3367.

Junker, J., Quoss, L., Valdez, J., Arandjelovic, M., Barrie, A., Campbell, G., Heinicke, S., Humle, T., Kouakou, C. Y., Kühl, H. S., Ordaz-Németh, I., Pereira, H. M., Rainer, H., Refisch, J., Sonter, L. & Sop, T. 2024. Threat of mining to African great apes. *Science Advances,* 10**,** eadl0335.

Kays, R., Hirsch, B., Caillaud, D., Mares, R., Alavi, S., Havmøller, R. W. & Crofoot, M. 2023. Multi-scale movement syndromes for comparative analyses of animal movement patterns. *Movement Ecology,* 11**,** 61.

Kearney, M., Phillips, B. L., Tracy, C. R., Christian, K. A., Betts, G. & Porter, W. P. 2008. Modelling species distributions without using species distributions: the cane toad in Australia under current and future climates. *Ecography,* 31**,** 423-434.

Kerle, J. & Burgman, M. 1984. Some Aspects of the Ecology of the Mammal Fauna of the Jabiluka Area. Northern Territory. *Wildlife Research,* 11**,** 207-222.

Kerley, L. L., Goodrich, J. M., Miquelle, D. G., Smirnov, E. N., Quigley, H. B. & Hornocker, M. G. 2002. Effects of Roads and Human Disturbance on Amur Tigers. *Conservation Biology,* 16**,** 97-108.

Kernohan, B. J., Gitzen, R. A. & Millspaugh, J. J. 2001. Analysis of animal space use and movements. *Radio tracking and animal populations.* Academic Press.

Kie, J. G. 2013. A rule-based ad hoc method for selecting a bandwidth in kernel home-range analyses. *Animal Biotelemetry,* 1**,** 13.

Kight, C. R. & Swaddle, J. P. 2011. How and why environmental noise impacts animals: an integrative, mechanistic review. *Ecology Letters,* 14**,** 1052-1061.

King, D. 1989. An assessment of the hazard posed to northern quolls (D*asyurus hallucatus*) by aerial baiting with 1080 to control dingoes. *Wildlife Research,* 16**,** 569–574.

König, S., Köhnke, M. C., Firle, A.-L., Banitz, T., Centler, F., Frank, K. & Thullner, M. 2019. Disturbance Size Can Be Compensated for by Spatial Fragmentation in Soil Microbial Ecosystems. *Frontiers in Ecology and Evolution,* 7.

Kotze, D. J., O'Hara, R. B. & Lehvävirta, S. 2012. Dealing with Varying Detection Probability, Unequal Sample Sizes and Clumped Distributions in Count Data. *PLOS ONE,* 7, e40923.

Krishna, Y. C., Kumar, A. & Isvaran, K. 2016. Wild Ungulate Decision-Making and the Role of Tiny Refuges in Human-Dominated Landscapes. *PLOS ONE,* 11**,** e0151748.

Kubinec, R. 2023. Ordered Beta Regression: A Parsimonious, Well-Fitting Model for Continuous Data with Lower and Upper Bounds. *Political Analysis,* 31**,** 519-536.

Kuznetsova, A., Brockhoff, P. B. & Christensen, R. H. B. 2015. Package 'lmertest'.

Laliberté, E., Legendre, P., Shipley, B. & Laliberté, M. 2014. Measuring functional diversity from multiple traits, and other tools for functional ecology. *R Package FD.*

Lasky, M. & Bombaci, S. 2023. Human-induced fear in wildlife: A review. *Journal for Nature Conservation,* 74**,** 126448.

Laundré, J. W., Hernández, L. & Altendorf, K. B. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology,* 79**,** 1401-1409.

Laundré, J. W., Hernández, L. & Ripple, W. J. 2010. The landscape of fear: ecological implications of being afraid. *The Open Ecology Journal,* 3.

Laurance, W. F., Nascimento, H. E. M., Laurance, S. G., Andrade, A., Ewers, R. M., Harms, K. E., Luizão, R. C. C. & Ribeiro, J. E. 2007. Habitat Fragmentation, Variable Edge Effects, and the Landscape-Divergence Hypothesis. *PLOS ONE,* 2**,** e1017.

Lefcheck, J. S. 2016. piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution,* 7**,** 573-579.

Legendre, P. & Legendre, L. 1998. *Numerical ecology: developments in environmental modelling,* Elsevier.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M. & Gonzalez, A. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters,* 7**,** 601-613.

Leigh, K. A., Zenger, K. R., Tammen, I. & Raadsma, H. W. 2012. Loss of genetic diversity in an outbreeding species: small population effects in the African wild dog (Lycaon pictus). *Conservation Genetics,* 13**,** 767-777.

Lewis, J. S., Spaulding, S., Swanson, H., Keeley, W., Gramza, A. R., VandeWoude, S. & Crooks, K. R. 2021. Human activity influences wildlife populations and activity patterns: implications for spatial and temporal refuges. *Ecosphere,* 12**,** e03487.

Lima, S. L. & Zollner, P. A. 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology & Evolution,* 11**,** 131-135.

Lindenmayer, D., Scheele, B. C., Lavery, T. & Likens, G. E. 2023. Biodiversity response to rapid successive land cover conversions in human-dominated landscapes. *Global Ecology and Conservation,* 45**,** e02510.

Linley, G. D., Pauligk, Y., Marneweck, C. & Ritchie, E. G. 2020. Moon phase and nocturnal activity of native Australian mammals. *Australian Mammalogy,* 43**,** 190-195.

Lotka, A. J. 1920. Analytical Note on Certain Rhythmic Relations in Organic Systems. *Proceedings of the National Academy of Sciences,* 6**,** 410-415.

Lund, U., Agostinelli, C. & Agostinelli, M. C. 2017. Package 'circular'. *Repository CRAN,* 775**,** 142.

Lundgren, E. J., Ramp, D., Rowan, J., Middleton, O., Schowanek, S. D., Sanisidro, O., Carroll, S. P., Davis, M., Sandom, C. J., Svenning, J. C. & Wallach, A. D. 2020. Introduced herbivores restore Late Pleistocene ecological functions. *Proc Natl Acad Sci USA,* 117**,** 7871-7878.

Mac Nally, R., Duncan, R. P., Thomson, J. R. & Yen, J. D. L. 2018. Model selection using information criteria, but is the “best” model any good? *Journal of Applied Ecology,* 55**,** 1441–1444.

MacArthur, R. H. & Pianka, E. R. 1966. On Optimal Use of a Patchy Environment. *The American Naturalist,* 100**,** 603-609.

Macdonald, K. J., Driscoll, D. A., Macdonald, K. J., Hradsky, B. & Doherty, T. S. 2023. Meta-analysis reveals impacts of disturbance on reptile and amphibian body condition. *Global Change Biology,* 29**,** 4949–4965.

Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., van Bentham, K., Bolker, B., Brooks, M. & Brooks, M. M. 2017. Package ‘glmmTMB’. *R Package Version 0.2. 0*.

Main, M. T., Davis, R. A., Blake, D., Mills, H. & Doherty, T. S. 2020. Human impact overrides bioclimatic drivers of red fox home range size globally. *Diversity and Distributions,* 26**,** 1083-1092.

Mänd, R., Tilgar, V., Lõhmus, A., Leivits & Agu 2005. Providing nest boxes for hole-nesting birds – Does habitat matter? *Biodiversity & Conservation,* 14**,** 1823–1840.

Maron, M., Brownlie, S., Bull, J. W., Evans, M. C., von Hase, A., Quétier, F., Watson, J. E. M. & Gordon, A. 2018. The many meanings of no net loss in environmental policy. *Nature Sustainability,* 1**,** 19–27.

Martin, J. K. & Martin, A. A. 2007. Resource Distribution Influences Mating System in the Bobuck (*Trichosurus cunninghami: Marsupialia*). *Oecologia,* 154**,** 227–236.

Martino, R., McCann, P., Kumar Ray, R. & van der Ende, O. 2021. Digging deeper: Trends in underground hard-rock mining for gold and base metals. McKinsey & Company.

Martins-Oliveira, A. T., Zanin, M., Canale, G. R., Costa, C. A. d., Eisenlohr, P. V., Melo, F. C. S. A. d. & Melo, F. R. d. 2021. A global review of the threats of mining on mid-sized and large mammals. *Journal for Nature Conservation,* 62**,** 126025.

Maslin, B. R. & van Leeuwen, S. 2008. New taxa of Acacia (Leguminosae: Mimosoideae) and notes on other species from the Pilbara and adjacent desert regions of Western Australia. *Nuytsia,* 18**,** 139–188.

Mata, C., Malo, J. E., Galaz, J. L., Cadorzo, C. & Lagunas, H. 2016. A three-step approach to minimise the impact of a mining site on vicuña (Vicugna vicugna) and to restore landscape connectivity. *Environmental Science and Pollution Research,* 23**,** 13626-13636.

Maxwell, S. L., Fuller, R. A., Brooks, T. M. & Watson, J. E. M. 2016. Biodiversity: The ravages of guns, nets and bulldozers. *Nature News,* 536**,** 143.

Mazerolle, M. J. & Mazerolle, M. M. J. 2017. Package ‘AICcmodavg’.

McCann, K. 2007. Protecting biostructure. *Nature,* 446**,** 29-29.

McDonald, P. J., Nano, C. E. M., Ward, S. J., Stewart, A., Pavey, C. R., Luck, G. W. & Dickman, C. R. 2017. Habitat as a mediator of mesopredator-driven mammal extinction. *Conservation Biology,* 31**,** 1183–1191.

McDonald, P. J., Stewart, A., Jensen, M. A. & McGregor, H. W. 2020. Topographic complexity potentially mediates cat predation risk for a critically endangered rodent. *Wildlife Research,* 47**,** 643–648.

McDonald, P. J., Stewart, A., Schubert, A. T., Nano, C. E. M., Dickman, C. R. & Luck, G. W. 2016. Fire and grass cover influence occupancy patterns of rare rodents and feral cats in a mountain refuge: implications for management. *Wildlife Research,* 43**,** 121-129.

McGill, B. J. 2003. A test of the unified neutral theory of biodiversity. *Nature,* 422**,** 881-885.

McGregor, H. W., Legge, S., Jones, M. E. & Johnson, C. N. 2014a. Landscape Management of Fire and Grazing Regimes Alters the Fine-Scale Habitat Utilisation by Feral Cats. *PLOS ONE,* 9.

McGregor, H. W., Legge, S., Jones, M. E. & Johnson, C. N. 2015. Feral cats are better killers in open habitats, revealed by animal-borne video. *PloS one,* 10**,** e0133915.

McGregor, R. A., Stokes, V. L. & Craig, M. D. 2014b. Does forest restoration in fragmented landscapes provide habitat for a wide-ranging carnivore? *Animal Conservation,* 17**,** 467-475.

McKenzie, N. L., van Leeuwen, S. & Pinder, A. M. 2009. Introduction to the Pilbara Biodiversity Survey, 2002–2007. *Records of the Western Australian Museum, Supplement,* 78.

McNab, B. K. 1963. Bioenergetics and the Determination of Home Range Size. *The American Naturalist,* 97**,** 133-140.

Meek, P. D., Ballard, G. A., Abell, J., Milne, H., Smith, D. & Fleming, P. J. S. 2024. Activity of dingoes (*Canis familiaris*) and their use of anthropogenic resources in the Strzelecki Desert, South Australia. *Wildlife Research,* 51**,** WR23083.

Meira, R. M. S. A., Peixoto, A. L., Coelho, M. A. N., Ponzo, A. P. L., Esteves, V. G. L., Silva, M. C., Câmara, P. E. A. S. & Meira-Neto, J. A. A. 2016. Brazil's mining code under attack: giant mining companies impose unprecedented risk to biodiversity. *Biodiversity and Conservation,* 25**,** 407-409.

Mercker, M., Schwemmer, P., Peschko, V., Enners, L. & Garthe, S. 2021. Analysis of local habitat selection and large-scale attraction/avoidance based on animal tracking data: is there a single best method? *Movement Ecology,* 9**,** 20.

Meredith, M. & Ridout, M. 2018. Overview of the overlap package. *R Proj* [Online]. Available: https://cran.r-project.org/web/packages/overlap/vignettes/overlap.pdf [Accessed 10 April 2019].

Meredith, M., Ridout, M. & Meredith, M. M. 2014. Package 'overlap'. *Estimates of coefficient of overlapping for animal activity patterns,* 3**,** 1.

Michel, E. S., Gullikson, B. S., Brackel, K. L., Schaffer, B. A., Jenks, J. A. & Jensen, W. F. 2020. Habitat selection of white-tailed deer fawns and their dams in the Northern Great Plains. *Mammal Research,* 65**,** 825–833.

Mitchell, L. J., White, P. C. L. & Arnold, K. E. 2019. The trade-off between fix rate and tracking duration on estimates of home range size and habitat selection for small vertebrates. *PLOS ONE,* 14**,** e0219357.

Møller, A. P. 2009. Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia,* 159**,** 849-858.

Molloy, S. W., Davis, R. A., Dunlop, J. A. & van Etten, E. J. B. 2017. Applying surrogate species presences to correct sample bias in species distribution models: a case study using the Pilbara population of the northern quoll. *Nature Conservation,* 18**,** 27–46.

Moore, H. A., Diete, R. L., Indigo, N. L., Cowan, M. A., Trewella, G. J. & Nimmo, D. G. 2024. Midnight siesta: Bimodal temporal activity observed in an endangered marsupial predator. *Austral Ecology,* 49**,** e13521.

Moore, H. A., Dunlop, J. A., Jolly, C. J., Kelly, E., Woinarski, J. C. Z., Ritchie, E. G., Burnett, S., van Leeuwen, S., Valentine, L. E., Cowan, M. A. & Nimmo, D. G. 2021a. A brief history of the northern quoll (*Dasyurus hallucatus*): a systematic review. *Australian Mammalogy*.

Moore, H. A., Dunlop, J. A., Jolly, C. J., Kelly, E., Woinarski, J. C. Z., Ritchie, E. G., Burnett, S., van Leeuwen, S., Valentine, L. E., Cowan, M. A. & Nimmo, D. G. 2022a. A brief history of the northern quoll (*Dasyurus hallucatus*): a systematic review. *Australian Mammalogy,* 44**,** 185–207.

Moore, H. A., Dunlop, J. A. & Nimmo, D. G. 2023. Habitat suitability correlates with mean population fitness of a threatened marsupial predator. *Wildlife Research,* 51**,** WR23023.

Moore, H. A., Dunlop, J. A., Valentine, L. E., Woinarski, J. C. Z., Ritchie, E. G., Watson, D. M. & Nimmo, D. G. 2019. Topographic ruggedness and rainfall mediate geographic range contraction of a threatened marsupial predator. *Diversity and Distributions,* 25**,** 1818–1831.

Moore, H. A., Michael, D. R., Dunlop, J. A., Valentine, L. E., Cowan, M. A. & Nimmo, D. G. 2022b. Habitat amount is less important than habitat configuration for a threatened marsupial predator in naturally fragmented landscapes. *Landscape Ecology,* 37**,** 935–949.

Moore, H. A., Michael, D. R., Ritchie, E. G., Dunlop, J. A., Valentine, L. E., Hobbs, R. J. & Nimmo, D. G. 2021b. A rocky heart in a spinifex sea: occurrence of an endangered marsupial predator is multiscale dependent in naturally fragmented landscapes. *Landscape Ecology,* 36**,** 1359–1376.

Moore, H. A., Valentine, L. E., Dunlop, J. A. & Nimmo, D. G. 2020. The effect of camera orientation on the detectability of wildlife: a case study from north-western Australia. *Remote Sensing in Ecology and Conservation,* 6**,** 546-556.

Morelli, T. L., Maher, S. P., Lim, M. C. W., Kastely, C., Eastman, L. M., Flint, L. E., Flint, A. L., Beissinger, S. R. & Moritz, C. 2017. Climate change refugia and habitat connectivity promote species persistence. *Climate Change Responses,* 4**,** 8.

Mori, A. S., Furukawa, T. & Sasaki, T. 2013. Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews,* 88**,** 349-364.

Moro, D., Dunlop, J. & Williams, M. R. 2019. Northern quoll persistence is most sensitive to survivorship of juveniles. *Wildlife Research,* 46**,** 165-175.

Mortensen, L. O., Chudzinska, M. E., Slabbekoorn, H. & Thomsen, F. 2021. Agent-based models to investigate sound impact on marine animals: bridging the gap between effects on individual behaviour and population level consequences. *Oikos,* 130**,** 1074-1086.

Moseby, K. E., Hodgens, P., Peacock, D., Mooney, P., Brandle, R., Lynch, C., West, R., Young, C. M., Bannister, H., Copley, P. & Jensen, M. A. 2021. Intensive monitoring, the key to identifying cat predation as a major threat to native carnivore (*Dasyurus geoffroii*) reintroduction. *Biodiversity and Conservation,* 30**,** 1–25.

Muff, S., Signer, J. & Fieberg, J. 2020. Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation. *Journal of Animal Ecology,* 89**,** 80–92.

Murphy, B. P. & Davies, H. F. 2014. There is a critical weight range for A ustralia's declining tropical mammals. *Global Ecology and Biogeography,* 23**,** 1058-1061.

Murray, M. G. & Illius, A. W. 2000. Vegetation modification and resource competition in grazing ungulates. *Oikos,* 89**,** 501-508.

Muthén, B. 2011. Applications of causally defined direct and indirect effects in mediation analysis using SEM in Mplus. Los Angeles, CA.

Najera-Zuloaga, J., Lee, D.-J., Arostegui, I. & Najera-Zuloaga, M. J. 2020. Package ‘PROreg’.

Nakagawa, S. & Schielzeth, H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution,* 4**,** 133-142.

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P. E. 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences,* 105**,** 19052-19059.

Nathan, R., Monk, C. T., Arlinghaus, R., Adam, T., Alós, J., Assaf, M., Baktoft, H., Beardsworth, C. E., Bertram, M. G., Bijleveld, A. I., Brodin, T., Brooks, J. L., Campos-Candela, A., Cooke, S. J., Gjelland, K. Ø., Gupte, P. R., Harel, R., Hellström, G., Jeltsch, F., Killen, S. S., Klefoth, T., Langrock, R., Lennox, R. J., Lourie, E., Madden, J. R., Orchan, Y., Pauwels, I. S., Říha, M., Roeleke, M., Schlägel, U. E., Shohami, D., Signer, J., Toledo, S., Vilk, O., Westrelin, S., Whiteside, M. A. & Jarić, I. 2022. Big-data approaches lead to an increased understanding of the ecology of animal movement. *Science,* 375**,** eabg1780.

Nathan, R., Spiegel, O., Fortmann-Roe, S., Harel, R., Wikelski, M. & Getz, W. M. 2012. Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *Journal of Experimental Biology,* 215**,** 986-996.

Neilson, E. W. & Boutin, S. 2017. Human disturbance alters the predation rate of moose in the Athabasca oil sands. *Ecosphere,* 8.

Newsome, A. E. 1971. Competition between wildlife and domestic livestock. *Australian Veterinary Journal,* 47**,** 577-586.

Newsome, T. M., Ballard, G.-A., Fleming, P. J. S., van de Ven, R., Story, G. L. & Dickman, C. R. 2014a. Human-resource subsidies alter the dietary preferences of a mammalian top predator. *Oecologia,* 175**,** 139-150.

Newsome, T. M., Ballard, G. A., Dickman, C. R., Fleming, P. J. S. & Howden, C. 2013a. Anthropogenic Resource Subsidies Determine Space Use by Australian Arid Zone Dingoes: An Improved Resource Selection Modelling Approach. *PLoS ONE,* 8.

Newsome, T. M., Ballard, G. A., Dickman, C. R., Fleming, P. J. S. & Van De Ven, R. 2013b. Home Range, activity and sociality of a top predator, the dingo: A test of the resource dispersion hypothesis. *Ecography,* 36**,** 914-925.

Newsome, T. M., Dellinger, J. A., Pavey, C. R., Ripple, W. J., Shores, C. R., Wirsing, A. J. & Dickman, C. R. 2014b. The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography,* 24**,** 1-11.

Newsome, T. M., Howden, C. & Wirsing, A. J. 2019. Restriction of anthropogenic foods alters a top predator's diet and intraspecific interactions. *Journal of Mammalogy,* 100**,** 1522-1532.

Newsome, T. M., Stephens, D., Ballard, G.-A., Dickman, C. R. & Fleming, P. J. S. 2013c. Genetic profile of dingoes (*Canis lupus dingo*) and free-roaming domestic dogs (*C. l. familiaris*) in the Tanami Desert, Australia. *Wildlife Research,* 40**,** 196-206.

Nichols, O. G. & Nichols, F. M. 2003. Long-term trends in faunal recolonization after bauxite mining in the Jarrah forest of Southwestern Australia. *Restoration Ecology,* 11**,** 261-272.

Nimmo, D. G., Avitabile, S., Banks, S. C., Bliege Bird, R., Callister, K., Clarke, M. F., Dickman, C. R., Doherty, T. S., Driscoll, D. A., Greenville, A. C., Haslem, A., Kelly, L. T., Kenny, S. A., Lahoz-Monfort, J. J., Lee, C., Leonard, S., Moore, H., Newsome, T. M., Parr, C. L., Ritchie, E. G., Schneider, K., Turner, J. M., Watson, S., Westbrooke, M., Wouters, M., White, M. & Bennett, A. F. 2019. Animal movements in fire-prone landscapes. *Biological Reviews,* 94**,** 981–998.

Nock, C. A., Vogt, R. J. & Beisner, B. E. 2016. Functional traits. *eLS***,** 1-8.

Northrup, J. M., Vander Wal, E., Bonar, M., Fieberg, J., Laforge, M. P., Leclerc, M., Prokopenko, C. M. & Gerber, B. D. 2022. Conceptual and methodological advances in habitat-selection modeling: guidelines for ecology and evolution. *Ecological Applications,* 32**,** e02470.

Oakwood, M. 1997. *The ecology of the northern quoll, Dasyurus hallucatus.* Doctor of Philosophy, Australian National University.

Oakwood, M. 2000. Reproduction and demography of the northern quoll, *Dasyurus hallucatus*, in the lowland savanna of northern Australia. *Australian Journal of Zoology,* 48**,** 519-539.

Oakwood, M. 2002. Spatial and social organization of a carnivorous marsupial *Dasyurus hallucatus*. *Journal of Zoology,* 257**,** 237–248.

Oakwood, M. 2004. Death after sex. *Biologist,* 51**,** 5-8.

Oakwood, M., Bradley, A. J. & Cockburn, A. 2001. Semelparity in a Large Marsupial. *Proceedings: Biological Sciences,* 268**,** 407-411.

Oakwood, M., Woinarski, J. C. Z. & Burnett, S. 2016. *Dasyurus hallucatus. The IUCN Red List of Threatened Species 2016* [Online]. Available: http://dx.doi.org/10.2305/IUCN.UK.2016-2.RLTS.T6295A21947321 [Accessed 14 May 2019].

Oberpriller, J., de Souza Leite, M. & Pichler, M. 2022. Fixed or random? On the reliability of mixed-effects models for a small number of levels in grouping variables. *Ecology and Evolution,* 12**,** e9062.

Oehler, M. W., Bleich, V. C., Bowyer, R. T. & Nicholson, M. C. 2005. Mountain sheep and mining: implications for conservation and management. *California Fish and Game,* 91**,** 149.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M. H. H., Oksanen, M. J. & Suggests, M. 2007. The vegan package. *Community ecology package,* 10**,** 719.

Osborne, M. J. & Rubinstein, A. 1994. *A course in game theory,* MIT press.

Osipova, L., Okello, M. M., Njumbi, S. J., Ngene, S., Western, D., Hayward, M. W. & Balkenhol, N. 2019. Using step-selection functions to model landscape connectivity for African elephants: accounting for variability across individuals and seasons. *Animal Conservation,* 22**,** 35-48.

Osterhout, M. J., Stewart, K. M., Wakeling, B. F., Schroeder, C. A., Blum, M. E., Brockman, J. C. & Shoemaker, K. T. 2024. Effects of large-scale gold mining on habitat use and selection by American pronghorn. *Science of The Total Environment,* 921**,** 170750.

Owusu, E. H., Ofori, B. Y. & Attuquayefio, D. K. 2018. The secondary impact of mining on primates and other medium to large mammals in forest reserves in southwestern Ghana. *The Extractive Industries and Society,* 5**,** 114-121.

Palmer, R., Anderson, H., Richards, B., Craig, M. D. & Gibson, L. 2021. Does aerial baiting for controlling feral cats in a heterogeneous landscape confer benefits to a threatened native meso-predator? *PLOS ONE,* 16**,** e0251304.

Pandey, A. C. & Kulhari, A. 2018. *Semi-supervised spatiotemporal classification and trend analysis of satellite images,* Singapore, Springer Singapore.

Paruelo, J. M., Epstein, H. E., Lauenroth, W. K. & Burke, I. C. 1997. ANPP Estimates from NDVI for the Central Grassland Region of the United States. *Ecology,* 78**,** 953-958.

Pearson, D. 2003. Giant pythons of the Pilbara. *Landscope,* 19**,** 32–39.

Pebesma, E. J. 2018. Simple features for R: standardized support for spatial vector data. *R J.,* 10**,** 439.

Penteriani, V., Delgado, M. D. M., Krofel, M., Jerina, K., Ordiz, A., Dalerum, F., Zarzo-Arias, A. & Bombieri, G. 2018. Evolutionary and ecological traps for brown bears Ursus arctos in human-modified landscapes. *Mammal Review,* 48**,** 180-193.

Peris, A., Closa, F., Marco, I., Acevedo, P., Barasona, J. A. & Casas-Díaz, E. 2020. Towards the comparison of home range estimators obtained from contrasting tracking regimes: the wild boar as a case study. *European Journal of Wildlife Research,* 66**,** 32.

Perkins, D. M., Hatton, I. A., Gauzens, B., Barnes, A. D., Ott, D., Rosenbaum, B., Vinagre, C. & Brose, U. 2022. Consistent predator-prey biomass scaling in complex food webs. *Nature Communications,* 13**,** 4990.

Perona, A. M., Urios, V. & López-López, P. 2019. Holidays? Not for all. Eagles have larger home ranges on holidays as a consequence of human disturbance. *Biological Conservation,* 231**,** 59-66.

Perry, G. & Pianka, E. R. 1997. Animal foraging: past, present and future. *Trends in Ecology & Evolution,* 12**,** 360–364.

Petchey, O. L. 2003. Integrating methods that investigate how complementarity influences ecosystem functioning. *Oikos,* 101**,** 323-330.

Pettorelli, N. 2013. *The normalized difference vegetation index*, Oxford University Press.

Poessel, S. A., Duerr, A. E., Hall, J. C., Braham, M. A. & Katzner, T. E. 2018. Improving estimation of flight altitude in wildlife telemetry studies. *Journal of Applied Ecology,* 55**,** 2064-2070.

Polfus, J. L., Hebblewhite, M. & Heinemeyer, K. 2011. Identifying indirect habitat loss and avoidance of human infrastructure by northern mountain woodland caribou. *Biological Conservation,* 144**,** 2637–2646.

Pollock, A. B. 1999. Notes on status, distribution and diet of northern quoll *Dasyurus hallucatus* in the Mackay-Bowen area, mideastern Queensland. *Australian Zoologist,* 31**,** 388–395.

Potter, L. C., Brady, C. J. & Murphy, B. P. 2019. Accuracy of identifications of mammal species from camera trap images: A northern Australian case study. *Austral Ecology,* 44**,** 473-483.

Potts, J. R. & Börger, L. 2023. How to scale up from animal movement decisions to spatiotemporal patterns: An approach via step selection. *Journal of Animal Ecology,* 92**,** 16-29.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators. *Research techniques in animal ecology: controversies and consequences,* 442**,** 65–110.

Qasem, L., Cardew, A., Wilson, A., Griffiths, I., Halsey, L. G., Shepard, E. L. C., Gleiss, A. C. & Wilson, R. 2012. Tri-Axial Dynamic Acceleration as a Proxy for Animal Energy Expenditure; Should We Be Summing Values or Calculating the Vector? *PLOS ONE,* 7**,** e31187.

QGIS Development Team 2020. QGIS Geographic Information System. Open Source Geospatial Foundation Project.

R Core Team 2023a. Package 'stats'.

R Core Team 2023b. R: A language and environment for statistical computing. *R Foundation for Statistical Computing*.

Ramanaidou, E. R. & Morris, R. C. 2010. A synopsis of the channel iron deposits of the Hamersley Province, Western Australia. *Applied Earth Science,* 119**,** 56–59.

Ranc, N., Cagnacci, F. & Moorcroft, P. R. 2022. Memory drives the formation of animal home ranges: Evidence from a reintroduction. *Ecology Letters,* 25**,** 716-728.

Recio, M. R., Mathieu, R., Denys, P., Sirguey, P. & Seddon, P. J. 2011. Lightweight GPS-Tags, One Giant Leap for Wildlife Tracking? An Assessment Approach. *PLOS ONE,* 6**,** e28225.

Rheault, H., Anderson, C. R., Bonar, M., Marrotte, R. R., Ross, T. R., Wittemyer, G. & Northrup, J. M. 2021. Some Memories Never Fade: Inferring Multi-Scale Memory Effects on Habitat Selection of a Migratory Ungulate Using Step-Selection Functions. *Frontiers in Ecology and Evolution,* 9.

Richardson, D. M., Bond, W. J., Dean, W. R. J., Higgins, S. I., Midgley, G. F., Milton, S. J., Powrie, L. W., Rutherford, M. C., Samways, M. J. & Schulze, R. E. 2000. Invasive alien species and global change: a South African perspective. *Invasive species in a changing world. Island Press, Washington, DC***,** 303-349.

Ricketts, T. H. 2001. The Matrix Matters: Effective Isolation in Fragmented Landscapes. *The American Naturalist,* 158**,** 87-99.

Ridout, M. & Linkie, M. 2009. Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics,* 14**,** 322-337.

Riley, S. J., DeGloria, S. D. & Elliot, R. 1999. Index that quantifies topographic heterogeneity. *intermountain Journal of sciences,* 5**,** 23–27.

Riotte-Lambert, L., Benhamou, S. & Chamaillé-Jammes, S. 2015. How memory-based movement leads to nonterritorial spatial segregation. *Am Nat,* 185**,** E103-16.

Robert, K. A., Lesku, J. A., Partecke, J. & Chambers, B. 2015. Artificial light at night desynchronizes strictly seasonal reproduction in a wild mammal. *Proceedings of the Royal Society B: Biological Sciences,* 282**,** 20151745.

Ruprecht, J. 1996. Arid Zone Hydrology: Pilbara Region of Western Australia. *Hydrology and Water Resources Symposium 1996: Water and the Environment.* Barton, ACT: Institution of Engineers, Australia.

Rus, A. I., McArthur, C., Mella, V. S. A. & Crowther, M. S. 2020. Habitat fragmentation affects movement and space use of a specialist folivore, the koala. *Animal Conservation,* 24**,** 26–37.

Sales Rosa, J. C., Campos, P. B. R., Nascimento, C. B., Souza, B. A., Valetich, R. & Sánchez, L. E. 2023. Enhancing ecological connectivity through biodiversity offsets to mitigate impacts on habitats of large mammals in tropical forest environments. *Impact Assessment and Project Appraisal,* 41**,** 333-348.

Sánchez-Montoya, M. M., Moleón, M., Sánchez-Zapata, J. A. & Tockner, K. 2016. Dry riverbeds: corridors for terrestrial vertebrates. *Ecosphere,* 7**,** e01508.

Sartor, C. C., Cushman, S. A., Wan, H. Y., Tirelli, F. P., Althoff, S. L., Eizirik, E., Trigo, T. C. & de Freitas, T. R. O. 2024. Prioritizing conservation areas to mitigate connectivity loss and local extinction risk of a small carnivore (*Leopardus guttulus*) in South America. *Biodiversity and Conservation,* 33**,** 1605–1622.

Schoener, T. W. 1971. Theory of Feeding Strategies. *Annual Review of Ecology and Systematics,* 2**,** 369-404.

Schulz, K. J., DeYoung, J. J. H., Seal Ii, R. R. & Bradley, D. C. 2017. *Critical mineral resources of the United States—Economic and environmental geology and prospects for future supply,* Reston, VA.

Schulz, M., Wilks, G. & Broome, L. 2012. Occupancy of spoil dumps by the Mountain Pygmy-possum *Burramys parvus* in Kosciuszko National Park. *Ecological Management & Restoration,* 13**,** 290–296.

Seaman, D. E., Millspaugh, J. J., Kernohan, B. J., Brundige, G. C., Raedeke, K. J. & Gitzen, R. A. 1999. Effects of Sample Size on Kernel Home Range Estimates. *The Journal of Wildlife Management,* 63**,** 739–747.

Sells, S. N., Costello, C. M., Lukacs, P. M., Roberts, L. L. & Vinks, M. A. 2023. Predicted connectivity pathways between grizzly bear ecosystems in Western Montana. *Biological Conservation,* 284**,** 110199.

Senior, K. L., Giljohann, K. M., McCarthy, M. A. & Kelly, L. T. 2023. A field test of mechanisms underpinning animal diversity in recently burned landscapes. *Journal of Applied Ecology,* 60**,** 146-157.

Sepúlveda, R. D. & Valdivia, N. 2016. Localised Effects of a Mega-Disturbance: Spatiotemporal Responses of Intertidal Sandy Shore Communities to the 2010 Chilean Earthquake. *PLOS ONE,* 11**,** e0157910.

Shaw, R. E., Spencer, P. B., Gibson, L. A., Dunlop, J. A., Kinloch, J. E., Mokany, K., Byrne, M., Moritz, C., Davie, H., Travouillon, K. J. & Ottewell, K. M. 2022. Linking life history to landscape for threatened species conservation in a multiuse region. *Conservation Biology,* 37**,** e13989.

Shine, R. 1986. Food Habits, Habitats and Reproductive Biology of Four Sympatric Species of Varanid Lizards in Tropical Australia. *Herpetologica,* 42**,** 346-360.

Shine, R. 2010. The Ecological Impact of Invasive Cane Toads (*Bufo Marinus*) in Australia. *The Quarterly Review of Biology,* 85**,** 253-291.

Signer, J. & Balkenhol, N. 2015. Reproducible home ranges (rhr): A new, user-friendly R package for analyses of wildlife telemetry data. *Wildlife Society Bulletin,* 39**,** 358–363.

Signer, J., Balkenhol, N., Ditmer, M. & Fieberg, J. 2015. Does estimator choice influence our ability to detect changes in home-range size? *Animal Biotelemetry,* 3**,** 16.

Signer, J., Fieberg, J. & Avgar, T. 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. *Ecology and Evolution,* 9**,** 880-890.

Signer, J. & Fieberg, J. R. 2021. A fresh look at an old concept: home-range estimation in a tidy world. *PeerJ,* 9**,** e11031.

Silverman, B. W. 1986. *Density estimation for statistics and data analysis*, CRC press.

Siqueira-Gay, J. & Sánchez, L. E. 2021. The outbreak of illegal gold mining in the Brazilian Amazon boosts deforestation. *Regional Environmental Change,* 21**,** 28.

Smit, I. P. J. & Grant, C. C. 2009. Managing surface-water in a large semi-arid savanna park: Effects on grazer distribution patterns. *Journal for Nature Conservation,* 17**,** 61–71.

Smith, B. P., Morrant, D. S., Vague, A.-L. & Doherty, T. S. 2020. High rates of cannibalism and food waste consumption by dingoes living at a remote mining operation in the Great Sandy Desert, Western Australia. *Australian Mammalogy,* 42**,** 230-234.

Sonter, L. J., Ali, S. H. & Watson, J. E. M. 2018. Mining and biodiversity: key issues and research needs in conservation science. *Proceedings of the Royal Society B: Biological Sciences,* 285**,** 20181926.

Sonter, L. J., Dade, M. C., Watson, J. E. M. & Valenta, R. K. 2020. Renewable energy production will exacerbate mining threats to biodiversity. *Nature Communications,* 11**,** 4174.

Sonter, L. J., Herrera, D., Barrett, D. J., Galford, G. L., Moran, C. J. & Soares-Filho, B. S. 2017. Mining drives extensive deforestation in the Brazilian Amazon. *Nature Communications,* 8**,** 1013.

Sonter, L. J., Lloyd, T. J., Kearney, S. G., Di Marco, M., O'Bryan, C. J., Valenta, R. K. & Watson, J. E. M. 2022. Conservation implications and opportunities of mining activities for terrestrial mammal habitat. *Conservation Science and Practice,* 4**,** e12806.

Sonter, L. J., Moran, C. J., Barrett, D. J. & Soares-Filho, B. S. 2014. Processes of land use change in mining regions. *Journal of Cleaner Production,* 84**,** 494-501.

Squires, J. R., DeCesare, N. J., Olson, L. E., Kolbe, J. A., Hebblewhite, M. & Parks, S. A. 2013. Combining resource selection and movement behavior to predict corridors for Canada lynx at their southern range periphery. *Biological Conservation,* 157**,** 187–195.

Stobo-Wilson, A. M., Cremona, T., Murphy, B. P. & Carthew, S. M. 2021. Resource availability drives variation in a marsupial glider’s home-range size. *Journal of Zoology,* 315**,** 199–212.

Stokes, V. L., Pech, R. P., Banks, P. B. & Arthur, A. D. 2004. Foraging behaviour and habitat use by Antechinus flavipes and Sminthopsis murina (Marsupialia: Dasyuridae) in response to predation risk in eucalypt woodland. *Biological Conservation,* 117**,** 331-342.

Stratmann, T. S. M., Dejid, N., Calabrese, J. M., Fagan, W. F., Fleming, C. H., Olson, K. A. & Mueller, T. 2021. Resource selection of a nomadic ungulate in a dynamic landscape. *PLOS ONE,* 16**,** e0246809.

Suglo, P., Effah, P., Acheampong, A. A., Sunkari, R. & Yeboah, A. 2021. Effects of Illegal Mining on the Environment, Economy, and Agricultural Productivity. *Biochemistry and Molecular Biology,* 6**,** 79-91.

Tang, L. & Werner, T. T. 2023. Global mining footprint mapped from high-resolution satellite imagery. *Communications Earth & Environment,* 4**,** 134.

Tang, W. & Bennett, D. A. 2010. Agent-based Modeling of Animal Movement: A Review. *Geography Compass,* 4**,** 682-700.

Tarabon, S., Bergès, L., Dutoit, T. & Isselin-Nondedeu, F. 2019. Maximizing habitat connectivity in the mitigation hierarchy. A case study on three terrestrial mammals in an urban environment. *Journal of Environmental Management,* 243**,** 340-349.

Taylor, P. D., Fahrig, L., Henein, K. & Merriam, G. 1993. Connectivity is a vital element of landscape structure. *Oikos***,** 571-573.

Theobald, E., Hosken, D. J., Foster, P. & Moyes, K. 2020. Mines and bats: the impact of open-pit mining on bat activity. *Acta Chiropterologica,* 22**,** 157-166.

Thomas, H., Cameron, S. F., Campbell, H. A., Micheli-Campbell, M. A., Kirke, E. C., Wheatley, R. & Wilson, R. S. 2021. Rocky escarpment versus savanna woodlands: comparing diet and body condition as indicators of habitat quality for the endangered northern quoll (*Dasyurus hallucatus*). *Wildlife Research,* 48**,** 434–443.

Thurfjell, H., Ciuti, S. & Boyce, M. S. 2014. Applications of step-selection functions in ecology and conservation. *Movement Ecology,* 2**,** 4.

Tilahun, A. & Teferie, B. 2015. Accuracy assessment of land use land cover classification using Google Earth. *Am. J. Environ. Prot,* 4**,** 193–198.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. 1997. The Influence of Functional Diversity and Composition on Ecosystem Processes. *Science,* 277**,** 1300-1302.

Torres, A., Ermgassen, S. O. S. E. z., Ferri-Yanez, F., Navarro, L. M., Rosa, I. M. D., Teixeira, F. Z., Wittkopp, C. & Liu, J. 2022. Unearthing the global impact of mining construction minerals on biodiversity. *bioRxiv***,** 2022.03.23.485272.

Trakhtenbrot, A., Nathan, R., Perry, G. & Richardson, D. M. 2005. The importance of long-distance dispersal in biodiversity conservation. *Diversity and Distributions,* 11**,** 173-181.

Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T. O., Dormann, C. F., Ewers, R. M., Fründ, J., Holt, R. D., Holzschuh, A., Klein, A. M., Kleijn, D., Kremen, C., Landis, D. A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W. H. & Westphal, C. 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews,* 87**,** 661-685.

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B., Alberts, S. C., Ali, A. H., Allen, A. M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J. L., Bertassoni, A., Beyer, D., Bidner, L., van Beest, F. M., Blake, S., Blaum, N., Bracis, C., Brown, D., de Bruyn, P. J. N., Cagnacci, F., Calabrese, J. M., Camilo-Alves, C., Chamaillé-Jammes, S., Chiaradia, A., Davidson, S. C., Dennis, T., DeStefano, S., Diefenbach, D., Douglas-Hamilton, I., Fennessy, J., Fichtel, C., Fiedler, W., Fischer, C., Fischhoff, I., Fleming, C. H., Ford, A. T., Fritz, S. A., Gehr, B., Goheen, J. R., Gurarie, E., Hebblewhite, M., Heurich, M., Hewison, A. J. M., Hof, C., Hurme, E., Isbell, L. A., Janssen, R., Jeltsch, F., Kaczensky, P., Kane, A., Kappeler, P. M., Kauffman, M., Kays, R., Kimuyu, D., Koch, F., Kranstauber, B., LaPoint, S., Leimgruber, P., Linnell, J. D. C., López-López, P., Markham, A. C., Mattisson, J., Medici, E. P., Mellone, U., Merrill, E., de Miranda Mourão, G., Morato, R. G., Morellet, N., Morrison, T. A., Díaz-Muñoz, S. L., Mysterud, A., Nandintsetseg, D., Nathan, R., Niamir, A., Odden, J., O'Hara, R. B., Oliveira-Santos, L. G. R., Olson, K. A., Patterson, B. D., Cunha de Paula, R., Pedrotti, L., Reineking, B., Rimmler, M., Rogers, T. L., Rolandsen, C. M., Rosenberry, C. S., Rubenstein, D. I., Safi, K., Saïd, S., Sapir, N., Sawyer, H., Schmidt, N. M., Selva, N., Sergiel, A., Shiilegdamba, E., Silva, J. P., Singh, N., et al. 2018. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science,* 359**,** 466.

Tucker, M. A., Schipper, A. M., Adams, T. S. F., Attias, N., Avgar, T., Babic, N. L., Barker, K. J., Bastille-Rousseau, G., Behr, D. M., Belant, J. L., Beyer, D. E., Blaum, N., Blount, J. D., Bockmühl, D., Pires Boulhosa, R. L., Brown, M. B., Buuveibaatar, B., Cagnacci, F., Calabrese, J. M., Černe, R., Chamaillé-Jammes, S., Chan, A. N., Chase, M. J., Chaval, Y., Chenaux-Ibrahim, Y., Cherry, S. G., Ćirović, D., Çoban, E., Cole, E. K., Conlee, L., Courtemanch, A., Cozzi, G., Davidson, S. C., DeBloois, D., Dejid, N., DeNicola, V., Desbiez, A. L. J., Douglas-Hamilton, I., Drake, D., Egan, M., Eikelboom, J. A. J., Fagan, W. F., Farmer, M. J., Fennessy, J., Finnegan, S. P., Fleming, C. H., Fournier, B., Fowler, N. L., Gantchoff, M. G., Garnier, A., Gehr, B., Geremia, C., Goheen, J. R., Hauptfleisch, M. L., Hebblewhite, M., Heim, M., Hertel, A. G., Heurich, M., Hewison, A. J. M., Hodson, J., Hoffman, N., Hopcraft, J. G. C., Huber, D., Isaac, E. J., Janik, K., Ježek, M., Johansson, Ö., Jordan, N. R., Kaczensky, P., Kamaru, D. N., Kauffman, M. J., Kautz, T. M., Kays, R., Kelly, A. P., Kindberg, J., Krofel, M., Kusak, J., Lamb, C. T., LaSharr, T. N., Leimgruber, P., Leitner, H., Lierz, M., Linnell, J. D. C., Lkhagvaja, P., Long, R. A., López-Bao, J. V., Loretto, M.-C., Marchand, P., Martin, H., Martinez, L. A., McBride, R. T., McLaren, A. A. D., Meisingset, E., Melzheimer, J., Merrill, E. H., Middleton, A. D., Monteith, K. L., Moore, S. A., Van Moorter, B., Morellet, N., et al. 2023. Behavioral responses of terrestrial mammals to COVID-19 lockdowns. *Science,* 380**,** 1059-1064.

Tuomainen, U. & Candolin, U. 2011. Behavioural responses to human-induced environmental change. *Biological Reviews,* 86**,** 640-657.

Turner, F. B. & Medica, P. A. 1982. The Distribution and Abundance of the Flat-Tailed Horned Lizard (Phrynosoma mcallii). *Copeia,* 1982**,** 815-823.

Tylianakis, J. M., Laliberté, E., Nielsen, A. & Bascompte, J. 2010. Conservation of species interaction networks. *Biological Conservation,* 143**,** 2270-2279.

USGS. 2023. *Earth Explorer* [Online]. Available: https://earthexplorer.usgs.gov/ [Accessed Accessed 15 January 2023].

van der Meer, E., Fritz, H., Blinston, P. & Rasmussen, G. S. A. 2014. Ecological trap in the buffer zone of a protected area: effects of indirect anthropogenic mortality on the African wild dog Lycaon pictus. *Oryx,* 48**,** 285-293.

van Donk, S., Shamoun-Baranes, J., van der Meer, J. & Camphuysen, K. C. J. 2019. Foraging for high caloric anthropogenic prey is energetically costly. *Movement Ecology,* 7**,** 17.

Van Moorter, B., Visscher, D., Benhamou, S., Börger, L., Boyce, M. S. & Gaillard, J.-M. 2009. Memory keeps you at home: a mechanistic model for home range emergence. *Oikos,* 118**,** 641-652.

Van Vreeswyk, A. M. E., Leighton, K. A., Payne, A. L. & Hennig, P. 2004. An inventory and condition survey of the Pilbara region, Western Australia. Perth: Department of Agriculture and Food.

Viana, D. S., Granados, J. E., Fandos, P., Pérez, J. M., Cano-Manuel, F. J., Burón, D., Fandos, G., Aguado, M. Á. P., Figuerola, J. & Soriguer, R. C. 2018. Linking seasonal home range size with habitat selection and movement in a mountain ungulate. *Movement Ecology,* 6**,** 1.

Vilella, M., Ferrandiz-Rovira, M. & Sayol, F. 2020. Coexistence of predators in time: Effects of season and prey availability on species activity within a Mediterranean carnivore guild. *Ecology and Evolution,* 10**,** 11408-11422.

Violet, C. & Gravel, D. 2019. Package 'omnivor'.

Virgós, E., Baniandrés, N., Burgos, T. & Recio, M. R. 2020. Intraguild Predation by the Eagle Owl Determines the Space Use of a Mesopredator Carnivore. *Diversity,* 12**,** 359.

von Takach, B., Ranjard, L., Burridge, C. P., Cameron, S. F., Cremona, T., Eldridge, M. D. B., Fisher, D. O., Frankenberg, S., Hill, B. M., Hohnen, R., Jolly, C. J., Kelly, E., MacDonald, A. J., Moussalli, A., Ottewell, K., Phillips, B. L., Radford, I. J., Spencer, P. B. S., Trewella, G. J., Umbrello, L. S. & Banks, S. C. 2022. Population genomics of a predatory mammal reveals patterns of decline and impacts of exposure to toxic toads. *Molecular Ecology,* 31**,** 5468-5486.

Wang, J., Rich, P. M., Price, K. P. & Kettle, W. D. 2004. Relations between NDVI and tree productivity in the central Great Plains. *International Journal of Remote Sensing,* 25**,** 3127-3138.

Wang, Y., Smith, J. A. & Wilmers, C. C. 2017. Residential development alters behavior, movement, and energetics in an apex predator, the puma. *PLOS ONE,* 12**,** e0184687.

Watchorn, D. J., Cowan, M. A., Driscoll, D. A., Nimmo, D. G., Ashman, K. R., Garkaklis, M. J., Wilson, B. A. & Doherty, T. S. 2022. Artificial habitat structures for animal conservation: design and implementation, risks and opportunities. *Frontiers in Ecology and the Environment,* 20**,** 301–309.

Watchorn, D. J., Dickman, C. R., Greenville, A., Wilson, B. A., Garkaklis, M. J., Driscoll, D. A., Hodgens, P., Hoadley, D., Groffen, H. & Doherty, T. S. 2024. Artificial refuges provide post-fire habitat for small vertebrates. *Biological Conservation,* 291**,** 110501.

Watchorn, D. J., Duncan, T. A. & Cowan, M. A. 2023. The risks and rewards of using artificial habitat structures for wildlife conservation. *Austral Ecology,* 48**,** 1207-1222.

Webb, S. L., Dzialak, M. R., Harju, S. M., Hayden-Wing, L. D. & Winstead, J. B. 2011. Effects of human activity on space use and movement patterns of female Elk. *Wildlife Society Bulletin,* 35**,** 261-269.

Werner, T. T., Bach, P. M., Yellishetty, M., Amirpoorsaeed, F., Walsh, S., Miller, A., Roach, M., Schnapp, A., Solly, P., Tan, Y., Lewis, C., Hudson, E., Heberling, K., Richards, T., Chia, H. C., Truong, M., Gupta, T. & Wu, X. 2020. A Geospatial Database for Effective Mine Rehabilitation in Australia. *Minerals,* 10, 745.

Whittington, J., Hebblewhite, M., Baron, R. W., Ford, A. T. & Paczkowski, J. 2022. Towns and trails drive carnivore movement behaviour, resource selection, and connectivity. *Movement Ecology,* 10**,** 17.

Williams, B. A., Venter, O., Allan, J. R., Atkinson, S. C., Rehbein, J. A., Ward, M., Di Marco, M., Grantham, H. S., Ervin, J., Goetz, S. J., Hansen, A. J., Jantz, P., Pillay, R., Rodríguez-Buriticá, S., Supples, C., Virnig, A. L. S. & Watson, J. E. M. 2020a. Change in Terrestrial Human Footprint Drives Continued Loss of Intact Ecosystems. *One Earth,* 3**,** 371-382.

Williams, H. J., Taylor, L. A., Benhamou, S., Bijleveld, A. I., Clay, T. A., de Grissac, S., Demšar, U., English, H. M., Franconi, N., Gómez-Laich, A., Griffiths, R. C., Kay, W. P., Morales, J. M., Potts, J. R., Rogerson, K. F., Rutz, C., Spelt, A., Trevail, A. M., Wilson, R. P. & Börger, L. 2020b. Optimizing the use of biologgers for movement ecology research. *Journal of Animal Ecology,* 89**,** 186-206.

Williamson, S. D., van Dongen, R., Trotter, L., Palmer, R. & Robinson, T. P. 2021. Fishing for Feral Cats in a Naturally Fragmented Rocky Landscape Using Movement Data. *Remote Sensing,* 13**,** 4925.

Wilson, R. P., Börger, L., Holton, M. D., Scantlebury, D. M., Gómez-Laich, A., Quintana, F., Rosell, F., Graf, P. M., Williams, H., Gunner, R., Hopkins, L., Marks, N., Geraldi, N. R., Duarte, C. M., Scott, R., Strano, M. S., Robotka, H., Eizaguirre, C., Fahlman, A. & Shepard, E. L. C. 2020. Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. *Journal of Animal Ecology,* 89**,** 161-172.

Woinarski, J. C. Z., Armstrong, M., Brennan, K., Fisher, A., Griffiths, A. D., Hill, B., Milne, D. J., Palmer, C., Ward, S., Watson, M., Winderlich, S. & Young, S. 2010. Monitoring indicates rapid and severe decline of native small mammals in Kakadu National Park, northern Australia. *Wildlife Research,* 37**,** 116-126.

Woinarski, J. C. Z., Burbidge, A. & Harrison, P. 2014. *The action plan for Australian mammals 2012*, CSIRO publishing.

Wynn, M. L., Clemente, C., Nasir, A. F. & Wilson, R. S. 2015. Running faster causes disaster: trade-offs between speed, manoeuvrability and motor control when running around corners in northern quolls (*Dasyurus hallucatus*). *J Exp Biol,* 218**,** 433–9.

Wysong, M. L., Hradsky, B. A., Iacona, G. D., Valentine, L. E., Morris, K. & Ritchie, E. G. 2020a. Space use and habitat selection of an invasive mesopredator and sympatric, native apex predator. *Movement Ecology,* 8**,** 18.

Wysong, M. L., Iacona, G. D., Valentine, L. E., Morris, K. & Ritchie, E. G. 2020b. On the right track: placement of camera traps on roads improves detection of predators and shows non-target impacts of feral cat baiting. *Wildlife Research,* 47**,** 557-569.

Zhuo, Y., Xu, W., Wang, M., Chen, C., da Silva, A. A., Yang, W., Ruckstuhl, K. E. & Alves, J. 2022. The effect of mining and road development on habitat fragmentation and connectivity of khulan (Equus hemionus) in Northwestern China. *Biological Conservation,* 275**,** 109770.

Zoellick, B. W., Harris, C. E., Kelly, B. T., O'Farrell, T. P., Kato, T. T. & Koopman, M. E. 2002. Movements and home ranges of San Joaquin kit foxes (*vulpes macrotis mutica*) relative to oil-field development. *Western North American Naturalist,* 62**,** 151-159.

zu Ermgassen, S. O. S. E., Baker, J., Griffiths, R. A., Strange, N., Struebig, M. J. & Bull, J. W. 2019. The ecological outcomes of biodiversity offsets under “no net loss” policies: A global review. *Conservation Letters,* 12**,** e12664.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. 2009. *Mixed effects models and extensions in ecology with R,* New York, Springer.


Woodie Woodie 44

Appendices

Appendix A: Supplementary material for Chapter 2

Table A1: The describing characteristics of each mining camp used to identify reference sites. The De Grey mining camp size and capacity includes the cattle station (Indee) buildings which were constructed from 1962.

Mining camp	**Year constructed**	**Size (ha)**	**Capacity (people)**	**NVIS Major Vegetation Subgroup**	**Topographic ruggedness index** median (IQR)	**Drainage line distance (m)** mean ± S.E.
Abydos	2013	17.11	160	Hummock grassland	0.375 (0.250 – 0.625)	512.98 ± 31.88
Cloudbreak	2008	60.87	1785	Mulga (*Acacia aneura*) woodlands +/- tussock grass +/- forbs	0.500 (0.250 – 0.625)	212.85 ± 18.00
De Grey (Indee)	2012 (1962)	21.79	114	Other sparse shrublands and sparse heathlands	0.375 (0.125 – 0.625)	2156.26 ± 25.14
Eliwana	2020	40.66	850	Mulga (*Acacia aneura*) woodlands +/- tussock grass +/- forbs	0.500 (0.375 – 0.750)	119.64 ± 14.83
Kantarma	2011	52.89	1852	Mulga (*Acacia aneura*) woodlands +/- tussock grass +/- forbs	0.500 (0.375 – 0.625)	210.03 ± 22.58
Roy Hill	2012	73.95	2500	Hummock grassland	0.500 (0.375 – 0.750)	249.19 ± 19.75
Solomon	2012	62.31	1776	Hummock grassland	0.500 (0.250 – 0.625)	183.66 ± 15.37
Woodie	2009	44.71	466	Hummock grassland	0.375 (0.250 – 0.625)	82.89 ± 10.02

Appendix A1

Mining camp definition

We define mining camps as the area of the mining footprint which accommodates staff and, in all cases, includes any available dining, sleeping, water treatment, or leisure infrastructure (e.g., gymnasiums, pools, tennis courts, lawn, or gardens). This does not include active mining areas where mineral extraction and machinery operate, vehicle washing bays, or large waste landfills. These excluded areas likely attract wildlife (e.g., due to resources such as food and water; Newsome et al., 2013a), or deter wildlife (e.g., due to disturbances such as artificial light or noise; Kight and Swaddle, 2011, Berger et al., 2020), but we focus primarily on mining camps in this study as they are often targeted for animal management—including feral cat (*Felis catus*), dingo (*Canis lupus dingo*), and rodent (*Rodentia* spp.) eradication, as well as dingo and livestock exclusion (e.g., by fencing)—due to a higher chance of human-wildlife conflict. Mining camps contain several potential resources including food waste, water, vegetation, shelter, and structural complexity (e.g., drain culverts and buildings) which may attract animals (Newsome et al., 2013b). The De Grey mining camp is constructed next to a cattle station homestead, so this extended footprint (including buildings belonging to the station) was included in the monitoring area of this camp. Two mining camps were surrounded by high exclusion fences to keep out livestock, but smaller animals could still move through the fence. Sites covered varying geographic locations and environmental characteristics across the Pilbara (Figure 2.1, Table A1). All landscapes were located on cattle stations, including mining camps.

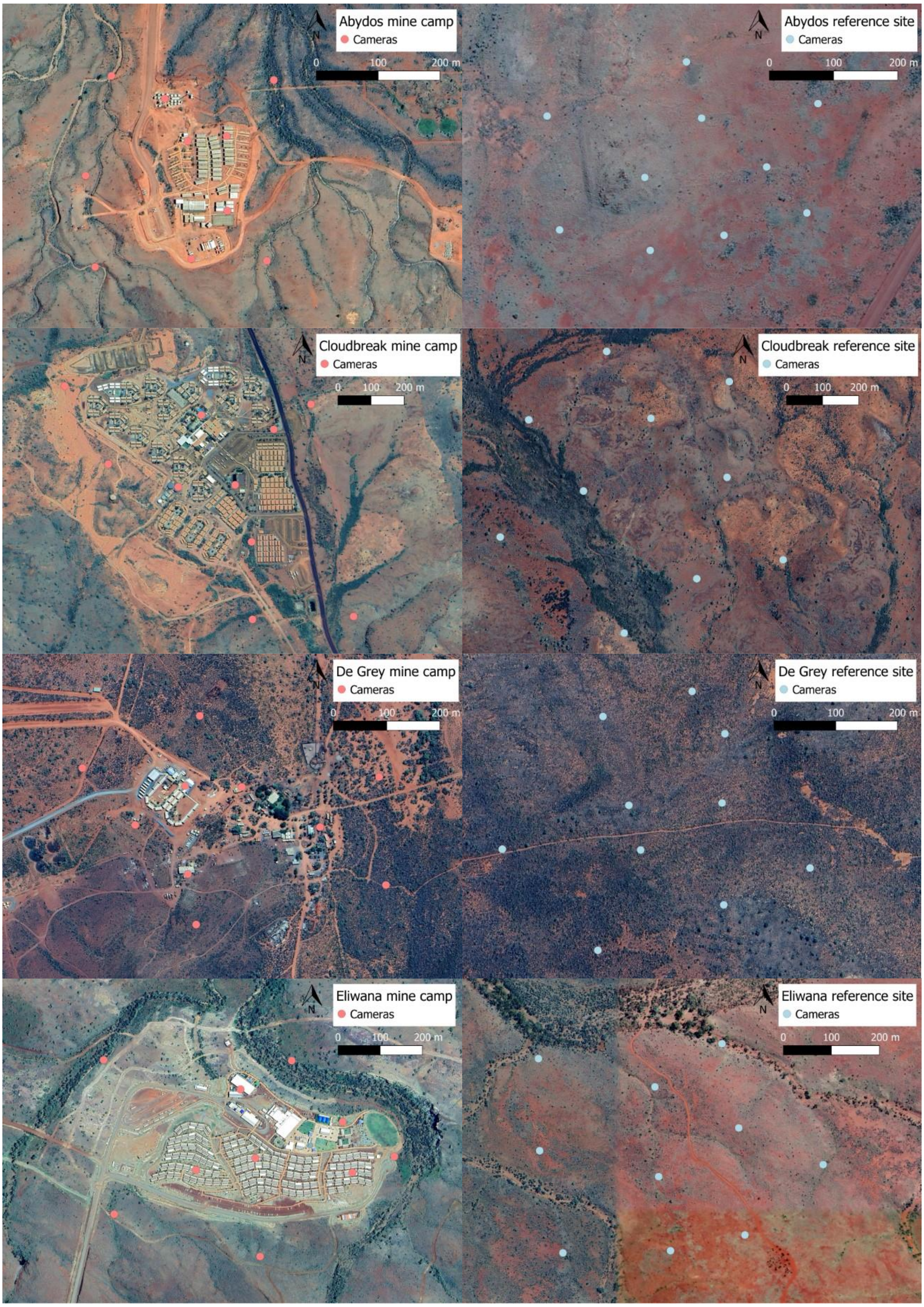


Figure A1: Camera placement for the Abydos, Cloudbreak, De Grey, and Eliwana mining camps and reference sites. Cameras at mining camps are represented by red points and cameras at reference sites are represented by blue points. Mining camps are shown in the left column and the matching reference sites are shown in the right column. Google satellite imagery was used here, accessed from QGIS (Map data ©2015 Google).

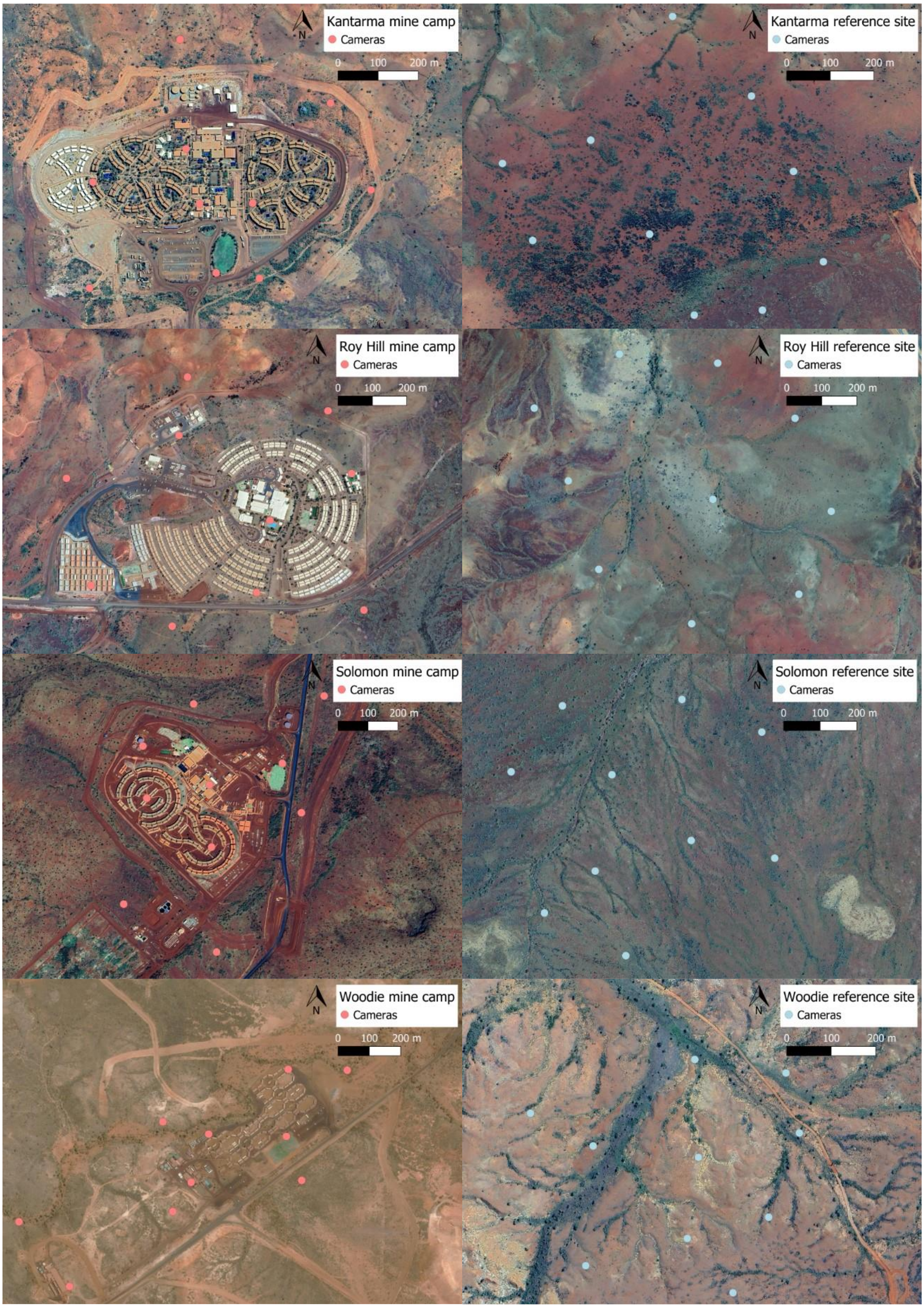


Figure A2: Camera placement for the Kantarma, Roy Hill, Solomon, and Woodie mining camps and reference sites. Cameras at mining camps are represented by red points and cameras at reference sites are represented by blue points. Mining camps are shown in the left column and the matching reference sites are shown in the right column. Google satellite imagery was used here, accessed from QGIS (Map data ©2015 Google).

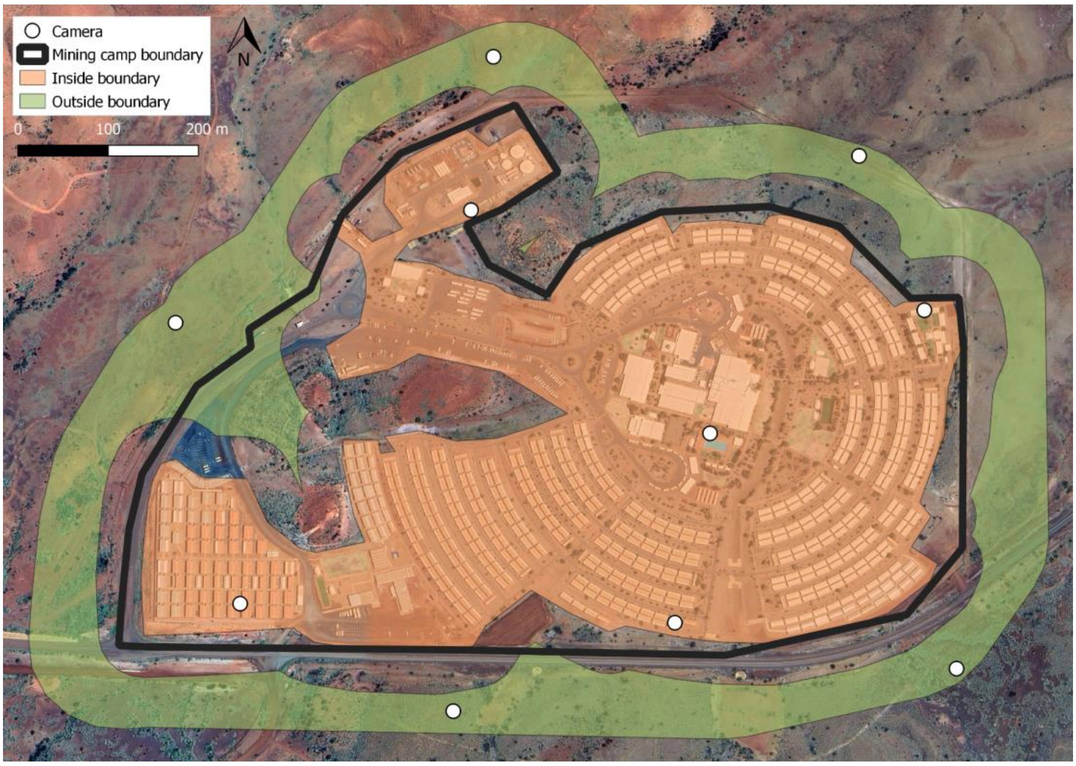


Figure A3: An example of the areas classed as inside mining camps (< 5 m from infrastructure; orange) and outside mining camps (> 50 m but < 100 m from infrastructure; green), at the Roy Hill mining camp where cameras were randomly placed. Camera locations are shown as white points (*n* = 5 in each area), and the mining camp boundary as a black line.

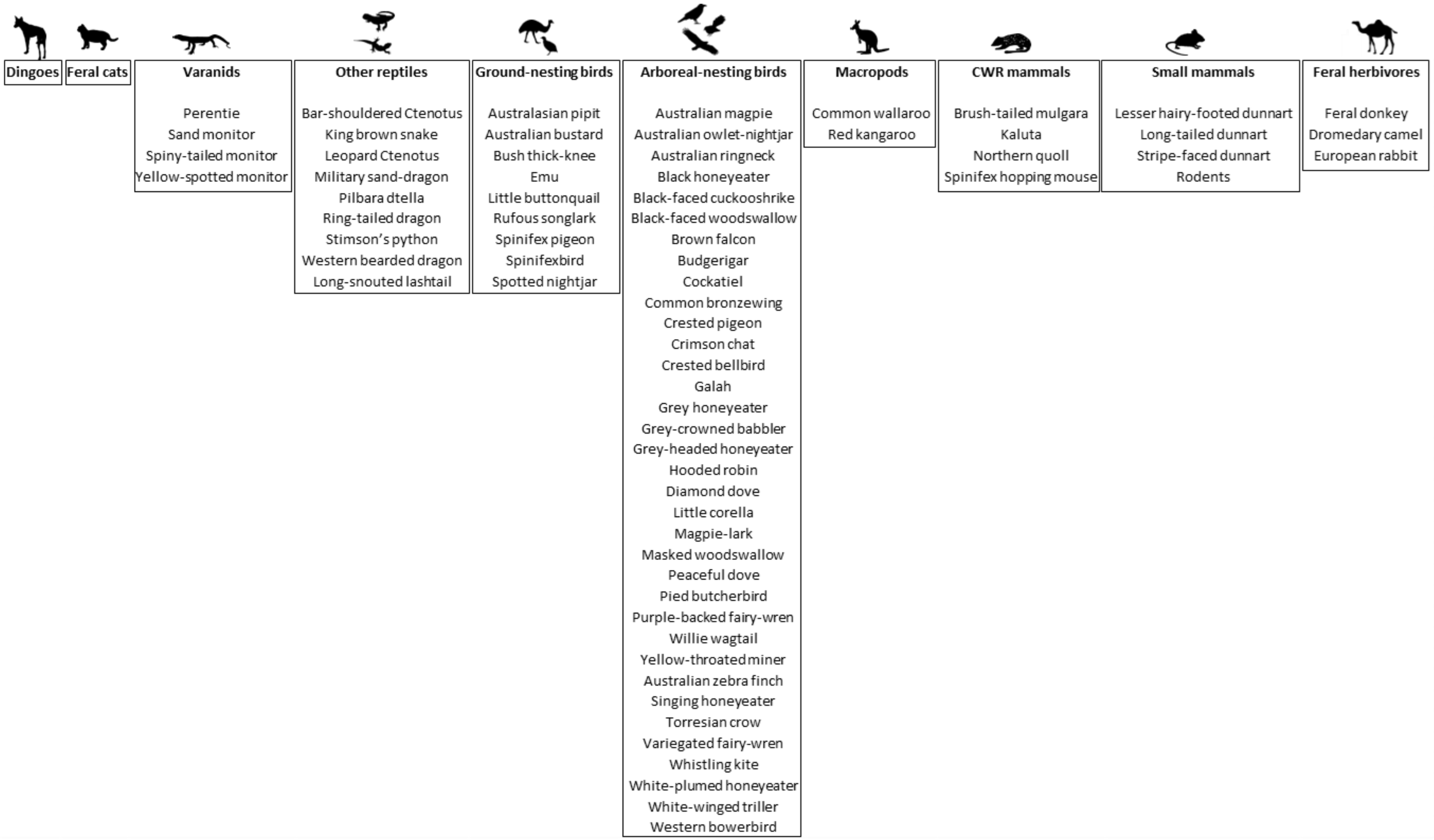
Appendix A2

Landscape selection

Given the high density of mining infrastructure in the Pilbara region (Environmental Protection Authority, 2014), finding independent reference landscapes was challenging. Thus, potential reference landscapes were placed ~ 20 km away from their paired mining camp and > 5 km from active mining disturbance, excluding roads for access, to ensure they were independent of mining camps and to limit detecting animals using natural and disturbed areas. Suitable reference landscapes had to have 1) a median topographic ruggedness index (TRI) within the inter-quartile range of the mining camp, and 2) a mean distance from drainage lines (e.g., creeks, rivers) which fell within the mean ± S.E. of the mining camp (all drainage lines close to our sites were dry during monitoring).

The topographic ruggedness index (TRI) is defined as the difference in elevation between a cell and the eight cells surrounding it (Riley et al., 1999). To create topographic ruggedness index rasters for each site, we sourced high-resolution radiometric terrain-corrected Digital Elevation Models (12.5 m scale) (ASF DAAC, 2022), and used the 'Terrain Ruggedness Index' function in QGIS (QGIS Development Team, 2020). We calculated the median TRI for each mining camp and potential reference site using the "extract" function of the 'raster' package in R (Hijmans et al., 2015).

To calculate the average distance from drainage lines for mining camps and potential reference sites, we downloaded the "Surface Hydrology Lines (National)" vector layer from Geoscience Australia (Crossman and Li, 2015). We converted this vector layer to a distance raster using the "rasterize" function in the 'raster' package in R. Each resulting cell of the raster (100 × 100 m) reflected the mean distance from a drainage lines. We calculated average distances from drainage lines for mining camps and potential reference sites by using the "extract" function in the 'raster' package in R (Hijmans et al., 2015).



Dingoes

Feral cats

Varanids
- Perentie
- Sand monitor
- Spiny-tailed monitor
- Yellow-spotted monitor

Other reptiles
- Bar-shouldered Ctenotus
- King brown snake
- Leopard Ctenotus
- Military sand-dragon
- Pilbara dtella
- Ring-tailed dragon
- Stimson's python
- Western bearded dragon
- Long-snouted lashtail

Ground-nesting birds
- Australasian pipit
- Australian bustard
- Bush thick-knee
- Emu
- Little buttonquail
- Rufous songlark
- Spinifex pigeon
- Spinifexbird
- Spotted nightjar

Arboreal-nesting birds
- Australian magpie
- Australian owlet-nightjar
- Australian ringneck
- Black honeyeater
- Black-faced cuckooshrike
- Black-faced woodswallow
- Brown falcon
- Budgerigar
- Cockatiel
- Common bronzewing
- Crested pigeon
- Crimson chat
- Crested bellbird
- Galah
- Grey honeyeater
- Grey-crowned babbler
- Grey-headed honeyeater
- Hooded robin
- Diamond dove
- Little corella
- Magpie-lark
- Masked woodswallow
- Peaceful dove
- Pied butcherbird
- Purple-backed fairy-wren
- Willie wagtail
- Yellow-throated miner
- Australian zebra finch
- Singing honeyeater
- Torresian crow
- Variegated fairy-wren
- Whistling kite
- White-plumed honeyeater
- White-winged triller
- Western bowerbird

Macropods
- Common wallaroo
- Red kangaroo

CWR mammals
- Brush-tailed mulgara
- Kaluta
- Northern quoll
- Spinifex hopping mouse

Small mammals
- Lesser hairy-footed dunnart
- Long-tailed dunnart
- Stripe-faced dunnart
- Rodents

Feral herbivores
- Feral donkey
- Dromedary camel
- European rabbit

Figure A4: The defined animal groups and the species that they include. See Table A2 for corresponding species names.

Appendix A3

Species functional traits

Animal functional traits collected were body mass (g), mean number of offspring per litter, primary dietary niche (e.g., vertivore, invertivore, nectarivore), primary lifestyle (e.g., terrestrial, arboreal), leg development (e.g., biped, quadruped), locomotion (e.g., cursorial, volant), primary diel activity (e.g., nocturnal, diurnal), reproduction method (i.e., oviparous, viviparous), and temperature regulation (i.e., endothermic, ectothermic).

Dietary data and predator-prey networks

We collated dietary information for all predators from published diet databases (Kissling et al., 2014, Tobias et al., 2022, Middleton et al., 2021, Wilman et al., 2014, Uetz and Etzold, 1996). For non-collated diets and where predation examples were limited for the region or species, we sourced information from published literature. This was done through targeted literature searches including the species name and “diet”. Where dietary information was limited geographically, we made inferences about likely prey in the Pilbara based on available dietary information and body mass. We identified all potential predatory links between co-occurring predators and prey across all landscapes and treatments. Links between predators and prey were realised if 1) there was empirical evidence of prior or potential predation, and 2) both the predator and prey species were present in the landscape.

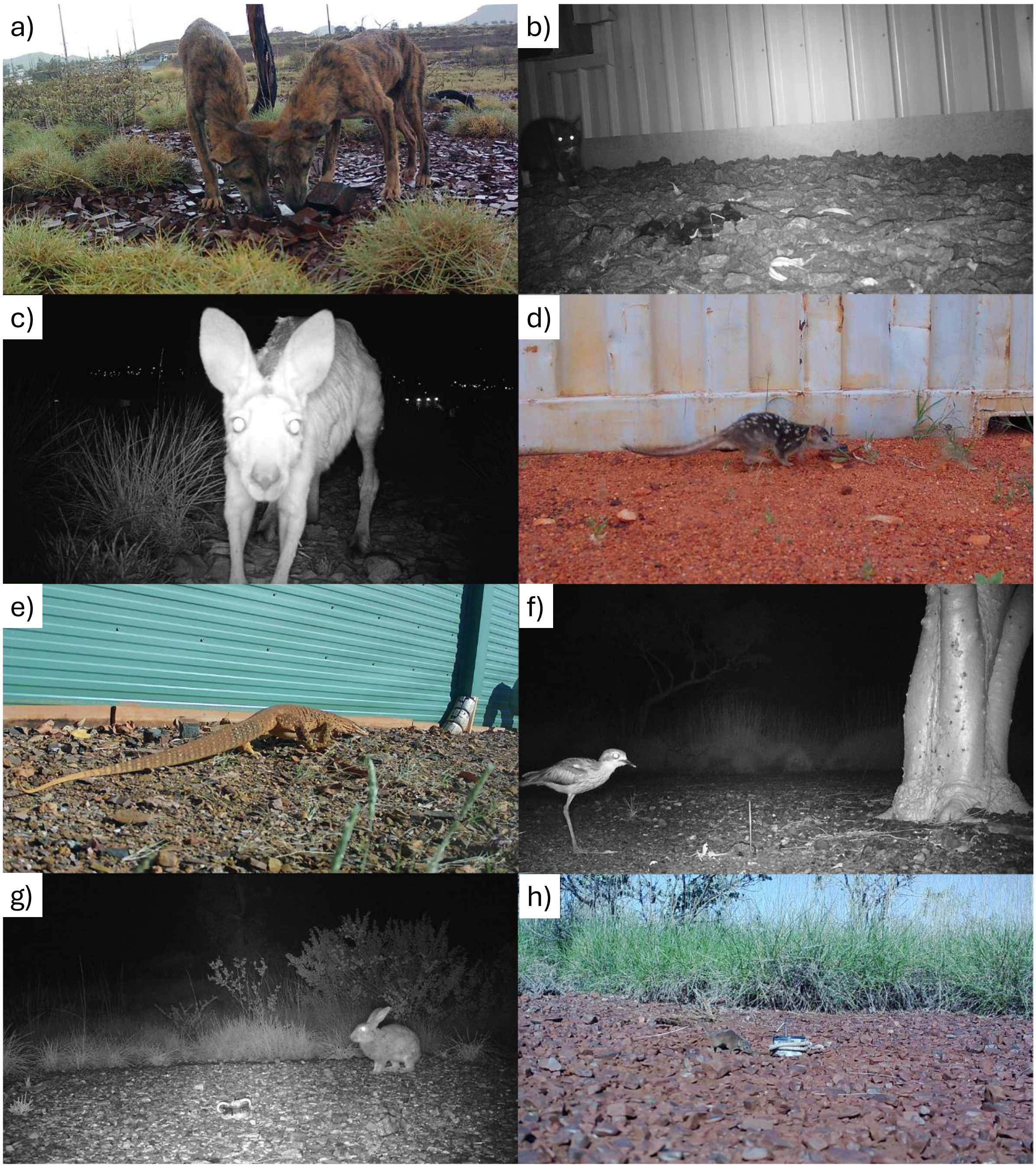


Figure A5: Some examples of species detected on camera traps inside and outside mining camps: a) dingoes (*Canis lupus dingo*), b) feral cat (*Felis catus*), c) common wallaroo (*Osphranter robustus*), d) northern quoll (*Dasyurus hallucatus*), e) yellow-spotted monitor (*Varanus panoptes*), f) bush thick-knee (*Burhinus grallarius*), g) European rabbit (*Oryctolagus cuniculus*), and h) kaluta (*Dasykaluta rosamondae*).

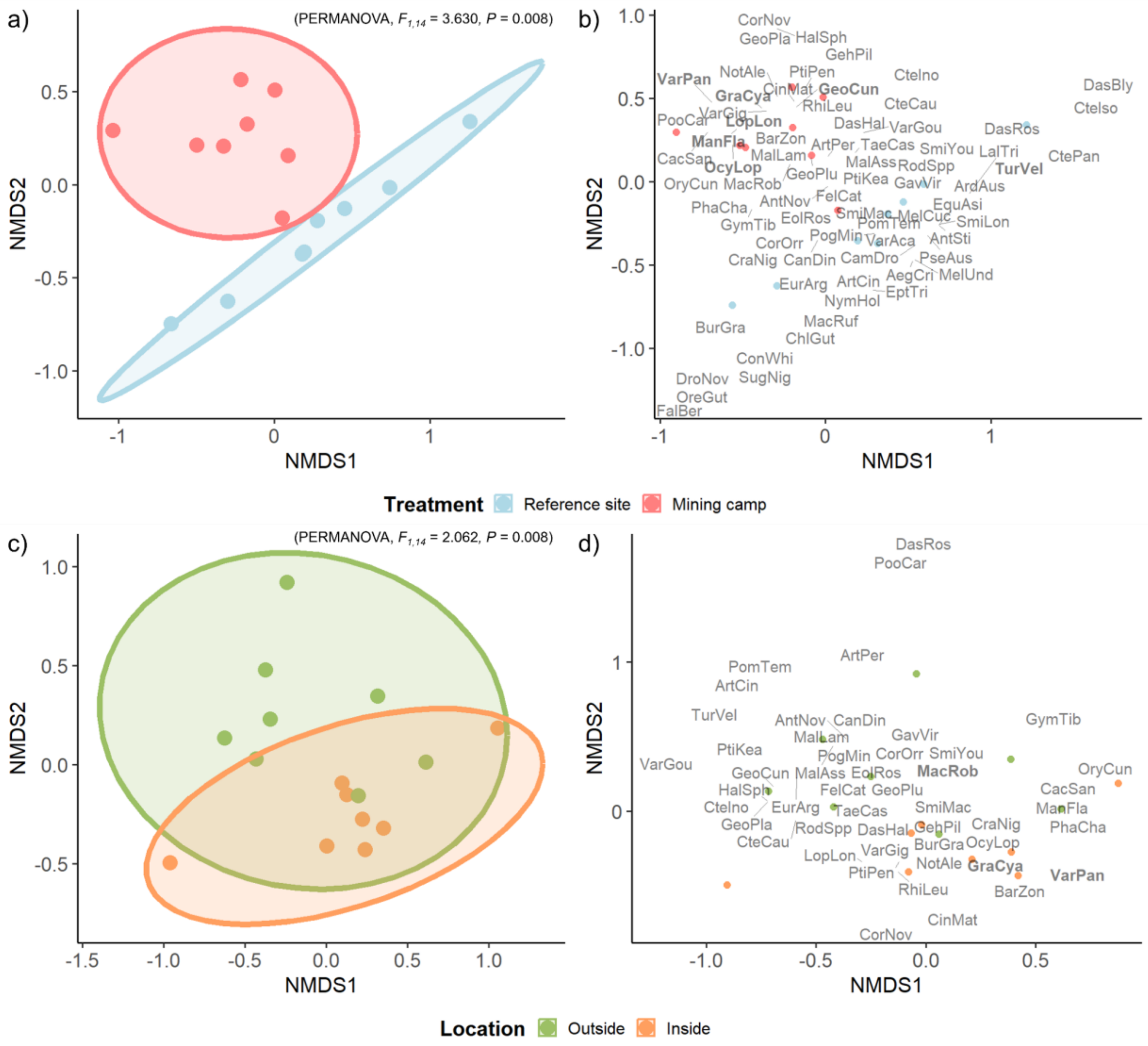


Figure A6: Non-metric multidimensional scaling (NMDS) plots showing species dissimilarities from camera trap data, with a) and c) showing ordinations between mining camps and reference sites, and inside versus outside mining camps, with 95% confidence ellipses. Points represent the species composition of a site, with closer points indicating similar compositions. Species codes are overlaid in b) and d). Axes (NMDS1 and NMDS2) were calculated using Bray-Curtis dissimilarity. Mining camps are shown in red, reference sites in blue, inside mining camps in orange, and outside mining camps in green. PERMANOVA results are located atop panels a) and c). See Table A2 for species codes.

Table A2: An index for species codes used during non-metric multidimensional scaling (NMDS) ordinations illustrating the dissimilarities in species compositions based on camera trapping data between mining camps and reference sites, and inside and outside mining camps.

NMDS Code	Common name	Species name
AegCri	Australian owlet-nightjar	*Aegotheles cristatus*
AntNov	Australasian pipit	*Anthus novaeseelandiae*
AntSti	Stimson's python	*Antaresia stimsoni*
ArdAus	Australian bustard	*Ardeotis australis*
ArtCin	Black-faced woodswallow	*Artamus cinereus*
ArtPer	Masked woodswallow	*Artamus personatus*
BarZon	Australian ringneck	*Barnardius zonarius*
BurGra	Bush thick-knee	*Burhinus grallarius*
CacSan	Little corella	*Cacatua sanguinea*
CamDro	Dromedary camel	*Camelus dromedarius*
CanDin	Dingo	*Canis lupus dingo*
ChlGut	Western bowerbird	*Chlamydera guttata*
CinMat	Rufous songlark	*Cincloramphus mathewsi*
ConWhi	Grey honeyeater	*Conopophila whitei*
CorNov	Black-faced cuckooshrike	*Coracina novaehollandiae*
CorOrr	Torresian crow	*Corvus orru*
CraNig	Pied butcherbird	*Cracticus nigrogularis*
CteCau	Ring-tailed dragon	*Ctenophorus caudicinctus*
CteIno	Bar-shouldered Ctenotus	*Ctenotus inornatus*
CteIso	Military sand-dragon	*Ctenophorous isolepsis*
CtePan	Leopard Ctenotus	*Ctenotus pantherinus*
DasBly	Brush-tailed mulgara	*Dasycercus blythi*
DasHal	Northern quoll	*Dasyurus hallucatus*
DasRos	Kaluta	*Dasykaluta rosamondae*
DroNov	Emu	*Dromaius novaehollandiae*
EolRos	Galah	*Eolophus roseicapilla*
EptTri	Crimson chat	*Epthianura tricolor*
EquAsi	Feral donkey	*Equus asinus*
EurArg	Spotted nightjar	*Eurostopodus argus*
FalBer	Brown falcon	*Falco berigora*
FelCat	Feral cat	*Felis catus*
GavVir	Singing honeyeater	*Gavicalis virescens*
GehPil	Pilbara dtella	*Gehyra pilbara*
GeoCun	Diamond dove	*Geopelia cuneata*
GeoPla	Peaceful dove	*Geopelia placida*
GeoPlu	Spinifex pigeon	*Geophaps plumifera*
GraCya	Magpie-lark	*Grallina cyanoleuca*
GymTib	Australian magpie	*Gymnorhina tibicen*
HalSph	Whistling kite	*Haliastur sphenurus*
LalTri	White-winged triller	*Lalage tricolor*
LopLon	Long-snouted lashtail	*Lophognathus longirostris*
MacRob	Common wallaroo	*Osphranter robustus*
MacRuf	Red kangaroo	*Osphranter rufus*
MalAss	Purple-backed fairy-wren	*Malurus assimilis*
MalLam	Variegated fairy-wren	*Malurus lamberti*
ManFla	Yellow-throated miner	*Manorina flavigula*
MelCuc	Hooded robin	*Melanodryas cucullata*
MelUnd	Budgerigar	*Melopsittacus undulatus*
NotAle	Spinifex hopping mouse	*Notomys alexis*
NymHol	Cockatiel	*Nymphicus hollandicus*

OcyLop	Crested pigeon	*Ocyphaps lophotes*
OreGut	Crested bellbird	*Oreoica gutturalis*
OryCun	European rabbit	*Oryctolagus cuniculus*
PhaCha	Common bronzewing	*Phaps chalcoptera*
PogMin	Western bearded dragon	*Pogona minor*
PomTem	Grey-crowned babbler	*Pomatostomus temporalis*
PooCar	Spinifexbird	*Poodytes carteri*
PseAus	King brown snake	*Pseudechis australis*
PtiKea	Grey-headed honeyeater	*Ptilotula keartlandi*
PtiPen	White-plumed honeyeater	*Ptilotula penicillata*
RhiLeu	Willie wagtail	*Rhipidura leucophrys*
RodSpp	Rodent	*Rodentia spp.*
SmiLon	Long-tailed dunnart	*Sminthopsis longicaudata*
SmiMac	Stripe-faced dunnart	*Sminthopsis macroura*
SmiYou	Lesser hairy-footed dunnart	*Sminthopsis youngsoni*
SugNig	Black honeyeater	*Sugomel nigrum*
TaeCas	Australian zebra finch	*Taeniopygia castanotis*
TurVel	Little buttonquail	*Turnix velox*
VarAca	Spiny-tailed monitor	*Varanus acanthurus*
VarGig	Perentie	*Varanus giganteus*
VarGou	Sand monitor	*Varanus gouldii*
VarPan	Yellow-spotted monitor	*Varanus panoptes*

Table A3: Raw camera detection events for each species and trap nights from each mining camp and reference landscape.

Treatment	Mining camps							
Mine site	Abydos	Cloudbreak	De Grey	Eliwana	Kantarma	Roy Hill	Solomon	Woodie
Trap nights	361	276	304	342	300	452	297	425
Australasian pipit	0	0	0	0	0	3	0	6
Australian bustard	0	0	0	0	0	0	0	0
Australian magpie	7	22	0	7	6	6	0	0
Australian owlet-nightjar	0	0	0	0	0	0	0	0
Australian ringneck	0	0	0	0	0	0	1	0
Australian zebra finch	1	0	1	0	0	0	2	5
Bar-shouldered Ctenotus	12	0	1	0	0	0	0	1
Black honeyeater	0	0	0	0	0	0	0	0
Black-faced cuckooshrike	0	0	0	2	0	0	0	0
Black-faced woodswallow	0	0	0	0	0	0	0	1
Brown falcon	0	0	0	0	0	0	0	0
Brush-tailed mulgara	0	0	0	0	0	0	0	0
Budgerigar	0	0	0	0	0	0	0	0
Bush thick-knee	0	0	2	0	0	0	0	0
Cockatiel	0	0	0	0	0	0	0	0
Common bronzewing	0	4	6	0	0	0	0	0
Common wallaroo	3	5	28	2	4	3	3	5
Crested bellbird	0	0	0	0	0	0	0	0
Crested pigeon	0	4	17	0	34	4	13	1
Crimson chat	0	0	0	0	0	0	0	0
Diamond dove	25	0	3	10	0	3	0	98
Dingo	2	0	0	10	0	13	17	0
Dromedary camel	0	0	0	0	0	0	0	0
Emu	0	0	0	0	0	0	0	0
European rabbit	0	3	0	0	13	2	0	0
Feral cat	2	0	3	7	1	0	6	10
Feral donkey	0	0	0	0	0	0	0	0
Galah	0	0	4	9	0	1	0	0
Grey honeyeater	0	0	0	0	0	0	0	0
Grey-crowned babbler	0	0	0	1	0	0	0	0
Grey-headed honeyeater	1	0	0	0	0	0	1	0
Hooded robin	0	0	0	0	0	0	0	0
Kaluta	0	0	0	0	0	8	0	0
King brown snake	0	0	0	0	0	0	0	0
Leopard Ctenotus	0	0	0	0	0	0	0	0
Lesser hairy-footed dunnart	0	0	2	0	0	1	0	0
Little buttonquail	1	0	0	1	0	0	0	0
Little corella	0	0	0	0	19	0	0	0
Long-snouted lashtail	12	1	0	6	1	0	1	2
Long-tailed dunnart	0	0	0	0	0	0	0	0

Magpie-lark	113	30	55	4	54	125	36	227
Masked woodswallow	0	0	0	0	0	2	1	0
Military sand-dragon	0	0	0	0	0	0	0	0
Northern quoll	24	0	24	0	0	2	0	0
Peaceful dove	0	0	0	0	0	0	0	1
Perentie	11	0	1	0	4	1	0	2
Pied butcherbird	0	0	0	0	2	0	2	1
Pilbara dtella	1	0	0	0	0	0	0	0
Purple-backed fairy-wren	0	0	0	0	0	0	6	0
Red kangaroo	0	0	0	0	0	0	0	0
Ring-tailed dragon	29	0	0	0	0	0	1	1
Rodent	16	0	47	36	26	2	19	17
Rufous songlark	0	0	0	0	0	0	2	1
Sand monitor	2	0	0	0	0	0	0	0
Singing honeyeater	0	0	1	0	0	1	2	0
Spinifex hopping mouse	0	0	1	0	0	0	0	0
Spinifex pigeon	51	0	4	3	8	6	22	17
Spinifexbird	0	0	0	0	0	3	0	0
Spiny-tailed monitor	0	0	0	0	0	0	0	0
Spotted nightjar	0	0	0	0	0	0	1	3
Stimson's python	0	0	0	0	0	0	0	0
Stripe-faced dunnart	0	0	2	1	6	0	15	0
Torresian crow	2	1	2	6	3	1	0	7
Variegated fairy-wren	0	0	0	0	0	0	1	0
Western bearded dragon	0	0	0	0	0	0	3	0
Western bowerbird	0	0	0	0	0	0	0	0
Whistling kite	0	0	0	0	0	0	0	1
White-plumed honeyeater	0	0	4	0	0	0	2	13
White-winged triller	0	0	0	0	0	0	0	0
Willie wagtail	19	3	6	7	0	0	1	332
Yellow-spotted monitor	0	5	5	0	14	13	0	8
Yellow-throated miner	9	109	13	0	40	14	26	5

Treatment	Reference landscapes							
Mine site	Abydos	Cloudbreak	De Grey	Eliwana	Kantarma	Roy Hill	Solomon	Woodie
Trap nights	297	320	306	340	301	267	259	419
Australasian pipit	0	0	0	0	0	13	0	1
Australian bustard	0	0	0	0	0	0	0	1
Australian magpie	0	9	0	0	5	5	1	2
Australian owlet-nightjar	0	0	0	6	0	1	2	0
Australian ringneck	0	0	0	0	0	0	0	0
Australian zebra finch	0	0	0	1	0	3	0	5
Bar-shouldered Ctenotus	0	0	4	0	0	0	0	2
Black honeyeater	0	0	0	0	1	0	0	0
Black-faced cuckooshrike	0	0	0	0	0	0	3	0
Black-faced woodswallow	0	0	0	0	0	0	0	0
Brown falcon	0	1	0	0	0	0	0	0

Brush-tailed mulgara	0	0	78	0	0	0	0	0
Budgerigar	17	0	1	0	0	15	7	0
Bush thick-knee	0	7	0	0	4	0	0	0
Cockatiel	0	0	0	0	0	16	0	0
Common bronzewing	0	1	0	0	2	0	0	0
Common wallaroo	8	2	0	0	0	2	2	1
Crested bellbird	0	12	0	0	3	0	0	0
Crested pigeon	0	1	0	0	1	0	0	0
Crimson chat	0	0	0	0	0	2	0	0
Diamond dove	0	0	0	0	1	2	0	0
Dingo	4	9	0	9	10	2	3	1
Dromedary camel	5	0	0	0	0	0	0	0
Emu	0	14	0	0	5	0	0	0
European rabbit	0	5	0	0	0	0	0	0
Feral cat	2	1	2	5	4	5	6	5
Feral donkey	0	0	0	8	0	0	0	0
Galah	0	0	0	0	0	0	4	0
Grey honeyeater	0	0	0	0	1	0	0	0
Grey-crowned babbler	0	0	0	2	0	0	0	0
Grey-headed honeyeater	0	0	0	0	0	0	1	0
Hooded robin	0	0	0	7	0	0	0	0
Kaluta	0	0	61	0	0	0	3	2
King brown snake	1	0	0	1	0	0	0	0
Leopard Ctenotus	0	0	2	1	0	0	0	0
Lesser hairy-footed dunnart	0	0	10	7	0	0	0	0
Little buttonquail	6	0	60	1	0	2	3	36
Little corella	0	0	0	0	0	0	0	0
Long-snouted lashtail	0	0	0	0	0	0	0	0
Long-tailed dunnart	0	0	0	10	0	0	0	0
Magpie-lark	0	0	0	6	2	2	0	0
Masked woodswallow	0	0	0	0	0	0	0	2
Military sand-dragon	0	0	24	0	0	0	0	3
Northern quoll	16	0	0	1	0	0	0	0
Peaceful dove	0	0	0	0	0	0	0	0
Perentie	0	0	0	0	1	0	0	0
Pied butcherbird	0	2	0	0	9	1	2	0
Pilbara dtella	0	0	0	0	0	0	0	0
Purple-backed fairy-wren	0	0	0	1	0	0	0	0
Red kangaroo	0	2	0	0	2	3	4	0
Ring-tailed dragon	0	0	2	1	0	1	0	2
Rodent	3	0	153	95	2	16	24	27
Rufous songlark	0	0	0	0	0	0	0	0
Sand monitor	1	0	0	0	0	0	0	0
Singing honeyeater	4	0	5	1	0	0	1	0
Spinifex hopping mouse	0	0	0	0	0	0	0	0
Spinifex pigeon	23	4	0	2	0	7	0	0
Spinifexbird	0	0	0	0	0	0	0	0

Spiny-tailed monitor	2	0	0	0	0	0	0	0
Spotted nightjar	2	24	0	0	0	0	1	2
Stimson's python	0	0	0	1	0	0	0	0
Stripe-faced dunnart	2	0	0	9	2	1	2	18
Torresian crow	0	28	0	34	5	5	1	2
Variegated fairy-wren	0	0	0	0	0	0	0	0
Western bearded dragon	1	0	0	1	1	0	1	2
Western bowerbird	0	1	0	0	0	0	1	0
Whistling kite	0	0	0	0	0	0	0	0
White-plumed honeyeater	0	0	0	0	0	0	0	1
White-winged triller	0	0	0	0	0	0	0	1
Willie wagtail	0	0	0	5	2	2	1	1
Yellow-spotted monitor	0	0	0	0	0	0	0	0
Yellow-throated miner	0	2	1	0	0	0	2	3

Table A4: Model outputs from GLMMs comparing animal group detections between mining camps and reference sites (intercept), and inside and outside (intercept) mining camps. Models which were significant at the $P < 0.05$ level have an asterisk following the *P* value.

Treatment	Model	Fixed effect	Estimate	Std. error	*Z* value	*P* value
Mining camp vs. reference site	Dingoes	Reference (intercept)	-4.65	0.56	-8.27	< 0.001
		Mine	-0.61	0.76	-0.81	0.419
	Feral cats	Reference (intercept)	-4.54	0.28	-16.33	< 0.001
		Mine	-0.20	0.34	-0.59	0.557
	Varanids	Reference (intercept)	-6.99	0.79	-8.90	< 0.001
		Mine	2.79	0.65	4.29	< 0.001*
	Other reptiles	Reference (intercept)	-4.87	0.58	-8.46	< 0.001
		Mine	0.04	0.79	0.06	0.956
	Ground-nesting birds	Reference (intercept)	-2.83	0.37	-7.56	< 0.001
		Mine	-0.69	0.54	-1.29	0.197
	Arboreal-nesting birds	Reference (intercept)	-2.37	0.24	-9.69	< 0.001
		Mine	1.56	0.34	4.58	< 0.001*
	Macropods	Reference (intercept)	-4.86	0.40	-12.28	< 0.001
		Mine	0.53	0.52	1.01	0.314
	CWR mammals	Reference (intercept)	-5.42	1.08	-5.03	< 0.001
		Mine	-0.78	0.92	-0.86	0.393
	Small mammals	Reference (intercept)	-2.95	0.62	-4.75	< 0.001
		Mine	-0.34	0.48	-0.71	0.480
	Feral herbivores	Reference (intercept)	-6.88	1.46	-4.70	< 0.001
		Mine	-0.30	1.54	-0.20	0.845
Inside vs. outside mining camp	Dingoes	Outside (intercept)	-6.95	2.87	-2.42	0.015
		Inside	-1.66	2.11	-0.78	0.433
	Feral cats	Outside (intercept)	-4.43	0.46	-9.67	< 0.001
		Inside	-1.42	0.46	-3.09	0.002*
	Varanids	Outside (intercept)	-5.85	0.80	-7.29	< 0.001
		Inside	2.03	0.85	2.38	0.017*
	Other reptiles	Outside (intercept)	-5.21	0.77	-6.81	< 0.001
		Inside	0.44	0.64	0.69	0.488
	Ground-nesting birds	Outside (intercept)	-3.15	0.46	-6.86	< 0.001
		Inside	-1.15	0.37	-3.09	0.002*
	Arboreal-nesting birds	Outside (intercept)	-1.30	0.34	-3.78	< 0.001
		Inside	0.55	0.44	1.25	0.211
	Macropods	Outside (intercept)	-3.68	0.35	-10.39	< 0.001
		Inside	-2.39	0.47	-5.08	< 0.001*
	CWR mammals	Outside (intercept)	-9.37	5.10	-1.84	0.066
		Inside	0.71	0.94	0.76	0.446
	Small mammals	Outside (intercept)	-3.32	0.65	-5.12	< 0.001
		Inside	-0.50	0.78	-0.64	0.521
	Feral herbivores	Outside (intercept)	-7.09	1.78	-3.99	< 0.001
		Inside	-0.25	0.47	-0.53	0.599

Table A5: Model outputs from GLMMs comparing Shannon diversity, functional richness, and functional dispersion, between (1) mining camps and reference sites (intercept), and (2) inside and outside (intercept) mining camps. Models which were significant at the $P < 0.05$ level have an asterisk following the *P* value.

Method	Treatment	Measure	Fixed effect	Estimate	Std. error	*Z* value	*P* value
Shannon diversity	Mining camp vs. reference site (1)	Total	Reference (intercept)	-3.41	0.15	-22.89	< 0.001
			Mine	-0.35	0.21	-1.68	0.092
		Mammal	Reference (intercept)	-4.65	0.12	-38.72	< 0.001
			Mine	-0.29	0.08	-3.52	< 0.001*
		Bird	Reference (intercept)	-4.00	0.20	-19.56	< 0.001
			Mine	-0.24	0.29	-0.83	0.406
		Reptile	Reference (intercept)	-5.01	0.18	-27.70	< 0.001
			Mine	-0.09	0.24	-0.36	0.719
	Inside vs. outside mining camp (2)	Total	Outside (intercept)	-2.89	0.16	-18.54	< 0.001
			Inside	-0.84	0.16	-5.19	< 0.001*
		Mammal	Outside (intercept)	-3.95	0.11	-34.85	< 0.001
			Inside	-0.67	0.15	-4.43	< 0.001*
		Bird	Outside (intercept)	-3.35	0.15	-22.72	< 0.001
			Inside	-0.78	0.17	-4.58	< 0.001*
		Reptile	Outside (intercept)	-4.84	0.15	-32.46	< 0.001
			Inside	0.33	0.11	3.01	0.003*

Method	Treatment	Measure	Fixed effect	Estimate	Std. Error	*T* value	*P* value
Functional richness	1	Total	Reference (intercept)	-6.90	0.21	-32.65	< 0.001
			Mine	-0.26	0.15	-1.80	0.072
	2	Total	Outside (intercept)	-7.22	0.43	-16.77	< 0.001
			Inside	-0.32	0.14	-2.27	0.023*
Functional dispersion	1	Total	Reference (intercept)	-7.56	0.16	-46.83	< 0.001
			Mine	-0.34	0.14	-2.37	0.018*
	2	Total	Outside (intercept)	-6.79	0.09	-73.48	< 0.001
			Inside	-0.03	0.07	-0.43	0.667

Table A6: The mean body mass (g) and number of offspring per year and the proportion of species with each categorical functional trait for each treatment.

Functional trait type	Trait	Landscape treatment		Location treatment	
		Mine	Reference	Inside	Outside
Mean body mass (g)		2580.77	8767.38	1585.76	3570.53
Mean offspring per breeding event		3.82	3.95	4.13	3.47
Dietary niche	Invertivore	0.45	0.44	0.37	0.43
	Omnivore	0.25	0.23	0.30	0.25
	Nectarivore	0.02	0.00	0.00	0.00
	Granivore	0.13	0.11	0.15	0.16
	Vertivore	0.11	0.15	0.11	0.11
	Folivore	0.04	0.08	0.07	0.05
Primary lifestyle	Terrestrial	0.63	0.63	0.73	0.68
	Insessorial	0.24	0.23	0.19	0.17
	Aerial	0.06	0.05	0.00	0.10
	Generalist	0.04	0.08	0.04	0.05
	Arboreal	0.02	0.00	0.04	0.00
Leg development	Biped	0.65	0.63	0.58	0.63
	Quadruped	0.35	0.33	0.42	0.37
	Limbless	0.00	0.03	0.00	0.00
Locomotion	Ambulatory	0.00	0.03	0.00	0.00
	Cursorial	0.31	0.30	0.31	0.34
	Saltatorial	0.04	0.05	0.08	0.05
	Scansorial	0.06	0.03	0.12	0.05
	Undulatory	0.00	0.03	0.00	0.00
	Volant	0.59	0.55	0.50	0.56
Primary diel activity	Cathemeral	0.00	0.03	0.00	0.00
	Crepuscular	0.08	0.08	0.15	0.10
	Diurnal	0.71	0.68	0.69	0.68
	Nocturnal	0.20	0.20	0.15	0.22
Reproduction method	Oviparous	0.80	0.77	0.73	0.76
	Viviparous	0.20	0.23	0.27	0.24
Temperature regulation	Ectotherm	0.16	0.17	0.19	0.15
	Endotherm	0.84	0.83	0.81	0.85

Table A7: The functional traits for each species.

Species	Body mass	Mean offspring	Dietary niche	Primary lifestyle	Leg development	Locomotion	Primary diel activity	Reproduction method	Temperature regulation
Australian Owlet-nightjar	45	3.265	Invertivore	Insessorial	Biped	Volant	Nocturnal	Oviparous	Endotherm
Stimson's Python	349.9	8.5	Invertivore, Vertivore	Terrestrial	Limbless	Undulatory	Nocturnal	Oviparous	Ectotherm
Australasian Pipit	26.4	3.85	Invertivore	Terrestrial	Biped	Volant	Diurnal	Oviparous	Endotherm
Australian Bustard	5500	1.555	Omnivore	Terrestrial	Biped	Volant	Diurnal	Oviparous	Endotherm
Black-faced Woodswallow	37.7	3.5	Invertivore	Aerial	Biped	Volant	Diurnal	Oviparous	Endotherm
Masked Woodswallow	34.7	2.7	Invertivore	Aerial	Biped	Volant	Diurnal	Oviparous	Endotherm
Australian Ringneck	141.6	5	Omnivore	Insessorial	Biped	Volant	Diurnal	Oviparous	Endotherm
Bush Thick-knee	695	2	Invertivore	Terrestrial	Biped	Volant	Nocturnal	Oviparous	Endotherm
Little Corella	472	2.6	Granivore	Terrestrial	Biped	Volant	Diurnal	Oviparous	Endotherm
Dromedary Camel	434000	1	Folivore	Terrestrial	Quadruped	Ambulatory	Diurnal	Viviparous	Endotherm
Dingo	20000	5	Vertivore	Terrestrial	Quadruped	Cursorial	Crepuscular	Viviparous	Endotherm
Western Bowerbird	138.5	2	Omnivore	Insessorial	Biped	Volant	Diurnal	Oviparous	Endotherm
Rufous Songlark	29	3	Invertivore	Terrestrial	Biped	Volant	Diurnal	Oviparous	Endotherm
Grey Honeyeater	9.8	2	Invertivore	Insessorial	Biped	Volant	Diurnal	Oviparous	Endotherm
Black-faced Cuckooshrike	115	2.45	Invertivore	Insessorial	Biped	Volant	Diurnal	Oviparous	Endotherm
Torresian crow	508.45	3.6	Omnivore	Generalist	Biped	Volant	Diurnal	Oviparous	Endotherm
Pied Butcherbird	124.1	3.7	Omnivore	Insessorial	Biped	Volant	Diurnal	Oviparous	Endotherm

Military sand-dragon	25	3	Invertivore	Terrestrial	Quadruped	Cursorial	Diurnal	Oviparous	Ectotherm
Ring-tailed dragon	15.28	5.7	Omnivore	Terrestrial	Quadruped	Cursorial	Diurnal	Oviparous	Ectotherm
Bar-shouldered Ctenotus	5.4	5	Invertivore	Terrestrial	Quadruped	Cursorial	Diurnal	Oviparous	Ectotherm
Leopard Ctenotus	14.73	6	Omnivore	Terrestrial	Quadruped	Cursorial	Cathemeral	Oviparous	Ectotherm
Brush-tailed Mulgara	83.8	6.25	Omnivore	Terrestrial	Quadruped	Cursorial	Nocturnal	Viviparous	Endotherm
Kaluta	32.17	7.32	Omnivore	Terrestrial	Quadruped	Cursorial	Nocturnal	Viviparous	Endotherm
Northern Quoll	538.75	6.595	Omnivore	Terrestrial	Quadruped	Scansorial	Nocturnal	Viviparous	Endotherm
Emu	38440	9.5	Omnivore	Terrestrial	Biped	Cursorial	Diurnal	Oviparous	Endotherm
Galah	300	3	Granivore	Terrestrial	Biped	Volant	Diurnal	Oviparous	Endotherm
Crimson Chat	11	3.165	Invertivore	Generalist	Biped	Volant	Diurnal	Oviparous	Endotherm
Domestic Donkey	325000	1	Folivore	Terrestrial	Quadruped	Ambulatory	Diurnal	Viviparous	Endotherm
Spotted Nightjar	97.5	1	Invertivore	Aerial	Biped	Volant	Nocturnal	Oviparous	Endotherm
Brown Falcon	547.5	2.895	Vertivore	Generalist	Biped	Volant	Diurnal	Oviparous	Endotherm
Domestic Cat	3300	3.69	Vertivore	Terrestrial	Quadruped	Cursorial	Crepuscular	Viviparous	Endotherm
Singing Honeyeater	24	2.145	Invertivore	Insessorial	Biped	Volant	Diurnal	Oviparous	Endotherm
Pilbara dtella	3.6	1	Invertivore	Arboreal	Quadruped	Scansorial	Nocturnal	Oviparous	Ectotherm
Diamond Dove	33	2	Granivore	Terrestrial	Biped	Volant	Diurnal	Oviparous	Endotherm
Peaceful Dove	48.9	2	Granivore	Terrestrial	Biped	Volant	Diurnal	Oviparous	Endotherm
Spinifex pigeon	95	2	Granivore	Terrestrial	Biped	Cursorial	Diurnal	Oviparous	Endotherm
Magpie-lark	88	3.5	Invertivore	Terrestrial	Biped	Volant	Diurnal	Oviparous	Endotherm
Australian Magpie	390	4	Invertivore	Terrestrial	Biped	Volant	Diurnal	Oviparous	Endotherm
Whistling Kite	775	2	Omnivore	Aerial	Biped	Volant	Diurnal	Oviparous	Endotherm
White-winged Triller	25.5	2	Invertivore	Insessorial	Biped	Volant	Diurnal	Oviparous	Endotherm

Long-snouted Lashtail	12.62	5	Invertivore	Terrestrial	Quadruped	Scansorial	Diurnal	Oviparous	Ectotherm
Common Wallaroo	32593.95	1	Folivore	Terrestrial	Biped	Saltatorial	Crepuscular	Viviparous	Endotherm
Red Kangaroo	40285.1	1	Folivore	Terrestrial	Biped	Saltatorial	Crepuscular	Viviparous	Endotherm
Purple-backed Fairy-wren	8	3	Invertivore	Insessorial	Biped	Volant	Diurnal	Oviparous	Endotherm
Variegated Fairy-wren	7.9	3.5	Invertivore	Insessorial	Biped	Volant	Diurnal	Oviparous	Endotherm
Yellow-throated miner	50.7	2.925	Invertivore	Insessorial	Biped	Volant	Diurnal	Oviparous	Endotherm
Hooded Robin	20.9	2.25	Invertivore	Insessorial	Biped	Volant	Diurnal	Oviparous	Endotherm
Budgerigar	32.5	1	Granivore	Generalist	Biped	Volant	Diurnal	Oviparous	Endotherm
Spinifex Hopping Mouse	33.67	3.9	Omnivore	Terrestrial	Quadruped	Cursorial	Nocturnal	Viviparous	Endotherm
Cockatiel	88.15	4.5	Granivore	Terrestrial	Biped	Volant	Diurnal	Oviparous	Endotherm
Crested Pigeon	190	2	Omnivore	Terrestrial	Biped	Volant	Diurnal	Oviparous	Endotherm
Crested Bellbird	63.3	3	Invertivore	Terrestrial	Biped	Volant	Diurnal	Oviparous	Endotherm
European Rabbit	1894.33	5.24	Folivore	Terrestrial	Quadruped	Saltatorial	Crepuscular	Viviparous	Endotherm
Common Bronzewing	335	1.915	Granivore	Terrestrial	Biped	Volant	Diurnal	Oviparous	Endotherm
Western bearded dragon	115.12	8.75	Omnivore	Terrestrial	Quadruped	Cursorial	Diurnal	Oviparous	Ectotherm
Grey-crowned Babbler	69.5	2.7	Invertivore	Generalist	Biped	Volant	Diurnal	Oviparous	Endotherm
Spinifexbird	23	3	Invertivore	Terrestrial	Biped	Volant	Diurnal	Oviparous	Endotherm
King Brown Snake	8144	13	Vertivore	Terrestrial	Limbless	Undulatory	Cathemeral	Oviparous	Ectotherm
Grey-headed Honeyeater	15.25	2	Invertivore	Insessorial	Biped	Volant	Diurnal	Oviparous	Endotherm

White-plumed Honeyeater	19.175	2.355	Omnivore	Insessorial	Biped	Volant	Diurnal	Oviparous	Endotherm
Willie Wagtail	20.7	2.8	Invertivore	Insessorial	Biped	Volant	Diurnal	Oviparous	Endotherm
Rodent	25	3.51875	Omnivore	Terrestrial	Quadruped	Cursorial	Nocturnal	Viviparous	Endotherm
Long-tailed Dunnart	18	3.62	Invertivore, Vertivore	Terrestrial	Quadruped	Cursorial	Nocturnal	Viviparous	Endotherm
Stripe-faced Dunnart	19.15	7	Invertivore	Terrestrial	Quadruped	Cursorial	Nocturnal	Viviparous	Endotherm
Lesser Hairy-footed Dunnart	10	5.5	Invertivore, Vertivore	Terrestrial	Quadruped	Cursorial	Nocturnal	Viviparous	Endotherm
Black Honeyeater	9.5	3	Nectarivore	Insessorial	Biped	Volant	Diurnal	Oviparous	Endotherm
Australian Zebra Finch	12.7	4.8	Omnivore	Insessorial	Biped	Volant	Diurnal	Oviparous	Endotherm
Little Buttonquail	46	3.58	Granivore	Terrestrial	Biped	Cursorial	Nocturnal	Oviparous	Endotherm
Spiny-tailed monitor	60	9.1	Invertivore, Vertivore	Terrestrial	Quadruped	Scansorial	Diurnal	Oviparous	Ectotherm
Perentie	2496	9.6	Invertivore, Vertivore	Terrestrial	Quadruped	Cursorial	Diurnal	Oviparous	Ectotherm
Sand Monitor	643	9.6	Invertivore, Vertivore	Terrestrial	Quadruped	Cursorial	Diurnal	Oviparous	Ectotherm
Yellow-spotted monitor	1467	7.65	Invertivore, Vertivore	Terrestrial	Quadruped	Cursorial	Diurnal	Oviparous	Ectotherm

Table A8: Model outputs from GLMMs comparing network metrics between mining camps and reference sites (Intercept), and inside and outside (Intercept) mining camps. Models which were significant at the *P* < 0.05 level have an asterisk following the *P* value.

Network metric	Fixed effect	Estimate	Std. error	Z value	*P* value
Num. of interactions	Intercept	-1.92	0.11	-17.80	< 0.001
	Mine	-0.09	0.15	-0.62	0.536
Connectance	Intercept	-7.64	0.11	-67.16	< 0.001
	Mine	-0.21	0.08	-2.64	0.008*
Link density	Intercept	-3.36	0.19	-18.01	< 0.001
	Mine	-0.15	0.21	-0.69	0.493
Nestedness	Intercept	-1.13	0.90	-1.25	0.211
	Mine	-1.45	0.76	-1.90	0.058
Num. of interactions	Intercept	-2.10	0.22	-9.64	< 0.001
	Inside	-0.63	0.24	-2.67	0.008
Connectance	Intercept	-6.95	0.15	-46.74	< 0.001
	Inside	0.31	0.19	1.61	0.106
Link density	Intercept	-3.44	0.21	-16.19	< 0.001
	Inside	-0.31	0.21	-1.49	0.136
Nestedness	Intercept	-0.55	0.91	-0.60	0.550
	Inside	-0.42	0.54	-0.78	0.436

Table A9: Temporal overlap of animal activity patterns at mining camps and reference sites, and inside and outside mining camps. Confidence intervals are included as well as the Δ type used to estimate overlap.

Treatment	Animal group	Overlap	Lower 95% CI	Upper 95% CI	Δ
Mining vs. Reference	Dingoes	0.76	0.58	0.87	Dhat1
	Feral cats	0.81	0.57	0.89	Dhat1
	Varanids	0.55	0.14	0.82	Dhat1
	Other reptiles	0.84	0.70	0.93	Dhat1
	Ground-nesting birds	0.61	0.55	0.72	Dhat4
	Arboreal-nesting birds	0.71	0.66	0.79	Dhat4
	Macropods	0.70	0.49	0.86	Dhat1
	CWR mammals	0.67	0.56	0.78	Dhat1
	Small mammals	0.94	0.86	0.96	Dhat4
	Feral herbivores	0.77	0.47	0.84	Dhat1
Inside vs. Outside	Dingoes	0.44	0.20	0.68	Dhat1
	Feral cats	0.61	0.20	0.79	Dhat1
	Varanids	0.60	0.35	0.83	Dhat1
	Other reptiles	0.78	0.60	0.91	Dhat1
	Ground-nesting birds	0.81	0.68	0.88	Dhat1
	Arboreal-nesting birds	0.97	0.90	0.97	Dhat4
	Macropods	0.62	0.23	0.76	Dhat1
	CWR mammals	0.68	0.41	0.87	Dhat1
	Small mammals	0.82	0.70	0.91	Dhat4
	Feral herbivores	0.55	0.21	0.76	Dhat1

Table A10: Temporal overlap of all animal group interactions at mining camps and reference sites. Confidence intervals are included as well as the Δ type used to estimate overlap.

Species 1	Species 2	Overlap	Lower 83% CI	Upper 83% CI	Treatment	Δ
Arboreal bird	Small mammal	0.18	0.17	0.27	Mining	Dhat4
Arboreal bird	CWR mammal	0.32	0.2	0.48	Mining	Dhat1
Arboreal bird	Macropod	0.34	0.27	0.42	Mining	Dhat1
Arboreal bird	Feral herbivore	0.07	0.1	0.14	Mining	Dhat1
CWR mammal	Small mammal	0.7	0.54	0.8	Mining	Dhat1
CWR mammal	Feral herbivore	0.83	0.76	0.89	Mining	Dhat1
Dingo	Arboreal bird	0.32	0.27	0.44	Mining	Dhat1
Dingo	Varanid	0.81	0.65	0.83	Mining	Dhat1
Dingo	Other reptile	0.72	0.57	0.8	Mining	Dhat1
Dingo	Small mammal	0.74	0.57	0.8	Mining	Dhat1
Dingo	Ground bird	0.41	0.36	0.55	Mining	Dhat1
Dingo	CWR mammal	0.74	0.65	0.85	Mining	Dhat1
Dingo	Macropod	0.27	0.22	0.4	Mining	Dhat1
Dingo	Feral cat	0.65	0.55	0.75	Mining	Dhat1
Dingo	Feral herbivore	0.27	0.21	0.39	Mining	Dhat1
Feral cat	Arboreal bird	0.16	0.11	0.26	Mining	Dhat1
Feral cat	Varanid	0.83	0.68	0.87	Mining	Dhat1
Feral cat	Other reptile	0.7	0.48	0.77	Mining	Dhat1
Feral cat	Small mammal	0.26	0.2	0.39	Mining	Dhat1
Feral cat	Ground bird	0.7	0.61	0.83	Mining	Dhat1
Feral cat	CWR mammal	0.14	0.09	0.25	Mining	Dhat1
Feral cat	Macropod	0.77	0.68	0.86	Mining	Dhat1
Feral cat	Feral herbivore	0.15	0.09	0.26	Mining	Dhat1
Ground bird	Arboreal bird	0.87	0.82	0.89	Mining	Dhat4
Ground bird	Small mammal	0.28	0.25	0.39	Mining	Dhat4
Ground bird	CWR mammal	0.4	0.27	0.55	Mining	Dhat1
Ground bird	Macropod	0.43	0.34	0.51	Mining	Dhat1
Ground bird	Feral herbivore	0.18	0.18	0.28	Mining	Dhat1
Macropod	Small mammal	0.79	0.71	0.87	Mining	Dhat1
Macropod	CWR mammal	0.73	0.55	0.81	Mining	Dhat1
Macropod	Feral herbivore	0.75	0.68	0.83	Mining	Dhat1
Other reptile	Arboreal bird	0.89	0.83	0.94	Mining	Dhat1
Other reptile	Small mammal	0.14	0.12	0.25	Mining	Dhat1
Other reptile	Ground bird	0.3	0.16	0.42	Mining	Dhat1
Other reptile	CWR mammal	0.82	0.74	0.88	Mining	Dhat1
Other reptile	Macropod	0.31	0.24	0.39	Mining	Dhat1
Other reptile	Feral herbivore	0.08	0.07	0.15	Mining	Dhat1
Small mammal	Feral herbivore	0.63	0.49	0.76	Mining	Dhat1
Varanid	Arboreal bird	0.83	0.79	0.91	Mining	Dhat1
Varanid	Other reptile	0.15	0.12	0.24	Mining	Dhat1
Varanid	Small mammal	0.31	0.18	0.43	Mining	Dhat1
Varanid	Ground bird	0.76	0.7	0.85	Mining	Dhat1
Varanid	CWR mammal	0.31	0.23	0.39	Mining	Dhat1
Varanid	Macropod	0.88	0.78	0.92	Mining	Dhat1
Varanid	Feral herbivore	0.09	0.08	0.16	Mining	Dhat1
Arboreal bird	Small mammal	0.51	0.50	0.60	Reference	Dhat4

Arboreal bird	CWR mammal	0.34	0.21	0.49	Reference	Dhat4
Arboreal bird	Macropod	0.43	0.33	0.59	Reference	Dhat1
Arboreal bird	Feral herbivore	0.10	0.13	0.18	Reference	Dhat1
CWR mammal	Small mammal	0.70	0.51	0.75	Reference	Dhat4
CWR mammal	Feral herbivore	0.58	0.54	0.64	Reference	Dhat1
Dingo	Arboreal bird	0.59	0.50	0.68	Reference	Dhat1
Dingo	Varanid	0.80	0.71	0.87	Reference	Dhat1
Dingo	Other reptile	0.70	0.58	0.81	Reference	Dhat1
Dingo	Small mammal	0.71	0.50	0.78	Reference	Dhat1
Dingo	Ground bird	0.70	0.59	0.76	Reference	Dhat1
Dingo	CWR mammal	0.71	0.55	0.79	Reference	Dhat1
Dingo	Macropod	0.29	0.23	0.44	Reference	Dhat1
Dingo	Feral cat	0.49	0.43	0.64	Reference	Dhat1
Dingo	Feral herbivore	0.19	0.07	0.31	Reference	Dhat1
Feral cat	Arboreal bird	0.32	0.27	0.47	Reference	Dhat1
Feral cat	Varanid	0.72	0.62	0.80	Reference	Dhat1
Feral cat	Other reptile	0.85	0.58	0.84	Reference	Dhat1
Feral cat	Small mammal	0.48	0.40	0.62	Reference	Dhat1
Feral cat	Ground bird	0.76	0.55	0.82	Reference	Dhat1
Feral cat	CWR mammal	0.14	0.09	0.26	Reference	Dhat1
Feral cat	Macropod	0.79	0.67	0.84	Reference	Dhat1
Feral cat	Feral herbivore	0.08	0.03	0.17	Reference	Dhat1
Ground bird	Arboreal bird	0.73	0.70	0.80	Reference	Dhat4
Ground bird	Small mammal	0.56	0.55	0.66	Reference	Dhat4
Ground bird	CWR mammal	0.49	0.37	0.63	Reference	Dhat4
Ground bird	Macropod	0.64	0.51	0.75	Reference	Dhat1
Ground bird	Feral herbivore	0.26	0.28	0.36	Reference	Dhat1
Macropod	Small mammal	0.70	0.55	0.78	Reference	Dhat1
Macropod	CWR mammal	0.78	0.52	0.81	Reference	Dhat1
Macropod	Feral herbivore	0.60	0.47	0.73	Reference	Dhat1
Other reptile	Arboreal bird	0.48	0.44	0.60	Reference	Dhat1
Other reptile	Small mammal	0.33	0.28	0.41	Reference	Dhat1
Other reptile	Ground bird	0.16	0.07	0.29	Reference	Dhat1
Other reptile	CWR mammal	0.31	0.28	0.42	Reference	Dhat1
Other reptile	Macropod	0.15	0.08	0.28	Reference	Dhat1
Other reptile	Feral herbivore	0.03	0.01	0.06	Reference	Dhat1
Small mammal	Feral herbivore	0.74	0.56	0.82	Reference	Dhat1
Varanid	Arboreal bird	0.33	0.16	0.53	Reference	Dhat1
Varanid	Other reptile	0.18	0.07	0.26	Reference	Dhat1
Varanid	Small mammal	0.10	0.01	0.21	Reference	Dhat1
Varanid	Ground bird	0.24	0.12	0.39	Reference	Dhat1
Varanid	CWR mammal	0.08	0.02	0.22	Reference	Dhat1
Varanid	Macropod	0.67	0.31	0.84	Reference	Dhat1
Varanid	Feral herbivore	0.00	0.00	0.02	Reference	Dhat1

Table A11: Temporal overlap of all animal group interactions inside and outside mining camps. Confidence intervals are included as well as the Δ type used to estimate overlap.

Species 1	Species 2	Overlap	Lower 83% CI	Upper 83% CI	Location
Arboreal bird	Small mammal	0.05	0.06	0.11	Inside
Arboreal bird	Macropod	0.05	0	0.17	Inside
Arboreal bird	CWR mammal	0.12	0.11	0.2	Inside
Arboreal bird	Feral herbivore	0.39	0.18	0.63	Inside
CWR mammal	Feral herbivore	0.46	0.29	0.67	Inside
CWR mammal	Small mammal	0.81	0.71	0.89	Inside
Dingo	Feral cat	0.32	0.09	0.45	Inside
Dingo	Small mammal	0.43	0.22	0.55	Inside
Dingo	Varanid	0.44	0.24	0.66	Inside
Dingo	Macropod	0.44	0.11	0.56	Inside
Dingo	Arboreal bird	0.47	0.26	0.62	Inside
Dingo	Ground bird	0.47	0.27	0.63	Inside
Dingo	CWR mammal	0.49	0.26	0.6	Inside
Dingo	Other reptile	0.5	0.29	0.66	Inside
Dingo	Feral herbivore	0.51	0.19	0.56	Inside
Feral cat	Varanid	0.02	0	0.06	Inside
Feral cat	Other reptile	0.02	0	0.08	Inside
Feral cat	Arboreal bird	0.05	0.02	0.13	Inside
Feral cat	Ground bird	0.05	0.01	0.14	Inside
Feral cat	Feral herbivore	0.41	0.17	0.61	Inside
Feral cat	Small mammal	0.65	0.39	0.85	Inside
Feral cat	Macropod	0.65	0.24	0.76	Inside
Feral cat	CWR mammal	0.71	0.42	0.81	Inside
Ground bird	Small mammal	0.06	0.05	0.15	Inside
Ground bird	Macropod	0.06	0	0.17	Inside
Ground bird	CWR mammal	0.12	0.1	0.24	Inside
Ground bird	Feral herbivore	0.4	0.17	0.61	Inside
Ground bird	Arboreal bird	0.96	0.83	0.95	Inside
Macropod	Feral herbivore	0.48	0.14	0.64	Inside
Macropod	CWR mammal	0.79	0.43	0.83	Inside
Macropod	Small mammal	0.95	0.46	0.87	Inside
Other reptile	Macropod	0.07	0	0.15	Inside
Other reptile	Small mammal	0.08	0.04	0.14	Inside
Other reptile	CWR mammal	0.12	0.07	0.21	Inside
Other reptile	Feral herbivore	0.39	0.14	0.52	Inside
Other reptile	Ground bird	0.81	0.67	0.88	Inside
Other reptile	Arboreal bird	0.82	0.73	0.9	Inside
Small mammal	Feral herbivore	0.49	0.29	0.64	Inside
Varanid	Small mammal	0.03	0.02	0.08	Inside
Varanid	Macropod	0.03	0	0.1	Inside
Varanid	CWR mammal	0.06	0.04	0.14	Inside
Varanid	Feral herbivore	0.36	0.13	0.53	Inside
Varanid	Ground bird	0.77	0.66	0.87	Inside
Varanid	Arboreal bird	0.78	0.74	0.87	Inside
Varanid	Other reptile	0.88	0.75	0.91	Inside

Arboreal bird	Small mammal	0.11	0.14	0.21	Outside
Arboreal bird	Feral herbivore	0.26	0.14	0.43	Outside
Arboreal bird	CWR mammal	0.34	0.25	0.48	Outside
Arboreal bird	Macropod	0.43	0.34	0.52	Outside
CWR mammal	Small mammal	0.67	0.5	0.8	Outside
CWR mammal	Feral herbivore	0.71	0.43	0.77	Outside
Dingo	Other reptile	0.19	0.16	0.34	Outside
Dingo	Arboreal bird	0.27	0.24	0.4	Outside
Dingo	Ground bird	0.37	0.3	0.5	Outside
Dingo	Varanid	0.46	0.31	0.62	Outside
Dingo	Feral cat	0.69	0.49	0.79	Outside
Dingo	Macropod	0.71	0.61	0.82	Outside
Dingo	Small mammal	0.72	0.57	0.79	Outside
Dingo	Feral herbivore	0.76	0.52	0.81	Outside
Dingo	CWR mammal	0.81	0.55	0.83	Outside
Feral cat	Other reptile	0.15	0.08	0.27	Outside
Feral cat	Arboreal bird	0.21	0.14	0.33	Outside
Feral cat	Ground bird	0.33	0.25	0.48	Outside
Feral cat	Varanid	0.39	0.21	0.55	Outside
Feral cat	Macropod	0.68	0.54	0.8	Outside
Feral cat	CWR mammal	0.71	0.47	0.78	Outside
Feral cat	Feral herbivore	0.74	0.42	0.77	Outside
Feral cat	Small mammal	0.8	0.66	0.86	Outside
Ground bird	Small mammal	0.24	0.23	0.37	Outside
Ground bird	Feral herbivore	0.36	0.21	0.52	Outside
Ground bird	CWR mammal	0.45	0.34	0.58	Outside
Ground bird	Macropod	0.52	0.42	0.62	Outside
Ground bird	Arboreal bird	0.82	0.76	0.87	Outside
Macropod	Small mammal	0.69	0.63	0.8	Outside
Macropod	Feral herbivore	0.72	0.48	0.8	Outside
Macropod	CWR mammal	0.75	0.55	0.82	Outside
Other reptile	Small mammal	0.07	0.07	0.17	Outside
Other reptile	Feral herbivore	0.19	0.09	0.38	Outside
Other reptile	CWR mammal	0.25	0.17	0.41	Outside
Other reptile	Macropod	0.34	0.27	0.45	Outside
Other reptile	Ground bird	0.77	0.68	0.84	Outside
Other reptile	Arboreal bird	0.89	0.8	0.94	Outside
Small mammal	Feral herbivore	0.72	0.48	0.82	Outside
Varanid	Small mammal	0.31	0.18	0.48	Outside
Varanid	Feral herbivore	0.44	0.2	0.6	Outside
Varanid	CWR mammal	0.53	0.31	0.63	Outside
Varanid	Macropod	0.59	0.37	0.66	Outside
Varanid	Other reptile	0.71	0.49	0.81	Outside
Varanid	Arboreal bird	0.8	0.56	0.85	Outside
Varanid	Ground bird	0.85	0.57	0.83	Outside

References

ASF DAAC 2022. ALOS PALSAR_Radiometric_Terrain_Corrected_high_res; Includes Material © JAXA/METI 2009. Accessed 30 June 2022 from https://asf.alaska.edu/data-sets/derived-data-sets/alos-palsar-rtc/alos-palsar-radiometric-terrain-correction/.

Berger, A., Lozano, B., Barthel, L. M. F. & Schubert, N. 2020. Moving in the Dark—Evidence for an Influence of Artificial Light at Night on the Movement Behaviour of European Hedgehogs (Erinaceus europaeus). *Animals,* 10**,** 1306.

Crossman, S. & Li, O. 2015. Surface Hydrology Lines (National). Geoscience Australia. Canberra.

Environmental Protection Authority 2014. Cumulative environmental impacts of development in the Pilbara region. Perth: The Government of Western Australia.

Hijmans, R. J., Van Etten, J., Cheng, J., Mattiuzzi, M., Sumner, M., Greenberg, J. A., Lamigueiro, O. P., Bevan, A., Racine, E. B. & Shortridge, A. 2015. Package 'raster'.

Kight, C. R. & Swaddle, J. P. 2011. How and why environmental noise impacts animals: an integrative, mechanistic review. *Ecology Letters,* 14**,** 1052-1061.

Kissling, W. D., Dalby, L., Fløjgaard, C., Lenoir, J., Sandel, B., Sandom, C., Trøjelsgaard, K. & Svenning, J.-C. 2014. Establishing macroecological trait datasets: digitalization, extrapolation, and validation of diet preferences in terrestrial mammals worldwide. *Ecology and Evolution,* 4**,** 2913-2930.

Middleton, O., Svensson, H., Scharlemann, J. P. W., Faurby, S. & Sandom, C. 2021. CarniDIET 1.0: A database of terrestrial carnivorous mammal diets. *Global Ecology and Biogeography,* 30**,** 1175-1182.

Newsome, T. M., Ballard, G. A., Dickman, C. R., Fleming, P. J. S. & Howden, C. 2013a. Anthropogenic Resource Subsidies Determine Space Use by Australian Arid Zone Dingoes: An Improved Resource Selection Modelling Approach. *PLoS ONE,* 8.

Newsome, T. M., Ballard, G. A., Dickman, C. R., Fleming, P. J. S. & Van De Ven, R. 2013b. Home Range, activity and sociality of a top predator, the dingo: A test of the resource dispersion hypothesis. *Ecography,* 36**,** 914-925.

QGIS Development Team 2020. QGIS Geographic Information System. Open Source Geospatial Foundation Project.

Riley, S. J., Degloria, S. D. & Elliot, R. 1999. Index that quantifies topographic heterogeneity. *intermountain Journal of sciences,* 5**,** 23–27.

Tobias, J. A., Sheard, C., Pigot, A. L., Devenish, A. J. M., Yang, J., Sayol, F., Neate-Clegg, M. H. C., Alioravainen, N., Weeks, T. L., Barber, R. A., Walkden, P. A., Macgregor, H. E. A., Jones, S. E. I., Vincent, C., Phillips, A. G., Marples, N. M., Montaño-Centellas, F. A., Leandro-Silva, V., Claramunt, S., Darski, B., Freeman, B. G., Bregman, T. P., Cooney, C. R., Hughes, E. C., Capp, E. J. R., Varley, Z. K., Friedman, N. R., Korntheuer, H., Corrales-Vargas, A., Trisos, C. H., Weeks, B. C., Hanz, D. M., Töpfer, T., Bravo, G. A., Remeš, V., Nowak, L., Carneiro, L. S., Moncada R., A. J., Matysioková, B., Baldassarre, D. T., Martínez-Salinas, A., Wolfe, J. D., Chapman, P. M., Daly, B. G., Sorensen, M. C., Neu, A., Ford, M. A., Mayhew, R. J., Fabio Silveira, L., Kelly, D. J., Annorbah, N. N. D., Pollock, H. S., Grabowska-Zhang, A. M., Mcentee, J. P., Carlos T. Gonzalez, J., Meneses, C. G., Muñoz, M. C., Powell, L. L., Jamie, G. A., Matthews, T. J., Johnson, O., Brito, G. R. R., Zyskowski, K., Crates, R., Harvey, M. G., Jurado Zevallos, M., Hosner, P. A., Bradfer-Lawrence, T., Maley, J. M., Stiles, F. G., Lima, H. S., Provost, K. L., Chibesa, M., Mashao, M., Howard, J. T., Mlamba, E., Chua, M. a. H., Li, B., Gómez, M. I., García, N. C., Päckert, M., Fuchs, J., Ali, J. R., Derryberry, E. P., Carlson, M. L., Urriza, R. C., Brzeski, K. E., Prawiradilaga, D. M., Rayner, M. J., Miller, E. T., Bowie, R. C. K., Lafontaine, R.-M., Scofield, R. P., Lou, Y., Somarathna, L., Lepage, D., Illif, M., Neuschulz, E. L., Templin, M., Dehling,

D. M., et al. 2022. AVONET: morphological, ecological and geographical data for all birds. *Ecology Letters*, 25**,** 581-597.

Uetz, P. & Etzold, T. 1996. The EMBL/EBI Reptile Database. *Herpetological Review*, 27**,** 174-175.

Wilman, H., Belmaker, J., Simpson, J., De La Rosa, C., Rivadeneira, M. M. & Jetz, W. 2014. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95**,** 2027-2027.

Appendix B: Supplementary material for Chapter 3

Table B1: Sites where northern quolls (*Dasyurus hallucatus*) were tracked in the Pilbara region, Western Australia between 2014 and 2018.

Site	Coordinates	Site description	Land use	Year(s)
Red Rock	(-20.88, 118.59)	Large patches of rocky habitat scattered along the seasonal Turner River, with spinifex sandplain and *Acacia* stands throughout.	Pastoral	2014 2015 2018
Python Pool	(-21.34, 117.25)	Rocky habitat including deep gorges nestled within spinifex sandplain and *Acacia* stands.	National Park	2014
Cattle Gorge	(-20.55, 120.25)	Decommissioned iron ore mine tenement with rocky habitat, spinifex sandplain, *Acacia* stands, and a small amount of disturbance (e.g., roads).	Mining tenement	2016
De Grey Ridge	(-20.84, 118.59)	Rocky habitat comprising a granite ridge surrounded by spinifex sandplain and *Acacia* stands.	Pastoral	2018

Table B2: Studies of northern quoll spatial movement in the Pilbara region of Western Australia which were used to analyse habitat selection and determinants of activity area size.

Study	Motivation	GPS unit & brand	Fix interval	Quolls collared (*n*)	Site(s)
Hernandez-Santin et al. (2020)	To measure northern quoll activity area	CatTrack® GPS logger backpack (Catnip Technologies, South Carolina, USA).	10 mins	5	Red Rock Python Pool
Biologic (2016)	To assess northern quoll interactions with mine pits.	FLR V Micro GPS collars (Telemetry Solutions, California, USA).	30 mins	3	Cattle Gorge
Cowan et al. (2020)	To locate occupied maternal northern quoll dens using VHF.	Custom made GPS collars with i-gotU components (Mobile Action Technology, Taipei, Taiwan).	5 mins	8	De Grey Ridge
H. Moore (unpubl. data)	To investigate the fine-scale movement and habitat interactions of northern quolls.	Custom made GPS collars with i-gotU components (Mobile Action Technology, Taipei, Taiwan).	1 min	9	Red Rock

Table B3: The parameters used during kernel density estimation for the measurement of northern quoll activity areas. Parameters show the buffer size, grid output, and the UTM zone for each individual (ID) when using the *ad hoc* method ($h_{ad\ hoc}$) (Kie, 2013), referred to as 'reference scaled' in the package "rhr" (Signer and Balkenhol, 2015).

Contributor	ID	X buffer (ha)	Y buffer (ha)	Grid output	UTM zone
Moore	23891	232	167	100 x 100	50S
Cowan	44751	321	277	100 x 100	50S
Moore	44828	188	157	100 x 100	50S
Moore	45146	132	208	100 x 100	50S
Moore	46324	267	246	100 x 100	50S
Hernandez-Santin	98322	1042	1493	100 x 100	50S
Hernandez-Santin	99027	1018	1528	100 x 100	50S
Hernandez-Santin	99464	1587	1400	100 x 100	50S
Hernandez-Santin	99531	425	895	100 x 100	50S
Moore	953815	374	410	100 x 100	50S
Moore	961514	190	209	100 x 100	50S
Biologic	E6CA67a	335	862	100 x 100	51S
Biologic	E6CA67b	250	620	100 x 100	51S
Biologic	E6CA67c	345	791	100 x 100	51S

Table B4: The characteristics of the 14 individual northern quoll tracking events. Sex is female (♀) or male (♂), and fix nights is the number of nights with a successful fix. This also includes the short-term activity area size and percentage cover of each habitat type for each individual northern quoll tracking event.

Site	ID	Year	Season	Sex	Weight (g)	Fix nights	Fixes	Short-term activity area size (ha)	Habitat cover (%)			
									Rocky habitat	Spinifex sandplain	*Acacia* stands	Riverbed
Red Rock	23891	2018	Winter	♀	420	4	363	8.83	28.52	63.02	2.48	5.98
De Grey Ridge	44751	2018	Spring	♀	410	7	389	22.96	3.13	38.29	58.57	0.00
Red Rock	44828	2018	Winter	♀	540	2	84	7.25	30.12	58.73	4.54	6.60
Red Rock	45146	2018	Winter	♀	420	4	974	7.60	30.08	53.30	2.51	14.12
Red Rock	46324	2018	Winter	♀	490	4	998	14.26	25.30	67.60	3.79	3.30
Python Pool	98322	2014	Spring	♂	730	7	351	274.66	6.00	78.77	15.23	0.00
Red Rock	99027	2014	Spring	♂	673	7	366	193.39	17.12	68.68	5.87	8.33
Red Rock	99464	2014	Spring	♂	540	7	387	340.54	1.80	80.92	13.43	3.85
Red Rock	99531	2015	Winter	♂	690	7	418	53.84	28.39	61.38	4.13	6.10
Red Rock	953815	2018	Winter	♀	600	3	400	17.76	27.29	58.90	7.07	6.74
Red Rock	961514	2018	Winter	♀	450	3	615	7.51	33.56	50.20	3.22	13.02
Cattle Gorge	E6CA67a	2016	Autumn	♀	430	7	81	124.06	23.62	45.44	19.43	0.00
Cattle Gorge	E6CA67b	2016	Autumn	♀	430	7	69	89.30	38.88	33.99	18.61	0.00
Cattle Gorge	E6CA67c	2016	Autumn	♀	430	7	73	128.62	30.14	40.06	18.69	0.00

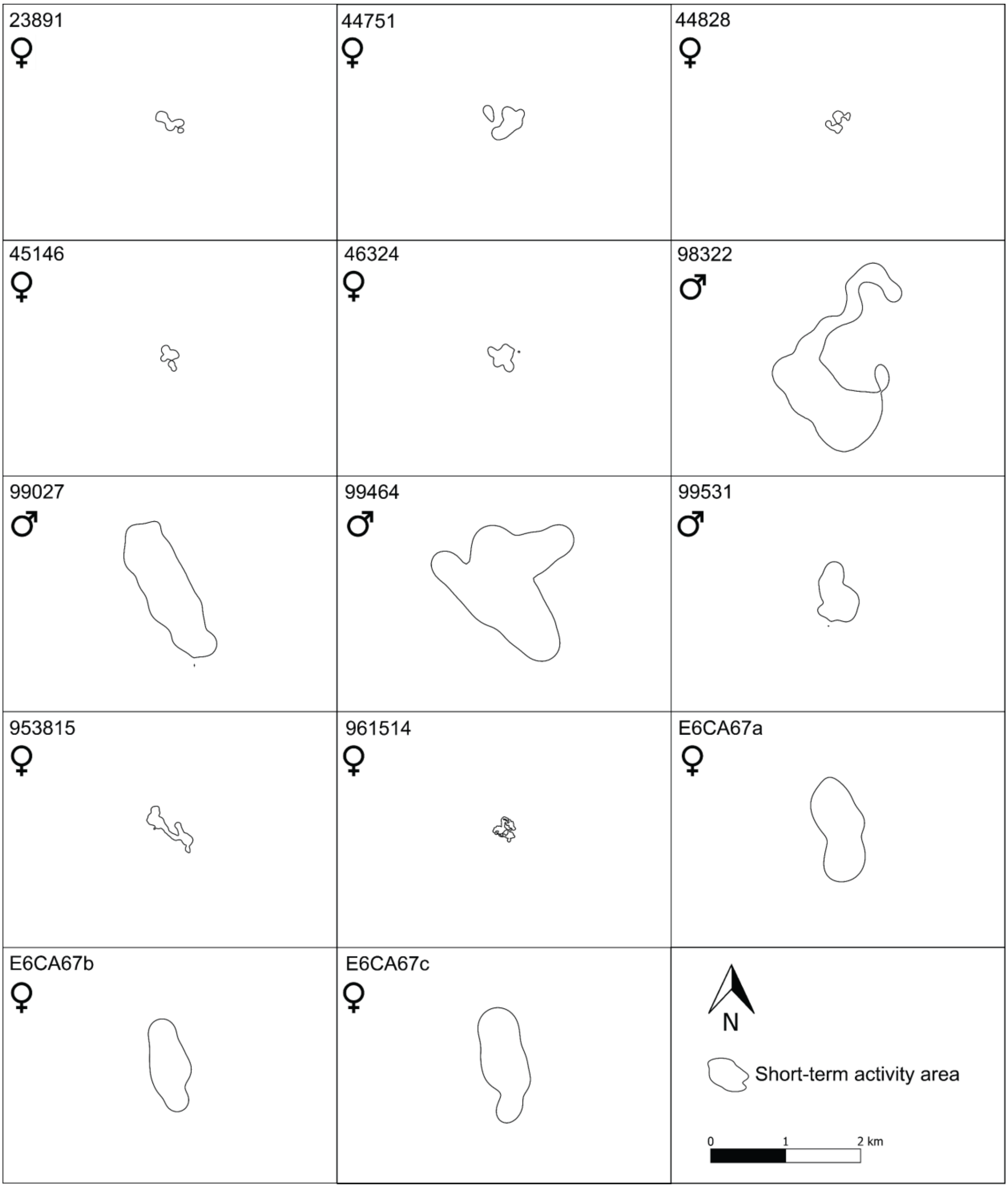


Figure B1: The used activity areas of northern quolls from the Pilbara region of Western Australia, estimated using kernel density estimation. Activity areas were estimated using the *ad hoc* method. All activity areas are on the same scale, represented by the scale bar.

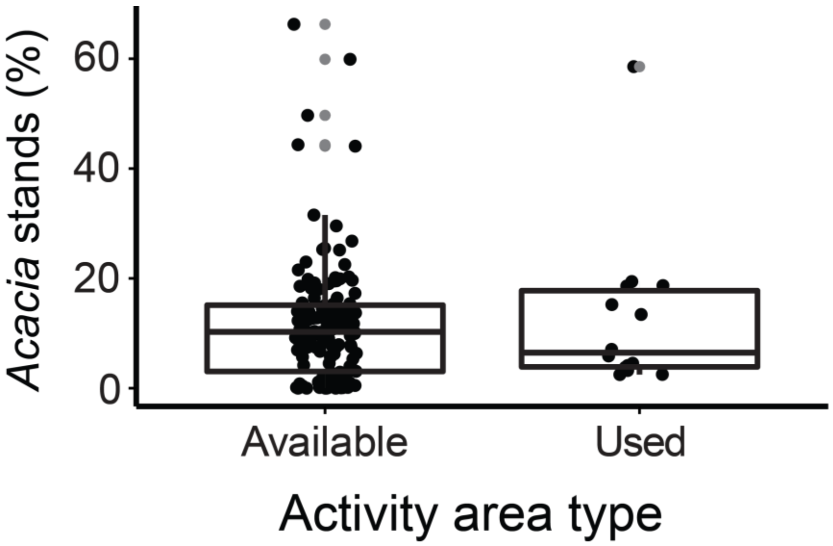


Figure B2: The proportional cover of *Acacia* stands within available (intercept) and used northern quoll activity areas. Black points represent data values and grey points represent outliers. The lack of red asterisks signifies no significant difference from the intercept. Boxplots show the distribution of the data for available and used activity areas.

References

Biologic 2016. Cattle Gorge and Callawa West Vertebrate Fauna Studies. Perth: Report prepared for BHP Billiton Iron Ore Pty Ltd: Biologic.

Cowan, M. A., Dunlop, J. A., Turner, J. M., Moore, H. A. & Nimmo, D. G. 2020. Artificial refuges to combat habitat loss for an endangered marsupial predator: How do they measure up? *Conservation Science and Practice,* 2**,** e204.

Hernandez-Santin, L., Henderson, M., Molloy, S. W., Dunlop, J. A. & Davis, R. A. 2020. Spatial ecology of an endangered carnivore, the Pilbara northern quoll. *Australian Mammalogy,* 43**,** 235–242.

Kie, J. G. 2013. A rule-based ad hoc method for selecting a bandwidth in kernel home-range analyses. *Animal Biotelemetry,* 1**,** 13.

Signer, J. & Balkenhol, N. 2015. Reproducible home ranges (rhr): A new, user-friendly R package for analyses of wildlife telemetry data. *Wildlife Society Bulletin,* 39**,** 358–363.

Appendix C: Supplementary material for Chapter 4

Appendix C1: Methods used to create environmental covariate layers for habitat selection analyses.

To create the map of habitat classifications, we applied semi-supervised classification of a normalised difference vegetation index (NDVI) layer (Pandey and Kulhari, 2018, Cowan et al., 2022, Leroux et al., 2018), derived from Sentinel-2 imagery (USGS, 2023). The NDVI layer for the habitat map was captured at a scale of 10 m and we used a consistent layer (captured in October 2021) for both tracking periods. Woodie Woodie had no fires between tracking periods and habitat features remained relatively consistent between time periods. NDVI is calculated using the near infrared (NIR) and red (RED) bands:

$$NDVI = \frac{NIR - RED}{NIR + RED}$$

For Sentinel 2 data the NIR band is band 8 and the RED band is band 4.

We used the semi-automatic classification (SCP) plugin (Congedo, 2016), in QGIS to classify habitat classifications from NDVI imagery. Classified habitats included spinifex grassland, riparian habitat (which was mostly associated with heavily vegetated creek lines), disturbed land, and water. To define all disturbed land accurately, we then overlaid a disturbance raster layer (converted from a vector) provided by *ConsMin* which reflected all mining disturbance in the landscape and was used for reporting at *Environmental Protection Authority (EPA)* standards. Finally, because rocky habitat is crucial for northern quolls in the Pilbara (Moore et al., 2022, Moore et al., 2021, Hernandez-Santin et al., 2016), we overlaid a northern quoll potential natural denning habitat raster layer (converted from a vector) which was digitised manually by *Western Wildlife* by outlining all visible rocky features from high-resolution aerial imagery. These features included rocky outcrops, gorges, and rocky mesas, as these are the areas which provide denning habitat for northern quolls in the Pilbara (Hernandez-Santin et al., 2022, Cowan et al., 2020). This resulted in a habitat raster of the following habitat types: spinifex grassland, riparian habitat (dense vegetation associated with creek lines), water, rocky habitat, and mining disturbed land. During breeding season, quolls were often tracked to dens within rocky waste dumps and mine pits, therefore, we split mining disturbed land into two types: 1) mine pits and waste dumps, and 2) other disturbed land (e.g., roads, buildings, and large cleared areas). The final map was cross-examined with the corresponding satellite imagery to ensure the accuracy of habitat feature classification (Tilahun and Teferie, 2015).

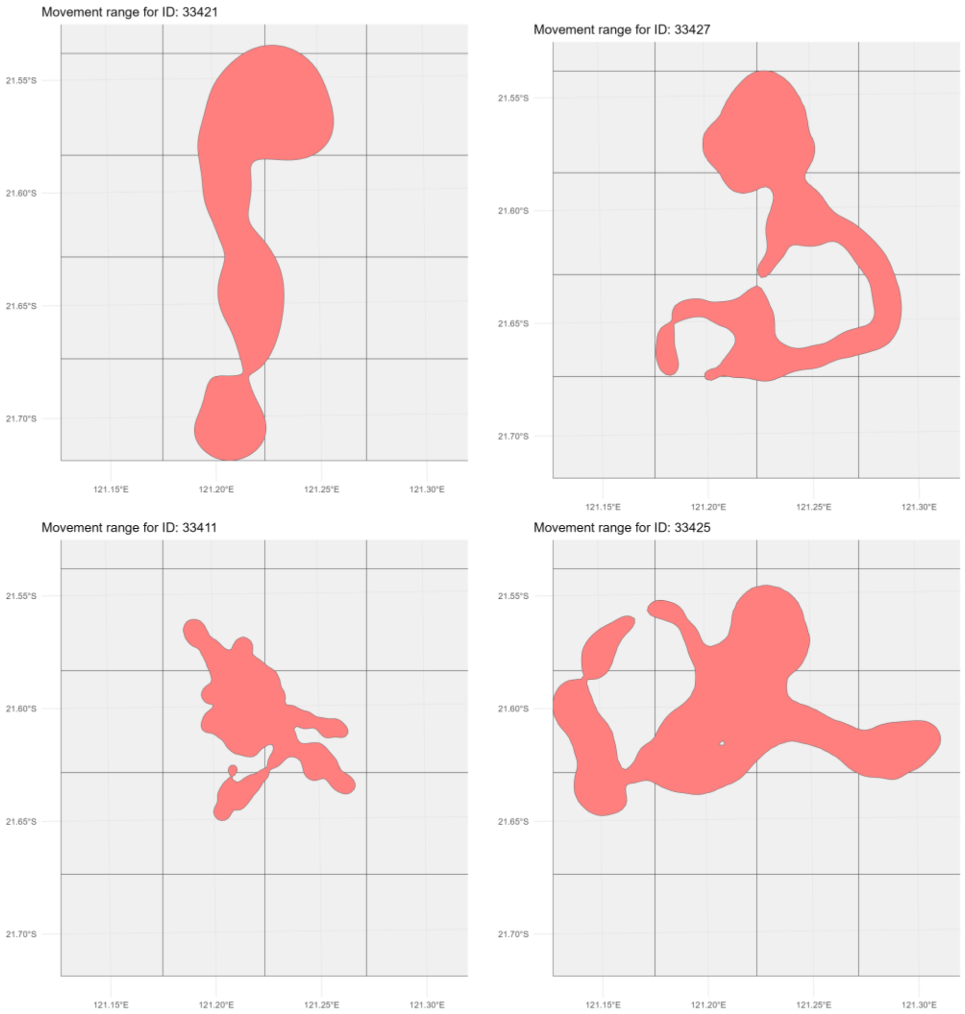
The topographic ruggedness index (TRI) is defined as the difference in elevation between a cell and the eight cells surrounding it (Riley et al., 1999). To create a TRI map for our landscape, we sourced a high-resolution radiometric terrain-corrected digital elevation model (12.5 m scale) (ASF DAAC, 2022), and used the 'Terrain Ruggedness Index' function in QGIS to calculate TRI for each cell (QGIS Development Team, 2020).

To create maps representing distance to disturbance and distance to potential denning habitat, we used the same disturbance and habitat vector layers provided by ConsMin that we used to create the habitat classification map. We converted these vector layers to distance rasters using the "rasterize" function in the 'raster' package in R. Each resulting cell of the respective rasters (10 m scale) reflected the distance from disturbed land or potential natural denning habitat.

To determine differences in environmental characteristics among habitat classifications, we extracted the mean NDVI value and the median topographic ruggedness for each habitat. To define the area from which to sample from, we combined the *observed* and *available* movement ranges (values were compared separately for *observed* and *available* ranges, but were very similar so they were combined for simplicity), using QGIS (QGIS Development Team, 2020). We clipped all habitat types to the combine *observed* and *available* area and extracted the NDVI and topographic ruggedness values using the 'extract' function in the "raster" package in R (R Core Team, 2023).

Table C1: The parameters used during kernel density estimation for the measurement of northern quoll movement ranges. Parameters show the buffer size, grid output, and the UTM zone for each individual (ID) when using the ad hoc method ($h_{ad\ hoc}$), referred to as 'reference scaled' in the package "rhr" (Signer and Balkenhol, 2015).

ID	X buffer (ha)	Y buffer (ha)	Grid output	UTM zone
33425	8857	4973	100 x 100	51S
33421	2835	9112	100 x 100	51S
33427	5565	7078	100 x 100	51S
33411	3862	4569	100 x 100	51S
33413	2889	1492	100 x 100	51S
33423	1819	1892	100 x 100	51S
33422	2083	1619	100 x 100	51S
33415	573	860	100 x 100	51S
33412	679	876	100 x 100	51S


Movement range for ID: 33421

Movement range for ID: 33427

Movement range for ID: 33411

Movement range for ID: 33425

Figure C1: Northern quoll movement ranges during breeding season used in analysis. Individual ID is in the top left of each plot and each grid square is 5 km wide. Latitude is on the Y axis and Longitude is on the X axis.

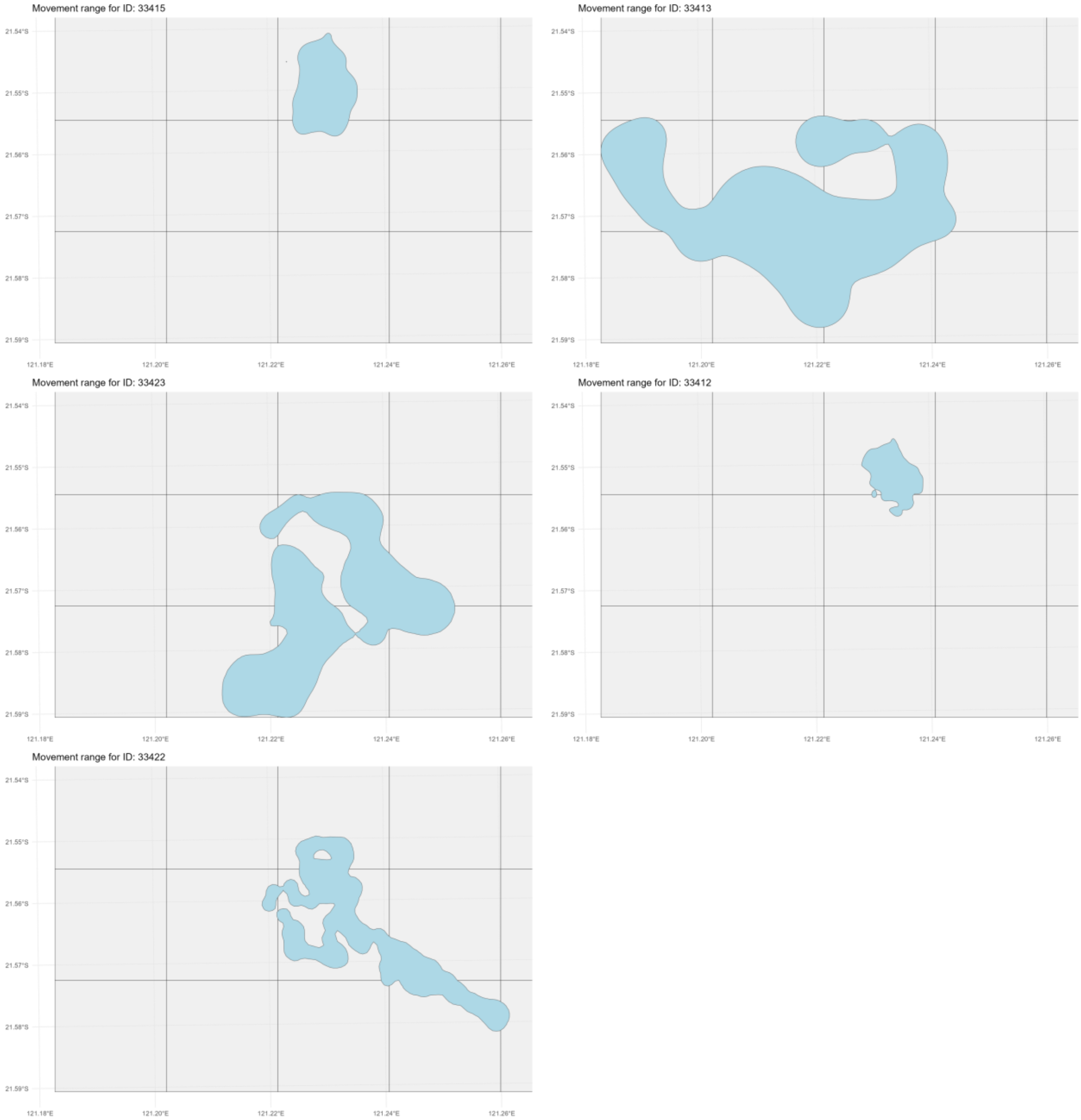


Figure C2: Northern quoll movement ranges during non-breeding season used in analysis. Individual ID is in the top left of each plot and each grid square is 2 km wide. Latitude is on the Y axis and Longitude is on the X axis.

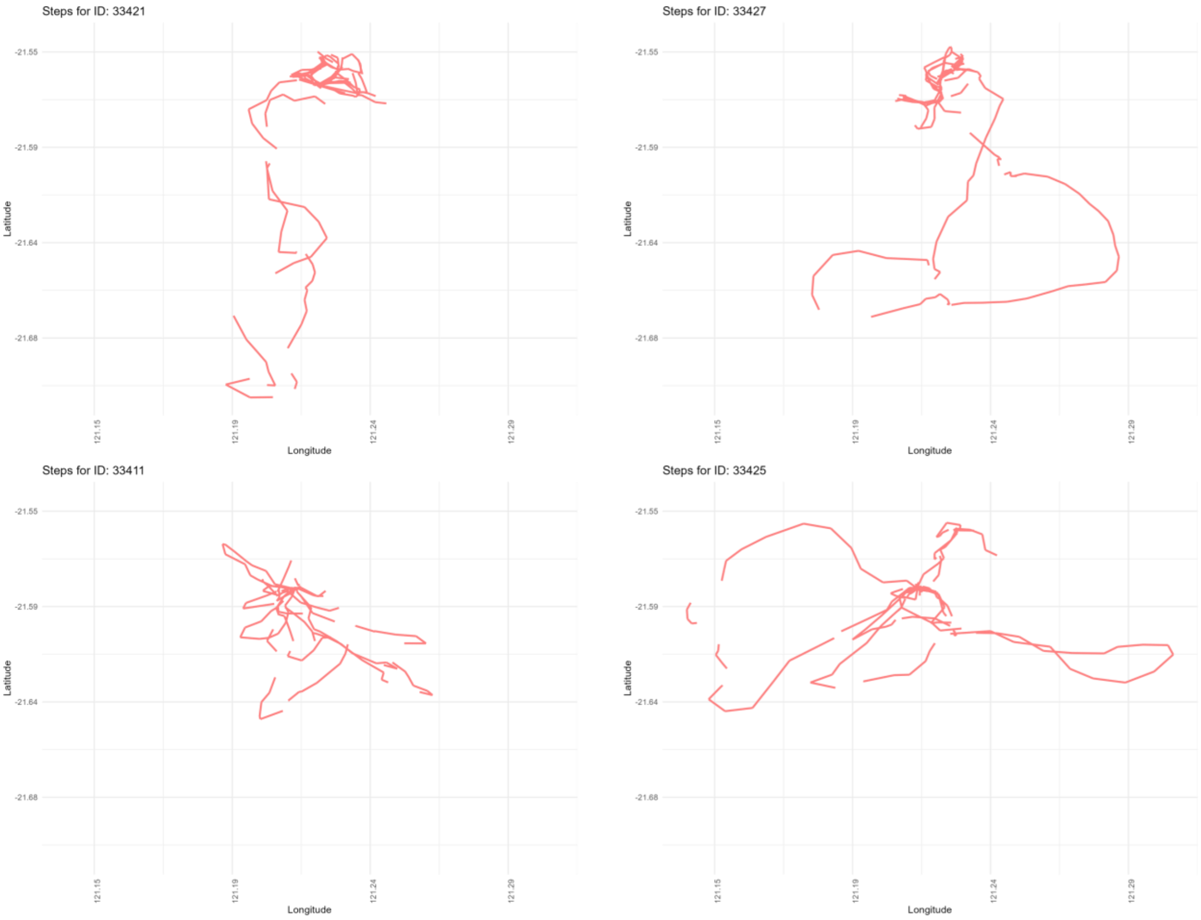


Figure C3: Northern quoll steps during breeding season used in analysis after data cleaning and removal of bursts with less than three steps. Individual ID is in the top left of each plot and each grid square is 5 km wide. Red lines signify steps.

Figure C4: Northern quoll steps during non-breeding season used in analysis after data cleaning and removal of bursts with less than three steps. Individual ID is in the top left of each plot and each grid square is 2 km wide. Blue lines signify steps.

Table C2: iSSF models compared to determine the habitat selection of northern quolls in a mining landscape. Models compared include variables: habitat = habitat classification (spinifex sandplain, dense vegetation, rocky habitat, mine pits and waste dumps, other disturbed land), sl = step length, ta = turn angle, TRI = topographic ruggedness, HD = distance from potential denning habitat, DD = distance from disturbance, and age = age. The global model for both seasons is highlighted in bold.

Season	Mod. Num.	Model	K	AICc	Δ AICc	AICc Wt	Cum. Wt	LL
Breeding	3	habitat + log(sl) + cos(ta) + TRI + HD	8	5620.36	0	0.56	0.56	-2802.16
	1	**habitat + log(sl) + cos(ta) + TRI + DD + HD**	**9**	**5621.62**	**1.26**	**0.3**	**0.86**	**-2801.79**
	2	habitat + log(sl) + cos(ta) + TRI + DD	8	5624.21	3.85	0.08	0.94	-2804.09
	4	habitat + log(sl) + cos(ta) + TRI	7	5624.76	4.4	0.06	1	-2805.37
	6	habitat + log(sl) + cos(ta) + DD + HD	8	5633.94	13.58	0	1	-2808.96
	5	habitat + log(sl) + cos(ta)	6	5634.24	13.88	0	1	-2811.11
	8	TRI + log(sl) + cos(ta)	3	5682.96	62.6	0	1	-2838.48
	7	DD + HD + log(sl) + cos(ta)	4	5716.15	95.79	0	1	-2854.07
Non-breeding	4	habitat + log(sl) + cos(ta) + TRI + age × (log(sl) + cos(ta))	9	3960.35	0	0.26	0.26	-1971.15
	3	habitat + log(sl) + cos(ta) + TRI + HD + age × (log(sl) + cos(ta))	10	3960.69	0.33	0.22	0.48	-1970.31
	2	habitat + log(sl) + cos(ta) + TRI + DD + age × (log(sl) + cos(ta))	10	3961.16	0.81	0.17	0.65	-1970.55
	1	**habitat + log(sl) + cos(ta) + TRI + DD + HD + age × (log(sl) + cos(ta))**	**11**	**3961.51**	**1.16**	**0.14**	**0.79**	**-1969.72**
	5	habitat + log(sl) + cos(ta) + age × (log(sl) + cos(ta))	8	3961.78	1.43	0.13	0.92	-1972.87
	6	habitat + log(sl) + cos(ta) + DD + HD + age × (log(sl) + cos(ta))	10	3962.67	2.32	0.08	1	-1971.3
	7	HD + DD + log(sl) + cos(ta) + age × (log(sl) + cos(ta))	6	4038.75	78.4	0	1	-2013.36
	8	TRI + log(sl) + cos(ta) + age × (log(sl) + cos(ta))	5	4049.64	89.29	0	1	-2019.81

Table C3: Outputs of Bayesian zero-inflated regression models for broad scale use of each habitat type, and linear mixed-effects models for broad movement ranges and their median topographic ruggedness, mean distance from disturbance, and mean distance from potential denning habitat. Significant relationships are highlighted in bold and denote differences in used movement ranges from the intercept. The intercept is the *available* movement range.

Response Variable	Parameter	Estimate	Est.Error	L-95% CI	U-95% CI	Rhat	Bulk_ESS	Tail_ESS
Spinifex grassland cover	Intercept	1.48	0.18	1.12	1.85	1	1886	1649
	Observed	-0.47	0.32	-1.06	0.18	1	4214	2534
Dense vegetation cover	Intercept	-3.6	0.15	-3.89	-3.33	1	2319	2468
	Observed	0.09	0.26	-0.46	0.57	1	4906	2642
Rocky habitat cover	Intercept	-3.54	0.3	-4.15	-2.93	1.01	1217	1526
	Observed	**1.09**	**0.24**	**0.6**	**1.55**	**1**	**3308**	**2686**
Mine pits and waste dumps cover	Intercept	-2.08	0.21	-2.49	-1.69	1	2226	2005
	Observed	-0.31	0.37	-1.1	0.35	1	2588	2133
Other disturbed land cover	Intercept	-2.29	0.22	-2.75	-1.87	1	2126	1988
	Observed	-0.45	0.34	-1.18	0.18	1	3857	2543
Median topographic ruggedness	Intercept	0.62	0.04	0.53	0.71	1	1059	1152
	Observed	**0.18**	**0.05**	**0.08**	**0.27**	**1**	**4515**	**2482**
Mean disturbance distance	Intercept	1262.35	222.46	802.68	1687.8	1	2674	2300
	Observed	**-888.2**	**425.81**	**-1739.21**	**-53.87**	**1**	**4726**	**2838**
Mean potential denning distance	Intercept	1335.18	151.84	1035.73	1635.3	1	2494	1666
	Observed	**-826.47**	**290.45**	**-1397.02**	**-254.15**	**1**	**3856**	**2719**

Table C4: The outputs of iSSFs for models which had substantial support from AICc ranking (Table C3). Models are separated by their model number for each season. Response variables which were significantly different from the intercept (p = <0.05) are highlighted in bold. The intercept for categorical habitat classifications was rocky habitat.

Season	Mod. num.	Response variable	Coef.	Std. error	z-value	*p*-value	Lower 95% CI	Upper 95% CI
Breeding	3	**Spinifex grassland**	**-1.17**	**0.14**	**-8.47**	**<0.001**	**0.24**	**0.41**
		Dense vegetation	**-0.69**	**0.32**	**-2.12**	**0.034**	**0.27**	**0.95**
		Mine pit and waste dump	**-0.85**	**0.18**	**-4.65**	**<0.001**	**0.30**	**0.61**
		Other disturbed land	**-0.97**	**0.22**	**-4.47**	**<0.001**	**0.25**	**0.58**
		log(step length)	**0.09**	**0.05**	**2.07**	**0.038**	**1.01**	**1.20**
		cosine(turn angle)	0.02	0.08	0.29	0.773	0.87	1.21
		Topographic ruggedness	**0.31**	**0.08**	**3.84**	**0.000**	**1.16**	**1.59**
		Distance from potential denning habitat	**0.00**	**0.00**	**2.54**	**0.011**	**1.00**	**1.00**
	1	**Spinifex grassland**	**-1.17**	**0.14**	**-8.47**	**<0.001**	**0.24**	**0.41**
		Dense vegetation	**-0.71**	**0.33**	**-2.18**	**0.030**	**0.26**	**0.93**
		Mine pit and waste dump	**-0.81**	**0.19**	**-4.33**	**<0.001**	**0.31**	**0.64**
		Other disturbed land	**-0.93**	**0.22**	**-4.24**	**<0.001**	**0.26**	**0.61**
		log(step length)	**0.09**	**0.05**	**2.09**	**0.0370**	**1.01**	**1.20**
		cosine(turn angle)	0.02	0.08	0.30	0.7675	0.87	1.21
		Topographic ruggedness	**0.31**	**0.08**	**3.84**	**0.0001**	**1.16**	**1.59**
		Distance from disturbance	0.00	0.00	0.87	0.3844	1.00	1.00
		Distance from potential denning habitat	**0.00**	**0.00**	**2.15**	**0.0314**	**1.00**	**1.00**
Non-breeding	4	**Spinifex grassland**	**-1.17**	**0.12**	**-9.75**	**<0.001**	**0.25**	**0.39**
		Dense vegetation	**-0.68**	**0.32**	**-2.08**	**0.037**	**0.27**	**0.96**
		Mine pit and waste dump	-0.13	0.37	-0.34	0.732	0.43	1.82
		Other disturbed land	-0.80	0.43	-1.85	0.064	0.19	1.05
		log(step length)	0.11	0.07	1.57	0.116	0.97	1.28
		cosine(turn angle)	0.13	0.26	0.51	0.609	0.69	1.89
		Topographic ruggedness	0.14	0.08	1.86	0.062	0.99	1.34
		Age × log(step length)	-0.03	0.03	-0.95	0.342	0.92	1.03
		Age × cosine(turn angle)	-0.14	0.17	-0.79	0.433	0.62	1.22
	3	**Spinifex grassland**	**-1.10**	**0.13**	**-8.42**	**<0.001**	**0.26**	**0.43**
		Dense vegetation	-0.61	0.33	-1.84	0.066	0.29	1.04
		Mine pit and waste dump	0.06	0.40	0.16	0.874	0.49	2.33
		Other disturbed land	-0.67	0.44	-1.51	0.132	0.22	1.22
		log(step length)	0.12	0.07	1.66	0.096	0.98	1.29
		cosine(turn angle)	0.13	0.26	0.50	0.615	0.69	1.88
		Topographic ruggedness	0.13	0.08	1.64	0.101	0.98	1.32
		Distance from potential denning habitat	0.00	0.00	-1.25	0.210	1.00	1.00
		Age × log(step length)	-0.03	0.03	-0.89	0.375	0.92	1.03
		Age × cosine(turn angle)	-0.14	0.17	-0.79	0.429	0.62	1.22

2	**Spinifex grassland**	**-1.17**	**0.12**	**-9.75**	**<0.001**	**0.25**	**0.39**
	Dense vegetation	**-0.68**	**0.32**	**-2.08**	**0.038**	**0.27**	**0.96**
	Mine pit and waste dump	-0.20	0.37	-0.52	0.601	0.39	1.71
	Other disturbed land	**-0.87**	**0.44**	**-1.99**	**0.047**	**0.18**	**0.99**
	log(step length)	0.10	0.07	1.37	0.172	0.96	1.27
	cosine(turn angle)	0.12	0.26	0.47	0.636	0.68	1.87
	Topographic ruggedness	**0.16**	**0.08**	**2.01**	**0.044**	**1.00**	**1.36**
	Distance from disturbance	0.00	0.00	-1.09	0.277	1.00	1.00
	Age × log(step length)	-0.02	0.03	-0.56	0.579	0.93	1.04
	Age × cosine(turn angle)	-0.13	0.17	-0.76	0.450	0.63	1.23
1	**Spinifex grassland**	**-1.10**	**0.13**	**-8.39**	**<0.001**	**0.26**	**0.43**
	Dense vegetation	-0.60	0.33	-1.83	0.067	0.29	1.04
	Mine pit and waste dump	-0.01	0.41	-0.01	0.989	0.45	2.20
	Other disturbed land	-0.73	0.45	-1.64	0.101	0.20	1.16
	log(step length)	0.10	0.07	1.45	0.147	0.96	1.28
	cosine(turn angle)	0.12	0.26	0.46	0.643	0.68	1.86
	Topographic ruggedness	0.14	0.08	1.79	0.074	0.99	1.34
	Distance from disturbance	0.00	0.00	-1.08	0.279	1.00	1.00
	Distance from potential denning habitat	0.00	0.00	-1.25	0.212	1.00	1.00
	Age × log(step length)	-0.01	0.03	-0.49	0.623	0.93	1.04
	Age × cosine(turn angle)	-0.13	0.17	-0.76	0.448	0.63	1.23
5	**Spinifex grassland**	**-1.22**	**0.12**	**-10.43**	**<0.001**	**0.23**	**0.37**
	Dense vegetation	**-0.76**	**0.32**	**-2.35**	**0.019**	**0.25**	**0.88**
	Mine pit and waste dump	-0.21	0.37	-0.59	0.558	0.39	1.65
	Other disturbed land	**-0.90**	**0.43**	**-2.09**	**0.036**	**0.18**	**0.94**
	log(step length)	0.10	0.07	1.40	0.161	0.96	1.26
	cosine(turn angle)	0.13	0.26	0.50	0.616	0.69	1.88
	Age × log(step length)	-0.02	0.03	-0.87	0.386	0.92	1.03
	Age × cosine(turn angle)	-0.13	0.17	-0.77	0.443	0.62	1.23

Table C5: The mean, standard deviation (SD), minimum (Min), and maximum (Max) Normalised Difference Vegetation Index (NDVI) values for each habitat classification in the *observed* and *available* landscapes. As well as the median, interquartile range (IQR), minimum, and maximum Topographic Ruggedness Index (TRI) in the *observed* and *available* landscapes.

NDVI		**Mean**	**SD**	**Min**	**Max**
	Spinifex grassland	0.16	0.04	0.03	0.64
	Dense vegetation	0.36	0.11	0.13	0.97
	Rocky habitat	0.19	0.05	0.07	0.62
	Mine pits & waste dumps	0.09	0.04	0.00	0.98
	Other disturbed land	0.11	0.04	0.00	0.65
TRI		**Median**	**IQR**	**Min**	**Max**
	Spinifex grassland	0.500	0.375	0.00	6.000
	Dense vegetation	0.375	0.375	0.00	5.500
	Rocky habitat	1.250	1.000	0.00	4.625
	Mine pits & Waste dumps	0.500	0.375	0.00	6.875
	Other disturbed land	0.500	0.375	0.00	5.875

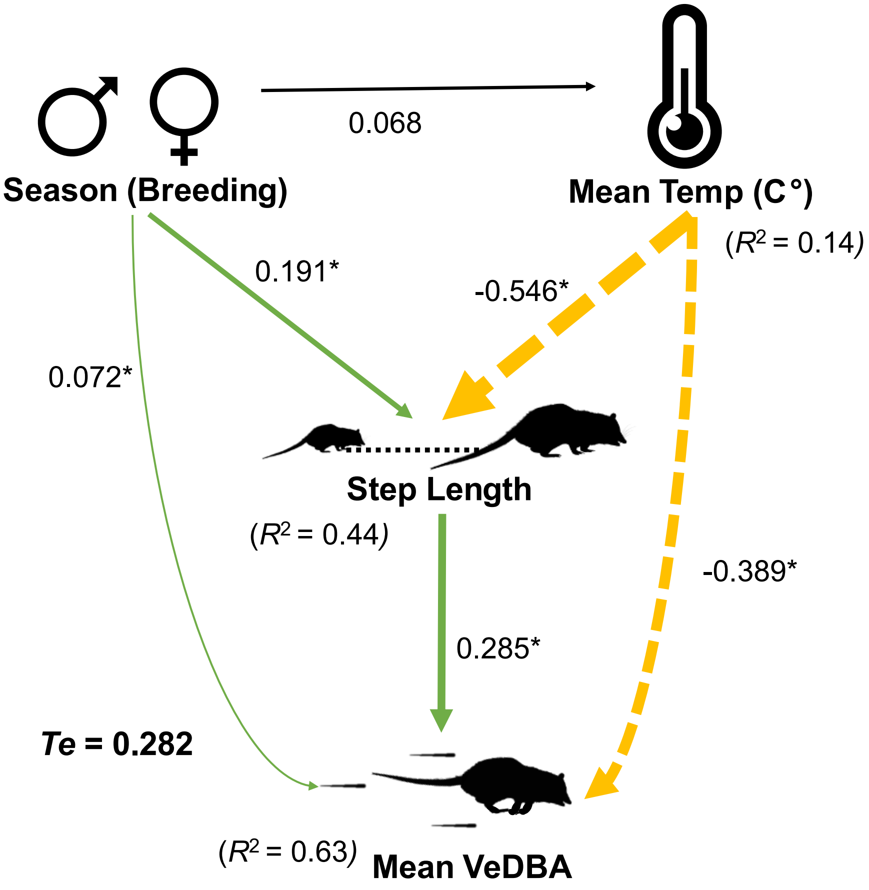


Figure C5: Relevant range coefficients for step length and mean VeDBA related to the influence of temperature and season (specifically, breeding season). Red dashed arrows represent a negative relationship and blue solid arrows represent a positive relationship. Arrow width shows the size of the effect, with wider arrows representing a larger effect. An asterisk signifies that the relationship is significant (p = <0.05) and the conditional R^2 value for step length and mean VeDBA is listed for each model, outlining the variance explained by the predictor variables. *Te* represents the total effect coefficient of season on mean VeDBA, both directly and mediated through step length. Icons adapted from Microsoft PowerPoint.

References

ASF DAAC 2022. ALOS PALSAR_Radiometric_Terrain_Corrected_high_res; Includes Material © JAXA/METI 2009. Accessed 30 June 2022 from https://asf.alaska.edu/data-sets/derived-data-sets/alos-palsar-rtc/alos-palsar-radiometric-terrain-correction/.

Congedo, L. 2016. Semi-Automatic Classification Plugin Documentation. Release 6.0.1.1.

Cowan, M. A., Dunlop, J. A., Turner, J. M., Moore, H. A. & Nimmo, D. G. 2020. Artificial refuges to combat habitat loss for an endangered marsupial predator: How do they measure up? *Conservation Science and Practice,* 2**,** e204.

Cowan, M. A., Moore, H. A., Hradsky, B. A., Jolly, C. J., Dunlop, J. A., Wysong, M. L., Hernandez-Santin, L., Davis, R. A., Fisher, D. O., Michael, D. R., Turner, J. M., Gibson, L. A., Knuckey, C. G., Henderson, M. & Nimmo, D. G. 2022. Non-preferred habitat increases the activity area of the endangered northern quoll (*Dasyurus hallucatus*) in a semi-arid landscape. *Australian Mammalogy,* 45**,** 138–150.

Hernandez-Santin, L., Goldizen, A. W. & Fisher, D. O. 2016. Introduced predators and habitat structure influence range contraction of an endangered native predator, the northern quoll. *Biological Conservation,* 203**,** 160–167.

Hernandez-Santin, L., Goldizen, A. W. & Fisher, D. O. 2022. Northern quolls in the Pilbara persist in high-quality habitat, despite a decline trajectory consistent with range eclipse by feral cats. *Conservation Science and Practice***,** e12733.

Leroux , L., Congedo , L., Bellón , B., Gaetano , R. & Bégué , A. 2018. Land cover mapping using Sentinel-2 images and the semi-automatic classification plugin: A northern Burkina Faso case study. *QGIS and Applications in Agriculture and Forest.*

Moore, H. A., Michael, D. R., Dunlop, J. A., Valentine, L. E., Cowan, M. A. & Nimmo, D. G. 2022. Habitat amount is less important than habitat configuration for a threatened marsupial predator in naturally fragmented landscapes. *Landscape Ecology,* 37**,** 935–949.

Moore, H. A., Michael, D. R., Ritchie, E. G., Dunlop, J. A., Valentine, L. E., Hobbs, R. J. & Nimmo, D. G. 2021. A rocky heart in a spinifex sea: occurrence of an endangered marsupial predator is multiscale dependent in naturally fragmented landscapes. *Landscape Ecology,* 36**,** 1359–1376.

Pandey, A. C. & Kulhari, A. 2018. *Semi-supervised spatiotemporal classification and trend analysis of satellite images,* Singapore, Springer Singapore.

QGIS Development Team 2020. QGIS Geographic Information System. Open Source Geospatial Foundation Project.

R Core Team 2023. R: A language and environment for statistical computing. *R Foundation for Statistical Computing*.

Riley, S. J., DeGloria, S. D. & Elliot, R. 1999. Index that quantifies topographic heterogeneity. *intermountain Journal of sciences,* 5**,** 23–27.

Signer, J. & Balkenhol, N. 2015. Reproducible home ranges (rhr): A new, user-friendly R package for analyses of wildlife telemetry data. *Wildlife Society Bulletin,* 39**,** 358–363.

Tilahun, A. & Teferie, B. 2015. Accuracy assessment of land use land cover classification using Google Earth. *Am. J. Environ. Prot,* 4**,** 193–198.

USGS 2023. Earth Explorer.

Appendix D: Supplementary material for Chapter 5

Appendix D1: Simulation model validation

For each model with 0, 1, 2, and 3 pairs of harmonics, as well as the observed data we calculated a range of summary statistics used to compare movement among models and observed quoll data. The summary statistics informed a principal component analysis (PCA) to assess similarities and differences between models following Forrest et al. (2024), Abrahms et al. (2017), and Kays et al. (2023). Summary statistics were:

- Mean step length
- Median step length
- Shape and scale of a Gamma distribution fitted to the step lengths
- Turn angle - concentration (k) of von Mises distribution
- Path sinuosity
- Path straightness
- Total distance, which is the displacement from initial location (i.e. distance between the first and last locations)
- 50% area of the KDE utilisation distribution
- 75% area of the KDE utilisation distribution
- 95% area of the KDE utilisation distributions
- The proportion of habitat at the end of each step which was rocky habitat (rocky habitat / total habitat)
- The proportion of habitat at the end of each step which was riparian habitat (riparian habitat / total habitat)
- The proportion of habitat at the end of each step which was spinifex grassland (spinifex grassland / total habitat)
- The proportion of habitat at the end of each step which was mine pits and waste dumps (mine pits and waste dumps / total habitat)
- The proportion of habitat at the end of each step which was other disturbed land (other disturbed land / total habitat)
- Mean distance from rocky habitat
- Median distance from rocky habitat
- Standard deviation for distance from rocky habitat
- Mean distance from mining disturbance
- Median distance from mining disturbance
- Standard deviation for distance from mining disturbance

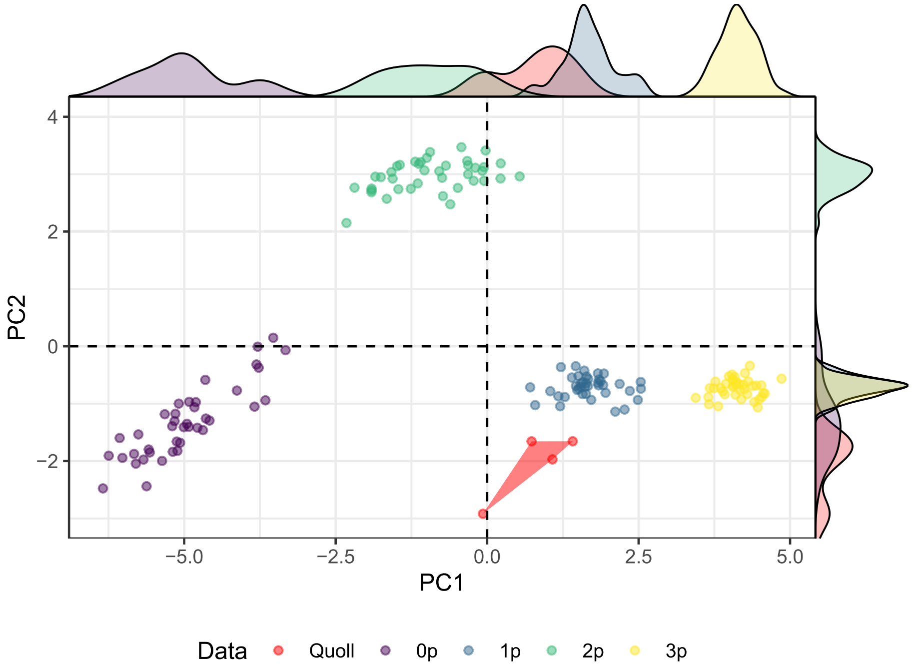


Figure D1: PCA plot of the summary movement metrics comparing simulations from iSSFs with 0, 1, 2, and 3 pairs of harmonics to the observed northern quoll data in the current mining landscape.

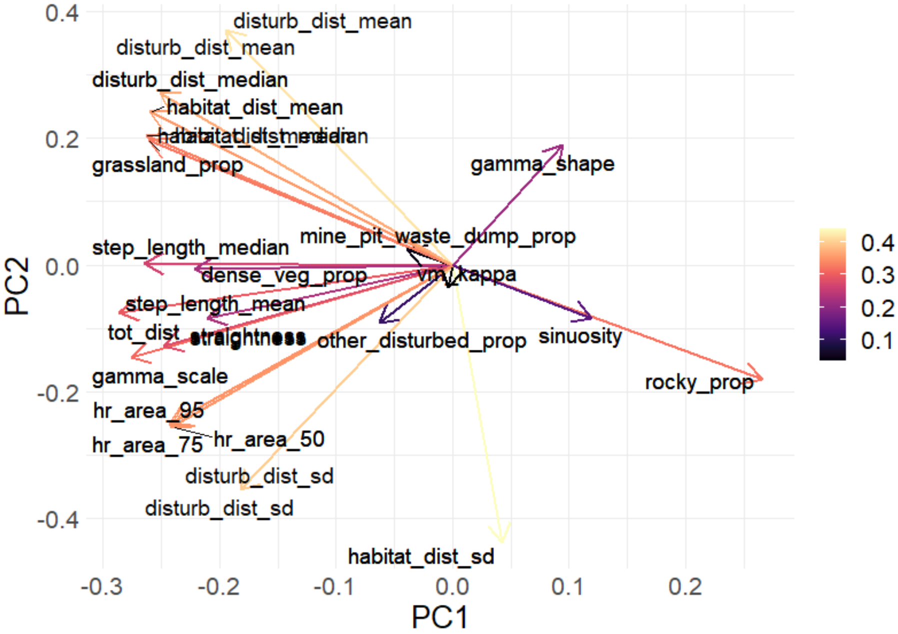


Figure D2: The **l**oadings plot relevant to the PCA in Figure D1 showing the importance of each summary statistic on the first two principal components. Arrows and colours indicate the direction and magnitude of influence by each statistic on PC1 and PC2.

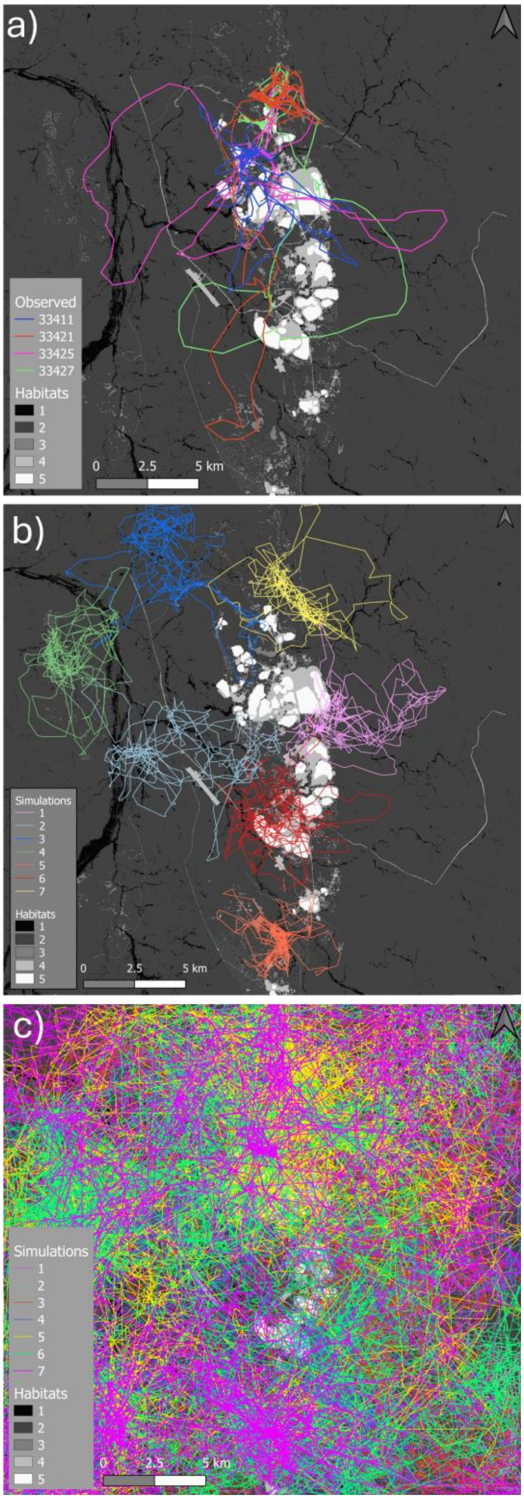


Figure D3: Maps depicting movement tracks in the current landscape of a) observed northern quolls (average 185 steps), b) a subset of seven simulations with the memory process included (480 steps per simulation), and c) a subset of seven simulations with the memory process omitted (8760 steps per simulation).

Appendix D2: Landscape map creation

For each of the four landscapes, we created three habitat maps, including i) a habitat type map, including riparian habitat, spinifex grassland, rocky habitat, mine pits and waste dumps, and other disturbed land (for mining landscapes), ii) a distance from rocky habitat map, and iii) a distance from mining disturbance map (all at a 10 m scale). See Cowan et al. (2024) for details on the creation of habitat maps for the current mining landscape and distance maps.

To create the 'non-mining landscape', we converted all 'other disturbed land' and 'waste dumps' from the 'current mining landscape' to spinifex grassland, given this habitat is often flat before mining disturbance (e.g., roads, run of mine (ROM) stockpile pads, mining camps, building infrastructure). Then, we placed rocky habitat patches within all 'mine pit' contiguous patches which were the same shape as the mine pit and equal to 30% of its' total area. Rocky habitat often makes up 30% of undisturbed Pilbara landscapes (Moore et al., 2022), and mining often targets rocky habitats for ore (Ramanaidou and Morris, 2010), therefore it can be presumed that mine pits once contained some amounts of surface rocky habitat. Thus formed the non-mining landscape.

To create the 'dispersed mining landscape', we randomly selected 58 contiguous rocky habitat patches from the 'non-mining landscape'—equal to the number of original mine pits and waste dumps—separated by a minimum of 680.05 m, which was 5 times the average nearest neighbour distance between mine pits in the 'current mining landscape' (136.01 m). We then relocated all 58 mine pits and waste dump patches to the centroid of a randomly paired selected rocky habitat patch. Some overlap was observed among relocated polygons, so a 59th polygon, equal in size to the difference between original and fragmented mine pits and waste dumps was added to a random rocky habitat patch, to ensure the same area was covered by mine pits and waste dumps across all mining landscapes (12.58 km^2). We then fit a buffer of other disturbed land around each fragmented mine pit and waste dump patch until the habitat covered the same total area as it did in the 'current mining landscape' (17.46 km^2). Rocky patches not selected for new mine pit patches were left undisturbed. Thus formed the dispersed mining landscape.

To create the ‘aggregated mining landscape’ we identified an existing mine polygon from (Tang and Werner, 2023), which was equal to the area of all mine pits and waste dumps in the ‘current mining landscape’. We then randomly placed it in the ‘non-mining landscape’ and fit a buffer of other disturbed land around the polygon until it covered the same total area as other disturbed land in the ‘current mining landscape’. Thus formed the aggregated mining landscape.

Checks were made in all cases to ensure the proportions of habitats in the three mining landscapes were within 0.10% of each other. Distance maps were created for rocky habitat and mine pits and waste dumps for all landscapes, as per Cowan et al. (2024).

Table D1: Model outputs from GLMMs comparing home range size, mean energetic costs, and revisitations among landscapes.

Analysis	Model	Landscape	Estimate	Std. error	Z value	P value
Home range size	Non-mining vs. mining	Intercept	17.15	0.03	651.80	<0.001
		Fragmented landscape	0.02	0.02	0.70	0.473
		Current landscape	0.05	0.02	2.00	0.042
		Consolidated landscape	-0.04	0.02	-1.80	0.078
Home range size	Mining composition	Intercept	17.19	0.03	638.50	<0.001
		Fragmented landscape	-0.03	0.02	-1.20	0.234
		Consolidated landscape	-0.09	0.02	-3.70	<0.001
Mean energetic cost	Non-mining vs. mining	Intercept	0.42	0.02	20.23	<0.001
		Fragmented landscape	0.11	0.00	48.52	<0.001
		Current landscape	0.14	0.00	59.05	<0.001
		Consolidated landscape	0.10	0.00	43.85	<0.001
Mean energetic cost	Mining composition	Intercept	0.56	0.02	25.77	<0.001
		Fragmented landscape	-0.02	0.00	-9.72	<0.001
		Consolidated landscape	-0.03	0.00	-14.57	<0.001
Revisitations	Non-mining vs. mining (rocky habitat)	Intercept	0.34	0.01	44.08	<0.001
		Fragmented landscape	0.02	0.00	6.94	<0.001
		Current landscape	0.03	0.00	9.06	<0.001
		Consolidated landscape	0.05	0.00	12.64	<0.001
	Non-mining vs. mining (spinifex grassland)	Intercept	0.04	0.00	14.43	<0.001
		Fragmented landscape	0.00	0.00	0.02	0.988
		Current landscape	0.00	0.00	0.59	0.555
		Consolidated landscape	0.01	0.00	1.45	0.148
	Non-mining vs. mining (riparian habitat)	Intercept	0.05	0.02	3.06	0.002
		Fragmented landscape	0.00	0.02	0.13	0.894
		Current landscape	0.01	0.02	0.50	0.618
		Consolidated landscape	0.02	0.02	0.96	0.337
Revisitations	Mining composition (rocky habitat)	Intercept	0.37	0.01	52.77	<0.001
		Fragmented landscape	-0.01	0.00	-1.95	0.052
		Consolidated landscape	0.01	0.00	3.84	<0.001
	Mining composition (spinifex grassland)	Intercept	0.04	0.00	15.28	<0.001
		Fragmented landscape	0.00	0.00	-0.56	0.573
		Consolidated landscape	0.00	0.00	0.85	0.394
	Mining composition (riparian grassland)	Intercept	0.06	0.01	4.24	<0.001
		Fragmented landscape	-0.01	0.02	-0.35	0.729
		Consolidated landscape	0.01	0.02	0.51	0.607
	Mining composition (mine pits and waste dumps)	Intercept	0.02	0.01	2.03	0.042
		Fragmented landscape	0.00	0.02	0.26	0.798
		Consolidated landscape	-0.01	0.02	-0.24	0.811
	Mining composition (other disturbed land)	Intercept	0.03	0.01	2.74	0.006
		Fragmented landscape	0.00	0.02	0.19	0.851
		Consolidated landscape	-0.01	0.02	-0.68	0.499

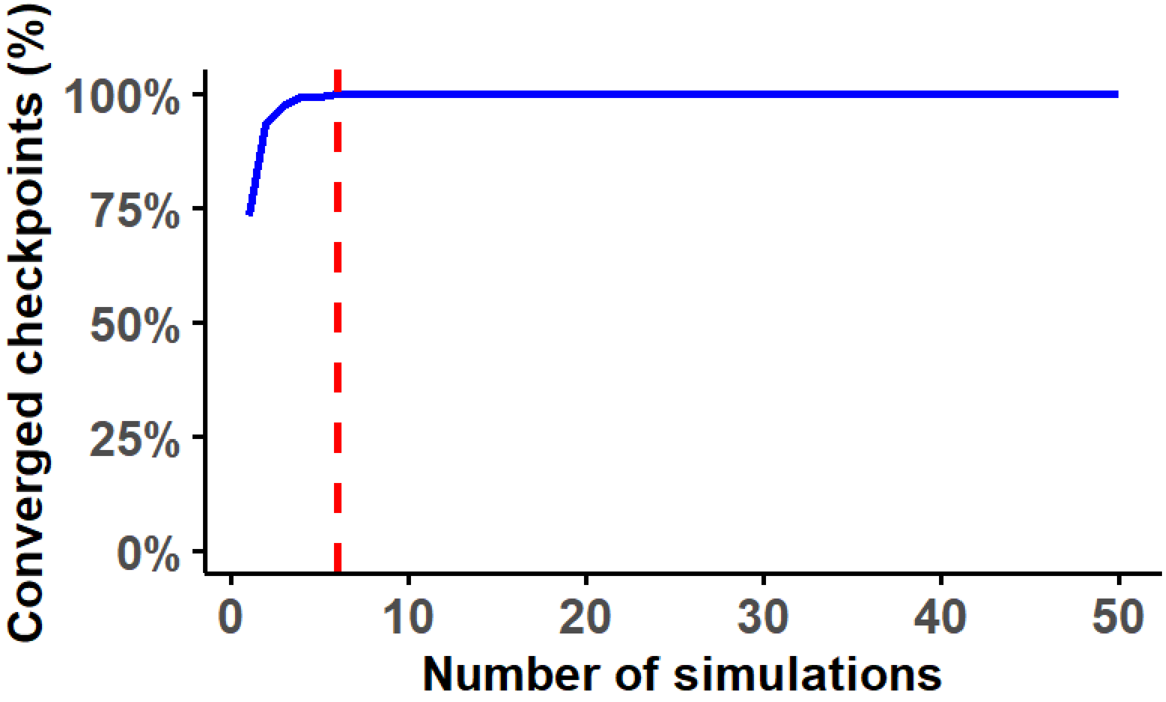


Figure D4: The blue line shows the proportion of converged checkpoints relative to the number of simulations tested. The dashed red line represents the point of convergence (6 simulations; 100% coverage of checkpoints).

Table D2: Model outputs from GLMMs comparing the average steps taken between rocky habitat patches.

Analysis	Model	Landscape	Estimate	Std. error	Z value	P value
Average steps	Non-mining vs. mining	Intercept	1.58	0.00	361.80	<0.001
		Fragmented landscape	0.24	0.01	35.10	<0.001
		Current landscape	0.35	0.01	51.10	<0.001
		Consolidated landscape	0.15	0.01	22.70	<0.001
	Mining composition	Intercept	1.94	0.01	355.80	<0.001
		Fragmented landscape	-0.12	0.01	-15.30	<0.001
		Consolidated landscape	-0.21	0.01	-29.00	<0.001

References

Abrahms, B., Seidel, D. P., Dougherty, E., Hazen, E. L., Bograd, S. J., Wilson, A. M., Weldon Mcnutt, J., Costa, D. P., Blake, S., Brashares, J. S. & Getz, W. M. 2017. Suite of simple metrics reveals common movement syndromes across vertebrate taxa. *Movement Ecology,* 5**,** 12.

Cowan, M. A., Dunlop, J. A., Gibson, L. A., Moore, H. A., Setterfield, S. A. & Nimmo, D. G. 2024. Movement ecology of an endangered mesopredator in a mining landscape. *Movement Ecology,* 12**,** 5.

Forrest, S. W., Pagendam, D., Bode, M., Drovandi, C., Potts, J. R., Perry, J., Vanderduys, E. & Hoskins, A. J. 2024. Simulating animal movement trajectories from temporally dynamic step selection functions. *bioRxiv***,** 2024.03.19.585696.

Kays, R., Hirsch, B., Caillaud, D., Mares, R., Alavi, S., Havmøller, R. W. & Crofoot, M. 2023. Multi-scale movement syndromes for comparative analyses of animal movement patterns. *Movement Ecology,* 11**,** 61.

Moore, H. A., Michael, D. R., Dunlop, J. A., Valentine, L. E., Cowan, M. A. & Nimmo, D. G. 2022. Habitat amount is less important than habitat configuration for a threatened marsupial predator in naturally fragmented landscapes. *Landscape Ecology,* 37**,** 935–949.

Ramanaidou, E. R. & Morris, R. C. 2010. A synopsis of the channel iron deposits of the Hamersley Province, Western Australia. *Applied Earth Science,* 119**,** 56–59.

Tang, L. & Werner, T. T. 2023. Global mining footprint mapped from high-resolution satellite imagery. *Communications Earth & Environment,* 4**,** 134.

Appendix E: High post-sex survival of the world's largest semelparous mammal

Published in *Austral Ecology* in September 2024.

Manuscript citation**:** Cowan, M. A., Dunlop, J. A., Hernandez-Santin, L., Heidrich, A., Knuckey, C. G. & Nimmo, D. G. (2024). High post-sex survival of the world's largest semelparous mammal. *Austral Ecology,* 49**,** e13595.

Received: 24 April 2024 | Revised: 1 July 2024 | Accepted: 8 September 2024
DOI: 10.1111/aec.13595

NATURAL HISTORY NOTE

High post-sex survival of the world's largest semelparous mammal

Mitchell A. Cowan[1,2] | **Judy A. Dunlop**[1,2,3] | **Lorna Hernandez-Santin**[4] | **Astrid Heidrich**[5] | **Chris G. Knuckey**[6] | **Dale G. Nimmo**[1]

[1]Gulbali Institute, School of Agricultural, Environmental and Veterinary Sciences, Charles Sturt University, Thurgoona, New South Wales, Australia

[2]School of Agriculture and Environment, The University of Western Australia, Crawley, Western Australia, Australia

[3]School of Molecular and Life Sciences, Curtin University, Bentley, Western Australia, Australia

[4]Centre for Mined Land Rehabilitation, Sustainable Minerals Institute, University of Queensland, St. Lucia, Queensland, Australia

[5]Spectrum Ecology and Spatial, Leederville, Western Australia, Australia

[6]Biologic Environmental Survey, East Perth, Western Australia, Australia

Correspondence
Mitchell A. Cowan, Gulbali Institute, School of Agricultural, Environmental and Veterinary Sciences, Charles Sturt University, 386 Elizabeth Mitchell Drive, Thurgoona, NSW 2640, Australia.
Email: mcowan@csu.edu.au; mitchcow96@gmail.com and mitchell.cowan@uwa.edu.au

Funding information
Charles Sturt University; Consolidated Minerals; Department of Biodiversity, Conservation and Attractions

Abstract

Males of the endangered northern quoll (*Dasyurus hallucatus*) are facultatively semelparous, often dying following their first breeding season. This is often driven by high breeding costs: males travel and mate extensively in breeding season, resulting in reduced body condition. Annual post-breeding survival rates for male northern quolls have been recorded between 0% and 12.5% across their range in northern Australia. We highlight an observed 50% survival rate of male northern quolls (3 of 6) living into their second year in a Pilbara mining landscape. High male survival here may be attributed to above average rainfall in the landscape and reduced breeding opportunities, due to low female abundance—likely driven by large amounts of unfavourable mining land. This likely led to lower hormonal stress associated with breeding for males, as well as increased resource availability. Given northern quoll population persistence is highly dependent on breeding success, high survival of male northern quolls may inadvertently stabilize populations if they can breed again in a second year, though this is yet to be observed in the Pilbara region. Nevertheless, semelparity of male northern quolls likely varies with environmental and demographic factors, demonstrating that northern quoll populations may be resilient to disturbance in an unpredictable semi-arid environment.

KEYWORDS
breeding, *Dasyurus hallucatus*, marsupial, northern quoll, semelparity

INTRODUCTION

Semelparity refers to a reproductive strategy where an individual allocates all of its resources to a single, often massive, reproductive event before dying (Cole, 1954). This strategy exists on a semelparity–iteroparity continuum, where iteroparous individuals reproduce multiple times over their lifespan (Hughes, 2017). Semelparity arises when adult survival is low or chances of reproduction are highly variable, such that channelling reproductive effort into a single breeding season can maximize the reproductive success of individuals, benefitting population persistence (Young, 2010). Survival after the first breeding season in semelparous species is uncommon, as the intense allocation of resources to reproduction significantly compromises an individual's fitness, and thus their survival (Cockburn, 1997; Lee & Cockburn, 1985). The subsequent reduction in competition for offspring allows new recruits to access more resources, increasing their survival probability (Fisher & Blomberg, 2011; Oakwood et al., 2001).

Globally, semelparity in mammals is rare, having developed in some form in only six genera of mammals (Lee & Cockburn, 1985). These include small male dasyurids such as *Antechinus* spp. (Braithwaite & Lee, 1979), dibblers (*Parantechinus apicalis*; Dickman & Braithwaite, 1992), kaluta (*Dasykaluta rosamondae*; Hayes et al., 2019), and *Phascogale* spp. (Cuttle, 1982; Old et al., 2021). Semelparity has also been observed in males of a larger dasyurid, the endangered northern quoll (*Dasyurus hal- lucatus*; 350–1000 g; Oakwood et al., 2001), making the northern quoll the world's largest mammal with any level of semelparity. Male northern quolls are facultatively semelparous, meaning individuals can occasionally sur- vive after breeding in some populations (Fisher et al., 2013). This differs from obligate semelparity seen in most smaller dasyurids, where males always die following their first breeding season due to immune system col- lapse (Fisher et al., 2013).

The northern quoll has faced significant range contraction in northern Australia, except in the semi-arid Pilbara region, which remains a stronghold for the species, likely due to the absence of the invasive and poisonous cane toad (*Rhinella marina*) (Moore et al., 2022). Pilbara northern quolls often mate between July and September, with exact timing influenced by rainfall (Moore et al., 2022). Northern quolls exhibit multiple paternity, with females able to sire litters of up to eight young, each with different paternity (Chan et al., 2020). Therefore, males mate extensively during breeding season, to breed with as many females as possible (Oakwood, 2000). Annual survival of male northern quolls into a second year has not been observed above 12.5%, because the intense breeding season leads to reduced body condition and function (Dickman & Braithwaite, 1992). Male northern quoll deterioration is different to the lethal immune system collapse seen in smaller dasyurids (Bradley, 1987; Fisher et al., 2013), likely caused by harsh environmental conditions and high energetic breeding costs (i.e., increased activity and reduced rest; Dickman & Braithwaite, 1992, Gaschk et al., 2023). We present an example of a northern quoll population from the Pilbara exhibiting unprecedented second-year male survival and provide some potential explanations for this unusual observation.

METHODS

We conducted two trapping surveys for northern quolls at the Woodie Woodie mine, an active manganese mine on Nyamal Country in the Pilbara, Western Australia (Cowan et al., 2024). Trapping occurred dur- ing part of the breeding season (September–October) in 2021 and non- breeding season (June–July) in 2022 and spanned an area just over 61 km^2. Northern quolls were captured in suitable habitats using wire cage traps (45 cm × 17 cm × 17 cm; Sheffield Wire Co., Welshpool, WA), baited with oats, peanut butter, and sardines (Dunlop et al., 2014). Trapping spanned 23 nights in 2021 and 18 nights in 2022 (Dunlop et al., 2014). Morphological measurements, including sex, weight, testes size (for males), hindfoot length, and tail circumference, were recorded (Cowan et al., 2024). Additionally, we collated published and unpublished northern quoll trapping data spanning 2010–2023 in the Pilbara to contextualize male survival rates across years (Hernandez-Santin et al., 2019; J. A. Dunlop, unpubl. data; C. G. Knuckey, unpubl. data; A. Heidrich, unpubl. data). All datasets were created using similar trapping methodologies and effort, and second-year males were identified using passive integrated transponder (PIT) tags (i.e., microchips) which were inserted into northern quolls upon first trapping (as per Dunlop et al., 2014). For one collated dataset (Hernandez-Santin et al., 2019), second-year males were identified through visual inspection of healed scars and hair growth—signs recorded by the authors in second-year microchipped males (Figure 1).

RESULTS AND DISCUSSION

Seven male northern quolls were recorded at Woodie Woodie in 2021, one of which was killed by a feral cat (*Felis catus*) during GPS tracking (Cowan et al., 2024). Of the six remaining males, three were recorded

FIGURE 1 Examples of male northern quolls in their first and second year. Purple and red circles show the hair loss by male quolls in September 2021 (breeding season) and subsequent recovery in June 2022 (non-breeding season) following breeding season. Yellow circles show the recovery of an area where a tick (*Ixodes* sp.) was found and removed.

surviving into their second year (50%). In 2022, second-year male northern quolls made up one-third of the male population recorded at Woodie Woodie—the most of any Pilbara population sampled between 2010 and 2023 (Figure 2). The collated datasets recorded only four other male northern quolls living into a second year in the Pilbara, in 2014 ($n = 2$), 2015, and 2023 (Table 1). Second-year males were not recorded in eight of the 14 survey years (Figure 2). The previous maximum survival rate of male northern quolls living into a second year in the Pilbara was ~5% (Hernandez-Santin et al., 2019). Annual male survival observed in other regional populations outside the Pilbara included 4% in the Kimberley (Schmitt et al., 1989) and 0% in the Northern Territory, specifically Kakadu and Groote Eylandt (Heiniger et al., 2020; Oakwood et al., 2001). One study in Kakadu recorded a 12.5% survival rate of males to a second breeding season in 1978 (Begg, 1981); however, most males in the Northern Territory die within 2 weeks of mating (Dickman & Braithwaite, 1992; Oakwood et al., 2001). Thus, our observed 50%

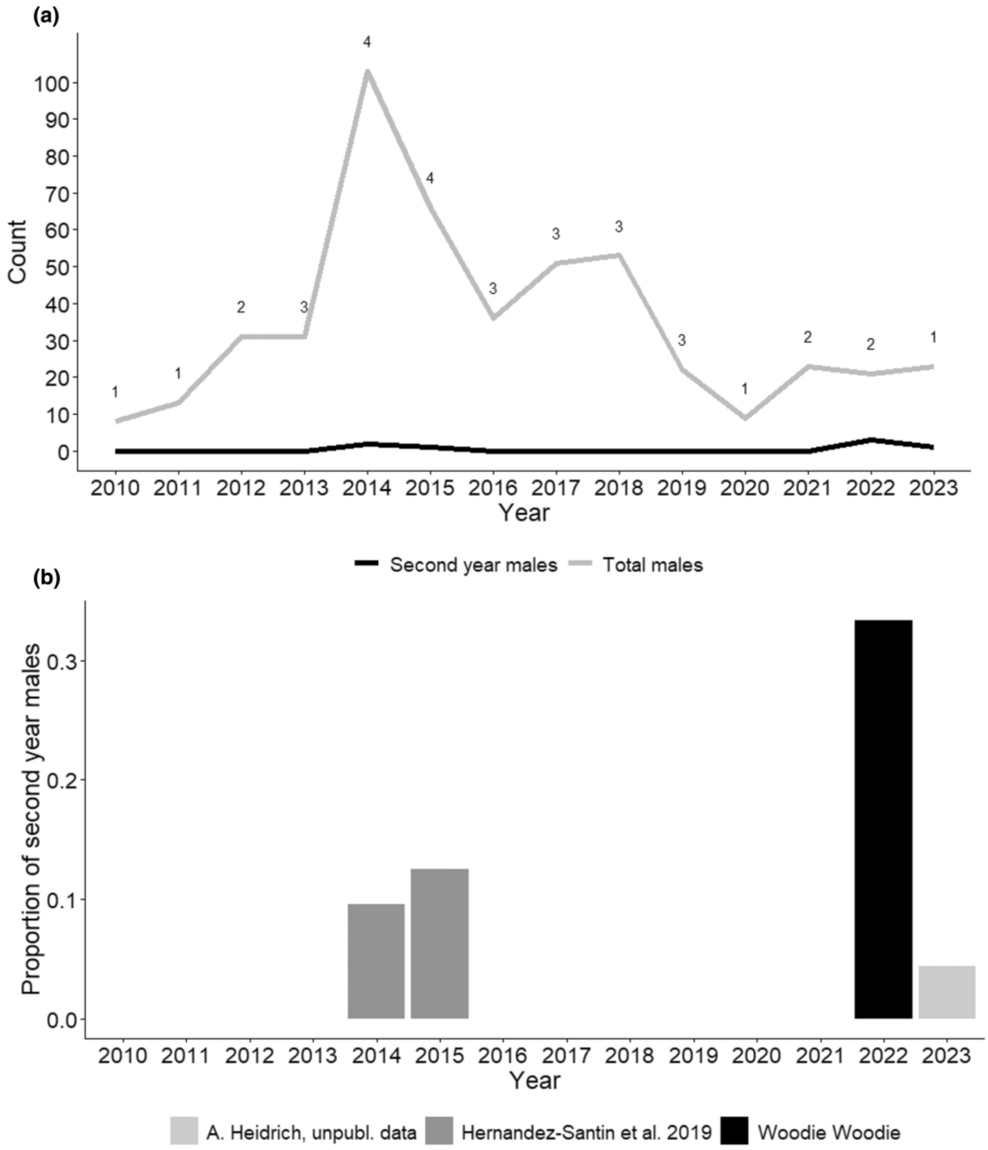


FIGURE 2 The (a) total number of male northern quolls trapped in the Pilbara using the five datasets from 2010 to 2023 (grey line), and the number of second-year males per year (black line)—numbers above lines reflect the number of datasets available for that year; and the (b) proportion of second-year males in each annual male population (relative to the annual population monitored in each dataset).

TABLE 1 Body condition statistics for Pilbara second-year males in their first year (where available) and second year.

ID	Month	Year	Age	Mass (g)	Pes (mm)	Tail circ. (mm)	Testes (mm)	Dataset
Q1	September	2021	1	690	36	54	–	Woodie Woodie
Q1	June	2022	2	600	33	45	21	
Q2	September	2021	1	640	38	50	24	
Q2	June	2022	2	805	34	65	15	
Q3	September	2021	1	680	36	50	–	
Q3	June	2022	2	700	35	55	22	
Q4	July	2022	1	710	–	–	–	A. Heidrich, unpubl. data
Q4	July	2023	2	–	–	–	–	
Q5	April	2015	2	525	44	50	11	Hernandez-Santin et al., 2019
Q6	April	2014	2	735	64	60	16	
Q7	May	2014	2	830	40	69	17	
			Year 1 mean	680	37	51	24	All
			Year 1 SE	15	1	1	–	
			Year 2 mean	734	41	59	18	All
			Year 2 SE	48	5	4	2	

Note: Dashes (−) mean data for that statistic were not recorded in that year.

survival rate (3 of 6) of males into a second year was the highest recorded of any northern quoll population.

Reasons for high male survival at Woodie Woodie in 2022 may include high resource abundance that year, indicated by improved second-year male body condition (i.e., increased weight and tail circumference; Table 1). Rainfall was above average in 2021 and 2022 (Bureau of Meteorology, 2024), likely supporting increased food availability. Hernandez-Santin et al. (2019) found very low food abundance for northern quolls during a drought in the summer of 2014/15, corresponding with reductions in northern quoll population size in 2015. However, despite the favourable conditions during our study, energy expenditure is expected to be higher in our study area than in the relatively undisturbed landscapes like that studied by Hernandez-Santin et al. (2019). This is because northern quolls move through energetically costly mining areas that typically lack food and other resources (Cowan et al., 2024). Given that the high energy demands of the breeding season are a leading factor driving male northern quoll mortality (Gaschk et al., 2023), any further increase to energetic costs, due to the presence of unfavourable mining areas, would be expected to reduce survival.

Further, the mechanism of semelparous male survival is dependent on the density of males as well as females (Fisher et al., 2013). Male northern quolls at Woodie Woodie made up 70% and 75% of the population in 2021 and 2022 respectively, much higher than annual percentages recorded across two comparably sized study areas (Dampier Archipelago, Indee Station) by Western Australia's Department of Biodiversity, Conservation and Attractions (DBCA) between 2014 and 2019 (male average = 57%; J. A. Dunlop, unpubl. data). This suggests that male northern quolls at Woodie Woodie should have increased breeding-associated stress and competition intensity than quolls at the DBCA monitored sites—driving lower survival (Fisher et al., 2013). As we saw the opposite, this does not help to explain the high survival of males at Woodie Woodie.

A more likely explanation for high male northern quoll survival during our study may be related to reduced breeding costs for males during the breeding season, due to low female abundance and reduced breeding opportunities. At Woodie Woodie, Cowan et al. (2024) recorded only three female northern quolls in 2021 and 2022, respectively (M. A. Cowan, unpubl. data), compared with an annual average of 11 females at the two similar sized study areas (Dampier Archipelago, Indee Station) monitored by DBCA between 2014 and 2019 (Dunlop et al., 2014; J. A. Dunlop, unpubl. data). Female northern quolls require high-quality denning habitats during the breeding season (Cowan et al., 2020; Oakwood, 1997), which are rare in mining landscapes, potentially leading to the observed scarcity of females. Low female northern quoll abundance in our study area likely resulted in few breeding opportunities for males—and thus low breeding costs—consequently increasing survival. A lack of female hormonal scent marking in the study area may have also worked to reduce male northern quoll breeding drive (Oakwood, 1997). In a captive setting with limited breeding opportunities, stable resources, and lower energetic costs, male northern quolls have been recorded living for up to 6 years (Oakwood, 1997). In a similar vein, reduced breeding costs could significantly increase free-living male northern quoll survival—as previously reported in female *Antechinus* spp. (Bradley et al., 1980).

One remaining question for northern quolls in the Pilbara is whether second-year males actually contribute to a second breeding season (Oakwood, 1997). There is evidence of second-year males breeding in the closed forest and open woodland habitats of Kakadu National Park (Begg, 1981; Schmitt et al., 1989), but this is yet to be observed in the semi- arid savannas of the Pilbara. It is likely that second-year male northern quolls at Woodie Woodie were within 2 months of breeding season in June 2022 (Shaw et al., 2022), given that a nearby population (~60 km away) began breeding in August (M. A. Cowan unpubl. data). Hernandez-Santin et al. (2019) found no evidence that male northern quolls contributed to a second breeding season in the Pilbara, although it was possible given im- proved body condition in their second year. It is also possible that second- year males have a reduced ability to breed, given they had smaller testes in their second than first years (Table 1).

The implications of high male survival in a landscape may include higher competition for new male recruits in the following breeding season. However, it may also inadvertently stabilize populations with limited breeding success in an unpredictable environment, allowing individuals another chance at breeding. This would be beneficial given northern quoll persistence relies heavily on the recruitment of young (Moro et al., 2019), but this is yet to be proven in Pilbara populations. Nevertheless, our observation reinforces that there is variability in male semelparity among northern quoll populations, likely influenced by environmental, population demographic, and behavioural factors, as suggested by Dickman and Braithwaite (1992). Future research may consider how exactly habitat quality and northern quoll demographics influence breeding success, and subsequently, male survival and population dynamics.

AUTHOR CONTRIBUTIONS

Mitchell A. Cowan: Conceptualization (lead); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); validation (equal); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Judy A. Dunlop:** Conceptualization (equal); data curation (equal); investigation (supporting); methodology (supporting); writing – review and editing (equal). **Lorna Hernandez-Santin:** Data curation (equal); writing – review and editing (equal). **Astrid Heidrich:** Data curation (equal); writing – review and editing (equal). **Chris G. Knuckey:** Data curation (equal); writing – review and editing (equal). **Dale G. Nimmo:** Conceptualization (equal); data curation (equal); methodology (equal); supervision (lead); writing – review and editing (equal).

ACKNOWLEDGEMENTS

We acknowledge the Nyamal people as the Traditional Owners of the land upon which fieldwork was undertaken. We thank Charles Sturt University, Consolidated Minerals, and the Department of Biodiversity, Conservation and Attractions (DBCA) for supporting the fieldwork for this study. Particular thanks to Luke Barrett, Rory Embleton, Jacqui Roberts, and Kaylee Prince for assisting with fieldwork. We also acknowledge contributions of data by Spectrum Ecology & Spatial, Biologic, DBCA, Fortescue Metals Group, Damien Cancilla, Todd Edwards, and the University of Queensland. Open access publishing facilitated by Charles Sturt University, as part of the Wiley - Charles Sturt University agreement via the Council of Australian University Librarians.

FUNDING INFORMATION

Fieldwork was funded by Charles Sturt University, Consolidated Minerals, and the Department of Biodiversity, Conservation and Attractions.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Given shared ownership and usage limitations of some data, raw trapping data can be requested from the corresponding author.

ORCID

Mitchell A. Cowan https://orcid.org/0000-0001-8432-5301
Judy A. Dunlop https://orcid.org/0000-0003-4842-0672
Dale G. Nimmo https://orcid.org/0000-0002-9814-1009

REFERENCES

Begg, R.J. (1981) The small mammals of Little Nourlangie Rock, NT III. Ecology of *Dasyurus hallucatus*, the northern quoll (Marsupialia: Dasyuridae). *Wildlife Research*, 8, 73–85.

Bradley, A.J. (1987) Stress and mortality in the red-tailed phascogale, *Phascogale calura* (Marsupialia: Dasyuridae). *General and Comparative Endocrinology*, 67, 85–100.

Bradley, A.J., Mcdonald, I.R. & Lee, A.K. (1980) Stress and mortality in a small marsupial (*Antechinus stuartii*, Macleay). *General and Comparative Endocrinology*, 40, 188–200.

Braithwaite, R.W. & Lee, A.K. (1979) A mammalian example of semelparity. *The American Naturalist*, 113, 151–155.

Bureau of Meteorology. (2024) *Climate data online*. Australian Government. Available at: http://www.bom.gov.au/climate/data/ [Accessed 25th February 2024].

Chan, R., Dunlop, J. & Spencer, P.B.S. (2020) Highly promiscuous paternity in mainland and island populations of the endangered northern quoll. *Journal of Zoology*, 310, 210–220.

Cockburn, A. (1997) Living slow and dying young: senescence in marsupials. In: Saunders, N. & Hinds, L. (Eds.) *Marsupial biology: recent research, new perspectives*. Sydney, NSW: University of New South Wales Press.

Cole, L.C. (1954) The population consequences of life history phenomena. *The Quarterly Review of Biology*, 29, 103–137.

Cowan, M.A., Dunlop, J.A., Gibson, L.A., Moore, H.A., Setterfield, S.A. & Nimmo, D.G. (2024) Movement ecology of an endangered mesopredator in a mining landscape. *Movement Ecology*, 12, 5.

Cowan, M.A., Dunlop, J.A., Turner, J.M., Moore, H.A. & Nimmo, D.G. (2020) Artificial refuges to combat habitat loss for an endangered marsupial predator: how do they measure up? *Conservation Science and Practice*, 2, e204.

Cuttle, P. (1982) Life history strategy of the dasyurid marsupial *Phascogale tapoatafa*. In: Archer, M. (Ed.) *Carnivorous marsupials*. Mosman, NSW: Royal Zoological Society of New South Wales Sydney, pp. 13–22.

Dickman, C.R. & Braithwaite, R.W. (1992) Postmating mortality of males in the dasyurid marsupials, *Dasyurus* and *Parantechinus*. *Journal of Mammalogy*, 73, 143–147.

Dunlop, J., Cook, A. & Morris, K. (2014) *Pilbara northern quoll project: surveying and monitoring Dasyurus hallucatus in the Pilbara, Western Australia*. Perth, WA: Department of Parks and Wildlife.

Fisher, D.O. & Blomberg, S.P. (2011) Costs of reproduction and terminal investment by females in a semelparous marsupial. *PLoS One*, 6, e15226.

Fisher, D.O., Dickman, C.R., Jones, M.E. & Blomberg, S.P. (2013) Sperm competition drives the evolution of suicidal reproduction in mammals. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 17910–17914.

Gaschk, J.L., Del Simone, K., Wilson, R.S. & Clemente, C.J. (2023) Resting disparity in quoll semelparity: examining the sex-linked behaviours of wild roaming northern quolls (*Dasyurus hallucatus*) during breeding season. *Royal Society Open Science*, 10, 221180.

Hayes, G.L.T., Simmons, L.W., Dugand, R.J., Mills, H.R., Roberts, J.D., Tomkins, J.L. et al. (2019) Male semelparity and multiple paternity confirmed in an arid-zone dasyurid. *Journal of Zoology*, 308, 266–273.

Heiniger, J., Cameron, S.F., Madsen, T., Niehaus, A.C. & Wilson, R.S. (2020) Demography and spatial requirements of the endangered northern quoll on Groote Eylandt. *Wildlife Research*, 47, 224–238.

Hernandez-Santin, L., Dunlop, J.A., Goldizen, A.W. & Fisher, D.O. (2019) Demography of the northern quoll (*Dasyurus hallucatus*) in the most arid part of its range. *Journal of Mammalogy*, 100, 1191–1198.

Hughes, P.W. (2017) Between semelparity and iteroparity: empirical evidence for a continuum of modes of parity. *Ecology and Evolution*, 7, 8232–8261.

Lee, A.K. & Cockburn, A. (1985) *Evolutionary ecology of marsupials*. Cambridge: University Press.

Moore, H.A., Dunlop, J.A., Jolly, C.J., Kelly, E., Woinarski, J.C.Z., Ritchie, E.G. et al. (2022) A brief history of the northern quoll (*Dasyurus hallucatus*): a systematic review. *Australian Mammalogy*, 44, 185–207.

Moro, D., Dunlop, J. & Williams, M.R. (2019) Northern quoll persistence is most sensitive to survivorship of juveniles. *Wildlife Research*, 46, 165–175.

Oakwood, M. (1997) *The ecology of the northern quoll*, Dasyurus hallucatus. Doctor of Philosophy, Australian National University.

Oakwood, M. (2000) Reproduction and demography of the northern quoll, *Dasyurus hallucatus*, in the lowland savanna of northern Australia. *Australian Journal of Zoology*, 48, 519–539.

Oakwood, M., Bradley, A.J. & Cockburn, A. (2001) Semelparity in a large marsupial. *Proceedings of the Biological Sciences*, 268, 407–411.

Old, J.M., Ong, O.T.W. & Stannard, H.J. (2021) Red-tailed phascogales: a review of their biology and importance as model marsupial species. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, 335, 217–227.

Schmitt, L.H., Bradley, A.J., Kemper, C.M., Kitchener, D.J., Humphreys, W.F. & How, R.A. (1989) Ecology and physiology of the northern quoll, *Dasyurus hallucatus* (Marsupialia, Dasyuridae), at Mitchell Plateau, Kimberley, Western Australia. *Journal of Zoology*, 217, 539–558.

Shaw, R.E., Spencer, P.B., Gibson, L.A., Dunlop, J.A., Kinloch, J.E., Mokany, K. et al. (2022) Linking life history to landscape for threatened species conservation in a multiuse region. *Conservation Biology*, 37, e13989.

Young, T.P. (2010) Semelparity and iteroparity. *Nature Education Knowledge*, 3, 2.

How to cite this article:
Cowan, M.A., Dunlop, J.A., Hernandez-Santin, L., Heidrich, A., Knuckey, C.G. & Nimmo, D.G. (2024) High post-sex survival of the world's largest semelparous mammal. *Austral Ecology*, 49, e13595. Available from: https://doi.org/10.1111/aec.13595

Appendix F: A review of progress of a research program for the endangered northern quoll (*Dasyurus hallucatus*) in the multi-use landscapes of the Pilbara

Published in *Australian Mammalogy* in June 2023.

***Manuscript citation*:** Gibson, L. A., Moore, H. A., Cowan, M. A., Craig, M. D., Nimmo, D. G., & Dunlop, J. A. (2023). A review of progress of a research program for the endangered northern quoll (*Dasyurus hallucatus*) in the multi-use landscapes of the Pilbara. *Australian Mammalogy*, 45, 251-263.

CSIRO PUBLISHING

REVIEW
https://doi.org/10.1071/AM22028

Australian MAMMALOGY
The Australian Mammal Society

A review of progress of a research program for the endangered northern quoll (*Dasyurus hallucatus*) in the multi-use landscapes of the Pilbara

L. A. Gibson[A,B,*], H. A. Moore[A,C], M. A. Cowan[C,D], M. D. Craig[A,B], D. G. Nimmo[D] and J. A. Dunlop[C,D]

For full list of author affiliations and declarations see end of paper

***Correspondence to:**
L. A. Gibson
Department of Biodiversity, Conservation and Attractions, Kensington, WA 6151, Australia
Email: lesley.gibson@dbca.wa.gov.au

Handling Editor:
Ross Goldingay

ABSTRACT

Maximising conservation outcomes for threatened species in multi-use landscapes is likely to require a multi-stakeholder, coordinated approach that is tenure blind. Here, we conduct a review of a research program targeting the endangered northern quoll (*Dasyurus hallucatus*) in the Pilbara region of Western Australia; an area with a high concentration of mining and pastoral activities. To inform ongoing investment to support northern quoll conservation, we identify future directions that either add value to research already undertaken or are based on the original priorities that have not been addressed. The original program was developed using a collaborative process involving workshops attended by multiple stakeholders to identify research priorities. To date, the program has significantly improved our knowledge of Pilbara northern quolls, particularly in relation to effective survey and monitoring techniques, the influence of habitat quantity, configuration, and composition on occupancy, movement ecology, population dynamics and structure, and the threat posed by introduced predators. The efficacy of artificial refuges that were created to replicate natural denning habitat has also been investigated. Suggested future research directions focus on refining the northern quoll regional monitoring program, understanding how interacting threats such as introduced predators, fire, and herbivore grazing influence northern quoll populations in the Pilbara, and how best to mitigate other threats such as mining associated activities and the impending cane toad invasion.

Keywords: conservation management, cumulative impacts, dasyurid, habitat quality, multi-use region, optimal monitoring, threat mitigation, threatened species.

Introduction

Effective conservation of biodiversity values in modified landscapes remains a major challenge (Fischer and Lindenmayer 2007; Watson *et al.* 2016). This is particularly so for multi-use landscapes where there are competing priorities for land use (Kremen and Merenlender 2018; Sonter *et al.* 2018), and cumulative impacts are likely to be significant (Mahon *et al.* 2019). Maximising conservation outcomes in this context requires a coordinated approach that balances the diverse needs of stakeholders (Campbell *et al.* 2015) and is applied across multiple land use tenures (Kearney *et al.* 2022).

The Pilbara region of Western Australia is recognised for its significant biodiversity and cultural values, as well as being important for its immense mineral wealth and extensive pastoral industry (McKenzie *et al.* 2009). This vast region also harbours a number of nationally threatened fauna species that are classified as *matters of national environmental significance* (MNES) by the Australian Government under its *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act; Australian Government 2013). These species are legally protected by the EPBC Act, so that any action by a development proponent that is likely to have a significant impact on them, needs to be referred to the Australian Government environment minister. If the minister decides that

Received: 10 November 2022
Accepted: 28 February 2023
Published: 11 April 2023

Cite this:
Gibson LA *et al.* (2023)
Australian Mammalogy
doi:10.1071/AM22028

the action is likely to have a significant impact, a formal environmental impact assessment is required in accordance with the EPBC approval process.

The northern quoll (*Dasyurus hallucatus*) is one of the listed threatened species in the Pilbara. This medium-sized (300–800 g) carnivorous marsupial is endemic to northern Australia, occurring in Queensland, the Northern Territory, and the Kimberley and Pilbara regions of Western Australia (Moore *et al.* 2019). The species is subject to a range of threats including habitat clearing, competition with and/or predation by introduced predators such as the red fox (*Vulpes vulpes*) and feral cat (*Felis catus*), herbivore grazing and inappropriate fire regimes that reduce vegetation cover, and the continued spread of the introduced and poisonous cane toad (*Rhinella marina*) across most of its range (Braithwaite and Griffiths 1994; Hill and Ward 2010; O'Donnell *et al.* 2010). Northern quolls lack immunity to cane toad toxins and quolls that ingest large toads typically die (Woinarski *et al.* 2010; Ujvari *et al.* 2013). This combination of threats has led to range contractions and local extinctions of northern quolls (Moore *et al.* 2019), and the species is currently listed as Endangered under both the EPBC Act and the *Western Australian Biodiversity Conservation Act 2016*. The Pilbara population is genetically distinct from other northern quoll populations (How *et al.* 2009; Woolley *et al.* 2015), and as cane toads are yet to reach this region, it is considered a stronghold for the species. However, the ongoing security of northern quolls in the Pilbara is tenuous, given modelling predicts cane toads will eventually invade this region from the Kimberley (Tingley *et al.* 2013; Southwell *et al.* 2017).

Habitat for northern quolls in the Pilbara tends to include areas highly prospective for mining, particularly iron-ore formations (Cramer *et al.* 2016). As a result, many mining proponents have undertaken targeted surveys of northern quolls as a requirement of their environmental impact assessments (Cramer *et al.* 2016). While these surveys have improved our understanding of the distribution of the species in the Pilbara, until recently, knowledge of the impacts of anthropogenic disturbances on northern quolls was rudimentary. This high level of uncertainty in relation to the likely impact of development activities on the northern quoll has resulted in funds being allocated to ecological research (Cramer *et al.* 2016). To better direct this funding, in 2013, the Western Australian Department of Biodiversity, Conservation and Attractions (DBCA) hosted a workshop, attended by scientists, environmental consultants, mining proponents and state and federal government agencies, to identify research priorities for the northern quoll in the Pilbara (Cramer *et al.* 2016). These priorities were further refined in a subsequent workshop in 2016 (Cramer and Dunlop 2018) and are documented in Table 1. Here, we review the progress of the ensuing research program against these priorities and identify future research directions to help ensure the ongoing persistence of the northern quoll in the Pilbara.

Research priorities – progress

Our review on progress of the Pilbara Northern Quoll Research Program (PNQRP) is framed around the eight research priorities outlined in Cramer and Dunlop (2018), ranked in order of importance according to workshop participants. Key outcomes for each priority are provided in Table 1 and described below.

Priority 1&2: assess and refine survey and monitoring protocols

Since its inception, the PNQRP has contributed more than 1700 northern quoll records to historical data (Dunlop *et al.* 2019). Surveys in new areas, in addition to those associated with mining developments, have significantly increased our knowledge on the distribution of the northern quoll in the Pilbara and allowed for the generation of species-specific distribution models (e.g. Molloy *et al.* 2017; Moore *et al.* 2019; Shaw *et al.* 2023). For example, following the discovery in 2012 of the northern quoll in Karlamilyi National Park, more than 150 km from the nearest known record (Turpin and Bamford 2015), additional surveys within and to the north of Karlamilyi, under the PNQRP, recorded new locations of the species (Dunlop *et al.* 2019). Further detections over the past few years in this location indicates that desert habitat on the extreme eastern edge of the Pilbara can support a low-density population of northern quolls (Dunlop *et al.* 2019).

Dunlop *et al.* (2014) revised and implemented a survey and monitoring protocol for several sites with known populations of northern quolls in the Pilbara, with the aim to obtain detailed information on population demographics and trends in abundance across these sites. Although this regional monitoring program was not established to implicitly measure management effectiveness, it does provide baseline data that may be useful for such assessments. Using this approach, annual surveys of northern quolls have been undertaken from 2014 to 2019 (Dunlop *et al.* 2019). Preliminary analyses of live trapping data, using a standard of 50 cage traps (i.e. 2 lines of 25 traps, with lines and traps spaced 50 m apart) for four nights (Dunlop *et al.* 2014) and capture–recapture analyses (Efford 2004), highlighted limitations of this approach to estimate population size due to the low number of recaptures of northern quolls (particularly of males, between sessions) for all but 2 of 15 sites (Dunlop *et al.* 2019).

Advancing technology has led to camera traps becoming a popular alternative to traditional live trapping methods (Wearn and Glover-Kapfer 2019). When applied to a species where individuals can be recognised via unique markings, camera imagery can be used to estimate abundance using mark-resight techniques (e.g. Hohnen *et al.* 2013). In the Pilbara, the potential use of camera traps to accurately identify individual northern quolls based on their spot

Table 1. Main outcomes of the Pilbara Northern Quoll Research Program against each research priority identified in Cramer and Dunlop (2018) and proposed future research directions.

Research priority	Outcomes	Future directions
Assessing and refining survey and monitoring protocols	• Improved understanding of the distribution of the northern quoll in the Pilbara (Molloy *et al.* 2017; Dunlop *et al.* 2019; Moore *et al.* 2019; Shaw *et al.* 2023). • Improved understanding of the application of capture–recapture techniques to estimate density based on standardised live trapping data, indicating that further refinement is required (Dunlop *et al.* 2019). • Identification of the survey effort required using either horizontally or vertically orientated cameras to detect northern quolls with a pre-specified level of confidence, with either orientation producing a similar result (Moore *et al.* 2020). • Identification of the cost-effectiveness of monitoring programs using either vertically orientated cameras or standard live trapping, with cameras identified as being a more cost-effective option (Moore *et al.* 2023).	• Update existing survey and monitoring protocols to include recommendations regarding a program based on camera traps, individual identification and mark-resight or occupancy analytical approaches that are fit-for-purpose. • Provide a guiding framework for regional monitoring of northern quolls that can be used by multiple stakeholders to better understand long-term population trends. • Investigate emerging technologies (e.g. artificial intelligence cameras) to improve effectiveness and efficiency of monitoring approaches.
Improving our understanding of fine-scale habitat use to identify areas of critical habitat	• Identification of the spatial configuration of suitable habitat that is likely to afford protection from threats such as introduced predators i.e. relatively contiguous rocky patches (Moore *et al.* 2022). • Improved understanding of fine-scale habitat use of northern quolls indicating the importance of well-connected and vegetated rugged rocky outcrops and riparian areas as critical habitat (Moore *et al.* 2021*a*; Cowan *et al.* 2022; Shaw *et al.* 2023). • Improved knowledge of the diet of northern quolls across the region revealing a broad omnivorous dietary niche typical of a habitat generalist (Dunlop *et al.* 2017).	• Incorporate spatial information into new population viability analyses (PVAs) to further improve accuracy. • Identify the characteristics of habitats that reduce predation risk for northern quolls during dispersal events.
Improving our understanding of population dynamics and structure	• Population viability analyses (PVA) indicated mortality of juvenile northern quolls may compromise the persistence of the species (Moro *et al.* 2019). • Improved population demographic data now available to update PVA models (Hernandez-Santin *et al.* 2019). • Confirmation that there is no obvious genetic structuring across the mainland meta-population of northern quolls with results of genetic relatedness indicating widespread dispersal of males (Spencer *et al.* 2013; Dunlop *et al.* 2019). • Genetic analyses identified reproductive strategies likely to maximise fitness of offspring, such as multiple paternity of northern quoll litters, and island females preferentially choosing smaller males, which has implications in terms of sourcing animals for translocations (Chan *et al.* 2020).	• Refine PVAs using improved information, such as survival rates of juveniles. • Identify source and sink populations of northern quolls in the Pilbara using fine-scale demographic information.
Assessing the impacts of introduced predators	• Demonstration that Felixer™ feral cat grooming traps can be used safely in the presence of northern quolls (Dunlop *et al.* 2020; Edwards and Nelson 2022). • Complementary projects provided evidence of the threat posed by feral cats through predation of northern quolls; *Eradicat*® feral cat baits can be safely applied in the presence of northern quolls; and aerial baiting using *Eradicat*® is beneficial to northern quolls (Cowan *et al.* 2020*a*; Palmer *et al.* 2020, 2021).	• Investigate changes in habitat use by northern quolls with sustained introduced predator management. • Further investigate the efficacy of Felixer™ feral cat grooming traps in reducing the impact of feral cats on northern quolls. • Further investigate the strategic management of feral cats using a combination of approaches (aerial and targeted ground baiting using *Eradicat*®, trapping) and the subsequent response of northern quolls.

(*Continued on next page*)

Table 1. (*Continued*)

Research priority	Outcomes	Future directions
Understanding the spread and impacts of cane toads	• Training northern quolls to avoid cane toads through conditioned-taste aversion has shown some promise in trials in the Kimberley (e.g. Indigo *et al.* 2018, 2019).	• Investigation of the uptake and potential longer-term aversion of cane toad sausages by northern quolls and non-target species in the Pilbara. • Identification of locations where northern quolls and cane toads are most likely to intersect to inform surveillance and targeted response (i.e. application of cane toad taste aversion baits).
Understanding interactions with infrastructure and built environments	• Identification of the characteristics of natural dens, indicating that northern quolls used natural dens which were cooler and deeper than other crevices available in the natural landscape (Cowan *et al.* 2020*b*) • Indication that artificially created refuges were warmer than occupied natural dens, had less complex vegetation, lower detections of mammal prey, and higher detections of feral cats (Cowan *et al.* 2020*b*).	• Investigation into optimising the design of artificial refuges in relation to surrounding landscape features (e.g. size, spatial arrangement, surrounding habitat) and microclimatic attributes (e.g. material, internal temperature). • Investigate the use of artificial refuges by northern quolls in relation to breeding, survival, and recruitment and quantify risks of predation. • Undertake field trials to assess the effectiveness of feral predator control and habitat restoration on northern quoll use of artificial refuges. • Determine how disturbances associated with mining (e.g. artificial light, altered resource and predator abundances) influence the movement and behaviour of northern quolls. • Better understand the cumulative impact of habitat loss due to mining in relation to northern quoll distribution and habitat connectivity.
Other research priorities (threat interactions)	• Effective threat mitigation is likely to benefit from a better understanding of how multiple interacting threats influence northern quoll populations (Moore *et al.* 2021*b*).	• Understand the extent to which fire and habitat degradation influences predation pressure on northern quolls. • Determine how interactions between threats influence habitat selection by northern quolls to inform threat mitigation. • Investigate the response of northern quoll occupancy and abundance to the management of interacting threats.

pattern was examined by placing 110 vertically orientated (downward facing) lured cameras (Fig. 1) deployed across 23 sites within a 6000 km^2 study area, with over 70% of images allowing for northern quolls to be identified (Moore *et al.* 2021*a*). A further study compared the use of horizontally and vertically oriented cameras to adequately detect northern quolls (Moore *et al.* 2020); it was assumed that the reduced field of view of the vertical camera orientation would influence the detection rate. However, only a small difference was identified with less survey effort required using horizontally orientated cameras to be 95% confident of northern quoll absence at a site (i.e. 24 compared to 32 nights).

The difference in cost effectiveness when using live trapping or vertically orientated cameras to detect changes in northern quoll occupancy was also examined by Moore *et al.* (2023). Regardless of whether the monitoring program aimed to detect a 30, 50, or 80% change in quoll occupancy, using cameras was always more cost effective than live trapping. The cost differential between the two monitoring methods increased as the program aimed to detect smaller changes in occupancy. While the most cost-effective camera monitoring designs used a similar number of sites to the most cost-effective live trap monitoring designs, camera designs were able to accrue greater survey effort by operating for a longer period of time at a much lower cost (Moore *et al.* 2023). When combined with the capacity to individually identify animals, camera trapping appears to be a substantially more efficient means of monitoring northern quoll population trends in the Pilbara.

Priority 3: improve our understanding of fine-scale habitat use to identify areas of critical habitat

Historically, survey effort for northern quolls in the Pilbara has typically been focused in mining areas for environmental impact assessment, and hence have been highly spatially biased (Cramer *et al.* 2016). Using an extended data set of northern quoll presence and adjusting for this bias, a predictive species distribution model was produced by Molloy *et al.* (2017). Moore *et al.* (2019) added to this work by

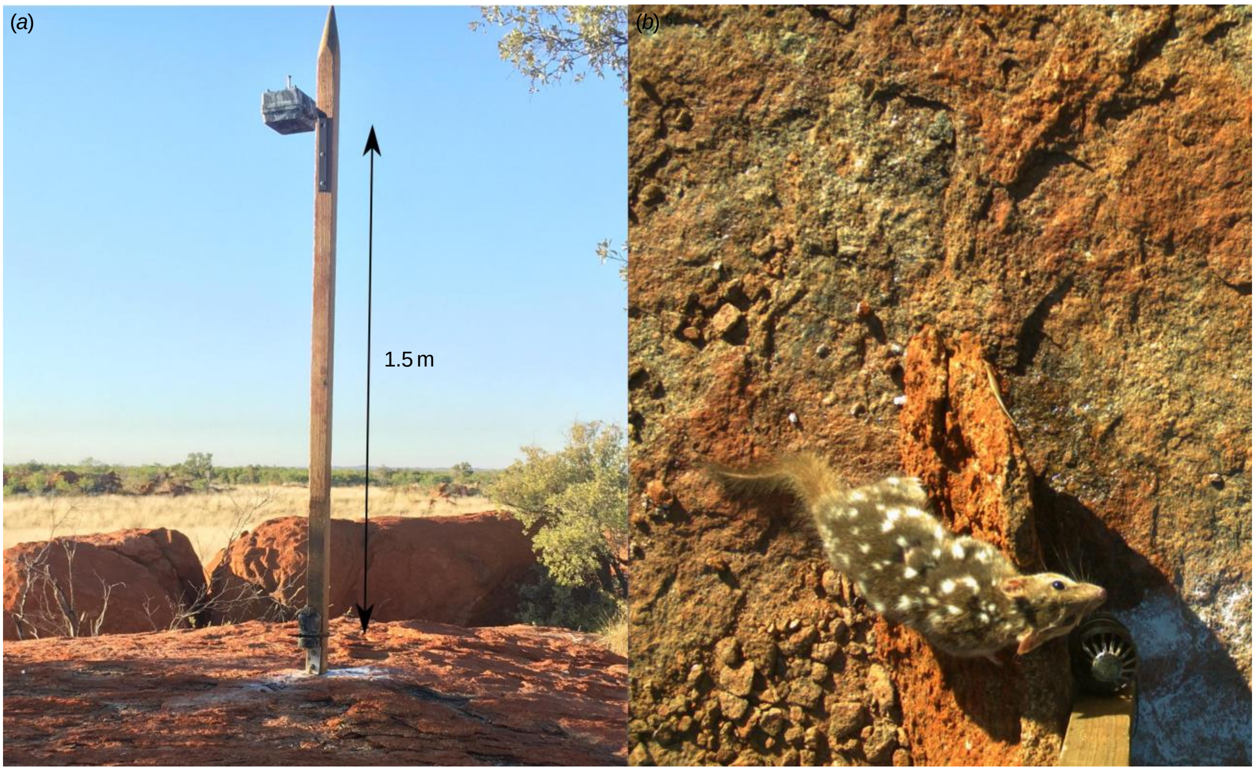


Fig. 1. (*a*) The 'downward-facing' camera approach used to survey Pilbara northern quolls, (*b*) An image of a northern quoll captured using a downward facing camera and showing dorsal spot patterning.

expanding the model beyond the Pilbara to include the entire species' range. While these models provide regional context for potentially suitable habitat for northern quolls (Fig. 2), further studies to identify the spatial distribution of refugial areas that provide protection from threats and are suitable for breeding were considered a priority in Cramer and Dunlop (2018) i.e. habitat that is critical for the survival of the species.

Moore *et al.* (2022) investigated the influence of the amount and configuration of rocky habitat on northern quoll occupancy and abundance. Study landscapes were comprised of rock outcrops which were fragmented to varying degrees by a matrix of spinifex grassland (Fig. 3). Spatial configuration of rocky habitat was more important than habitat quantity (i.e. the area of rocky habitat within a landscape) in terms of predicting northern quoll occupancy and abundance, which both declined with increasing fragmentation. This response is likely driven by predation risk, given that movement between many small disjunct patches of habitat across spinifex sandplains exposes quolls to enhanced predation risk (Hernandez-Santin *et al.* 2016). Northern quoll abundance also increased with increasing topographical ruggedness and previous wet season rainfall, supporting the results of broader species distribution modelling by Molloy *et al.* (2017), Moore *et al.* (2019) and Shaw *et al.* (2023).

Habitat use by northern quolls at the patch (i.e. contiguous rock outcrop), within-patch, and landscape scales, using the same set of sites as above was further examined by Moore *et al.* (2021*a*). Northern quolls preferred rocky out- crops that also had greater vegetation cover <0.5 m in height and a higher number of den crevices (within- patch), had smaller amounts of edge habitat relative to patch area (patch) and were embedded in a landscape with more rocky outcrops (landscape). Quolls were scarce in the surrounding grassland, but when they used it, they remained close to the rocky habitat and preferred areas of high vegetation cover (i.e. less affected by fire). These results indicate that habitat critical for northern quolls con- stitutes large areas of highly concentrated, complex rocky habitat. A recent study suggests this is driven by shelter (i.e. den) availability as a critical component of habitat quality (Hernandez-Santin *et al.* 2022). Management actions that facilitate habitat connectivity (e.g. predator control) and maximise vegetation cover (e.g. reduced grazing and fire) are likely to be important for protecting this habitat.

Cowan *et al.* (2022) used GPS telemetry to further refine understanding of northern quoll habitat use. Northern quolls preferentially selected areas that were more topographically rugged and had a higher percentage cover of rocky habitat and riverbed than the surrounding habitat. They avoided areas with a high percentage of spinifex sandplain, and their

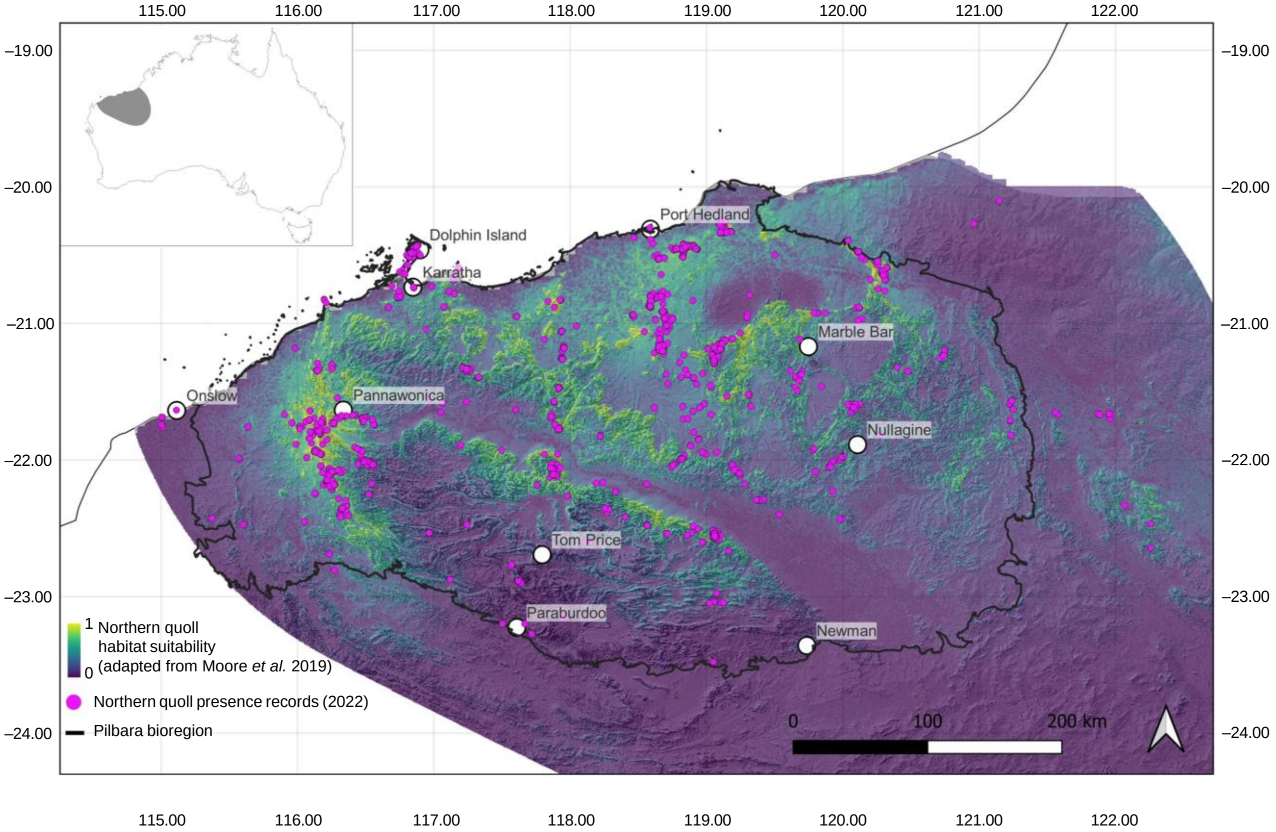


Fig. 2. Habitat suitability map generated using MaxEnt for the northern quoll in the Pilbara. Adapted from Moore *et al.* (2019).

Fig. 3. Typical configuration of rocky habitat preferred by northern quolls in the Pilbara.

area of activity increased in size with increasing cover of spinifex sandplain (Cowan *et al.* 2022). These results are consistent with the results discussed above, and suggest that northern quolls need to travel further to access sufficient resources in areas where their preferred rocky habitat is scarce, necessitating higher energy expenditure and potentially exposing them to predation by feral cats (Hernandez-Santin *et al.* 2016). The preferential use of riverbeds is likely to be related to the ease of movement between patches of rocky habitat. Using a landscape genetics approach, Shaw *et al.* (2023) demonstrated that dispersal of Pilbara northern quolls was facilitated by proximity to water, suggesting that dense vegetation along watercourses provides protection from predators.

To further understand the dietary requirements of northern quolls within their habitats, Dunlop *et al.* (2017) undertook a dietary analysis of 498 scats collected across 325 locations in the Pilbara. Northern quolls demonstrated a broad dietary niche, suggestive of an opportunistic dietary strategy, with no obvious environmental drivers. Invertebrates made up most of their diet, although they also consumed a wide range of vertebrates (mammals, birds, reptiles, frogs), as well as molluscs, carrion, and plant material (e.g. seeds, fruits, and flowers). High dietary overlap between introduced predators (i.e. cats and foxes) and other quoll species has been reported (Glen and Dickman 2008; Glen *et al.* 2011; Moseby *et al.* 2022), how- ever these studies have also indicated that the broad and flexible diet of quolls is likely to reduce the intensity of this competitive interaction. While not investigated in Dunlop *et al.* (2017), this is also likely to be the case for the northern quoll, although foxes are not widespread in the Pilbara and northern quolls appear to spatially avoid feral cats (see Priority 5).

Priority 4: population dynamics and structure

The Pilbara northern quoll population is genetically distinct, being separated from the nearest Kimberley population by approximately 500 km of the arid Great Sandy Desert, with no evidence of contemporary gene flow (How *et al.* 2009; Spencer *et al.* 2013; Hohnen *et al.* 2016; von Takach *et al.* 2022). Spencer *et al.* (2013) further indicated that the Pilbara population is a single genetic cluster, with a similar level of genetic diversity between locations, implying wide- spread dispersal across the sampled region. Genotyping of an additional 1844 tissue samples from the Pilbara region, along with 660 samples from the Kimberley and 164 from the Northern Territory, collected between 2012 and 2018, confirmed that Pilbara northern quolls formed a homogeneous group with no obvious genetic structuring across the mainland meta-population (Dunlop *et al.* 2019). No sampled location showed any sign of recent or historical population bottlenecks and heterozygosity was high (~70%) at all mainland sites. Genetic relatedness within sampled locations indicated that dispersal occurred over 1–2 km for females and up to 30 km for males. These results reflect findings of other studies which show that female quolls are highly site philopatric and remain within a relatively small home range, whereas males disperse widely in the breeding season (e.g. Oakwood 2002; Henderson 2015). Shaw *et al.* (2023) also explored genetic structure in Pilbara northern quolls and identified only a weak east- west split. Their results also suggested limited barriers to dispersal, although silt/clay plains showed the highest resistance, presumably due to lack of vegetation cover and rocky habitat, and likely higher exposure to predators.

Chan *et al.* (2020) compared paternity of litters and mate choice of northern quolls between a local mainland and island population (Dolphin Island). Multiple paternity was evident regardless of location, with the young from every litter having multiple fathers; in some litters, each offspring had a different father. Such a competitive mating strategy is likely to enhance the fitness of offspring and may explain the selection for die-off of males after their first breeding season (Fisher *et al.* 2013). Mate choice was only evident in the island population with females selecting smaller males, and island females also consistently had fewer nipples (6 cf. 8 on the mainland; Chan *et al.* 2020). These differences are likely to be driven by limited resources on islands, as invest- ment in fewer and smaller offspring mean a reduced require- ment for resources (Lawlor 1982).

Knowledge of the demographics of local northern quoll populations in the Pilbara has also been improved through the study of Hernandez-Santin *et al.* (2019). Focusing on two mainland sites (Indee Station and Millstream Chichester National Park), results showed that apparent survivorship for both males and females varied primarily between sea- sons, with variation between years being of a smaller mag- nitude. This study also showed that the probability of an individual entering the population – which is a combination of immigration and juvenile recruitment – varied with season and between males and females but not between years. The difference between sexes is likely due to male-biased dispersal rather than differing juvenile recruitment. Male population size also increased from April to June and then reached its lowest point in September, likely due to male die-off (Oakwood 2004)

Using data on abundance and demographics from the annual monitoring program, combined with data from the literature, a population viability analysis (PVA) simulated the trajectories of a northern quoll population under a range of scenarios (Moro *et al.* 2019). The PVA model predicted a 99% probability that northern quoll populations would persist in the Pilbara over the next 20 years. However, population viability was sensitive to increases in juvenile mortality, with immediate declines in population size predicted with increases in juvenile mortality as low as 5%. As such, management actions that maximise survival of juvenile northern quolls (e.g. introduced predator control) are likely to facilitate the persistence of this species in the region.

Priority 5: assessing the impacts of introduced predators

Cowan *et al.* (2020*a*) provided evidence of the impact of feral cats (*Felis catus*) on northern quolls in the Pilbara with cats predating 8 of 41 radio-collared individuals over a period of approximately 4 months. This study is supported by the results of Palmer *et al.* (2020) whereby 17 of 135 feral cat scats collected across the same area contained northern quoll remains, including the Passive Integrated Transponder (PIT) tag of one individual. Woolley *et al.* (2019) also report records of predation of northern quolls by feral cats. The limited distribution of the European red fox (*Vulpes vulpes*) in the Pilbara (Moro *et al.* 2021) means they likely pose a lesser threat than feral cats (Woinarski 2014). Annual surveys from 2016 to 2018 on Dolphin Island off the Pilbara coast detected both northern quolls and foxes in all 3 years, although the number of fox detections was low, ranging from five to eight (Birch and Dunlop 2019). The threat of dingoes (*Canis familiaris*) to Pilbara northern quolls is unknown, although there is evidence of dingoes predating northern quolls in the Northern Territory and Queensland (Doherty *et al.* 2019; Moore *et al.* 2021*b*). As top predators, dingoes may also play a role in regulating both feral cat and fox populations (Hernandez-Santin *et al.* 2016).

In a complementary study to the PNQRP, Palmer *et al.* (2021) explored the effectiveness of landscape scale feral cat control in the Pilbara and the benefits it provided to northern quolls. *Eradicat*® (i.e. sausage-style baits containing the toxin sodium fluoroacetate or 1080; Algar *et al.* 2007) was applied aerially at a treatment site and an unbaited refer- ence site over 4 years. While they found evidence of mortality of GPS-collared feral cats, camera trap monitoring indicated no significant effect of baiting on feral cat detections. Even so, northern quolls responded positively and, over time, expanded their range beyond rocky outcrops. As supported by other studies (e.g. Hernandez-Santin *et al.* 2016), it appears that rugged rocky habitat preferred by northern quolls in the Pilbara buffers them to some extent from feral cat predation. A related study by Williamson *et al.* (2021) also indicated avoidance of topographically complex rocky habitats by feral cats.

The operational use of *Eradicat*® is currently not permitted in areas where northern quolls are likely to be present, as the risk to this species in the wild had not been assessed at the time the bait was registered in Western Australia (Palmer *et al.* 2021). In an important first step in assessing this risk, Cowan *et al.* (2020*a*) demonstrated that northern quolls were unlikely to be susceptible to poison baiting using *Eradicat*®. This study assessed survivorship of free-ranging radio-collared northern quolls at a baited (21 individuals) and unbaited (20 individuals) site before and after the aerial application of *Eradicat*® and found no evidence that northern quolls consumed aerially distributed baits, or died, as a result of the baiting program. As an alternative tool to poison baiting, Dunlop *et al.* (2020) trialled an automated feral cat grooming trap (the 'Felixer™') for feral cat management in the Pilbara (see Read *et al.* 2019; Moseby *et al.* 2020). In-built algorithms allow the Felixer™ unit to identify the shape and movement of a cat using an array of LiDAR sensors as it passes, which then ejects a lethal dose of toxic 1080 gel onto the cat's fur that is ingested by grooming. Photographs are taken every time the detection beams are crossed, enabling refinement of the technology with different suites of non-target species. Three units (Model 3, Thylation, SA) first trialled in non-toxic photo-only mode recorded 24 feral cats, with 11 identified as targets. Northern quolls passed the Felixer™ units on 226 occasions, and a further 11 other categories of non-target animals and were never identified as a target from over 1000 occasions. In a further trial using toxic mode, 14 cats were detected, with six identified as targets (Edwards and Nelson 2022). Of the two quolls detected, neither were identified as a target. These early results indicate that Felixer™ units can be used safely in the presence of northern quolls in the Pilbara. The units could provide local relief from feral cat predation, targeted around important habitats, feral cat sources or sinks, or their movement pathways.

Priority 6: understanding the spread and impact of cane toads

The primary cause of the most recent decline of northern quolls across northern Australia has been attributed to the spread of the toxic introduced cane toad, with the complete collapse of some populations in Queensland and the Northern Territory (Woinarski *et al.* 2010, 2015). In terms of mitigation, training northern quolls to avoid cane toads through conditioned-taste aversion (CTA), using a nausea inducing thiabendazole-laced sausage or non-lethal juvenile toad that makes them unwell, prior to their reintroduction to an area, has shown some promise (Cremona *et al.* 2017*a*; Jolly *et al.* 2018). Small field trials in the Kimberley region have also demonstrated that a high proportion of northern quolls will take a 'toad sausage' on their first encounter and that some individuals develop a longer-term aversion to them (Indigo *et al.* 2018, 2019). A more recent study suggests the efficacy of the method is highly dependent on cultural transmission of toad avoidance (i.e. mothers teaching their offspring to avoid toads; Indigo *et al.* 2021). One study that trialled CTA on three northern quoll populations in the Kimberley found no evidence of a positive impact compared to four control populations (Indigo *et al.* 2023). Further testing of the delivery and uptake of CTA baits is required to better understand the likely effectiveness of this method.

Southwell *et al.* (2017) used structured decision making to explore the optimal locations of barriers to the movement of cane toads into the Pilbara from the Kimberley, and the costs of various water source management options. The practicality and feasibility of putting these into practice have raised some questions, particularly in relation to the confounding influence of land uses, such as irrigated agriculture (Galloway *et al.* 2022), and widespread flooding associated with cyclones in the vicinity of the proposed barrier (D. Pearson pers. comm.). While the PNQRP has yet to invest in cane toad research, clearly much is still to be learnt about the spread and impacts of cane toads on northern quolls in the relatively arid and topographically complex landscapes of the Pilbara. Given that the occurrence of northern quolls is negatively correlated with increasing distance to water (Molloy *et al.* 2017; Moore *et al.* 2019), an overlap in distribution with the cane toad is likely (Kearney *et al.* 2008). Current projections under climate change also predict an increase in intensity of heavy rainfall events in the Pilbara (Sudmeyer 2016), which may facilitate the spread of cane toads in this region.

Priority 7: interactions with infrastructure and built environments

In areas disturbed by mining activity, northern quolls have been shown to use structures in the vicinity of accommodation villages, and raw material stockpiles such as rock quarries (Dunlop *et al.* 2015), as well as culverts under railway lines (Ecoscape 2019). Cowan *et al.* (2020*b*) also showed that northern quolls will use artificial refuges (large piles of waste rock or concrete slabs and gravel arranged by earth moving vehicles) purposely created as denning habitat. Here, we define denning habitat as that which is suitable for breeding and raising young to independence (see Cowan *et al.* 2020*b*). Adult and juvenile northern quolls were recorded using 2 of 10 monitored artificial refuges.

Artificial refuges had similar internal temperatures to occupied natural dens but had much less cover and structural complexity of surrounding vegetation than natural dens (Cowan *et al.* 2020*b*). Feral cat visitation was much higher at artificial refuges, and detections of northern quoll prey items were much lower compared to occupied natural dens, suggesting an increased risk of predation and food scarcity (Cowan *et al.* 2020*b*). Further studies are required on how to design artificial refuges so they more closely approximate the environmental characteristics of natural dens to increase their ability to be a reliable conservation intervention (see Cowan *et al.* 2021; Watchorn *et al.* 2022).

Priority 8: other research opportunities: understanding the influence of interacting threats

Many of the studies undertaken as part of the PNQRP have implications in terms of managing threats influencing northern quoll populations in the Pilbara, but research specifically addressing the complexity of how multiple interacting threats influence northern quoll populations is currently lacking (Moore *et al.* 2021*b*). For example, extensive and frequent fires, along with overgrazing, is likely to increase predation risk to northern quolls by reducing vegetation cover (Cremona *et al.* 2017*b*; Jolly *et al.* 2018). Introduced predators may actively make expeditions to hunt in areas that have been recently burnt by intense fires (McGregor *et al.* 2015). Dispersal routes along watercourses (Shaw *et al.* 2023) may be pinch points, particularly given these areas are often heavily grazed in the Pilbara (McKenzie *et al.* 2009) and there is evidence that feral cats also favour riparian habitats (Williamson *et al.* 2021).

Northern quolls are likely to be most vulnerable during the breeding season when males are ranging widely in search of females, and later when young are dispersing (Hernandez-Santin *et al.* 2016). At East Alligator River in the Northern Territory, late dry season fires reduced the available cover for juvenile quolls when they began forag- ing, with dog and dingo predation a major source of mortal- ity (Cremona *et al.* 2017*b*). As increases in juvenile mortality may lead to local extinction of populations (Moro *et al.* 2019), better understanding the interactions between predation, fire, and grazing may be critical to effectively conserving Pilbara northern quoll populations. While clearly more empirical studies are required to improve our knowledge on how introduced predators respond to fire (Geary *et al.* 2020), applying feral cat control soon after a fire (wild or planned) is one strategy that may help alleviate predation pressure (Hradsky 2020).

Future research

While significant progress has been made towards improving our understanding of the Pilbara northern quoll population, this review has also identified future research directions to inform ongoing investment of funds to support northern quoll conservation (summarised in Table 1). Some of these are derived from research already undertaken, and others are original priorities which have yet to be studied in detail. Refinement of the annual regional monitoring program is needed given the analytical limitations of live trapping data from sites with apparently low abundance. An important area requiring further investigation is understanding how multiple interacting threats influence north- ern quoll populations in the Pilbara, particularly the synergistic threats of introduced predators, fire, and herbi- vore grazing (see Geary *et al.* 2019; Doherty *et al.* 2023). The influence of other threats, and their effective manage- ment, namely the impending cane toad invasion and cumu- lative impacts of mining associated activities remain poorly understood.

A recently commenced research project is investigating the influence of mining disturbance on the movement ecology and behaviour of northern quolls, including interactions with infrastructure and surrounding habitat (M. Cowan pers. comm.). The propensity for northern quolls to recolonise disturbed areas or artificial habitat is also unclear. While it appears that northern quolls will use purposely created artificial refuges, it is unknown whether they will continue to use them long-term and if they are suitable for breeding or supporting populations. More research is also needed on the optimal design of artificial refuges to maximise their potential as a conservation option.

One of the biggest concerns for the ongoing persistence of northern quolls in the Pilbara is the arrival of cane toads in this region, and the unknown consequences in this relatively arid and topographically complex landscape. Future research should focus on the potential hotspots for cane toads within the Pilbara taking climate change into consid- eration and where these areas overlap with northern quoll habitat, to direct targeted management.

Conclusions

Ecological knowledge of the Pilbara northern quoll population has been substantially improved as a result of the PNQRP. Survey and monitoring techniques have evolved with technological and analytical advances, and many studies summarised in this review demonstrate the application of these emerging approaches. Data collected using camera traps have improved our ability to measure changes in occupancy and abundance of northern quolls in the Pilbara. In combination with spatially explicit GPS-telemetry, genetic and environmental data, this has in turn allowed for assessments of habitat use from the regional to local scale, including the size, shape, and configuration of suitable habitat. We now have strong evidence-based support that contemporary habitat critical for Pilbara northern quolls constitutes topographically complex, contiguous, and well vegetated rocky areas that are important for denning. A recent study suggests this is driven by shelter availability as an important component of habitat quality (Hernandez-Santin *et al.* 2022). Evidence also suggests riparian areas are important as dispersal corridors for this population.

Monitoring data from several sites across the Pilbara indicate many subpopulations occur at apparently low density, although lack of genetic structure among them suggests widespread dispersal. As such, it appears northern quolls can move across suboptimal habitat such as the lowland plains surrounding rocky areas. Genetic studies also indicate male-biased dispersal and greater movements by males than female quolls, particularly during the breeding season. Given that high juvenile mortality is predicted to compro- mise the persistence of northern quolls, the importance of protecting dispersing young males is apparent. Effective management of introduced predators, particularly feral cats, and foxes where they are most prevalent, to facilitate movement of dispersing males, and connectivity between fragmented northern quoll populations, is likely to be cru- cial. Targeting areas surrounding critical habitat, including in recently burnt areas and along riparian areas, is likely to maximise management outcomes, given that feral cats have also shown preference for the latter. The results of this program and associated complementary research can now help inform the allocation of funding (including offsets) to on-ground conservation management actions that directly benefit northern quolls in the Pilbara.

References

Algar, D., Angus, G. J., Williams, M. R., and Mellican, A. E. (2007). Influence of bait type, weather and prey abundance on bait uptake by feral cats (*Felis catus*) on Peron Peninsula, Western Australia. *Conservation Science Western Australia* **6**, 109–149.

Australian Government (2013). 'Matters of national environmental significance: Significant impact guidelines.' (Department of Energy and Environment: Canberra, Australia.)

Birch, N., and Dunlop, J. (2019). 'Inventory of the Burrup Peninsula and Dolphin Island Animal Species.' (Department of Biodiversity, Conservation and Attractions: Perth, Australia.)

Braithwaite, R. W., and Griffiths, A. D. (1994). Demographic variation and range contraction in the northern quoll, *Dasyurus hallucatus* (Marsupialia: Dasyuridae). *Wildlife Research* **21**, 203–217. doi:10.1071/WR9940203

Cairns, K. M., Crowther, M. S., Nesbitt, B., and Letnic, M. (2022). The myth of wild dogs in Australia: are there any out there? *Australian Mammalogy* **44**, 67–75. doi:10.1071/AM20055

Campbell, C. A., Lefroy, E. C., Caddy-Retalic, S., Bax, N., Doherty, P. J., Douglas, M. M., Johnson, D., Possingham, H. P., Specht, A., Tarte, D., and West, J. (2015). Designing environmental research for impact. *Science of the Total Environment* **534**, 4–13. doi:10.1016/j.scitotenv. 2014.11.089

Chan, R., Dunlop, J., and Spencer, P. B. S. (2020). Highly promiscuous paternity in mainland and island populations of the endangered Northern Quoll. *Journal of Zoology* **310**, 210–220. doi:10.1111/jzo. 12745

Cowan, M., Moro, D., Anderson, H., Angus, J., Garretson, S., and Morris, K. (2020*a*). Aerial baiting for feral cats is unlikely to affect survivorship of northern quolls in the Pilbara region of Western Australia. *Wildlife Research* **47**, 589–598. doi:10.1071/WR19141

Cowan, M. A., Dunlop, J. A., Turner, J. M., Moore, H. A., and Nimmo, D. G. (2020*b*). Artificial refuges to combat habitat loss for an endangered marsupial predator: How do they measure up? *Conservation Science and Practice* **2**, e204.

Cowan, M. A., Callan, M. N., Watson, M. J., Watson, D. M., Doherty, T. S., Michael, D. R., Dunlop, J. A., Turner, J. M., Moore, H. A., Watchorn, D. J., and Nimmo, D. G. (2021). Artificial refuges for wildlife conservation: what is the state of the science? *Biological Reviews* **96**, 2735–2754. doi:10.1111/brv.12776

Cowan, M. A., Moore, H. A., Hradsky, B. A., Jolly, C. J., Dunlop, J. A., Wysong, M. L., Hernandez-Santin, L., Davis, R. A., Fisher, D. O., Michael, D. R., Turner, J. M., Gibson, L. A., Knuckey, C. G., Henderson, M., and Nimmo, D. G. (2022). Non-preferred habitat increases the activity area of the endangered northern quoll (*Dasyurus hallucatus*) in a semi-arid landscape. *Australian Mammalogy* doi:10.1071/AM22006

Cramer, V., and Dunlop, J. A. (2018). 'The ecology of the northern quoll (Dasyurus hallucatus) in the Pilbara bioregion, Western Australia: Project plans for 2016–2020.' (Department of Biodiversity, Conservation and Attractions: Perth, Australia.)

Cramer, V. A., Dunlop, J., Davis, R., Ellis, R., Barnett, B., Cook, A., Morris, K., and Van Leeuwen, S. (2016). Research priorities for the northern quoll (*Dasyurus hallucatus*) in the Pilbara region of Western Australia. *Australian Mammalogy* **38**, 135–148. doi:10.1071/ AM15005

Cremona, T., Spencer, P., Shine, R., and Webb, J. K. (2017*a*). Avoiding the last supper: parentage analysis indicates multi-generational survival of re-introduced 'toad-smart' lineage. *Conservation Genetics* **18**, 1475–1480. doi:10.1007/s10592-017-0973-3

Cremona, T., Crowther, M. S., and Webb, J. K. (2017*b*). High mortality and small population size prevent population recovery of a reintroduced mesopredator. *Animal Conservation* **20**, 555–563. doi:10.1111/ acv.12358

Doherty, T. S., Davis, N. E., Dickman, C. R., Forsyth, D. M., Letnic, M., Nimmo, D. G., Palmer, R., Ritchie, E. G., Benshemesh, J., Edwards, G., Lawrence, J., Lumsden, L., Pascoe, C., Sharp, A., Stokeld, D., Myers, C., Story, G., Story, P., Triggs, B., Venosta, M., Wysong, M., and Newsome, T. M. (2019). Continental patterns in the diet of a top predator: Australia's dingo. *Mammal Review* **49**, 31–44. doi:10.1111/ mam.12139

Doherty, T. S., Geary, W. L., Miritis, V., and Watchorn, D. J. (2023). Multiple Threats Affecting the Marsupials of Australasia: Impacts and Management. In 'American and Australasian Marsupials'. (Eds N. C. Cáceres, C. R. Dickman.) (Springer: Cham.) doi:10.1007/978-3-030-88800-8_53-1

Dunlop, J., Cook, A., and Morris, K. (2014). 'Pilbara northern quoll project: Surveying and monitoring *Dasyurus hallucatus* in the Pilbara, Western Australia.' (Department of Parks and Wildlife: Perth, Australia.)

Dunlop, J., Cook, A., Rayner, K., and Lees, J. (2015). Use of quarry infrastructure by the Pilbara northern quoll *Dasyurus hallucatus*. Final Report May 2010 - June 2013. (Department of Parks and Wildlife: Perth, Australia.)

Dunlop, J. A., Rayner, K., and Doherty, T. S. (2017). Dietary flexibility in small carnivores: a case study on the endangered northern quoll, *Dasyurus hallucatus*. *Journal of Mammalogy* **98**, 858–866. doi:10.1093/jmammal/gyx015

Dunlop, J., Birch, N., Moore, H., and Cowan, M. (2019). Pilbara Northern Quoll Research Program: 2018 Annual Report. (Department of Biodiversity, Conservation and Attractions: Perth, Australia.)

Dunlop, J., Birch, N., Davie, H., Nelson, J., and Read, J. (2020). 'Felixer™ feral cat grooming trap trials in the presence of northern quolls.' (Department of Biodiversity, Conservation and Attractions: Perth, Australia.)

Ecoscape (2019). 'Rail Culvert Fauna Monitoring 2018.' (Ecoscape: Perth, Australia.)

Edwards, T., and Nelson, J. (2022). 'Felixer™ feral cat grooming trap trials in the presence of northern quolls 2022.' (Fortescue Metals Group: Perth, Australia.)

Efford, M. (2004). Density estimation in live-trapping studies. *Oikos* **106**, 598–610. doi:10.1111/j.0030-1299.2004.13043.x

Fischer, J., and Lindenmayer, D. B. (2007). Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* **16**, 265–280. doi:10.1111/j.1466-8238.2007.00287.x

Fisher, D. O., Dickman, C. R., Jones, M. E., and Blomberg, S. P. (2013). Sperm competition drives the evolution of suicidal reproduction in mammals. Proceedings of the National Academy of Science 110, 17910-17914. doi:10.1073/pnas.131069111

Galloway, P., Simons, J., Holmes, K., and van Gool, D. (2022). Land and Water Resources for Irrigated Agriculture in the Pilbara. Resource Management Technical Report 426. (Department of Primary Industries and Regional Development, Western Australian Government: Perth.)

Geary, W. L., Nimmo, D. G., Doherty, T. S., Ritchie, E. G., and Tulloch, A. I. T. (2019). Threat webs: Reframing the co-occurrence and interactions of threats to biodiversity. *Journal of Applied Ecology* **56**, 1992–1997. doi:10.1111/1365-2664.13427

Geary, W. L., Doherty, T. S., Nimmo, D. G., Tulloch, A. I. T., and Ritchie, E. G. (2020). Predator responses to fire: A global systematic review and meta-analysis. *Journal of Animal Ecology* **89**, 955–971. doi:10.1111/1365-2656.13153

Glen, A. S., and Dickman, C. R. (2008). Niche overlap between marsupial and eutherian carnivores: does competition threaten the endangered spotted-tailed quoll? *Journal of Applied Ecology* **45**, 700–707. doi:10.1111/j.1365-2664.2007.01449.x

Glen, A. S., Pennay, M., Dickman, C. R., Wintle, B. A., and Firestone, K. B. (2011). Diets of sympatric native and introduced carnivores in the Barrington Tops, eastern Australia. *Austral Ecology* **36**, 290–296. doi:10.1111/j.1442-9993.2010.02149.x

Henderson, M. (2015). The effects of mining infrastructure on northern quoll movement and habitat. Masters thesis, Edith Cowan University, Perth, Australia.

Hernandez-Santin, L., Goldizen, A. W., and Fisher, D. O. (2016). Introduced predators and habitat structure influence range contraction of an endangered native predator, the northern quoll. *Biological Conservation* **203**, 160–167. doi:10.1016/j.biocon.2016.09.023

Hernandez-Santin, L., Dunlop, J. A., Goldizen, A. W., and Fisher, D. O. (2019). Demography of the northern quoll (*Dasyurus hallucatus*) in the most arid part of its range. *Journal of Mammalogy* **100**, 1191–1198. doi:10.1093/jmammal/gyz092

Hernandez-Santin, L., Goldizen, A. W., and Fisher, D. O. (2022). Northern quolls in the Pilbara persist in high-quality habitat, despite a decline trajectory consistent with range eclipse by feral cats. *Conservation Science and Practice* **4**, e12733. doi:10.1111/csp2.12733

Hill, B. M., and Ward, S. J. (2010). 'National Recovery Plan for the Northern Quoll *Dasyurus hallucatus*.' (Department of Natural Resources, Environment, the Arts and Sport: Darwin, Australia.)

Hohnen, R., Ashby, J., Tuft, K., and McGregor, H. (2013). Individual identification of northern quolls (*Dasyurus hallucatus*) using remote cameras. *Australian Mammalogy* **35**, 131–135. doi:10.1071/AM12015

Hohnen, R., Tuft, K. D., Legge, S., Hillyer, M., Spencer, P. B. S., Radford, I. J., Johnson, C. N., and Burridge, C. P. (2016). Rainfall and topography predict gene flow among populations of the declining northern quoll (*Dasyurus hallucatus*). *Conservation Genetics* **17**, 1213–1228. doi:10.1007/s10592-016-0856-z

How, R. A., Spencer, P. B. S., and Schmitt, L. H. (2009). Island populations have high conservation value for northern Australia's top marsupial predator ahead of a threatening process. *Journal of Zoology* **278**, 206–217. doi:10.1111/j.1469-7998.2009.00569.x

Hradsky, B. A. (2020). Conserving Australia's threatened native mammals in predator-invaded, fire-prone landscapes. *Wildlife Research* **47**, 1–15. doi:10.1071/WR19027

Indigo, N., Smith, J., Webb, J. K., and Phillips, B. (2018). Not such silly sausages: Evidence suggests northern quolls exhibit aversion to toads after training with toad sausages. *Austral Ecology* **43**, 592–601. doi:10.1111/aec.12595

Indigo, N., Smith, J., Webb, J. K., and Phillips, B. L. (2019). Bangers and cash: Baiting efficiency in a heterogeneous population. *Wildlife Society Bulletin* **43**, 669–677. doi:10.1002/wsb.1012

Indigo, N. L., Jolly, C. J., Kelly, E., Smith, J., Webb, J. K., and Phillips, B. L. (2021). Effects of learning and adaptation on population viability. *Conservation Biology* **35**, 1245–1255. doi:10.1111/cobi.13691

Indigo, N. L., Kelly, E., Smith, J., Webb, J. K., and Phillips, B. L. (2023). Can conditioned taste aversion be deployed at a landscape level to mitigate the impact of invasive cane toads on northern quolls? *Wildlife Research* doi:10.1071/WR21151

Jolly, C. J., Kelly, E., Gillespie, G. R., Phillips, B., and Webb, J. K. (2018). Out of the frying pan: Reintroduction of toad-smart northern quolls to southern Kakadu National Park. *Austral Ecology* **43**, 139–149. doi:10.1111/aec.12551

Kearney, S. G., Carwardine, J., Reside, A. E., Adams, V. M., Nelson, R., Coggan, A., Spindler, R., and Watson, J. E. M. (2022). Saving species beyond the protected area fence: Threats must be managed across multiple land tenure types to secure Australia's endangered species. *Conservation Science and Practice* **4**, e617. doi:10.1111/csp2.617

Kearney, M., Phillips, B. L., Tracy, C. R., Christian, K. A., Betts, G., and Porter, W. P. (2008). Modelling species distributions without using species distributions: the cane toad in Australia under current and future climates *Ecography* **31**(4), 423–434. doi:10.1111/j.0906-7590.2008.05457.x

Kremen, C., and Merenlender, A. M. (2018). Landscapes that work for biodiversity and people. *Science* **362**, eaau6020. doi:10.1126/science.aau6020

Lawlor, T. E. (1982). The evolution of body size in mammals: evidence from insular populations in Mexico. *The American Naturalist* **119**, 54–72. doi:10.1086/283890

Mahon, C. L., Holloway, G. L., Bayne, E. M., and Toms, J. D. (2019). Additive and interactive cumulative effects on boreal landbirds: winners and losers in a multi-stressor landscape. *Ecological Applications* **29**, e01895. doi:10.1002/eap.1895

McGregor, H., Legge, S., Jones, M. E., and Johnson, C. N. (2015). Feral cats are better killers in open habitats, revealed by animal-borne video. *PLoS One* **10**, e0133915. doi:10.1371/journal.pone.0133915

McKenzie, N. L., Van Leeuwen, S., and Pinder, A. M. (2009). Introduction to the Pilbara Biodiversity Survey, 2002–2007. *Records of the Western Australian Museum, Supplement* **78**, 3–89. doi:10.18195/issn.0313-122x.78(1).2009.003-089

Molloy, S. W., Davis, R. A., Dunlop, J. A., and Van Etten, E. J. B. (2017). Applying surrogate species presences to correct sample bias in species distribution models: A case study using the Pilbara population of the Northern Quoll. *Nature Conservation* **18**, 27–46. doi:10.3897/natureconservation.18.12235

Moore, H. A., Dunlop, J. A., Valentine, L. E., Woinarski, J. C. Z., Ritchie, E. G., Watson, D. M., and Nimmo, D. G. (2019). Topographic ruggedness and rainfall mediate geographic range contraction of a threatened marsupial predator. *Diversity and Distributions* **25**, 1818–1831. doi:10.1111/ddi.12982

Moore, H. A., Valentine, L. E., Dunlop, J. A., and Nimmo, D. G. (2020). The effect of camera orientation on the detectability of wildlife: a case study from north-western Australia. *Remote Sensing in Ecology and Conservation* **6**, 546–556. doi:10.1002/rse2.158

Moore, H. A., Michael, D. R., Ritchie, E. G., Dunlop, J. A., Valentine, L. E., Hobbs, R. J., and Nimmo, D. G. (2021*a*). A rocky heart in a spinifex sea: occurrence of an endangered marsupial predator is multiscale dependent in naturally fragmented landscapes. *Landscape Ecology* **36**, 1359–1376. doi:10.1007/s10980-021-01207-9

Moore, H. A., Dunlop, J. A., Jolly, C. J., Kelly, E., Woinarski, J. C., Ritchie, E. G., Burnett, S., van Leeuwen, S., Valentine, L. E., and Cowan, M. A. (2021*b*). A brief history of the northern quoll (*Dasyurus hallucatus*): A systematic review. *Australian Mammalogy* **44**, 185–207. doi:10.1071/AM21002

Moore, H. A., Michael, D. R., Dunlop, J. A., Valentine, L. E., Cowan, M. A., and Nimmo, D. G. (2022). Habitat amount is less important than habitat configuration for a threatened marsupial predator in natu- rally fragmented landscapes. *Landscape Ecology* **37**, 935–949. doi:10.1007/s10980-022-01411-1

Moore, H. A., Dunlop, J. A., Geyle, H. M., Greenwood, L., and Nimmo, D. G. (2023). First you get the money, then you get the power: comparing the cost and power of monitoring programs to detect changes in occupancy of a threatened marsupial predator. *Conservation Science and Practice* **5**, e12881. doi:10.1111/csp2.12881

Moro, D., Dunlop, J., and Williams, M. R. (2019). Northern quoll persistence is most sensitive to survivorship of juveniles. *Wildlife Research* **46**, 165–175. doi:10.1071/WR18010

Moro, D., Morris, K., van Leeuwen, S., and Davie, H. (2021). A framework of integrated research for managing introduced predators in the Pilbara bioregion, Western Australia. *Australian Mammalogy* **43**, 265–276. doi:10.1071/AM20025

Moseby, K. E., McGregor, H., and Read, J. L. (2020). Effectiveness of the Felixer grooming trap for the control of feral cats: A field trial in arid South Australia. *Wildlife Research* **47**, 599–609. doi:10.1071/WR19132

Moseby, K. E., Jensen, M. A., and Tatler, J. (2022). Dietary flexibility and high predator efficacy facilitate coexistence in a novel predator interaction. *Journal of Mammalogy* **103**, 124–135. doi:10.1093/jmammal/gyab120

Oakwood, M. (2002). Spatial and social organization of a carnivorous marsupial *Dasyurus hallucatus* (Marsupialia: Dasyuridae). *Journal of Zoology* **257**, 237–248. doi:10.1017/S0952836902000833

Oakwood, M. (2004). Death after sex. *Biologist* **51**, 5–8.

O'Donnell, S., Webb, J. K., and Shine, R. (2010). Conditioned taste aversion enhances the survival of an endangered predator imperilled by a toxic invader. *Journal of Applied Ecology* **47**, 558–565. doi:10.1111/j.1365-2664.2010.01802.x

Palmer, R., Anderson, H., and Richards, B. (2020). Predator control baiting and monitoring program, Yarraloola and Red Hill, Pilbara region, Western Australia. 2019 Annual report – Year 5. (Department of Biodiversity, Conservation and Attractions: Perth.)

Palmer, R., Anderson, H., Richards, B., Craig, M. D., and Gibson, L. (2021). Does aerial baiting for controlling feral cats in a heterogeneous landscape confer benefits to a threatened native meso-predator? *PLoS One* **16**, e0251304. doi:10.1371/journal.pone.0251304

Read, J. L., Bowden, T., Hodgens, P., Hess, M., McGregor, H., and Moseby, K. (2019). Target specificity of the felixer grooming "trap". *Wildlife Society Bulletin* **43**, 112–120. doi:10.1002/wsb.942

Shaw, R. E., Spencer, P. B., Gibson, L. A., Dunlop, J. A., Kinloch, J. E., Mokany, K., Byrne, M., Moritz, C., Davie, H., Travouillon, K. J., and Ottewell, K. M. (2023). Linking life history to landscape for threatened species conservation in a multi-use region. *Conservation Biology* **37**, e13989. doi:10.1111/cobi.13989

Sonter, L. J., Ali, S. H., and Watson, J. E. M. (2018). Mining and biodiversity: key issues and research needs in conservation science. *Proceedings of the Royal Society B: Biological Sciences* **285**, 20181926. doi:10.1098/rspb.2018.1926

Southwell, D., Tingley, R., Bode, M., Nicholson, E., and Phillips, B. L. (2017). Cost and feasibility of a barrier to halt the spread of invasive cane toads in arid Australia: incorporating expert knowledge into model-based decision-making. *Journal of Applied Ecology* **54**, 216–224. doi:10.1111/1365-2664.12744

Spencer, P. B. S., How, R. A., Hillyer, M., Cook, A., Morris, K., Stevenson, C., and Umbrello, L. (2013). Genetic Analysis of Northern Quolls from the Pilbara Region of Western Australia. (Murdoch University: Perth, Australia).

Sudmeyer, R. (2016). 'Climate in the Pilbara, Bulletin 4873.' (Department of Agriculture and Food: Perth, WA)

Tingley, R., Phillips, B. L., Letnic, M., Brown, G. P., Shine, R., and Baird, S. J. E. (2013). Identifying optimal barriers to halt the invasion of cane toads *Rhinella marina* in arid Australia. *Journal of Applied Ecology* **50**, 129–137. doi:10.1111/1365-2664.12021

Turpin, J. M., and Bamford, M. J. (2015). A new population of the northern quoll (*Dasyurus hallucatus*) on the edge of the Little Sandy Desert, Western Australia. *Australian Mammalogy* **37**, 86–91. doi:10.1071/AM13045

Ujvari, B., Oakwood, M., and Madsen, T. (2013). Queensland northern quolls are not immune to cane toad toxin. *Wildlife Research* **40**, 228–231. doi:10.1071/WR13011

von Takach, B., Ranjard, L., Burridge, C. P., Cameron, S. F., Cremona, T., Eldridge, M. D. B., Fisher, D. O., Frankenberg, S., Hill, B. M., Hohnen, R., Jolly, C. J., Kelly, E., MacDonald, A. J., Moussalli, A., Ottewell, K., Phillips, B. L., Radford, I. J., Spencer, P. B. S., Trewella, G. J., Umbrello, L. S., and Banks, S. C. (2022). Population genomics of a predatory mammal reveals patterns of decline and impacts of exposure to toxic toads. *Molecular Ecology* **31**, 5468–5486. doi:10.1111/mec.16680

Watchorn, D. J., Cowan, M. A., Driscoll, D. A., Nimmo, D. G., Ashman, K. R., Garkaklis, M. J., Wilson, B. A., and Doherty, T. S. (2022). Artificial habitat structures for animal conservation: design and implementation, risks and opportunities. *Frontiers in Ecology and the Environment* **20**, 301–309. doi:10.1002/fee.2470

Watson, J. E. M., Jones, K. R., Fuller, R. A., Marco, M. D., Segan, D. B., Butchart, S. H. M., Allan, J. R., McDonald-Madden, E., and Venter, O. (2016). Persistent disparities between recent rates of habitat conversion and protection and implications for future global conservation targets. *Conservation Letters* **9**, 413–421. doi:10.1111/conl.12295

Wearn, O. R., and Glover-Kapfer, P. (2019). Snap happy: camera traps are an effective sampling tool when compared with alternative methods. *Royal Society Open Science* **6**, 181748. doi:10.1098/rsos.181748

Williamson, S. D., van Dongen, R., Trotter, L., Palmer, R., and Robinson, T. P. (2021). Fishing for feral cats in a naturally fragmented rocky landscape using movement data. *Remote Sensing* **13**, 4925. doi:10.3390/rs13234925

Woinarski, J. C. Z. (2014). Northern Quoll. In 'The Action Plan for Australian Mammals 2012'. (Eds A. Burbidge, P. Harrison, J. C. Z. Woinarski.) pp. 76–81. (CSIRO Publishing: Melbourne.)

Woinarski, J. C. Z., Armstrong, M., Brennan, K., Fisher, A., Griffiths, A. D., Hill, B., Milne, D. J., Palmer, C., Ward, S., Watson, M., Winderlich, S., and Young, S. (2010). Monitoring indicates rapid and severe decline of native small mammals in Kakadu National Park, northern Australia. *Wildlife Research* **37**, 116–126. doi:10.1071/WR09125

Woinarski, J. C. Z., Burbidge, A. A., and Harrison, P. L. (2015). Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences* **112**, 4531–4540. doi:10.1073/pnas.1417301112

Woolley, P. A., Krajewski, C., and Westerman, M. (2015). Phylogenetic relationships within *Dasyurus* (Dasyuromorphia: Dasyuridae): Quoll systematics based on molecular evidence and male characteristics. *Journal of Mammalogy* **96**, 37–46. doi:10.1093/jmammal/gyu028

Woolley, L. A., Geyle, H. M., Murphy, B. P., Legge, S. M., Palmer, R., Dickman, C. R., Augusteyn, J., Comer, S., Doherty, T. S., Eager, C., Edwards, G., Harley, D. K. P., Leiper, I., McDonald, P. J., McGregor, H. W., Moseby, K. E., Myers, C., Read, J. L., Riley, J., Stokeld, D., Turpin, J. M., and Woinarski, J. C. Z. (2019). Introduced cats *Felis catus* eating a continental fauna: inventory and traits of Australian mammal species killed. *Mammal Review* **49**, 354–368. doi:10.1111/ mam.12167

Data availability. Data sharing is not applicable as no new data were generated or analysed during this study.

Conflicts of interest. The authors declare no conflict of interest.

Declaration of funding. The Pilbara Northern Quoll Research Program was supported by environmental offsets and industry funding provided by Atlas Iron, BHP, Fortescue Metals Group, Main Roads Western Australia, Metals X Ltd, Process Minerals International, Rio Tinto and Roy Hill.

Acknowledgements. We thank Rainer Chan, Tim Doherty, Dorian Moro and Peter Spencer for their contribution to the PNQRP (post-2016). We are grateful to Leonie Valentine, David Watson, Euan Ritchie, and James Turner for supervising PhD and Honours students involved in the program. Trials of Felixer™ feral cat grooming traps were in collaboration with John Read, Roy Hill and Fortescue Metals Group. Russell Palmer and Robyn Shaw kindly shared information in relation to their complementary studies in the Pilbara. Joanne Potts conducted the mark–recapture analyses. We thank Stephen van Leeuwen and Keith Morris for their support of the program, and Dr Ross Goldingay and an anonymous reviewer for their useful comments on the manuscript. We are appreciative of the field and logistical assistance provided by Hannah Anderson, Sophie Arnall, Neil Birch, Gareth Catt, Jacob Champney, Lachlan Crossley, Harriet Davie, Brent Johnson, Joanne King, Kirsten Marmion, Mike Robinson, Kelly Rayner, Zac Sims, Elizabeth Trevenen, Matthew Verdouw and Alicia Whittington. We acknowledge the Traditional Owners of the Pilbara and their representative bodies: KJ Martu Indigenous Knowledge Program, Murujuga Aboriginal Corporation, Yindjibarndi Aboriginal Corporation, Banyjima, Kurrama and Innawonga people, Kariyarra Aboriginal Corporation, Nyamal Aboriginal Corporation, Karlka Aboriginal Corporation, Puutu Kunti Kurrama and Pinkura Aboriginal Corperation, Wanparta Aboriginal Corporation, Wanparta Aboriginal Corporation Ngarluma Aboriginal Corporation, Wirrawandi Aboriginal Corporation, Wanparta Aboriginal Corporation, Palyku-Jartayi Aboriginal Corporation.

Author affiliations

[A]Department of Biodiversity, Conservation and Attractions, Kensington, WA 6151, Australia.

[B]School of Biological Sciences, University of Western Australia, Crawley, WA 6009, Australia.

[C]School of Agriculture and Environment, University of Western Australia, Crawley, WA 6009, Australia.

[D]Gulbali Institute, School of Agricultural, Environmental and Veterinary Sciences, Charles Sturt University, Albury, NSW 2640, Australia.

Appendix G: A brief history of the northern quoll (*Dasyurus hallucatus*): a systematic review

Published in *Australian Mammalogy* in August 2021.

Manuscript citation**:** Moore, H.A., Dunlop, J.A., Jolly, C.J., Kelly, E., Woinarski, J.C.Z., Ritchie, E.G., Burnett, S., van Leeuwen, S., Valentine, L.E., Cowan, M.A., Nimmo, D. G. (2022). A brief history of the northern quoll (*Dasyurus hallucatus*): a systematic review. *Australian Mammalogy*, 44, 185–207.

CSIRO PUBLISHING

Australian Mammalogy
https://doi.org/10.1071/AM21002

Review

A brief history of the northern quoll (*Dasyurus hallucatus*): a systematic review

Harry A. Moore[A,B,J], Judy A. Dunlop[A,B,C,D], Chris J. Jolly[A], Ella Kelly[E], John C. Z. Woinarski[F], Euan G. Ritchie[G], Scott Burnett[H], Stephen van Leeuwen[I], Leonie E. Valentine[B], Mitchell A. Cowan[A] and Dale G. Nimmo[A]

[A]Institute for Land, Water and Society, School of Environmental Science, Charles Sturt University, Albury, NSW 2640, Australia.
[B]School of Biological Sciences, University of Western Australia, Crawley, WA 6009, Australia.
[C]Department of Biodiversity, Conservation and Attractions, Bentley Delivery Centre, Locked Bag 104, Perth, WA, Australia.
[D]Western Australian Feral Cat Working Group, Mandurah, WA 6210, Australia.
[E]Department of Environment, Land, Water and Planning, Nicholson Street, East Melbourne, Vic. 3002, Australia.
[F]Threatened Species Recovery Hub, National Environmental Science Program, Charles Darwin University, Darwin, NT 0810, Australia.
[G]Centre for Integrative Ecology and School of Life and Environmental Sciences, Deakin University, Burwood, Vic. 3125, Australia.
[H]PO Box 1219, Maleny, Qld 4552, Australia.
[I]School of Molecular and Life Sciences, Curtin University, Bentley, WA 6102, Australia.
[J]Corresponding author. Email: harryamos@live.com.au

Abstract. In response to Australia's current extinction crisis, substantial research efforts have been targeted towards some of the most imperilled species. One such species is the northern quoll (*Dasyurus hallucatus*), a marsupial predator that has recently suffered substantial declines in range and is now listed as Endangered. We conducted a systematic review of all literature relevant to the conservation and ecology of northern quolls. We reviewed 143 studies, including research articles, government and industry reports, theses, and books, and quantified research effort in terms of topic, location, and publication period. We then summarised research relevant to northern quoll taxonomy, genetics, distribution, habitat associations, diet, reproduction, movement, threats, management, and Indigenous knowledge. Research effort was higher between 2011 and 2020 than the previous four decades combined. Northern quolls in the Northern Territory were the most studied, followed by the Pilbara, the Kimberley, and Queensland populations. Most studies focused on northern quoll distribution and habitat, management, and threats – primarily cane toads, predation, and fire. We conclude with a non-exhaustive list of ten future research directions. If pursued, these future research directions should provide information critical to managing and conserving northern quolls.

Keywords: biodiversity conservation, dasyurids, *Dasyurus hallucatus*, Endangered species, extinction crisis, habitat management, imperilled species, mammal extinction, marsupial predator, northern quolls, research studies, systematic literature reviews.

Received 14 January 2021, accepted 13 July 2021, published online 26 August 2021

Introduction

Biodiversity conservation and management is most effective when derived from a robust evidence base (Salafsky *et al.* 2019). Despite an ever growing of ecological information (Bornmann and Mutz 2015), there remains a considerable gap between the science of conservation biology and the on-ground implementation of evidence-based policy (Knight *et al.* 2008; Evans and Cvitanovic 2018; Rose *et al.* 2019). One reason for this is that conservation practitioners can struggle to access, interpret, and synthesise an increasingly dispersed and voluminous body of scientific literature (Pullin and Knight 2005). Similar problems are encountered by researchers, leading to repetition and redundancy in ecological science (Pulsford *et al.* 2016). Systematic literature reviews are one means of overcoming these

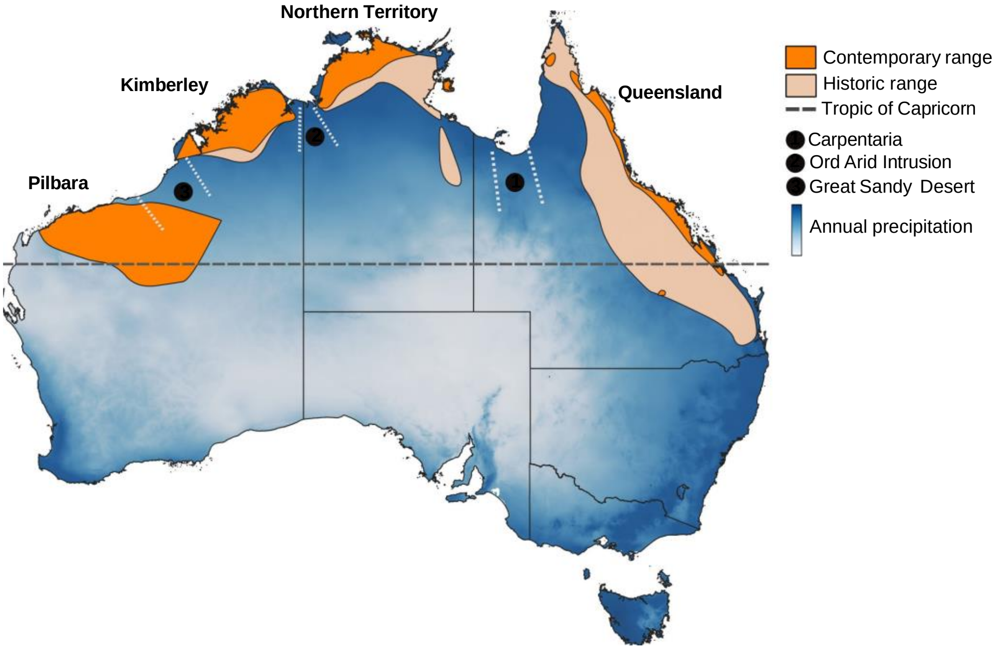


Fig. 1. The historic and contemporary range of the northern quoll (*Dasyurus hallucatus*). Figure adapted from (Moore *et al.* 2019). Note that islands occupied by the northern quolls (except Groote Eylandt) are not depicted, but are listed in Supplementary material S2.

issues by identifying, selecting, and appraising research on a predefined topic, drawing out evidence-based management implications and critical knowledge gaps for further research (Moher *et al.* 2009).

Australia's contemporary mammal extinction rate is the globe's highest (Woinarski *et al.* 2019*a*). Yet more Australian mammals are forecast to become extinct within the next two decades (Geyle *et al.* 2018). In response to this crisis, increased research effort has been directed towards Australian species that have suffered population contractions over the last 240 years (Fleming and Bateman 2016). One such species is the northern quoll (*Dasyurus hallucatus*) – a medium-sized marsupial predator (240–1120 g) endemic to northern Australia. Prior to European colonisation, northern quolls were distributed across much of northern Australia (Braithwaite and Griffiths 1994), but have since suffered substantial declines (Fig. 1) (Moore *et al.* 2019). As such, northern quolls are listed as Endangered both nationally (TSSC 2005) and globally (Oakwood *et al.* 2016).

Due to their ongoing and precipitous decline, much of the research focused on the ecology and conservation of northern quolls has occurred within the last two decades. However, accessing this research can be challenging, largely because it is spread across a diverse and dispersed literature (e.g. books, journals, government and consultant's reports, and theses). To help overcome this barrier, we conducted a systematic review of all literature relevant to the ecology and conservation of northern quolls across their entire range.

The complexities of species conservation are such that multiple disciplinary approaches are often required to achieve meaningful progress (Dick *et al.* 2016). With this in mind, we take a deliberately broad approach to our review. We summarise research related to the northern quoll's diet, distribution and habitat associations, genetics and taxonomy, reproduction, movement, and threats and management. We also summarise available Indigenous knowledge related to the northern quoll's ecology. We identify and discuss knowledge gaps throughout and provide a non-exhaustive list of future research directions for the northern quoll. If applied, we believe these future research directions could provide knowledge critical to improving the conservation of northern quolls.

Materials and methods

Database compilation

We followed the approach used by Ashman *et al.* (2019) to collate relevant literature for this review. Three electronic databases were searched (Web of Science, Scopus and Google Scholar) on 17 August 2020 using the search terms 'northern quoll' OR '*Dasyurus hallucatus*'. The search was updated on 15 April 2021. Search terms were located in publication title, abstract, keywords and main text. Searches retrieved studies from a range of categories including peer-reviewed literature, MSc and PhD theses, government and publicly available industry reports, and government action and recovery plans. Studies were reviewed in a three-step process (Fig. 2). First, duplicates were removed, then titles and/or abstracts were screened to detect the terms 'northern quoll' or '*Dasyurus hallucatus*', or a reference to a broader community of species that was likely to include northern quolls, for example, 'tropical mammals of Australia'. Lastly, full texts were reviewed. Studies were excluded if they were not immediately relevant to the ecology and conservation of the species. Therefore, for example, studies that focused solely on the physiology or anatomy of northern quolls were removed unless the publication made explicit reference to the relevance of their findings to ecology or conservation of wild populations (e.g. predator-aversion trials conducted in captivity).

Data retrieved

For each of the 143 studies that were included in the final analysis, we recorded date of publication, study population(s) (if applicable), and study site(s) (if applicable). Study populations were adapted from Moore *et al.* (2019) and comprise four largely spatially segregated units: Queensland, Northern Territory, the Kimberley region of Western Australia, and the Pilbara region (including the neighbouring Little Sandy and Great Sandy Desert bioregions) of Western Australia. We also extracted home range estimates from studies that listed them. We pooled publication dates into six categories: prior to 1980, 1981–1990, 1991–2000, 2001–2010, 2011–2020, 2021–2030. We used decadal increments to categorise studies given they were fine enough to detect changes in research effort through time, but also coarse enough to capture a substantial number of studies within each increment. We then categorised studies into one or more of nine topics, adapted from Ashman *et al.* (2019):

- taxonomy and genetics,
- distribution, declines and habitat associations,
- diet (prey choice, scat composition),
- reproduction,
- movement,
- threats,
- conservation management (direct management actions, legislation, action and recovery plans),
- Indigenous knowledge, and
- miscellaneous (methods, reviews, albinism).

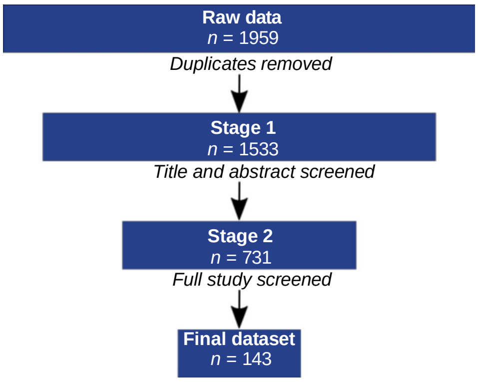


Fig. 2. Flow diagram of studies included and excluded from review.

Threats

For studies that included the topic ‘threats’, we categorised the threats examined within the publication according to threat categories adapted from the National Recovery Plan (Hill and Ward 2010). Threat categories adapted from the recovery plan included the introduced and toxic cane toad (*Rhinella marina*), feral cat (*Felis catus*) and dingo/dog (*Canis* spp.) predation, fire, grazing, habitat clearing, mining, disease, feral predator baiting, and vehicle strikes.

Topic summary and future research needs

We provide written summaries for all research topics included in the review except for ‘behaviour’, which is discussed within the management section, and ‘miscellaneous’, which is discussed throughout. Within summaries, we discuss important findings in the context of the ecology and conservation of northern quolls. We also identify and discuss knowledge gaps to highlight areas that may require future research. We finish by providing a non-exhaustive list of ten future research areas that could be useful to refine management action(s) to conserve northern quolls.

Results and discussion

The temporal distribution of the 143 studies shows a substantial increase in research effort in recent years (Fig. 3) (Supplementary material S1). The earliest study included in our analysis was published from 1926 (Thomas 1926) and the most recent was published in May 2021 (Moore *et al.* 2021). Most studies were conducted between 2011 and 2020 (86), and few studies were conducted prior to 1981 (2) (Fig. 3).

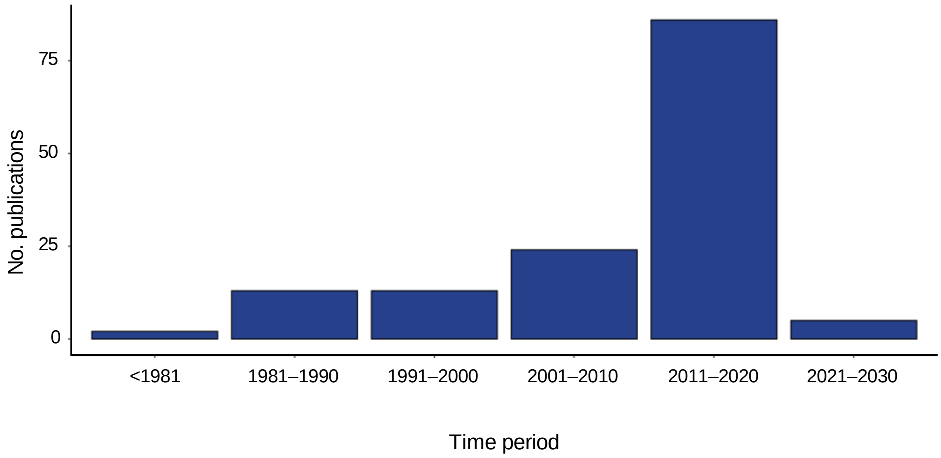


Fig. 3. Research relevant to the conservation and ecology of northern quoll (*Dasyurus hallucatus*) categorised by publication date.

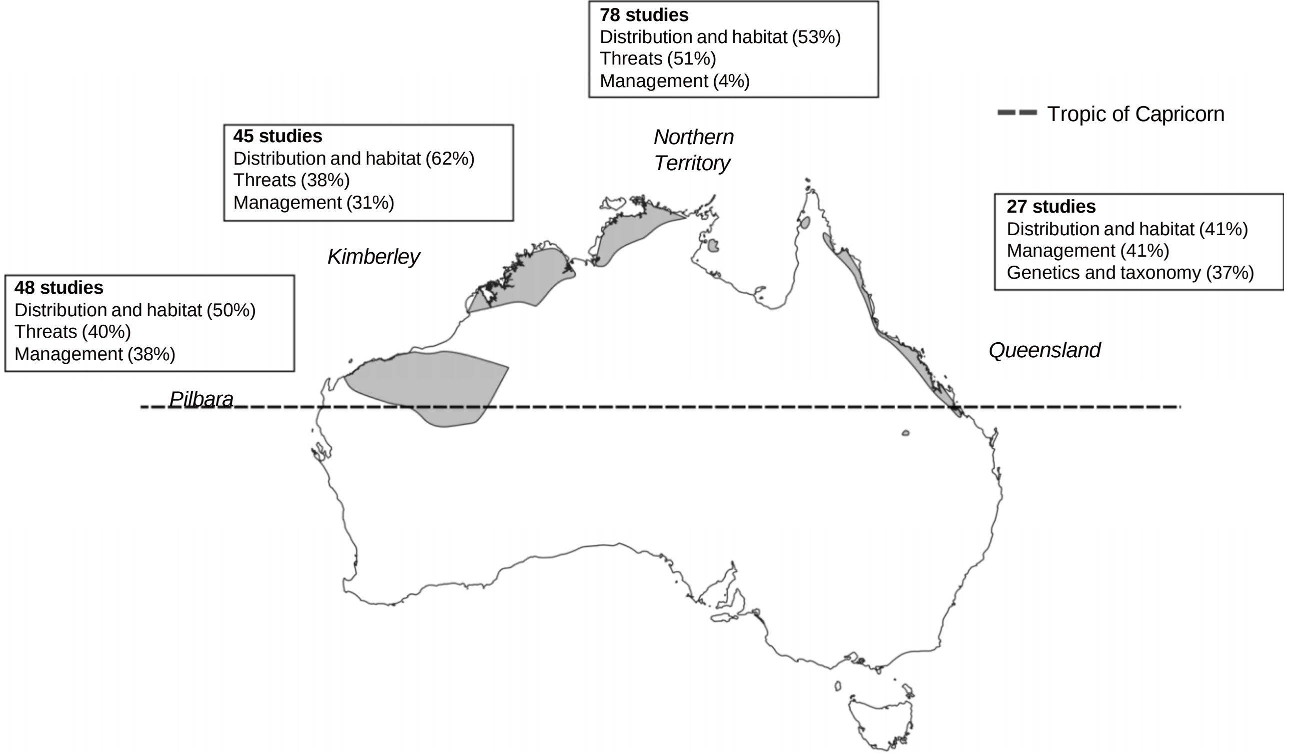
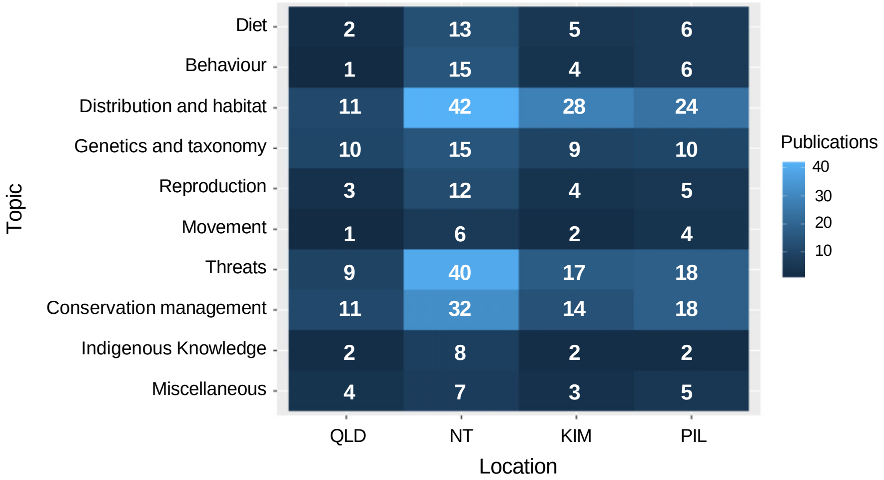


Fig. 4. Research relevant to the conservation and ecology of northern quoll (*Dasyurus hallucatus*) mapped by population. Insets represent top three research topics within each population. Dark grey area represents northern quoll contemporary distribution (prior to year 2000) adapted from (Moore *et al*. 2019).



	QLD	NT	KIM	PIL
Diet	2	13	5	6
Behaviour	1	15	4	6
Distribution and habitat	11	42	28	24
Genetics and taxonomy	10	15	9	10
Reproduction	3	12	4	5
Movement	1	6	2	4
Threats	9	40	17	18
Conservation management	11	32	14	18
Indigenous Knowledge	2	8	2	2
Miscellaneous	4	7	3	5

Fig. 5. Research relevant to the conservation and ecology of northern quolls (*Dasyurus hallucatus*) categorised by research topic and location.

The region with the most studies was the Northern Territory (78), followed by the Pilbara (48), the Kimberley (45), and Queensland (27) (Fig. 4). We identified 18 studies which were at least partly laboratory based. Each of the nine study topics were represented at least once within studies included in this review (Fig. 5). It is important to note that we found a limited amount of grey literature in this review and, as such, a number of environmental impact assess- ments (and the implications of their findings) were likely missed.

Taxonomy and genetics

We identified 21 studies relevant to northern quoll taxonomy, covering all major populations. Northern quolls (*Dasyurus hallucatus* Gould 1842) were described by John Gould (1842) from two specimens collected at Port Essington in the Northern Territory. They are the smallest of six *Dasyurus* species: including the spotted-tailed quoll (*D. maculatus*), western quoll (*D. geoffroii*), eastern quoll (*D. viverrinus*), bronze quoll (*D. spartacus*), and New Guinean quoll (*D. albopunctatus*). The latter two species are only found in Papua New Guinea and Indonesia. The current range of the northern quoll overlaps with the current range of the northern subspecies of spotted tailed quoll (*Dasyurus maculatus gracilis*) in North Queensland. In the Pilbara, subfossil evidence suggests northern quolls overlap with the historic distribution of the western quoll (Baynes and McDowell 2010).

In 1926, northern quolls were separated into four subspecies, based largely on the width of the skull at the nasals: *D. h. hallucatus* (Northern Territory to central Queensland); *D. h. predator* (Cape York, Queensland); *D. h. exilis* (the Kimberley); and *D. h. nesaeus* (Groote Eylandt) (Thomas 1926). No Pilbara specimens were included in this examination. Although these subspecies are no longer recognised (Jackson *et al.* 2015), there is now genetic evidence to suggest northern quolls in each of the four major populations (Queensland, Northern Territory, the Kimberley and the Pilbara) do represent distinct lineages. Firestone *et al.* (2000) suggest northern quoll cytochrome b sequences from Queensland and the Northern Territory are at least as divergent as those between western quolls and the bronze quoll. Woolley *et al.* (2015) and Hohnen *et al.* (2016*b*) found that the Northern Territory and Kimberley northern quoll populations are genetically divergent, and How *et al.* (2009) found the same for Kimberley and Pilbara populations. The results of more recent morphological examinations are mixed: Umbrello (2018) found significant differences in skull size, dentition, and external characteristics between Queensland, Northern Territory, Kimberley, and Pilbara populations, whereas Viacava *et al.* (2020) found few consistent differences. Some island populations separated from the mainland by permanent sea channels (Bigge, Boongaree, Koolan), as well as less permanent channels (Dolphin Island) also appear genetically divergent from mainland populations (How *et al.* 2009; Spencer *et al.* 2017; Chan *et al.* 2020). However, this is not the case for Groote Eylandt quolls, which genetically align with the mainland Northern Territory population (Woolley *et al.* 2015).

The disjunct distribution of mainland northern quolls, accompanied by the genetic and morphological differences between populations, correspond to biogeographical barriers across northern Australia (Bowman *et al.* 2010). Separating the Queensland and Northern Territory populations is the Carpentaria Gap; a series of clay pans that limit dispersal between Cape York and the rest of the Australian monsoonal tropics for a range of taxa (Bowman *et al.* 2010). For example, the Carpentaria Gap separates a recently recognised species of glider, *Petaurus ariel*, from its sister species, *Petaurus notatus* (Cremona *et al.* 2020). Similarly, the gap between the Northern Territory and Kimberley populations aligns with the Ord Arid Intrusion, which divides sandstone blocks between Arnhem Land in the Northern Territory and the Kimberley (Bowman *et al.* 2010), and acts as a dispersal barrier for other species that use rocky habitat, such as rock-wallabies (*Petrogale* spp.) (Potter *et al.* 2012). The Kimberley and Pilbara populations of northern quoll are separated by the Great Sandy Desert – an extensive dune system often implicated in the isolation of both species and populations (Edwards *et al.* 2017).

The taxonomic status of the northern quoll may not yet be fully resolved. Lack of taxonomic clarity has previously hampered conservation efforts in other taxa (Peterson 2006; Pickett *et al.* 2020). In the case of the northern quoll, understanding if populations should be treated as distinct taxonomic units or are genetically similar enough to be intermixed is likely to have important management implications, particularly in relation to cross-population translocations (as discussed in the 'Management' section). As such, further clarification of the extent to which northern quoll populations differ both genetically and morphologically should be a priority for future research. Other research related to northern quoll genetics are discussed within the 'Management' section.

Distribution, habitat associations, and geographic range contraction

A total of 80 studies were included in the 'Distribution, declines, and habitat associations' topic, with the most focused on the Northern Territory population ($n = 42$), followed by the Kimberley ($n = 28$), Pilbara ($n = 24$), and Queensland populations ($n = 11$) (Fig. 5).

Prior to European colonisation, the geographic range of northern quolls incorporated much of northern Australia above the Tropic of Capricorn (90˚ South) and within 200 km of the coastline (but likely extended inward much further (Braithwaite and Griffiths 1994; Turpin and Bamford 2014) covering a total area of over 1.2 million km^2. Average annual rainfall across this area varies substantially, ranging from 220 mm in the eastern extent of the Pilbara, to nearly 4500 mm in the Wet Tropics of northern Queensland (BOM 2020). Similarly, average maximum temperature in the warmest months ranges from 42.1˚C in the Pilbara to 25.5˚C in southern Queensland (BOM 2020). Northern quolls naturally occur on at least 32 islands, mostly off the Northern Territory and Kimberley (Supplementary material S2). Many of these are relatively free from human disturbance and lack introduced predators and/or cane toads (Woinarski *et al.* 2007; How *et al.* 2009). In the Northern Territory, northern quolls are particularly associated with large, remote, and rugged islands (Woinarski *et al.* 2007), although they are notably absent from two large Northern Territory islands – Bathurst (2600 km^2) and Melville (5786 km^2). In 2003 and 2017, northern quolls were translocated to three islands outside of their historical geographic range in the Northern Territory (Rankmore *et al.* 2008; Kelly 2018) (see 'Management' section).

Northern quolls occur across a broad range of habitat types including tropical and monsoonal rainforest, *Eucalyptus* woodlands, *Eucalyptus* open forests, lowland savanna, vine thickets, on beaches, and amongst human settlements (Pollock 1980; Begg 1981; Schmitt *et al.* 1989; Braithwaite and Griffiths 1994; Oakwood 1997), but appear most abundant in rugged and rocky landscapes, including rocky hills, patches of granite outcrops, boulder-strewn slopes, rocky creek lines, and gorges (Calaby

Fig. 6. Northern quoll habitat: (*a*) Hazelwood Gorge, Queensland; (*b*) East Alligator River, Northern Territory; (*c*) Charnley River Wildlife Sanctuary, the Kimberley, Western Australia; and (*d*) Indee station, the Pilbara, Western Australia. Image credits: (*a*) Dennis Jeffery; (*b*) Catherine Marshall; (*c*) Naomi Indigo; and (*d*) Daniel Bohorquez Fandino.

1973; McKenzie *et al.* 1975; Begg 1981; Kitchener *et al.* 1981; Schmitt *et al.* 1989; Braithwaite and Griffiths 1994; Oakwood 1997; Pollock 1999; Olds *et al.* 2016; Molloy *et al.* 2017; Ibbett *et al.* 2018; Moore *et al.* 2021) (Fig. 6). This preference may be due to rocky habitats holding permanent water and more food resources than surrounding habitats (Braithwaite and Griffiths 1994; Burnett 1997). However, evidence from some studies suggests diet is unlikely to be a key factor explaining the northern quolls preference for rocky habitat: Oakwood (1997) and Hernandez Santin (2017) found limited evidence that quoll selected rocky habitat based on differences in intrinsic dietary resources. Further, Thomas *et al.* (2021) found quolls occupying rocky habitat consumed a narrower range of prey resources than quolls that occurred in nearby savanna woodland, and also displayed lower body condition.

Another factor linking quolls to rocky habitats is the availability of shelter, particularly dens – small, enclosed spaces that northern quolls use as either short-term shelter sites (temporary den) or semi-permeant dwellings used to raise offspring (natal den). Northern quolls den in tree hollows (both alive and dead), termite mounds, logs, and goanna burrows (Oakwood 1997). In more arid regions in which trees and logs are scarce (e.g. the Pilbara), rocky crevices within granite boulder piles and rocky mesas are critical for providing both temporary and natal den sites for northern quolls (Cowan *et al.* 2020*b*). In the Pilbara, Cowan *et al.* (2020*b*) found rocky dens act as thermal refuges, being buffered from extreme external temperatures, which often exceeded safe temperatures for northern quolls (i.e. ≥36.5°C; Cooper and Withers 2010). Even in habitats where alternative den sites are available (e.g. tree hollows and logs), females selectively den in rocky habitat, and there is some evidence that females with home ranges comprised of more rocky habitat survive longer (Oakwood 1997). Rocky dens also provide refuge from predators, and there is evidence that feral cats and dingoes are less likely to occur in rugged, rocky habitats (Hernandez-Santin *et al.* 2016; Hohnen *et al.* 2016*a*).

Since European colonisation – and particularly within the past 50 years (Braithwaite and Griffiths 1994) – the geographic range of northern quolls has declined by at least 45.2% and the volume of their ecological niche has also declined substantially (Moore *et al.* 2019). Declines have been most severe in Queensland, where >400 000 km^2 of former habitat is now unoccupied, constituting a range contraction of .75% (Moore *et al.* 2019). The Northern Territory is the second most affected population, which has experienced a 58% range contraction (115 024 km^2), mostly from the more arid southern extent of their historic distribution (Braithwaite and Griffiths 1994; Ziembicki *et al.* 2013; Moore *et al.* 2019; von Takach *et al.* 2020). The Kimberley population has seen a 17% decline, equating to 25 986 km^2 of lost range; (Moore *et al.* 2019), whereas the Pilbara – the most arid region currently supporting northern quoll populations – has so far seen little to no evidence of decline (Spencer *et al.* 2013; Moore *et al.* 2019).

These broadscale declines in geographic range arise through numerous local declines and extincitons that have been well documented. For example, Burnett and Zwar (2009) found no evidence to suggest northern quolls persist in the southern Mary River catchment north of Brisbane, despite the known occurrence of historic populations. Populations in Far North Queensland have also been subject to substantial decline. For example, Perry *et al.* (2015) and Burnett (1997) found northern quolls are largely absent from sizeable areas of Cape York Peninsula where they once occurred. In the Northern Territory, Ibbett *et al.* (2018) found northern quoll trap success in Kakadu National Park was significantly lower in 2002 than it was in 1980 (Begg 1981) and Woinarski *et al.* (2011*b*) found northern quoll abundance was lower at sites within Kakadu in 2007–2009 than it was in 2001–2004.

There are clear spatial patterns in the decline and persistence of northern quoll populations. In Queensland, the Northern Territory, and the Kimberly, topographically simple landscapes that receive low rainfall and are distant from permanent water have seen extremely severe declines (Burnett 1997; Pollock 1999; Woinarski *et al.* 2008; Radford *et al.* 2014; Moore *et al.* 2019), and areas that would have historically been marginal habitat have seen the greatest declines (Moore *et al.* 2019). Hence, extant populations tend to occur in topographically rugged areas with high annual rainfall (Moore *et al.* 2019). The extent of decline across populations corresponds with the length of time that the population has co-occurred with the introduced cane toad (see threat section). Persisting mainland populations of northern quolls now exist on the Central Mackay coast, Wet Tropics, Einasleigh Uplands and Cape York Penin- sula bioregions in Queensland, the Arnhem Plateau, Darwin Coastal Plain, Daly Basin, Pine Creek bioregions, and Groote Eylandt in the Northern Territory, the Central and North Kimberley bioregions, Dampierland, and the Pilbara, Great Sandy and Little Sandy Deserts bioregions.

Diet

We identified 30 studies that examined the diet of the northern quoll, representing all study populations, with the most studies conducted in the Northern Territory. A large number of these studies ($n = 14$) focused on the consumption of cane toads, or baits designed to kill feral cats and dingos ($n = 7$) by quolls, and are discussed in the 'threats' section below. Northern quolls are omnivorous, opportunistic foragers that consume a range of invertebrate, vertebrate, and plant species. Research examining sex-based dietary difference is scarce; however, there is some evidence that females northern quoll consume less vertebrate prey items than males, probably because females are typically smaller in mass (Oakwood 1997).

Invertebrates are a dominant feature in the diets of northern quolls across all populations, with beetles (Coleoptera), grasshoppers (Orthoptera), ants (Hymenopterans) and spiders (Arachnida) appearing most frequently within scats (Dixon and Huxley 1985; Oakwood 1997; Pollock 1999; Radford 2012; Dunlop *et al.* 2017). Indigenous people from Arnhem Land in the Northern Territory also observed northern quolls feeding on *wai* (worms), grubs, and moths (Dixon and Huxley 1985). In Kakadu National Park (Northern Territory), Oakwood (1997) found invertebrate consumption peaked in the early dry season, coinciding with the arrival of juveniles into the popula- tion. In the Pilbara, invertebrate occurrence in the northern quoll diets decreases with the occurrence of rodents and plant mate- rial, potentially indicating invertebrates may be a staple food item, but not always preferred (Dunlop *et al.* 2017).

A diverse range of vertebrate prey also appear in the diet of northern quolls, including rodents (*Melomys burtoni*, *Pseudomys delicatulus*, *Pseudomys hermannsbergensis*, *Rattus rattus*, *Rattus sordidus*, *Zyzomys argurus*), rabbits (*Oryctolagus cuniculus*), other dasyurids (*Dasykaluta rosamondae*, *Ningaui timeleyai*, *Pseudantechinus* sp., *Sminthopsis macroura*, *Sminthopsis youngsoni*), gliders (*Petaurus* spp.), possums (*Trichosurus vulpecula*), bandicoots (*Isoodon auratus*, *Isoodon macrourus*), bats (*Nyctophilus* spp., *Rhinonicteris aurantia*), birds, lizards (Scincidae spp., Agamidae spp., Varanidae spp., Gekkonidae spp.), snakes, and frogs (Dixon and Huxley 1985; Oakwood 1997; Pollock 1999; Radford 2012; Dunlop *et al.* 2017). Larger mammals including kangaroos (*Osphranter* spp.), cows (*Bos taurus*), cats (*Felis catus*) and dogs/dingoes (*Canis* spp.) have also been recorded in northern quoll scats (Dunlop *et al.* 2017), presumably consumed as carrion. In the Kimberley, northern quolls consume a larger proportion of larger prey, such as golden bandicoots (*Isoodon auratus*), in recently burnt habitats, potentially because hunting this prey item is easier when vegetation cover is reduced (Radford 2012).

Plant material has been recorded in the diet of northern quolls in the Northern Territory (Oakwood 1997), the Kimberley (Radford 2012), and the Pilbara (Dunlop *et al.* 2017), and is typically comprised of fleshy fruits, seeds, and flowers. In the Northern Territory, Oakwood (1997) found fruits from wild grape plants (*Ampellocissus acetose*) were the most common plant material to appear in northern quoll diets, with peak consumption occurring in the late dry to early wet season. In the Pilbara, native figs (*Ficus* spp.) were the most frequently recorded plant group within northern quoll scats, occurring within 16.1% of total scats measured (Dunlop *et al.* 2017).

Reproduction

We identified 17 studies related to northern quoll reproduction. Northern quolls typically breed during the dry season – between June and July in Queensland, May and June in the Northern Territory, June to October in the Kimberley, and July to September in the Pilbara. Variation in the timing of breeding also occurs within populations and between years, mostly driven by variation in rainfall (Schmitt *et al.* 1989; Braithwaite and Griffiths 1994; Oakwood 2000). Male northern quolls are known to exhibit semelparity, a reproductive strategy where animals only breed once in their lifetime, characterised by increased levels of testosterone followed by rapid condition loss, with individuals rarely living longer than 11 months (Oakwood *et al.* 2001), although survival varies.

In the Northern Territory, most male quolls die within two weeks of mating (Dickman and Braithwaite 1992; Oakwood 2004*a*), although a small percentage may survive to a second breeding season (Begg 1981; Schmitt *et al.* 1989). Female survival is also very low in the Northern Territory (typically less than ,40% between years), although they can survive for up to 3 years (Braithwaite and Griffiths 1994; Oakwood 2000; Cremona *et al.* 2017*b*). In the Kimberley, Schmitt *et al.* (1989) found 4% of males and 37% of females survived to reach a second breeding season. In the Pilbara, just over 5% of males and 40% of females survive to a second breeding season (Hernandez-Santin *et al.* 2019). On Groote Eylandt, Heiniger *et al.* (2020) found 0% of males and 39.6% of females survived to their second year. They also found 8.7% of females survived to their third year.

A consequence of large annual die-offs in the adult population of northern quolls is that the likelihood of population persistence is heavily reliant on offspring survivorship. For example, in the Pilbara, an increase in mean juvenile mortality of 5% could potentially result in a 20% decline in overall population size (Moro *et al.* 2019). One strategy northern quolls may use to increase juvenile survival is polyandry, where females mate with multiple males to increase genetic diversity among offspring, conferring a group net fitness benefit. For example, a recent study found that 100% of examined northern quoll litters (*n* = 16) had young sired by multiple males, and in some litters, every offspring was fathered by a different male (Chan *et al.* 2020).

It is possible that risks associated with semelparity are likely counterbalanced by benefits derived from reduced competition between males and offspring in areas where resources are limited. As such, Cook (2010*b*) suggested male die off may be less pronounced in populations where resources are plentiful. However, more recent studies suggest this may not necessarily be the case: Heiniger *et al.* (2020) found complete semelparity was observed in northern quoll populations on Groote Eylandt where resources are sufficient to support high quoll densities. Further research is required to better understand the evolutionary drivers and consequences of semelparity in northern quolls.

Following mating, females undergo a gestation period of between 21 and 25 days before giving birth (Oakwood 2000). Mothers have between five and nine nipples (normally eight) (Begg 1981; Braithwaite and Griffiths 1994), and Chan *et al.* (2020) found that females on a small Pilbara island consistently had six nipples compared to eight on the adjacent mainland.

Although up to 17 young can be born (Nelson and Gemmell 2003), nipple number determines the maximum number of young that can be carried after birth. Braithwaite and Griffiths (1994) found that, on average, females that lived closer to creek lines – areas that are more productive than surrounding habitat and likely more conducive to reproduction – had more nipples than females that lived further from creek lines. Once young are attached to a nipple, mortality over the following 3 months ranges from less than 2% (Oakwood 2000) to 86% (Braithwaite and Griffiths 1994). Young are deposited in dens at roughly two and a half months of age (Oakwood 2000), are independently foraging at 4 months, and are trappable by 5 months of age (Oakwood 1997). Young are weaned by 6 months and disperse shortly thereafter (Oakwood 2000).

We found little information regarding northern quoll reproduction in Queensland. For example, no research included in this review documented whether quolls in Queensland show evidence of complete or partial annual male die-off, as observed in other regions (Oakwood *et al.* 2001). Documenting the post-breeding survival rate of northern quolls in Queensland will allow managers to better estimate the risk of Queensland subpopulations becoming locally extinct.

Movement

We identified 12 studies that investigated the movement ecology of northern quolls, which were spread across all regions (Fig. 5). Seven of these studies included home range estimates, calculated using three different methods (delimiting supposed home range, minimum convex polygon, and 95% minimum convex polygon) (Table 1). Across all home range studies, a general trend appears to be that male home ranges are typically larger than female home ranges. This was especially apparent during the breeding season, when males move large distances in search of females. In the Northern Territory, Oakwood (2002) found that males occupied a much larger home range (84 ± 16 ha) than females (34.8 ± 6.4 ha). The difference was largest in the breeding season when males expanded their home range to seek mating opportunities (Oakwood 2002). These males also travelled further between dens (average = 1.9 km) than females (average = 1.2 km). Similarly, on Groote Eylandt, Heiniger *et al.* (2020) found the average home range of male northern quolls (215 ± 58.4 ha) to be four times larger than that of females (53.1 ± 38.8 ha), although this was largely due to male quolls expanding their home ranges by an average of 300% during the breeding season. Prior to the start of breeding season, average home range sizes were larger for females (79.0 ± 58.8 ha) than they were for males (72.9 ± 24.4 ha) (Heiniger *et al.* 2020).

In the Kimberley, (Cook 2010*a*) found home ranges were on average larger for males (64 ± 37 ha) than females (7 ± 2 ha). Maximum distance between dens was also greater for males (1.2 km) than females (0.4 km). Schmitt *et al.* (1989) found quolls moved further between successive trap locations in the breeding season (104 ± 99 m) when compared to the non-breeding season (61 ± 82 m). In the Pilbara, average male home range estimates were between 2.7 and 28.6 times larger than female home range estimates (Table 1). Similar to the Northern Territory and Kimberly populations, male quolls in the Pilbara appear to move further in the breeding season when compared to the non-breeding season (Schmitt *et al.* 1989; Oakwood 2002; Hernandez-Santin *et al.* 2021). Although we did not find any direct measurements of home range for northern quolls in Queensland, Burnett *et al.* (2013) provides a mean half maximum distance moved for 25 individuals (334.6 m), suggesting a crude circular home range estimate of 35 ha.

Lab-based studies investigating northern quoll locomotion have found northern quolls tend to sacrifice speed in favour of manoeuvrability in order to avoid making mistakes (Wynn *et al.* 2015; Amir Abdul Nasir *et al.* 2017). On Groote Eylandt,

Table 1. Northern quoll (*Dasyurus hallucatus*) home range estimates (ha) sourced from studies included in review
MCP, minimum convex polygon; DSHR, delimiting supposed home range

Author	Location	Home range estimate (ha)		Data type	Method
		Female	Male		
Oakwood (2002)	Northern Territory	34.8 ± 6.4 *n* = 7	84.1 ± 16 *n* = 8	VHF	MCP
Heiniger *et al.* (2020)	Northern Territory (Groote Eylandt)	53.07 ± 38.77 *n* = 10	215.4 ± 58.24 *n* = 29	GPS	MCP
Schmitt *et al.* (1989)	Kimberley	2.30 ± 1.20 *n* = 7	1.80 ± 1.60 *n* = 2	TRAP	DSHM
Cook (2010*b*)	Kimberley	7 ± 2 *n* = 11	64 ± 37 *n* = 11	VHF	MCP
King (1989)	Pilbara	168 ± 32.25 *n* = 4	464.75 ± 200.245 *n* = 4	VHF	MCP
Cowan *et al.* (2020*a*)	Pilbara (Red hill)	13.8 ± 6.6 *n* = 10	301.4 ± 108.9 *n* = 10	VHF	MCP
Cowan *et al.* (2020*a*)	Pilbara (Yarraloola)	32.5 ± 10.7 *n* = 10	931.1 ± 259.9 *n* = 11	VHF	MCP
Hernandez-Santin *et al.* (2021)	Pilbara	4 *n* = 1	193 ± 55 *n* = 8	GPS	95% MCP

northern quolls with greater agility when moving around corners are more likely to survive their first 21 months of life than quolls that move slower around corners, potentially because they are better at avoiding predators, such as dingoes, feral cats, and birds of prey (Rew-Duffy *et al.* 2020).

Although male-biased dispersal is common in other dasyurids, evidence for this in northern quolls is limited (Oakwood 2002). Further research is required to better understand patterns in northern quoll dispersal. However, there is evidence that male northern quolls disperse further than females (Oakwood 2000) and male consecutive dens can be up to 4 km apart (Cook 2010*b*). In the Kimberley, genetic data suggests that habitats with higher annual rainfall and lower topographical ruggedness are likely to facilitate increased dispersal between subpopulations (Hohnen *et al.* 2016*b*).

Threats

A total of 70 studies included the topic 'threats', most of which were focused on northern quolls in the Northern Territory (*n* = 40), with substantially fewer studies focused on the Pilbara (*n* = 18), the Kimberley (*n* = 17) or Queensland (*n* = 9) (Fig. 7).

Cane toads

The most commonly investigated threat was cane toads (*n* = 22). In 1935, cane toads (*Rhinella marina*) were introduced to a research station near Cairns, Queensland, Australia (17°04′S, 145°47′E) (Lever 2001). From there, toads quickly expanded their distribution into other parts of Queensland. Cane toads first invaded the Northern Territory in the 1980s (Freeland and Martin 1985), reached Kakadu National Park in 2001 (Woinarski *et al.* 2002) and progressed through to Western Australia *c.* 2009.

Like some other native predators, northern quolls that attempt to consume cane toads rapidly succumb to their novel and potent defensive toxins (Shine 2010). Oakwood (2004*b*) found 31% of radio-tracked quoll mortalities in Kakadu were likely caused by cane toads, whereas O'Donnell *et al.* (2010) found 29%, and Jolly *et al.* (2018*a*) found 85% of toad-naïve quolls and 18% of toad-trained quolls died as a result of attempting to consume cane toads.

In far north Queensland, Burnett (1997) presented anecdotal evidence that cane toads were the cause of northern quoll extirpation between 1983 and 1995. Although northern quoll populations in the Northern Territory exhibited declines prior to toad arrival (Woinarski *et al.* 2001; Ziembicki *et al.* 2013; Ibbett *et al.* 2018), rapid declines, often to extirpation, followed the invasion front (Woinarski *et al.* 2010, 2011*b*). In the Kimberley, Indigo (2020) found northern quoll populations declined by 86–96% following toad arrival, despite these populations being repeatedly exposed to thiabendazole-laced cane toad sausages – a technique shown to elicit toad-aversion in captive quolls (see management section). Despite these declines, there is evidence that northern quolls can co-exist successfully with cane toads, for instance, in central Queensland, where toads and quolls have co-existed for over 80 years (Sabath *et al.* 1981). Although it has been confirmed that Queensland northern quolls (and likely all other populations of northern quolls) are not physiologically resistant to cane toad toxins (Ujvari *et al.* 2013), natural variation in quoll behavioural responses to toads may have made some quolls less vulnerable to toad related mortality than others (see 'Management' section).

Predation

Feral cats and dingoes are considered the most active predators to northern quolls across the majority of their range (Hill and Ward 2010), and this was reflected in the number of northern quoll studies that included reference to feral cat or dingo/dog predation (*n* = 15 and *n* = 21, respectively). Feral cats were introduced onto the Australian mainland with the arrival of the 'first fleet' of British colonists (Abbott 2008). As such, northern quolls have had limited evolutionary exposure to feral cats as predators and limited opportunity to adapt to feral cat

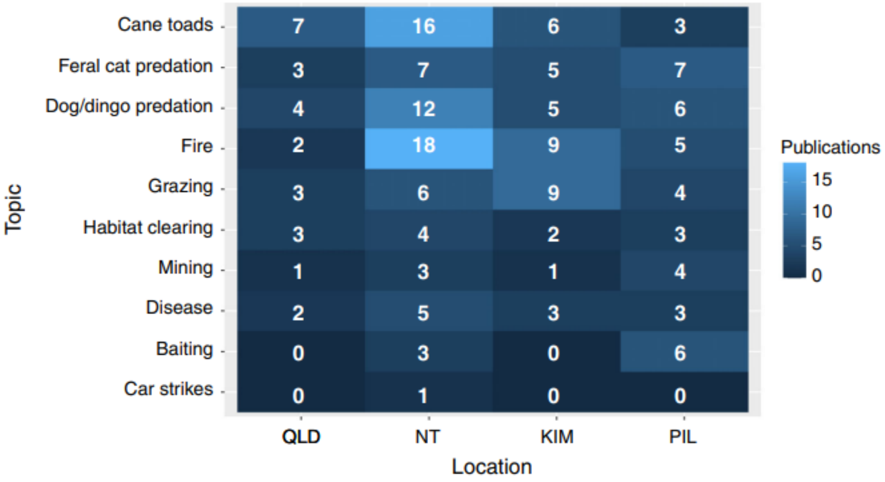


Fig. 7. Research relevant to threatening processes for northern quolls (*Dasyurus hallucatus*) categorised by threat and location. Threat categories were derived from the 'National Recovery Plan for the Northern Quoll' (Hill and Ward 2010).

predation risk (,240 years). By contrast, northern quolls have co-existed with dingoes across their historical range for up to 8000 years (Cairns and Wilton 2016; Zhang *et al.* 2020). This suggests the impacts of dingoes, and potentially their close relatives, domestic dogs, are unlikely to threaten the persistence of northern quolls on their own, but instead are amplified when acting in conjunction with other threats such as altered fire regimes, livestock grazing, habitat loss, and predation from feral cats (Geary *et al.* 2019*b*). Another introduced predator, the red fox (*Vulpes vulpes*), is also likely to depredate on northern quolls in some areas of their southern distribution (Cramer *et al.* 2016), although foxes are not present across the majority of the northern quoll range in northern Australia (Saunders *et al.* 2010).

In the Mackay Bowen region of Queensland, Pollock (1999) recorded eleven occurrences of quoll mortality as a result of domestic dogs and one record of predation by a black-headed python (*Aspidites melanocephalus*). This author also recorded predation by domestic or feral cats; but the number of quolls killed was not recorded. Cat predation on northern quolls in Queensland has also been recorded in the Rockhampton and Cape Upstart regions (Burnett pers. comm., 2020). In Kakadu National Park, Northern Territory, Oakwood (2000) tracked 9 of 15 radio-tracked quolls to their death as a result of predation (dingo = 4, feral cat = 2, owl = 1, king brown snake, *Pseudechis australis* = 1, olive python, *Liasis olivaceus* = 1). Cremona *et al.* (2017*a*) found three of four quolls tracked to their death likely died of dingo/dog predation. Similarly, Jolly *et al.* (2018*a*) found at least 7 of 19 quolls were killed by dingoes. However, it's possible this number over represents the threat of dingoes, given that quolls in this case were breed on a predator free island, and thus were likely naïve to dingo predatory cues. In the Pilbara, Cowan *et al.* (2020*a*) found 6 of 41 collared northern quolls died as result of feral cat predation and two from dingo predation.

In a behavioural study, quolls from mainland Queensland were shown to recognise and avoid the scent of cats and dingoes, as did their captive born young, suggesting a genetic basis for predator recognition, including recognition of the introduced feral cat (Jolly *et al.* 2018*b*). However, quolls that had been translocated to Astell Island to conserve them against the impacts of cane toads appeared to have lost the ability to recognise dingoes and cats, after only 13 generations (Jolly *et al.* 2018*b*). The capacity of northern quolls to detect their predators could explain why Hernandez-Santin *et al.* (2016) found northern quolls avoided areas used by feral cats. The loss of antipredator traits observed on Astell Island may explain the role of dingo predation in the rapid extirpation of quolls during a reintroduction attempt (Jolly *et al.* 2018*a*). Unfortunately, any attempts to train quolls to recognise dingoes as predators in captivity failed to impart predator aversion on quolls prior to reintroduction (Jolly *et al.* 2020).

Fire

A large number of studies ($n = 24$) considered the impacts of fire on northern quolls. We found no studies that recorded evidence of northern quoll mortality as a direct result of fire; however, we did find evidence from several populations that fire can have negative impacts on northern quoll populations. In the Northern Territory, Begg (1981) found that fire delayed northern quoll breeding and reduced the mean number of young that left the pouch, Oakwood (1997) found 55% of female northern quolls perished soon after fire in Kakadu, and Kerle and Burgman (1984) found that, although northern quolls were common just after fire (<1 year), they declined in the following year. Corbett (2003) and Andersen *et al.* (2005) found northern quolls were more abundant at unburnt sites than burnt sites. Griffiths and Brook (2015) found modelled recruitment was 20% lower after late dry season fire.

In the Kimberley, Radford *et al.* (2015) found northern quolls were less abundant at sites with larger extents of habitat burnt within the previous year, high fire frequency, and a greater distance from unburnt patches. Ondei *et al.* (2021) found northern quolls were only detected at rainforest sites, which burn less frequently than adjacent savanna sites, where no northern quolls were detected. Finally, in the Pilbara, Hernandez-Santin *et al.* (2016) found northern quolls were negatively associated with habitat that had been recently burnt.

There are multiple mechanisms that could explain observed negative impacts of fire on northern quolls. It is possible that food may be scarce immediately following fire, which reduces overall habitat suitability. For example, in the Kimberley, Radford and Andersen (2012) found the total number of invertebrates – a key prey item for northern quoll – declined by 80–90% in the week following fire. However, this same study found invertebrates were rapidly restored following the first wet season after fire, and there was no significant difference in invertebrate numbers between pre- and post-fire sessions within a year (Radford 2012). This study also found quolls consumed higher proportions of vertebrate prey following small-scale fires, presumably because the simplified post-fire landscape facilitated improved predation success on these more energetically valuable prey items.

Another probable mechanism is that fire increases predation risk, as a result of reduced ground-layer vegetation cover (Kerle and Burgman 1984; Oakwood 1997). Interactions between fire and predation have previously been implicated in the decline of numerous Australian mammals (Woinarski *et al.* 2010; Leahy *et al.* 2016; Hradsky *et al.* 2017; McGregor *et al.* 2017), particularly for species like northern quolls that fall within a critical weight range (CWR) of species most vulnerable to predation from feral cats, foxes and dingoes (Woinarski 2015). It is important to note that some studies have not found fire to have a negative impact on northern quolls. Woinarski *et al.* (2004) found northern quolls near Darwin in the Northern Territory were more common at sites burnt annually, compared to sites that were long unburnt. Similarly, von Takach *et al.* (2020) did not find fire frequency to be an important determinant of northern quoll niche contraction across the Top End of the Northern Territory. In the Kimberley, Cook (2010*a*) found fire had little impact on northern quoll home range size, even when an animal's entire home range was burnt. These contrasting results highlight that the impact of fire on northern quolls is likely to be context-specific. This is further demonstrated by Radford *et al.* (2020), who found northern quolls declined under prescribed burning in woodland habitats, but increased under prescribed burning in sandstone habitat. Additional research is required to further investigate the context-specific impacts of fire on northern quoll populations across their range.

Grazing

Overgrazing by feral and managed livestock has long been implicated in the decline of Australia's mammal fauna (Woinarski *et al.* 2011*b*). Here, we identified 11 studies which discuss the impacts of over-grazing on northern quolls. The primary mechanism by which over-grazing is thought to impact northern quolls is through the removal of ground-level vegetation, which likely exposes quolls to increased levels of predation (Oakwood 1997). Water-hole eutrophication and soil-erosion caused by livestock, as well as extensive tree removal by graziers, are also likely to impact northern quolls. Braithwaite and Griffiths (1994) suggest the combined impacts of grazing by feral ungulates are likely to have contributed to the decline of northern quolls across their range and similar assessments are also made elsewhere (Oakwood 1997; Woinarski *et al.* 2011*b*; Radford *et al.* 2015). However, it is important to note that quolls do appear to persist at some sites where heavy grazing occurs (Woinarski *et al.* 2008; Hill and Ward 2010; H. A. Moore, pers comms.).

Habitat clearing

We identified six studies that discussed the impact of habitat clearing on northern quoll populations. Habitat clearing has been implicated as a factor in northern quoll declines prior to the year 2000, particularly in Queensland and the Northern Territory (Braithwaite and Griffiths 1994; Hill and Ward 2010; Jones *et al.* 2014). However, despite the subsequent introduction of environmental legislation such as the *Environment Protection and Biodiversity Conservation Act 1999* (*EPBC Act*), designed to protect species from such direct human impacts, habitat clearing is likely continuing to threaten northern quoll populations. For example, in the period between 2000 and 2017, an estimated 1.6 million ha of potential northern quoll habitat was legally cleared (Ward *et al.* 2019). Northern quolls may be particularly sensitive to direct habitat loss because they require large areas (at least 220 km^2) for population persistence (Brook *et al.* 2011): they show strong negative responses to habitat fragmentation (Rankmore 2006), and critical habitat features, such as hollows in trees and logs used for shelter, are commonly removed during land clearing and take many years to form (Woinarski and Westaway 2008).

Mining

There were few studies ($n = 6$) that investigated the response of northern quolls to disturbance because of mining/resource development. This is surprising, especially for the Pilbara population, where the scale of overlap between mining activity and northern quoll habitat is likely to be greatest—91% of the Pilbara bioregion is occupied by mining tenement (Environmental Protection Authority 2014). Here, rocky ridges and mesas, which are known to be important habitat for northern quolls (e.g. Moore *et al.* 2021), are frequently destroyed by mining companies targeting deposits of iron ore and gold (Cramer *et al.* 2016). Surrounding granite outcrops and tor fields are also quarried for rail formation ballast, rock armour for port infrastructure and basic raw materials for road construction. We found two studies from the Pilbara which examined the impact of mining-related habitat clearing on quolls, including a govern- ment report that found northern quolls persist at two rocky sites located in close proximity to a recently installed rail line (Dunlop *et al.* 2015), and an MSc thesis with similar findings at the same sites (Henderson 2015).

In addition to destroying habitat, mining activity can also impact species by introducing contaminants into the environment which can bioaccumulate, reducing the health of animals within affected areas (Nawab *et al.* 2015). For example, Amir Abdul Nasir *et al.* (2018*b*) found airborne manganese dust from Groote Eylandt Mining Company (a BHP Billiton subsidiary) was absorbed by northern quolls living in close proximity to mining operations. Groote Eylandt quolls accumulated manganese within their hair, testes, and brain. Quolls with higher manganese body burdens were slower at manoeuvring around corners than manganese-free quolls, which may reduce their capacity to capture prey and escape predators (Amir Abdul Nasir *et al.* 2018*a*).

Other threats

Other potential threats or sources of mortality for northern quolls are vehicle strikes (Oakwood 1997) and toxoplasmosis. However, Oakwood and Pritchard (1999) found no evidence of toxoplasmosis from 28 road-killed quolls in Kakadu National Park. Although it is clear from this review that northern quolls are exposed to multiple threats across their range, our understanding as to whether such threats to quolls are coincidentally or causally linked is poorly understood, and this can limit our capacity to manage threats effectively (Doherty *et al.* 2015). For example, although targeted baiting for larger predators, such as canids or foxes, may result in short-term alleviation of pressure from one predator on the northern quoll (Jolly *et al.* 2018*a*), in the long term it could potentially increase predation by mesopredators such as feral cats (Marlow *et al.* 2015). Additionally, total isolation from predators (i.e. in havens) can cause rapid evolutionary loss of antipredator traits that may not be easily reinstated (Jolly *et al.* 2018*b*; Jolly and Phillips 2021). Similarly, although it has been suggested that fire may increase the susceptibility of northern quolls to predation (Oakwood 1997), our understanding of how the timing, scale, or intensity of fire influences predator–prey relationships remains limited for most ecosystems and species (Geary *et al.* 2019*a*). Recognising and understanding how these threats interact may facilitate more targeted management interventions potentially leading to more desirable conservation outcomes (see Geary *et al.* 2019*b*).

Indigenous knowledge

Incorporation of Indigenous Australians and their knowledge into management actions is listed in three of eight recovery plan objectives for northern quolls (Hill and Ward 2010). A recent study found 63% of the northern quolls current range, as defined by the IUCN, occurs within the lands of Indigenous Australians (O'Bryan *et al.* 2020). We identified eight studies that incorporated Indigenous knowledge as part of this review, two of which included Indigenous rangers or ranger groups as co-authors (Jolly *et al.* 2021; Kelly *et al.* 2021).

The name 'quoll', is derived from an indigenous name for northern quolls, 'Je-Quoll', recorded by Joseph Banks near Cooktown in North Queensland, 1770 (Beaglehole 1963). Other names were used by Indigenous Australians to describe northern quolls across northern Australia, and many of these are recorded by (Abbott 2013). Using local Indigenous vernacular names may help acknowledge the strong connections Aboriginal people share with Australia's fauna and flora that were honed over thousands of years of coexistence (Burbidge *et al.* 1988).

The most comprehensive summary of Indigenous knowledge about northern quolls is provided by Oakwood (1997). Like other quoll species (Attenbrow and Attenbrow 1987), northern quolls were consumed as food by Aboriginal people. However, there are mixed reports as to their palatability (Oakwood 1997). For example, northern quolls were considered 'good tucker' by the Gunwinggu people of West Arnhem Land (Goodfellow 1993). By contrast, *barkuma* (northern quolls) were not enjoyed as much by people of East Arnhem Land due to the *buggan tumero* (big smell) of the flesh (Dixon and Huxley 1985). Indigenous Australians of East Arnhem Land mentioned northern quolls as being numerous in *diltji* (open forest with grass) and also along beaches where cover is available, where they are said to shelter in hollow fallen logs and amongst stone.

In the Sir Edward Pellew Group of Islands of the Northern Territory, *karnbulanyi* (male northern quoll) or *a-kaliba* (female northern quoll) were also used as a food source (Bradley *et al.* 2006). Yanyuwa Elders from the Pellew Islands said northern quolls were once common, but younger people are less familiar with the species, and some of these island populations of quolls have been extirpated (Woinarski *et al.* 2011*a*). Further, the terms *karnbulanyi* and *a-kaliba* were later also used to describe feral cats (Bradley *et al.* 2006). Ziembicki *et al.* (2013) used Indigenous knowledge collated through a series of interviews across multiple communities in the Northern Territory to assess the extent and timing of regional mammal declines. This collation of information across communities found that range contractions were particularly pronounced for northern quolls, with the majority of decline recognised to have occurred in the 20 years prior to interviews taking place (1985–2009), and in the south of their range. Both cane toads and feral cats were implicated by observers as contributing factors in the declines, along with changing fire regimes associated with the cessation of Indigenous land management practises (Ziembicki *et al.* 2013).

There is significant Indigenous knowledge of the northern quoll across Australia (Abbott 2013, authors' pers. obs.). Although some traditional knowledge has been included in a handful of studies, there is a great potential for future integration into research and management of the remaining northern quoll populations. Recently, some research groups have worked closely with Indigenous rangers and Traditional Owners to improve the conservation of northern quolls in northern Australia. Indigenous people and their knowledge are actively involved in researching and conserving northern quoll populations. One way is through Indigenous ranger programs, such as the Dhimurru, Jawoyn, Kenbi, Warddeken, and Marthakal ranger programs in the Northern Territory, the Uunguu ranger program in the Kimberley, Martu – Kanyirninpa Jukurrpa in the Great Sandy and Little Sandy Deserts and the Budadee, Murujuga, and Yindjibarndi ranger programs in the Pilbara. As part of these programs, Indigenous Australians play an important role in land management and in surveying and monitoring northern quolls, typically on lands with which they share a strong cultural connection and are part of the Indigenous estate (Jacobsen *et al.* 2020).

Conservation management

In 1993, despite recognition of a potential national decline in geographic range of 10–50%, the conservation status of northern quolls was recognised as 'apparently stable' in an action plan for the conservation of Australian marsupials and monotremes (Kennedy 1992). Four years later, a similar action plan listed northern quolls as 'lower risk (near threatened)' (Maxwell *et al.* 1996). In 2005, the northern quoll was listed as Endangered under the *EPBC Act*, which enacts legal responsibility for consideration in environmental impact assessments and management actions, such as the development of conservation advice and a recovery plan. Northern quolls were later listed as

Critically Endangered in the Northern Territory and Endangered in Western Australia, but have remained listed as Least Concern in Queensland. In 2010, a strategic set of management priorities for the northern quoll was outlined in the 'National Recovery Plan for the Northern Quoll' (Hill and Ward 2010), which included eight specific objectives: (1) prevent cane toads from reaching offshore islands where northern quolls are present; (2) foster the recovery of northern quolls in populations where they coexist with cane toads; (3) halt northern quoll declines in areas where cane toads are present; (4) or absent; (5) maintain secure populations for future translocations; (6) increase knowledge of disease; (7) reduce the impacts of feral predators on northern quolls; and (8) raise public awareness of the plight of the northern quoll.

We have identified four primary management actions which have so far been applied and documented in detail that aim to achieve these objectives. These are (1) the use of islands as reserve populations through translocations, (2) cane toad control and aversion techniques, (3) feral predator control, and (4) the creation of artificial habitat.

Islands

Islands can be important tools for species conservation by harbouring species at risk from threats present on the mainland (Ringma *et al.* 2018). The translocation of northern quolls to three islands (Astell Island, Pobassoo Island, and Indian Island) off the coast of Northern Territory between 2003 and 2017 (Rankmore *et al.* 2008; Jolly and Phillips 2021; Kelly *et al.* 2021) has produced several positive outcomes. On Astell and Pobassoo Islands, northern quoll populations increased from a total of 64 to 5600 individuals in the 5 years that followed translocations (Rankmore *et al.* 2008) and populations appeared to maintain genetic diversity at least in the short term (Cardoso *et al.* 2009). Although the translocated populations exhibited some decline following their initial booms, both have now stabilised with high survival and recruitment rates compared to mainland populations (Griffiths *et al.* 2017).

In contrast to the Astell and Pobassoo Islands translocations, the Indian Island population declined sharply within a year of individuals being released and is now unlikely to be viable (Kelly *et al.* 2021). In addition to cane toad related mortality, the failure of the Indian Island translocation was likely contributed to by the extremely unfortunate timing of two major stochastic events (fire and cyclone) in the establishment year (Kelly *et al.* 2021). It is plausible that, had the timing of these events been different, the introduced quoll population on Indian Island may have taken a different trajectory (Kelly *et al.* 2021). The primary purpose of the Indian Island translocation, rather than establishing an insurance population, was to experimentally measure the selection on toad-smart genes and, thus, test the effectiveness of targeted gene flow (see below) (Kelly *et al.* 2021). This also probably influenced the fate of the population, as the experiment required quolls to be released onto an island with a resident toad population and a release cohort with appropriate population demographics (i.e. proportion of toad-smart individuals) meaning release numbers were small ($n = 54$).

Where quolls have been introduced to island arks for the purposes of setting up insurance populations, the success rate has been 100% (Griffiths *et al.* 2017). However, it is important to consider that an objective of northern quoll island introductions is to create insurance populations which can be used for future mainland reintroductions (Hill and Ward 2010). As such, it will be important for those planning future island translocations to consider the impacts of isolation on quolls in terms of both genetic diversity (Cardoso *et al.* 2009) and predator naivety (Jolly and Phillips 2021) in order to maximise the success of future mainland reintroductions. Translocation planners should also consider the impact northern quolls may have on prey species occupying islands that quolls are translocated to, which, in the short-term, are unlikely to be equipped with appropriate behaviours to avoid being depredated by quolls (Jolly *et al.* 2021). Given the right circumstances, translocations to mainland locations within the northern quoll's historic range could also be considered. This could include properties managed in terms of both predators and fire by conservations organisation such as the Australian Wildlife Conservancy and Bush Heritage Australia, or through the Australian Government's Indigenous Protected Areas program.

Cane toad control and aversion techniques

Although established toad populations are largely impossible to eradicate with existing tools (Tingley *et al.* 2017), several studies have assessed the feasibility of controlling the spread of cane toads by capitalising on their vulnerability to desiccation and blocking access to large artificial water bodies (Brook *et al.* 2011; Southwell *et al.* 2017; Tingley *et al.* 2013, 2017; Gregg *et al.* 2019). Southwell *et al.* (2017) suggest barriers blocking toad access to water between the Kimberley and the Pilbara could be constructed for AU$4.5 million, with such a mechanism potentially capable of stopping toad invasion from the Kimberley to the Pilbara region, even for scenarios with extremely high rainfall. Initial field trials have been successful, with toads surviving a maximum of 5 days without access to surface water under the conditions where barriers would be installed (Gregg *et al.* 2019). However, it is important to note that the desire of the Western Australian government and that of the pastoral industry to drought-proof the north-west pastoral industry through the increased development of alternative agriculture practises (new crops and fodder) and intensification in pastoral diversification such as central pivot irrigation (e.g. La Grange region) will limit the effectiveness of strategies based on rendering water sources inaccessible to toads. Similarly, this method of restricting toad movement will not address breaches in biosecurity procedures which enable toads to reach the Pilbara within plant nursey stock and fresh food produce from the Kimberley and Northern Territory growing regions and as hitchhikers with tourists and industrial/mining equipment.

In populations where cane toads are already established, persisting northern quolls are now 'toad-smart' and are less willing to depredate toads than quolls that have no previous exposure to toads (Kelly and Phillips 2017). This behaviour has been shown to be heritable, with offspring of toad-smart quolls being shown to innately avoid cane toads on their first encounter, suggesting rapid adaptive response in toad-impacted populations (Kelly and Phillips 2017, 2019). To induce similar toad-smart behaviour in toad-naïve quolls, conditioned taste aversion (CTA) trials have recently been used to alter northern quoll predatory behaviour in captivity (O'Donnell *et al.* 2010; Webb *et al.* 2015; Cremona *et al.* 2017*b*; Indigo *et al.* 2018; Kelly *et al.* 2018; Jolly *et al.* 2018*a*) and have shown promise. CTA techniques used to train quolls to avoid toads typically use cane toad flesh laced with a nausea inducing dose of thiabendazole that deters quolls from subsequently eating cane toad flesh once released. Quolls trained with non-lethal toad meals generally avoided the consumption of live and dead toads when tested in captivity (Indigo *et al.* 2018) and survived longer in the wild then toad-naïve quolls (O'Donnell *et al.* 2010; Jolly *et al.* 2018*a*).

Despite the success of CTA trials on laboratory-trained quolls, buffering wild northern quolls against cane toads using CTA techniques has proved more difficult. For example, recent unpublished research found CTA trials conducted within and adjacent to Mornington Wildlife Sanctuary in the Kimberley did not reduce toad impacts on the quoll populations (Indigo 2020). Several contributing factors are thought to be potentially responsible for the failure of these trials, including: (i) the decay of toad aversion with time since CTA exposure (Indigo *et al.* 2018); (ii) ineffective delivery rates of the toad sausages; and (iii) ineffective dose rates of thiabendazole within sausages (Indigo 2020). Although it has been demonstrated that intergenerational persistence of CTA trained quolls can occur in the wild following translocation (Cremona *et al.* 2017*b*), the mechanism by which toad-avoidance behaviour is transmitted across generations – via genetic or cultural means – remains unclear. Discerning the transmission mechanisms is made considerably more difficult by the fact a certain proportion of quolls, irrespective of training, have a natural tendency to avoid attacking cane toads (Kelly and Phillips 2017). The efficacy of CTA as a management strategy is largely dependent on a single factor: whether quolls can confer the learnt toad-aversion lesson between generations via trained mothers teaching their young (cultural transmission). Recently, population viability models demonstrated that the efficacy of CTA as a conservation strategy for northern quolls requires cultural transmission rates (mother training young) of >70% to prevent local extinction (Indigo *et al.* 2021). Unfortunately, there is currently no evidence that quolls have the ability or tendency to train their young to avoid cane toads (Indigo *et al.* 2021). Therefore, the transmission of behavioural aversion of cane toads in toad-averse quoll populations (e.g. Queensland) likely proceeds via genetic inheritance rather that cultural transmission.

Another cane toad mitigation strategy that could be implemented as part of future northern quoll management efforts is targeted gene flow, where quolls with heritable toad-smart genes are introduced into naïve populations to enhance their adaptive capacity (Kelly and Phillips 2016, 2019). In 2017, the first and only trial of targeted gene flow in northern quolls involved releasing 54 CTA trained northern quolls onto toad infested Indian Island. The released quolls were composed of toad-smart genotypes from Queensland, hybrid toad-smart and toad-naive genotypes (Queensland × Northern Territory) and toad-naive genotypes from Northern Territory. The aim of the trial was to test if selection pressure in the form of cane toads would drive toad smart genes to spread throughout the introduced quoll population with each generation. Although northern quolls failed to establish a population on Indian Island (details discussed above), genetic data collected the year after the translocation indicated selection toward toad-smarts had occurred after only a single generation (Kelly 2018; Kelly *et al.* 2021). The study also demonstrated the successful hybridisation of Queensland and Northern Territory northern quolls, with viable F2 hybrids and backcrosses observed, suggesting outbreeding depression (a potential barrier to the success of targeted gene flow) is not an issue for this species (Kelly *et al.* 2021).

Feral predator control

Dingo and wild dog control has occurred across much of mainland Australia for well over a century (Allen and Sparkes 2001). Dingo control is particularly common in pastoral areas and is mostly conducted via the deployment of meat baits containing 1080 (sodium monofluoroacetate) (Twigg *et al.* 2000). Sodium monofluoroacetate is a poisonous compound produced naturally by plants, mostly in the genus *Gastrolobium*, most of which occur in the southwest of Western Australia. Although it is typically most lethal to animals without an evolved tolerance, this depends on both the dose rate and number of baits consumed (McIlroy 1981, 1982). Using aircraft to deploy baits (aerial baiting) has dramatically increased the scale at which predator control can feasibility be implemented (Thomson 1986).

At sites where 1080 baits are deployed, dingo densities can be reduced (Thomson 1986; Twigg *et al.* 2000), although there are several examples of baiting programs failing to produce a decline in dingo densities (McIlroy *et al.* 1986; Kennedy *et al.* 2021). Northern quolls do eat 1080 baits (Calver *et al.* 1989), but the baits themselves do not appear to negatively affect quoll population sizes (King 1989). However, due to differences in their evolutionary exposure history to plants containing sodium monofluoroacetate occurring, some populations of northern quoll are likely to be more vulnerable to 1080 poisoning than others (Twigg *et al.* 2003). Although dingo control, if successful, may reduce dingo-related mortality in quolls, it may also have complex and unintended indirect effects (Dickman *et al.* 2009; Brook *et al.* 2012), such as mesopredator release (Crooks and Soulé 1999; Ritchie and Johnson 2009) of feral cats. However, there is conflicting evidence regarding whether feral cats are indeed released following dingo control in northern Australia (Brook *et al.* 2012; Kennedy *et al.* 2012; Leo *et al.* 2019; Stobo-Wilson *et al.* 2020).

Feral cats can also be controlled using poison baits, albeit much less effectively (Algar *et al.* 2007), and with the risk of unintentionally killing dingoes (e.g Wysong *et al.* 2020). New baits engineered specifically for cats such as Eradicat™, 5 and Hisstory™ are now being trialled (Woinarski *et al.* 2019*b*; Johnston *et al.* 2013, 2020). A five-year trial is currently underway investigating the impact of a large-scale Eradicat™ baiting program on northern quolls, as well as other species vulnerable to cat predation such as Rothschild's rock wallabies (*Petrogale rothschildi*) and Pilbara olive pythons (*Liasis olivaceus barroni*) (Morris *et al.* 2015). Preliminary results suggest feral cat baiting does have a positive effect on northern quoll populations (Palmer 2019), without any direct impacts to the quolls themselves (Moro *et al.* 2019; Cowan *et al.* 2020*a*). However, confounding factors related to rainfall and fire justify the need for further research to measure benefits of feral cat baiting for northern quolls. Other technology, such as the Felixer feral cat grooming trap (Thylation), are in the process of being tested for efficacy in targeting feral cats in the presence of native fauna (Read *et al.* 2019).

Artificial habitat

Northern quolls, like several other CWR species in Australia, require structural complexity in the form of logs, tree hollows, termite mounds, or rocky outcrops to use as refuges (Oakwood 1997*a*), and reductions in habitat complexity because of fire or habitat clearing can expose these species to increased rates of predation (Oakwood 1997*a*). One way of mitigating these effects may be through the use of artificial refuges (Cramer *et al.* 2016), which provide quolls with shelter from predation and climatic exposure where natural refuges have been removed. So far, artificial refuges designed for northern quolls have been deployed in several locations across the Pilbara (Cramer *et al.* 2016; Cowan *et al.* 2020*b*). Each of these artificial refuges trialled were constructed in response to habitat loss as a result of mining (Cramer *et al.* 2016; Cowan *et al.* 2020*b*). Cowan *et al.* (2020*b*) found that although artificial refuges closely replicated the thermal conditions created by natural dens, the surrounding environment was typically less complex, potentially contributing to greater feral cat visitation and lower prey availability. It is possible that improving restoration efforts in the area surrounding refuges may increase their suitability for northern quolls, but this has yet to be tested. Overall, there remain many gaps in our knowledge of the capacity of artificial refuges to act as quoll habitat. Far more research on quoll use, survival, and breeding (among other things) within artificial refuges is required before they can be implemented as an evidence-based intervention in response to habitat loss or degradation (Cowan *et al.* 2021).

Future research directions

Northern quolls have been the subject of considerable research, which has improved our understanding of their threats and provided a useful basis for conservation management. However, the species remains threatened and continues to decline, with more resolute and strategic management required. Further research that addresses key knowledge gaps can contribute significantly to improving the effectiveness of conservation management for the northern quoll, and hence its overall conservation outlook. Here, we provide a non-exhaustive list of future research directions based on knowledge gaps evident from our review. If applied, each could be used to fine-tune and redirect management actions to improve conservation outcomes for northern quolls.

We acknowledge that a separate but overlapping set of research priorities have been identified for the Pilbara population (Cramer *et al.* 2016), including: (i) develop appropriate and standardised survey and monitoring methods; (ii) improve our understanding of habitat requirements; (iii) better understand the population dynamics of the northern quoll in the Pilbara; (iv) better understand key threats (cane toads, feral predators, mining infrastructure) and the interactions of these threats; and (v) determine the ability of the northern quoll to recolonise disturbed areas or colonise artificial habitat. We reiterate the importance of these research priorities to the conservation of Pilbara northern quolls.

1. Resolving taxonomy

Although no subspecies of northern quoll are currently recognised, several studies have found clear genetic distinctions among the four major populations based on microsatellite data, which are separated from one another by established biogeographic boundaries (Firestone *et al.* 2000; How *et al.* 2009; Woolley *et al.* 2015; Hohnen *et al.* 2016*b*). Determining if major populations should be treated as distinct taxonomic units is likely to be critical in informing future management interventions such as targeted gene flow and genetic rescue, where quolls from one population are translocated to another (see management section). The use of more recently available genetic techniques such as genome-wide single nucleotide polymorphisms (SNPs) analysis are likely to be important in addressing whether these genetic divergences warrant taxonomic recognition and/or whether significant evolutionary units should be assigned to populations and managed differently.

2. The status of Queensland northern quolls

The Queensland population of northern quoll previously occupied a larger area than any other northern quoll population and has since undergone larger declines than any other northern quoll population (Moore *et al.* 2019). Yet, we found a disproportionally small number of studies on Queensland northern quolls (although research in Queensland is ongoing). Queensland northern quolls have not been comprehensively surveyed and there are no published studies which provide estimates of abundance or density for this population (but see Woinarski *et al.* 2008). An explanation for this could be that northern quolls remain listed as 'least concern' under the *Queensland Nature Conservation Act* (*1992*), and, therefore, research funding provided by the state government for threatened species may not have been prioritised for Queensland northern quolls. We acknowledge the northern quoll research currently underway in Queensland (e.g. S. Burnett unpubl. data; G. Trewella unpubl. data), but suggest an increased research effort is valid given the scale of declines that have occurred. Further research may assist in assessing whether persisting northern quoll populations are stable, declining, or recovering, and could help prioritise conservation efforts.

3. Understand mechanisms allowing the persistence and resistance of northern quoll populations during cane toad invasions

In contrast to a trend of severe and rapid decline following the arrival of cane toads, some northern quoll populations do survive the initial wave of a toad invasion (Woinarski *et al.* 2008; Kelly and Phillips 2017). However, apart from a small selection of broad-scale habitat predictors (Woinarski *et al.* 2008), we have little knowledge of population-specific characteristics that best predict a population's short-term likelihood of surviving a toad invasion. Understanding the initial patterns of persistence may be useful in forecasting the probability of quoll population persistence in areas yet to be invaded by cane toads (i.e. southern Kimberley, Pilbara), potentially allowing us to prioritise the management of these areas. Such lessons are likely to improve our understanding of the mechanisms and circumstances underlying a quoll populations' persistence following cane toad invasion, but may also provide an increased mechanistic understanding of how these impacts and recoveries may play out in populations of other Australian predators that are threatened with extinction via the impacts of cane toads.

In addition to investigating factors facilitating quoll persistence through cane toad invasions, an important future research direction may be to assess if there are any signs of recovery. Have northern quolls returned to sites from which they were previously lost, and if so, what population/habitat characteristics have allowed for this return? Answering these questions are likely to provide information critical to the success of future assisted recolonisations – currently one of our most promising tools for conserving northern quolls (discussed above). This will first require the re-surveying of sites from which northern quolls have previously been confirmed to be absent following cane toad invasion (of which there are now many) to assess whether recoveries have occurred. Secondly, the physical and genetic characteristics of the recolonising quolls, along with the make-up of the recolonised habitat should be compared with sites where quolls have remained absent. Given northern quolls in Queensland have co-existed with cane toads for longer than any other northern quoll population, it is likely that recovery following cane toad-caused decline is most likely to be apparent in the Queensland population. As such, we recommend future studies addressing these questions focus on the Queensland population.

1. Quantifying the impacts of mining

Mining activity occurs across the northern quolls entire range, including important cane toad-free populations, such as Groote Eylandt and the Pilbara. Yet, few studies (see threats section) have investigated the impact of mining on northern quoll populations. As such, determining the extent to which mining activity is likely to influence the persistence of northern quoll population should be addressed in future research. This is especially true for the Pilbara populations, where overlap between the northern quolls geographic range and mining tenure is high (Cramer *et al.* 2016). In relation to mining activity specifically, Cramer *et al.* (2016) identify the impacts of linear infrastructure on northern quoll movement and the ability of the northern quoll to recolonise disturbed areas or artificial habitat as key research areas. In addition to these areas, we suggest future studies investigate secondary impacts of mining activity on northern quoll populations, such as increased predator densities surrounding mining camps driven by increased resource subsidies (e.g. food, water).

2. Population isolation and genetic rescue

A consequence of the northern quolls recent geographic decline is that many populations are now smaller and more isolated. Inbreeding and loss of genetic diversity is often unavoidable in small, isolated populations, increasing their extinction risk due to inbreeding depression (i.e. loss of fitness from low genetic diversity) and lowered adaptive potential (Frankham *et al.* 2017; Ralls *et al.* 2020). Island populations of northern quolls are particularly vulnerable to these risks, and previous work has shown they have lower genetic diversity compared to populations on the mainland (Cardoso *et al.* 2009). We recommend future studies expand on this work by including additional sites—both on islands as well as the mainland populations (Flanagan *et al.* 2018). Where isolated quoll populations are showing signs of genetic degradation, it would be wise to consider mixing populations via translocation to increase genetic diversity and adaptive potential (Aitken and Whitlock 2013; Frankham 2015; Whiteley *et al.* 2015).

3. Unwinding interacting threats

Northern quolls face multiple co-occurring threats across their range; however, limited research has investigated if and how these threats interact synergistically. Studies of other native mammals occurring in northern Australia demonstrate that threats may compound one another and management that addresses only individual threats in isolation of others may be ineffective (Legge *et al.* 2019). A better understanding northern quoll 'threat webs' (a group of co-occurring threats that may have additive or non-additive impacts on each other) may improve land managers' ability to focus efforts toward ultimate threats rather than proximate threats – hopefully with improved conservation outcomes (Geary *et al.* 2019*b*). Understanding the synergistic impacts of predation, fire, and grazing on northern quolls across their existing range is likely to be important, particularly in areas where populations are already significantly degraded by toads. Currently, there is limited evidence that feral cats are driving declines in northern quolls, although the impacts of feral cats are potentially significant. Given the scale of feral cat impacts on the declining mammal fauna of northern Australia (Woinarski *et al.* 2019*b*) we suggest that the impacts of feral cats on quoll populations be investigated as a matter of priority.

An important tool in untangling these threats is the use of manipulative experiments, where at least one threat within a system is controlled (typically as part of conservation management activities), such that its relative impact on northern quoll populations can be measured in context to co-occurring threats. Although experiments of this nature are already underway (e.g. Palmer 2019), opportunities for further research are likely to exist in areas where threat management (e.g. controlled burns, predator baiting) within northern quoll habitat is planned or actively occurring already.

4. Predicting the impact of climate change

Climate change poses an extreme risk to global biodiversity (Steffen 2009), yet we found little mention of it in literature related to northern quolls. Across the northern quolls geographic range, the impacts of climate change are likely to include increased temperatures, rainfall variability, increased proportion of extreme rainfall events, and less frequent cyclones (NESP 2018). Projected changes to total annual rainfall are uncertain, although decreases in total rainfall are more likely than increases (NESP 2018). Measuring the extent to which changes in rainfall will impact resource availability and breeding success for northern quoll, among other northern Australian mammals, has obvious implications for the conservation of the species. In addition to changes in rainfall, average temperatures across Northern Australia will continue to increase and there will be more days with extreme maximum temperatures (NESP 2018). Understanding if these changes will lead to increased northern quoll mortality or reduced reproductive output as a result of thermal stress, and the implications this would have for population persistence, should be a future research priority. Identifying potential climate refugia for northern quolls (areas that they will likely persist in under various climate change scenarios) where management efforts can be concentrated should also form a future research focus.

1. Further incorporation of Indigenous knowledge

Recognition of the knowledge held by the Indigenous people of Australia – often termed 'two-way' or 'right-way' science – has improved our ecological understanding of many species (e.g. Horstman and Wightman 2001; Telfer and Garde 2006; Butler *et al.* 2012; Bohensky *et al.* 2013). There is significant Indigenous knowledge of the northern quoll across northern Australia (Abbott 2013). Some traditional knowledge has been included in a handful of studies (Dixon and Huxley 1985; Woinarski *et al.* 2011*a*; Ziembicki *et al.* 2013), but there is significant potential for future integration of traditional knowledge into research and on-ground management of the remaining northern quoll populations. Indigenous knowledge could potentially be important in detecting of unknown isolated populations in remote areas of the Western Desert. Given that such a large proportion of the known distribution of northern quolls is on the Indigenous Estate, future research and conservation endeavours should seek to be more inclusive of Indigenous stakeholders and aim to incorporate increased involvement of Indigenous Australians in such efforts.

2. Harnessing the heritability of toad avoidance behaviour

Individuals within quoll populations that survive the initial invasion of toads and continue to persist in sympatry with toads do so because they are innately averse to attacking toads (Kelly and Phillips 2017; Moore *et al.* 2019). Thus, if populations can avoid local extinction, natural selection should be rapidly acting upon heritable toad-averse traits. Harnessing the heritability of this behaviour forms the basis of targeted gene flow strategies (discussed above). Initial targeted gene flow trials using northern quolls have documented some encouraging results, however, additional research required to enhance this technique such that it can be applied on a broader scale. This may be achieved by utilising recent advancements in genetic technology to identify areas of the quolls genome that are most useful in predicting toad adverse behaviours in quolls. Future research in this area may also include attempting additional translocation trials, where captivity-bred quolls with genetic tendances to avoid toads are inserted into quoll populations predicted to be impacted by invading cane toads.

3. The role of artificial refuges

Initial trials have shown some potential for artificial refuges to provide thermally appropriate denning habitat in areas of disturbed or degraded habitat (Cowan *et al.* 2020*b*). However, this approach is not yet proven, and further research is required to determine whether artificial refuges can be a viable management tool for future northern quoll conservation. For example, evidence that northern quolls willingly use artificially constructed refuges as breeding habitat is currently lacking. Further trials, potentially incorporating differing complimentary actions (i.e. invasive predator control), are therefore required in order to address this knowledge gap. We also still have a limited understanding of the dimensions of artificially constructed den sites that maximise northern quoll use. This is particularly important in relation to natal dens. For example, existing artificial refuges range from 9 to 150 m^2 in size, but offer shallower crevices compared to those northern quolls use in natural habitat (Cowan *et al.* 2020*b*). Future experiments should aim to test different sizes or arrangements of artificial refuges to determine how differences in these variables alter the thermal conditions of the refuges, and northern quoll use and survival. We also recommend that artificial refuges are trialled for northern quolls in habitats impacted by disturbances other than mining, such as fire and intense grazing, such as has already been trialled for smaller dasyurids (Bleicher and Dickman 2020).

Conflict of interests

The authors declare no conflict of interests.

Declaration of funding

H.A.M. was supported by a scholarship from the Institute of Land, Water and Society operating funds from the Faculty of Science at Charles Sturt University. L.E.V. was funded by the Australian Government's National Environmental Science Program through the Threatened Species Recovery Hub. D.G.N. was supported by an Australian Research Council Early Career Researcher Award (DECRA).

Acknowledgements

We thank Naomi Indigo for her assistance with this review. We also thank two reviewers and the editor for useful comments on an earlier version of the manuscript.

References

Abbott, I. (2008). The spread of the cat, *Felis catus*, in Australia: re-examination of the current conceptual model with additional information. *Conservation Science Western Australia* **7**(1), 1–17.

Abbott, I. (2013). Extending the application of Aboriginal names to Australian biota:'*Dasyurus*'(Marsupialia: Dasyuridae) species. *Victorian Naturalist, The* **130**(3), 109.

Aitken, S. N., and Whitlock, M. C. (2013). Assisted gene flow to facilitate local adaptation to climate change. *Annual review of ecology, evolution, and systematics* **44**, 367–388. doi:10.1146/ANNUREV-ECOLSYS-110512–135747

Algar, D., Angus, G., Williams, M., and Mellican, A. (2007). Influence of bait type, weather and prey abundance on bait uptake by feral cats (*Felis catus*) on Peron Peninsula, Western Australia. *Conservation Science Western Australia* **6**(1), 109.

Allen, L., and Sparkes, E. (2001). The effect of dingo control on sheep and beef cattle in Queensland. *Journal of Applied Ecology* **38**(1), 76–87. doi:10.1046/J.1365-2664.2001.00569.X

Amir Abdul Nasir, A. F., Clemente, C. J., Wynn, M. L., and Wilson, R. S. (2017). Optimal running speeds when there is a trade-off between speed and the probability of mistakes. *Functional Ecology* **31**(10), 1941–1949. doi:10.1111/1365-2435.12902

Amir Abdul Nasir, A. F., Cameron, S. F., Niehaus, A. C., Clemente, C. J., von Hippel, F. A., and Wilson, R. S. (2018*a*). Manganese contamination affects the motor performance of wild northern quolls (*Dasyurus* *hallucatus*). *Environmental Pollution* **241**, 55–62. doi:10.1016/J.ENVPOL.2018.03.087

Amir Abdul Nasir, A. F., Cameron, S. F., von Hippel, F. A., Postlethwait, J., Niehaus, A. C., Blomberg, S., and Wilson, R. S. (2018*b*). Manganese accumulates in the brain of northern quolls (*Dasyurus hallucatus*) living near an active mine. *Environmental Pollution* **233**, 377–386. doi:10.1016/J.ENVPOL.2017.10.088

Andersen, A. N., Cook, G. D., Corbett, L. K., Douglas, M. M., Eager, R. W., Russell-Smith, J., Setterfield, S. A., Williams, R. J., and Woinarski, J. C. (2005). Fire frequency and biodiversity conservation in Australian tropical savannas: implications from the Kapalga fire experiment. *Austral Ecology* **30**(2), 155–167. doi:10.1111/J.1442-9993.2005.01441.X

Ashman, K. R., Watchorn, D. J., and Whisson, D. A. (2019). Prioritising research efforts for effective species conservation: a review of 145 years of koala research. *Mammal Review* **49**(2), 189–200. doi:10.1111/MAM.12151

Attenbrow, V., and Attenbrow, V. (1987). 'The Upper Mangrove Creek catchment: a study of quantitative changes in the archaeological record.' (University of Sydney.)

Baynes, A., and McDowell, M. C. (2010). The original mammal fauna of the Pilbara biogeographic region of north-western Australia. *Records of the Western Australian Museum* **Part 1**, 285–298. doi:10.18195/ISSN.0313-122X.78(1).2010.285-298

Beaglehole, J. C. (1963). 'The Endeavour Journal of Joseph Banks, 1768-1771.' ([Sydney]: Trustees of the Public Library of New South Wales.)

Begg, R. J. (1981). The small mammals of Little Nourlangie Rock, NT III. Ecology of *Dasyurus hallucatus*, the northern quoll (Marsupialia: Dasyuridae). *Wildlife Research* **8**(1), 73–85. doi:10.1071/WR9810073

Bleicher, S. S., and Dickman, C. R. (2020). On the landscape of fear: shelters affect foraging by dunnarts (Marsupialia, *Sminthopsis* spp.) in a sandridge desert environment. *Journal of Mammalogy* **101**(1), 281–290. doi:10.1093/JMAMMAL/GYZ195

Bohensky, E., Butler, J., and Davies, J. (2013). Integrating indigenous ecological knowledge and science in natural resource management: perspectives from Australia. *Ecology and Society* **18**(3). doi:10.5751/ES-05846-180320

BOM (2020). Climate Data Online. Bureau of Meteorology. Available at http://www.bom.gov.au/climate/data/

Bornmann, L., and Mutz, R. (2015). Growth rates of modern science: A bibliometric analysis based on the number of publications and cited references. *Journal of the Association for Information Science and Technology* **66**(11), 2215–2222. doi:10.1002/ASI.23329

Bowman, D. M., Brown, G., Braby, M., Brown, J., Cook, L. G., Crisp, M., Ford, F., Haberle, S., Hughes, J., and Isagi, Y. (2010). Biogeography of the Australian monsoon tropics. *Journal of Biogeography* **37**(2), 201–216. doi:10.1111/J.1365-2699.2009.02210.X

Bradley, J., Holmes, M., Marrngawi, D. N., Karrakayn, A. I., Wuwarlu, J. M., and Ninganga, I. (2006). Yumbulyumbulmantha ki-Awarawu: all kinds of things from country: Yanyuwa ethnobiological classification. *Aboriginal and Torres Strait Islander Studies Unit Research Report Series* **6**.

Braithwaite, R. W., and Griffiths, A. D. (1994). Demographic variation and range contraction in the northern Quoll, *Dasyurus hallucatus* (Marsupialia: Dasyuridae). *Wildlife Research* **21**(2), 203–217. doi:10.1071/WR9940203

Brook, B. W., Whitehead, P. J., and Dingle, J. K. (2011). 'Potential cane toad short to medium term control techniques: the biological feasibility and cost of exclusion as a mitigating control strategy.' (Department of the Environment and Heritage.)

Brook, L. A., Johnson, C. N., and Ritchie, E. G. (2012). Effects of predator control on behaviour of an apex predator and indirect con- sequences for mesopredator suppression. *Journal of applied ecology* **49**(6), 1278–1286. doi:10.1111/J.1365-2664.2012.02207.X

Burbidge, A. A., Johnson, K. A., Fuller, P. J., and Southgate, R. (1988). Aboriginal knowledge of the mammals of the central deserts of Australia. *Wildlife Research* **15**(1), 9–39. doi:10.1071/WR9880009

Burnett, S. (1997). Colonizing cane toads cause population declines in native predators: reliable anecdotal information and management implications. *Pacific Conservation Biology* **3**(1), 65–72. doi:10.1071/PC970065

Burnett, S., and Zwar, A. (2009). 'Quolls (*Dasyurus maculatus* and *D. hallucatus*) in the southern Mary River catchment, south-east Queensland.' (Wildlife Preservation Society of Queensland: Sippy Downs.)

Burnett, S., Shimizu, Y., and Middleton, J. (2013). Distribution and abundance of the Northern quoll (*Dasyurus hallucatus*) in far north Queensland. Report prepared by the University of the Sunshine Coast, Sunshine Coast for Ratch Australasia.

Butler, J. R., Tawake, A., Skewes, T., Tawake, L., and McGrath, V. (2012). Integrating traditional ecological knowledge and fisheries management in the Torres Strait, Australia: the catalytic role of turtles and dugong as cultural keystone species. *Ecology and Society* **17**, 1–19. doi:10.5751/ES-05165-170434

Cairns, K. M., and Wilton, A. N. (2016). New insights on the history of canids in Oceania based on mitochondrial and nuclear data. *Genetica* **144**(5), 553–565. doi:10.1007/S10709-016-9924-Z

Calaby, J. (1973). Mammals. In 'Alligator Rivers region environmental factfinding study: wildlife'. (CSIRO Division of Wildlife Research: Canberra.)

Calver, M., King, D., Bradley, J., Gardner, J., and Martin, G. (1989). An assessment of the potential target specificity of 1080 predator baiting in Western-Australia. *Wildlife Research* **16**(6), 625–638. doi:10.1071/WR9890625

Cardoso, M. J., Eldridge, M. D., Oakwood, M., Rankmore, B., Sherwin, W. B., and Firestone, K. B. (2009). Effects of founder events on the genetic variation of translocated island populations: implications for conservation management of the northern quoll. *Conservation Genetics* **10**(6), 1719–1733. doi:10.1007/S10592-008-9774-Z

Chan, R., Dunlop, J., and Spencer, P. (2020). Highly promiscuous paternity in mainland and island populations of the endangered northern Quoll. *Journal of Zoology* **310**(3), 210–220. doi:10.1111/JZO.12745

Cook, A. (2010*a*). Fire effect on habitat use and home-range of the northern quoll, *Dasyurus hallucatus*. Masters of Science thesis. University of Western Austalia, Perth, WA.

Cook, A. (2010*b*). 'Habitat use and home-range of the northern quoll, *Dasyurus hallucatus*: effects of fire.' (University of Western Australia.)

Cooper, C. E., and Withers, P. C. (2010). Comparative physiology of Australian quolls (Dasyurus; Marsupialia). *Journal of Comparative Physiology B* **180**(6), 857–868. doi:10.1007/S00360-010-0452-3

Corbett, L. (2003). Terrestrial vertebrates. In 'Fire in tropical savannas: the Kapalga experiment'. (Eds A. N. Andersen, G. D. Cook and R. J. Williams) pp. 126–152. (Springer-Verlag: New York.)

Cowan, M., Moro, D., Anderson, H., Angus, J., Garretson, S., and Morris, K. (2020*a*). Aerial baiting for feral cats is unlikely to affect survivorship of northern quolls in the Pilbara region of Western Australia. *Wildlife Research* **47**, 589–598. doi:10.1071/WR19141

Cowan, M. A., Dunlop, J. A., Turner, J. M., Moore, H. A., and Nimmo, D. G. (2020*b*). Artificial refuges to combat habitat loss for an endangered marsupial predator: how do they measure up? *Conservation Science and Practice* **2**(6), 204. doi:10.1111/CSP2.204

Cowan, M. A., Callan, M. N., Watson, M. J., Watson, D. M., Doherty, T. S., Michael, D. R., Dunlop, J. A., Turner, J. M., Moore, H. A., and Watchorn, D. J. (2021). Artificial refuges for wildlife conservation: what is the state of the science? *Biological Reviews*. doi:10.1111/brv.12776

Cramer, V. A., Dunlop, J., Davis, R., Ellis, R., Barnett, B., Cook, A., Morris, K., and van Leeuwen, S. (2016). Research priorities for the northern quoll (*Dasyurus hallucatus*) in the Pilbara region of Western Australia. *Australian Mammalogy* **38**(2), 135–148. doi:10.1071/AM15005

Cremona, T., Crowther, M., and Webb, J. K. (2017*a*). High mortality and small population size prevent population recovery of a reintroduced mesopredator. *Animal Conservation* **20**(6), 555–563. doi:10.1111/ACV.12358

Cremona, T., Spencer, P., Shine, R., and Webb, J. K. (2017*b*). Avoiding the last supper: parentage analysis indicates multi-generational survival of re-introduced 'toad-smart'lineage. *Conservation genetics* **18**(6), 1475–1480. doi:10.1007/S10592-017-0973-3

Cremona, T., Baker, A. M., Cooper, S. J., Montague-Drake, R., Stobo-Wilson, A. M., and Carthew, S. M. (2020). Integrative taxonomic investigation of *Petaurus breviceps* (Marsupialia: Petauridae) reveals three distinct species. *Zoological Journal of the Linnean Society*. doi:10.1093/ZOOLINNEAN/ZLAA060

Crooks, K. R., and Soule´, M. E. (1999). Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* **400**(6744), 563. doi:10.1038/23028

Dick, M., Rous, A. M., Nguyen, V. M., and Cooke, S. J. (2016). Necessary but challenging: multiple disciplinary approaches to solving conservation problems. *Facets* **1**(1), 67–82. doi:10.1139/FACETS-2016-0003

Dickman, C., and Braithwaite, R. W. (1992). Postmating mortality of males in the dasyurid marsupials, *Dasyurus* and *Parantechinus*. *Journal of Mammalogy* **73**(1), 143–147. doi:10.2307/1381875

Dickman, C. R., Glen, A. S., and Letnic, M. (2009). Reintroducing the dingo: can Australia's conservation wastelands be restored. *Reintroduction of top-order predators* **238**, 269. doi:10.1002/9781444312034.CH11

Dixon, J. M., and Huxley, L. (1985). 'Donald Thomson's mammals and fishes of northern Australia.' (Nelson.)

Doherty, T. S., Dickman, C. R., Nimmo, D. G., and Ritchie, E. G. (2015). Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. *Biological Conservation* **190**, 60–68. doi:10.1016/J.BIOCON.2015.05.013

Dunlop, J., Johnson, B., Rayner, K., and Morris, K. (2015). Northern quoll trapping surveys at Wall Creek and Mesa 228. Report prepared for Roy Hill Pty Ltd. Department of Parks and Wildlife, Kensington.

Dunlop, J. A., Rayner, K., and Doherty, T. S. (2017). Dietary flexibility in small carnivores: a case study on the endangered northern quoll, *Dasyurus hallucatus*. *Journal of Mammalogy* **98**(3), 858–866. doi:10.1093/JMAMMAL/GYX015

Edwards, R. D., Crisp, M. D., Cook, D. H., and Cook, L. G. (2017). Congruent biogeographical disjunctions at a continent-wide scale: quantifying and clarifying the role of biogeographic barriers in the Australian tropics. *PLoS One* **12**(4), e0174812. doi:10.1371/JOURNAL.PONE.0174812

Environmental Protection Authority (2014). 'Cumulative environmental impacts of development in the Pilbara region.' (Western Australia Government: Perth.)

Evans, M. C., and Cvitanovic, C. (2018). An introduction to achieving policy impact for early career researchers. *Palgrave Communications* **4**(1), 1–12. doi:10.1057/S41599-018-0144-2

Firestone, K. B., Houlden, B. A., Sherwin, W. B., and Geffen, E. (2000). Variability and differentiation of microsatellites in the genus *Dasyurus* and conservation implications for the large Australian carnivorous marsupials. *Conservation Genetics* **1**(2), 115–133. doi:10.1023/A:1026578821339

Flanagan, S. P., Forester, B. R., Latch, E. K., Aitken, S. N., and Hoban, S. (2018). Guidelines for planning genomic assessment and monitoring of locally adaptive variation to inform species conservation. *Evolutionary Applications* **11**(7), 1035–1052. doi:10.1111/EVA.12569

Fleming, P. A., and Bateman, P. W. (2016). The good, the bad, and the ugly: which Australian terrestrial mammal species attract most research? *Mammal Review* **46**(4), 241–254. doi:10.1111/MAM.12066

Frankham, R. (2015). Genetic rescue of small inbred populations: meta-analysis reveals large and consistent benefits of gene flow. *Molecular Ecology* **24**(11), 2610–2618. doi:10.1111/MEC.13139

Frankham, R., Ballou, J. D., Ralls, K., Eldridge, M., Dudash, M. R., Fenster, C. B., Lacy, R. C., and Sunnucks, P. (2017). 'Genetic management of fragmented animal and plant populations.' (Oxford University Press: Oxford, UK.)

Freeland, W. J., and Martin, K. C. (1985). The rate of range expansion by *Bufo marinus* in Northern Australia, 1980-84. *Wildlife Research* **12**(3), 555–559. doi:10.1071/WR9850555

Geary, W. L., Doherty, T. S., Nimmo, D. G., Tulloch, A. I., and Ritchie, E. G. (2019*a*). Predator responses to fire: a global systematic review and meta-analysis. *Journal of Animal Ecology* **89**, 955–971. doi:10.1111/1365-2656.13153

Geary, W. L., Nimmo, D. G., Doherty, T. S., Ritchie, E. G., and Tulloch, A. I. (2019*b*). Threat webs: reframing the co-occurrence and interactions of threats to biodiversity. *Journal of Applied Ecology* **56**(8), 1992–1997. doi:10.1111/1365-2664.13427

Geyle, H. M., Woinarski, J. C., Baker, G. B., Dickman, C. R., Dutson, G., Fisher, D. O., Ford, H., Holdsworth, M., Jones, M. E., and Kutt, A. (2018). Quantifying extinction risk and forecasting the number of impending Australian bird and mammal extinctions. *Pacific Conservation Biology* **24**(2), 157–167. doi:10.1071/PC18006

Goodfellow, D. (1993) 'Fauna of Kakadu and the Top End.' (Wakefield Press: Kent Town, SA)

Gould, J. (1842). Characters of a new species of Perameles, and a new species of *Dasyurus*. *Proceedings of the Zoological Society of London* **10**, 41–42.

Gregg, E. A., Tingley, R., and Phillips, B. L. (2019). The on-ground feasibility of a waterless barrier to stop the spread of invasive cane toads in Western Australia. *Conservation Science and Practice* e74. doi:10.1111/CSP2.74

Griffiths, A. D., and Brook, B. W. (2015). Fire impacts recruitment more than survival of small-mammals in a tropical savanna. *Ecosphere* **6**(6), 1–22. doi:10.1890/ES14-00519.1

Griffiths, A. D., Rankmore, B., Brennan, K., and Woinarski, J. C. (2017). Demographic evaluation of translocating the threatened northern quoll to two Australian islands. *Wildlife Research* **44**(3), 238–247. doi:10.1071/WR16165

Heiniger, J., Cameron, S. F., Madsen, T., Niehaus, A. C., and Wilson, R. S. (2020). Demography and spatial requirements of the endangered northern quoll on Groote Eylandt. *Wildlife Research* **47**(3), 224–238. doi:10.1071/WR19052

Henderson, M. (2015). 'The effects of mining infrastructure on northern quoll movement and habitat.' (Edith Cowan University: Perth.)

Hernandez Santin, L. (2017). Ecology and predator associations of the northern quoll (*Dasyurus hallucatu*s) in the Pilbara. PhD Thesis, School of Biological Sciences, The University of Queensland, Brisbane. doi:10.14264/UQL.2017.661

Hernandez-Santin, L., Goldizen, A. W., and Fisher, D. O. (2016). Introduced predators and habitat structure influence range contraction of an endangered native predator, the northern quoll. *Biological Conservation* **203**, 160–167. doi:10.1016/J.BIOCON.2016.09.023

Hernandez-Santin, L., Dunlop, J. A., Goldizen, A. W., and Fisher, D. O. (2019). Demography of the northern quoll (*Dasyurus hallucatus*) in the most arid part of its range. *Journal of Mammalogy* **100**, 1191–1198. doi:10.1093/JMAMMAL/GYZ092

Hernandez-Santin, L., Henderson, M., Molloy, S. W., Dunlop, J. A., and Davis, R. A. (2021). Spatial ecology of an endangered carnivore, the Pilbara northern quoll. *Australian Mammalogy* **43**, 235–242. doi:10.1071/AM19052

Hill, B. M., and Ward, S. J. (2010). 'National recovery plan for the northern quoll *Dasyurus hallucatus*.' (Department of Natural Resources, Environment, The Arts and Sport: Darwin.)

Hohnen, R., Tuft, K., McGregor, H. W., Legge, S., Radford, I. J., and Johnson, C. N. (2016*a*). Occupancy of the invasive feral cat varies with habitat complexity. *PLoS One* **11**(9), e0152520. doi:10.1371/JOURNAL.PONE.0152520

Hohnen, R., Tuft, K. D., Legge, S., Hillyer, M., Spencer, P. B., Radford, I. J., Johnson, C. N., and Burridge, C. P. (2016*b*). Rainfall and topography predict gene flow among populations of the declining northern quoll (*Dasyurus hallucatus*). *Conservation Genetics* **17**(5), 1213–1228. doi:10.1007/S10592-016-0856-Z

Horstman, M., and Wightman, G. (2001). Karparti ecology: recognition of Aboriginal ecological knowledge and its application to management in north-western Australia. *Ecological Management & Restoration* **2**(2), 99–109. doi:10.1046/J.1442-8903.2001.00073.X

How, R., Spencer, P., and Schmitt, L. (2009). Island populations have high conservation value for northern Australia's top marsupial predator ahead of a threatening process. *Journal of Zoology* **278**(3), 206–217. doi:10.1111/J.1469-7998.2009.00569.X

Hradsky, B. A., Mildwaters, C., Ritchie, E. G., Christie, F., and Di Stefano, J. (2017). Responses of invasive predators and native prey to a prescribed forest fire. *Journal of Mammalogy* **98**(3), 835–847. doi:10.1093/JMAMMAL/GYX010

Ibbett, M., Woinarski, J., and Oakwood, M. (2018). Declines in the mammal assemblage of a rugged sandstone environment in Kakadu National Park, Northern Territory, Australia. *Australian Mammalogy* **40**(2), 181–187. doi:10.1071/AM17011

Indigo, N. L. (2020). Safeguarding the northern quoll. Can we mitigate cane toad impacts through conditioned taste aversion? PhD thesis. University of Technology, Sydney.

Indigo, N., Smith, J., Webb, J. K., and Phillips, B. (2018). Not such silly sausages: evidence suggests northern quolls exhibit aversion to toads after training with toad sausages. *Austral Ecology* **43**(5), 592–601. doi:10.1111/AEC.12595

Indigo, N. L., Jolly, C. J., Kelly, E., Smith, J., Webb, J. K., and Phillips, B. L. (2021). Effects of learning and adaptation on population viability. *Conservation Biology*. doi:10.1111/COBI.13691

Jackson, S., Jackson, S. M., and Groves, C. (2015). 'Taxonomy of Australian mammals.' (CSIRO Publishing: Melbourne.)

Jacobsen, R., Howell, C., and Read, S. (2020). Australia's Indigenous land and forest estate: separate reporting of Indigenous ownership, management and other special rights. Technical report 20.15. Australian Bureau of Agricultural and Resource Economics and Sciences, Department of Agriculture, Water and the Environment. Available at https://www.agriculture.gov.au/abares/forestsaustralia/publications/indigenous-estate-report

Johnston, M., O'Donoghue, M., Holdsworth, M., Robinson, S., Herrod, A., Eklom, K., Gigliotti, F., Bould, L., and Little, N. (2013). 'Field assessment of the Curiosity® bait for managing feral cats in the Pilbara.' (Arthur Rylah Institute for Environmental Research, Department of Sustainability and Environment: Heidelberg, Vic.)

Johnston, M., Algar, D., O'Donoghue, M., Morris, J., Buckmaster, T., and Quinn, J. (2020). Efficacy and welfare assessment of an encapsulated para-aminopropiophenone (PAPP) formulation as a bait-delivered toxicant for feral cats (*Felis catus*). *Wildlife Research* **47**(8), 686–697. doi:10.1071/WR19171

Jolly, C. J., and Phillips, B. L. (2021). Effects of rapid evolution due to predator-free conservation on endangered species recovery. *Conservation Biology* **35**, 383–385. doi:10.1111/COBI.13521

Jolly, C. J., Kelly, E., Gillespie, G. R., Phillips, B., and Webb, J. K. (2018*a*). Out of the frying pan: reintroduction of toad-smart northern quolls to southern Kakadu National Park. *Austral Ecology* **43**(2), 139–149. doi:10.1111/AEC.12551

Jolly, C. J., Webb, J. K., and Phillips, B. L. (2018*b*). The perils of paradise: an endangered species conserved on an island loses antipredator behaviours within 13 generations. *Biology Letters* **14**(6), 20180222. doi:10.1098/RSBL.2018.0222

Jolly, C. J., Webb, J. K., Gillespie, G. R., and Phillips, B. L. (2020). Training fails to elicit behavioral change in a marsupial suffering evolutionary loss of antipredator behaviors. *Journal of Mammalogy* **101**(4), 1108–1116. doi:10.1093/JMAMMAL/GYAA060

Jolly, C. J., Smart, A. S., Moreen, J., Webb, J. K., Gillespie, G. R., and Phillips, B. L. (2021). Trophic cascade driven by behavioural fine-tuning as naïve prey rapidly adjust to a novel predator. *Ecology* **102**, e03363. doi:10.1002/ECY.3363

Jones, M. E., Burnett, S., Claridge, A. W., Fancourt, B., Kortner, G., Morris, K., Peacock, D., Troy, S., and Woinarski, J. (2014). Australia's surviving marsupial carnivores: threats and conservation. In 'Carnivores of Australia: past, present and future'. (Eds A. Glen and C. Dickman) pp. 197–240. (CSIRO Publishing: Melbourne.)

Kelly, E. (2018). Targeted gene flow for conservation: northern quolls and the invasive cane toad. PhD thesis. School of BioSciences, The University of Melbourne.

Kelly, E., and Phillips, B. L. (2016). Targeted gene flow for conservation. *Conservation Biology* **30**(2), 259–267. doi:10.1111/COBI.12623

Kelly, E., and Phillips, B. L. (2017). Get smart: native mammal develops toad-smart behavior in response to a toxic invader. *Behavioral Ecology* **28**(3), 854–858. doi:10.1093/BEHECO/ARX045

Kelly, E., and Phillips, B. L. (2019). Targeted gene flow and rapid adaptation in an endangered marsupial. *Conservation Biology* **33**(1), 112–121. doi:10.1111/COBI.13149

Kelly, E., Phillips, B. L., and Webb, J. K. (2018). Taste overshadows less salient cues to elicit food aversion in endangered marsupial. *Applied Animal Behaviour Science* **209**, 83–87. doi:10.1016/J.APPLANIM.2018.09.003

Kelly, E., Jolly, C. J., Indigo, N., Smart, A., Webb, J., and Phillips, B. (2021). No outbreeding depression in a trial of targeted gene flow in an endangered Australian marsupial. *Conservation Genetics* **22**, 23–33. doi:10.1007/S10592-020-01316-Z

Kennedy, M. (1992) 'Australasian marsupials and monotremes: an action plan for their conservation.' (IUCN)

Kennedy, M., Phillips, B. L., Legge, S., Murphy, S. A., and Faulkner, R. A. (2012). Do dingoes suppress the activity of feral cats in northern Australia? *Austral Ecology* **37**(1), 134–139. doi:10.1111/J.1442-9993.2011.02256.X

Kennedy, M., Kreplins, T., O'Leary, R., and Fleming, P. (2021). Responses of dingo (*Canis familiaris*) populations to landscape-scale baiting. *Food Webs* **27**, e00195. doi:10.1016/J.FOOWEB.2021.E00195

Kerle, J. A., and Burgman, M. (1984). Some aspects of the ecology of the mammal fauna of the Jabiluka Area. Northern Territory. *Wildlife Research* **11**(2), 207–222. doi:10.1071/WR9840207

King, D. R. (1989). An assessment of the hazard posed to northern quolls (*Dasyurus hallucatus*) by aerial baiting with 1080 to control dingoes. *Australian Wildlife Research* **16**(5), 569–574. doi:10.1071/WR9890569

Kitchener, D., Keller, L., Chapman, A., McKenzie, N., Start, A., and Kenneally, K. (1981). Observations on mammals of the Mitchell Plateau area, Kimberley, Western Australia. In 'Biological Survey of Mitchell Plateau and Admiralty Gulf, Kimberley, Western Australia.' pp. 123–168. (Western Australian Museum: Perth.)

Knight, A. T., Cowling, R. M., Rouget, M., Balmford, A., Lombard, A. T., and Campbell, B. M. (2008). Knowing but not doing: selecting priority conservation areas and the research–implementation gap. *Conservation Biology* **22**(3), 610–617. doi:10.1111/J.1523-1739.2008.00914.X

Leahy, L., Legge, S. M., Tuft, K., McGregor, H. W., Barmuta, L. A., Jones, M. E., and Johnson, C. N. (2016). Amplified predation after fire suppresses rodent populations in Australia's tropical savannas. *Wildlife Research* **42**(8), 705–716. doi:10.1071/WR15011

Legge, S., Smith, J. G., James, A., Tuft, K. D., Webb, T., and Woinarski, J. C. (2019). Interactions among threats affect conservation management outcomes: Livestock grazing removes the benefits of fire management for small mammals in Australian tropical savannas. *Conservation Science and Practice* **1**(7), e52. doi:10.1111/CSP2.52

Leo, V., Reading, R. P., Gordon, C., and Letnic, M. (2019). Apex predator suppression is linked to restructuring of ecosystems via multiple ecological pathways. *Oikos* **128**(5), 630–639. doi:10.1111/OIK.05546

Lever, C. (2001). 'The cane toad: the history and ecology of a successful colonist.' (Westbury Academic and Scientific Publishing: Otley, West Yorkshire, UK.)

Marlow, N. J., Thomas, N. D., Williams, A. A., Macmahon, B., Lawson, J., Hitchen, Y., Angus, J., and Berry, O. (2015). Cats (*Felis catus*) are more abundant and are the dominant predator of woylies (*Bettongia penicillata*) after sustained fox (*Vulpes vulpes*) control. *Australian Journal of Zoology* **63**(1), 18–27. doi:10.1071/ZO14024

Maxwell, S., Burbidge, A. A., and Morris, K. (1996). Spotted-tailed Quoll (SE mainland and Tas); recovery outline. In 'The Action Plan for Australian Marsupials and Monotremes.' pp. 85–87. Environment Australia, Canberra, ACT.

McGregor, H. W., Cliff, H. B., and Kanowski, J. (2017). Habitat preference for fire scars by feral cats in Cape York Peninsula, Australia. *Wildlife Research* **43**(8), 623–633. doi:10.1071/WR16058

McIlroy, J. (1981). The sensitivity of Australian animals to 1080 poison. II. Marsupial and eutherian carnivores. *Wildlife Research* **8**(2), 385–399. doi:10.1071/WR9810385

McIlroy, J. (1982). The sensitivity of Australian animals to 1080 poison. III. Marsupial and eutherian herbivores. *Wildlife Research* **9**(3), 487–503. doi:10.1071/WR9820487

McIlroy, J., Cooper, R., Gifford, E., Green, B., and Newgrain, K. (1986). The effect on wild dogs, *Canis familiaris*, of 1080 poisoning campaigns in Kosciusko National Park, NSW. *Wildlife Research* **13**(4), 535–544. doi:10.1071/WR9860535

McKenzie, N., Chapman, A., and Youngson, W. (1975). Mammals of the prince regent river reserve, north-west Kimberley, Australia. *Wildlife Research Bulletin* **3**, 69.

Moher, D., Liberati, A., Tetzlaff, J., and Altman, D. G. (2009). Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. *Annals of internal medicine* **151**(4), 264–269. doi:10.7326/0003-4819-151-4-200908180-00135

Molloy, S. W., Davis, R. A., Dunlop, J. A., and van Etten, E. J. (2017). Applying surrogate species presences to correct sample bias in species distribution models: a case study using the Pilbara population of the northern Quoll. *Nature Conservation* **18**, 25. doi:10.3897/NATURECONSERVATION.18.12235

Moore, H. A., Dunlop, J. A., Valentine, L. E., Woinarski, J. C., Ritchie, E. G., Watson, D. M., and Nimmo, D. G. (2019). Topographic ruggedness and rainfall mediate geographic range contraction of a threatened marsupial predator. *Diversity and Distributions* **25**(12), 1818–1831. doi:10.1111/DDI.12982

Moore, H. A., Michael, D. R., Ritchie, E. G., Dunlop, J. A., Valentine, L. E., Hobbs, R. J., and Nimmo, D. G. (2021). A rocky heart in a spinifex sea: occurrence of an endangered marsupial predator is multiscale dependent in naturally fragmented landscapes. *Landscape Ecology* **36**(5), 1359–1376. doi:10.1007/S10980-021-01207-9

Moro, D., Dunlop, J., and Williams, M. R. (2019). Northern quoll persistence is most sensitive to survivorship of juveniles. *Wildlife Research* **46**(2), 165–175. doi:10.1071/WR18010

Morris, K., Cowan, M., Angus, J., Anderson, H., Garretson, S., Algar, D., and Williams, M. (2015). The northern quoll cat bait uptake and survivorship study, Yarraloola Land Management Area, Pilbara Region, WA: Yandicoogina JSW and Oxbow Project, Threatened Species Offset Plan. Western Australian Department of Parks and Wildlife, Perth.

Nawab, J., Khan, S., Shah, M. T., Khan, K., Huang, Q., and Ali, R. (2015). Quantification of heavy metals in mining affected soil and their bioaccumulation in native plant species. *International Journal of Phytoremediation* **17**(9), 801–813. doi:10.1080/15226514.2014.981246

Nelson, J. E., and Gemmell, R. T. (2003). Birth in the northern quoll, *Dasyurus hallucatus* (Marsupialia: Dasyuridae). *Australian Journal of Zoology* **51**(2), 187–198. doi:10.1071/ZO02016

NESP (2018). Our changing climate: How will rainfall change in Northern Australia over this century? Available at https://nespclimate.com.au/wp-content/uploads/2018/06/Northern-Australia-6pp_WEB.pdf

Oakwood, M. (1997). The ecology of the northern quoll, *Dasyurus hallucatus*. PhD thesis thesis. Australian National University, Canberra.

Oakwood, M. (2000). Reproduction and demography of the northern quoll, *Dasyurus hallucatus*, in the lowland savanna of northern Australia. *Australian Journal of Zoology* **48**(5), 519–539. doi:10.1071/ZO00028

Oakwood, M. (2002). Spatial and social organization of a carnivorous marsupial *Dasyurus hallucatus* (Marsupialia: Dasyuridae). *Journal of Zoology* **257**(2), 237–248. doi:10.1017/S0952836902000833

Oakwood, M. (2004*a*). Death after sex. *Biologist* **51**(1), 5–8.

Oakwood, M. (2004*b*). The effect of cane toads on a marsupial carnivore, the northern quoll, *Dasyurus hallucatus*. Parks Australia.

Oakwood, M., and Pritchard, D. (1999). Little evidence of toxoplasmosis in a declining species, the northern quoll (*Dasyurus hallucatus*). *Wildlife Research* **26**(3), 329–333. doi:10.1071/WR97105

Oakwood, M., Bradley, A. J., and Cockburn, A. (2001). Semelparity in a large marsupial. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **268**(1465), 407–411. doi:10.1098/RSPB.2000.1369

Oakwood, M., Woinarski, J., and Burnett, S. (2016). *Dasyurus hallucatus*. The IUCN Red List of Threatened Species. Available at https://www.iucnredlist.org/species/6295/21947321

O'Bryan, C. J., Garnett, S. T., Fa, J. E., Leiper, I., Rehbein, J. A., Ferna´ndez-Llamazares, A´ ., Jackson, M. V., Jonas, H. D., Brondizio, E. S., Burgess, N. D., Robinson, C. J., Zander, K. K., Molna´r, Z., Venter, O., and Watson, J. E. M. (2020). The importance of indigenous peoples' lands for the conservation of terrestrial mammals. *Conservation Biology* **35**(3), 1002–1008. doi:10.1111/cobi.13620

O'Donnell, S., Webb, J. K., and Shine, R. (2010). Conditioned taste aversion enhances the survival of an endangered predator imperilled by a toxic invader. *Journal of Applied Ecology* **47**(3), 558–565. doi:10.1111/J.1365-2664.2010.01802.X

Olds, L. G., Myers, C., Reside, J., Madani, G., Dudley, A., Potter, S., Martin, R., Boona, E., Waina, T., and Taggart, D. A. (2016). Small terrestrial mammals on Doongan Station, in the Northern Kimberley bioregion, Western Australia. *Australian Mammalogy* **38**(2), 164–176. doi:10.1071/AM15004

Ondei, S., Prior, L. D., McGregor, H. W., Reid, A. M., Johnson, C. N., Vigilante, T., Goonack, C., Williams, D., and Bowman, D. M. (2021). Small mammal diversity is higher in infrequently compared with frequently burnt rainforest–savanna mosaics in the north Kimberley, Australia. *Wildlife Research* **48**, 218–229. doi:10.1071/WR20010

Palmer, R. (2019). Predator control baiting and monitoring program, Yarraloola and Red Hill, Pilbara Region, Western Australia. 2016 Annual Report – Year 2. Department of Biodiversity, Conservation and Attractions, Perth.

Perry, J. J., Vanderduys, E. P., and Kutt, A. S. (2015). More famine than feast: pattern and variation in a potentially degenerating mammal fauna on Cape York Peninsula. *Wildlife Research* **42**(6), 475–487. doi:10.1071/WR15050

Peterson, A. T. (2006). Taxonomy is important in conservation: a preliminary reassessment of Philippine species-level bird taxonomy. *Bird Conservation International* **16**(2), 155–173. doi:10.1017/S0959270906000256

Pickett, B. D., Wallace, E. M., Ridge, P. G., and Kauwe, J. S. (2020). Lingering taxonomic challenges hinder conservation and management of global bonefishes. *Fisheries* **45**(7), 347–358. doi:10.1002/FSH.10438

Pollock, K. H. (1980). 'Capture-recapture models: a review of current methods, assumptions and experimental design.' (Citeseer: North Carolina, USA.)

Pollock, A. (1999). Notes on status, distribution and diet of northern quoll *Dasyurus hallucatus* in the Mackay-Bowen area, mideastern Queensland. *Australian Zoologist* **31**(2), 388–395. doi:10.7882/AZ.1999.040

Potter, S., Eldridge, M. D., Taggart, D. A., and Cooper, S. J. (2012). Multiple biogeographical barriers identified across the monsoon tropics of northern Australia: Phylogeographic analysis of the brachyotis group of rock-wallabies. *Molecular Ecology* **21**(9), 2254–2269. doi:10.1111/J.1365-294X.2012.05523.X

Pullin, A. S., and Knight, T. M. (2005). Assessing conservation management's evidence base: a survey of management-plan compilers in the United Kingdom and Australia. *Conservation Biology* **19**(6), 1989–1996. doi:10.1111/J.1523-1739.2005.00287.X

Pulsford, S. A., Lindenmayer, D. B., and Driscoll, D. A. (2016). A succession of theories: purging redundancy from disturbance theory. *Biological Reviews* **91**(1), 148–167. doi:10.1111/BRV.12163

Radford, I. J. (2012). Threatened mammals become more predatory after small-scale prescribed fires in a high-rainfall rocky savanna. *Austral Ecology* **37**(8), 926–935. doi:10.1111/J.1442-9993.2011.02352.X

Radford, I. J., and Andersen, A. N. (2012). Effects of fire on grass-layer savanna macroinvertebrates as key food resources for insectivorous vertebrates in northern Australia. *Austral Ecology* **37**(6), 733–742. doi:10.1111/J.1442-9993.2012.02413.X

Radford, I. J., Dickman, C. R., Start, A. N., Palmer, C., Carnes, K., Everitt, C., Fairman, R., Graham, G., Partridge, T., and Thomson, A. (2014). Mammals of Australia's tropical savannas: a conceptual model of assemblage structure and regulatory factors in the Kimberley region. *PloS One* **9**(3), e92341. doi:10.1371/JOURNAL.PONE. 0092341

Radford, I. J., Gibson, L. A., Corey, B., Carnes, K., and Fairman, R. (2015). Influence of fire mosaics, habitat characteristics and cattle disturbance on mammals in fire-prone savanna landscapes of the northern Kimberley. *PLoS One* **10**(6). doi:10.1371/JOURNAL.PONE.0130721

Radford, I. J., Woolley, L.-A., Corey, B., Vigilante, T., Hatherley, E., Fairman, R., Carnes, K., and Start, A. N. (2020). Prescribed burning benefits threatened mammals in northern Australia. *Biodiversity and Conservation* **29**(9), 2985–3007. doi:10.1007/S10531-020-02010-9

Ralls, K., Sunnucks, P., Lacy, R. C., and Frankham, R. (2020). Genetic rescue: A critique of the evidence supports maximizing genetic diversity rather than minimizing the introduction of putatively harmful genetic variation. *Biological Conservation* **251**, 108784. doi:10.1016/J.BIOCON.2020.108784

Rankmore, B. R. (2006). 'Impacts of habitat fragmentation on the vertebrate fauna of the tropical savannas of Northern Australia; with special reference to medium-sized mamals.' (Charles Darwin University.)

Rankmore, B., Griffiths, A., Woinarski, J., Ganambarr, B., Taylor, R., Brennan, K., Firestone, K., and Cardoso, M. (2008). Island translocation of the northern quoll Dasyurus hallucatus as a conservation response to the spread of the cane toad *Chaunus (Bufo) marinus* in the Northern Territory, Australia. Report to the Australian Government's Natural Heritage Trust. Department of Natural Resources, Environment and the Arts, Darwin.

Read, J. L., Bowden, T., Hodgens, P., Hess, M., McGregor, H., and Moseby, K. (2019). Target specificity of the Felixer grooming ''trap''. *Wildlife Society Bulletin* **43**(1), 112–120. doi:10.1002/WSB.942

Rew-Duffy, M., Cameron, S. F., Freeman, N. J., Wheatley, R., Latimer, J. M., and Wilson, R. S. (2020). Greater agility increases probability of survival in the endangered northern quoll. *Journal of Experimental Biology* **223**(15). doi:10.1242/JEB.218503

Ringma, J., Legge, S., Woinarski, J., Radford, J., Wintle, B., and Bode, M. (2018). Australia's mammal fauna requires a strategic and enhanced network of predator-free havens. *Nature Ecology & Evolution* **2**(3), 410. doi:10.1038/S41559-017-0456-4

Ritchie, E. G., and Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* **12**(9), 982–998. doi:10.1111/J.1461-0248.2009.01347.X

Rose, D. C., Amano, T., Gonza´lez-Varo, J. P., Mukherjee, N., Robertson, R. J., Simmons, B. I., Wauchope, H. S., and Sutherland, W. J. (2019). Calling for a new agenda for conservation science to create evidence-informed policy. *Biological Conservation* **238**, 108222. doi:10.1016/J.BIOCON.2019.108222

Sabath, M. D., Boughton, W. C., and Easteal, S. (1981). Expansion of the range of the introduced toad Bufo marinus in Australia from 1935 to 1974. *Copeia* 676–680. doi:10.2307/1444573

Salafsky, N., Boshoven, J., Burivalova, Z., Dubois, N. S., Gomez, A., Johnson, A., Lee, A., Margoluis, R., Morrison, J., and Muir, M. (2019). Defining and using evidence in conservation practice. *Conservation Science and Practice* **1**(5), e27. doi:10.1111/CSP2.27

Saunders, G. R., Gentle, M. N., and Dickman, C. R. (2010). The impacts and management of foxes *Vulpes vulpes* in Australia. *Mammal Review* **40**(3), 181–211. doi:10.1111/J.1365-2907.2010.00159.X

Schmitt, L., Bradley, A., Kemper, C., Kitchener, D., Humphreys, W., and How, R. (1989). Ecology and physiology of the northern quoll, *Dasyurus hallucatus* (Marsupialia, Dasyuridae), at Mitchell Plateau, Kimberley, Western Australia. *Journal of Zoology* **217**(4), 539–558. doi:10.1111/J.1469-7998.1989.TB02510.X

Shine, R. (2010). The ecological impact of invasive cane toads (*Bufo marinus*) in Australia. *The Quarterly Review of Biology* **85**(3), 253–291. doi:10.1086/655116

Southwell, D., Tingley, R., Bode, M., Nicholson, E., and Phillips, B. L. (2017). Cost and feasibility of a barrier to halt the spread of invasive cane toads in arid Australia: incorporating expert knowledge into model-based decision-making. *Journal of Applied Ecology* **54**(1), 216–224. doi:10.1111/1365-2664.12744

Spencer, P., How, R., Hillyer, M., Cook, A., Morris, K., Stevenson, C., and Umbrello, L. (2013). Genetic analysis of northern quolls from the Pilbara region of Western Australia. Murdoch University: Perth. Final report.

Spencer, P. B., Sandover, S., Nihill, K., Wale, C. H., How, R. A., and Schmitt, L. H. (2017). Living in isolation: ecological, demographic and genetic patterns in northern Australia's top marsupial predator on Koolan Island. *Australian Mammalogy* **39**(1), 17–27. doi:10.1071/AM16004

Steffen, W. (2009). 'Australia's biodiversity and climate change.' (CSIRO Publishing: Melbourne.)

Stobo-Wilson, A. M., Stokeld, D., Einoder, L. D., Davies, H. F., Fisher, A., Hill, B. M., Mahney, T., Murphy, B. P., Stevens, A., and Woinarski, J. C. (2020). Habitat structural complexity explains patterns of feral cat and dingo occurrence in monsoonal Australia. *Diversity and Distributions* **26**, 832–842. doi:10.1111/DDI.13065

Telfer, W. R., and Garde, M. J. (2006). Indigenous knowledge of rock kangaroo ecology in western Arnhem Land, Australia. *Human Ecology* **34**(3), 379–406. doi:10.1007/S10745-006-9023-3

Thomas, O. (1926). LXVII. – The local races of *Dasyurus hallucatus*. *Annals and Magazine of Natural History* **18**(107), 543–544. doi:10.1080/00222932608633550

Thomas, H., Cameron, S. F., Campbell, H. A., Micheli-Campbell, M. A., Kirke, E. C., Wheatley, R., and Wilson, R. S. (2021). Rocky escarpment versus savanna woodlands: comparing diet and body condition as indicators of habitat quality for the endangered northern quoll (*Dasyurus hallucatus*). *Wildlife Research*. doi:10.1071/WR20032

Thomson, P. (1986). The effectiveness of aerial baiting for the control of dingoes in north-western Australia. *Wildlife Research* **13**(2), 165–176. doi:10.1071/WR9860165

Tingley, R., Phillips, B. L., Letnic, M., Brown, G. P., Shine, R., and Baird, S. J. (2013). Identifying optimal barriers to halt the invasion of cane toads *Rhinella marina* in arid Australia. *Journal of Applied Ecology* **50**(1), 129–137. doi:10.1111/1365-2664.12021

Tingley, R., Ward-Fear, G., Schwarzkopf, L., Greenlees, M. J., Phillips, B. L., Brown, G., Clulow, S., Webb, J., Capon, R., and Sheppard, A. (2017). New weapons in the toad toolkit: a review of methods to control and mitigate the biodiversity impacts of invasive cane toads (*Rhinella marina*). *The Quarterly Review of Biology* **92**(2), 123–149. doi:10.1086/692167

TSSC (2005). Northern quoll (*Dasyurus hallucatus*). Available at http://www.environment.gov.au/biodiversity/threatened/assessments/dasyurus-hallucatus-2005

Turpin, J. M., and Bamford, M. J. (2014). A new population of the northern quoll (Dasyurus hallucatus) on the edge of the Little Sandy Desert, Western Australia. *Australian Mammalogy* **37**(1), 86–91.

Twigg, L. E., Eldridge, S. R., Edwards, G. P., Shakeshaft, B. J., dePreu, N. D., and Adams, N. (2000). The longevity and efficacy of 1080 meat baits used for dingo control in central Australia. *Wildlife Research* **27**(5), 473–481. doi:10.1071/WR99044

Twigg, L. E., Martin, G. R., Eastman, A. F., and Kirkpatrick, W. E. (2003). Sensitivity of some Australian animals to sodium fluoroacetate (1080): additional species and populations, and some ecological considerations. *Australian Journal of Zoology* **51**(5), 515–531. doi:10.1071/ZO03040

Ujvari, B., Oakwood, M., and Madsen, T. (2013). Queensland northern quolls are not immune to cane toad toxin. *Wildlife Research* **40**(3), 228–231. doi:10.1071/WR13011

Umbrello, L. S. (2018). Evolution and diversification of dasyurid marsupials of the Australian arid zone. PhD thesis. School of Biological Sciences, University of Western Australia.

Viacava, P., Blomberg, S. P., Sansalone, G., Phillips, M. J., Guillerme, T., Cameron, S. F., Wilson, R. S., and Weisbecker, V. (2020). Skull shape of a widely distributed, endangered marsupial reveals little evidence of local adaptation between fragmented populations. *Ecology and Evolution* **10**(18), 9707–9720. doi:10.1002/ECE3.6593

von Takach, B., Scheele, B. C., Moore, H., Murphy, B. P., and Banks, S. C. (2020). Patterns of niche contraction identify vital refuge areas for declining mammals. *Diversity and Distributions* **26**, 1467–1482. doi:10.1111/DDI.13145

Ward, M. S., Simmonds, J. S., Reside, A. E., Watson, J. E., Rhodes, J. R., Possingham, H. P., Trezise, J., Fletcher, R., File, L., and Taylor, M. (2019). Lots of loss with little scrutiny: the attrition of habitat critical for threatened species in Australia. *Conservation Science and Practice* **1**, e117. doi:10.1111/CSP2.117

Webb, J., Legge, S., Tuft, K., Cremona, T., and Austin, C. (2015). Can we mitigate cane toad impacts on northern quolls? Final report. Charles Darwin University, Darwin. Available at http://www.nespnorthern.edu.au/wp-content/uploads/2015/10/4.1.35_can_we_mitigate_cane_toad_impacts_on_northern_quolls_-_final_report.pdf

Whiteley, A. R., Fitzpatrick, S. W., Funk, W. C., and Tallmon, D. A. (2015). Genetic rescue to the rescue. *Trends in Ecology & Evolution* **30**(1), 42–49. doi:10.1016/J.TREE.2014.10.009

Woinarski, J. C. (2015). Critical-weight-range marsupials in northern A ustralia are declining: a commentary on Fisher *et al.* (2014). 'The current decline of tropical marsupials in Australia: is history repeating?' *Global Ecology and Biogeography* **24**(1), 118–122. doi:10.1111/GEB.12165

Woinarski, J., and Westaway, J. (2008). Hollow formation in the *Eucalyptus miniata–E. tetrodonta* open forests and savanna woodlands of tropical northern Australia. Final report to Land and Water Australia. Department of Natural Resources, Environment, The Arts and Sport, Darwin.

Woinarski, J., Milne, D., and Wanganeen, G. (2001). Changes in mammal populations in relatively intact landscapes of Kakadu National Park, Northern Territory, Australia. *Austral Ecology* **26**(4), 360–370. doi:10.1046/J.1442-9993.2001.01121.X

Woinarski, J., Watson, M., and Gambold, N. (2002). Vertebrate monitoring and resampling in Kakadu National Park. Parks and Wildlife Commission of the Northern Territory, Palmerston, NT.

Woinarski, J., Risler, J., and Kean, L. (2004). Response of vegetation and vertebrate fauna to 23 years of fire exclusion in a tropical *Eucalyptus* open forest, Northern Territory, Australia. *Austral Ecology* **29**(2), 156–176. doi:10.1111/J.1442-9993.2004.01333.X

Woinarski, J., Rankmore, B., Fisher, A., Brennan, K., and Milne, D. (2007). The natural occurrence of northern quolls .*Dasyurus hallucatus* on islands of the Northern Territory: assessment of refuges from the threat posed by cane toads *Bufo marinus*. *Report to Natural Heritage Trust*, 1–40.

Woinarski, J., Oakwood, M., Winter, J., Burnett, S., Milne, D., Foster, P., Myles, H., and Holmes, B. (2008). Surviving the toads: patterns of persistence of the northern quoll *Dasyurus hallucatus* in Queensland. Report to The Australian Government's Natural Heritage Trust. Available at https://denr.nt.gov.au/__data/assets/pdf_file/0003/255081/qld_quolls_finalreport.pdf

Woinarski, J., Armstrong, M., Brennan, K., Fisher, A., Griffiths, A., Hill, B., Milne, D., Palmer, C., Ward, S., and Watson, M. (2010). Monitoring indicates rapid and severe decline of native small mammals in Kakadu National Park, northern Australia. *Wildlife Research* **37**(2), 116–126. doi:10.1071/WR09125

Woinarski, J., Ward, S., Mahney, T., Bradley, J., Brennan, K., Ziembicki, M., and Fisher, A. (2011*a*). The mammal fauna of the Sir Edward Pellew island group, Northern Territory, Australia: refuge and death-trap. *Wildlife Research* **38**(4), 307–322. doi:10.1071/WR10184

Woinarski, J. C., Legge, S., Fitzsimons, J. A., Traill, B. J., Burbidge, A. A., Fisher, A., Firth, R. S., Gordon, I. J., Griffiths, A. D., and Johnson, C. N. (2011*b*). The disappearing mammal fauna of northern Australia: context, cause, and response. *Conservation Letters* **4**(3), 192–201. doi:10.1111/J.1755-263X.2011.00164.X

Woinarski, J., Braby, M., Burbidge, A., Coates, D., Garnett, S., Fensham, R., Legge, S., McKenzie, N., Silcock, J., and Murphy, B. (2019*a*). Reading the black book: the number, timing, distribution and causes of listed extinctions in Australia. *Biological Conservation* **239**, 108261. doi:10.1016/J.BIOCON.2019.108261

Woinarski, J. C., Legge, S. M., and Dickman, C. R. (2019*b*). 'Cats in Australia: companion and killer.' (CSIRO Publishing: Melbourne.)

Woolley, P. A., Krajewski, C., and Westerman, M. (2015). Phylogenetic relationships within *Dasyurus* (Dasyuromorphia: Dasyuridae): quoll systematics based on molecular evidence and male characteristics. *Journal of Mammalogy* **96**(1), 37–46. doi:10.1093/JMAMMAL/GYU028

Wynn, M. L., Clemente, C., Nasir, A. F. A. A., and Wilson, R. S. (2015). Running faster causes disaster: trade-offs between speed, manoeuvrability and motor control when running around corners in northern quolls (*Dasyurus hallucatus*). *Journal of Experimental Biology* **218**(3), 433–439. doi:10.1242/JEB.111682

Wysong, M. L., Iacona, G. D., Valentine, L. E., Morris, K., and Ritchie, E. G. (2020). On the right track: placement of camera traps on roads improves detection of predators and shows non-target impacts of feral cat baiting. *Wildlife Research* **47**(8), 557–569. doi:10.1071/WR19175

Zhang, S.-j., Wang, G.-D., Ma, P., Zhang, L.-l., Yin, T.-T., Liu, Y.-h., Otecko, N. O., Wang, M., Ma, Y.-p., and Wang, L. (2020). Genomic regions under selection in the feralization of the dingoes. *Nature Communications* **11**(1), 1–10. doi:10.1038/S41467-020-14515-6

Ziembicki, M., Woinarski, J., and Mackey, B. (2013). Evaluating the status of species using Indigenous knowledge: novel evidence for major native mammal declines in northern Australia. *Biological Conservation* **157**, 78–92. doi:10.1016/J.BIOCON.2012.07.004

Appendix H: A technological advancement in artificial refuges for an endangered marsupial predator

Published in *Conservation Science and Practice* in June 2023.

Manuscript citation**:** Cowan, M. A., Callan, M. N., Tippler, C., & Nimmo, D. G. (2023). A technological advancement in artificial refuges for an endangered marsupial predator. *Conservation Science and Practice,* 5, e12981.

DOI: 10.1111/csp2.12981

SCIENTIFIC IMPACT PAPER

Conservation Science and Practice
A Journal of the Society for Conservation Biology
Open Access

WILEY

A technological advancement in artificial refuges for an endangered marsupial predator

Mitchell A. Cowan [1,2] | Michael N. Callan [3] | Carl Tippler [3] | Dale G. Nimmo [1]

[1]Gulbali Institute, School of Agricultural, Environmental and Veterinary Sciences, Charles Sturt University, Thurgoona, New South Wales, Australia

[2]School of Agriculture and Environment, University of Western Australia, Crawley, Western Australia, Australia

[3]Habitat Innovation and Management, Wollongong, New South Wales, Australia

Correspondence
Mitchell A. Cowan, Gulbali Institute, School of Agricultural, Environmental and Veterinary Sciences, Charles Sturt University, Thurgoona, NSW, 2640, Australia.
Email: mcowan@csu.edu.au

Funding information
Fortescue Metals Group

With ongoing habitat destruction, conservationists and land managers are increasingly looking to human-made alternatives to provide shelter to wildlife (Cowan et al., 2021, Watchorn et al., 2022). In the Pilbara region of Western Australia, mining companies are required to offset habitat destruction that affects species of conservation significance. These offsets are often in the form of compensation approaches—including the creation of artificial habitat—so it is critical that compensation measures are effective. One such species of conservation significance is the northern quoll (*Dasyurus hallucatus*), which is impacted by the destruction of rugged and rocky denning habitat during mining (Moore et al., 2022). In many cases, mining companies have looked to artificial refuges as a potential offset tool to provide denning habitat for quolls—historically created as large piles of rocky material with internal crevices formed by the variation in material used.

Cowan et al. (2020) investigated the ability of these artificial refuge designs to imitate natural northern quoll dens and published their findings in *Conservation Science and Practice*. Artificial refuges had internal microclimates reflective of those inside natural dens but were much shallower and had less complex surrounding habitat. Artificial refuges also had higher visitations of feral cats (*Felis catus*), a predator of northern quolls. Northern quoll visitation was extremely low at artificial refuges, while feral cats were observed raising young within one artificial refuge, highlighting the potentially negative impacts of these structures if not designed appropriately.

These findings had important conservation implications and sparked much activity in this space. Collaboration among industry, government, engineers, designers, consultants, and species experts has led to at least one project aimed at advancing the development of artificial refuges for northern quolls. *Habitat Innovation and Management*—experts in artificial habitat design and manufacture—in collaboration with industry partner *Fortescue Metals Group* and northern quoll experts, developed a reproducible artificial refuge for northern quolls (Figure 1). The artificial refuge considers the internal denning requirements of northern quolls (e.g., depth), as described by Cowan et al. (2020), as well as environmental threats such as extreme temperatures, fire, and heavy rain that are common in the Pilbara. The artificial refuge is constructed using linear low-density polyethylene (LLDPE) to which a flame-retardant additive is applied to increase fire resistance. Manufacture of the refuge is

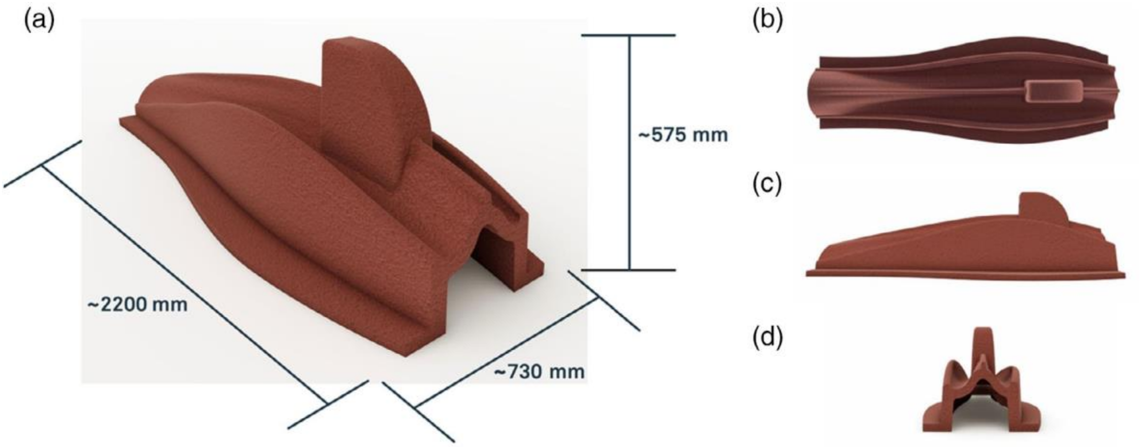


FIGURE 1 The Habitech Quoll Den© created by Habitat Innovation and Management in collaboration with species experts, engineers, designers, and industry. Shown here are the (a) dimensions, (b) top view, (c) side view, and (d) front view of the refuge.

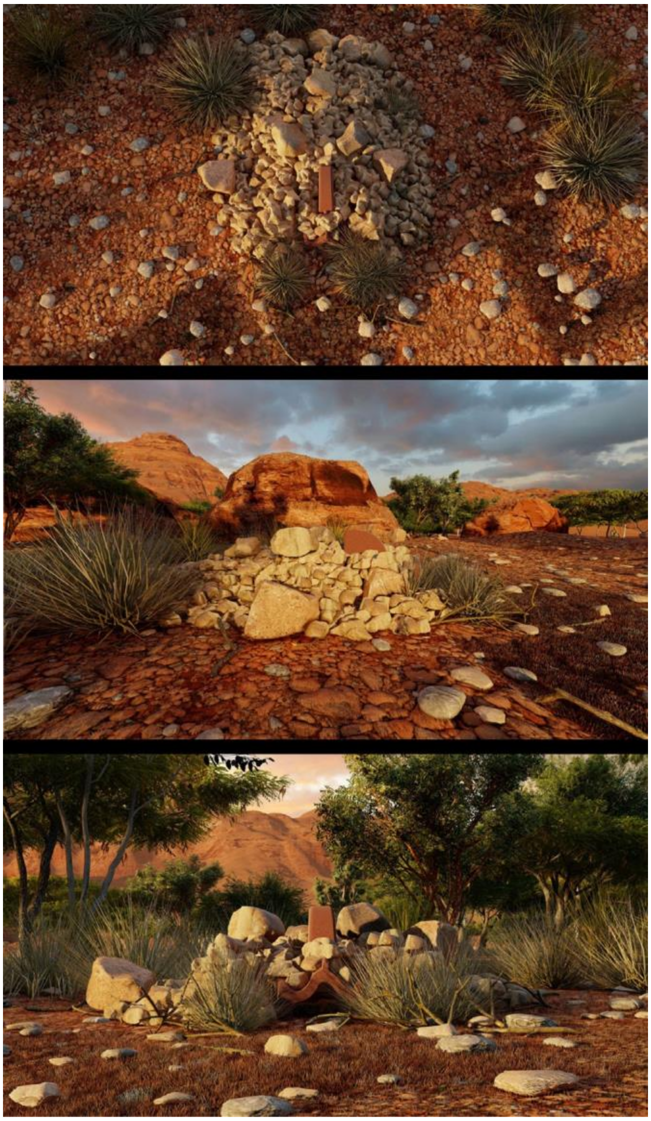


FIGURE 2 Rendered 3D models of the Habitech Quoll Den© in situ. Top: top view, middle: side view, bottom: front view.

achieved using rotational molding which involves rotating a heated mold filled with LLDPE, where the softened material spreads around the walls of the mold, forming the required shape. The artificial refuge incorporates features critical to the ecological needs of northern quolls, including an air-circulating vent, an escape shelf, and an entrance which can be configured with natural or artificial materials to exclude larger predators such as feral cats. The refuge is designed to be easily deployed in the field and covered with layers of soil and rocks to assist in thermal buffering, fire protection, and habitat complexity (Figure 2).

Future research will include field testing of the refuges alongside management techniques such as invasive predator control and vegetation restoration. This will help to determine if these artificial refuges can support breeding populations of northern quolls long term.

AUTHOR CONTRIBUTION

All authors conceived the idea for the manuscript and contributed to writing, editing, and approved final submission. Writing was led by Mitchell A. Cowan. The concept and design of the artificial refuge was led by Michael N. Callan and Carl Tippler at Habitat Innovation and Management with input from Mitchell A. Cowan and Dale G. Nimmo.

ACKNOWLEDGMENTS

We thank the editor and reviewers for their thoughtful reviews on this manuscript.

CONFLICT OF INTEREST STATEMENT

Michael N. Callan and Carl Tippler are Directors of Habitat Innovation and Management.

DATA AVAILABILITY STATEMENT

No data were used in this manuscript.

ORCID

Mitchell A. Cowan https://orcid.org/0000-0001-8432-5301

REFERENCES

Cowan, M. A., Callan, M. N., Watson, M. J., Watson, D. M., Doherty, T. S., Michael, D. R., Dunlop, J. A., Turner, J. M., Moore, H. A., Watchorn, D. J., & Nimmo, D. G. (2021). Artificial refuges for wildlife conservation: What is the state of the science? *Biological Reviews*, *96*, 2735–2754.

Cowan, M. A., Dunlop, J. A., Turner, J. M., Moore, H. A., & Nimmo, D. G. (2020). Artificial refuges to combat habitat loss for an endangered marsupial predator: How do they measure up? *Conservation Science and Practice*, *2*, e204.

Moore, H. A., Dunlop, J. A., Jolly, C. J., Kelly, E., Woinarski, J. C. Z., Ritchie, E. G., Burnett, S., Van Leeuwen, S., Valentine, L. E., Cowan, M. A., & Nimmo, D. G. (2022). A brief history of the northern quoll (*Dasyurus hallucatus*): A systematic review. *Australian Mammalogy*, *44*, 185–207.

Watchorn, D. J., Cowan, M. A., Driscoll, D. A., Nimmo, D. G., Ashman, K. R., Garkaklis, M. J., Wilson, B. A., & Doherty, T. S. (2022). Artificial habitat structures for animal conservation: Design and implementation, risks and opportunities. *Frontiers in Ecology and the Environment*, *20*, 301–309.

How to cite this article: Cowan, M. A., Callan, M. N., Tippler, C., & Nimmo, D. G. (2023). A technological advancement in artificial refuges for an endangered marsupial predator. *Conservation Science and Practice*, e12981. https://doi.org/10.1111/csp2.12981

Appendix I: Movement patterns of two northern quolls after a large wildfire

Published in *Austral Ecology* in April 2024.

Manuscript citation**:** Cowan, M. A., Nyamal Rangers, Dunlop, J. A., Moore, H. A. & Nimmo, D. G. 2024. Movement patterns of two northern quolls after a large wildfire. *Austral Ecology*, 49, e13569.

Received: 12 April 2024 | Revised: 20 June 2024 | Accepted: 15 July 2024

DOI: 10.1111/aec.13569

NATURAL HISTORY NOTE

Movement patterns of two northern quolls after a large wildfire

M. A. Cowan[1,2] | **Nyamal Rangers**[3] | **J. A. Dunlop**[1,2,4] | **H. A. Moore**[2,5] | **D. G. Nimmo**[1]

[1]Gulbali Institute, School of Agricultural, Environmental and Veterinary Sciences, Charles Sturt University, Thurgoona, New South Wales, Australia

[2]School of Agriculture and Environment, The University of Western Australia, Crawley, Western Australia, Australia

[3]Nyamal Aboriginal Corporation, Port Hedland, Western Australia, Australia

[4]School of Molecular and Life Sciences, Curtin University, Bentley, Western Australia, Australia

[5]Department of Biodiversity, Conservation and Attractions, Kensington, Western Australia, Australia

Correspondence
M. A. Cowan, Gulbali Institute, School of Agricultural, Environmental and Veterinary Sciences, Charles Sturt University, 386 Elizabeth Mitchell Drive, Thurgoona, NSW 2640, Australia.
Email: mitchell.cowan@uwa.edu.au

Abstract

Understanding how animals respond to fire is crucial for conservation efforts in fire-prone regions across the world. How fire affects animal movement is of particular interest, as it determines access to resources, exposure to risks, and connectivity of populations. We report on observations of the movement patterns and habitat selection of two northern quolls (*Dasyurus hallucatus*, an endangered marsupial predator), one male and one female, in the Pilbara region of Western Australia. We employed GPS tracking and integrated step selection functions to analyse habitat preferences in relation to fire, and used accelerometry data to assess the energetic costs of using burnt areas. The male northern quoll avoided recently burnt areas, likely due to increased energetic demands and predation risks during the breeding season. In contrast, the female northern quoll neither avoided nor preferred burnt areas, but showed a preference for rocky areas. The female appeared to move through burnt areas to access suitable breeding habitat. The movement patterns observed in the two individuals might reflect a broader pattern of sex-specific responses to fire, but further research is required to confirm how general the pattern is. Our observations indicate that fire can influence northern quoll movement, with female dependence on rocky areas increasing use of suboptimal habitats, and male avoidance of burnt areas raising potential implications for breeding dispersal and population dynamics. Given the expected increases in fire size and frequency, further research on northern quoll responses to fire in the Pilbara is needed to determine if the pattern we observed is consistent across the broader population.

KEYWORDS
Dasyurus hallucatus, fire, habitat connectivity, movement ecology, refuge

INTRODUCTION

Fire plays a vital role in shaping ecosystems globally (Kelly et al., 2020). While animals often survive individual fire events (Jolly et al., 2022), post-fire population declines are common due to reductions in resources such as vegetative cover (Fox, 1982), which provides food resources and protection from predators (Doherty et al., 2022). Survival after fire is therefore dependent on animals navigating transformed landscapes (Nimmo et al., 2019). Given that fire regimes around the world are changing

(Bowman et al., 2020), understanding how fire affects animal movement is an urgent research priority (Nimmo et al., 2019).

The northern quoll (*Dasyurus hallucatus*)—marlarlparra in Nyamal language—is an endangered marsupial mesopredator that occurs across many fire-prone ecosystems of northern Australia (Moore, Dunlop, et al., 2022). Altered fire regimes are listed as a threat to the northern quoll (Department of the Environment, 2024), and declines in both abundance and recruitment have been observed immediately after fire, as well as in the years following (Andersen et al., 2008; Begg et al., 1981). One of the primary mechanisms thought to be driving post-fire declines is the removal of vegetation cover, leading to reduced structural complexity and increased exposure to predation from larger predators (e.g. feral cats, *Felis catus*, and dingoes, *Canis dingo*) (Hill & Ward, 2010). In parts of the northern quolls' tropical range, feral cats are most active in areas with high fire frequencies (Trewella et al., 2023).

The Pilbara region in Western Australia remains a stronghold for northern quolls within their contemporary range, largely due to the absence of toxic cane toads—an invasive species lethal to northern quolls when consumed (Moore et al., 2019). Northern quoll habitat in the Pilbara is mostly characterized by rugged rocky mesas and outcrops (Moore et al., 2021), which provide an abundance of deep crevices that northern quolls use to shelter from extreme temperatures and predators during the day (Cowan et al., 2020; Hernandez-Santin et al., 2022; Moore et al., 2019). Surrounding these rocky areas are expanses of highly flammable spinifex (*Triodia* spp.) grasslands that northern quolls move through to supplement foraging and access additional rocky areas (Moore et al., 2021). Movement through grasslands is likely to carry an elevated risk for northern quolls, given predators such as feral cats and dingoes are more common in them, particularly after fire (Hernandez-Santin et al., 2016). Despite extensive research on northern quolls in the Pilbara region over the past decade, our understanding of how fire shapes quoll movement in rugged rocky areas or open spinifex grasslands remains extremely limited (Gibson et al., 2023; Moore, Dunlop, et al., 2022). To help fill this gap, we report on observa- tions of two northern quolls that were tracked in the vicinity of a recent fire during a project that monitored quoll movements within the Pilbara. These individuals were intended to be control animals for a study investigating the influence of mining on northern quoll movements—providing a baseline against which movements by quolls in mining landscapes could be compared—but incidentally provided information on how quolls navigate fire-affected landscapes.

METHODS

Monitoring was undertaken in August and September 2022 at Ripon Hills, a rugged landscape on Nyamal country, in the Pilbara. The landscape is comprised of rugged rocky outcrops and cliffs scattered within spinifex grasslands, and vegetated riparian zones along creeks and gorges (Figure 1). This area experienced a large (~5000 ha), hot summer wildfire 7 months before the study, which burned the vegetation surrounding rocky outcrops, as well as vegetation on top of rocky outcrops in some cases (Figure 1). This resulted in simpler vegetation structure in burnt areas compared to unburnt areas (Figure 1), even 7 months post-fire—spinifex grasslands can take up to 20 years to reach full maturity after wildfire (Burrows et al., 2009). As part of a broader study by Cowan et al. (2024), a 1-year-old male and 2-year-old female northern quoll were monitored for 15 and 14 days, respectively, using LiteTrack 20 RF GPS collars (Lotek, Havelock North). GPS collars

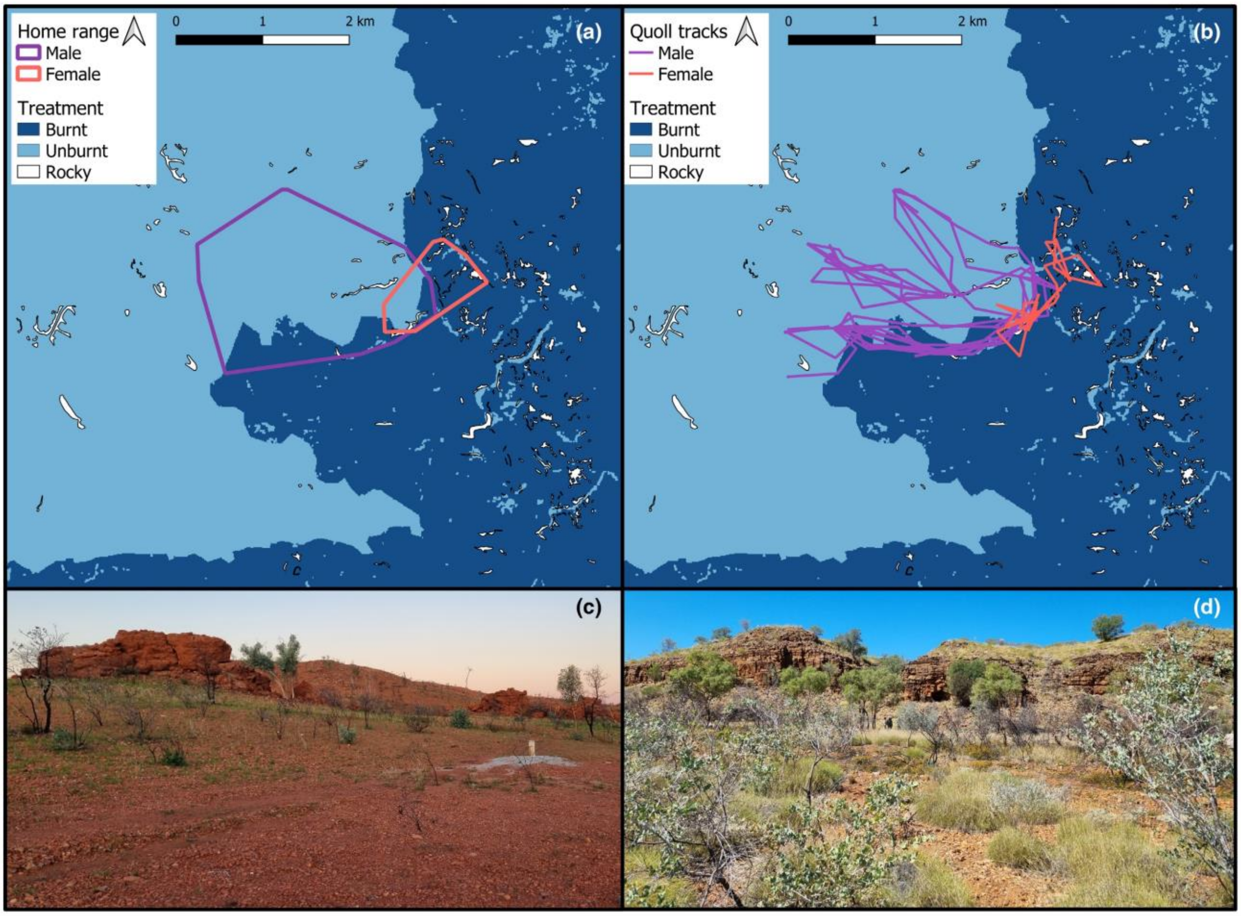


FIGURE 1 Maps showing burnt, unburnt and rocky areas with northern quoll (a) home ranges and (b) observed movement steps overlaid. Photographs show examples of (c) burnt areas and (d) unburnt areas, with rocky areas present in the background of each.

contained accelerometers and recorded GPS fixes and mean vectorial dynamic body acceleration (VeDBA; a proxy for energy expenditure; Qasem et al., 2012) every 30 min from 6 PM to 6 AM, the northern quolls' active phase. Data were processed following Cowan et al. (2024), and the fire scar was mapped using NDVI data from Sentinel 2 imagery from August 2022 (Figure 1). Rocky areas were digitized from satellite imagery and include exposed scarps or arrangements of rock that likely contain crevices.

To investigate northern quoll movement across burnt, unburnt, and rocky areas, we determined home ranges by calculating 95% minimum convex polygons (MCPs) from GPS points for each individual (Hernandez-Santin et al., 2020). We then calculated the proportion of burnt, unburnt and rocky areas within each home range. We converted GPS points to ‘movement steps’ (connecting subsequent GPS fixes) and standardized them for time as per Cowan et al. (2024). We then applied an integrated step selection function (iSSF) as per Cowan et al. (2024), comparing northern quoll movement steps with five random potential steps—modelled using Gamma-distributed step lengths and von Mises-distributed turning angles (Avgar et al., 2016). Endpoints were categorized into burnt/unburnt and rocky/ non-rocky (Appendix S1). We fit separate iSSF models for the male and female northern quoll, with the step type as the response variable, and the endpoint type, the natural logarithm of step length, and the cosine of the turning angle included as categorical predictors. Step ID was used as a stratifying term to match observed and random steps. Models were fitted in the ‘amt’ package in R (Signer et al., 2019).

To assess differences in energy expenditure (mean VeDBA), we calculated the proportion of recently burnt and unburnt areas along each movement step and calculated the mean VeDBA (±S.E) for steps that were ≥50% in burnt areas and unburnt areas (Appendix S2).

RESULTS AND DISCUSSION

Recently burnt areas covered 19.36% of the male northern quoll's home range and 63.09% of the female's home range. Rocky areas comprised 1.25% and 6.05% of the male and female's home range respectively (Figure 1). The movement track of the male northern quoll suggested avoidance of the burnt area (Figure 1), and this was supported by the iSSF. According to the iSSF, the male neither preferred nor avoided rocky areas (Figure 2). The female northern quoll did not prefer or avoid the burnt area, but favoured rocky areas over non-rocky areas (Figure 2).

The tracking period coincided with the beginning of breeding season, during which male northern quolls travel extensively to find mates, incurring high energy costs (Gaschk et al., 2023; Moore, Dunlop, et al., 2022). When northern quoll steps were predominantly (i.e. ≥50%) within the burnt area, they incurred a higher energy use (mean VeDBA ± SE: 2.06 ± 0.04) than when steps were predominantly in unburnt areas (1.78 ± 0.08). Increased VeDBA (and higher energy use) indicates faster movements in the burnt area by northern quolls, likely driven by reduced foraging opportunities and shelter availability, and increased predation risks.

The apparent avoidance of burnt areas by the male northern quoll has parallels with their avoidance of mining areas (Cowan et al., 2024). Although recently mined areas and recently burnt areas are different in many ways, they share in common a lack of complex vegetation structure (Fox et al., 1996). Hence, they might also share similar risks for northern quolls, particularly in terms of predation pressure, which is often more intense in areas with less complex vegetation (Doherty et al., 2023). Indeed, feral cats have been documented to move directly towards fire scars, presumably to hunt (McGregor et al., 2014). Therefore, the male avoidance of burnt areas is likely due to the heightened energetic costs and predatory risks during an already energetically demanding time. Large fires within the Pilbara's already naturally fragmented landscape might further reduce

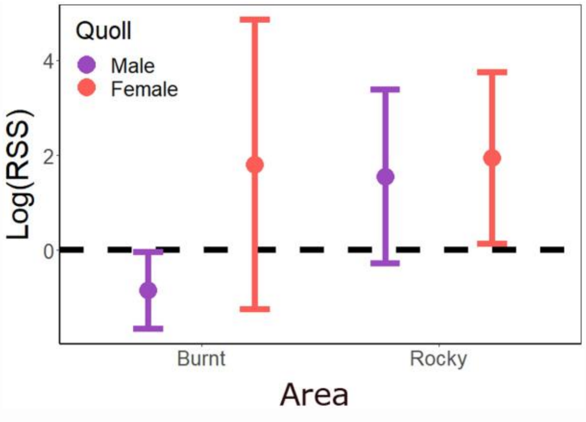


FIGURE 2 The log relative selection strength (RSS) for burnt and rocky areas. Points reflect the RSS and bars reflect 95% CIs. The dashed line represents the intercept RSS for each model (unburnt/non-rocky areas). A clear difference between treatments is observed if CIs do not cross the intercept.

landscape connectivity for male northern quolls (Shaw et al., 2022), potentially impacting population dynamics (Moore, Michael, et al., 2022; Radford et al., 2015).

Unlike the male, the female northern quoll neither preferred nor avoided burnt areas, but favoured rocky areas. During breeding season, female northern quolls depend on rocky areas for denning (Cowan et al., 2020), while males are more willing to disperse (Cowan et al., 2022). Rocky areas contain deep crevices that are unaffected by fire and which likely act as post-fire refuges for female northern quolls, reducing predation risk and buffering impacts of fire (Lees et al., 2021). However, the reliance on rocky areas may constrain the capacity of female northern quolls to shift their movement in response to fire, resulting in greater use of burnt areas. This may result in sublethal impacts. For example, female black-tailed deer (*Odocoileus hemionus columbianus*) in the USA displayed high site fidelity after fire, potentially contributing to reduced body condition (Kreling et al., 2021). There may be delayed impacts of fire on female northern quolls that are yet to materialize. For example, Kerle and Burgman (1984) found that northern quolls in the Northern Territory were common after fire, but declined the following year, and Griffiths and Brook (2015) showed that modelled northern quoll recruitment decreased by 20% following fire.

We have described the movement of a male and female northern quoll in a post-fire landscape, exploring the potential influence of fire on their movement and energy use, highlighting intraspecific differences in the response to fire between sexes. As male northern quolls use spinifex grasslands to disperse more than females (Cowan et al., 2022), large fires likely affect their movement more than females, potentially reducing interactions with female northern quolls and breeding success. The female's movement underscores the crucial role of rocky refuges in mitigating disturbance effects. It is likely that a range of factors (e.g. sex, diet, reproductive period) influenced northern quoll movement. Based on our limited sample size, it would seem that fire is one of these. With fires expected to grow in size and frequency in many regions, conservation strategies may include the protection of rocky areas and Indigenous fire stewardship that reduces the likelihood of large fires (Bliege Bird et al., 2012; Greenwood et al., 2024). More research into northern quoll responses to fire, including tracking the movements of a much larger number of animals at varying stages of disturbance (e.g. before, during, and after fire), is required to properly inform ecological fire management (Gibson et al., 2023). Furthermore, unwinding the interaction of fire with other threats, such as predation and grazing on northern quolls, is likely to be particularly important to their conservation, given that these threats occur together across their entire range (Moore, Dunlop, et al., 2022).

AUTHOR CONTRIBUTIONS

M. A. Cowan: Conceptualization (lead); data curation (lead); formal analysis (lead); writing – original draft (lead); writing – review and editing (lead). **Nyamal Rangers:** Data curation (supporting); writing – review and editing (supporting). **J. A. Dunlop:** Conceptualization (supporting); data curation (supporting); writing – review and editing (supporting). **H. A. Moore:** Writing – review and editing (supporting). **D. G. Nimmo:** Conceptualization (supporting); writing – review and editing (supporting).

ACKNOWLEDGEMENTS

We would like to acknowledge Charles Sturt University, Consolidated Minerals, the Nyamal Aboriginal Corporation, and the Department of Biodiversity, Conservation and Attractions for supporting the fieldwork for this study. Particular thanks to Marc Wohling, Abbey Ernst, Kaylee Prince, Luke Barrett, Rory Embleton, Kerryn Forster and Sam Covich-Lindsay for assisting with fieldwork. Open access publishing facilitated by Charles Sturt University, as part of the Wiley - Charles Sturt University agreement via the Council of Australian University Librarians.

FUNDING INFORMATION

Fieldwork was funded by Charles Sturt University, Consolidated Minerals, the Nyamal Aboriginal Corporation, and the Department of Biodiversity, Conservation and Attractions.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data used for analyses are in the Appendices S1 and S2, but GPS locations have been omitted. To request GPS locations please contact the corresponding author.

ORCID

M. A. Cowan https://orcid.org/0000-0001-8432-5301
J. A. Dunlop https://orcid.org/0000-0003-4842-0672
D. G. Nimmo https://orcid.org/0000-0002-9814-1009

REFERENCES

Andersen, A.N., Cook, G.D., Corbett, L.K., Douglas, M.M., Eager, R.W., Russell-Smith, J. et al. (2008) Fire frequency and biodiversity conservation in Australian tropical savannas: implications from the Kapalga fire experiment. *Austral Ecology*, 30, 155–167.

Avgar, T., Potts, J.R., Lewis, M.A. & Boyce, M.S. (2016) Integrated step selection analysis: bridging the gap between resource selection and animal movement. *Methods in Ecology and Evolution*, 7, 619–630.

Begg, R., Martin, K. & Price, N. (1981) The small mammals of little Nourlangie rock, NT. V. The effects of fire. *Wildlife Research*, 8, 515–527.

Bliege Bird, R., Codding, B.F., Kauhanen, P.G. & Bird, D.W. (2012) Aboriginal hunting buffers climate-driven fire-size variability in Australia's spinifex grasslands. *Proceedings of the National Academy of Sciences*, 109, 10287–10292.

Bowman, D.M.J.S., Kolden, C.A., Abatzoglou, J.T., Johnston, F.H., Van Der Werf, G.R. & Flannigan, M. (2020) Vegetation fires in the Anthropocene. *Nature Reviews Earth and Environment*, 1, 500–515.

Burrows, N.D., Ward, B. & Robinson, A. (2009) Fuel dynamics and fire spread in spinifex grasslands of the Western Desert. *The Proceedings of the Royal Society of Queensland*, 115(69), 76.

Cowan, M.A., Dunlop, J.A., Gibson, L.A., Moore, H.A., Setterfield, S.A. & Nimmo, D.G. (2024) Movement ecology of an endangered mesopredator in a mining landscape. *Movement Ecology*, 12, 5.

Cowan, M.A., Dunlop, J.A., Turner, J.M., Moore, H.A. & Nimmo, D.G. (2020) Artificial refuges to combat habitat loss for an endangered marsupial predator: how do they measure up? *Conservation Science and Practice*, 2, e204.

Cowan, M.A., Moore, H.A., Hradsky, B.A., Jolly, C.J., Dunlop, J.A., Wysong, M.L. et al. (2022) Non-preferred habitat increases the activity area of the endangered northern quoll (*Dasyurus hallucatus*) in a semi-arid landscape. *Australian Mammalogy*, 45, 138–150.

Department of the Environment. (2024) *Dasyurus hallucatus in species profile and threats database*. Canberra: Department of the Environment.

Doherty, T.S., Geary, W.L., Jolly, C.J., Macdonald, K.J., Miritis, V., Watchorn, D.J. et al. (2022) Fire as a driver and mediator of predator–prey interactions. *Biological Reviews*, 97, 1539–1558.

Doherty, T.S., Watchorn, D.J., Miritis, V., Pestell, A.J.L. & Geary, W.L. (2023) Cats, foxes and fire: quantitative review reveals that invasive predator activity is most likely to increase shortly after fire. *Fire Ecology*, 19, 22.

Fox, B.J. (1982) Fire and mammalian secondary succession in an Australian coastal heath. *Ecology*, 63, 1332–1341.

Fox, B.J., Fox, M.D., Taylor, J.E., Jackson, G.P., Simpson, J., Higgs, P. et al. (1996) Comparison of regeneration following burning, clearing or mineral sand mining at Tomago, NSW: I. Structure and growth of the vegetation. *Australian Journal of Ecology*, 21, 184–199.

Gaschk, J.L., Del Simone, K., Wilson, R.S. & Clemente, C.J. (2023) Resting disparity in quoll semelparity: examining the sex-linked behaviours of wild roaming northern quolls (Dasyurus hallucatus) during breeding season. *Royal Society Open Science*, 10, 221180.

Gibson, L.A., Moore, H.A., Cowan, M.A., Craig, M.D., Nimmo, D.G. & Dunlop, J.A. (2023) A review of progress of a research program for the endangered northern quoll (*Dasyurus hallucatus*) in the multi-use landscapes of the Pilbara. *Australian Mammalogy*, 45, 251–263.

Greenwood, L., Bliege Bird, R., Mcguire, C., Jadai, N., Price, J., Skroblin, A. et al. (2024) Indigenous pyrodiversity promotes plant diversity. *Biological Conservation*, 291, 110479.

Griffiths, A.D. & Brook, B.W. (2015) Fire impacts recruitment more than survival of small-mammals in a tropical savanna. *Ecosphere*, 6, art99.

Hernandez-Santin, L., Goldizen, A.W. & Fisher, D.O. (2016) Introduced predators and habitat structure influence range contraction of an endangered native predator, the northern quoll. *Biological Conservation*, 203, 160–167.

Hernandez-Santin, L., Goldizen, A.W. & Fisher, D.O. (2022) Northern quolls in the Pilbara persist in high-quality habitat, despite a decline trajectory consistent with range eclipse by feral cats. *Conservation Science and Practice*, 4, e12733.

Hernandez-Santin, L., Henderson, M., Molloy, S.W., Dunlop, J.A. & Davis, R.A. (2020) Spatial ecology of an endangered carnivore, the Pilbara northern quoll. *Australian Mammalogy*, 43, 235–242.

Hill, B.M. & Ward, S.J. (2010) National recovery plan for the northern quoll Dasyurus hallucatus. Department of Natural Resources, Environment, The Arts and Sport, Darwin.

Jolly, C.J., Dickman, C.R., Doherty, T.S., Van Eeden, L.M., Geary, W.L., Legge, S.M. et al. (2022) Animal mortality during fire. *Global Change Biology*, 28, 2053–2065.

Kelly, L.T., Giljohann, K.M., Duane, A., Aquilué, N., Archibald, S., Batllori, E. et al. (2020) Fire and biodiversity in the Anthropocene. *Science*, 370, eabb0355.

Kerle, J. & Burgman, M. (1984) Some aspects of the ecology of the mammal Fauna of the Jabiluka area. Northern Territory. *Wildlife Research*, 11, 207–222.

Kreling, S.E.S., Gaynor, K.M., Mcinturff, A., Calhoun, K.L. & Brashares, J.S. (2021) Site fidelity and behavioral plasticity regulate an ungulate's response to extreme disturbance. *Ecology and Evolution*, 11, 15683–15694.

Lees, D.M., Watchorn, D.J., Driscoll, D.A. & Doherty, T.S. (2021) Microhabitat selection by small mammals in response to fire. *Australian Journal of Zoology*, 69, 67–79.

Mcgregor, H.W., Legge, S., Jones, M.E. & Johnson, C.N. (2014) Landscape Management of Fire and Grazing Regimes Alters the fine-scale habitat utilisation by feral cats. *PLoS One*, 9, e109097.

Moore, H.A., Dunlop, J.A., Jolly, C.J., Kelly, E., Woinarski, J.C.Z., Ritchie, E.G. et al. (2022) A brief history of the northern quoll (*Dasyurus hallucatus*): a systematic review. *Australian Mammalogy*, 44, 185–207.

Moore, H.A., Dunlop, J.A., Valentine, L.E., Woinarski, J.C.Z., Ritchie, E.G., Watson, D.M. et al. (2019) Topographic ruggedness and rainfall mediate geographic range contraction of a threatened marsupial predator. *Diversity and Distributions*, 25, 1818–1831.

Moore, H.A., Michael, D.R., Dunlop, J.A., Valentine, L.E., Cowan, M.A. & Nimmo, D.G. (2022) Habitat amount is less important than habitat configuration for a threatened marsupial predator in naturally fragmented landscapes. *Landscape Ecology*, 37, 935–949.

Moore, H.A., Michael, D.R., Ritchie, E.G., Dunlop, J.A., Valentine, L.E., Hobbs, R.J. et al. (2021) A rocky heart in a spinifex sea: occurrence of an endangered marsupial predator is multiscale dependent in naturally fragmented landscapes. *Landscape Ecology*, 36, 1359–1376.

Nimmo, D.G., Avitabile, S., Banks, S.C., Bliege Bird, R., Callister, K., Clarke, M.F. et al. (2019) Animal movements in fire-prone landscapes. *Biological Reviews*, 94, 981–998.

Qasem, L., Cardew, A., Wilson, A., Griffiths, I., Halsey, L.G., Shepard, E.L.C. et al. (2012) Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we Be summing values or calculating the vector? *PLoS One*, 7, e31187.

Radford, I.J., Gibson, L.A., Corey, B., Carnes, K. & Fairman, R. (2015) Influence of fire mo- saics, habitat characteristics and cattle disturbance on mammals in fire-prone savanna landscapes of the northern Kimberley. *PLoS One*, 10, e0130721.

Shaw, R.E., Spencer, P.B., Gibson, L.A., Dunlop, J.A., Kinloch, J.E., Mokany, K. et al. (2022) Linking life history to landscape for threatened species conservation in a multiuse region. *Conservation Biology*, 37, e13989.

Signer, J., Fieberg, J. & Avgar, T. (2019) Animal movement tools (amt): R package for man- aging tracking data and conducting habitat selection analyses. *Ecology and Evolution*, 9, 880–890.

Trewella, G.J., Cremona, T., Nevard, H. & Murphy, B.P. (2023) Habitat structure facilitates coexistence of native and invasive mesopredators in an Australian tropical savanna. *Wildlife Research*, 50, 1058–1070.