THE ECOLOGY OF AN INSULAR POPULATION OF NORTHERN QUOLL *DASYURUS HALLUCATUS*

Jai Thomas

BSc. Environmental Science (1st Class Hons)

Submitted in fulfilment of the requirements for the degree of
Doctor of Philosophy

Environmental and Conservation Sciences
Murdoch University
2020

Dasyurus hallucatus, Koolan Island. Illustration by E. Harradine.

Abstract

The northern quoll (*Dasyurus hallucatus*) is the smallest of the four quoll species endemic to Australia, and has suffered significant recent declines due to the spread of a number of threatening processes including ingestion of the toxic cane toad, altered fire regimes, and habitat loss and modification. In many areas, the species has survived by persisting in rocky country but populations are fragmented and isolated. In the recent mining boom of Western Australia many areas where the northern quoll has persisted were targeted for mining, and there have been an increasing number of mining projects needing to manage and mitigate impacts to populations of this species. There are also a number of conservation initiatives in progress that aim to buffer the northern quoll from the continuing threat of exotic species and habitat modification. However, the northern quoll is a cryptic species that occurs in remote areas and research to date has been limited by logistic constraints and sampling difficulty. On Koolan Island, the northern quoll has persisted despite a long history of mining for iron ore (1934 – 1940; 1965 - 1993; 2006 - present). Therefore, this thesis aimed to study the ecology of Koolan Island northern quolls to better understand the population dynamics, diet and habitat use of an island population, and examine any interactions with modified areas.

Fieldwork undertaken between 2014 and 2017 on Koolan Island was combined with a mark-recapture dataset spanning 13 years (2006 - 2018). The dataset was analysed using both spatial and non-spatial capture recapture methods to examine the population dynamics of northern quolls on Koolan Island. Using both methods aided in circumventing the analytical constraints of the study design, which was typical of many long-term monitoring programs in that it was spatially inconsistent (trap location varied) between years. Females were rarely captured between years, with no male recaptures suggesting a near-complete male die-off before the next breeding season. Apart from a decline in 2010-2011 following a cyclone, the population remained relatively stable and was not in continuous decline between 2006-2018 (~12.65 individuals/ km^2). Using estimates of seniority (the probability that an individual present in year t was also present in year $t – 1$), recruitment was found to drive population change (seniority = 0.18; 95% CI 0.12–0.27).

Dietary analysis was conducted using scats collected across the island from 2014 - 2017, with a total 448 scats from both anthropogenic and native habitat types. Closed capture models were used to examine differences in diet between anthropogenic and native habitat to contrast the wet and dry season, and Fisher's Exact Tests were used to determine if prey were consumed relative to their availability. A total of 32 food items were detected in the northern quoll diet, with the most commonly consumed foods including invertebrates (beetles/cockroaches, crickets/grasshoppers, centipedes, crustaceans), skinks, and major fruiting plants found on the island (*Ficus* sp. and fruit of the stinking passionflower *Passiflora foetida*). Closed capture analysis indicated that diet composition was influenced by both season and habitat type. Invertebrates were the most commonly consumed food type by far, in particular beetles/cockroaches which were consumed more often than would be expected based on their availability in the environment ($P < 0.001$). Fruits were consumed in moderate amounts (found in 43.1% of scats), and vertebrates were consumed the least in both modified and unmodified habitats and across seasons.

Given population dynamics are driven by recruitment, juvenile survival is likely to be critical to the persistence of the northern quoll. The northern quoll is dependent on its mother for the first stage of life, and young are deposited in dens while the female forages at night. Therefore, this thesis also investigated the characteristics of dens selected by females during the young in den phase to better understand den attributes that may influence selection by this species. A total of 22 dens were located by tracking females captured in both anthropogenic and native habitats. The structural and habitat attributes of these dens were compared with similar available ‘dens’ in the surrounding area using logistic regression. Temperature and humidity of used dens (n = 22), available dens (n = 24) and ambient sites (n = 12) were also measured to determine the microclimatic properties of selected dens. Dens were found in trees (n = 4), rock crevices (n = 12), and underground (n = 6), with no dens found in anthropogenic areas. One den was located in an area with commenced but not complete rehabilitation (earthworks undertaken). Using generalised additive mixed models (GAMM), used dens appeared to provide a more stable temperature and humidity throughout the day than both available den sites and ambient conditions. Rocky dens had more stable microclimates than dens in trees or earth. Aerial cover (canopy and/or rocky cover) and number of entrances best predicted female den selection during the young in den period.

Overall, my findings indicate that northern quolls on Koolan Island currently exist in a stable population and take advantage of certain resources available in modified areas, appearing relatively resilient to the anthropogenic habitat modification that has occurred to date. Of particular interest is their use of the stinking passionflower, which is the subject of weed control programs on the island. The high level of invertebrate consumption across seasons and habitats, particularly beetles and cockroaches, indicates the importance of this food item to island populations. Low vertebrate consumption may be due to prey availability on the island, or reflect the smaller body size compared to mainland populations. While northern quolls appear to forage in both modified and unmodified environments, maternal den use seems heavily reliant on native habitat, indicating that suitable denning habitat in undisturbed areas must be preserved for a population to persist. Denning habitats that provide a stable microclimate, aerial cover and multiple entry/exit points are likely to be preferred by females during the young in den period and may support juvenile survival at a critical life stage.Collectively, the research detailed in this thesis contains pertinent information on population dynamics, diet, and den site selection to inform conservation efforts across northern Australia and worldwide that target cryptic, rare and endangered mammals.

Table of Contents

Abstract iii

List of Figures ix

List of Tables xi

Statement of Original Authorship xii

Acknowledgements xv

Chapter 1: Introduction 1

1.1 Threats to Biodiversity in Australia's Wet-Dry Tropics 1

1.2 Mining and Wildlife Management 2

1.3 Value of Baseline Data for Rare and Endangered Species 3

1.4 This study 7

1.5 Thesis Outline 9

1.6 References 13

Chapter 2: A synthesis of the literature regarding the biology and ecology of the northern quoll (*Dasyurus hallucatus*) 19

2.1 Introduction 19

2.2 Life History 22

2.3 Movement and habitat use 30

2.4 Threats and conservation 41

2.5 Conclusion 47

2.6 References 53

Chapter 3: Analysis of mine site monitoring data using spatial and non-spatial capture recapture models reveals the population dynamics of an endangered marsupial 62

3.1 Abstract 62

3.2 Introduction 63

3.3 Methods 69

3.4 Results 80

3.5 Discussion 85

3.6 References 96

3.7 Ethics 102

Chapter 4: The influence of season and habitat on the diet of an insular population of an endangered marsupial 103

4.1 Abstract 103

4.2 Introduction 104

4.3 Methods 107

4.4 Results 116
4.5 Discussion...124
4.6 References 134
4.7 Supplementary Information 141

Chapter 5: Nursery den site selection by the northern quoll (*Dasyurus hallucatus*) 142

5.1 Abstract...142
5.2 Introduction 142
5.3 Methods 146
5.4 Results 156
5.5 Discussion...163
5.6 References 170
5.7 Supplementary Information 175

Chapter 6: General Discussion 1756

6.1 Insular populations of northern quoll...176
6.2 Response to habitat modification...181
6.3 Rehabilitation actions for the northern quoll 185
6.4 Management implications for the cane toad 188
6.5 challenges and learnings from this study 190
6.6 Directions for future research 193
6.7 References: 197

Appendix 201

Appendix A Used and available den sites on Koolan Island 201

List of Figures

Figure 2.1. Life history of the northern quoll *Dasyurus hallucatus*, with reference to data chapters in this thesis. As detailed in Section 2.2, the timing associated with each life history stage vary across this species' range. 23

Figure 3.1. Koolan Island, Western Australia 70

Figure 3.2. Trap lines used on Koolan Island from 2006 – 2018, showing location in relation to mine and associated infrastructure. Note that not all trap lines were used each year. 72

Figure 3.3. Annual density per square kilometre estimated using spatially explicit capture recapture methods, shown with 95% confidence intervals. 81

Figure 3.4. Association between finite population change and (a) material moved (tonnes), (b) average manning level, (c) SPEI12 and (d) SPEI24. Blue lines are model-derived. 82

Figure 3.5. Model averaged estimates of apparent female survival over the years 2012 - 2018. 84

Figure 4.1. Location of Koolan Island in the Kimberley region, Western Australia, showing the mining and accommodation footprint (anthropogenic habitat type; orange), and sampled scat locations (grey dots). 108

Figure 4.2. %Volume for all food items detected in scats by (a) habitat type, (b) wet/dry season, and (c) broad food group classification. Error bars represent 95% bootstrap confidence intervals. 118

Figure 4.3. Diet estimates from Program MARK using fine-scale food item categorisation across native (Nat) and anthropogenic (Anthro) habitat types and wet and dry season. Error bars represent 95% confidence intervals. 121

Figure 4.4. Diet estimates from Program MARK using broad-scale food item categorisation across the wet and dry seasons. Error bars represent 95% confidence intervals. 121

Figure 4.5. Standardised Levins' niche breadth calculated for (a) wet versus dry season, and (b) native versus anthropogenic habitat types. 122

Figure 4.6. Comparison of food item occurrence in scats and traps in both natural and antrhopogenic habitat types, and combined across habitat types. Comparison is limited to food items detected in both scats and traps. 124

Figure 5.1. Location of Koolan Island showing used dens (triangle), available dens (circle) and ambient sites (square). 149

Figure 5.2. Mean estimates and 95% confidence intervals for (a) temperature measures and (b) humidity measures. Note that range and rate represent median values with bootstrapped 95% confidence intervals. 158

Figure 5.3. Predictions from Generalised Additive Mixed Models of the (a) daily temperature (°C) and (b) daily humidity (%) for used dens, available dens and ambient sites. Blue lines represent ambient sites, red lines represent used dens, and green lines represent available dens. Grey shaded areas indicate 95% confidence intervals. 159

Figure 5.4. Predictions from Generalised Additive Mixed Models of the (a) daily temperature (°C) and (b) daily humidity (%) for used dens in rock, earth and wood substrate. Ambient sites have been included for comparison. Grey dots are observed values. Grey shaded areas indicate 95% confidence intervals. 160

Figure 5.5. Structural and habitat characteristics of used and available northern quoll den sites on Koolan Island, including (a) number of potential entrances, (b) % vegetation cover, (c) % rock cover, (d) elevation (metres), (e) % aerial cover, and (f) vegetation condition using the scale detailed in EPA (2016). Black dots represent suspected outliers. 162

Figure 6.1. Life history of the northern quoll Dasyurus hallucatus, with reference to data chapters in this thesis.. 176

List of Tables

Table 2.1. Home range estimates of the northern quoll 37

Table 3.1. Model selection results for spatially explicit capture recapture estimates. K is the number of parameters. AIC is Akaike's Information Criterion. △AIC shows the difference between the model AIC and the AIC of the highest ranked model. AIC_{wi} is the relative likelihood of the model normalised to sum to 1. b denotes an effect of previous capture; session denotes a year effect; g denotes an effect of sex. 81

Table 3.2. Model selection results for female northern quoll apparent survival and seniority (Pradel Robust Design). Phi denotes survival, gamma denotes seniority, p denotes probability of capture, c denotes probability of recapture, session denotes year. See Table 3.1 for an explanation of table column headings... 83

Table 3.3. Model selection results for the top 12 of 48 candidate models for female northern quoll apparent survival and recruitment (Pradel Robust Design). Phi denotes survival, f denotes recruitment, p denotes probability of capture, c denotes probability of recapture, session denotes year, and habitat denotes the effect of habitat. See Table 3.1 for an explanation of table column headings. 85

Table 4.1. Percentage frequency of occurrence (%FO) and percentage volume (%VO) for food items detected in northern quoll scats, compared to other studies. (-) denotes data not available. 117

Table 4.2. Model sets and model results used to describe the diet of the northern quoll on Koolan Island using fine-scale categorisation. *K* = number of parameters; AIC = Akaike's Information Criterion; △AIC = Delta AIC. 120

Table 4.3. Model sets and model results used to describe the diet of the northern quoll on Koolan Island using the categories invertebrate, vertebrate, fruit. *K* = number of parameters; QAICc = Quasi-corrected Akaike's Information Criterion corrected for small sample size; △QAICc = Delta QAICc. 120

Table 4.4. Exact test of goodness of fit results comparing the occurrence of each prey category in pitfall and funnel traps and scats of the northern quoll. *p<0.05; **p<0.01; ***p<0.001. 'Native' refers to habitat in areas outside the mining and infrastructure footprint that have not been previously cleared. 'Anthropogenic' means areas within the mining and infrastructure footprint (shown in Figure 4.1). 123

Table 5.1. Habitat variables recorded at each used and available den. 151

Table 5.2. Parameter estimates and AICc values for candidate models within ≤ 2AIC of the top model. 162

Statement of Original Authorship

I declare that this thesis is my own account of my research and contains as its main content work which has not been previously submitted for a degree at any tertiary education institution.

Signature: __________________________

Preface

Each data chapter (Chapters 3-5) presents my PhD research and has been written for submission for journal publication. Therefore there is repetition of the description of study site and species throughout. While each data chapter has been formatted as a journal submission, the tables and figures have been re-numbered sequentially throughout the thesis for consistency and ease of reference.

Data chapters are bracketed by an introduction (Chapter 1), literature review (Chapter 2) and conclusion (Chapter 6), which explain the links between papers, place the research in a broader context and explore the application of this research and future directions.

This project was funded by Mount Gibson Iron Ltd. and commenced in 2014 with the aim to better understand the ecology of island populations of northern quoll, and to inform measures to minimise and mitigate impacts to this species as a result of mining activities on Koolan Island.

Monitoring data used in Chapter 3 were collected by contractors engaged by Mount Gibson Iron Ltd. over a 13 year period (most recently by Dr Mitch Ladyman, Animal Plant Mineral). I assisted with fieldwork for annual monitoring from 2014 - 2017.

Field equipment was provided by Mount Gibson Iron Ltd. and supplemented with self-sourced materials. Dr Joe Fontaine provided data loggers for use in Chapter 5. I organised, led and undertook all fieldwork for Chapters 4 and 5. When collecting data for Chapter 5, I was occasionally accompanied by John Tomich (Mount Gibson Iron Ltd).

I undertook all logistical planning, study design and statistical analysis. I also reviewed the literature and wrote and revised the chapters/papers with scientific and editorial input from my supervisors.

One paper presented in this thesis has been submitted for publication, and two have been prepared for submission. Each paper refers to “we” in acknowledgement of the contributions of co-authors, who are as follows:

Chapter	Manuscript	Contributions
3	Thomas, J., Fontaine, J., Mills, H. & Spencer, P. (submitted). Analysis of mine site monitoring data using spatial and non-spatial capture recapture models reveals the population dynamics of an endangered marsupial.	J Thomas 80% J Fontaine 10% Mills H 5% Spencer P 5%
4	Thomas, J., Fontaine, J., Mills, H. & Spencer, P. (in prep.). The influence of season and habitat on the diet of an insular population of an endangered marsupial.	J Thomas 80% J Fontaine 10% Mills H 5% Spencer P 5%
5	Thomas, J., Fontaine, J., Mills, H. & Spencer, P. (in prep.). Nursery den site selection by the northern quoll (*Dasyurus hallucatus*)	J Thomas 80% J Fontaine 10% Mills H 5% Spencer P 5%

Ethics

This study was undertaken with approval from the Department of Biodiversity, Conservation and Attractions under the former *Wildlife Conservation Act 1950* (Licences 08-000719-1 and 08-001011-1), and ethics approval from Murdoch University (Permit IRMA2865/16).

Acknowledgements

I would first like to acknowledge the Dambimangari, the traditional owners of the land on which this study was conducted.

I would like to sincerely thank my supervisors Dr Joe Fontaine, Assoc. Prof. Peter Spencer and Dr Harriet Mills for thinking of me when the project came about, and for sticking with me through this at times stressful and arduous project.

Thanks to Dr Mitch Ladyman for approaching Murdoch University with this project and for your enthusiasm and willingness to bring me on board for the annual monitoring surveys. Thanks also for giving up your own time over many cups of coffee to discuss parts of the project.

I would also like to thank Mount Gibson Iron Ltd. for facilitating ongoing access to the island, even when mine operations ceased temporarily, and for significant logistical support including equipment, vehicles, transport and accommodation. In particular I wish to thank John Tomich for assistance in the field, and for his persistent support to ensure the project continued when logistics and external factors threatened its completion. I thank you also for the many hours of long conversation shared on the island. I would also like to thank Graham Taylor, Chris Taylor, Beau Zoranich, Al Yates, Alistair Stirling, Damon Farrell, Mitch Harding, Dave Rayfield and Darren Margetts. Thank you for your help with equipment and for the comradery; the work ethic that you demonstrated inspired me to keep moving forward.

Thank you to the Department of Biodiversity, Conservation and Attractions for the loan of equipment when everything else broke. Chapter 5 would have been significantly more difficult without this help. Thanks in particular to Russell Palmer for organising the equipment loan, as well as your early advice and assistance regarding the diet study and scat collection.

Thanks to my partner Elysia for her perpetual encouragement and for the countless hours spent reading over early drafts. No words could describe my gratitude and appreciation.

Lastly, I would like to give special thanks to Professor Rick Shine and Melanie Elphick, who gave me my opportunity to pursue a career in wildlife biology. Without that opportunity I would never have gone to university and been exposed to the people and places that opened my eyes and changed my life profoundly. I will be forever grateful for the opportunities I was given through and following my association with the Shine Lab.

Chapter 1: Introduction

1.1 THREATS TO BIODIVERSITY IN AUSTRALIA’S WET-DRY TROPICS

Extinction rates are increasing globally, especially for vertebrate species. At least 200 extinctions have been documented in the last century, and a third or more are in current decline (Ceballos et al. 2017). Widespread impacts associated with anthropogenic land use are considered the main drivers of vertebrate declines worldwide (Ellis et al. 2010; Troyer et al. 2014; Newbold et al. 2015). However, the examination of such a complex and intertwined suite of impacts is difficult, as their effects are often entangled with the natural variability of the species’ environment and demography (Brigatti et al. 2016). Without a thorough understanding of a species’ ecology and the natural variability of their population dynamics, the task of quantifying the causes of decline can be formidable.

Australian mammal species comprise a third of the global mammal extinctions since the year 1500, with the majority occurring in the southern-most half of the continent (Woinarski et al. 2011; Fisher et al. 2014). This statistic is unenviable given that Australia has only 6% of the world’s mammal species (Fisher et al. 2014). The effects of European settlement, predation from primarily feral cats and foxes, and changes to land use and management, are considered to have driven the majority of Australian mammal declines (Woinarski et al. 2015). Due to its sparse human population, largely-natural vegetation cover and lack of red foxes (*Vulpes vulpes*), it was assumed that mammal species inhabiting the wet-dry tropics of the north were free from the threatening processes that have resulted in the decline of their southern counterparts (Woinarski et al. 2007, Garnett et al. 2010; Woinarski et al. 2011). The

Kimberley region of northern Western Australia is one example of the country's wet-dry tropics and due to its extraordinary plant and animal diversity is recognised as a National Biodiversity Hotspot (http://www.environment.gov.au/biodiversity/hotspots /-national-hotspots.htm) with a portion listed as world heritage area by UNESCO (https://whc.unesco.org/en/list/1094).

The region has been relatively resilient to most human-associated disturbances as a result of both its size and isolation (Fitzsimmons et al. 2010; Woinarski et al. 2010). However, recent evidence from a range of sources suggests as many as 22 marsupial species in the northern tropics have suffered declines and range reductions beginning around 1970 (Fitzsimons et al. 2010). Additionally, the abundance of three species (the northern brush-tailed phascogale, *Phascogale pirata*; northern quoll, *Dasyurus hallucatus*; fawn antechinus, *Antechinus bellus*) are observed to have declined by more than 90% in some areas (Fitzsimons et al. 2010; Woinarski et al. 2011). Given the lack of extensive habitat modification in northern Australia, there has been growing conjecture as to the drivers of declines in this region.

In a study of mammal declines in northern Australia, Woinarski et al. (2011) note that tropical mammal declines show more or earlier declines from lower rainfall and "topographically simple" or less rugged areas, with slower declines in higher rainfall and more rugged areas, and islands (see Southgate et al. 1996; Woinarski et al. 1999; Woinarski 2000; Firth et al. 2006).

1.2 MINING AND WILDLIFE MANAGEMENT

As many as 400 large mines are currently active within Australia (Geoscience Australia 2018), and although mining accounts for less than one percent of land use within Australia (Hancock 1993; ABARES 2018), localised impacts can be intensive. These impacts can act on both a local and regional scale, and amongst others include habitat loss and degradation, the facilitation of invasive species, or contributions to air, water and noise pollution (Hancock 1993).

One of the most pervasive impacts of mining is the large scale clearing of land and the construction of mining infrastructure. These impacts have parallels with other intensive land uses such as residential areas and agriculture, which may lead to a reduction in food resources, shelter and breeding habitat, and result in patches of land that impede the dispersal of fauna (Environmental Law Alliance Worldwide 2010). Globally, habitat loss as a result of mining has been identified as a threat to the continued existence of 216 reptiles, 225 amphibians, 266 mammals, and 322 species of bird (IUCN 2013).

While the mining industry has modified large areas of habitat within Australia, the industry is also well-placed to gather important data on wildlife populations that other agencies are unable to focus on given logistical and financial constraints. The life of a mine is typically longer than the three to four-year studies that dominate the literature, and mining companies are often required to conduct regular monitoring of impacted fauna populations as part of their approval to mine. However, the data that arise from these studies are rarely peer reviewed and published (Costello and Wieczorek 2014; Addison et al. 2015). This represents an important gap and opportunity in Australia's adaptive management framework for managing rare and endangered species in modified landscapes.

1.3 VALUE OF BASELINE DATA FOR RARE AND ENDANGERED SPECIES

Since human population growth and its associated resource requirements are predicted to increase well into the future, finding creative solutions to maintain viable wildlife populations is becoming a crucial societal challenge (Ripple et al. 2014). Our ability to predict the impacts of disturbance and identify effective management solutions is underpinned by the need for sound knowledge of a species' population dynamics, natural history and ecology (McDonald et al. 2012). This has proven difficult for many cryptic and low-density species that are hard to study and may already be limited to small remnant populations (Karanth et al. 2006). Challenges in studying Australia's vertebrate fauna are common relative to other, better studied regions such as the USA or Western Europe. This is due to a generally less-productive landscape, with many fauna occurring at low densities either naturally or following decline (e.g. Lollback et al. 2015). The Australian landscape also presents many logistical challenges to sampling due to a lack of infrastructure and difficult accessibility in remote areas (e.g. Vernes et al. 2009). When compounded with the nocturnal habits and secretive behaviour of many species, the application of methods that require direct observation and recaptures can be problematic (Bain et al. 2014).

In spite of the challenging and often costly sampling conditions present in Australia, the continual pursuit of ecological data is driven by the increasing extent and effect of threatening processes such as land use change, fire, and feral species (Woinarski et al. 2015). The ultimate goal of collecting these data is for its direct application to conservation efforts to avert population crashes and localised (or complete) extinction, as demonstrated by classic examples from other parts of the world. For example, the recovery of the Mauritius kestrels *Falco punctatus* using habitat enhancement for nest sites, supplementary feeding and predator control would have been impossible without a knowledge of the species provided by studies such as Temple (1977) and McKelvey (1977), and later Jones and Owadally (1985; 1988). In the US, the black-footed ferret (*Mustela nigripes*) has been brought back from the brink of extinction following reintroduction programs and management actions extending to important prey species. In this case, management decisions have been informed by knowledge of important habitat characteristics (Biggins et al. 1993; 2006; Luce 2004), resource selection relating to diet (Jachowski 2007), and seasonal changes in movement and habitat use (Richardson et al. 1987).

1.3.1 Population dynamics

Threatened species often become threatened due to a range of processes. The examination of these processes can be difficult as their effects are often mixed with the impacts of environmental variation and demographic fluctuations (Brigatti et al. 2016). To disentangle the confounding effects of demographic and environmental influences, it is necessary to gain a thorough understanding of the natural variability and drivers of a species' population dynamics. This includes a study of annual variability in population size and density, and the influence of recruitment and survival on these measures (Kersting and García-March 2017). However, these studies must be conducted over many generations and years to identify patterns and isolate the population dynamics from the effects of environmental variation (Krebs 1991), which is often logistically or financially unfeasible.

1.3.2 Diet

Ensuring that wildlife populations have sufficient food, water and shelter for adequate survival and reproduction are of primary concern to conservation management. Through examining a species' diet and foraging strategy, we may also identify predatory or competitive relationships with other fauna, and resources that should be maintained for that species' persistence (Darimont et al. 2009). Further, these studies can be used to examine whether diet changes with habitat type and modification, or across a species' range. This knowledge has direct application to the planning and implementation of conservation initiatives. For example, when islands or mainland sites are considered for use in relocation or translocation programs, dietary information can be used to determine the suitability of candidate sites in sustaining a viable population of the study species (DeYoung et al. 2000) and to assess the population post-translocation (e.g. Kinley and Newhouse 2008; Stannard et al. 2010). Such information may also indicate whether translocation will have negative impacts on the pre-existing island fauna through unsustainable predation or competition.

Studies of diet in areas with habitat modification can also provide information towards understanding human-wildlife interactions, where anthropogenic areas may provide subsidies (Johnson and St-Laurent 2011). Understanding wildlife interactions with anthropogenic areas can be informed by understanding the scale to which a species has a specialised or generalist diet. While specialist species are more likely to be adversely impacted by habitat alterations that influence resource availability (Boyles and Storm 2007), generalist species are more flexible to changes in food availability, and more likely to be able to take advantage of novel food sources (e.g. Lowry et al. 2013; Newsome et al. 2014).

1.3.3 Denning habitat

For species that require specific microhabitats for shelter, denning or nesting, site availability likely influences population distribution and limits individual survival and reproductive success (Lesmeister et al. 2008; Carter et al. 2012). Denning and nesting requirements may also change as a result of seasonal variation, i.e. a shift between summer and winter dens, or between breeding and non-breeding periods (Ross et al. 2010). Most studies that have examined the drivers of den site selection identify characteristics that provide stable microclimatic conditions and/ or protection from predators (e.g. Fernández and Palomares 2000; Lutermann et al. 2010; Ross et al. 2010; Maziarz and Wesolowski 2013; Amat-Valero et al. 2014), while some have also suggested that proximity to suitable foraging habitat is a factor in the den site selection process (Henner et al. 2004). Dens that provide protection from adverse weather conditions and predators are likely to be particularly important for species that rely on recruitment success for population growth, as altricial juveniles in dens are more susceptible to mortality than adults (Serena and Soderquist 1989; Lutermann et al. 2010).

Given the importance of available suitable den sites to population viability, understanding the characteristics of selected den sites can be extremely beneficial in identifying high quality habitat, improving habitat quality, and planning for rehabilitation. Studies such as McGregor et al. (2014) have studied den use by dasyurids to recommend a higher proportion of log microhabitats be provided in rehabilitated areas. Alternatively, studies such as Saunders et al. (2014) have demonstrated the success of artificial nesting habitat that replicates natural nesting microhabitats and can be used to increase the reproductive output of an area. Therefore, studies on den site use may have direct and practical applications to species management and recovery.

1.4 THIS STUDY

Prior to European settlement, quolls occurred across most of Australia, including many of its offshore islands (Jones et al. 2014). However, out of the four largely carnivorous species, one has disappeared from the mainland (eastern quoll) and the remaining three have undergone significant range retractions and population declines (Woinarski et al. 2014). The processes driving these declines are numerous and often interact to compound impacts (Johnson 2006; Jones et al. 2014). In recent times the northern quoll (*Dasyurus hallucatus*), previously regarded as the most secure carnivorous marsupial given its large northern-tropical distribution across relatively intact landscapes, has suffered local population extinctions as a result of altered fire regimes, habitat loss and modification, impacts from introduced predators and predation on the invasive and toxic cane toad *Rhinella marinus* (Oakwood 2004; O'Donnell et al. 2010). Consequently, northern quolls now exist as several disjunct populations on the mainland and on several islands (How et al. 2009). In the near future, cane toads are projected to spread over the remainder of the northern quoll's range in Western Australia (Hill and Ward 2010). Aside from the current and future threat posed by the cane toad, the relatively recent and rapid growth of the resource sector has had an increasing level of impact to northern quoll habitat.

A detailed review of the current knowledge of the northern quoll is provided in Chapter 2. The northern quoll has declined across most of its range in Queensland and the Northern Territory (Hill and Ward 2010). Relatively intact populations still exist in the Kimberley and Pilbara regions of Western Australia; however, several of these populations occur in close proximity to mining operations (DPaW 2013). One such population occurs on Koolan Island in the Kimberley region of Western Australia. Mining has occurred on the island intermittently since the early 1900's, nevertheless large areas of the island are relatively undisturbed and northern quolls appear to occur on the island at densities greater than those that have been reported for other populations (Spencer et al. 2017). The high abundance of northern quolls combined with a disturbance gradient from highly disturbed mining pits to undisturbed woodlands and rocky outcrops provides a valuable opportunity to study how these factors influence population size, habitat use and diet.

This thesis aims to fill an important gap in the current knowledge of the population dynamics and resource use of the northern quoll. This in turn will contribute to the conservation management of the species both on islands and the mainland, and provide much-needed data that can contribute to the management of habitat to maintain populations of the northern quoll in modified landscapes, including land under rehabilitation, across the species' range. This study also addresses the need to further understand how biodiversity values relating to fauna can be integrated into rehabilitation processes. The findings of this study will contribute to the management of generalist predators worldwide that exist in modified landscapes or are subject to conflict with humans and anthropogenic land uses.

1.5 THESIS OUTLINE

Each chapter of this thesis is written as a standalone research journal article. Each chapter contributes towards the common goal of this thesis; to better understand the underlying population dynamics and resource use of the northern quoll *Dasyurus hallucatus* in an area modified by anthropogenic activity (mining) but not subject to other decline drivers such as predators, cane toad, or altered fire regimes present on the nearby mainland. Research topics were chosen based on the data available for the species at the inception of candidature, and the need for data to inform pertinent decision-making regarding the management of this species in and around modified areas. By structuring the thesis in this way, we are able to answer targeted questions that increased our understanding of the northern quoll's underlying biology and response to anthropogenic land use, and direct focus to future research areas.

Briefly, the chapters are as follows:

Chapter 2: A synthesis of the literature regarding the biology and ecology of the northern quoll (*Dasyurus hallucatus*)

This chapter synthesises the published literature on the range, distribution, ecology and biology of the northern quoll including a discussion on its semelparous life history and current gaps in the literature.

Chapter 3: Analysis of mine site monitoring data using spatial and non-spatial capture recapture models reveals the population dynamics of an endangered marsupial

This chapter uses a dataset typical of species monitoring programs in Australia undertaken for the purpose of legislative reporting, and demonstrates how this information can be maximised to gain insight into the population dynamics of endangered species. Given the widespread practice of species monitoring in accordance with development approvals for habitat modification, this study has implications for how we look at an under-utilised data-source across the country. The study also has important considerations for developing monitoring programs going forward, to minimise difficulties in modelling those datasets.

The data are important as it is the first to clearly demonstrate that northern quoll populations oscillate over time, and focuses on the conservation value of islands in providing long-term security for threatened species.

Chapter 4: The influence of season and habitat on the diet of an insular population of endangered marsupial

This study provides the first in-depth study of diet of the northern quoll in the Kimberley region of Western Australia and of an island population of this species. Understanding the importance of various prey items in a disturbed environment can also support informed species conservation during all stages of development. In habitats modified by anthropogenic land uses, fauna have the potential to become habituated to artificial environments, and as a result, reliant on the associated resources they provide. Understanding if and/or how the northern quoll uses novel food sources can identify beneficial and detrimental resource use so that negative interactions between northern quolls and anthropogenic land uses are minimised.

The findings of this study will contribute to the ongoing conservation of the northern quoll in identifying suitable relocation and translocation sites. It will also assist in identifying completion criteria for rehabilitation activities that aim to support this species.

Chapter 5: Nursery den site selection by the northern quoll (*Dasyurus hallucatus*)

This study is the first of its kind in Australia for northern quolls of the wet-dry tropics. The study will enable us to understand if and/or how micro-climate and habitat characteristics influence den site selection.

This chapter is complementary to Chapter 4 in identifying the characteristics of northern quoll habitat that contribute to their ongoing persistence in an area, whether that be native, modified or rehabilitated.

Chapter 6: General discussion

This chapter synthesises the findings of this thesis to provide a general discussion of population dynamics and resource use by the northern quoll in and around modified habitat. The data presented in this thesis are then used to discuss management implications for this species both on Koolan Island and in similar environments.

The outcomes of this thesis include the incorporation of its findings into the adaptive management framework for the northern quoll on Koolan Island, including objectives for rehabilitation as described in the mine closure plan for the island. The findings can also be applied to other populations of this species across its range, especially in island and insular environments, and may assist managers in predicting the effects of habitat disturbance on populations of the northern quoll.

1.6 REFERENCES

Addison, P. F. E., Flander, L. B., & Cook, C. N. (2015). Are we missing the boat? Current uses of long-term biological monitoring data in the evaluation and management of marine protected areas. *Journal of Environmental Management*, *149*, 148-156.

Amat-Valero, M., Calero-Torralbo, M. A., Václav, R., & Valera, F. (2014). Cavity types and microclimate: implications for ecological, evolutionary, and conservation studies. *International Journal of Biometeorology*, *58*, 1983-1994.

Australian Bureau of Agricultural and Resource Economics (ABARES) (2018) *Land use in Australia – at a glance*. Retrieved from http://www.agriculture.gov.au/abares/aclump/land-use.

Bain, K., Wayne, A., & Bencini, R. (2014). Overcoming the challenges of measuring the abundance of a cryptic macropod: Is a qualitative approach good enough? *Wildlife Research, 41*, 84.

Biggins, D. E., Miller, B. J., Hanebury, L. R., Oakleaf, B., Farmer, A. H., Crete, R., & Dood, A. (1993). A technique for evaluating black-footed ferret habitat. *Management of prairie dog complexes for the reintroduction of the black-footed ferret.* US Fish and Wildlife Service Biological Report, 13, 73-88.

Biggins, D. E., Godbey, J. L., Matchett, M. R., & Livieri, T. M. (2006). Habitat preferences and intraspecific competition in black-footed ferrets. *Recovery of the black-footed ferret–progress and continuing challenges*. U.S. Geological Survey Scientific Investigations Report 2005–5293, Washington, D.C., USA.

Boyles, J.G., & Storm, J.J. (2007). The perils of picky eating: dietary breadth is related to extinction risk in insectivorous bats. PLoS ONE, 2, e672.

Brigatti, E., Vieira, M. V., Kajin, M., Almeida, P. J. A. L., De Menezes, M. A., & Cerqueira, R. (2016). Detecting and modelling delayed density-dependence in abundance time series of a small mammal (*Didelphis aurita*). *Scientific Reports, 6*, 19553.

Carter, A., Luck, G. W., & Wilson, B. P. (2012). Ecology of the red fox (*Vulpes vulpes*) in an agricultural landscape. 1. Den-site selection. *Australian Mammalogy*, *34*, 145-154.

Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, *114*, E6089-E6096.

Costello, M. J., & Wieczorek, J. (2014). Best practice for biodiversity data management and publication. *Biological Conservation*, *173*, 68-73.

Darimont, C. T., Paquet, P. C., & Reimchen, T. E. (2009). Landscape heterogeneity and marine subsidy generate extensive intrapopulation niche diversity in a large terrestrial vertebrate. *Journal of Animal Ecology*, *78*, 126-133.

Department of Parks and Wildlife (DPaW) (2013). *Pilbara northern quoll regional monitoring guidelines*. Department of Parks and Wildlife, Perth.

DeYoung, R. W., Hellgren, E. C., Fulbright, T. E., Robbins, W. F., & Humphreys, I. D. (2000). Modeling nutritional carrying capacity for translocated desert bighorn sheep in western Texas. *Restoration Ecology, 8*, 57-65.

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

Environmental Law Alliance Worldwide (2010). Guidebook for evaluating mining project EIAs. *Environmental Law Alliance Worldwide, Eugene, Oregon*.

Fernández, N., & Palomares, F. (2000). The selection of breeding dens by the endangered Iberian lynx (Lynx pardinus): implications for its conservation. *Biological Conservation*, *94*, 51-61.

Firth, R.S.C., Woinarski, J.C.Z., Brennan, K.G., & Hempel, C. (2006) Environmental relationships of the brush-tailed rabbit-rat *Conilurus penicillatus* and other small mammals on the Tiwi Islands, northern Australia. *Journal of Biogeography, 33,*1820–1837.

Fisher, D.O., Johnson, C.N., Lawes, M.J., Fritz, S.A., McCallum, H., Blomberg, S.P., VanDerWal, J., Abbott, B., Frank, A., Legge, S. and Letnic, M. (2014). The current decline of tropical marsupials in Australia: is history repeating?. *Global Ecology and Biogeography*, *23*, 181-190.

Fitzsimons, J., Legge S., Traill B., Woinarski J. (2010) *Into Oblivion? The disappearing native mammals of Northern Australia*. The Nature Conservancy, Melbourne.

Garnett, S. T., Woinarski, J. C., Crowley, G. M., & Kutt, A. S. (2010). *Biodiversity conservation in Australian tropical rangelands* (pp. 191-234). Wiley-Blackwell: Chichester, UK.

Geoscience Australia. (2018). Minerals Basics. Geoscience Australia, Canberra. Retrieved from http://www.ga.gov.au/minerals/basics.html.

Hancock, P. (1993). *Green & Gold: Sustaining mineral wealth, Australians and their environment*. Centre for Resource and Environmental Studies, Australian National University.

Henner, C. M., Chamberlain, M. J., Leopold, B. D., & Burger Jr, L. W. (2004). A multi-resolution assessment of raccoon den selection. *The Journal of wildlife management*, *68*, 179-187.

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.

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.

IUCN. (2013). The IUCN Red List of Threatened Species. Version 2013.2. Retrieved from http://www.iucnredlist.org.

Jachowski, D. S. (2007). *Resource selection by Black-footed Ferrets in relation to the spatial distribution of prairie dogs*. University of Missouri (M.S. Thesis), Columbia, Missouri, USA.

Johnson, C. (2006). *Australia's mammal extinctions: a 50000 year history* (pp. 1-278). Cambridge University Press.

Johnson, C. J., & St-Laurent, M. H. (2011). Unifying framework for understanding impacts of human developments on wildlife. In *Energy development and wildlife conservation in Western North America* (pp. 27-54). Island Press, Washington, DC.

Jones, C. G., & Owadally, A. W. (1985). The status ecology and conservation of the Mauritius kestrel. *Conservation Studies on Raptors*, *211*, 222.

Jones, C. G., & Owadally, A. W. (1988). The life histories and conservation of the Mauritius kestrel Falco punctatus, pink pigeon Columba mayeri and echo parakeet Psittacula eques. *Proceedings of the Royal Society of Arts and Sciences of Mauritius*, *5*, 79-130.

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. *Carnivores of Australia (A. S. Glen and CR Dickman, eds.). CSIRO Publishing, Collingwood, Victoria, Australia*, 197-240.

Karanth, K. U., Nichols, J. D., Kumar, N. S., & Hines, J. E. (2006). Assessing tiger population dynamics using photographic capture–recapture sampling. *Ecology*, *87*, 2925-2937.

Kersting, D. K., & García-March, J. R. (2017). Long-term assessment of recruitment, early stages and population dynamics of the endangered Mediterranean fan mussel *Pinna nobilis* in the Columbretes Islands (NW Mediterranean). *Marine environmental research*, *130*, 282-292.

Kinley, T. A., & Newhouse, N. J. (2008). Ecology and translocation-aided recovery of an endangered badger population. *The Journal of Wildlife Management*, *72*, 113-122.

Krebs, C. J. (1991). The experimental paradigm and long-term population studies. *Ibis*, *133*, 3-8.

Lesmeister, D. B., Gompper, M. E., & Millspaugh, J. J. (2008). Summer resting and den site selection by eastern spotted skunks (*Spilogale putorius*) in Arkansas. *Journal of Mammalogy*, *89*, 1512-1520.

Lollback, G. W., Mebberson, R., Evans, N., Shuker, J. D., & Hero, J. M. (2015). Estimating the abundance of the bilby (Macrotis lagotis): a vulnerable, uncommon, nocturnal marsupial. *Australian Mammalogy*, *37*, 75-85.

Lowry, H., Lill, A., & Wong, B. (2013). Behavioural responses of wildlife to urban environments. *Biological Reviews*, *88*, 537-549.

Luce, R. J. (2004, January). Areas where habitat characteristics could be evaluated to identify potential black-footed ferret reintroduction sites and develop conservation partnerships. In Roelle, J. E., Miller, B. J., Godbey, J. L. &

Biggins, D. E. (eds) *Recovery of the Blackfooted Ferret – progress and continuing challenges.* U.S. Geological Survey Scientific Investigations Report 2005-5293, Washington, D.C., USA.

Lundholm, J. T., & Richardson, P. J. (2010). Mini-Review: Habitat analogues for reconciliation ecology in urban and industrial environments. *Journal of Applied Ecology*, *47*, 966-975.

Lutermann, H., Verburgt, L., & Rendigs, A. (2010). Resting and nesting in a small mammal: sleeping sites as a limiting resource for female grey mouse lemurs. *Animal Behaviour, 79*, 1211-1219.

Maziarz, M., & Wesołowski, T. (2013). Microclimate of tree cavities used by Great Tits (Parus major) in a primeval forest. *Avian Biology Research, 6*, 47-56.

McDonald, L. L., Erickson, W. P., Boyce, M. S., & Alldredge, J. R. (2012). Modeling vertebrate use of terrestrial resources. *The wildlife techniques manual, 1*, 410-429.

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

McKelvey, D. S. (1977). The Mauritius kestrel some notes on its breeding biology behaviour and survival potential. *Hawk Trust Annual Report, 8*, 19-21.

Newbold, T., Hudson, L.N., Hill, S.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B. and Day, J. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, *520*, 45.

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

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.

Oakwood M. (2004). *The effect of cane toads on a marsupial carnivore, the northern quoll, Dasyurus hallucatus*. Report to Parks Australia.

Richardson, L., Clark, T. W., Forrest, S. C., & Campbell, T. M. (1987). Winter ecology of black-footed ferrets (*Mustela nigripes*) at Meeteetse, Wyoming. *The American Midland Naturalist, 117*(2), 225-239.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P. and Schmitz, O.J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, 343, 1241484.

Ross, S., Kamnitzer, R., Munkhtsog, B., & Harris, S. (2010). Den-site selection is critical for Pallas's cats (Otocolobus manul). *Canadian Journal of Zoology, 88,* 905-913.

Saunders, D.A., Dawson, R., Doley, A., Lauri, J., Le Souef, A., Mawson, P., Warren, K. and White, N. (2014). Nature conservation on agricultural land: a case study of the endangered Carnaby's Cockatoo *Calyptorhynchus latirostris* breeding at Koobabbie in the northern wheatbelt of Western Australia. *Nature Conservation, 9,* 19-43.

Serena, M. & Soderquist, T. R. (1989). Nursery dens of Dasyurus geoffroii (Marsupialia: Dasyuridae), with notes on nest building behaviour. *Australian Mammal Society, 12*, 35-36.

Southgate, R., Palmer, C., Adams, M., Masters, P., Triggs, B., & Woinarski, J. (1996) Population and habitat characteristics of the Golden Bandicoot (*Isoodon auratus*) on Marchinbar Island, Northern Territory. *Wildlife Research, 23,* 647–664.

Spencer, P. B., Sandover, S., Nihill, K., Wale, C. H., How, R. A., & 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.

Stannard, H. J., Caton, W., & Old, J. M. (2010). The diet of red-tailed phascogales in a trial translocation at Alice Springs Desert Park, Northern Territory, Australia. *Journal of Zoology*, *280*, 326-331.

Temple, S. A. (1977). The status and conservation of endemic kestrels on Indian Ocean islands. In *World Conference on Birds of Prey, Vienna, 1-3 October 1975: Report on Proceedings* (pp. 74-81).

Vernes, K., Freeman, M., & Nesbitt, B. (2009). Estimating the density of free-ranging wild horses in rugged gorges using a photographic mark–recapture technique. *Wildlife Research, 36*, 361-367.

Woinarski, J.C.Z. (2000) The conservation status of rodents in the monsoonal tropics of the Northern Territory. *Wildlife Research, 27,* 421–435.

Woinarski, J.C.Z., Palmer, C., Fisher, A., Southgate, R., Masters, P., & Brennan, K. (1999) Distributional patterning of mammals on the Wessel and English Company islands, Arnhem Land, Northern Territory, Australia. *Australian Journal of Zoology, 47*, 87–111.

Woinarski, J.C.Z., Mackey, B., Nix, H., & Traill, B. (2007) The Nature of Northern Australia: natural values, ecological processes and future prospects. *ANU e-press*, Canberra.

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 (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., Legge, S., Fitzsimons, J. A., Traill, B. J., Burbidge, A. A., Fisher, A., Firth, R.S., Gordon, I. J., Griffiths, A.D., Johnson, C.H. & McKenzie, N.L. (2011). The disappearing mammal fauna of northern Australia: context, cause, and response. *Conservation Letters*, 4, 192-201.

Woinarski, J., Burbidge, A., & Harrison, P. (2014). Action Plan for Australian Mammals 2012. CSIRO Publishing, Melbourne.

Woinarski, J.C., 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*, pp.4531-4540.

World Bank and the International Finance Corporation (2002). *Mining and Development, It's Not Over When It's Over: Mine Closure Around the World*. International Finance Corporation, Washington, DC.

Chapter 2: A synthesis of the literature regarding the biology and ecology of the northern quoll (*Dasyurus hallucatus*)

2.1 INTRODUCTION

Australia has one of the most unique mammal assemblages, with up to 87% of Australia’s terrestrial mammal fauna occurring nowhere else in the world (Woinarski et al. 2015). Unfortunately, over the last 200 years Australia has also had the highest rate of mammal extinctions, with the extinction of more than 10% of the country’s endemic terrestrial mammal species (Woinarski et al. 2015). This is a startling statistic when one considers that since European settlement only one species of terrestrial mammal has gone extinct in North America (Woinarski et al. 2015), which is a larger country, has ~15x the human population and experienced European colonization 300+ years earlier (Flannery 2002). Extinctions and declines in Australia have been greatest in small to medium species (50-1500g critical weight range) inhabiting the more arid parts of the continent (Short and Turner 1994; McKenzie et al. 2007) with recent evidence suggesting this is now occurring in tropical Australia as well (Fitzsimons et al. 2010; Wionarski et al. 2011).

Factors that may increase the susceptibility of Australian mammals to anthropogenic impacts associated with European settlement include the existence of an ancient landscape with highly weathered, nutrient-poor soils and long-term climate stability that has promoted persistence in place over dispersal, thereby leading to the development of species poorly adapted to changes in land use (Jones et al. 2003). Furthermore, unlike North America where species of canids and felids occur naturally, Australian species did not co-evolve with predators similar to the introduced fox (*Vulpes vulpes*) and cat (*Felis catus*), and are therefore highly susceptible to predation by these species (Jones et al. 2003). A loss of mammal taxa at all trophic levels across Australia has likely impacts for ecosystem function by altering or affecting fire regimes, decomposition, soil properties, species dispersal, and interspecific interactions such as predation and competition (Glen and Dickman 2005; Letnic and Koch 2010; Fleming et al. 2014).

There is increasing global awareness of the important role that predatory species play in ecosystem function (Terborgh et al. 2001; Sergio et al. 2005; Ripple et al. 2014). Predator species also exert an influence upon the abundance and resource use of other predator species. The restoration of grey wolf to Yellowstone National Park in the United States and subsequent shifts towards historic conditions across a range of trophic levels illustrates the importance of native predators through competition and intraguild predation (Berger et al. 2008). This in turn has flow-on effects to their prey, with the potential to influence the cover and structure of vegetation communities (Ripple and Beschta 2004).

Australia has the world's most diverse assemblage of marsupial carnivores (Jones et al. 2014). Like placental carnivores, marsupial carnivores can occupy top trophic levels in ecosystems (Purvis et al. 2001). Marsupial predators occur at lower numbers than their prey, and often require the use of large areas in order to acquire sufficient food resources (Jones et al. 2014). In addition, the lifespan of these species is short (frequently one to two years), and they are therefore highly susceptible to introduced threats that combine with the pre-existing effects of environmental and demographic stochasticity on mortality and recruitment (Lee and Cockburn 1985;

Jones et al. 2014). Of the six species for which other animals comprise a substantial portion of their diet, one has become extinct (Tasmanian tiger; *Thylacinus cynocephalus*), and the others have suffered human-induced declines in range and abundance (Burnett 2001). Should Australia lose additional marsupial predators, their absence may lead to further extinctions as invasive predators are released from competitive suppression (Johnson 2014).

The genus *Dasyurus* (commonly referred to as quolls) includes six species, four of which are endemic to Australia (Van Dyck and Strahan 2008). Prior to European settlement, these species potentially occupied the niche of top order predator in many ecosystems, however over the last 200 years all have undergone substantial reductions in range and abundance (Burnett 2001). The eastern quoll (*Dasyurus viverrinus*) is believed to be extinct on the mainland and is now found only in Tasmania, the spotted-tail quoll (*Dasyurus maculatus*) has declined from parts of its former range in Victoria (Belcher and Darrant 2006), and the chuditch (*Dasyurus geoffroii*) was once found in over 70% of mainland Australia but is now restricted to a small pocket in south-western Australia (Serena et al. 1991; Burbidge and Eisenberg 2006). The study species of this thesis, the northern quoll (*Dasyurus hallucatus*), once occupied a range of habitats across northern Australia and is now restricted to several disjunct populations within Queensland, the Northern Territory, and the Kimberley and Pilbara regions of Western Australia (How et al. 2009).

How et al. (2009) suggest that the northern quoll is a top-order predator in many ecosystems, and is therefore an important regulator of species at lower trophic levels. Subsequently, impacts to populations of the northern quoll could potentially affect the function of entire ecosystems. Due to the combined effects of predation by feral cats and altered fire regimes (Begg 1981; Braithwaite 1996; Oakwood 2000, Oakwood and Foster 2008; Woinarski et al. 2001) over the last century, the northern quoll has declined over the eastern and central parts of its former range and is now absent in many areas within northern Queensland and the Northern Territory (Braithwaite and Griffiths 1994; Oakwood 1997). More recently, as a result of its propensity to prey upon anurans, the spread of the toxic cane toad *Rhinella marinus* is believed to have hastened the northern quoll's decline in many areas (Burnett 1997; Oakwood 2004; Oakwood and Foster 2008).

This chapter will synthesise the literature relating to the biology of the northern quoll, in order to identify aspects of the species' life history and ecology that may make it susceptible to decline under certain disturbance regimes. Secondly, the existing research will be examined in order to identify any knowledge gaps that might inform future research, while also considering the logistical constraints that must be overcome when studying the northern quoll.

2.2 LIFE HISTORY

The key aspects of an organism's life cycle include birth, survival (death), mating and reproduction. Unsurprisingly, these key life history traits are subject to intense natural selection, and many diverse strategies have evolved that maximise reproductive fitness including differential lifespan, fecundity and age to sexual maturity (Stearns 1989). However, it is important to note that life history traits seldom evolve in isolation, such that trade-offs occur when one trait increases at the consequence of another (Stearns 1989). Dasyurids have a range of life history strategies along a spectrum of semelparous (death following a single reproductive event) to iteroparous (species that may reproduce multiple times in their lifetime), based on the frequency of oestrus, age of sexual maturity, seasonality of breeding, and the duration and time of male reproductive effort (Lee et al. 1982). The northern quoll is often referred to as a 'Strategy 1' species, being mono-oestrous, maturing at 11 months of age and subject to a male die-off shortly after their first mating season (Dickman and Vieria 2012).

This review will use the term 'life history' as defined by Stearns (1992), who defined life history to include the "key events in an organism's lifetime that are moulded by natural selection to increase the number of offspring produced that survive to reproduction". These key events, often referred to as life history traits or components, refers to the age at first reproduction, the number of times an individual reproduces, the number of offspring produced per litter, and life expectancy (Dickman and Vieira 2012).

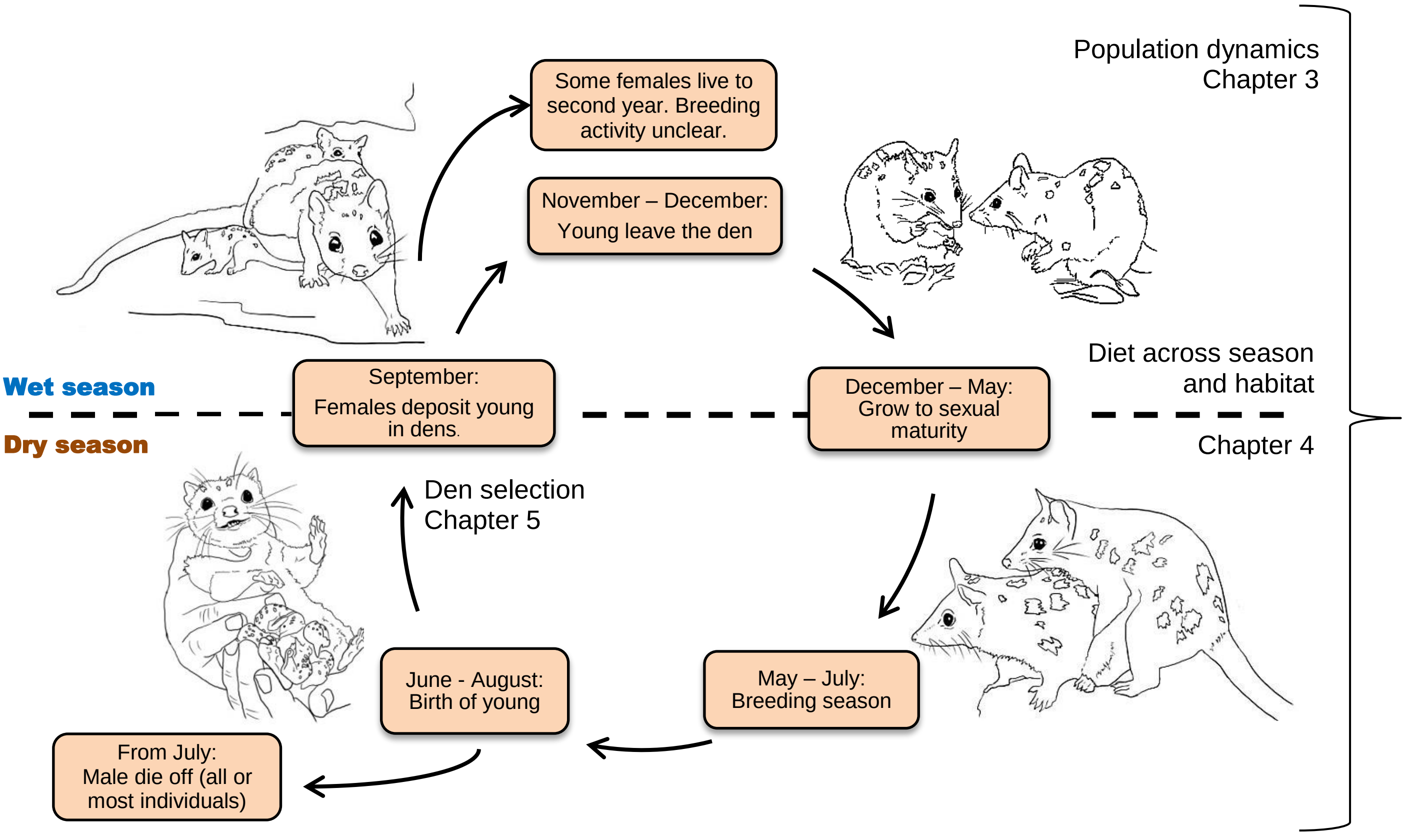


Figure 2.1. Life history of the northern quoll *Dasyurus hallucatus*, with reference to data chapters in this thesis. As detailed in Section 2.2, the timing associated with each life history stage vary across this species' range.

2.2.1 Mating

Female northern quolls are physiologically polyoestrus, but functionally mono-oestrus (one oestrus cycle per year), and reproductive events are highly synchronised within populations (Oakwood 2000). However, the timing of reproductive events such as the onset of mating and subsequent births can vary across years within a population, and geographically between populations (Oakwood 2000; Nelson and Gemmell 2003). For example, mating has been observed between late May to early June at Kapalga Research Station N.T. (Oakwood 2000) and between late July and August on the Mitchell Plateau, Kimberley W.A. (Schmitt et al. 1989) (Figure 2.1). Based on the age of wounds on the scapular region of females (presumably caused by males during mating), Oakwood (2000) suggested that most mating occurs within a two-week period. The rate of change of photoperiod has been observed to influence the onset of reproductive behaviour in several species of small dasyurids belonging to the *Antechinus stuartii- A. flavipes* complex in eastern Australia (McAllen et al. 2006). Although mating across quoll species coincides with some of the shortest photoperiods of the year, and when photoperiodic change is the least (McAllen 2003), Oakwood (2000) and Nelson and Gemmell (2003) suggest that there are additional cues other than photoperiod that initiate reproduction in northern quolls.

Throughout the mating period, females may be visited by as many as four males per night (Oakwood 2002). These males travel large distances to visit multiple females within a few days, presumably to determine their reproductive status (Oakwood 2002). Litters of the closely related spotted-tail quoll are known to be fathered by more than one male, and males have been observed to sire offspring in more than one litter by separate females (Glen et al. 2009). Based on the roving strategy exhibited by male northern quolls during the mating period (Oakwood 2002) it is possible that multiple paternity exists in this species as well, however it is yet to be determined.

2.2.2 Reproduction

The gestation period in northern quolls is believed to be between 21-25 days (Aitken et al. 1996). Depending on geographic location, births occur between mid to late June and August (Braithwaite and Griffiths 1994; Begg 1981; Dixon and Huxley 1985; Schmitt et al. 1989; Oakwood 1997; 2000) (Figure 2.1). The latest births were recorded in September by King and King (1989) within a population on the Fortescue River in the Pilbara region of Western Australia. At any given locality all female quolls give birth within a few weeks (Nelson and Gemmell 2003), and the majority of females within a population appear to breed within a given year. For example, Begg (1981) reported that 91% of females that were trapped in July had pouched young.

Females have been observed to reproduce over two successive years (Dickman and Braithwaite 1992; Oakwood 2000; Spencer et al. 2010). One female was observed to live for three years, but did not reproduce in her third season and was later found dead (Spencer et al. 2010). Females produce an average of six young (Begg 1981), with some litters exceeding the number of teats (usually eight) a female possesses. For example, Nelson and Gemmell (2003) reported between six and seventeen young at birth within a sample of female quolls. When the pouches were examined 12 hours later, the number of young had decreased to eight in five individuals, and as few as six in another.

From birth, northern quoll juveniles are altricial, depending on the mother for up to six months (Oakwood 1997). Females carry young in the pouch for between 60 - 70 days (Begg 1981; Oakwood 2002). In most populations, pouched young are deposited in a den from mid-late August to mid-September at approximately nine weeks of age (Begg 1981; Schmitt 1989; Oakwood 1997; Oakwood 2000). During this time, the young are left in a succession of nursery dens while the mother forages at night (Oakwood 2000; 2002). Although it has not been assessed directly, juvenile mortality appears to be highest during the period when young are left in the den (Begg 1981; Oakwood 2000). For example, Oakwood (2000) estimated juvenile mortality to be approximately 62%, or as high as 72% if the impacts of maternal mortality are considered.

Independent young are first observed in November, weighing between 100 to 150 grams (Braithwaite and Griffiths 1994) (Figure 2.1). However, Oakwood (1997) observed enlarged teats on females for a further four weeks, suggesting that young may continue to suckle for up to one month after leaving the den.

2.2.3 Post-mating male mortality

For reasons not yet confirmed, a number of dasyurids experience post-mating male mortality. A single spermatogenic wave prior to a highly synchronised and brief mating period followed by complete male die-off has been found to occur in all species of antechinus (Woolley 1966), both species of phascogale (Bradley 1997; Mills et al 1999) and the little red kaluta (*Dasykaluta rosamondae*; Woolley 1991), all of which are members of the subfamily Dasyurinae (Tyndale-Biscoe 2005). However, of the four quoll species that occur in Australia, three show no evidence of this phenomenon. Interestingly, the northern quoll exhibits a high instance of post-mating male mortality, with complete post-mating die-off being observed in at least one population (Dickman and Braithwaite 1992; Oakwood 1997; Oakwood et al. 2001). Dickman and Braithwaite (1992) first observed this phenomenon in a population of the northern quoll inhabiting lowland savanna at the Kapalga research station in the Northern Territory. Based on mark-recapture data collected between 1985 and 1987, no marked males were thought to have survived through to a second breeding season. Further investigation of the Kapalga population utilising both trapping and radio-telemetry methods confirmed complete male die-off for this population (Oakwood 1997; 2000; Oakwood et al. 2001; Oakwood 2002). Oakwood (1997) found that most males died within two weeks after the mating season in late May to early July. Although complete post-mating male die-off has not been observed in all studied populations, males consistently undergo a period of physical decline during the mating period including a considerable loss of weight, loss of fur, increased parasite load and the presence of wounds (Begg 1981; Schmitt et al. 1989; Oakwood et al. 2001).

The northern quoll appears to differ in the terminal physiological and pathological changes that have been reported in the smaller species of dasyurid that experience post-mating mortality. For instance, in species of *Antechinus* and *Phascogale*, the proximate cause of death is believed to be an elevation of stress hormones (cortisol) that converts protein into energy but also leads to a suppression of immune and inflammatory systems, and consequently leads to haemorrhage from stress induced gastric ulceration (Bradley 2003). In contrast, Oakwood et al. (2001) found no evidence of elevated cortisol levels in a study population of the northern quoll during the breeding season. Furthermore, post-mortem examination of road-killed males conducted at this time found no evidence of gastric ulceration, and the proximate cause of death for most males found deceased during telemetry studies was motor vehicles and predation. Moreover, unlike other dasyurid species that experience spermatogenic failure (such that sperm production ceases before the mating season), the northern quoll continues to produce sperm throughout the breeding season, and potentially into a second year of life (Oakwood et al. 2001). Based on these findings the physical decline in condition is consistent with what has been observed for other dasyurids; however, the proximate cause and physiological mechanism that leads to death appears to differ.

2.2.4 Hypotheses for the evolution of semelparity

Six hypotheses have been proposed to explain why semelparity occurs within small insectivorous marsupials. The first suggests that semelparity has evolved in response to pre-existing biological and environmental conditions (Braithwaite and Lee 1979; Tyndale-Biscoe 2005). Tyndale-Biscoe (2005) proposes that the long lactation period experienced by marsupials limits females to one litter per season, and that the production of offspring must occur within a constrained time period so that energetically demanding activities such as lactation and weaning coincide with the time of year when adequate food resources are available (wet season). Furthermore, environmental causes of mortality are rife in small mammals, and males are not always likely to survive for more than one year (Tyndale-Biscoe 2005). Therefore, this strategy may have evolved in northern quolls so that males can maximise their reproductive potential within a limited timeframe.

The second hypothesis suggests that an ancestor of the northern quoll may have at one time developed semelparity as an adaptation to environmental conditions or biological traits that are no longer relevant, and are as such phylogenetically predisposed to this life history attribute (Oakwood et al. 2001). In contrast, other authors have suggested that semelparity is a consequence of the accumulation of deleterious and fatal mutations following breeding (Humphries and Stevens 2001), and that extreme male promiscuity has evolved to counterbalance a poor survival rate of breeding females, therefore increasing the chances that genes will be passed on to the next generation of offspring even if one or more females do not survive (Kraaijeveld et al. 2003). The fifth and final hypothesis has been advanced by a number of authors, including Braithwaite and Lee (1979), Diamond (1982) and Green et al. (1991), and suggests that annual male die-off prevents competition with the next generation of individuals. However, this altruistic adaptation has not been suggested by more recent studies, and may be the least plausible of the five hypotheses in light of successive research.

A recent paper by Fisher et al. (2013) suggests that sperm competition has driven the evolution of semelparity in dasyurids. The study showed that marsupial predators with a shorter breeding season correlated with a greater seasonal predictability of prey abundance, and that the last month of lactation or weaning was associated with the month in which prey abundance was greatest. This high seasonal influence is proposed to have led to the selection of shorter annual breeding seasons, as females acquire fitness benefits by timing lactation and weaning to coincide with maximum food abundance. A brief mating season increases male competition for females, and intensifies the level of sperm competition between males.

While sperm competition may have led to the evolution of semelparity in ancestral dasyurids, and may have fitness benefits for several of the smaller dasyurid species, a number of inherent biological traits of the northern quoll challenge the plausibility of this hypothesis. For instance, the northern quoll does not undergo spermatogenic failure prior to the mating season (Oakwood et al. 2001), which suggests that they may have the potential to breed in a second season. Secondly, while other dasyurids have increased levels of cortisol to turn protein into energy at the expense of the individual's longevity, male northern quolls do not have increased levels of cortisol during the mating season (Oakwood et al. 2001). Furthermore, incomplete post-mating male die-off observed in most populations of northern quoll (e.g. Schmitt et al. 1989; Spencer et al. 2010; Cook 2010) instead adds weight to the hypothesis proposed by Oakwood et al. (2001), suggesting that this species is subject to 'ancestral baggage', or a phylogenetic predisposition to a semelparous life history. However, there are still many aspects that require clarification, and further research regarding the potential of males that survive to another mating season to sire offspring is still required to advance the debate.

2.3 MOVEMENT AND HABITAT USE

2.3.1 Habitat use

Sufficient resources such as food and habitat are essential for the maintenance and growth of animal populations (Manly et al. 2007). Therefore, identifying key resources and understanding their importance is vital for the management of threatened species such as the northern quoll. Habitat can be defined as “an area with a combination of resources (e.g. food, water, cover) and environmental conditions (temperature, precipitation, presence or absence of predators and competitors) that promotes occupancy by individuals of a given species (or population) and allows individuals to survive and reproduce” (Morrison et al 2006). Northern quolls appear to be habitat generalists; they have been observed to use a number of different habitat types, including woodland, forest, vine thickets, mangroves and rocky hills in the form of mesas, plateaus and granite boulder fields (Oakwood 1997; Pollock 1999). In addition, they have been noted to use anthropogenically modified environments, including rural and urban areas, and mine sites (Pollock 1999; DPaW 2013). For example, a telemetry study conducted by DPaW (2013) in the Pilbara region of

Western Australia observed individuals moving in and out of multiple habitats, including human infrastructures such as a workshop and a quarry. Further, a mark-recapture study conducted on the same population in the Pilbara region found that northern quolls were more abundant in disturbed areas than in undisturbed areas (DPaW 2013). The authors suggested that excavation of the area, which resulted in pools of permanent water and complex rock piles, created a greater number of microhabitats. This in turn is thought to have increased floristic diversity and productivity compared to the undisturbed habitat, resulting in greater prey density or diversity and producing higher quality foraging habitat (DPaW 2013).

Several authors have suggested a relationship between the presence of northern quolls and sources of permanent fresh water (Braithwaite and Griffiths 1994; Pollock 1999). For example, 57% of records examined by Pollock (1999) from the Mackay-Bowen area between 1994 and 1996 were within 200 metres of permanent fresh water. In addition, Braithwaite and Griffiths (1994) observed a relationship between the teat length of females and scrotum width of males and proximity to water, which they suggest indicated a preference of these areas by reproductive individuals. However, the species is also known to persist on islands in the Kimberley and Pilbara regions where permanent water is absent, and a study of northern quolls in Kakadu National Park, Northern Territory by Oakwood (2002) did not observe a similar trend.

The importance of rocky habitats in the wet dry tropics as areas of mammalian diversity and endemism has been noted previously (e.g. Freeland et al. 1988). Likewise, there is evidence to suggest that rocky habitats support denser populations of northern quolls than other habitats that have been studied. For example, Braithwaite and Griffiths (1994) reported mean capture rates per 100 trap nights of between 0.6 and 1.3 northern quolls for lowland savannah habitat in Kakadu National Park, whereas Begg (1981) and Schmitt et al. (1989) recorded a rate of 1.9 and 1.6 northern quolls per 100 traps nights, respectively, at rocky sites. Additionally, a survey of remnant populations in north-coastal Queensland found abundance to be greatest at coastal sites where large boulders were present (Foster and Oakwood pers comm, as cited in Hill and Ward 2010), and Woinarski et al. (2007) found the presence of northern quolls on islands to be related to a measure of topographic ruggedness or complexity.

There is also evidence that survival is higher in rocky habitat compared to other habitat types. Oakwood (1997) found that females whose home ranges included rocky habitat were more likely to survive to a second breeding season. Moreover, the nine instances of predation recorded by Oakwood (1997) were evenly recorded in forest, woodland and creek habitat, however none were recorded in rocky hills. Further evidence that rocky areas provide important habitat for northern quolls is provided by Woinarski et al. (2008), which showed that declines of the northern quoll in Queensland have mostly been restricted to lowland, less rugged areas.

With consideration to the importance of rocky habitat, other habitat types may also be required for population persistence in an area. In a study of northern quolls on the fringes of Darwin, Rankmore and Price (2004) noticed that in habitat fragments within a rural mosaic, northern quolls were absent from fragments with less than 65% woodland within a four kilometre area. This may suggest that woodlands are a vital component of the landscape for foraging or dispersal purposes. In addition, findings by Oakwood (1997) that habitat use differs between life stages suggest the importance of multiple habitat types. For example, in her study of northern quoll den site and habitat use, females were predominantly caught in rocky habitat, except for the period September - November when they had young in nursery dens. During this period, females were caught most often in forest (Oakwood 1997). In addition, when juvenile males first became trappable in mid-late November, they were more likely to be caught in rocky hills than at other times of the year (Oakwood 1997). As juvenile males completed weaning, dispersed and became sexually mature, their use of forest habitat increased (Oakwood 1997). A more recent study on the genetic structure of northern quoll on a landscape scale found populations separated by open plains were more genetically similar (Hohnen et al. 2016). These findings suggest that while rocky habitats may act as refuges, other habitats are likely to be vital for dispersal and foraging.

2.3.2 Den site selection

For species that exhibit denning behaviour, dens may be important for several reasons including protection from predators, protection from environmental hazards (e.g. fire), thermoregulation and social contact (Godsell 1983; Cockburn and Lazenby-Cohen 1992; Lindenmayer et al. 1996; Oakwood 1997). Northern quolls are nocturnal, spending the daytime hours within a den site (Van Dyck 2008). Based on the current literature, northern quolls do not appear to be highly specialised when it comes to den site selection. The species has been reported to den in tree hollows (living and dead), rock crevices, logs, termite mounds and burrows (Oakwood 1997). They have also been observed to den in various types of human infrastructure such as timber piles, underneath house verandas, within ceilings, and once within the frame of a washing machine (Pollock 1999) and a vehicle engine (Burnett 2008). Oakwood (1997) reported evidence of den site preferences within lowland savannah habitat in

Kakadu National Park where live trees and rock crevices were used more often than other den types. Unfortunately, Oakwood (1997) was unable to quantify the relative availability of all den types, so live tree hollows and rock crevices may have been the most common den types within the study area and not the most preferred. In addition, while Braithwaite and Griffiths (1994) suggest that den sites close to water sources are preferred, Oakwood (1997) found no such relationship.

Both sexes of northern quolls den solitarily and only one instance of den sharing has been recorded, where the two females were presumed to be mother and daughter (Oakwood 1997). In addition, northern quolls have rarely been found to inhabit a den previously used by another individual, and on occasions where this has been observed the initial occupant had died, and a considerable time lapse (greater than eight months) had occurred (Oakwood 2002). Therefore, it is unlikely that den sites are important for social contact.

Northern Australia is prone to annual fires that vary in size and intensity (Russell-Smith et al. 2003). Oakwood (1997) proposed that denning behaviour may aid in the survival of northern quolls within fire-prone areas. However, if this was the case one would expect northern quolls to predominantly use den sites that were intrinsically fire resistant, such as termite mounds and rocky habitat. In contrast, Oakwood (1997) found that live and dead trees formed a large portion of den sites used by the species. Moreover, her observation of females shifting habitat use from rocky hills to forest during the late dry season (when the risk of intense fires is greatest) suggests that fire avoidance does not have a major influence on den site selection.

In addition to seasonal fires, northern Australia has a tropical climate and is subject to consistently high temperatures throughout the year (mean annual minimum and maximum 20.8 and 34.9, respectively; BoM 2015). The use of termite mounds by females has been observed to increase during the three month period from mid-August to November, when females left young in nursery dens during foraging activity (Oakwood 1997). Some goanna species are known to lay eggs in termite mounds, purportedly due to stable microclimatic properties present within mounds (Pianka 2004). As juvenile northern quolls are altricial for several months after birth and have little fur, it is possible that termite mounds are used by northern quolls for their thermoregulatory benefits (Oakwood 1997). In addition, the synchrony between periods of northern quoll activity and cooler parts of the day (leaving den sites before dusk and returning before dawn) provides further evidence that dens may provide protection from climatic extremes.

However, other species of *Dasyurus* in more temperate regions are also nocturnal (Dickman and Vieira 2012; Dyck and Strahan 2008), and therefore the denning behaviour of the northern quoll may have evolved in response to other pressures. Given a large proportion of Australian predators are diurnal, one may postulate that the ancestral species of the northern quoll evolved this denning behaviour and nocturnality in order to avoid predation from and competition with other predatory species. Findings from Oakwood (1997) suggesting that predation is lowest and survival is greater in rocky habitats, combined with the knowledge that rocky habitat includes a higher density of available den sites such as fissures, cracks and crevices, further supports this hypothesis.

2.3.3 Movement and home range

Movement and home range estimates vary between the studies for which they have been reported. Movement estimates range from maximum distances of 6-7 kilometres for both sexes (Koolan Island in the Kimberley region of W.A.; Spencer et al. 2010), 4.2 km for males and 0.69 km for females (Mitchell Plateau, Kimberley region of W.A; Cook 2010), 3.5 km (a single male tracked near Fortescue River, Pilbara W.A; King and King 1989), and 0.94 km for males and 1.16 km for females (Little Nourlangie Rock, Arnhem Land, N.T; Begg 1981). Although a difference in habitat types between the study sites is likely to have had an influence on the observed variation between estimates, movement estimates were also likely to have been influenced by differences in the duration, timing and methodology between studies. For example, Spencer et al. (2010) recorded the greatest distances moved by both sexes of northern quoll; however the study was also the longest, including monthly trapping data collected over a three year period.

Spencer et al. (2010) suggest that the movement patterns of males and females differ. For example, female movements were observed to be greatest during the pouched young and young in den period, whereas males appeared to move further than females in October, when the male population consisted of individuals who had survived the mating season. Begg (1981) observed a similar pattern with peak female activity recorded in July-August and October. However, in contrast to Spencer et al. (2010) peak male activity was recorded in July, around the time of mating. Braithwaite and Griffiths (1994) reported a gradual increase of female movements up until the breeding season, after which movements declined until December when immature females were detected in the population. Male movements increased until the males were sexually mature, and large movements were detected from post reproductive males (Braithwaite and Griffiths 1994). King and King (1989) also report a single male moving a great distance, following the breeding season in the Pilbara region of Western Australia.

Reports of mean and maximum home range size for northern quolls based on the minimum convex polygon method vary between study locations (Table 2.1). Evidence suggesting seasonal difference in home range size or activity area is inconclusive. For example, Oakwood (2002) observed that the home range of males appeared to increase during the mating season; however this was based on one individual. Additionally, Cook (2010) observed that of the four individuals monitored, increases in home range during the dry season were only observed for one male and one female. No noticeable difference was observed for the other male, and the other female's home range was smaller during the dry season. Based on the aforementioned observations of seasonal changes in movement extent, and evidence that resources such as food are more abundant during the wet season (Cook 2010), a seasonal difference in home range size is plausible as individuals may need to disperse further during the dry season to seek out adequate resources.

Table 2.1. Home range estimates of the northern quoll

Location	Sex	Mean Home Range (ha)	Maximum Home Range (ha)	Reference
Mitchell Plateau, WA	Female	11.6	-	Cook (2010)
Mitchell Plateau, WA	Male	74.8	-	Cook (2010)
Kakadu NP, NT	Female	35 ± 8	66	Oakwood (2002)
Mitchell Plateau, WA	Female	2.3	-	Schmitt et al. (1989)
Mitchell Plateau, WA	Male	1.8	-	Schmitt et al. (1989)
Fortescue River, WA	Female	219.7	-	King and King (1989)
Fortescue River, WA	Male	382.4	-	King and King (1989)

Measures of home range overlap suggest that females may be territorial, at least during some periods of the year. Oakwood (2002) did not observe an overlap between the home ranges of females that were radio tracked at her study site in Kakadu National Park. However, the home ranges of males overlapped with other males, as well as other females (Oakwood 2002). Based on these and other observations, such as the tendency of males to visit multiple females nightly during the mating season, Oakwood (2002) suggested that females maintain discrete home ranges that are determined by resource availability, whereas males are wide-ranging with home ranges that are likely determined by the density of females within the area. Similarly, Cook (2010) observed the home ranges of males to overlap with those from both sexes during the wet season; however during the dry season they only overlapped with those of females. Home ranges of females during the wet season did not overlap with other females, but during the dry season the ranges of females overlapped in at least one of her study sites.

In contrast, King and King (1989) found considerable overlap in the home ranges of individuals of both sexes recorded during their study. The maintenance of female territories has important consequences on the perceived carrying capacity of an environment for northern quolls, as resource availability becomes restricted to individuals based on the home range they are able to maintain. Therefore, if abundance is used to determine habitat preference and territoriality is not considered, a correlation between habitat and abundance may be a function of the distribution of dominant and non-dominant individuals rather than an indication of preferred habitat.

Differences in habitat between the study sites and the duration of study may have influenced these results, and it is possible that additional northern quolls were not recorded during the aforementioned studies and may have had overlapping home ranges that went unnoticed. Furthermore, in order for the minimum convex polygon method to produce a reliable estimate, locations must be continually recorded until such a point that the area within the polygon no longer increases (Odum and Kuenzler 1955). Of the four studies that report home range estimates for northern quolls, two studies do not mention if this was achieved (King and King 1989; Schmitt et al. 1989), Cook (2010) only had sufficient data to estimate the home range of one male, and Oakwood (2002) was unable to obtain sufficient data to reach an asymptote for males. In addition, location data throughout the year were not constant and were only collected from diurnal den site locations, which does not account for nocturnal movements. Therefore, estimates of home range size, evidence of temporal pattern in home range size and socio-spatial organisation requires further exploration for this species.

2.3.4 Diet

Northern quolls have been described as predatory generalist or opportunistic omnivores (Oakwood 1997). A study conducted at Kakadu National Park based on analysis of scats and stomach contents of road-killed individuals found northern quolls to prey upon a wide range of insects (particularly of the Order Coleoptera and Orthoptera), mammals, birds and bird eggs, reptiles, frogs, and at least nine species of fleshy fruit (Oakwood 1997). A more recent study of the northern quoll diet in the Pilbara region based on scat analysis found the species to experience a varied diet of mammals, reptiles, invertebrates and plant material (Dunlop et al. 2017). A population of northern quoll in the Mackay-Bowen area of Northern Queensland was mainly insectivorous, with small mammals forming a minor component of scats (Pollock 1999). However, this study was limited to the analysis of 26 scats, and may have resulted in an underestimation of amphibian prey due to the difficulty in detecting amphibian species in scat analysis (Oakwood 1997). Crustacean fragments have also been detected in scats, suggesting that the northern quoll may forage along water courses (Pollock 1999; Dunlop et al. 2017).

Oakwood (1997) found the composition of food items to change throughout the year, presumably as they became more or less abundant. For example, fleshy fruits accounted for 60% of the volume of scats from the late wet to early dry season, while invertebrate consumption peaked in the late-dry to wet season, and vertebrate consumption peaked in the mid-dry season (Oakwood 1997). Diet preference did not differ between the sexes; however females consumed fewer vertebrates than males (Oakwood 1997). The northern quoll is thought to forage terrestrially, however Pollock (1999) recorded the presence of hair from a species of glider (*Petauridae*) in a single scat, birds and bird eggs were detected by Oakwood (1997), and birds and bats were detected by Dunlop et al. (2017). The northern quoll has also been observed to feed on human food refuse, and Pollock (1999) reports an individual from the Cathu State Forest area in Northern Queensland to be observed feeding on domestic cat food. The impacts of food subsidisation on the northern quoll is unknown, but has been shown to alter behaviour and movement patterns in other species (e.g. Newsome et al. 2014; Newsome et al. 2015).

Populations across the Pilbara region studied by Dunlop et al. (2017) varied 3-fold in niche breadth, however neither niche breadth nor the presence of food items correlated with any environmental or biogeophysical drivers. Dunlop et al. (2017) suggested that vertebrates were a preferred prey item when available, while invertebrates were consumed more frequently than any other food item. The findings of this study suggest that the northern quoll is able to adjust its diet based on food availability.

2.4 THREATS AND CONSERVATION

Several factors and processes have been suggested to contribute to northern quoll population declines, and pose a potential threat to the long-term persistence of the species. Broadly, these include habitat destruction and degradation, invasive species, and disease.

2.4.1 Habitat Destruction and Degradation

Altered Fire Regimes

Changes to existing fire regimes has been proposed as a threatening process for many of northern Australia’s threatened or declining species, including the northern quoll (Woinarski 1990; Oakwood 1997; 2000; Woinarski et al. 2004; 2005; McKenzie et al. 2007; Legge et al. 2008). As Indigenous Australians were displaced from traditional lands and moved to larger communities, and with European settlement, the fire regime has shifted from one consisting of frequent, patchy fires of less intensity to more expansive, intense fires (Woinarski et al., 2001; Woinarski et al., 2007). Fires may result in the mortality of individual animals, but it is also likely that the indirect effects of fire pose great risks to the long-term persistence of northern quolls in a given area (Hill and Ward 2010; Radford 2010). For example, frequent and extensive, intense fires in savannah woodlands have been observed to result in a reduction in habitat complexity by decreasing the abundance of large hollow trees and fallen logs (Woinarski et al. 2001). These habitat features are known to be used by northern quolls as diurnal den sites in some habitats (Oakwood, 1997). In addition to habitat modification, inappropriate fire regimes can also reduce the abundance of both prey species (Radford 2012) and the availability of vegetative food resources, as some species require a specific fire regime in order to produce fruit (Vigilante and Bowman 2004).

The causal link between fire and declines in small mammals such as the northern quoll is often speculative in nature (Radford 2010), however recent studies shed increasing light on this relationship (Griffiths and Brook 2015). Studies investigating the effect of fire on body weight and condition (Oakwood 2000), abundance (Woinarski et al. 2004) and change in home range size (Cook 2010) detected no detrimental effects to northern quolls related to fire. Woinarski et al. (2004) found that northern quolls and several other species were significantly more abundant at a site that was burnt annually when compared to a site were fire had been excluded for 23 years, but in another study found that northern quolls had declined in an area subject to a landscape-scale fire experiment four years prior (Woinarski et al. 2001). However, Griffiths and Brook (2015) found that fires impacted mammal populations through recruitment rather than adult survival, and that the timing of fires can have varying levels of impact on the northern quoll. The authors found that population recruitment responded negatively to late-dry season fire, which corresponds to a time when young are in pouches or deposited in dens. It is likely that the frequency, intensity and timing of fires are all factors that may impact northern quoll populations (Griffiths and Brook 2015).

Grazing

Habitat degradation resulting from over-grazing by livestock and feral herbivores has been linked to small mammal declines in northern Australia, but again, the exact mechanism is poorly understood (McKenzie et al. 2007). Overgrazing and trampling can result in a simplification of vegetation structure and the reduction of ground layer cover (Smitet et al. 2001). This reduction in cover has the potential to expose small mammals, such as northern quolls, to increased predation pressure from feral cats (Fleischner 1994; Keesing 1998). Disturbed vegetation as a result of grazing can also be more susceptible to weed invasion (Hobbs 2001), and in many circumstances pastoral lands may even be planted with invasive grass species to make it more suitable for grazing (Cook and Dias 2006). Hill and Ward (2010) suggest that the unusually high density and stiffness of exotic pasture grasses such as gamba grass (*Andropogon gayanus*) may impede northern quoll movements and thus decrease foraging efficiency. In addition, as they produce biomass greater than that of native grasses, weed species can potentially facilitate fire events of greater intensity, which are more likely to both cause direct mortality and exacerbate habitat degradation (Rossiter et al. 2003; Hill and Ward 2010).

Northern quoll populations in areas of the Pilbara have been in decline since the 1980s, corresponding with habitat degradation resulting from altered fire regimes, overgrazing and mining activities (McKenzie et al. 2007; Hill and Ward 2010; Cramer et al. 2016; Dunlop et al. 2017). Furthermore, remnant populations of northern quoll are known to persist in parts of Queensland with below-average cattle densities (Burnett 1997). However, as is the case with determining a strong causal relationship between other threatening processes and population declines of the northern quoll, there is evidence that both supports and challenges the perception that grazing pressure is a true threat to the species. As such, northern quolls are also known to occur in areas subject to heavy grazing pressure (Foster and Oakwood pers. com. 2008, as cited in Hill and Ward 2010).

Indirect impacts of habitat degradation

An overview of the factors contributing to habitat degradation is incomplete without an acknowledgement of the effect they have on habitat fragmentation, and the impact this may have on the northern quoll. A study by Rankmore and Price (2004) detected a negative response of the northern quoll to fragmentation, finding the species absent from fragments surrounded by less than 50% woodland within a four kilometre radius. With consideration to the species' requirement for multiple habitat types, and the knowledge that in certain areas some habitat types will be restricted, complete clearing of areas for urban development, mining and agriculture within the northern quoll's distribution is likely to at times co-occur with restricted habitat types and have a large impact on this species' ability to move through or effectively utilise an area (Hill and Ward 2010).

2.4.2 Feral Predators

Direct predation by and/or competition with introduced carnivores has also been proposed as a potential threat to northern quoll persistence (Hill and Ward 2010). Predation pressure from feral carnivores, such as the European red fox *Vulpes vulpes* and the domestic cat *Felis catus* has been linked to the extinction of at least 15 mammal species in Australia during the last 100 years (Johnson 2006; Woinarski et al. 2015). While the impact of the European red fox on northern quolls has not been assessed, authors such as Morris et al. (2003) and Glen et al. (2010; 2011) suggest that the fox has had a considerable impact on other species of quoll via competition and predation. Given the range of both species overlaps in areas of the Pilbara and in central and south eastern Queensland, it is very possible that these species interact, with negative consequences for the northern quoll (King and Smith 1985; Hill and Ward 2010).

The feral cat is now considered to be the foremost driver of small mammal declines in northern Australia (Fisher et al. 2014). Indeed, most declining mammal species fall within the favoured prey-size of feral cats (Dickman 1996; Fisher et al. 2014), that are capable of the wide-scale extirpation of native prey species even at relatively low densities (Frank et al. 2014). In contrast, island populations of declining species remain relatively stable on islands where feral cats do not occur or have been extirpated (Woinarski et al. 2011). While there is no direct evidence demonstrating a significant negative effect on northern quolls, there are reports of feral cats predating on northern quolls (Pollock 1999; Burnett 2000; Oakwood 2000; O’Donnell et al. 2010). It is of interest to note that although feral cats have existed in northern Australia for well over 100 years (Abbott 2002), mammal declines have only been detected over the last 20-30 years (Woinarski et al. 2011). However, it is believed that changes to traditional fire management practices in recent times have reduced ground cover and exacerbated feral cat predation on many of northern Australia’s small mammals, thus leading to decline (Oakwood 2000; McGregor et al. 2014).

In addition to cats and foxes, there is evidence of predation on northern quolls by domestic and wild dogs (*Canis lupus*) and dingos (*Canis dingo*), suggesting that they may supress northern quoll populations in some areas (Oakwood 2000; Cremona et al. 2017a). However, dingos are thought to supress feral cat and fox numbers in areas where they co-occur, and it has been noted that in areas of northern Queensland where northern quolls persist, dingos occur and feral cats and foxes are scarce or absent (Burnett unpublished, as cited by Jones et al. 2014). Therefore, northern quolls and dingos may be able to co-occur in some areas.

2.4.3 Cane Toads

The northern quoll is known to feed on the toxic cane toad, the ingestion of which is fatal and poses a risk to both mainland and island populations (O’Donnell et al. 2010). Cane toads were introduced to Northern Queensland in 1935 in an attempt to control two species of beetles that were predating on commercial crops of sugar cane

(Barton 1997). Since then, they have spread rapidly along coastal Queensland into Northern New South Wales, across much of the wet-dry tropics of the Northern Territory, and crossed the Western Australian border in 2009 (Shine 2010). The skin of the cane toad is toxic at all life stages (Hayes et al. 2009), producing potent bufogenins and bufotoxins (Zug and Zug 1979). As their main impact is via lethal toxic ingestion, the species most at risk are large predatory species (several species of reptile and the northern quoll) that have a propensity to prey upon anurans (Shine 2010). There is strong evidence that the colonisation of cane toads in certain areas of northern Australia is followed by the local extinction of northern quolls, presumably caused by quolls predating on toads (Burnett 1997; Woinarski et al. 2008). For example, shortly after the arrival of cane toads in Kakadu National Park, a significant decline in northern quoll numbers was observed and several populations went extinct (Watson and Woinarski 2004; Oakwood 2008). However, several populations have persisted in parts of Queensland where cane toads have occurred for a long period of time (Pollock 1999), and some northern quoll populations were already declining prior to the arrival of cane toads (Braithwaite and Griffiths 1994). Interestingly, a study of populations that have persisted alongside cane toads has found these northern quolls to be ‘toad-smart’, and less likely to predate on toads (Kelly and Phillips 2017). This indicates that some populations may have the ability to adapt behaviours to avoid this toxic prey species.

2.4.4 Disease

It has been suggested that disease has contributed to both the extinction of eastern quolls on mainland Australia, and the decline of the chuditch in parts of Western Australia (Peacock and Abbott 2014). As the current pattern of decline exhibited by the northern quoll mirrors that of its southern cousins, disease has likewise been proposed as a potential mechanism behind their decline (Hill and Ward 2010). Based on historical records, Peacock and Abbott (2014) proposed that canine distemper or a similar disease may have contributed to the decline of eastern quolls in southern Australia. The authors also found evidence suggesting that quoll declines may have resulted from a skin infection caused by the flea *Uropsylla tasmanica*. However, in their study of northern quoll ecto- and endo-parasites, Oakwood and Spratt (2000) did not detect the presence of *Uropsylla tasmanica*, and suggest that parasitism is unlikely to have contributed to the decline of the northern quoll.

Toxoplasmosis has also been suggested as a contributing factor to the declines of quoll species in southern Australia (Shepherd and Mahood 1978). However, pathology conducted on northern quoll tissue and blood samples taken from road-killed individuals near Kakadu National Park did not detect the presence of the protozoan parasite *Toxoplasma gondii* (Oakwood and Pritchard 1999). Although patterns of northern quoll decline in northern Australia are similar to that which has been observed for southern species of *Dasyurus*, there is thus far no evidence to support the proposition that disease is an important contributing factor to their decline.

2.5 CONCLUSION

2.5.1 Threats

Identifying and understanding the extrinsic factors driving the decline of the northern quoll is one of the primary areas of interest for their conservation management (Hill and Ward 2010). On a landscape scale, northern quoll habitat has been degraded over large areas as a result of widespread pastoralism and altered fire regimes (Hill and Ward 2010). Griffiths and Brook (2015) suggest that fires during the late-dry season are likely to have a greater impact on population viability than fires during other times of the year. While northern quolls may be capable of surviving some fire events, further information on how the extent and intensity influence the impact of fire on this species, and how habitat type interacts with these effects, would be valuable.

It is likely that habitat degradation has a synergistic relationship with other threats, such as the occurrence of introduced species. Feral cats are one such species that are suggested to capitalise on areas of degraded habitat, especially woodland habitat, which may experience a loss of ground cover and leave native species increasingly exposed (McGregor et al. 2014). With consideration to the influence that habitat type is likely to have on the manifestation of synergistic threats, it is likely that an increase in the research surrounding northern quoll habitat use and den site selection may in turn offer further insight into the effect of threats such as predation by feral cats, altered fire regimes, and grazing pressure.

When threats are considered independently, the toxic cane toad appears to be the most pervasive threat to the northern quoll. Novel methods such as conditioned taste aversion have been trialled both in captivity and in the field to discourage the predation of cane toads (O’Donnell et al. 2010; Cremona et al. 2017b; Indigo et al. 2018). Results have indicated that this approach may provide a level of protection against mortality via ingestion of this invasive species. In a study of 50 reintroduced ‘toad-smart’ quolls into Kakadu National Park, Cremona et al. (2017b) found that trained individuals survived in a toad-infested landscape, and reproduced successfully. Of the 50 northern quolls released, 22 were recaptured, with three ‘toad-smart’ females confirmed to have reproduced successfully.

2.5.2 Movement ecology

Movement and home range estimates appear to vary dramatically between the studies in which they have been reported. Most likely, this is a consequence of habitat type, the time of year the study was undertaken, duration of the study and the methods used to estimate these measurements. However, from the available information it is logical to assume that movement patterns differ both between males and females, and between seasons. The studies conducted on northern quoll movement to date strongly indicate that northern quolls are capable of moving large distances. It is likely that given the influence of seasonal rainfall on productivity within northern Australia, individuals may need to disperse farther to seek out adequate food resources. Northern quoll populations separated by open plains and within high rainfall areas have a low genetic distance, indicating immigration and emigration between these populations (Hohnen et al. 2016). However, this behaviour also makes the northern quoll increasingly likely to encounter additional threats, such as feral cats, cane toads, and vehicles. Therefore, further research is required in order to understand when northern quolls move larger distances, and whether dispersal is influenced by a search for food resources or a mate.

One aspect of their ecology that may also influence movement is territoriality. Measures of home range overlap by Oakwood (2002) and Cook (2010) suggest that females may be territorial, at least for part of the year, while males move large distances to maximise female encounters. However, these studies are limited by the methods used to collect the data. Where mark-recapture techniques were used, the area of inference is limited to the trapping grid, while telemetry studies have used daytime locations that restrict point data to den sites only. Mark-recapture studies also assume that all females were captured within a given area, and therefore do not consider that some untrapped females exist within the home range of other females. It is important to determine whether females are territorial, as this can inform how the carrying capacity of an environment for northern quolls is measured. If territoriality does occur and is not considered during density estimates, interpretation of the data may be misconstrued to reflect habitat quality, and not a result of the distribution of dominant and subordinate females.

However, when addressing the gaps in knowledge and considering the limitations of previous research, it must be appreciated that field studies within the northern quoll's distribution are inhibited by significant logistic and practical constraints. Heavy seasonal rainfall across northern Australia restricts access to many areas during the wet season, making it at times extremely difficult to collect year-round data. Furthermore, the northern quoll is a cryptic and wide-ranging species, and is therefore difficult to track using telemetry methods. Where telemetry is used, animals must be either tracked for a limited period or captured frequently in order to adjust the collars to match their rapid growth rate, while transmitters must be small enough to meet the ethical requirements for this smallest member of the *Dasyurus* genus, whilst still including the necessary technology to capture the data required.

2.5.3 Semelparity

The decline of the northern quoll is a primary concern to conservation management in northern Australia, not least of which due to the large gaps in knowledge that surround this species' biology and ecological traits. Undoubtedly, one of the most intriguing aspects of its biology that makes populations of the northern quoll susceptible to endangerment is the post-mating mortality that males experience. As has been previously stated by Oakwood (2000), semelparity increases the chance of a local extinction. Should recruitment fail in any given year due to extrinsic factors causing high juvenile mortality, few females and no males would be available to mate in the following year, increasing the likelihood of a severe population crash (Cremona et al. 2017a). Based on a synthesis of the literature, it seems most plausible that semelparity in the northern quoll has evolved in response to a shortened female breeding period that must ensure lactation and weaning coincides with periodic invertebrate abundance, which is in turn tied to the seasonal cycles in rainfall characteristic of tropical Australia (Tyndale-Biscoe 2005). When compounded with the short lifespan of small marsupials, the male northern quoll is forced to expend all energy during one reproductive event in order to maximise their reproductive potential.

While further studies that seek to clarify the proximate and ultimate causes for semelparity in northern quolls may increase our understanding of why it has evolved in some species, it may add little to inform their conservation. A complete male die-off will only negatively impact population dynamics if the species has a monogamous mating system (i.e. one male per female) and suffers from low male recruitment in a given year. Therefore, it is of importance to determine whether multiple paternity exists in populations of northern quoll, and whether males that survive into their second mating season are capable of breeding.

2.5.4 Habitat use

Interestingly and in contrast to many other endangered species, the northern quoll has been observed to inhabit a wide range of habitats both native and anthropogenic in nature, and is also a dietary generalist (Oakwood 1997; Pollock 1999; DPaW 2013). Therefore, it is of interest to ascertain the factors that influence habitat use by this species. A significant step in the conservation of the northern quoll would be to determine how different habitats influence survival. Studies such as Oakwood (1997) and Woinarski et al. (2008) have suggested that survival may be higher in rocky habitat. However, the specific attributes of rocky habitat that make it important to the northern quoll are unknown, and therefore future studies should focus on confirming the importance of rocky areas and clarifying the resources and benefits that they provide. Furthermore, other habitat types should not be ignored, as studies such as Rankmore and Price (2008) have shown that woodlands are likely to be highly important for foraging and dispersal, and Oakwood (1997) has shown habitat use to differ between life stages. This information would not only aid decision making regarding the protection of habitat for the northern quoll, but would also inform rehabilitation activities that aim to facilitate recolonisation by this species.

Part of this research, but also significant enough to form a main point of focus, is the selection of den sites by this species. Den site use by the northern quoll is likely to provide protection from both predation and exposure to extreme weather conditions. Data related to den site selection has previously suggested no preferences (e.g. Oakwood 1997), however studies have not yet explored microclimatic characteristics of den sites, nor structural characteristics such as depth, width, or number of access points or ‘openings’. A potential and major implication of this research would be to inform the production of artificial den sites, to supplement areas of degraded habitat where northern quolls either still occur or may colonise in the future.

Given the importance of recruitment to the persistence of northern quoll populations, female and juvenile survival may be more important to population viability than that of adult males. This, added with the shorter lifespan and large movements characteristic of males, may mean that studies that target female and juvenile habitat use and survival may be more pertinent to the conservation of the species.

2.6 REFERENCES

Abbott, I. (2002). Origin and spread of the cat, *Felis catus,* on mainland Australia, with a discussion of the magnitude of its early impact on native fauna. *Wildlife Research*, 29(1), 51-74.

Aitkin, L., Nelson, J., and Shepherd, R. (1996). Development of hearing and vocalization in a marsupial, the northern quoll, *Dasyurus hallucatus*. *Journal of Experimental Zoology*, 276(6), 394-402.

Barton, D. P. (1997). Introduced animals and their parasites: The cane toad, *Bufo marinus,* in Australia. *Australian Journal of Ecology*, 22(3), 316-324.

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

Belcher, C. A., and Darrant, J. P. (2006). Habitat use by tiger quoll (*Dasyurus maculatus*)(Marsupialia: Dasyuridae) in south-eastern Australia. *Journal of Zoology,* 269(2), 183-190.

Berger, K. M., Gese, E. M., and Berger, J. (2008). Indirect effects and traditional trophic cascades: a test involving wolves, coyotes, and pronghorn. *Ecology*, 89(3), 818-828.

BoM (2015) Climate Data Online. Monthly climate statistics for Kununurra, Darwin and Cairns. *http://www.bom.gov.au/climate/data/*. [Accessed on 7 April 2015].

Bradley, A. J. (1997). Reproduction and life history in the red-tailed phascogale, *Phascogale calura* (Marsupialia: Dasyuridae): the adaptive-stress senescence hypothesis. *Journal of Zoology*, 241(4), 739-755.

Bradley, A. J. (2003). Stress, hormones, and mortality in small carnivorous marsupials. In: *Predators with Pouches: the Biology of Carnivorous Marsupials* (Jones, M., Dickman, C., Archer, M., eds.). CSIRO Press, Sydney, pp. 250–263.

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.

Braithwaite, R. W., and Lee, A. K. (1979). A mammalian example of semelparity. *American Naturalist*, 151-155.

Burbidge, A.A. and Eisenberg, J.F. (2006). Conservation and management. In: *Marsupials* (Armati, P.J., Dickman, C.R., Hume, I.D., eds.). Cambridge University Press, Cambridge, pp. 299–330.

Burnett S. (1997). Colonising cane toads cause population declines in native predators: reliable anecdotal information and management implications. *Pacific Conservation Biology, 3,* 65-72.

Burnett, S. (2008). Quolls in the Townsville area: a summary of current knowledge. Progress report to The New Townsville City and BDTNRM.

Burnett, S. E. (2001). Ecology and conservation status of the northern spot-tailed quoll, *Dasyurus maculatus* with reference to the future of Australia's marsupial carnivores (Unpublished doctoral dissertation). James Cook University, Townsville, Australia.

Cockburn, A., and Lazenby-Cohen, K. A. (1992). Use of nest trees by *Antechinus stuartii*, a semelparous lekking marsupial. *Journal of Zoology*, 226(4), 657-680.

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

Cook, G. D., and Dias, L. (2006). Turner Review No. 12. It was no accident: deliberate plant introductions by Australian government agencies during the 20th century. *Australian Journal of Botany*, 54(7), 601-625.

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.

Cremona, T., Crowther, M. S., and Webb, J. K. (2017a). High mortality and small population size prevent population recovery of a reintroduced mesopredator. *Animal Conservation*, *20*(6), 555-563.

Cremona, T., Spencer, P., Shine, R., and Webb, J. K. (2017b). Avoiding the last supper: parentage analysis indicates multi-generational survival of re-introduced ‘toad-smart’ lineage. *Conservation Genetics*, *18*(6), 1475-1480.

Diamond, J.M. (1982) Big-bang reproduction and ageing in male marsupial mice. *Nature*, 298(5870), 115–116.

Dickman, C. R. (1996). Impact of exotic generalist predators on the native fauna of Australia. *Wildlife Biology*, 2(3), 185-195.

Dickman, C. R., and Braithwaite, R. W. (1992). Postmating mortality of males in the dasyurid marsupials, *Dasyurus* and *Parantechinus*. *Journal of Mammalogy*, 73(1), 143-147.

Dickman, C.R., and Vieira, E. (2012) Ecology and life histories. In: *Marsupials* (Armati, P.J., Dickman, C.R., Hume, I.D., eds.).Cambridge University Press, Cambridge, pp. 199–228.

Dixon, J. M., and Huxley, L. (1985). *Donald Thomson’s Mammals and Fishes of Northern Australia*. Nelson, Melbourne.

DPaW (2013). BHP Billiton Iron Ore Pilbara Northern Quoll Monitoring Project, Department of Parks and Wildlife, Perth.

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 Sciences*, 110(44), 17910-17914.

Fisher, D. O., Johnson, C. N., Lawes, M. J., Fritz, S. A., McCallum, H., Blomberg, S. P., ... and Kutt, A. (2014). The current decline of tropical marsupials in Australia: is history repeating?. *Global Ecology and Biogeography*, 23(2), 181-190.

Fitzsimons, J., Legge, S., Traill, B.J. and Woinarski, J.C.Z. (2010) *Into Oblivion: the disappearing native mammals of northern Australia*. The Nature Conservancy, Melbourne. Available at: http://www.nature.org/australia (accessed 26 May 2015).

Flannery, T. (2010). *The Eternal Frontier: An Ecological History of North America and Its Peoples*. Text Publishing, Melbourne.

Fleischner, T. L. (1994). Ecological costs of livestock grazing in western North America. *Conservation Biology*, 629-644.

Fleming, P. A., Anderson, H., Prendergast, A. S., Bretz, M. R., Valentine, L. E., and Hardy, G. E. S. (2014). Is the loss of Australian digging mammals contributing to a deterioration in ecosystem function?. *Mammal Review*, *44*(2), 94-108.

Frank, A. S., Johnson, C. N., Potts, J. M., Fisher, A., Lawes, M. J., Woinarski, J. C., Tuft, K., Radford, I. J., Gordon, I. J., Collis, M. A. & Legge, S. (2014). Experimental evidence that feral cats cause local extirpation of small mammals in Australia's tropical savannas. *Journal of Applied Ecology*, 51(6), 1486-1493.

Freeland, W. J., Winter, J. W., and Raskin, S. (1988). Australian rock-mammals: a phenomenon of the seasonally dry tropics. *Biotropica*, 70-79.

Glen, A. S., & Dickman, C. R. (2005). Complex interactions among mammalian carnivores in Australia, and their implications for wildlife management. *Biological Reviews*, *80*(3), 387-401.

Glen, A. S., Cardoso, M. J., Dickman, C. R., & Firestone, K. B. (2009). Who's your daddy? Paternity testing reveals promiscuity and multiple paternity in the carnivorous marsupial *Dasyurus maculatus* (Marsupialia: Dasyuridae). *Biological Journal of the Linnean Society*, 96(1), 1-7.

Glen, A. S., De Tores, P. J., Sutherland, D. R., & Morris, K. D. (2010). Interactions between chuditch (*Dasyurus geoffroii*) and introduced predators: a review. *Australian Journal of Zoology*, 57(5), 347-356.

Glen, A. S., Pennay, M., Dickman, C. R., Wintle, B. A., & Firestone, K. B. (2011). Diets of sympatric native and introduced carnivores in the Barrington Tops, eastern Australia. *Austral Ecology*, 36(3), 290-296.

Godsell, J. (1983). Ecology of the Eastern Quoll *Dasyurus viverrinus*,(Dasyrudae: Marsupialia) (Unpublished doctoral dissertation). Australian National University, ACT, Australia.

Green, B., Newgrain, K., Catling, P., & Turner, G. (1991). Patterns of prey consumption and energy use in a small carnivorous marsupial, *Antechinus stuartii. Australian Journal of Zoology*, 39(5), 539-547.

Griffiths, A. D., & Brook, B. W. (2015). Fire impacts recruitment more than survival of small-mammals in a tropical savanna. *Ecosphere*, *6*(6), 1-22.

Hayes, R. A., Crossland, M. R., Hagman, M., Capon, R. J., and Shine, R. (2009). Ontogenetic variation in the chemical defences of cane toads (*Bufo marinus*): toxin profiles and effects on predators. *Journal of Chemical Ecology*, 35(4), 391-399.

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.

Hobbs, R. J. (2001). Synergisms among habitat fragmentation, livestock grazing, and biotic invasions in southwestern Australia. *Conservation Biology,* 15(6), 1522-1528.

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(3), 206-217.

Humphries, S., and Stevens, D. J. (2001). Reproductive biology: Out with a bang. *Nature*, 410(6830), 758-759.

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*.

Johnson, C.N. (2014) The rise and fall of large marsupial carnivores. In: *Carnivores of Australia: Past, Present and Future* (Glen, A.S., Dickman, C.R., eds.). CSIRO Publishing, Collingwood, pp. 331-362.

Jones, M. E., Burnett, S., Claridge, A. W., Fancourt, B., Kortner, G., Morris, K., ... and Woinarski, J. (2014). Australia's surviving marsupial carnivores: threats and conservation. In: *Carnivores of Australia: Past, Present and Future* (Glen, A.S., Dickman, C.R., eds.). CSIRO Publishing, Collingwood, pp.197-240.

Jones, M. E., Oakwood, M., Belcher, C. A., Morris, K., Murray, A., Woolley, P. A., ... and Burnett, S. (2003). Carnivore concerns: problems, issues and solutions for conserving Australasia’s marsupial carnivores. In*: Predators with Pouches: the Biology of Carnivorous Marsupials* (Jones, M.E., Dickman, C.R., Archer, M., eds.). CSIRO Publishing, Collingwood, pp.422-434.

Keesing, F. (1998). Impacts of ungulates on the demography and diversity of small mammals in central Kenya. *Oecologia*, 116(3), 381-389.

King D.R. and Smith L.A. (1985). The distribution of the European red fox (*Vulpes vulpes*) in Western Australia. *Records of the Western Australian Museum* 12: 197-205.

King, D. R., and King, D. R. (1989). An Assessment of the Hazard Posed to Northern Quolls (*Dasyurus hallucatus*) by Aerial Baiting With 1080 to Control Dingoes. *Wildlife Research,* 16(5), 569-574.

Kraaijeveld, K., Kraaijeveld-Smit, F. J., and Adcock, G. J. (2003). Does female mortality drive male semelparity in dasyurid marsupials?. *Proceedings of the Royal Society of London B: Biological Sciences*, 270(Suppl 2), S251-S253.

Lee, A. K., Woolley, P., and Braithwaite, R. W. (1982). Life history strategies of dasyurid marsupials. In: *Carnivorous Marsupials* (Archer, M., ed.). Royal Zoological Society of New South Wales, Sydney, pp. 1-11.

Legge, S., Murphy, S., Heathcote, J., Flaxman, E., Augusteyn, J., and Crossman, M. (2008). The short-term effects of an extensive and high-intensity fire on vertebrates in the tropical savannas of the central Kimberley, northern Australia. *Wildlife Research*, 35(1), 33-43.

Letnic, M., and Koch, F. (2010). Are dingoes a trophic regulator in arid Australia? A comparison of mammal communities on either side of the dingo fence. *Austral Ecology*, *35*(2), 167-175.

Lindenmayer, D. B., Welsh, A., Donelley, C. F., and Meggs, R. A. (1996). Use of nest trees by the mountain brushtail possum (*Trichosurus caninus*)(Phalangeridae: Marsupialia). I. Number of occupied trees and frequency of tree use. *Wildlife Research*, 23(3), 343-361.

Manly, B. F. L., McDonald, L., Thomas, D., McDonald, T. L., and Erickson, W. P. (2007*). Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Springer Science and Business Media, New York.

McAllan, B. M. (2003). Timing of reproduction in carnivorous marsupials. In: *Predators with Pouches: the Biology of Carnivorous Marsupials* (Jones, M.E., Dickman, C.R., Archer, M., eds.). CSIRO Publishing, Collingwood, pp. 147-167.

McGregor, H. W., Legge, S., Jones, M. E., and Johnson, C. N. (2014) Landscape management of fire and grazing regimes alters the fine-Scale habitat utilisation by feral cats. *PLoS ONE* 9(10): e109097. doi:10.1371/journal.pone.0109097

McKenzie, N. L., Burbidge, A. A., Baynes, A., Brereton, R. N., Dickman, C. R., Gordon, G., ... and Woinarski, J. C. Z. (2007). Analysis of factors implicated in the recent decline of Australia's mammal fauna. *Journal of Biogeography*, 34(4), 597-611.

Millis, A. L., Taggart, D. A., Bradley, A. J., Phelan, J., and Temple-Smith, P. D. (1999). Reproductive biology of the brush-tailed phascogale, *Phascogale tapoatafa* (Marsupialia: Dasyuridae). *Journal of Zoology*, 248(03), 325-335.

Morris, K., Johnson, B., Orell, P., Gaikhorst, G., Wayne, A., and Moro, D. (2003). Recovery of the threatened chuditch (Dasyurus geoffroii): a case study. In: *Predators with Pouches: the Biology of Carnivorous Marsupials* (Jones, M.E., Dickman, C.R., Archer, M., eds.). CSIRO Publishing, Collingwood, pp. 435-451.

Morrison, M. L., Marcot, B., & Mannan, W. (2006). *Wildlife-habitat Relationships: Concepts and Applications*. Island Press, Washington, DC.

Nelson, J. E., & Gemmell, R. T. (2003). Birth in the northern quoll, *Dasyurus hallucatus* (Marsupialia: Dasyuridae). *Australian Journal of Zoology*, 51(2), 187-198.

Newsome, T. M., Ballard, G. A., Fleming, P. J., van de Ven, R., Story, G. L., & Dickman, C. R. (2014). Human-resource subsidies alter the dietary preferences of a mammalian top predator. *Oecologia*, *175*(1), 139-150.

Newsome, T. M., Dellinger, J. A., Pavey, C. R., Ripple, W. J., Shores, C. R., Wirsing, A. J., & Dickman, C. R. (2015). The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography*, *24*(1), 1-11.

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.

Oakwood, M. (1997). The ecology of the northern quoll, Dasyurus hallucatus (Unpublished doctoral dissertation). The Australian National University, ACT, Australia.

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 Royal Society of London. Series B: Biological Sciences, 268*(1465), 407-411.

Oakwood, M. (2002). Spatial and social organization of a carnivorous marsupial *Dasyurus hallucatus* (Marsupialia: Dasyuridae). *Journal of Zoology*, 257(02), 237-248.

Oakwood M. (2004). The effect of cane toads on a marsupial carnivore, the northern quoll, *Dasyurus hallucatus*. Report to Parks Australia.

Oakwood, M., and Foster, P. (2008). Monitoring extinction of the northern quoll. Report to the Australian Academy of Science, Canberra.

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.

Oakwood, M., and Spratt, D. M. (2000). Parasites of the northern quoll, *Dasyurus hallucatus* (Marsupialia: Dasyuridae) in tropical savanna, Northern Territory. *Australian Journal of Zoology*, 48(1), 79-90.

Oakwood, M., Bradley, A. J., and Cockburn, A. (2001). Semelparity in a large marsupial. *Proceedings of the Royal Society of London B: Biological Sciences*, 268(1465), 407-411.

Odum, E. P., & Kuenzler, E. J. (1955). Measurement of territory and home range size in birds. *The Auk*, 128-137.

Peacock, D., and Abbott, I. (2014). When the 'native cat'would 'plague': historical hyperabundance in the quoll (Marsupialia: Dasyuridae) and an assessment of the role of disease, cats and foxes in its curtailment. *Australian Journal of Zoology*, 62(4), 294-344.

Pianka, E. R. (2004). Monitors, Goannas, and Earless Monitors (Varanidae). In: *Grzimek's Animal Life Encyclopedia, 2nd edition* (Evans, A. V., Garrison, R. W., & Schlager, N.). Gale Publishing, Detroit,Vol. 7, pp. 359-368.

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(2), 388-395.

Purvis, A., Mace, G.M., and Gittleman, J.L., (2001). Past and future carnivore extinctions: a phylogenetic perspective. In: *Carnivore Conservation* (Gittleman, J.L., Funk, S.M., Macdonald, D., Wayne,R.K. eds.). Cambridge University Press, Cambridge, pp. 11–34.

Radford, I. J. (2010b). Fire regimes and regional biodiversity declines in north-west Australian tropical savannas. Review of knowledge and recommendations for future research. *Conservation Science Western Australia*, 7, 469-479.

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.

Rankmore BR and Price OF (2004) The effects of habitat fragmentation on the vertebrate fauna of tropical woodlands, Northern Territory. In: *Australian Forest Ecology* (second edition) (Lunney, D., ed.). Royal Zoological Society of New South Wales, Mosman, pp. 452-473.

Ripple, W. J., and Beschta, R. L. (2004). Wolves and the ecology of fear: can predation risk structure ecosystems?. *BioScience*, 54(8), 755-766.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., ... and Wirsing, A. J. (2014). Status and ecological effects of the world’s largest carnivores. *Science*, 343(6167), 1241484.

Rossiter, N. A., Setterfield, S. A., Douglas, M. M., and Hutley, L. B. (2003). Testing the grass-fire cycle: alien grass invasion in the tropical savannas of northern Australia. *Diversity and Distributions*, 9(3), 169-176.

Russell-Smith, J., Yates, C., Edwards, A., Allan, G. E., Cook, G. D., Cooke, P., ... and Smith, R. (2003). Contemporary fire regimes of northern Australia, 1997–2001: change since aboriginal occupancy, challenges for sustainable management. *International Journal of Wildland Fire*, 12(4), 283-297.

Schmitt, L. H., Bradley, A. J., Kemper, C. M., Kitchener, D. J., Humphreys, W. F., and 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(4), 539-558.

Serena, M., Soderquist, T. R., and Morris, K. D. (1991). Western Australian Wildlife Management Program No. 7: The Chuditch. Department of Conservation and Land Management, Como, WA.

Sergio, F., Newton, I., and Marchesi, L. (2005). Conservation: Top predators and biodiversity. *Nature*, 436(7048), 192-192.

Shepherd, N. C., and Mahood, I. T. (1978). The potential effect of feral dogs and cats on Australian native fauna. *Australian Advances in Veterinary Science*, 108.

Shine, R. (2010). The ecological impact of invasive cane toads (*Bufo marinus*) in Australia. *The Quarterly Review of Biology*, 85(3), 253-291.

Short, J., and Turner, B. (1994). A test of the vegetation mosaic hypothesis: a hypothesis to explain the decline and extinction of Australian mammals. *Conservation Biology*, 8(2), 439-449.

Smit, R., Bokdam, J., Den Ouden, J., Olff, H., Schot-Opschoor, H., and Schrijvers, M. (2001). Effects of introduction and exclusion of large herbivores on small rodent communities. *Plant Ecology*, 155(1), 119-127.

Spencer, P. B. S., How, R. A and Schmitt, L. H. (2010). The Northern Quoll Population on Koolan Island: Molecular and Demographic Analysis. Unpublished Report for Mount Gibson Iron Limited.

Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional Ecology*, 259-268.

Stearns, S. C. (1992). *The Evolution of Life Histories* (Vol. 249). Oxford: Oxford University Press.

Terborgh, J., Lopez, L., Nunez, P., Rao, M., Shahabuddin, G., Orihuela, G., ... and Balbas, L. (2001). Ecological meltdown in predator-free forest fragments. *Science*, 294(5548), 1923-1926.

Tyndale-Biscoe, C.H. (2005) Life of Marsupials. CSIRO Publishing, Melbourne.

Van Dyck, S., and Strahan, R. (Eds.). (2008). *The Mammals of Australia*. New Holland Pub Pty Limited, Chatswood.

Vigilante, T., and Bowman, D. M. J. S. (2004). Effects of individual fire events on the flower production of fruit-bearing tree species, with reference to Aboriginal people's management and use, at Kalumburu, North Kimberley, Australia. *Australian Journal of Botany*, 52(3), 405-416.

Watson, M., and Woinarski, J. C. Z. (2004). Vertebrate Monitoring and Re-sampling in Kakadu National Park: Year 3, 2003-04. Department of Infrastructure, Planning and Environment.

Woinarski J.C.Z., Milne D.J. and Wanganeen, G. (2001). Changes in mammal populations in relatively intact landscapes of Kakadu National Park, Northern Territory, Australia. *Austral Ecology* 26:360-370.

Woinarski, J. C. Z. (1990). Effects of fire on the bird communities of tropical woodlands and open forests in northern Australia. *Australian Journal of Ecology*, 15(1), 1-22.

Woinarski, J. C. Z., Oakwood, M., Winter, J., Burnett, S., Milne, D., Foster, P., Myles, H. & 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.

Woinarski, J. C. Z., 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.

Woinarski, J. C. Z., Ward, S., Mahney, T., Bradley, J., Brennan, K., Ziembicki, M., and Fisher, A. (2011). The mammal fauna of the Sir Edward Pellew island group, Northern Territory, Australia: refuge and death-trap. *Wildlife Research*, 38(4), 307-322.

Woinarski, J. C. Z., Williams, R. J., Price, O., and Rankmore, B. (2005). Landscapes without boundaries: wildlife and their environments in northern Australia. *Wildlife Research*, 32(5), 377-388.

Woinarski, J. C., 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(15), 4531-4540.

Woinarski, J. C., Legge, S., Fitzsimons, J. A., Traill, B. J., Burbidge, A. A., Fisher, A., ... and Ziembicki, M. (2011). The disappearing mammal fauna of northern Australia: context, cause, and response. *Conservation Letters*, 4(3), 192-201.

Woinarski, J., Mackey, B., Nix, H., and Traill, B. (2007). *The Nature of Northern Australia: Its Natural Values, Ecological Processing and Future Prospects*. ANU E Press.

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 The Australian Government’s Natural Heritage Trust.

Woinarski, J.C.Z., Milne, D.J., and Wanganeen, G. (2001). Changes in mammal populations in relatively intact landscapes in Kakadu National Park, Northern Territory, Australia. *Austral Ecology* 26, 360-370.

Woolley, P. (1966). Reproduction in *Antechinus spp*. and other dasyurid marsupials. In *Symposia of the Zoological Society of London* (Vol. 15, pp. 281-294). The Society.

Woolley, P. A. (1991). Reproduction in *Dasykaluta rosamondae* (Marsupialia, Dasyuridae)-Field and Laboratory Observations. *Australian Journal of Zoology*, 39(5), 549-568.

Zug, G. R., and Zug, P. B. (1979). *The Marine Toad, Bufo marinus: a Natural History Resume of Native Populations*. Smithsonian Institution Press, Washington, DC.

Chapter 3: Analysis of mine site monitoring data using spatial and non-spatial capture recapture models reveals the population dynamics of an endangered marsupial

3.1 ABSTRACT

The examination of the intrinsic drivers of population dynamics for a species are essential in planning successful conservation management strategies and minimising the impacts of threatening processes. For endangered species, it is commonplace for regulators to require monitoring programs yet monitoring data are rarely published. Unpublished monitoring data, particularly when collected over many years, present an important opportunity to gain inference that would otherwise involve an intensive resource output to obtain, but presents key challenges if study design has not been developed for the appropriate analyses. We used a 13-year dataset collected by a mining company to monitor the local population of the threatened northern quoll, *Dasyurus hallucatus*, to explore the application of spatial and non-spatial capture recapture methods to examine the population dynamics of this species. Spatially explicit capture recapture (SECR) methods proved more useful than non-spatial capture recapture in maximising use of the entire dataset, as variability in trap location limited non-spatial analysis to a six year period. SECR estimates of population density suggest that the population was relatively stable between 2006 and 2018, with a decline between 2009–2011 and subsequent recovery in 2012-2013. Finite population change correlated with the prior two-year average standardised precipitation evapotranspiration index, which may reflect a link between primary productivity and food availability for the northern quoll. Using a retrospective approach with estimates of

seniority (the probability that an individual present in year *t* was also present in year *t – 1*) to assess the relative contribution of survival and recruitment to population change, we found that recruitment had a much stronger influence on population change than survival (seniority = 0.18 95% CI 0.12–0.27). The importance of recruitment to population change suggests that the timing of activities for conservation management may be critical for this species, as juvenile mortality may influence the success of management activities. We suggest that if monitoring datasets made even small improvements to study design, their utility to gain inference on population dynamics and contribute to conservation research would increase substantially.

3.2 INTRODUCTION

Extinction rates are increasing globally, especially for iconic taxa such as vertebrates where at least 200 extinctions have been documented in the last century and a third or more are in current decline (Ceballos et al., 2017). Widespread impacts associated with anthropogenic land use are considered the main drivers of vertebrate declines worldwide (Ellis et al., 2010; Troyer et al., 2014; Newbold et al., 2015). However, the examination of such a complex and intertwined suite of impacts is difficult, as their effects are often entangled with the natural variability of the species' environment and demography (Brigatti et al., 2016). Without a thorough understanding of the natural variability of a species' population dynamics, the task of quantifying the causes of decline can be formidable.

Another important, yet relatively under-discussed, component of species management is the regulation of development to manage impacts to threatened species and communities. Regulatory frameworks around the world have adopted a range of tools and instruments to minimise the impacts that land clearing and subsequent anthropogenic land use has on resident wildlife populations (Gibbons & Lindenmayer, 2007; Redpath et al., 2013; Evans et al., 2016). For example, activities approved in Australia under the federal *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act) (‘controlled actions’) are subject to approval conditions that may necessitate the monitoring of conservation significant species. Where these approval conditions are implemented, proponents are often engaged in long-term monitoring programs. However, while environmental regulation has given rise to a number of monitoring activities, the data collected are rarely peer reviewed and/or published. This has also been found to be true for monitoring undertaken both by private industry as well as conservation management agencies (Costello & Wieczorek, 2014; Addison et al., 2015). Thus, the practical application of long-term monitoring data to species conservation is currently limited.

Monitoring programs examine seasonal or annual variation in the size, density and/or vital rates of a population. In many cases, these programs aim to monitor a population’s response to extrinsic variation or disturbance, so that management actions are implemented in a timely manner to increase the probability of successful intervention (Lindenmayer et al., 2013; Evans et al., 2016). A successful monitoring program is carefully planned to address clear objectives (Lindenmayer et al., 2012). This requires a thorough understanding of the species’ biology to ensure the correct parameters are measured, and the implementation of methodology that provides adequate statistical power to detect and quantify change (Schorr et al., 2012; Lindenmayer et al., 2013). However, monitoring frequently is limited by the financial resources and expertise available, which therefore limits the level of insight provided by monitoring data (Evans et al., 2016). The most basic monitoring programs for vertebrate populations use estimates of capture indices such as capture per unit effort (e.g. captures per trap nights), which fail to take into account the influence of imperfect detection in estimates of population size, density and demographic rates (MacKenzie et al., 2005). A number of studies have identified variability in the capture probability of species among years (e.g. Smith et al., 1984), which make capture indices invalid as a tool to estimate relative abundance in many circumstances (Wilson et al., 1996). This variability in capture probability, or imperfect detection, introduces bias into estimates of population change. Where that bias covaries with an impact, analyses risk overlooking population change resulting from intrinsic or extrinsic factors. The development of improved software packages such as MARK (White & Burnham, 1999) addressed this issue by allowing users to model detection probability with group-specific, time-specific and individual-specific covariates (White, 2005). The introduction of these methods to population dynamics research has seen a broad improvement in how population dynamics are measured and interpreted, with authors such as Borchers and Efford (2008) and Royle et al. (2013) continuing to refine and improve the tools available to quantify and understand population change.

The need for best practice abundance estimation is particularly acute in Australia; globally a third of mammal extinctions since 1500 have been Australian mammals, with the majority occurring in the southern-most half of the continent (Woinarski et al., 2011; Fisher et al., 2014). The effects of European settlement, primarily feral cat and fox predation and changes to land use and management, are considered to have driven the majority of Australian mammal declines (Woinarski et al., 2015). Due to its sparse human population, largely-native vegetation cover and lack of red foxes, it was assumed that mammals inhabiting the wet-dry tropics of the north were free from the threatening processes that have caused declines of their southern counterparts (Woinarski et al., 2007, Garnett et al., 2010; Woinarski et al., 2011). However, recent evidence from a range of sources suggests as many as 22 marsupial species in the northern tropics have suffered declines and range reductions since around 1970 (Fitzsimons et al., 2010). For example, the abundance of three species (the northern brush-tailed phascogale, *Phascogale pirate*;

northern quoll, *Dasyurus hallucatus*; fawn antechinus, *Antechinus bellus*) are observed to have declined by more than 90% in some areas (Fitzsimons et al., 2010; Woinarski et al., 2011a).

The northern quoll has suffered a 75% range reduction from across the northern third of the continent, withdrawing to discrete, fragmented populations across northern Australia (Braithwaite & Griffiths, 1994; Hill & Ward, 2010). The factors driving these declines are widely considered to include altered fire regimes (Andersen et al., 1998; Fisher et al., 2003; Vigilante, 2001), increased grazing pressure (Legge et al., 2011), and the effects of introduced species including the exotic cane toad (Oakwood, 2000; Start et al., 2012; Gibson & McKenzie, 2012; Fisher et al., 2014). As a result of its contracted range and the threats posed to its persistence, the northern quoll is listed as endangered under the IUCN Red List of Threatened Species and the Australian EPBC Act (Oakwood et al., 2008).

The northern quoll is an omnivorous, partially semelparous marsupial that experiences a near complete male die-off following their annual breeding season (Oakwood, 2000). This makes the northern quoll, which already exists in fragmented populations, highly susceptible to environmental stochasticity and the combined impacts of threatening processes. It is expected that certain threats to the northern quoll will increase in effect over time, such as habitat loss and degradation associated with increased development, and the spread of the cane toad across the range of the northern quoll (Hill & Ward, 2010). To counter the species' decline, the response in Australia has been twofold; a recent increase in the research of northern quoll biology and threat responses (e.g. Hohen et al., 2016; Hernandez-Santin et al., 2016; Dunlop et al., 2017; Jolly et al., 2017; Cremona et al., 2017), and a regulatory response including the production of a management plan (Hill &

Ward, 2010) and the consideration of impacts to this species in both federal and state decision making for development proposals.

However, while a number of studies have examined the pathways for the effects of threatening processes on the northern quoll (e.g. ingestion of the toxic cane toad, O'Donnell et al., 2010; increased predation by feral and native predators, Cremona et al., 2017), no studies have sought to examine the underlying drivers of population dynamics in the absence of stressors. Further, and most likely due to the logistical constraints of island research, there has been a geographic bias in the literature towards mainland populations of northern quoll (e.g. Begg, 1981; Schmitt et al., 1989; Dickman & Braithwaite, 1992; Oakwood, 2000; 2002; Nelson & Gemmell, 2003; Woinarski et al., 2007; 2008; Spencer et al., 2010; DPaW, 2013; Cremona et al., 2017; Dunlop et al., 2017, but see How et al., 2009; Spencer et al., 2017 and Griffiths et al., 2017). Due to their isolation, islands are considered to be of high conservation value to the long-term persistence of the northern quoll, particularly in their perceived ability to secure populations from the rapid spread of the cane toad (How et al., 2009; Hill & Ward, 2010). Given the recognised importance of island populations in contributing to the long-term conservation of the species, this presents an important knowledge gap.

Given the lack of long-term data for isolated populations of northern quoll, we looked to an underutilised source to seek inference. We used a long-term monitoring dataset of the northern quoll collected by a mining company to examine its population dynamics in an island setting (Koolan Island). Islands present an ideal opportunity to study species population dynamics, as they are often not subject to the entire suite of threats and processes present on the mainland (e.g. Gibson & McKenzie, 2012) and offer the logistical advantage of studying a population confined to a known area of habitat. Koolan Island is one of 2,633 island in the North Kimberley region, a National Biodiversity Hotspot of Australia (http://www.environment.gov.au/biodiversity/hotspots/national-hotspots.htm). Many of these islands may prove highly valuable to the conservation management of the northern quoll through both the protection of existing populations, and translocation programs (Cardoso et al., 2009). For this reason, it is pertinent to seek a further understanding of how the population dynamics of isolated populations of the northern quoll operate in island environments.

We used a mark-recapture dataset spanning 13 continuous years to conduct our analysis which, while being the longest timeframe of any published research on the northern quoll, is uncommon amongst vertebrate studies and particularly rare for tropical species. Most studies surveying mammal presence and abundance in the Kimberley region have occurred over relatively short periods, and studies to examine the drivers of population dynamics of the northern quoll have previously targeted relocated and translocated populations (Cremona et al., 2017; Griffiths et al., 2017). This study also demonstrates the use of capture recapture analysis applied to a dataset collected for analysis using capture per unit effort. Our aim was to estimate demographic parameters and investigate population dynamics in an isolated population using a long-term dataset and a combination of spatial and non-spatial capture mark recapture methods. We were also interested in examining changes in vital rates between modified (anthropogenic) and unmodified (native habitat) parts of the island. We estimated survival, seniority, recruitment and population density, and modelled the impact of habitat type on survival and recruitment. We hypothesised that (1) population density would change between years and be related to climate (food availability) and intensity of mining activity (disturbance) (Dickman et al., 2001), (2) given the short lifespan of the northern quoll, population change would be influenced more strongly by recruitment than survival (Cremona et al., 2017) and (3) survival and recruitment would vary between the mining footprint and the western, less disturbed, side of the island (Fox & Jones, 2004). We also examined the challenges and opportunities of using a dataset created from methods based on capture per unit effort calculations as a case study in demonstrating how monitoring data can be maximised in their application to conservation management.

3.3 METHODS

3.3.1 Study area

Koolan Island (Latitude -16.1, Longitude 123.8; Figure 3.1) is located one kilometre from the Australian mainland in the Buccaneer Archipelago of the west Kimberley, Western Australia, approximately 130 kilometres north of Derby. Koolan island is 2,712 hectares in size, making it one of the largest islands in the region. It is located within the interzone of the Northern Kimberley and Dampierland Interim Biogeographic Regionalisation for Australia (IBRA) bioregions (Thackway & Cresswell, 1995) and has a Proterozoic sandstone lithology (Tyler & Griffin, 1993). This lithology is represented on the island by rugged slopes, ridges, and uplands mantled with rock scree and shallow skeletal soils, with eucalypt savanna woodlands over hummock grass (McKenzie et al., 1995). The landform is incised by ephemeral creek lines across the island that flow during the wet season. A flora and vegetation survey undertaken by Keighery et al. (1995) recorded five major vegetation units on the island, the most widespread being *Eucalyptus miniata – Eucalyptus confertiflora* open woodland generally over *Triodia* hummock grassland and a variable shrub layer. Mangrove communities and vine forest also occur on the island, as do several weed species including rubber vine (*Cryptostegia madagascariensis*) and stinking passionflower (*passiflora foetida* var. *hispida*) (Keighery et al., 1995; J. Thomas pers. obs). Koolan Island is one of the best-studied islands of the Kimberley region in terms of biodiversity, and has been found to have a high diversity of vertebrates considering the island's size and restricted habitat diversity (McKenzie et al., 1995).

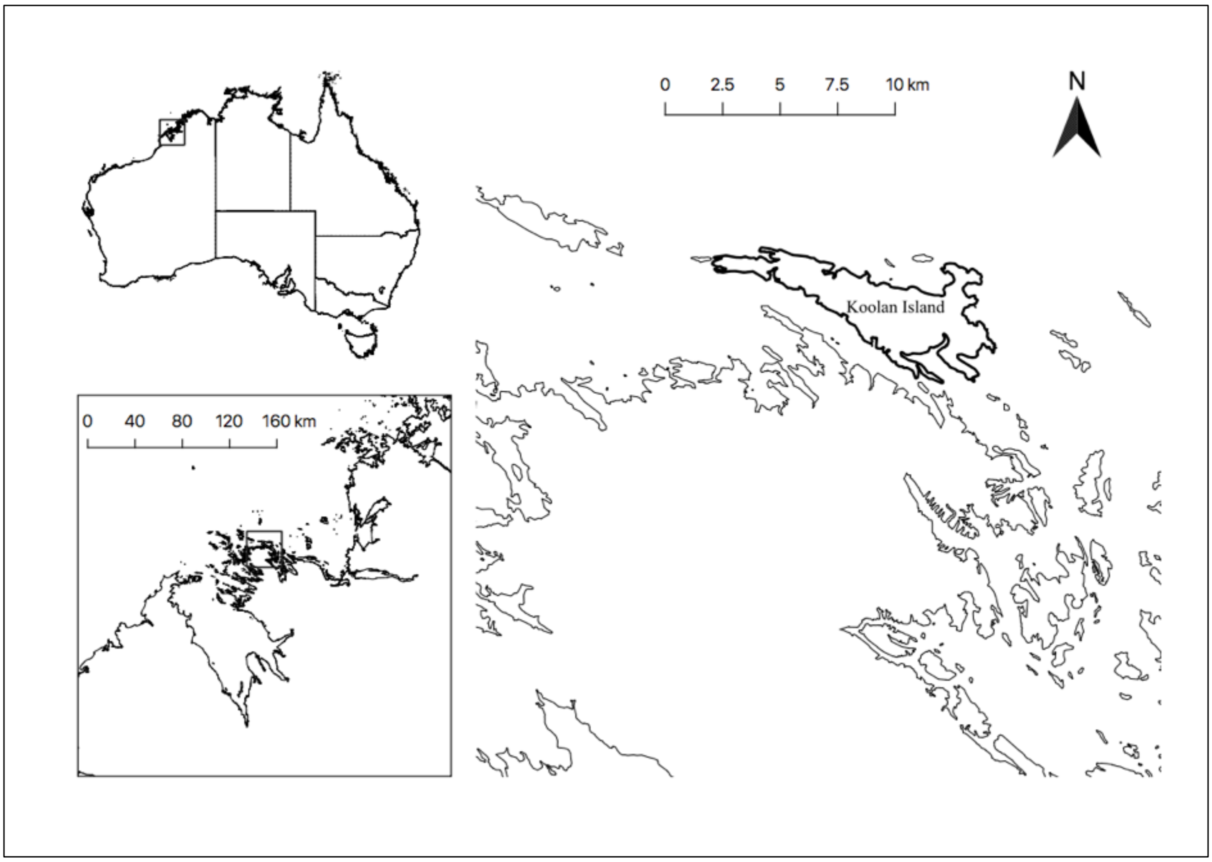


Figure 3.1. Koolan Island, Western Australia

Climatically, Koolan Island is located in the wet-dry tropics of northern Australia and experiences a sub-humid climate with an average annual rainfall of 790 millimetres (BoM, 2018). The wet season extends from December to April, with the majority of rainfall (75%) occurring in January to March (BoM, 2018). Typical of the wet-dry tropics, there is little variation in mean maximum temperature throughout the year (28 – 35C), and a noticeable increase in humidity from January - March (BoM, 2018).

High grade haematite (iron ore) occurs on Koolan island, and an iron ore mine was operated by BHP on Koolan Island from 1965 to 1993, before shutting down for a period of 13 years, and reopened by Mount Gibson Mining Limited from 2006 to present. The mine (open pit) and associated infrastructure occur over approximately one-third of the island (Figure 3.2), with activity on the island similar year-round. The existence of infrastructure on the island has allowed it to be one of the most-studied islands in the Kimberley (McKenzie et al., 1978, 1995; Abbott & Burbidge, 1995; Keighery et al., 1995; Maryan & Reinhold, 2009).

3.3.2 Study species

The northern quoll occurs in mostly fragmented populations across the Pilbara and Kimberley regions of Western Australia, Queensland, and the northern third of the Northern Territory (Hill & Ward, 2010). It is one of four species of the genus *Dasyurus* endemic to Australia, which are nocturnal and occupy the niche of either top-order or mesopredator in a wide range of Australia's habitat types (Maxwell et al., 1996; Burnett, 2001; How et al., 2009; Cremona et al., 2017; Dunlop et al., 2017). The northern quoll has been observed in woodland, forest, vine thickets, mangroves and rocky hills in the form of mesas, plateaus and granite boulder fields, and in anthropogenic environments (Oakwood, 1997, Pollock, 1999; DPaW, 2013). Northern quolls are short-lived and exhibit partial semelparity; males undergo a post-mating die-off, while females have been found to survive into a second and third year in some populations (Dickman & Braithwaite, 1992; Oakwood, 2000; Spencer et al., 2010). The species is known to forage and consume a wide range of food sources, including insects, mammals, birds, reptiles, frogs and fruit (Oakwood, 1997; Dunlop et al., 2017).

3.3.3 Data collection

A mark-recapture program to monitor the status of the northern quoll population has occurred on Koolan Island since 2006, with trapping undertaken on an annual basis in order to comply with conditions of approval to mine under the EPBC Act. During the period of 2006 – 2018, trapping was conducted between March – June each year before the mating season when both adult males and females are present in the population. Data collected November 2008 were not included given the lack of a male cohort during this time of year. Each year, six to nine trap lines were deployed across the island. Each trap line consisted of 25 or 50 traps, with traps spaced 25 metres apart (total of 275 – 300 traps per year; Figure 3.2). Traps were opened between dusk and dawn for five or six consecutive nights, and baited using standard universal bait of peanut butter, rolled oats and sardines. Captured quolls were marked with a microchip to enable identification of recaptured individuals. In 2012, a trap line of 100 traps was also introduced in the western portion of the island, further from the mining footprint, to compare population size between modified and largely unmodified portions of the island (see T15, Figure 3.2).

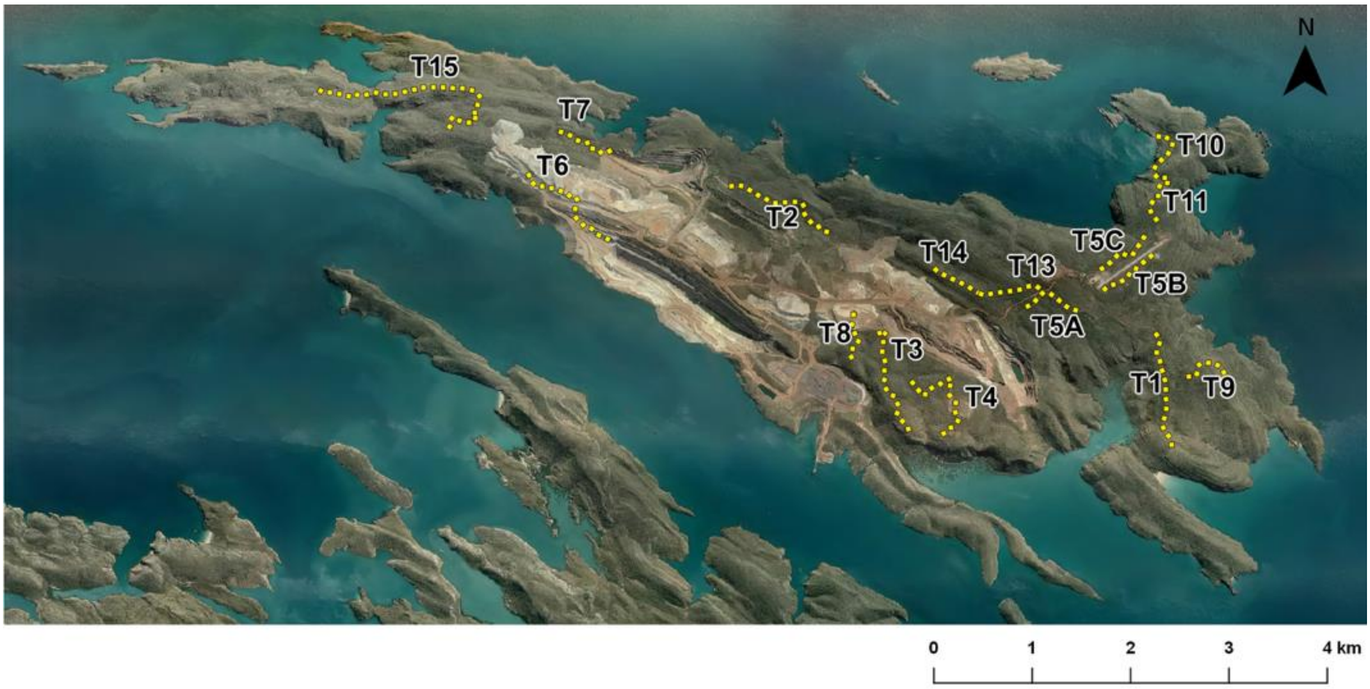


Figure 3.2. Trap lines used on Koolan Island from 2006 – 2018, showing location in relation to mine and associated infrastructure. Note that not all trap lines were used each year.

3.3.4 Data analysis

In order to estimate changes in population density between years and examine the contribution of vital rates to population change, analyses were conducted over several stages and used both spatial and non-spatial methods. By applying both of these methods to our dataset, we strengthened the inference in understanding the drivers of population dynamics for the northern quoll, and how factors such as habitat modification impacts population change.

Spatial CMR Analysis

Spatially explicit capture-recapture (SECR) methods differ from standard methods of capture-recapture analysis in that the capture probability for an individual at a specific trap is a function of the distance between that individual's activity centre and the trap location (Efford, 2004; Borchers & Efford, 2008). We obtained estimates of annual density using maximum likelihood based SECR methods (Borchers & Efford, 2008) using the "secr" package (version 3.1.5, Efford, 2018a) in the statistical program R (version 3.5.0, R Development Core Team, 2018). SECR is comprised of a 'state model' that describes probabilistically the distribution of animal activity centres, and an 'observation model' that describes the probability of observing (capturing) an individual given the distance between its activity centre and the trap location (Borchers, 2012). The distribution of activity centres is most commonly treated as a homogeneous Poisson point process, and several monotonically decreasing detection functions have been used to model the observation process including the half-normal, exponential, and hazard rate detection functions (Efford, 2004; Efford et al., 2009; Royle et al., 2013). SECR methods allow for a number of realistic accommodations in study design including (a) heterogeneity amongst individuals in their exposure to detectors (traps), which is a key source of bias in non-spatial estimators (*sensu* Gardner et al., 2009; Efford & Fewster, 2013), (b) estimates of population density that relate to a specific area rather than ad-hoc estimates of effective trapping area (Royle et al., 2013), and (c) designs where sampling is not continuous across space through time (i.e. changes in location and/or number of traps, as was the case in this study) (Marques et al., 2011; Sollmann et al., 2012; Zimmermann et al., 2013).

Specification of a SECR model involves three steps: (1) choosing a mask, (2) choosing the detection function, and (3) deciding whether to keep parameter values constant or to model them as a function of covariates.

A habitat mask is used to define an area where potential individual activity centres can occur. We used the boundary of Koolan Island derived from the GEODATA Coast dataset (Geoscience Australia, 2004) to apply a habitat mask thereby including 100% of the terrestrial portion of Koolan Island as potential quoll habitat. To avoid bias whilst maximising computational run time, the influence of buffer width and cell size was assessed retrospectively by fitting models with different buffer widths and cell sizes and inspecting density estimates for any bias, as demonstrated in Efford (2018b). Using this methodology, we chose a grid cell spacing of 100 metres and a buffer width of two kilometres.

In order to model the probability of capture as a function of the distance of an animal's activity centre from a trap, we used a multinomial observation model with an exponential detection function. Although the multinomial observation model was developed for use with multi-catch trap data, simulations suggest that density estimates using the multi-catch likelihood is only slightly biased for single-catch data, provided that the level of trap saturation (percentage of traps filled with captured animals per night) is less than 85% (Efford et al., 2009). This study met the trap saturation requirements. Therefore, the multinomial observation model was determined to be suitable for analysis and its use assumed to have a minimal bias on density estimates.

A detection function explains the probability of detecting an animal given the distance of the animal's activity centre from a trap location. A detection function is described by two parameters; g0 (probability of detecting an individual when its home range centre is at trap location), and sigma (a descriptor for how detection probability declines as a function of distance) (Borchers & Efford, 2008; Royle et al., 2013). To determine the most appropriate detection function to use in our analysis, we ran two preliminary analyses; one where the half-normal detection function was used in the observation model, and the other with the exponential detection function. We then used Akaike's Information Criteria (AIC) (Akaike, 1974) to determine which model best fit the data as suggested by Efford (2018c). AIC is a measure of goodness of fit and model complexity, whereby the 'best' (lowest) score is given to the model with the best AIC value (Burnham & Anderson, 2002). The top model contained the exponential detection function while the model containing the half-normal detection function was not supported, with a △AIC value >10. Therefore, according to the framework described by Burnham and Anderson (2002; see below), the exponential detection function was chosen for our final analysis.

In order to obtain annual estimates of population density and associated measures of variance (confidence intervals; CIs), we ran five multi-session SECR models where density varied by session, where g0 varied by session, varied if an individual had previously been captured (behavioural response; e.g. 'trap-happy' vs. 'trap-shy') and was constant, and sigma varied by session, differed by sex and was constant (Table 3.1). Models where g0 and sigma varied by session were included to account for unmeasured variables (e.g. food and water availability) that likely vary between years and may influence capture probability. In addition, a behavioural response for g0 was included as there is evidence from other studies conducted on small mammals that capture probability changes depending on previous capture (Otis et al., 1978; Tanaka, 1980; Seber, 1982). An effect of sex on sigma was included as previous studies on the northern quoll suggests that males move greater distances than females (Cook, 2010), which means that sigma would likely be different between the two sexes. A model where density was held constant was not included as preliminary analysis indicated that density varied between years. Additionally, combinations of these effects on the detection function parameters were not included as preliminary attempts resulted in failure to estimate variance.

Once density estimates were obtained we looked for relationships between external (environmental and anthropogenic) factors and population change. As density estimates between successive years are likely to be correlated we used finite population change (λ) as the response variable, being the ratio of density at year $t + 1$ to year t. As the monitoring program did not measure fine scale environmental variables concurrent with trapping sessions we were limited by the data available and chose annual measures to match the time scale of monitoring activity. We obtained data to calculate two measures that represent a proxy for mining activity including material moved (tonnes of ore and waste rock moved per year) and manning level (average number of staff on site each year). To examine the effects of climate variability and change on the northern quoll population we used the standardised precipitation evapotranspiration index (SPEI). SPEI is a climate index that combines precipitation and temperature data and considers precipitation lost due to evapotranspiration (Vincente-Serrano et al., 2010). We used data inputs from SPEIbase (Beguería et al., 2010) to examine the relationship between λ and the average SPEI over the 12 months prior to trapping (SPEI12), and the average SPEI over the 24 months prior to trapping (SPEI24).

Preliminary analyses of the standardised residuals by graphical means suggested non-normality, heteroscedasticity or presence of outliers for λ ~ material moved, λ ~ manning levels, and λ ~ SPEI12. Therefore for these three models we used Kendall's tau to determine the strength of association and estimated the slope of the regression line using the Theil-Sen estimator (Theil 1950; Sen 1968) to determine the magnitude of effect. To test the hypothesis that Kendall's tau and the Theil-Sen estimate for slope were equal to 0, we used a percentile bootstrap method described in Wilcox (2016) with 1000 bootstrap samples. For this part of the analysis R functions described in Wilcox (2016) and the R package WRS (Wilcox & Schönbrodt, 2014) were used. The model λ ~ SPEI24 did not violate any assumptions so we used a simple linear regression to determine the strength of association between these two variables. The influence of the predictor variables on λ were assessed independently from each other due to the small sample size (n = 9).

Non-spatial CMR analysis

In order to obtain estimates of annual survival and recruitment and assess the relative importance of survival and recruitment to population growth, we used two different parameterisations of a robust design version of Pradel's model; one that estimates survival and seniority (see below), and one that estimates survival and recruitment (Pradel, 1996) using program MARK (White and Burnham, 1999) through the RMark package (version 2.2.4, Laake, 2013; Laake & Rexstad, 2018) in the R software environment (version 3.5.0, R Development Core Team, 2018). The robust design method was used as the relative precision of parameter estimates tends to be better using the robust design's two levels of sampling (Kendall 2019). The model allows for the estimation of apparent survival (phi), seniority (gamma), per capita recruitment (f), capture probability (p) and recapture probability (c).

Seniority is defined as the probability that an individual present in year t was also present in year t – 1 (Pradel, 1996, Nichols et al., 2000). Therefore, it represents the proportion of the population that is composed of surviving individuals from the previous year (i.e. not new recruits). We used the retrospective approach as in Nichols et al. (2000) to assess the relative contribution of survival and recruitment to population change. Using this approach, recruitment was considered to have a greater proportional effect on population change if the gamma parameter was <0.50, while survival was considered to have a greater proportional effect on population change if the gamma parameter was >0.50.

Over the entire dataset, only one male was recaptured in two successive years. Therefore, near-zero male survivorship was assumed, and males were excluded from this part of the analysis. We ran two analyses to examine (1) whether female survival changed between years, the relative contribution of survival and recruitment on population change, and whether this varied between years, and (2) the influence of habitat and year on survival and recruitment.

For the first analysis, we used trap lines from within the mining footprint (i.e. excluding the western trap line) that were surveyed between 2012 and 2018. Trapping conducted between 2006 and 2011 was subject to the addition and removal of trap lines between years, and were therefore excluded in order to meet the assumption of the Pradel model, whereby the study area must be constant over time (Franklin, 2001). We modelled capture and recapture probability as constant by year, and constant over all years. We also modelled capture as equal to recapture and constant by year and constant over all years. Unlike the spatial CMR models, non-spatial CMR models are not able to deal with varying trap usage. Therefore, we did not model within-year variation in capture or recapture because although each trap line was operational for five occasions, not all trap lines were operational on the same nights, but were treated that way in the model. We modelled both phi and gamma as constant over all years and as different by year.

In the second analysis, both trap lines within the mining footprint and in the western portion of the island (Figure 3.2) were used to examine the influence of habitat and year on survival and recruitment. Habitat in the western portion of the island is outside the mining footprint and relatively undisturbed, and therefore provides a comparison against ‘disturbed’ habitat in and adjacent to the mining footprint. In this analysis, we were restricted to using data from 2014 to 2018, as for the first two years of use, trapping in the western portion was subject to high variability in the number of traps used and the number of occasions over which trapping was conducted. Both capture and recapture were modelled the same as in the first analysis, but survival and recruitment were modelled as functions of year + habitat, year, habitat, and constant. We did not include a model in the final analysis with an interaction between habitat and year on survival or recruitment because initial attempts resulted in failure to estimate some parameters.

At present, there are no methods available to assess goodness of fit for robust design models. However, we inspected the beta values and real parameter estimates, in addition to their associated standard errors and confidence intervals, for any signs that parameters were not well estimated (such as extreme large values or standard errors of 0). Any models that met these criteria were excluded from further analysis.

Model selection was conducted using AIC and associated measures such as ΔAIC and AIC_{wi}. Following Burnham and Anderson (2002), we used a ΔAIC of 2 as our threshold for a model being competitive.

Where multiple models have ΔAIC values < 4, there is substantial evidence that no one model best describes the data. To account for model selection uncertainty, we used model averaging to obtain estimates of parameters (Burnham & Anderson, 2002). We used model averaging to obtain estimates of parameters where more than one model had a △AIC <4.

Following this, we examined the 95% confidence intervals for the beta coefficients of these models. If the 95% confidence intervals overlapped zero, we took this to indicate no effect.

Finally, for the 2012 – 2018 analysis, the model-averaged estimates of survival and seniority were used to produce estimates of *f* by the fundamental relationships between gamma, phi and *f* as described in detail by Williams et al. (2002). The delta method was used to calculate standard errors for all derived parameters (Powell, 2007).

3.4 RESULTS

There were 1311 captures of 753 individuals of *D. hallucatus,* including 316 females and 437 males. Marked individuals were rarely recaptured within trapping sessions (mean captures per individual = 1.75; minimum = 1 and maximum = 6).

3.4.1 Spatially explicit capture-recapture

Out of the candidate model set, a SECR model where g0 varied by session and sigma varied by session ranked first, with an AIC_{wi} = 100% (Table 3.1). Therefore, all further inference was based on this model. Session-specific estimates of g0 ranged between 0.01 (95% CI 0.004–0.02) in 2011, and 0.18 (95% CI 0.179–0.182) in 2016. Session-specific estimates of sigma ranged between 95.26 m (95% CI 55.87–162.41) in 2013, and 403.63 m (95% CI 239.24–680.96) in 2011. Estimates of annual density (Figure 3.3) from model *g0~session, sigma~session* ranged between 19 individuals km^{-2} in June 2013 (95% CI 9-40) to 3 individuals per square kilometre in April 2011 (95% CI 2–6).

Table 3.1. Model selection results for spatially explicit capture recapture estimates. K is the number of parameters. AIC is Akaike's Information Criterion. △AIC shows the difference between the model AIC and the AIC of the highest ranked model. AIC_{wi} is the relative likelihood of the model normalised to sum to 1. b denotes an effect of previous capture; session denotes a year effect; g denotes an effect of sex.

Model	K	AIC	△AIC	AIC_{wi}
D~session g0~session sigma~session	36	10400.49	0	1
D~session g0~b sigma~1	15	10472	71.509	0
D~session g0~1 sigma~1	14	10491.91	91.419	0
D~session g0~b sigma~g	16	11364.38	963.889	0
D~session g0~1 sigma~g	15	11383.4	982.909	0

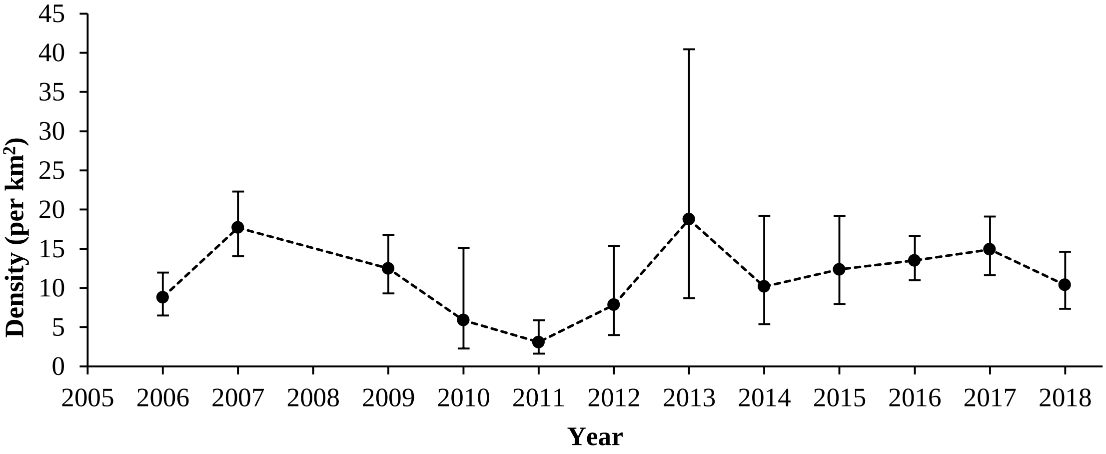


Figure 3.3. Annual density per square kilometre estimated using spatially explicit capture recapture methods, shown with 95% confidence intervals.

There was no correlation between finite population change with material moved (τ_{Kendall} = -0.28, p = 0.38; $\beta_{\text{Thiel Sen}}$ = -7.51e-09, SE = 2.74e-08, p = 0.37) manning level (τ_{Kendall} = -0.17, p = 0.46; $\beta_{\text{Thiel Sen}}$ = -6.05e-04, SE = 1.70e-03, p = 0.46) or SPEI12 (τ_{Kendall} = 0.22, p = 0.54; $\beta_{\text{Thiel Sen}}$ = 0.17, SE = 0.57, p = 0.60). SPEI24 had a positive correlation with finite population change ($r_{Pearson}$ = 0.66, p = 0.05; β = 0.91, SE = 0.39, p = 0.05) (Figure 3.4).

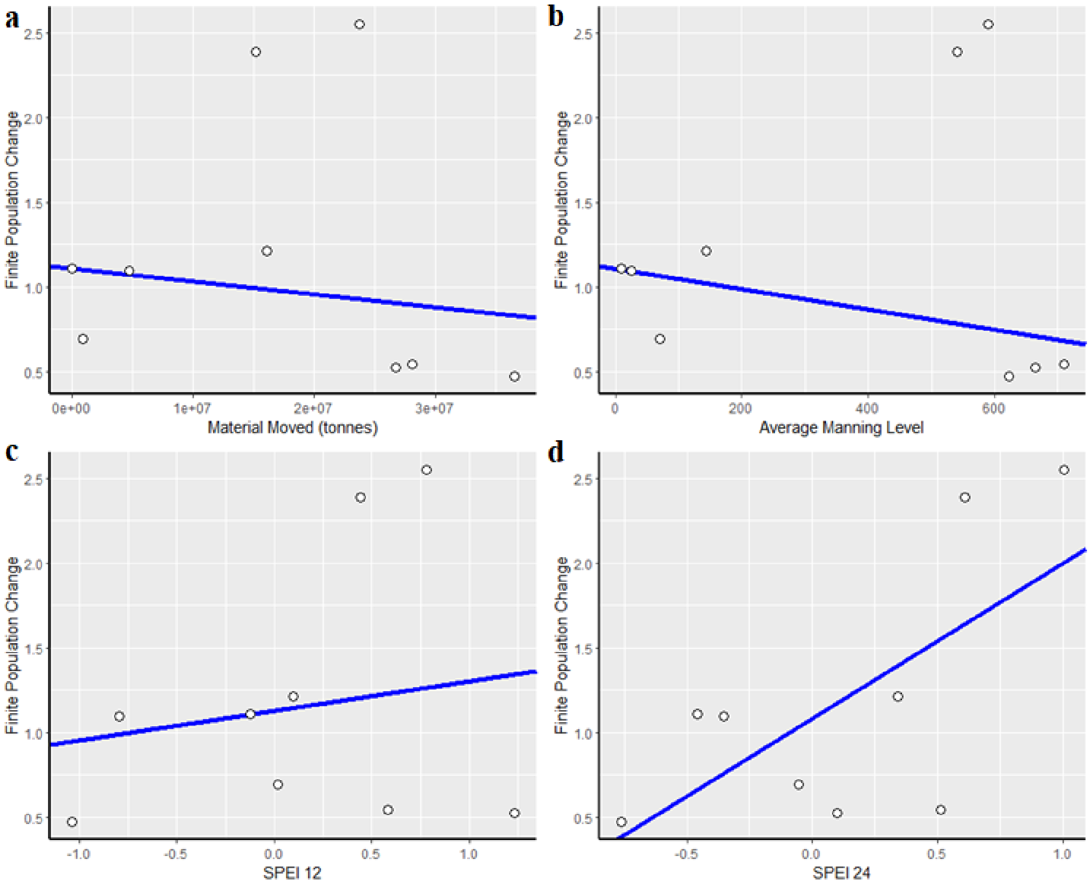


Figure 3.4. Association between finite population change and (a) material moved (tonnes), (b) average manning level, (c) SPEI12 and (d) SPEI24. Blue lines are model-derived.

3.4.2 Non-spatial capture-recapture

Initial attempts to run a model where all parameters varied by session resulted in poor estimates of several parameters. Therefore, the only sub-models of the capture probabilities that we included in the final analysis were *p=c ~ session*, *p~1* and *c~1*, and *p=c ~1*.

Effect of survival and recruitment on population change

In the 2012 – 2018 analysis to examine both if female survival differed between years and the relative contribution to survival and recruitment on population change (as given by the estimate of seniority), the top model (*phi~1*, *gamma~1*, *p=c ~ session*) had an AIC_{wi} of 83%. The next best model for this analysis contained survival differing by year and seniority as constant, and capture equal to recapture but different between years (△AIC =

4.7). Inspection of the 95% confidence intervals for the beta coefficients from the second-best model for survival overlapped 0, suggesting there was no difference in survival between years. In addition, model averaged estimates of annual survival show considerable overlap between years (Figure 3.5), and therefore further inference was based upon estimates from the top model. The estimate of seniority from the top model was 0.18 (95% CI 0.12–0.27), indicating that recruitment has a much stronger impact on population change than survival. There was no evidence that seniority varied significantly between 2012–2018, and model averaged estimates showed little to no variation. The estimate of survival from the top model was 0.19 (95% CI 0.13–0.27). Estimates of annual recruitment probability derived from the model averaged estimates of survival and seniority ranged from 0.90 (SE ± 0.40) for 2013, and 0.82 (SE ± 0.30) for 2016. Effectively, this suggests that each female from time (i) contributed 0.82 - 0.90 females to time (i + 1) (Cooch and White 2017).

Table 3.2. Model selection results for female northern quoll apparent survival and seniority (Pradel Robust Design). Phi denotes survival, gamma denotes seniority, p denotes probability of capture, c denotes probability of recapture, session denotes year. See Table 3.1 for an explanation of table column headings.

Model	K	AIC	△AIC	AIC_{wi}
Phi(~1)Gamma(~1)p(~session)c()	9	1815.06	0	0.83
Phi(~year)Gamma(~1)p(~session)c()	14	1818.96	3.90	0.12
Phi(~1)Gamma(~year)p(~session)c()	14	1820.7	5.64	0.05
Phi(~year)Gamma(~year)p(~session)c()	19	1828.32	13.26	0.00
Phi(~1)Gamma(~year)p(~1)c(~1)	9	1842.71	27.65	0.00
Phi(~year)Gamma(~1)p(~1)c(~1)	9	1844.03	28.97	0.00
Phi(~1)Gamma(~1)p(~1)c(~1)	4	1846.02	30.96	0.00
Phi(~1)Gamma(~year)p(~1)c()	8	1847.89	32.82	0.00
Phi(~year)Gamma(~1)p(~1)c()	8	1849.23	34.17	0.00
Phi(~1)Gamma(~1)p(~1)c()	3	1851.23	36.17	0.00
Phi(~year)Gamma(~year)p(~1)c(~1)	14	1851.26	36.20	0.00
Phi(~year)Gamma(~year)p(~1)c()	13	1856.56	41.50	0.00

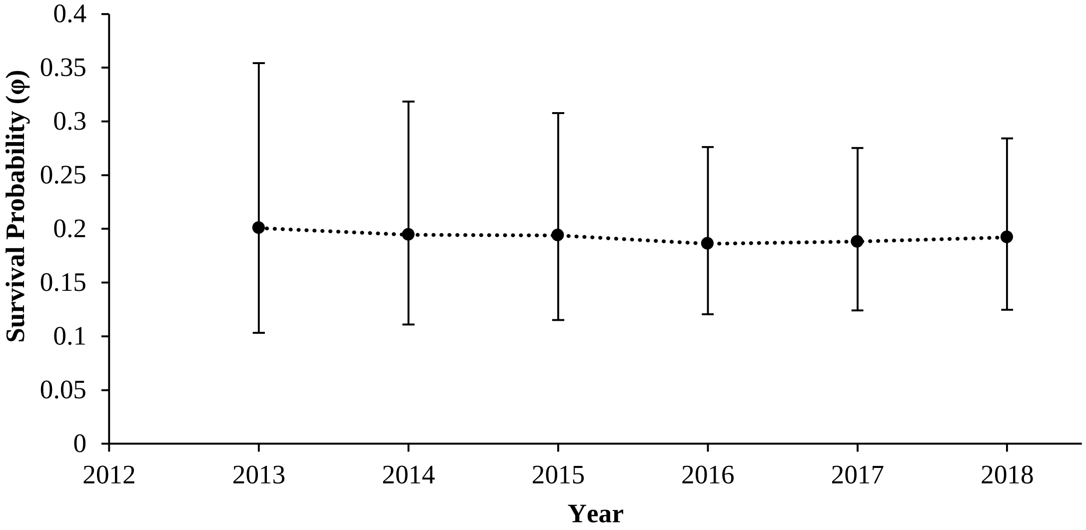


Figure 3.5. Model averaged estimates of apparent female survival over the years 2012 - 2018.

Effect of habitat and time on survival and recruitment

The top model for the analysis to examine the effect of habitat and year on survival and recruitment between 2014 – 2018 was *phi~1, f~1, p=c ~ session* (AIC_{wi} = 0.37). However, an additional three models had △AIC values < 4 (Table 3.3). Two models included habitat having an influence on recruitment, and one included recruitment varying by year. An examination of the beta coefficients and the 95% confidence intervals of these effects revealed that the confidence intervals included zero, indicating a lack of clear evidence for year or habitat influencing recruitment. Therefore, we based our inferences of survival and recruitment solely on the top model. Estimates from the top model of survival and recruitment were 0.17 (95% CI 0.12–0.25) and 0.75 (95% CI 0.58–0.87) respectively.

Table 3.3. Model selection results for the top 12 of 48 candidate models for female northern quoll apparent survival and recruitment (Pradel Robust Design). Phi denotes survival, f denotes recruitment, p denotes probability of capture, c denotes probability of recapture, session denotes year, and habitat denotes the effect of habitat. See Table 3.1 for an explanation of table column headings.

Model	K	AIC	△AIC	AIC_{wi}
Phi(~1)f(~1)p(~session)c()	7	1786.56	0	0.37
Phi(~1)f(~habitat)p(~session)c()	8	1787.991	1.43	0.18
Phi(~habitat)f(~1)p(~session)c()	8	1788.347	1.79	0.15
Phi(~1)f(~session)p(~session)c()	10	1789.666	3.11	0.08
Phi(~habitat)f(~habitat)p(~session)c()	9	1789.971	3.41	0.07
Phi(~1)f(~habitat + session)p(~session)c()	11	1791.089	4.53	0.04
Phi(~habitat)f(~session)p(~session)c()	11	1791.467	4.91	0.03
Phi(~session)f(~1)p(~session)c()	10	1792.216	5.66	0.02
Phi(~habitat)f(~habitat + session)p(~session)c()	12	1793.076	6.52	0.01
Phi(~session)f(~habitat)p(~session)c()	11	1793.648	7.09	0.011
Phi(~habitat + session)f(~1)p(~session)c()	11	1793.935	7.38	0.01
Phi(~session)f(~session)p(~session)c()	13	1795.541	8.98	0.00

3.5 DISCUSSION

Understanding how the population dynamics of a species operates in the absence of immigration, emigration and threatening processes is important because it provides insight into the underlying fluctuations of a population as influenced by the species' life history and provides a level of predictive power in managing populations exposed to potential threats (Schorr, 2012; Troyer et al., 2014). We analysed a dataset collected to monitor a population using a capture index (captures per trap-night) in order to demonstrate the possibilities in maximising the value of these data by applying more sophisticated methods yielding stronger inference with less potential for problematic bias. In doing so we gained important insight on the underlying population dynamics of the northern quoll and the challenges facing isolated populations of this semelparous marsupial. The study period is the longest thus far for a pre-existing (non-relocated) population of northern quoll, with previous inference gained from a maximum of three to four years. As a result, the findings below contribute not only to the future conservation management of this species, but to our overall understanding of how dasyurids operate in the wet-dry tropics of Australia.

3.5.1 Population trends

We were able to gain estimates of annual density using spatially explicit capture recapture methods using data that could not be analysed using non-spatial capture recapture methods, due to high levels of variability in trap location across years (2006 – 2012). Spatially explicit capture recapture models indicate that the population was subject to fluctuations, but had the capacity to restabilise within the period studied. Furthermore, non-spatial capture recapture analysis indicates that survival and recruitment did not vary significantly in the second half of the study period.

Our density estimates (3 - 19 animals km^{-2}) are lower than those presented for northern quolls on other islands (173 - 287 animals km^{-2} on Astell Island, 115 - 157 animals km^{-2} on Pobasso Island, Griffiths et al., 2017). This difference may be related to the dynamics of the translocated populations on Astell and Pobasso Islands, due to the presence of larger areas of better quality habitat on those islands, or differences in how density is estimated between studies (Obbard et al., 2010). We note that our analysis assumed density across the island was homogenous and future work could evaluate this assumption. Based on the data available in this study, we were not able to take this into account. While animals have been observed using artificial habitat within the mining footprint, finer-scale analysis of density across habitats on the island may result in better density estimates. This assumption notwithstanding, spatially explicit capture recapture methods proved useful in identifying population trends over the 13 year study period.

We also examined the effect of four potential drivers of finite population change using estimates from the spatial CMR analysis. Neither of the measures for mining activity showed a relationship with population change. While we note that manning levels and material moved are only a small subset of the potential factors to describe mining operations, a lack of relationship with finite population change is interesting given the recommencement of mining activities in 2006. Given the associated increase in traffic and activity, this had the potential to exert a negative influence over population growth through increased human-wildlife interactions. In a study of the northern quoll in the Northern Territory, Oakwood (1997) noted that the species has been observed foraging from human food sources (bin raiding). Observations by the authors and mining staff on the island indicate that quolls explore anthropogenic areas and may be capable of exploiting artificial resources (see Chapter 4; J. Tomich, pers comm.). This may in part buffer the northern quoll population from other potential negative impacts of mining, but presents its own particular challenges such as managing animal access to human food and food waste, and shelter areas that may risk the animal becoming trapped or harmed.

Although further analysis is required to fully understand the interactions between northern quolls and mining operations, it appears that over the period of this study the local northern quoll population was resilient to environmental variability and not in a continuous decline. However, it is pertinent to note that the majority of habitat modification regarding the mine occurred during its previous operations in the 1960s and 1990s, and the effect of this historic habitat loss was not able to be quantified.

We did find a relationship between population change and the average SPEI index of the two years prior to trapping. It should be noted that finite population change was derived from point estimates of density and did not include associated uncertainty, and the relationship appears to be driven largely by the last two time periods (see Figure 3.4d). Therefore, any inference obtained from this analysis should be viewed in light of these limitations. Nonetheless, SPEI index is know to correlate with net primary productivity in an environment (Chen et al., 2013), and our results may reflect the impact of food resource availability on population growth. The two-year time period is of interest and may reflect the response time between rainfall and ecosystem-level changes in the wet-dry tropics of Australia. A study by Thibault et al. (2010) examining ecosystem-level responses to rainfall in an arid environment found that time lags in response to rainfall increased with trophic level, with plants responding to same-season precipitation and insectivores responding to precipitation in the previous year. The underlying logic that a time-lag reflects the time required for primary consumers (e.g. invertebrates) to convert primary productivity into increased biomass is reasonably applied to our study area. Identifying such responses and their time lags aid in understanding both fundamental population dynamics as well as management challenges; a lag of up to two years is a crucial consideration for regulatory authorities as well as conservation managers anticipating a response to management actions.

3.5.2 Recruitment

This was the first study to examine the endogenous drivers of population dynamics for the northern quoll in a natural population without the threats present on the mainland. Our study confirms suggestions by Cremona et al. (2017), who used population viability analyses to suggest that recruitment is most important to the persistence of reintroduced populations of this species. We found that annual variability in population change is strongly reliant on recruitment. The importance of recruitment in short-lived species has been identified in a number of studies (e.g. Schorr, 2012; Troyer et al., 2014) but is particularly important for semelparous or partially semelparous species where individuals may breed only once in their lifetime (e.g. Sale et al., 2008). Recent studies of the didelphid marsupials of South America, analogous to the dasyurids of Australasia, have identified full or partial semelparity and the importance of recruitment in driving population growth (Leiner et al., 2008; Baladron et al., 2012; Puida & Paglia, 2015).

The findings of this study demonstrate the considerable dependence that isolated populations of the northern quoll have on annual recruitment success. Our study population suffered a significant drop in population density in 2009 – 2011, which followed a cyclone in December 2009. Northern quolls have been observed to bear young later on Koolan Island than has been reported for other populations, and the cyclone occurred at a time in the annual cycle when the young were likely to have just become independent or may have still been deposited in their mother’s den (thereby being at a maximum level of susceptibility to environmental perturbations). Cyclones impact ecosystems through both intense rainfall and flooding, and the effects of high winds or ‘wind storms’. These high velocity winds cause vegetation damage and habitat-scale impacts through stem and branch breakage, uprooting trees and other vegetation, and defoliation (Brokaw & Walker, 1991; Zimmerman et al., 1994; Burslem et al., 2000). The timing of the cyclone may have impacted recruitment through direct mortality of individuals (especially those denning in trees), or by impacts to foraging habitat and food resources. Interestingly, Cremona et al. (2017) also observed a population crash in this species that coincided with cyclonic flooding in March, while Griffiths et al. (2017) noted no population-scale impact from two cyclones that occurred in March 2005 and April 2006.

Our study population shows resilience to disturbance by recovering to pre-decline levels over the following two years, with no conceivable assistance from recruitment via immigration. While our data show that in favourable environmental conditions an isolated population can recover from a significant decrease in population size, it does highlight the challenges that isolated populations of this species face. Had a second extreme weather event occurred in the following years, or another threat been introduced to the population (i.e. cane toads), it is reasonable to expect that the population would not have recovered. In particular, our results may indicate that a frequency of catastrophic events every three years or less may require management intervention for isolated populations of this species. For smaller populations or those that have very low genetic diversity (e.g. Adolphus Island or Dolphin Island; Spencer et al. 2017), less frequent or even a standalone cataclysmic event may put a population on a one-way trajectory to decline.

The susceptibility of isolated populations of northern quoll has important conservation implications for translocated or reintroduced populations, as long-term resources should be allocated for ongoing monitoring and the implementation of active management strategies at short notice. In a genetic study of the northern quoll population on Koolan Island, Spencer et al. (2017) found that while the population was not genetically depauperate and had no indication of a recent or long-term bottleneck, it had only a third of the allelic diversity present in mainland populations. This, coupled with the influence of demographic stochasticity on small populations and the species' dependence on recruitment success, makes isolated populations of the northern quoll particularly susceptible to changes in their environment. A recent study demonstrated a successful translocation program on two islands but attributed this success to the presence of high quality habitat and the absence of threatening factors, thus necessitating ongoing management to monitor for environmental change (Griffiths et al., 2017). Such changes may be in the form of environmental stochasticity and the impact of severe weather events, or the introduction of new threats such as the toxic cane toad, currently considered to be the primary biosecurity risk to island populations of northern quoll (Hill & Ward, 2010).

In contrast, the findings of this study alongside Hohnen et al. (2016), Cremona et al. (2017) and Griffiths et al. (2017) may suggest that northern quoll persistence is most stable in a metapopulation dynamic, and that conservation efforts would be best spent on creating or maintaining subpopulations with sufficient connectivity between them. In an analysis of gene flow amongst populations across the Kimberley region, Hohnen et al. (2016) found that individuals separated by open plains and within high rainfall areas were more closely related. This suggests that in favourable conditions and habitats, northern quolls may have the ability to emigrate between populations, thus supplementing recruitment in subpopulations.

The strong influence of recruitment on population change, as demonstrated by our estimates of seniority, has important consequences for the timing of activities that affect conservation management. Our results indicate that impacts to northern quoll habitat will have the greatest potential for impact when juveniles are present in a population. Therefore, the impacts of habitat loss and modification may be minimised by excluding these activities from June to November. This is supported by a study of the impact of fire on four small mammal species in northern Australia, where Griffiths and Brook (2015) hypothesised that late dry season fire may impact northern quoll populations more than early dry season fire via elevated juvenile mortality. Furthermore, this information could be used to justify sourcing individuals for translocation programs just prior to the breeding season. This is illustrated by Griffiths et al. (2017), who observed a successful translocation of individuals sourced from mainland populations in the months between juveniles becoming independent and the breeding season (February – March) for a six year period post-release. Similarly, feral predator management targeted in the period where young are deposited in dens (September to November) could lead to better population outcomes via increased recruitment.

3.5.3 Survival

Based on the long-term trapping data used in this study, male survival appears to be generally constant between years. The estimates of female survival in this study make for an interesting comparison with prior studies conducted on the mainland and in translocated populations. We found an annual female survival rate of 19%. Following the reintroduction of northern quolls on the mainland, Cremona et al. (2017) found annual female survival to be 23.69%, which is similar to the female survival rate estimated in our study. However, northern quolls in their study were subject to canid predation, which is not a threat to northern quolls on Koolan Island. In two translocated populations of northern quolls on islands, Griffiths et al. (2017) found female survival to be 63% in the years following the initial translocation, attributing a high survival rate to the absence of predators and presence of high quality habitat in the form of rocky woodland. In our study, the population was largely stable and without cane toads or feral predators. The island does contain rocky areas, but the proportion of rocky woodland on Koolan Island to the islands studied by Griffiths et al. (2017) may differ. As a ‘natural’ (i.e. not translocated) population, the Koolan Island northern quoll population may be more affected by density dependence than newly translocated populations. Further, northern quolls used in translocation were sourced from the mainland, and may have had an increased ability to exploit available resources than their island counterparts given their larger size (How et al., 2009). Additional research would be beneficial to further explore differences in adult survival between island populations of this species.

Juvenile northern quolls are altricial for three months following birth, relying solely on the mother to provide food (Oakwood, 2000). Therefore, females with young must expend a high amount of energy foraging each night to obtain sufficient food to maintain themselves and support their offspring. Females on Koolan island are smaller but have similar litter sizes to their mainland counterparts (Spencer et al., 2017), and therefore may be more reliant on nightly foraging success to maintain body condition during this time. Given the toll this period must take on adult females, it is possible that the low survival rate on the island reflects the impact of the breeding season on small females, and that females surviving to a second year are those that did not successfully raise young in their first year. This may be because they did not accrue sufficient energy reserves before the breeding season, or they had juveniles that perished during the young in den phase, thus allowing them to increase their net energy gain from foraging activities. This may have interesting implications for recruitment success. Age-dependent reproductive success has been demonstrated in a number of studies (e.g. Wooller et al., 1990; Dugdale et al., 2011), and the potential for first and second-year females to vary in their ability to rear a higher number of young has not previously been explored.

3.5.4 Capture recapture methods and study design

Our study used a combination of spatially explicit and non-spatial capture recapture methods to examine population trends over time. We observed that, while density decreased over two years following a significant weather event in 2009, the population recovered in the following years to a level similar to that prior to the cyclone. Using capture recapture models to examine population change over time provides context to year-by-year fluctuations. This is key when considering the application of ‘trigger points’ in monitoring programs to implement management interventions (or, as in many circumstances where monitoring is conditional to legislative development approval, to trigger compliance action). If simplistic trigger points (for example, a drop in captures per trap-night in any one year to a minimum threshold) are used, especially without *a priori* knowledge of baseline population dynamics, a drop in captures may be mistaken for a downwards trajectory when it is in fact within the normal range of population size for that population. Further, monitoring that does not simultaneously consider external forces on population dynamics (such as cyclonic events) may lead to incorrect assumptions as to what is causing the decline.

Despite a number of resources being available to assist in the design of monitoring programs (e.g. Pollock et al., 2002; Kéry & Schmid, 2004; Lindenmayer, 1999; Goldsmith, 2012), a review by Lindenmayer et al. (2013) found that many conservation monitoring programs could be improved in their data collection methodology and designated trigger points. The same is likely to be true for monitoring undertaken by industry to comply with their regulatory responsibilities to monitor threatened species potentially affected by approved development. The improved consideration of monitoring program methods and analysis in regulatory decision making when development is approved would result in more meaningful data to not only understand the monitored population on a local scale, but also contribute to the wider knowledge of how that species varies within its range. Data collection methodology presented a key challenge in our study. While the use of spatial and non-spatial capture recapture methods extracted more information from the monitoring program than what is possible using calculations of captures per trap night, the complexity involved in circumnavigating variation in trap effort and location with a relatively low recapture rate required a significantly larger amount of time and resources than if this variation was minimised (Rovero et al., 2013). In these datasets, more effort is often placed on maintaining a number of ‘trap nights’ than maintaining spatial consistency (i.e., if a trap line could not be used, a new one was created). We suggest here that resources would be better spent on ensuring a smaller set of trap lines were used in consistent locations between years, and if possible, for longer than five days (Silver et al., 2004; Tobler & Powell, 2013). This would likely increase the recapture rate and therefore the quantitative power of analysis. Recent efforts on Koolan Island support this approach, with trapping over nine days and 100 traps yielding a recapture rate of 2.3, compared with 1.7 in our study (M. Ladyman pers comm.).

3.5.5 Conclusions

Mining companies have comparatively more stable financial resources, and are motivated by an obligation to monitor populations to allow extraction activities to continue. Where development and extraction are ongoing, such as for many mining operations, monitoring may continue for 5 – 20 years. It stands to reason that wildlife conservation managers explore the wider applications of these monitoring programs, as has been done in mine rehabilitation in its contribution to understanding rehabilited ecosystems (e.g. Doley & Audet, 2013; Lee et al., 2013; Craig et al., 2014; Laarmann et al., 2015).

When regulators approve monitoring programs to manage populations potentially affected by proposed development, consideration should be given to maximise the potential applications of the data when impacts to threatened species habitat is approved. This could be facilitated through defining aspects of the methodology that may not usually be considered, for example ensuring that trapping effort and spatial coverage is the same each year, and considering environmental variation in its ability to impact both the population and capture probability (Willson et al., 2011). Further, improving industry and government’s capacity to separate exogenous environmental influences (i.e. climate) from management activities imparts more certainty to both regulators and proponents, thereby increasing the effectiveness of regulation and transparency around the state of managed populations.

3.6 REFERENCES

Abbott, I., & Burbidge, A.A. (1995). The occurrence of mammal species on the islands of Australia: a summary of existing knowledge. *CALMscience, 1,* 259–324.

Addison, P. F. E., Flander, L. B., & Cook, C. N. (2015). Are we missing the boat? Current uses of long-term biological monitoring data in the evaluation and management of marine protected areas. *Journal of Environmental Management*, *149*, 148-156.

Akaike, H. (1974). A new look at the statistical model identification. *IEEE transactions on automatic control*, *19*(6), 716-723.

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *The Journal of Wildlife Management*, *74*(6), 1175-1178.

Beguería, S., Vicente-Serrano, S.M., & y Angulo, M., (2010). A multi-scalar global drought data set: the SPEIbase: A new gridded product for the analysis of drought variability and impacts. *Bulletin of the American Meteorological Society. 91*, 1351-1354.

BOM (Bureau of Meteorology). (2018). Climate Data Online. Retrieved from http://www.bom.gov.au/climate/data/index.shtml?bookmark=136.

Borchers, D. (2012). A non-technical overview of spatially explicit capture–recapture models. *Journal of Ornithology, 152*(2), 435-444.

Borchers, D. L., & Efford, M. G. (2008). Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometric*s, *64*(2), 377-385.

Brigatti, E., Vieira, M. V., Kajin, M., Almeida, P. J. A. L., De Menezes, M. A., & Cerqueira, R. (2016). Detecting and modelling delayed density-dependence in abundance time series of a small mammal (*Didelphis aurita*). *Scientific Report*s, *6,* 19553.

Brokaw, N.V.L. & Walker, L.R. (1991) Summary of the effects of Caribbean hurricanes on vegetation. *Biotropica*, 23, 442-447.

Burnham, K. P. & Anderson, D. R. (2002). Model selection and multimodel inference: a practical information-theoretic approach. *Ecological Modelling.* Springer Science & Business Media, New York, New York, USA.

Burslem, D. F. R. P., Whitmore, T. C., & Brown, G. C. (2000). Short-term effects of cyclone impact and long-term recovery of tropical rain forest on Kolombangara, Solomon Islands. *Journal of Ecology*, 88(6), 1063-1078.

Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, *114*(30), E6089-E6096.

Chen, T., Van der Werf, G. R., De Jeu, R. A. M., Wang, G., & Dolman, A. J. (2013). A global analysis of the impact of drought on net primary productivity. *Hydrology and Earth System Sciences*, *17,* 3885-3894.

Clutton-Brock, T., & Sheldon, B. C. (2010). Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution*, *25*(10), 562-573.

Costello, M. J., & Wieczorek, J. (2014). Best practice for biodiversity data management and publication. *Biological Conservation*, *173*, 68-73.

Cooch, E. & White, G. (2017). *Program MARK: A gentle introduction*. Colorado State University, Colorado U.S.A.

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

Craig, M. D., Grigg, A. H., Hobbs, R. J., & Hardy, G. E. S. J. (2014). Does coarse woody debris density and volume influence the terrestrial vertebrate community in restored bauxite mines? *Forest Ecology and Management*, *318*, 142-150.

Cremona, T., Crowther, M. S., & Webb, J. K. (2017). High mortality and small population size prevent population recovery of a reintroduced mesopredator. *Animal Conservation*, *20*, 555-563.

Dickman, C. R., Haythornthwaite, A. S., McNaught, G. H., Mahon, P. S., Tamayo, B., & Letnic, M. (2001). Population dynamics of three species of dasyurid marsupials in arid central Australia: a 10-year study. *Wildlife Research, 28*(5), 493-506.

Doley, D., & Audet, P. (2013). Adopting novel ecosystems as suitable rehabilitation alternatives for former mine sites. *Ecological Processes, 2*(1), 22.

Duffy, J.E. (2003). Biodiversity loss, trophic skew and ecosystem functioning. *Ecology letters*, *6*(8), 680-687.

Dugdale, H. L., Pope, L. C., Newman, C., Macdonald, D. W., & Burke, T. (2011). Age-specific breeding success in a wild mammalian population: selection, constraint, restraint and senescence. *Molecular Ecology*, *20*(15), 3261-3274.

Efford, M. (2004). Density estimation in live-trapping studies. *Oikos*, *106*(3), 598-610.

Efford, M. (2018a). A tutorial on fitting spatially explicit capture-recapture models in *secr*. Retrieved from http://www.otago.ac.nz/density/pdfs/secr-tutorial.pdf.

Efford, M. (2018b). Habitat masks in the package *secr*. Retrieved from http://www.otago.ac.nz/density/pdfs/secr-habitatmasks.pdf.

Efford, M. G. (2015). secr: Spatially explicit capture-recapture models. *R package version*, *2*(4).

Efford, M. G., & Fewster, R. M. (2013). Estimating population size by spatially explicit capture–recapture. *Oikos*, *122*(6), 918-928.

Efford, M. G., Borchers, D. L., & Byrom, A. E. (2009). Density estimation by spatially explicit capture–recapture: likelihood-based methods. In *Modeling demographic processes in marked populations* (255-269). Springer, Boston, MA.

Ellis, E. C., Goldewijk, K. K., Siebert, S., Lightman, D. & Ramankutty, N. (2010). Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography 19*(5), 589–606.

Evans, D.M., Che-Castaldo, J.P., Crouse, D., Davis, F.W., Epanchin-Niell, R., Flather, C.H., Frohlich, R.K., Goble, D.D., Li, Y.W., Male, T.D., Master, L.L., Moskwik, M.P., Neel, M.C., Noon, B.R., Parmesan, C., Schwartz, M.W., Scott, J.M., Williams, B.K. Species recovery in the United States: Increasing the effectiveness of the Endangered Species Act. *Ecological Society of America*, 20, 1-28.

Fox, J. C., & Jones, M. E. (2004). Spotted-tailed quoll (*Dasyurus maculatus maculatus*). Linking landscape ecology and management to population viability analysis, 173.

Gardner, B., Royle, J. A., & Wegan, M. T. (2009). Hierarchical models for estimating density from DNA mark–recapture studies. *Ecolog*y, *90*(4), 1106-1115.

Garnett, S. T., Woinarski, J. C., Crowley, G. M., & Kutt, A. S. (2010). *Biodiversity conservation in Australian tropical rangelands* (191-234). Wiley-Blackwell: Chichester, UK.

Geoscience Australia. (2004). Geodata Coast 100K. Geoscience Australia, Canberra. Retrieved from https://data.gov.au/dataset/geodata-coast-100k-2004.

Gibbons, P., & Lindenmayer, D. B. (2007). Offsets for land clearing: no net loss or the tail wagging the dog? *Ecological Management & Restoration*, *8*(1), 26-31.

Gibson, L. A., & McKenzie, N. L. (2012). Identification of biodiversity assets of selected Kimberley islands: background and implementation. *Records of the Western Australian Museum, Supplement, 81*, 1-14.

Goldsmith, F. B. (2012). *Monitoring for conservation and ecology* (Vol. 3). Springer Science & Business Media.

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.

How, R. A., Spencer, P. B. S., & 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.

Jeppsson, T., & Forslund, P. (2012). Can life history predict the effect of demographic stochasticity on extinction risk? *The American Naturalist*, *179*(6), 706-720.

Keighery, G. J., Gibson, N., Kenneally, K. F., & Mitchell, A. A. (1995). Biological inventory of Koolan Island, Western Australia. 2. Fora and vegetation. *Records of the Western Australian Museum, 17*, 237–248.

Kendall, W.L. (2019) The ‘Robust Design’. Program MARK: ‘A Gentle Introduction’, 19th ed. (eds E. Cooch & G.C. White), pp. 15-01–15-40.

Kéry, M., & Schmid, H. (2004). Monitoring programs need to take into account imperfect species detectability. *Basic and applied ecology*, *5*(1), 65-73.

Komsta, L. (2019). mblm: Median-Based Linear Models. R package version 0.12.1.

Retrieved from https://CRAN.R-project.org/package=mblm.

Laake, J. L. (2013). RMark: an R interface for analysis of capture-recapture data with MARK: US Department of Commerce. *National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center*.

Laake, J., & Rexstad, E. (2014). Appendix C. RMark-an alternative approach to building linear models in MARK. *Program MARK: A Gentle Introduction. 13th edition.* Retrieved from http://www. phidot. org/software/mark/docs/book.

Laarmann, D., Korjus, H., Sims, A., Kangur, A., Kiviste, A., & Stanturf, J. A. (2015). Evaluation of afforestation development and natural colonization on a reclaimed mine site. *Restoration ecology*, *23*(3), 301-309.

Lee, J., Finn, H., & Calver, M. (2013). Feeding activity of threatened black cockatoos in mine-site rehabilitation in the jarrah forest of south-western Australia. *Australian Journal of Zoology*, *61*(2), 119-131.

Leiner, N. O., E. Z. F. Setz, & W. R. Silva. (2008). Semelparity and factors affecting the reproductive activity of the Brazilian slender opossum (*Marmosops paulensis*) in Southeastern Brazil. *Journal of Mammalogy 89*(1), 153–158.

Lindenmayer, D. B. (1999). Future directions for biodiversity conservation in managed forests: indicator species, impact studies and monitoring programs. *Forest Ecology and Management*, *115*(2-3), 277-287.

Lindenmayer, D. B., Piggott, M. P., & Wintle, B. A. (2013). Counting the books while the library burns: why conservation monitoring programs need a plan for action. *Frontiers in Ecology and the Environment*, *11*(10), 549-555.

Lindenmayer, D.B., Gibbons, P., Bourke, M.A.X., Burgman, M., Dickman, C.R., Ferrier, S., Fitzsimons, J., Freudenberger, D., Garnett, S.T., Groves, C. & Hobbs, R.J. (2012). Improving biodiversity monitoring. *Austral Ecology*, *37*(3), 285-294.

MacKenzie, D. I., Nichols, J., Sutton, N., Kawanishi, K., & Bailey, L. L. (2005). Improving inferences in population studies of rare species that are detected imperfectly. *Ecology*, *86*(5), 1101-1113.

Maryan, B., & Reinhold, L. (2009). Additions to the terrestrial herpetofauna of Koolan and Dirk Hartog Islands. *Western Australian Naturalist (Perth) 27*, 18–24.

Maxwell, S., Burbidge, A. A. & Morris, K. (1996). *The 1996 Action Plan for Australian Marsupials and Monotremes*. Australasian Marsupial and Monotreme Specialist Group, IUCN Species Survival Commission, Gland, Switzerland.

McKenzie, N. L., Burbidge, A. A., Chapman, A., & Youngson, W. K. (1978). Mammals. In ‘*The Islands of the North-west Kimberley*’. (Eds A. A. Burbidge and N. L. McKenzie.) 22–28. Western Australian Wildlife Research Centre, Department of Fisheries and Wildlife: Perth.

McKenzie, N. L., Fontanini, L., Lindus, N. V., & Williams, M. R. (1995). Biological inventory of Koolan Island, Western Australia. 2. Zoological notes. *Records of the Western Australian Museum 17*, 249–266.

Newbold, T., Hudson, L.N., Hill, S.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B. & Day, J. (2015). Global effects of land use on local terrestrial biodiversity. *Nature, 520*(7545), 45.

Nichols, J. D., Hines, J. E., Lebreton, J. D., & Pradel, R. (2000). Estimation of contributions to population growth: a reverse-time capture–recapture approach. *Ecology*, *81*(12), 3362-3376.

Oakwood, M. (1997). The ecology of the northern quoll, *Dasyurus hallucatus* (Unpublished doctoral dissertation). The Australian National University, ACT, Australia.

Oakwood, M., Woinarski, J. & Burnett, S. (2008). *Dasyurus hallucatus. The IUCN Red List of Threatened Species 2008*: e.T6295A12600197. Retrieved from http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T6295A12600197.en.

Obbard, M. E., Howe, E. J., & Kyle, C. J. (2010). Empirical comparison of density estimators for large carnivores. *Journal of Applied Ecology*, *47*(1), 76-84.

Otis, D. L., Burnham, K. P., White, G. C., & Anderson, D. R. (1978). Statistical inference from capture data on closed animal populations. *Wildlife monographs*, (62), 3-135.

Pollock, K. H., Nichols, J. D., Simons, T. R., Farnsworth, G. L., Bailey, L. L., & Sauer, J. R. (2002). Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics: The official journal of the International Environmetrics Society*, *13*(2), 105-119.

Puida, D. B. C., & Paglia, A. P. (2015). Primary productivity and the demography of Gracilinanus agilis, a small semelparous marsupial. *Journal of Mammalogy*, *96*(1), 221-229.

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienne, Austria. Retrieved from https://www.R-project.org/.

Redpath, S.M., Young, J., Evely, A., Adams, W.M., Sutherland, W.J., Whitehouse, A., Amar, A., Lambert, R.A., Linnell, J.D., Watt, A. & Gutierrez, R.J. (2013). Understanding and managing conservation conflicts. *Trends in ecology & evolution*, *28*(2), 100-109.

Rovero, F., Zimmermann, F., Berzi, D., & Meek, P. (2013). "Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. *Hystrix*, *24*(2).

Royle, J. A., Chandler, R. B., Sollmann, R., & Gardner, B. (2013). *Spatial capture-recapture.* Academic Press.

Sale, M. G., Wilson, B. A., & Arnould, J. P. (2008). Factors influencing population dynamics in island and mainland populations of the swamp antechinus (*Antechinus minimus*). *Australian Journal of Zoology*, *56*(3), 187-194.

Schorr, A. (2012) Using a temporal symmetry model to assess population change and recruitment in the Preble's meadow jumping mouse (*Zapus hudsonius preblei*). *Journal of Mammology*, *93*(5), 1273-1282.

Seber, G.A.F. (1982) The Estimation of Animal Abundance and Related Parameters. Griffin, London.

Sen, P. K. (1968). Estimates of the regression coefficient based on Kendall's tau. *Journal of the American statistical association*, *63*(324), 1379-1389.

Silver, S.C., Ostro, L.E., Marsh, L.K., Maffei, L., Noss, A.J., Kelly, M.J., Wallace, R.B., Gómez, H. & Ayala, G. (2004). The use of camera traps for estimating jaguar P*anthera onca* abundance and density using capture/recapture analysis. *Oryx*, *38*(2), pp.148-154.

Smith, L. M., Brisbin, I. L., & White, G. C. (1984). An evaluation of total trapline captures as estimates of furbearer abundance. *The Journal of wildlife management*, *48*(4), 1452-1455.

Sollmann, R., Gardner, B., & Belant, J. L. (2012). How does spatial study design influence density estimates from spatial capture-recapture models?. *PloS One, 7*(4), e34575.

Spencer, P. B., Sandover, S., Nihill, K., Wale, C. H., How, R. A., & 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.

Tanaka, R. (1980). Controversial problems in advanced research on estimating population densities of small rodents. *Researches on Population Ecology, 22*(2), 1-67.

Thackway, R & Cresswell, I. (1995). An Interim Biogeographic Regionalisation for Australia. Australian Nature Conservation Agency, Canberra.

Theil, H. (1950). A rank-invariant method of linear and polynomial regression analysis. I, II and III. *Proceedings of Koninklijke Nederlandse Akademie van Wetenschappen*, 53, (pp. 386–392) (521–525, 1397–1412).

Thibault, K. M., Ernest, S. M., White, E. P., Brown, J. H., & Goheen, J. R. (2010). Long-term insights into the influence of precipitation on community dynamics in desert rodents. *Journal of Mammalogy, 91*(4), 787-797.

Tobler, M. W., & Powell, G. V. (2013). Estimating jaguar densities with camera traps: problems with current designs and recommendations for future studies. *Biological Conservation*, *159*, 109-118.

Troyer, E. M., Cameron Devitt, S. E., Sunquist, M. E., Goswami, V. R., & Oli, M. K. (2014). Density dependence or climatic variation? Factors influencing survival, recruitment, and population growth rate of Virginia opossums. *Journal of Mammalogy*, *95*(2), 421-430.

Tyler, I. M., & Griffin, T. J. (1993). ‘Yampi Western Australia (second edition) Sheet SE51–3 International Index. 1: 250,000 Geological Series – Explanatory notes.’ Geological Survey of Western Australia: Perth.

Venables, W.N & Ripley, B.D. (2002) Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0.

Vicente-Serrano, S. M., Beguería, S., & López-Moreno, J. I. (2010). A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *Journal of Climate, 23*(7), 1696-1718.

White, G. C. (2005). Correcting wildlife counts using detection probabilities. *Wildlife Research*, *32*(3), 211-216.

White, G. C., & Burnham, K. P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study*, *46*(sup1), S120-S139.

Wilcox, R. R. (2016). Understanding and applying basic statistical methods using R. John Wiley & Sons.

Wilcox, R.R., & Schönbrodt, F.D. (2014). The WRS package for robust statistics in R (version 0.24). Retrieved from http://r-forge.r-project.org/projects/wrs/.

Willson, J. D., Winne, C. T., & Todd, B. D. (2011). Ecological and methodological factors affecting detectability and population estimation in elusive species. *The Journal of Wildlife Management*, *75*(1), 36-45.

Wilson, D. E., Cole, R. F., Nichols, J. D., & Foster, M. S. (1996). *Measuring and monitoring biological diversity. Standard methods for mammals* (No. 599.05248 M4).

Woinarski, J.C., Burbidge, A.A. & 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*(15), 4531-4540.

Wooller, R. D., Bradley, J. S., Skira, I. J., & Serventy, D. L. (1990). Reproductive success of short-tailed shearwaters Puffinus tenuirostris in relation to their age and breeding experience. *The Journal of Animal Ecology*, *59(1)* 161-170.

Zimmermann, F., Breitenmoser-Würsten, C., Molinari-Jobin, A., & Breitenmoser, U. (2013). Optimizing the size of the area surveyed for monitoring a Eurasian lynx (*Lynx lynx*) population in the Swiss Alps by means of photographic capture–recapture. *Integrative zoology, 8*(3), 232-243.

Zimmerman, J.K., Everham, E.M. III, Waide, R.B., Lodge, D.J., Taylor, C.M. & Brokaw, N.V.L. (1994) Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. *Journal of Ecology*, 82, 911-922.

3.7 ETHICS

Data used in this chapter were collected in accordance with Licence SF010242 in accordance with the WA *Wildlife Conservation Regulations 1970*.

Chapter 4: The influence of season and habitat on the diet of an insular population of an endangered marsupial

4.1 ABSTRACT

The diet and feeding ecology of a species may vary across both space and time, with the food items consumed and trophic niche breadth often differing across populations, geographic locations and seasons. The northern quoll (*Dasyurus hallucatus*) is a predatory marsupial that occurs across tropical and semi-arid northern Australia and is in steep decline due to habitat loss and ingestion of the toxic cane toad. Here we present a quantitative analysis of the diet of an insular population, using 448 scats from Koolan Island in the Kimberley region of Western Australia. We used closed-capture models and Fisher's Exact Tests to examine if diet differed between anthropogenic and native habitats, or between seasons, and if prey was selected or consumed relative to their availability in the environment. We also calculated an index for niche breadth and measures of percentage frequency of occurrence and percentage volume to compare our findings with results from populations in other mainland locations. We found that invertebrates comprised the majority of the northern quoll's diet, and that diet was influenced by both season and habitat type. The food items consumed at the highest frequency and volume were cockroaches and beetles, which were eaten more than would be expected based on their availability. Fruit was consumed in moderate amounts, including the stinking passionflower *Passiflora foetida*, which is an environmental weed in Australia. Niche breadth (0.27; 95% CI 0.23 – 0.31) was comparable to mainland sites, which may be due to a lack of competition from other species on Koolan Island. Scat analysis suggests that the northern quoll feeds within modified habitat, and individuals are likely to move between anthropogenic and unmodified areas on the island in search of food. Our findings provide

valuable insight to inform habitat management for this species both on islands and in similar habitats within the wet dry tropics of Australia.

4.2 INTRODUCTION

The availability of suitable food resources can influence growth and survival, breeding success, and also population dynamics of a species (Miller et al. 2014), making dietary studies valuable to decision making in conservation management (Putman 1984; Doherty et al. 2018). A species' feeding ecology is primarily constrained by its morphological and physiological specialisations (Tremblay & Cherel 2003). Additionally, feeding ecology is influenced by changes in food availability (temporal and geographic) or developmental needs (ontogenetic shifts) (Darimont 2009; Newsome et al. 2014; Samplonius et al. 2016; Stenset et al. 2016). Given these variables and the influence they may exert on a population, it is vital for conservation managers to have a detailed understanding of the diet and feeding strategy of target species (Atkins et al. 2018).

Several factors influence a species' diet at any one time, including not only the quality and availability of food items but also prey preferences, hunger, risk, and spatiotemporal fluctuations in prey availability (Murdoch 1969; Dale et al. 1994; Hayward 2006; Newsome et al. 2014). Research into the feeding ecology of a species that captures both geographic and seasonal intraspecific variation in diet can therefore provide a more complete picture of the species' niche flexibility. This is particularly true for species with distributions spanning multiple bioregions and areas with substantial seasonal fluxes in the diversity and abundance of food. This information has important consequences for *in-situ* management, by informing habitat enhancement, and *ex-situ* management, as it assists in the identification of translocation sites, and (in instances where diverging adaptive trajectories or ecotypes are identified) may influence the selection of source populations.

Key demographic factors directly influenced by food availability include individual growth, the number of young produced and juvenile survival (McKinnon et al. 2012). This is especially important for short-lived species that reproduce only once or twice in their lifetime, as a low abundance of food during the breeding season may have a significant influence on population dynamics. Further, species that must leave their young unattended to forage (particularly single-parent species) must adapt their optimal foraging strategy to not only maximise their net energy gain, but also do so in a manner that minimises the risk of predation on juveniles (Panzacchi et al. 2010).

Important sources of variation in food availability and diet span not just broad spatial scales but also across island versus mainland and native versus modified habitats (Darimont et al. 2009). Variation in diet between mainland and island predators is exemplified by species such as the wolf (*Canis lupus*) in British Columbia, where variation in diet was considered to be a function of the differences in habitat, competition, and prey availability (Darimont et al. 2004; 2009). In a comparative study of island and mainland populations of pine marten (*Martes martes*), a wider trophic niche breadth in island populations was attributed to the absence of competing species found on the mainland (Clevenger 1993). Further, when species are identified to be able to adapt to different environments, they may also be more predisposed to adapting to modified environments and new food sources, such as those introduced with anthropogenic land use (e.g. Newsome et al. 2014)

The northern quoll (*Dasyurus hallucatus*) is considered to be an opportunistic omnivore or generalist predator (Oakwood 1997; Pollock 1999; Dunlop et al. 2017). Over the past 100 years the species experienced gradual declines as a result of altered fire regimes and feral predators (Braithwaite & Griffiths 1994; Maxwell et al. 1996). In 2008 the northern quoll was listed as endangered under the IUCN Red List of Threatened Species due to habitat loss and modification, and the ingestion of the toxic cane toad *Rhinella marinus* (Oakwood et al. 2008). The northern quoll's distribution has declined from across most of the northern third of Australia to isolated populations (Braithwaite & Griffiths 1994; Hill & Ward 2010), but is known to occur on at least six and 11 islands off the coast of the Northern Territory and Western Australia, respectively (Hill & Ward 2010).

Management measures to stem declines of the northern quoll currently include mainland based trials of conditioned-taste-aversion to cane toad ingestion (Webb et al. 2015; Jolly et al. 2018; Indigo et al. 2018), translocation and reintroduction programs (Cremona et al. 2017; Griffiths et al. 2017), and the management of populations amongst changing land uses (Hill & Ward 2010; Cramer et al. 2016). Conservation actions for the northern quoll are prioritised in areas within the species' range that are not yet subject to the spread of the toxic cane toad (Dunlop et al. 2017). This includes island populations, which provide a higher probability of maintaining biosecurity against invasive species (Hill & Ward 2010). While a thorough understanding of feeding ecology is essential for *ex-situ* and *in-situ* management, there is currently little information on the diet of island populations of northern quoll, populations that occur in or near anthropogenic land uses, or whether diet changes as a function of season or biological period.

This study examines the feeding ecology of the northern quoll on Koolan Island, located off the coast of the Kimberley region in northern Western Australia. Northern quolls on the island coexist with a long-term mining operation, where individuals are observed both in native habitat and around anthropogenic infrastructure. We analysed 448 scats collected from across Koolan Island to (a) quantify the diet of northern quolls on a tropical island, (b) determine if diet changes in native versus anthropogenic habitat, or between seasons, and (c) determine whether the northern quoll's feeding ecology is preferential or based on prey availability. We expected northern quolls would be opportunistic (Oakwood 1997; Dunlop et al. 2017); exhibit a preference towards high-energy food sources (Potter et al. 2018); and for diet to vary between habitat types and season to take advantage of available food sources (Oakwood 1997).

4.3 METHODS

4.3.1 Study area

Koolan Island is located in the tropical Kimberley region of Western Australia, approximately 130 kilometres north of Derby (Figure 4.1). The island is 2,712 hectares and is located one kilometre from the mainland, across from the Yampi Peninsula. The Kimberley region is in the wet-dry tropics of northern Australia and is broadly characterised by tropical savannah habitat with a eucalypt tree canopy, grass understorey, and a generally sparse shrub layer (Radford et al. 2015). Within this matrix, small patches of rainforest and riparian forest also occur. While broad-scale clearing has not occurred across the Kimberley region, the landscape has been modified by long-term cattle grazing, mining, and feral herbivore and predatory species such as cattle, horses, goats, cats and foxes (Legge et al. 2011a; 2011b).

Koolan Island has a highly seasonal climate that is representative of its location in the wet-dry tropics, with a wet season that extends from December to March. On average, 75% of annual rainfall (790 mm) occurs between January and March (BoM 2018). While long-term temperature data are not available for the site, nearby Cygnet Bay (85.8km from Koolan Island) experiences a mean maximum temperature of 32.4°C and mean minimum temperature of 21°C (BoM 2018).

The islands off the Kimberley coast were isolated from the mainland between 8,000 and 10,000 years ago (Nix & Kalma 1972) and are considered to be representative of the vegetation communities on the adjacent mainland (Lyons et al. 2014). There are five major vegetation units on Koolan Island, with the most widespread unit being *Eucalyptus miniata* – *Corymbia confertiflora* open woodland generally over *Triodia* hummock grassland and a variable shrub layer (Keighery et al. 1995). This vegetation unit covers approximately 80% of the non-disturbed area of the island (Figure 4.1; Beard 1979; Keighery et al. 1995).

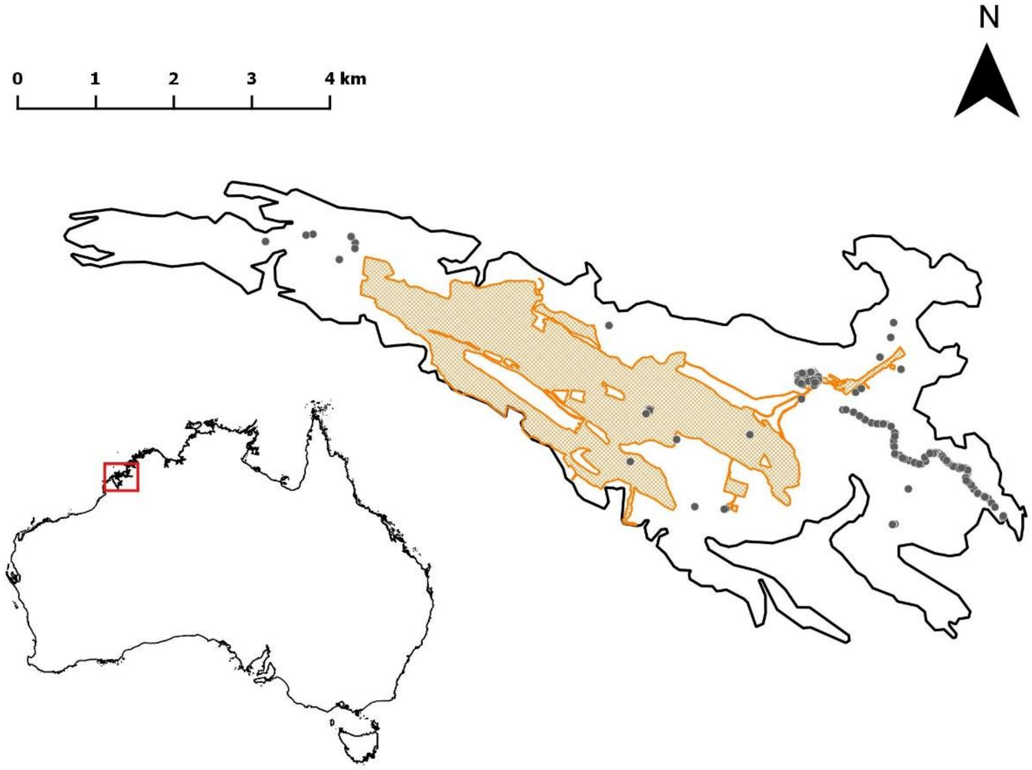


Figure 4.1. Location of Koolan Island in the Kimberley region, Western Australia, showing the mining and accommodation footprint (anthropogenic habitat type; orange), and sampled scat locations (grey dots).

Flora and vegetation surveys on the islands have identified 629 plant taxa (MBS Environmental 2012). The island contains two species of *Ficus* (*Ficus aculeata* var. *indecora*, *Ficus virens* Aiton), which are known to provide an important food resource for many species (Shanahan et al. 2001). As a result of human activity on the island since the 1960s, there are also several weed species present, including the stinking passionflower (*Passiflora foetida* var. *hispida*). Weed species are much more prevalent within modified habitat on the island

(Keighery et al. 1995), and are suppressed where possible by spot-spraying and physical removal through the mine's weed management program.

Koolan Island contains a nested subset of fauna found on the Kimberley mainland. Zoological surveys have identified a total of 51 invertebrate, 44 reptile, three anuran, 151 bird and 24 mammal species (McKenzie et al. 1995; MBS Environmental 2012). The northern quoll is the largest mammalian predator on the island, with other predators of equal or larger size including varanids (*Varanus glebopalma*), crocodiles (*Crocodylus porosus*), snakes (including large pythons such as *Liasis olivaceus*), owls (*Ninox* spp.) and numerous other birds of prey (McKenzie et al. 1995).

Excluding the Aboriginal heritage of the Kimberley islands, recent history of Koolan Island has been characterised by anthropogenic activity since the 1960s. An open-pit iron ore mine was operational on the island from 1965 to 1993. During this time, the island contained a small townsite of 850 people that was removed by 1993 (Keighery et al. 1995). The mine was reopened in 2006 and mining activity is ongoing, supported by mining and accommodation infrastructure including a small airstrip. The anthropogenic history of the island offers an exceptional opportunity to compare the diet of the northern quoll in both modified and relatively intact areas of native habitat. Areas cleared for mining, accommodation and supporting infrastructure or undergoing rehabilitation (referred to as 'anthropogenic areas' in this study) cover approximately 30% of the island (see Figure 4.1). The remaining areas are considered 'native' habitat (habitat in areas outside the mining and infrastructure footprint that have not been previously cleared).

4.3.2 Data collection

We collected northern quoll scats on the island (Figure 4.1) from March 2015 to November 2017, across all seasons. Scats were collected during pre-planned searches in modified habitat (around village infrastructure on the island), and native habitat (accessed using tracks within the eastern portion of the island), and opportunistically across the island while conducting other activities (weed surveys; annual northern quoll monitoring, Chapter 3; telemetry, Chapter 5). Pre-planned searches were conducted for 2-3 hours each time over 57 days in total. Search effort included 31 days in anthropogenic habitat and 32 days in native habitat, with 37 days during the dry season and 20 days during the wet season. Only scats that appeared to be recently deposited (i.e. showing no signs of degradation) were collected, to ensure scats were representative of the season. Scats were placed in sealable paper envelopes and labelled, and a location recorded at each scat location. Mean scats collected per search occasion ranged from 6-9 depending on anthropogenic (9) vs. native (6) habitat, or dry season (8) vs. wet season (7).

To determine if northern quoll diet was a function of availability, we used 20 trap lines containing pitfall and funnel traps in both anthropogenic (n = 10) and native (n = 10) habitat types to capture potential prey items. Each trap line was open for three sessions from June, August and November 2017, with four nights per session. Trap lines consisted of one 10 litre bucket dug into the ground situated in the middle of a 300 mm high, 10 m long drift fence of aluminium fly wire with two funnel traps positioned at each end (total of four funnel traps per trap line). Trap lines were opened at dusk, and checked and closed within three hours of dawn. Captured prey items were identified in accordance with the taxonomic categories used in the scat analysis (see below). Presence/absence of prey items per trap was recorded, with availability measured as the number of trap nights that a prey item belonging to a certain taxonomic group was captured in a trap.

Pit-trapping was only able to be conducted in the dry season owing to logistical limitations and animal welfare.

4.3.3 Scat analysis

Scats were analysed by a specialist (G. Story, Scats About, Majors Creek, New South Wales, Australia). Scats were oven-dried at 100°C for 12 hours, before being placed in nylon fine-weave mesh bags, washed in a washing machine and allowed to air dry. Once dried, food items from undigested animal and vegetative remains were identified and classified as belonging to one of 32 categories based on their taxonomic group (Table 4.1). Relative volumes of remains were visually estimated under a microscope with the aid of a superimposed reference grid, and each food item was expressed as a percentage of the volume of each scat.

4.3.4 Data analysis

Frequency of occurrence and percentage volume

To enable comparisons with previous studies, we calculated frequency of occurrence (%FO; the number of scats that contain food items of that category as a percentage of all sampled scats), and percentage volume (%VO; the volume of that food item in the scats expressed as a percentage of the total volume of all food items in the scats).

Data analysis

Diet analysis can lead to pseudoreplication, as each sampling unit (scat) usually contains more than one food item which are assumed to be independent of one another (Lemons et al. 2010; McVey et al. 2013). Recording each food item as present or absent in a scat yields a similar data structure to capture mark recapture data, and thus allows the use of closed capture mark recapture models to analyse diets and estimate diet selection accurately (Lemons et al. 2010).

In order to examine the relative frequency of food items consumed by the northern quoll across seasons and habitat type, we analysed diet data using Huggins' (1989) models for closed populations using program MARK (White & Burnham 1999) through the RMark package (version 2.2.4, Laake 2013; Laake & Rexstad 2014) in the R software environment (version 3.5.0, R Development Core Team 2018). This analysis required several assumptions similar to those of a standard closed-capture analysis (Lemons et al. 2010). Firstly, we assumed that scats represented independent samples of the diet. We believe this is reasonable as we avoided the sampling of co-located scats. For example, where latrine sites were identified with multiple scats present only one scat was sampled from the site. Secondly, we assume that food groups were equally available to all individuals within a specific class (e.g. all northern quolls inhabiting anthropogenic areas). The final assumption is that dietary items within samples were identified correctly. Given that the analysis of scat content was conducted by an expert with multiple years' experience, we believe that this assumption is reasonable.

We calculated the overdispersion parameter $\hat{c}$ using a goodness of fit statistic (Anderson et al. 1994; Burnham & Anderson 2002; Williams et al. 2002; McVey et al. 2013). Where $\hat{c}$ was greater than 1.5, we used quasi-corrected Akaike Information Criterion (QAICc) values for our analysis (Anderson et al. 1994). Where $\hat{c}$ was less than 1.5, we used Akaike Information Criterion values (Akaike 1974).

To detect trends and patterns at different taxonomic scales, we ran both fine-scale and broad-scale analyses. For the broad-scale analysis, we classified each of the original 32 categories of food items as vertebrate, invertebrate or fruit. This enabled us to compare the importance of broad 'food groups' (e.g. insects versus vertebrates) and the importance of more specific taxa in the diet of the northern quoll.

Measuring the frequency of occurrence can overestimate the importance of small food items. For example, small items (i.e. ants or termites) that are consumed regularly but do not have an important contribution to the predatory species' energy gain may appear as frequently as larger food items (such as rodents), therefore overestimating their importance in that species' diet (Klare et al. 2011). To minimise bias from overestimating the importance of food items that occurred at low volumes in our fine-scale analysis, we excluded trace food items that comprised $< 5\%$ of individual scats and occurred in $< 5\%$ of the total volume of all scats (Lemons et al. 2010). After trace food items were removed from the data seven food categories remained, including beetle/cockroach, grasshopper/cricket, centipede, crustacean, skink, *Ficus* sp., and *Passiflora foetida*. Each scat was characterised by a vector of three (broad scale) and seven (fine scale) 0s (absent) and 1s (present) in a multinomial sequence of food items from each category (Lemons et al. 2010).

Trophic niche breadth

To examine the influence of season and habitat on the uniformity of food resources being consumed by the northern quoll, and to enable comparisons with other studies, we subjected the results of the scat analysis to re-sampling with bootstrapping in R and calculated Levins' standardised index for niche breadth (Levins 1968; Hurlbert 1978):

$$\hat{B}_A = \frac{\left(\frac{1}{\sum p_i^2}\right) - 1}{n - 1}$$

where $\hat{B}_A$= Levins' standardised niche breadth, p_i = proportion of occurrence of each food resource in the diet and n = number of possible resources. $\hat{B}_A$ values range from 0 (specialist) to 1 (generalist), where $\hat{B}_A > 0.6$ is considered high, and $\hat{B}_A < 0.4$ is considered to be low (Novakowski et al. 2008).

To compare niche breadth between seasons, we grouped the data from the scat analysis into wet and dry season categories. Bootstrapping was used due to its ability to generate variance estimates for the data. We used bootstrap resampling to generate 1000 new samples equalling the sample size of each group (n (all scats) = 448; n (native habitat) = 184; n (anthropogenic habitat) = 264; n (wet season) = 137; n (dry season) = 311), and calculated standardised Levins' niche breadth for each of these new samples. Given prey items within a scat are not independent of each other we resampled the scat, and not the frequency or volume of prey items independently of each other. We then used the bootstrapped data to generate means and percentile confidence intervals for Levins' standardised index for niche breadth. To investigate if there was a statistically significant difference in Levins' standardised index for niche breadth between wet and dry season, we obtained p-values by using the bootstrap test as described in Gardener (2014). We then repeated these methods to test for a difference in niche breadth between anthropogenic and native habitat types.

To enable comparisons with other studies, we also calculated Levins' standardised niche breadth using all data (no habitat or season grouping) using food item categories as per Dunlop et al. (2017). These food item categories included rodents, marsupials, bats, birds, reptiles, crustaceans, molluscs, insects and vegetation. Frogs and carrion were detected in Dunlop et al. (2017) but were either not recorded (frogs), or not reliably identified (carrion) in our study and were therefore not considered. As the food categorisation by Dunlop et al. (2017) was broader than that used in our study, it had the potential to underestimate niche breadth. Therefore, we also repeated this step using the food item categories outlined in Table 4.1.

Prey availability

Prey availability was assessed in terms of the frequency of occurrence of each prey category in pitfall and funnel traps. Frequency of occurrence of each prey category was calculated as the total number of pitfall or funnel traps across all trap-nights containing a particular prey category divided by the total number of pitfall or funnel traps analysed across all trap-nights, grouped by species and habitat type. It is acknowledged that variance may occur between the capture probability of prey items in pit and funnel traps, and the probability of these prey being detected by a northern quoll during foraging activities.

Differences in the frequency of occurrence of prey items caught in traps between habitat types (anthropogenic versus native) were compared using Fisher's Exact Tests. Where no difference in the occurrence of a particular prey item was detected, habitat types were pooled. Where the occurrence of a prey item was different between habitats, occurrence was grouped by habitat.

To determine whether the northern quoll's diet on the island was selective or based on availability, the frequency of occurrence of prey food items in the diet was compared with its observed frequency of occurrence in the pitfall and funnel traps using Fisher's Exact Tests. This was done separately for each food category. Individual Fisher's Exact Tests were used instead of other methods (e.g. selection ratios) as the sample size was relatively small and the trap data was limited to a subset of the food items detected in scats.

4.4 RESULTS

We collected a total of 448 northern quoll scats from March 2015 to November 2017 (32 months). A total of 32 different food items were identified in the scats collected, with a mean of 4.0 food items detected in each scat (range 1-10) (Table 4.1; Figure 4.2). Animal prey included beetles/cockroaches, caterpillars, grasshopper/crickets, ants/termites, spiders, cocoons, crustaceans, millipedes, snails, northern quolls, native rock rats, fruit bats, microbats, birds, skinks, snakes and geckos. Eleven fruit species were identified in scats, with the most abundant being fig (*Ficus* spp.) and stinking passionflower (*Passiflora foetida*). General vegetation was also found in scats, as was anthropogenic waste (rubbish).

4.4.1 Effect of habitat and season

For the fine-scale diet data (seven food categories), we fit eight models with three unique variables (season, habitat, year) to the data (Table 4.2). Models were only fit with main effects because initial attempts to fit models with interactions failed to estimate several parameters. The top model to explain the food items present in scats included habitat type and season and was well supported relative to other models, with a weight of 94% (Table 4.2). Our second-best model (△AIC = 5.87) included year, habitat and season. Overall, we interpret these results to indicate that the diet of the northern quoll varies between the wet and dry season, and across native and anthropogenic habitats.

Table 4.1. Percentage frequency of occurrence (%FO) and percentage volume (%VO) for food items detected in northern quoll scats, compared to other studies. (-) denotes data not available.

	This study		**Dunlop et al. 2017**		**Oakwood 1997**
Food item	**%FO**	**%VO**	**%FO**	**%VO**	**%FO**
Beetle/ cockroach	58.0	25.3	47.6	12.4	90.0
Ant/ termite	38.0	4.9	52.0	6.6	51.0
Centipede	24.1	10.6	10.8	4.8	-
Grasshopper/ cricket	22.8	6.5	39.0	13.4	82.0
Crustacean	7.1	4.1	6.6	3.2	-
Snail	4.9	1.0	3.4	0.6	2.0
Unidentified invertebrate	1.8	0.4	3.6	1.5	-
Cocoon	1.6	0.4	-	-	-
Grub/ caterpillar	1.3	1.0	17.8	9.0	-
Spider	0.5	<0.1	5.0	0.5	-
Millipede	0.2	<0.1	1.8	0.6	-
Invertebrate	84.8	54.2	90.2	54.3	
Skink	20.8	7.0	13	3.4	12
Bird	4.0	2.1	11.8	5.3	-
Snake	2.7	1.3	3.6	1	9
Zyzomys argurus	1.1	0.6	9.2	6.6	-
Gecko	1.1	0.6	1.2	0.3	4
Dasyurus hallucatus	0.7	0.4	19.2	2.1	10
Pteropus Alecto	0.2	0.2	-	-	-
Microbat	0.2	0.2	0.8	0.4	-
Vertebrate	30.4	12.4	43.4	24.7	
Passiflora foetida	23.7	15.5	-	-	1
Ficus sp.	8.9	5.3	16.1	58.2	-
Seed 3	5.8	3.6	-	-	-
Seed 4	4.9	2.4	-	-	-
Ampelocissus acetosa	3.8	2.3	-	-	-
Seed 2	3.1	2.0	-	-	-
Seed 5	0.5	0.2	-	-	-
Bush tomato	0.2	0.1	-	-	-
Seed 6	0.2	0.2	-	-	-
Seed 7	0.2	0.2	-	-	-
Seed 8	0.2	<0.1	-	-	-
Fruit	43.1	31.8	22.2	15.5	-
Vegetation	3.6	1.3	5.4	2.1	-
Rubbish	0.6	0.4	-	-	-

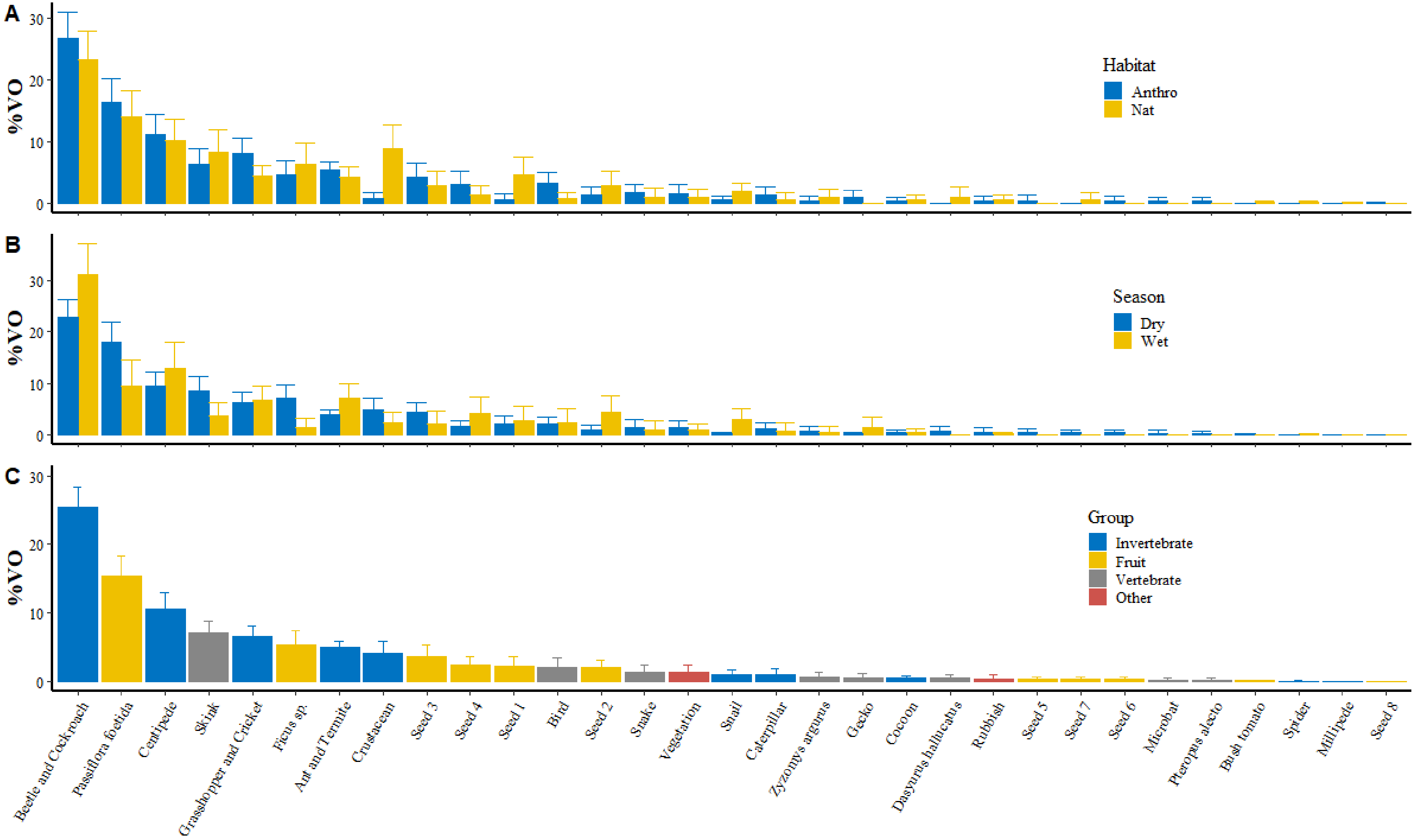


Figure 4.2. %Volume for all food items detected in scats by (a) habitat type, (b) wet/dry season, and (c) broad food group classification. Error bars represent 95% bootstrap confidence intervals.

Inspection of estimates of proportion obtained from the top model suggest that beetles and cockroaches were consumed more than any other food type in both seasons and habitat types, with more eaten during the wet season than the dry season (Figure 4.3). *Passiflora foetida* was consumed more commonly than *Ficus* spp., with more *Ficus* spp. eaten in the dry season than the wet season. Other food types showed no significant difference in consumption between the wet and dry seasons. Crustaceans showed the strongest habitat variation out of any food item, with almost all scats containing crustaceans found in native habitat.

Next, in order to see whether habitat type or season influenced the diet at a higher level, we fit eight models with three unique variables (season, habitat, year) to the broad-scale data (invertebrate, vertebrate, fruit/ seed; Table 4.3). The only competitive model ($\triangle$QAICc$\leq$ 2) included season as a predictor for northern quoll diet, with all other models having low weights. This model accounted for 64% of the model weights. Our second-best model ($\triangle$QAICc = 2.12) included intercept only.

The estimates of proportions obtained from the top model indicates that overall, invertebrates are eaten more than both vertebrates and fruits/ seeds during both the wet and dry seasons (Figure 4.4). The food type that appears to be most affected by season is vertebrates with more vertebrates consumed during the dry season (estimated occurrence in 31% of scats versus 19% in the dry season). Invertebrates and fruit both had overlapping confidence intervals between wet and dry season consumption, indicating that there was no significant difference in consumption between the wet and dry seasons at this level.

Table 4.2. Model sets and model results used to describe the diet of the northern quoll on Koolan Island using fine-scale categorisation. *K* = number of parameters; AIC = Akaike's Information Criterion; △AIC = Delta AIC.

Model	K	AIC	△AIC	Model weight
habitat + season	21	2735.56	0	0.94
year + habitat + season	35	2741.43	5.87	0.05
season	14	2744.41	8.85	0.01
year + season	28	2752.60	17.04	0.00
habitat	14	2762.27	26.70	0.00
year + habitat	28	2765.93	30.37	0.00
intercept	7	2773.67	38.11	0.00
year	21	2779.24	43.68	0.00

Table 4.3. Model sets and model results used to describe the diet of the northern quoll on Koolan Island using the categories invertebrate, vertebrate, fruit. *K* = number of parameters; QAICc = Quasi-corrected Akaike's Information Criterion corrected for small sample size; △QAICc = Delta QAICc.

Model	K	QAICc	△QAICc	Model weight
season	6	813.15	0	0.64
intercept	3	815.27	2.12	0.22
habitat + season	9	817.95	4.80	0.06
year + season	12	818.94	5.79	0.04
habitat	6	819.93	6.78	0.02
year	9	820.49	7.34	0.02
year + habitat + season	15	823.90	10.75	0.00
year + habitat	12	825.43	12.28	0.00

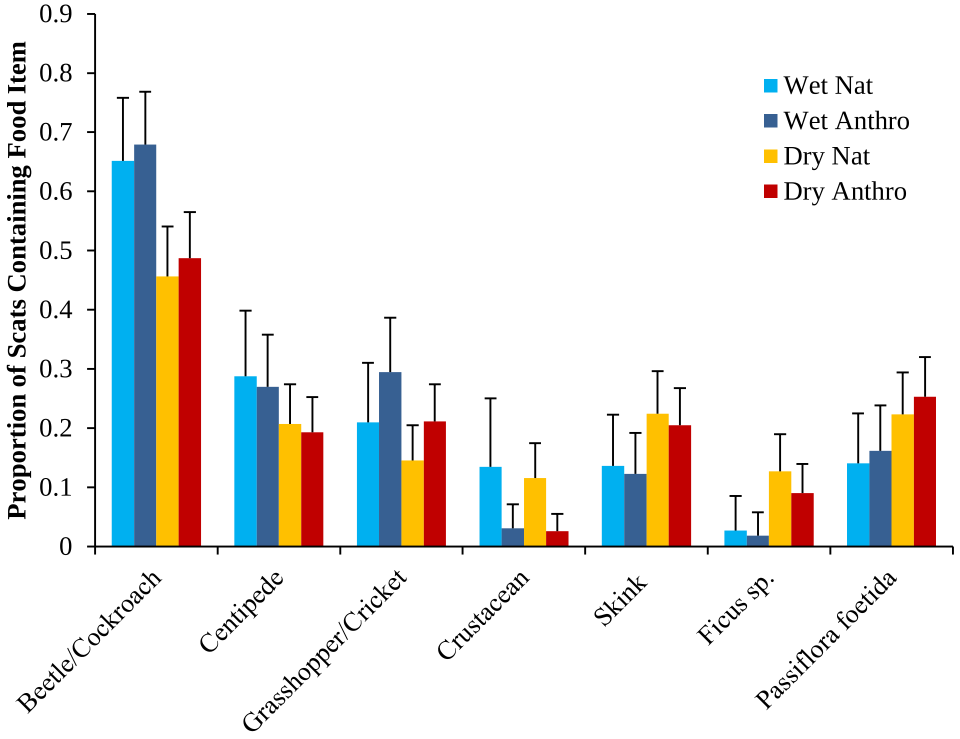


Figure 4.3. Diet estimates from Program MARK using fine-scale food item categorisation across native (Nat) and anthropogenic (Anthro) habitat types and wet and dry season. Error bars represent 95% confidence intervals.

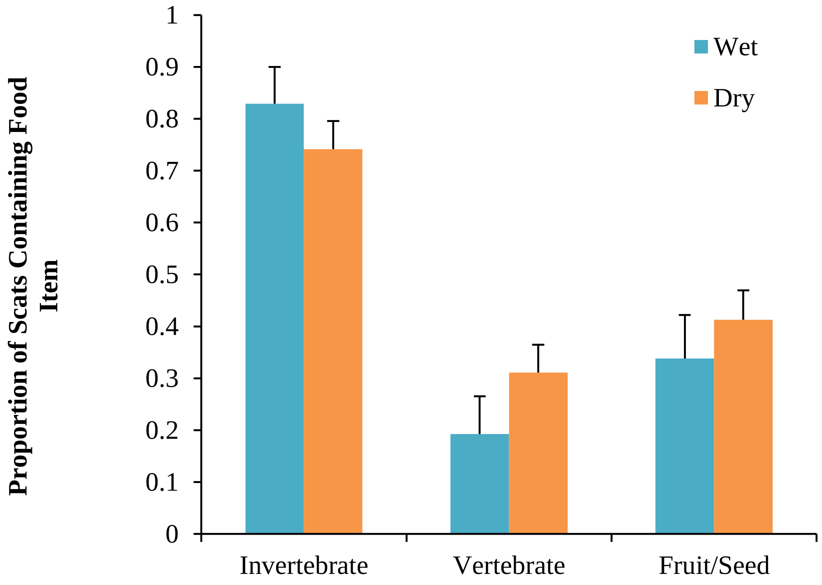


Figure 4.4. Diet estimates from Program MARK using broad-scale food item categorisation across the wet and dry seasons. Error bars represent 95% confidence intervals.

4.4.2 Niche breadth

Standardised Levins' niche breadth did not appear to differ between the wet and dry seasons (p = 0.756; Figure 4.5a). Mean niche breadth was lower in anthropogenic habitat (0.28) than native habitat (0.36), however the p value obtained from the bootstrapped test (p = 0.107) and overlapping confidence intervals suggests that the evidence of a difference is weak (Figure 4.5b). Niche breadth for all data (no habitat or season grouping) was 0.27 (95% CI 0.23 – 0.31). Using the food categories described in Dunlop et al. (2017), niche breadth for the island was 0.23 (95% CI 0.20 – 0.27).

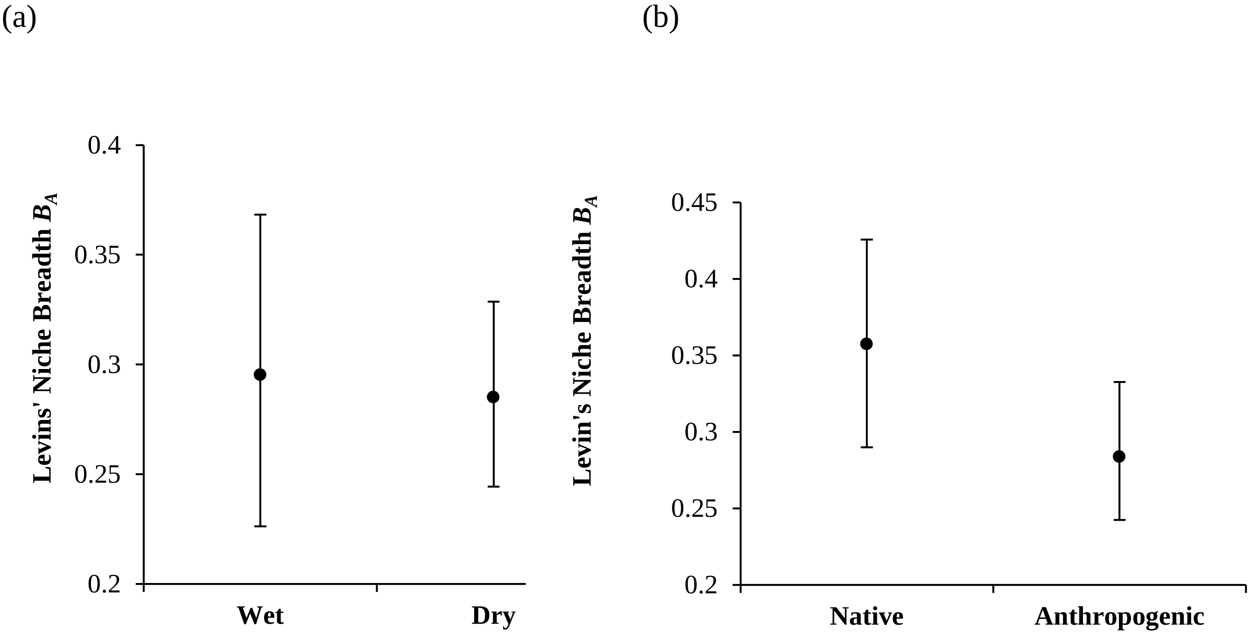


Figure 4.5. Standardised Levins' niche breadth calculated for (a) wet versus dry season, and (b) native versus anthropogenic habitat types.

4.4.3 Diet and prey availability

Six taxonomic groups were detected in pit and funnel traps (beetles/ cockroaches, skink, spider, centipede, snake, grasshopper/ crickets). Excluding food items that occurred in scats at trace volumes < 5%, four prey taxa were detected in both trapping and scat analysis, including beetles/cockroaches, centipedes, grasshopper/ crickets, and skinks. Results from

Fisher’s Exact Tests suggest that the availability of grasshoppers/crickets was higher in anthropogenic than native habitat ($p < 0.001$). Beetles/ cockroaches ($p = 0.75$), centipedes ($p = 0.26$) and skinks ($p = 0.16$) showed no difference in availability between habitat types.

Three of the four prey taxa showed deviation from observed (in scats) and expected (in pitfall and funnel traps) availability (Table 4.4). The northern quoll did not consume skinks in proportions relative to their high availability in the environment ($p < 0.01$). Comparatively, the northern quoll consumed more beetles/cockroaches than would be expected based on their availability in the environment ($p < 0.001$). Grasshopper/crickets were eaten more than would be expected in native habitat ($p < 0.05$), but were consumed in proportions relative to their availability in anthropogenic habitat ($p = 0.9$). There was no significant difference in the observed and expected values for centipedes, indicating that they were consumed in proportions relative to their availability.

Table 4.4. Exact test of goodness of fit results comparing the occurrence of each prey category in pitfall and funnel traps and scats of the northern quoll. *$p<0.05$; **$p<0.01$; ***$p<0.001$. ‘Native’ refers to habitat in areas outside the mining and infrastructure footprint that have not been previously cleared. ‘Anthropogenic’ means areas within the mining and infrastructure footprint (shown in Figure 4.1).

Food item	Pooled habitat	
Beetle/ cockroach	Greater frequency in scats than traps***	
Centipede	No difference in frequency between scats and traps	
Skink	Lower frequency in scats than traps**	
	Native	Anthropogenic
Grasshopper/ cricket	Greater frequency in scats than traps *	No difference in frequency between scats and traps

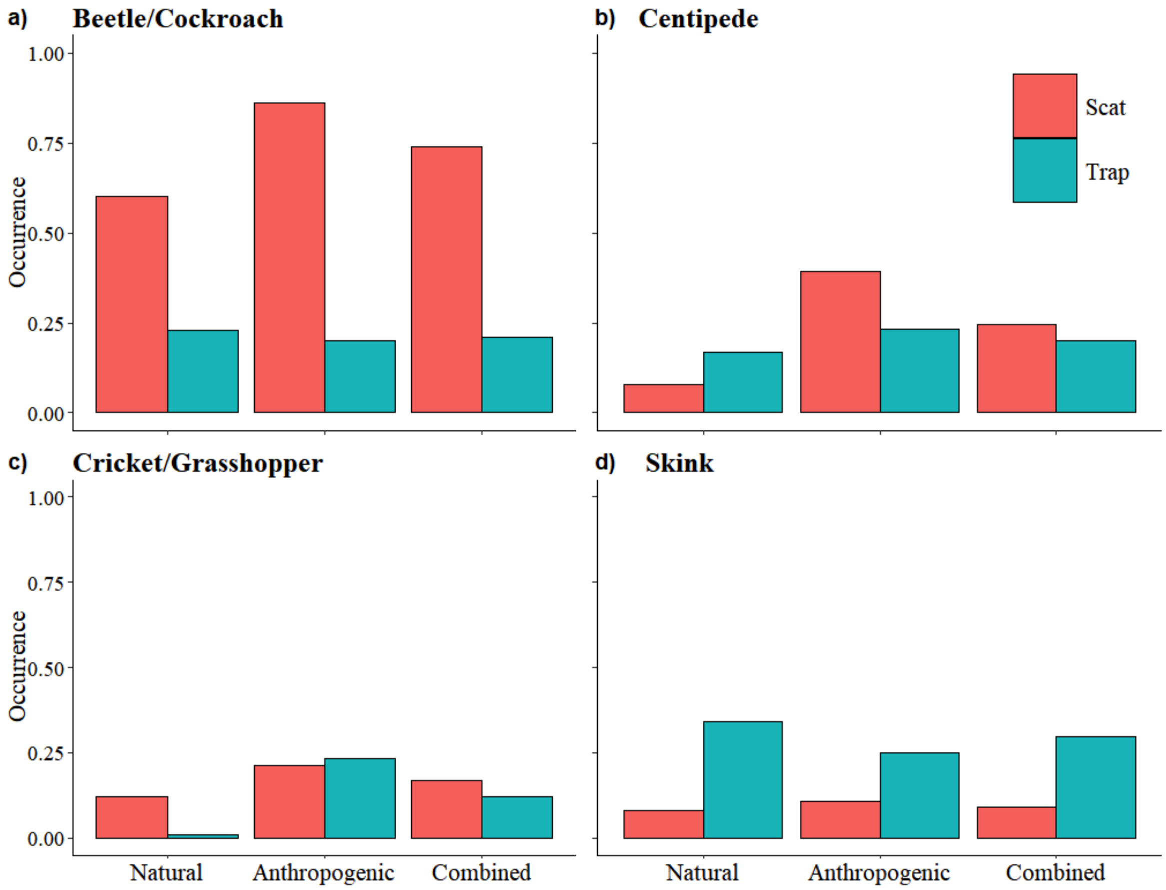


Figure 4.6. Comparison of food item occurrence in scats and traps in both natural and antrhopogenic habitat types, and combined across habitat types. Comparison is limited to food items detected in both scats and traps.

4.5 DISCUSSION

4.5.1 Diet selection and the influence of season and habitat

Closed capture models indicated that the frequency of food items consumed by quolls was best predicted by both season and habitat type. Parameter estimates indicated that more beetles and cockroaches were consumed in the wet season compared with the dry season, and more figs were consumed in the dry season than the wet season. Seasonal differences in diet are likely to be a result of ecosystem-level changes driven by the rainfall of the wet-dry tropics. Precipitation in tropical environments is known to influence net primary productivity and seasonal changes in plant (Murphy 1986; O’Connell 1989), invertebrate (Wolda & Fisk 1981), and vertebrate populations (e.g. Troyer et al. 2014).

Our findings are consistent with studies by Pollock (1999), Oakwood (1997), and Dunlop et al. (2017), where insects were dominant in the diet of the northern quoll. In our study, invertebrates were eaten significantly more than both vertebrates and fruit in both seasons and habitat types, and overall comprised 54% of the total volume of scats. Of the invertebrates, beetles and cockroaches were the most frequently and highest volume food item consumed by the northern quoll on Koolan Island across both habitat types and seasons, detected in 58% of scats and comprising 25% of the volume of all scats (Table 4.1). These findings are considerably higher than that for the northern quoll in the Pilbara region (%FO 47.6; %VO 12.4; Dunlop et al. 2017). Comparable levels of cockroach and beetle consumption was observed between anthropogenic and native habitat, while more were consumed in the wet season than the dry season. Assuming that our invertebrate trapping data (20 trap-lines x 12 nights trapping = 240 trap nights) accurately reflect availability of prey, more beetles and cockroaches were eaten than would be expected based on their availability in the environment, suggesting that northern quolls are selectively feeding on these prey items.

Previous studies of insectivores have found that their foraging strategy maximised the net energy gain by targeting invertebrates that provided the greatest net energy yield (Fisher & Dickman 1993; Brooks et al. 1996). Beetles and cockroaches are large compared to many invertebrates, and contain a high amount of energy, protein and lipids (Potter et al. 2018). However, beetles and cockroaches have exoskeletons with large amount of chitin, which contain bound protein that is difficult to digest (Finke 2007). Previous studies have found small dasyurids are able to digest a high portion of protein from insect diets (Stannard et al. 2014), and the northern quoll may also be physiologically adapted to invertebrate digestion. Given the nutritional value of beetles and cockroaches, combined with their size and abundance in the environment, the net energy gained from predating and feeding on beetles and cockroaches may be higher than for other invertebrates, vertebrates and fruit.

Both centipedes and grasshoppers (Order: Orthoptera) were consumed at moderate frequencies and volumes (Table 4.1). Centipedes appear to be consumed proportionate to their availability in the environment. The consumption of Orthoptera in anthropogenic habitat was proportionate to their high abundance, while more were consumed in native habitat than would be expected. Pollock (1999), Oakwood (1997), and Dunlop et al. (2017) also found Orthoptera to comprise a high proportion of invertebrates consumed by the northern quoll, being the second or third-most frequently consumed invertebrate. This may reflect a preference for grasshoppers and crickets, which are suggested by Potter et al. (2018) to be relatively high in energy, and easier to digest than more chitinous invertebrates.

The northern quoll’s diet appears to undertake seasonal shifts, whereby more vertebrates are consumed in the dry season (however, they are still consumed at lower frequencies than invertebrates or fruit in both seasons). Eight species of vertebrate were detected in the scats of northern quolls on Koolan Island, with some larger species (e.g. snakes, fruit bats; *Pteropus alecto*) likely to be consumed as carrion. Oakwood (1997) found that the consumption of vertebrates also peaked in the dry season in Kakadu National Park, Northern Territory, and suggested that the consumption of vertebrates correlated with their availability in the environment. While Dunlop et al. (2017) found that invertebrates were consumed more than any other group, the authors suggest that larger prey items, such as rodents, are preferred over invertebrates when available. We suggest that seasonal variation in vertebrate consumption is linked to the northern quoll’s life history. During the dry season, the northern quoll population is comprised of adults (Oakwood 1997; Oakwood 2000). Size-constrained predator prey relationships are well-documented in the literature (Polis & McCormick 1986;

Warren & Lawton 1987; Dickman 1988; Owen-Smith & Mills 2008), and dasyurid prey species are known to increase with the size of the individual (Fisher & Dickman 1993). During the dry season, the adult population is more likely to capture and subdue vertebrates than the juveniles present in the population during the wet season. However, northern quolls on Koolan Island are smaller than their mainland counterparts (max. 475 g vs 600 g; How et al. 2009), which may further constrain their ability to capitalise on most vertebrates on Koolan island. Interestingly, skinks, the vertebrate eaten most often and at the largest volumes, were consumed less than would be expected based on their availability. Our study assessed the availability of skinks using pitfall and funnel traps, which were opened at dusk and closed shortly after dawn, which would have captured skinks with crepuscular activity. Therefore, traps may have overestimated the availability of skinks to the northern quoll, which forages nocturnally. This notwithstanding, vertebrates are consumed significantly less than invertebrates in both the wet and the dry season, indicating that vertebrates are used to supplement the diet of the northern quoll rather than form a dominant component of this species' diet.

Northern quolls on Koolan Island appear to supplement their mainly insectivorous diet with fruits in both the wet and dry season. Fruits, specifically fig and stinking passionflower, comprise a relatively high portion of the northern quoll's diet on Koolan Island. Our data indicate a higher frequency of fruits and seeds in the diet of the northern quoll (%FO 43.1; %VO 31.8) than a previous study from the Pilbara region (%FO 29.2; %VO 18.8) (Dunlop et al. 2017), but lower than a study of northern quolls in the wet-dry tropics of mainland Australia (Oakwood 1997; volume up to 60%). Figs were present in 9% of scats, similar to the 10% recorded by Dunlop et al. (2017). Many *Ficus* spp. yield large crops of edible fruit that are high in calcium (O'Brien et al. 1998), making it an important food source for many vertebrates (Shanahan et al. 2001). However, the nutritional value of figs compared to other available fruits appears to vary across *Ficus* species (Milton et al. 1982; Ko et al. 1998; Shanahan 2000). Two species of *Ficus* occur on Koolan Island; *Ficus aculeata* var. *indecora*, and *Ficus virens* Aiton. While three of the ~350 *Ficus* spp. have a year-round fruiting season that is considered to make them a key resource in tropical forests, the two species on Koolan Island have seasonal flowering periods (Western Australian Herbarium 1998-). The availability of figs at our study site is therefore variable between seasons and between years. Oakwood (1997) found the consumption of fruits by the northern quoll was proportionate to their availability in the environment, which is also likely to be the case on Koolan Island. While fruits such as the stinking passionflower exist as prostrate vines and would be encountered during ground-based foraging, figs may be more likely to be encountered when they ripen and fall to the ground. The availability of figs may therefore be subject to seasonal variation in competition from birds, fruit bats and other arboreal feeders that forage on the fruit before it falls to the ground. This notwithstanding, figs are likely to be an important food source for the northern quoll, and this study increases our understanding of ecosystem dynamics between a generalist predator and *Ficus* spp.

We found that the most common fruit consumed by the northern quoll was the stinking passionflower *Passiflora foetida*, occurring in 23.4% of scats. Dunlop et al. (2017) also recorded *P. foetida* in the scats of northern quolls on the mainland, but at apparently much lower frequencies than in our study. Stinking passionflower is a weed of environmental concern in Australia, and is known to be disadvantageous to many species where it is invasive (Freeman & Ezzy 2011; Gerlach 2011; Somaweera et al. 2011). However, fruits of the stinking passionflower are relatively high in energy (73 kcal per 100 g) and protein (6.5% per 100 g) (Hoe & Siong 1999). Corlett (2005) suggested that in Hong Kong where *P. foetida* is also invasive, this plant provided a viable food resource for a number of bird species as it has fruit available for most of the year, unlike many native fruit species. This is also likely to be true on Koolan Island, and the stinking passionflower may provide a reliable resource when other food sources are less available.

Dunlop et al. (2017) suggests that the northern quoll may increase its consumption of fruits and vegetative material where insects and reptiles are less available, or where it is subjected to competitive exclusion from small vertebrates by feral cats. There are no feral cats on Koolan Island, and few other species that are likely to directly compete with the northern quoll for food resources. The importance of fruits may also be higher for northern quolls in the wet-dry tropics of Australia than for those in the semi-arid Pilbara region (also see Oakwood 1997), perhaps reflecting a higher availability of fruits or other community-level differences between ecosystems. Another possibility is that the reliance on fruits is a function of the smaller size of northern quolls on Koolan Island compared to the mainland (How et al. 2009). This difference in size may mean that northern quolls on the island are less able to exploit medium to larger vertebrates, and compensate with supplementing their diet with fruits. The proportion of fruit consumed by northern quolls on Koolan Island suggests that fruits are an important resource to this species, and possibly more so than for northern quolls in the Pilbara region.

4.5.2 Trophic niche breadth

Season and habitat were found to have no influence on northern quoll trophic niche breadth. Overall niche breadth on the island using Levins standardised index of niche breadth was 0.27. When using food categories as in Dunlop et al. (2017), niche breadth for the island (0.23; 95% CI 0.20 – 0.27) was comparable to the niche breadth recorded in the Pilbara region (0.21) and larger than six of ten Pilbara sites overall. Koolan Island has lower faunal diversity than the mainland (McKenzie et al. 1995), particularly in regard to small mammals, which is expected to result in a lower diversity of available prey species. Interestingly, an island larger in size than Koolan Island was included in the study by Dunlop et al. (2017) and reported to have a relatively small niche breadth (0.17). The niche of insular populations has been linked to levels of competition and the range of food resources available (e.g. Darimont et al. 2004; Keogh et al. 2005; Meiri et al. 2007). In cases where island populations have a larger niche breadth than their mainland counterparts, this has been attributed to reduced competition on the island that allows species to exploit food resources with more uniformity, and a wider niche of available resources (sometimes associated with coastal habitat) (Clevenger 1993; Stronen et al. 2014; Runemark et al. 2015; Crego et al. 2018; but see Novosolov 2018). Dunlop et al. (2017) suggest that the northern quoll competes with other medium-sized mammals in the Pilbara region, including feral cats (*Felis catus*) and foxes (*Vulpes vulpes*). Feral cats and foxes are absent on Koolan Island, and there are no other species likely to directly compete with the northern quoll. The recorded trophic niche breadth in the study population is likely to be influenced by the balance between prey availability and competition, whereby a lower diversity of available prey items on the island versus the mainland reduces the potential niche breadth, and the absence of competing animals present on the mainland increases the potential niche breadth.

4.5.3 Conservation management

Use of anthropogenic habitat

From the analyses conducted, differences in the frequency of food items between native and anthropogenic habitat was most pronounced for Orthoptera, which were more frequently detected in traps within anthropogenic than native habitat, and crustaceans, which were nearly always detected in scats in native habitat. There were no food items that were exclusively recorded in one habitat type. The drivers of habitat-level differences in the diet of a mobile species can be difficult to detect, especially where those habitat types are adjacent. In a previous study, northern quolls were suggested to move several kilometres on Koolan Island between captures (Spencer et al. 2017). Crustaceans, associated with coastal environments, were mostly detected in scats in native habitat, but also detected at low levels in anthropogenic habitat, indicating that quolls are moving across the island to maximise use of a variety of available food resources.

Anthropogenic habitat on the island contains a variety of invertebrates, skinks and fruits (particularly *P. foetida*, which thrives in disturbed habitats; Global Invasive Species Database 2018), and while the island is managed to limit the access by wildlife to human waste, small levels of rubbish were detected in northern quoll scats (Table 4.1). A wide range of generalist species have been found to exploit resources in anthropogenic habitats (e.g. Riley 2007; Berland et al. 2008; Beatty et al. 2013). Northern quolls appear to be flexible in their feeding ecology to take advantage of food sources when they are abundant, or conversely, to rely on a food source when other items are scarce (Dunlop et al. 2017). Similar behaviour was observed in spotted genets (*Genetta tigrina*) in South Africa, whereby the species was found to eat invertebrates associated with urban environments in winter, when insects were less common in their natural environment (Widdows & Downs 2015). However, while northern quolls can exploit food resources in modified habitat, this does not diminish the importance of accessible native habitat for foraging activities. Further, increased use of anthropogenic habitat also increases the chance of human-wildlife conflict (Widdows & Downs 2015). Therefore, managing species with generalist tendencies may also necessitate species management measures to address the increased risk of human wildlife conflict.

Rehabilitation and habitat management

When the goal of restoration includes the provision of habitat for particular species, broad land-based targets or ‘bottom-up’ approaches may be inadequate in identifying the biotic and abiotic factors required for that species (Miller & Hobbs 2007). In these cases, both landscape scale (bottom-up) and organism-based (top-down) considerations are needed, as the conditions that contribute to one species’ persistence may not correlate with landscape variables such as dominant vegetation type (Morrison 2013). Our findings indicate that northern quolls on Koolan Island have a generalist diet of invertebrates, vertebrates and vegetative material comprised mostly of fruits, and habitats that support these food items should be considered when managing native habitat for the northern quoll and setting rehabilitation objectives. The majority of prey items consumed are ground-dwelling (beetles and cockroaches, centipedes, crickets and grasshoppers, crustaceans, skinks) suggesting that northern quolls on Koolan Island primarily feed on the ground. The fruit species consumed most, *P. foetida*, also occurs on the ground as a prostrate vine, while other fruits may be consumed once they have ripened and fallen from the tree or shrub. The theory that the northern quoll is primarily a ground-based forager is supported by Oakwood (1997). The northern quoll relies on aural and olfactory cues to detect prey at night (Pellis et al. 1992). Northern quolls observed foraging at night on Koolan Island were always on the ground, exhibiting strong responses to movement in the leaf litter (J Thomas, pers. obs). Leaf litter correlates with the richness and abundance of a number of invertebrates, including cockroaches, beetles and ants (Sayer 2006; Tarli et al. 2014; Grimbacher et al. 2018), and this habitat component is therefore likely to be important for the northern quoll. Given the consistency of our findings with other studies in the wet-dry tropics (Pollock 1999; Oakwood 1997), these inferences may be used to set rehabilitation criteria both on Koolan Island and in similar environments to ensure sufficient food resources are available for the successful recolonisation of rehabilitated areas by the northern quoll. Based on our findings, suitable rehabilitation objectives may include measures of ground-dwelling invertebrate abundance, particularly beetles and cockroaches, and the availability of fruits (i.e. figs) that provide a supplementary food resource throughout the year.

In addition to invertebrates, our findings show that northern quolls supplement their diet with a variety of fruits, and in particular feed on the stinking passionflower at relatively high frequencies and volumes. From a management perspective, the use of stinking passionflower by the northern quoll presents an ideological conflict between weed management and the management of a threatened species. In terms of weed management, northern quolls may contribute to seed dispersal for *P. foetida*, should seeds remain viable after digestion (Dunlop et al. 2017). From a species management perspective, stinking passionflower provides a food resource for the northern quoll that may help populations to persist when other food items are less available, and increase the overall carrying capacity of an area. If weed management practices are successful, this may in turn impact the local northern quoll population. While this study provides some insight into the relationship between *P. foetida* and the northern quoll, the nuances of this relationship (for example, whether the prevalence of stinking passionflower has the potential to impact the availability of other prey items) should be further explored before informing any conservation management decisions.

4.6 REFERENCES

Anderson, D. R., Burnham, K. P. & White, G. C. (1994). AIC model selection in overdispersed capture–recapture data. *Ecology, 75*, 1780–1793.

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control, 19,* 716-723.

Atkins, Z. S., Clemann, N., Schroder, M., Chapple, D. G., Davis, N. E., Robinson, W. A., Wainer, J. & Robert, K. A. (2018). Consistent temporal variation in the diet of an endangered alpine lizard across two south-eastern Australian sky-islands. *Austral Ecology*, *43,* 339-351.

Beard, J.S. (1979). *Vegetation Survey of Western Australia. Kimberley* 1: 1 *000 000 vegetation Series.* University of Western Australia Press, Nedlands.

Beatty, W. S., Beasley, J. C., & Rhodes Jr, O. E. (2013). Habitat selection by a generalist mesopredator near its historical range boundary. *Canadian Journal of Zoology*, *92,* 41-48.

Berland, A., Nelson, T., Stenhouse, G., Graham, K., & Cranston, J. (2008). The impact of landscape disturbance on grizzly bear habitat use in the Foothills Model Forest, Alberta, Canada. *Forest Ecology and Management*, *256*, 1875-1883.

BOM (Bureau of Meteorology) (2018) Climate Data Online. Retrieved from http://www.bom.gov.au/climate/data/index.shtml?bookmark=136.

Braithwaite, R. W. & Griffiths, A. D. (1994). Demographic variation and range contraction in the Northern Quoll, *Dasyurus hallucatus* (Marsupalia: Dasyuridae). *Wildlife Research, 21*, 203-217.

Brooks, S. J., Calver, M. C., Dickman, C. R., Meathrel, C. E., & Bradley, J. S. (1996). Does intraspecific variation in the energy value of a prey species to its predators matter in studies of ecological energetics? A case study using insectivorous vertebrates. *Ecoscience, 3*, 247-251.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. Springer Science & Business Media.

Clevenger, A. P. (1993). Pine marten (*Martes martes* Linné, 1758) comparative feeding ecology in an island and mainland population of Spain. *Zeitschrift fur Saugetierkunde*, *58,* 212-212.

Corlett, R. T. (2005). Interactions between birds, fruit bats and exotic plants in urban Hong Kong, South China. *Urban Ecosystems*, *8,* 275-283.

Cramer, V. A., Dunlop, J., Davis, R., 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.

Crego, R. D., Jiménez, J. E., & Rozzi, R. (2018). Potential niche expansion of the American mink invading a remote island free of native-predatory mammals. *PloS One*, *13,* e0194745.

Cremona, T., Crowther, M. S., & Webb, J. K. (2017). High mortality and small population size prevent population recovery of a reintroduced mesopredator. *Animal Conservation*, *20*, 555-563.

Dale, B. W., Adams, L. G., & Bowyer, R. T. (1994). Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. *Journal of Animal Ecology, 63*, 644-652.

Darimont, C. T., Price, M. H. H., Winchester, N. N., Gordon-Walker, J., & Paquet, P. C. (2004). Predators in natural fragments: foraging ecology of wolves in British Columbia's central and north coast archipelago. *Journal of Biogeography*, *31*, 1867-1877.

Darimont, C. T., Paquet, P. C., & Reimchen, T. E. (2009). Landscape heterogeneity and marine subsidy generate extensive intrapopulation niche diversity in a large terrestrial vertebrate. *Journal of Animal Ecology, 78*, 126-133.

Dickman, C. R. (1988). Body size, prey size, and community structure in insectivorous mammals. *Ecology, 69*, 569-580.

Doherty, T.S., Davis, N.E., Dickman, C.R., Forsyth, D.M., Letnic, M., Nimmo, D.G. Newsome, T.M. (2018). Continental patterns in the diet of a top predator: Australia's dingo. *Mammal Review,* doi:10.1111/mam.12139.

Dunlop, J. A., 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*(3), 858-866.

Finke, M. D. (2007). Estimate of chitin in raw whole insects. *Zoo Biology*, *26*, 105-115.

Fisher, D. O., & Dickman, C. R. (1993). Body Size-Prey relationships in insectivorous marsupials: Tests of three hypotheses. *Ecology*, *74*, 1871-1883.

Freeman, A., & Ezzy, L. (2011). *Recommendations for pest control to protect the Gulf snapping turtle (Elseya lavarackorum) in the Middle Gorge area of Boodjamulla National Park*. Department of Environment and Resource Management.

Gardener, M. (2014). *Community ecology: analytical methods using R and Excel*. Pelagic Publishing Ltd., Exeter.

Gerlach, J. (2011). Conservation of the Seychelles sheath-tailed bat *Coleura seychellensis* from 1997–2011 and future prospects. *Phelsuma*, *19*, 54-68.

Global Invasive Species Database. (2018). Species profile: *Passiflora foetida*. Retrieved from http://www.iucngisd.org/gisd/species.php?sc=341.

Griffiths, A. D., Rankmore, B., Brennan, K., & Woinarski, J. C. (2017). Demographic evaluation of translocating the threatened northern quoll to two Australian islands. *Wildlife Research*, *44*, 238-247.

Grimbacher, P. S., Edwards, W., Liddell, M. J., Nelson, P. N., Nichols, C., Wardhaugh, C. W., & Stork, N. E. (2018). Temporal variation in abundance of leaf litter beetles and ants in an Australian lowland tropical rainforest is driven by climate and litter fall. *Biodiversity and Conservation, 27*, 2625-2640.

Hayward, M.W. (2006). Prey preferences of the spotted hyaena (*Crocuta crocuta*) and degree of dietary overlap with the lion (*Panthera leo*). *Journal of Zoology, 270*, 606–614.

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.

Hoe, V. B., & Siong, K. H. (1999). The nutritional value of indigenous fruits and vegetables in Sarawak. *Asia Pacific Journal of Clinical Nutrition, 8,* 24-31.

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.

Huggins, R. M. (1989). On the statistical analysis of capture experiments. *Biometrika, 76,* 133–140.

Hurlbert, S. H. (1978). The measurement of niche overlap and some relatives. *Ecology, 59,* 67-77.

Indigo, N., Smith, J., Webb, J. K., & 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.

Jolly, C. J., Kelly, E., Gillespie, G. R., Phillips, B., & 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.

Keighery, G. J., Gibson, N., Kenneally, K. F., & Mitchell, A. A. (1995). Biological inventory of Koolan Island, Western Australia 1. Flora and vegetation. *Records of the Western Australian Museum*, *17*, 237-248.

Keogh, J. S., Scott, I. A. W. & Hayes, C. (2005). Rapid and repeated origin of insular gigantism and dwarfism in Australian tiger snakes. *Evolution,* 59, 226–233.

Klare, U., Kamler, J. F., & Macdonald, D. W. (2011). A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Review, 41*, 294-312.

Ko, I. W. P., Corlett, R. T. & Xu, R-J. (1998). Sugar composition of wild fruits in Hong Kong, China. *Journal of Tropical Ecology, 14,* 381–387.

Laake, J. L. (2013). RMark: an R interface for analysis of capture-recapture data with MARK: US Department of Commerce. *National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center*.

Laake, J., & Rexstad, E. (2014). Appendix C. RMark-an alternative approach to building linear models in MARK. *Program MARK: A Gentle Introduction. 13th edition.* Retrieved from http://www. phidot. org/software/mark/docs/book.

Legge S, Kennedy MS, Lloyd R, Murphy SA, & Fisher A (2011a) Rapid recovery of mammal fauna in the central Kimberley, northern Australia, following the removal of introduced herbivores. *Austral Ecology, 36*, 791–799.

Legge S., Murphy S., Kingswood R., Maher B., & Swan D. (2011b). EcoFire: restoring the biodiversity values of the Kimberley region by managing fire. *Ecological Management & Restoration*, *12*, 84–92.

Lemons, P. R., Sedinger, J. S. , Herzog, M. P., Gipson, P. S. & Gilliand, R. L. (2010). Landscape effects on diets of two canids in northwestern Texas: a multinomial modeling approach. *Journal of Mammalogy, 91*, 66–78.

Levins, R. (1968). *Evolution in Changing Environments: Some Theoretical Explorations*. Princeton University Press, Princeton, NJ.

Lyons, M. N., Keighery, G. J., Gibson, L. A., & Handasyde, T. (2014). Flora and vegetation communities of selected islands off the Kimberley coast of Western Australia. *Records of the Western Australian Museum Supplement*, *81*, 205-244.

Maxwell, S., Burbidge, A. A. & Morris, K. (1996). *The 1996 Action Plan for Australian Marsupials and Monotremes*. Australasian Marsupial and Monotreme Specialist Group, IUCN Species Survival Commission, Gland, Switzerland.

MBS Environmental (2012) *Koolan Island iron ore mine and port facility project. Significant fauna species management plan*. Unpublished report prepared for Mount Gibson Iron Limited.

McKenzie, N. L., Fontanini, L., Lindus, N. V., & Williams, M. R. (1995). Biological inventory of Koolan Island, Western Australia 2. Zoological notes. *Records of the Western Australian Museum*, *17*, 249-266.

McKinnon, L., Picotin, M., Bolduc, E., Juillet, C. & Bêty, J. (2012). Timing of breeding, peak food availability, and effects of mismatch on chick growth in birds nesting in the High Arctic. *Canadian Journal of Zoology*, *90*, 961-971.

McVey, J. M., Cobb, D. T., Powell, R. A., Stoskopf, M. K., Bohling, J. H., Waits, L. P., & Moorman, C. E. (2013). Diets of sympatric red wolves and coyotes in northeastern North Carolina. *Journal of Mammalogy*, *94*, 1141-1148.

Meiri, S., Dayan, T., & Simberloff, D. (2007). Guild composition and mustelid morphology—character displacement but no character release. *Journal of Biogeography, 34*, 2148–2158.

Miller, J. R., & Hobbs, R. J. (2007). Habitat restoration—Do we know what we're doing? *Restoration Ecology*, *15*, 382-390.

Miller, R. A., Carlisle, J. D., & Bechard, M. J. (2014). Effects of prey abundance on breeding season diet of Northern Goshawks (*Accipiter gentilis*) within an unusual prey landscape. *Journal of Raptor Research*, *48*, 1-12.

Milton, K., Windsor, D. M., Morrison, D. W., & Estribi, M. A. (1982). Fruiting phenologies of two neotropical Ficus species. *Ecology, 63*, 752-762.

Morrison, M. L. (2013). *Wildlife restoration: techniques for habitat analysis and animal monitoring* (Vol. 1). Island Press.

Murdoch, W.W. (1969). Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological monographs*, *39*, 335-354.

Murphy, P. (1986). Ecology of tropical dry forest. *Annual Review of Ecology and Systematics*, *17*, 67-88.

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

Nix, H. A., Kalma, J. D., & Walker, D. (1972). *Bridge and Barrier: the natural and cultural history of Torres Strait.* Department of Biogeography and Geomorphology, Research School of Pacific Studies, ANU, Canberra.

Novakowski, G. C., Hahn, N. S., & Fugi, R. (2008). Diet seasonality and food overlap of the fish assemblage in a pantanal pond. *Neotropical Ichthyology*, *6*, 567-576.

Novosolov, M., Rodda, G. H., Gainsbury, A. M., & Meiri, S. (2018). Dietary niche variation and its relationship to lizard population density. *Journal of Animal Ecology*, *87*, 285-292.

O'Connell, M. A. (1989). Population dynamics of neotropical small mammals in seasonal habitats. *Journal of Mammalogy, 70*, 532-548.

O'Brien, T. G., Kinnaird, M. F., Dierenfeld, E. S., Conklin- Brittain, N. L., Wrangham, R. W., & Silver, S. C. (1998). What's so special about figs? *Nature, 392*, 668.

Oakwood, M. (1997). The ecology of the northern quoll, Dasyurus hallucatus (Unpublished doctoral dissertation). The Australian National University, ACT, Australia.

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., Woinarski, J. & Burnett, S. (2008). *Dasyurus hallucatus. The IUCN Red List of Threatened Species 2008*: e.T6295A12600197. Retrieved from http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T6295A12600197.en.

Owen-Smith, N., & Mills, M. G. (2008). Predator–prey size relationships in an African large-mammal food web. *Journal of Animal Ecology*, *77*, 173-183.

Panzacchi, M., Herfindal, I., Linnell, J. D., Odden, M., Odden, J., & Andersen, R. (2010). Trade-offs between maternal foraging and fawn predation risk in an income breeder. *Behavioral Ecology and Sociobiology*, *64*, 1267-1278.

Pellis, S. M., Vanderlely, R., & Nelson, J. E. (1992). The roles of vision and vibrissae in the predatory behaviour of Northern Quolls Dasyurus Hallucatus (Marsupialia: Dasyuridae). *Austral Mammalogy, 15*, 55-60.

Polis, G., & McCormick, S. J. (1986). Patterns of resource use and age structure among species of desert scorpion. *Journal of Animal Ecology*, *55*, 59-73.

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, T. I., Stannard, H. J., Greenville, A. C., & Dickman, C. R. (2018). Understanding selective predation: Are energy and nutrients important?. *PloS one*, *13*, e0201300.

Putman, R. J. (1984). Facts from faeces. *Mammal review, 14*(2), 79–97.

Radford, I. J., Gibson, L. A., Corey, B., Carnes, K., & 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*, e0130721.

Riley, E. P. (2007). Flexibility in diet and activity patterns of *Macaca tonkeana* in response to anthropogenic habitat alteration. *International Journal of Primatology*, *28*, 107-133.

Runemark, A., Sagonas, K., & Svensson, E. I. (2015). Ecological explanations to island gigantism: dietary niche divergence, predation, and size in an endemic lizard. *Ecology*, *96*, 2077-2092.

Samplonius, J. M., Kappers, E. F., Brands, S., & Both, C. (2016). Phenological mismatch and ontogenetic diet shifts interactively affect offspring condition in a passerine. *Journal of Animal Ecology, 85*, 1255-1264.

Sayer, E. J. (2006). Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biological reviews, 81*, 1–31.

Shanahan, M. (2000). *Ficus* seed dispersal guilds: ecology, evolution and conservation implications. Ph.D. thesis. University of Leeds, UK.

Shanahan, M., So, S., Compton, S. G., & Corlett, R. (2001). Fig-eating by vertebrate frugivores: a global review. *Biological Reviews*, *76*, 529-572.

Spencer, P. B., Sandover, S., Nihill, K., Wale, C. H., How, R. A., & 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*, 17-27.

Somaweera, R., Webb, J. K., & Shine, R. (2011). It's a dog-eat-croc world: dingo predation on the nests of freshwater crocodiles in tropical Australia. *Ecological Research*, *26*, 957.

Stannard, H. J., McAllan, B. M., & Old, J. M. (2014). Dietary composition and nutritional outcomes in two marsupials, *Sminthopsis macroura* and *S. crassicaudata*. *Journal of Mammalogy*, *95*, 503-515.

Stenset, N. E., Lutnæs, P. N., Bjarnadóttir, V., Dahle, B., Fossum, K. H., Jigsved, P., Johansen, T. Neumann, W. Opseth, O., Ronning, O. & Steyaert, S. M. (2016). Seasonal and annual variation in the diet of brown bears *Ursus arctos* in the boreal forest of southcentral Sweden. *Wildlife Biology*, *22*, 107-116.

Stronen, A. V., Navid, E. L., Quinn, M. S., Paquet, P. C., Bryan, H. M., & Darimont, C. T. (2014). Population genetic structure of gray wolves (*Canis lupus*) in a marine archipelago suggests island-mainland differentiation consistent with dietary niche. *BMC ecology*, *14*, 11.

Tarli, V. D., Pequeno, Pedro A. C. L, Franklin, E., Morais, J. W., Souza, J. L. P., Oliveira, A. H. C., & Guilherme, D. R. (2014). Multiple environmental controls on cockroach assemblage structure in a tropical rain forest. *Biotropica, 46*, 598-607.

Tremblay, Y., & Cherel, Y. (2003). Geographic variation in the foraging behaviour, diet and chick growth of rockhopper penguins. *Marine ecology progress series, 251*, 279-297.

Troyer, E. M., Cameron Devitt, S. E., Sunquist, M. E., Goswami, V. R., & Oli, M. K. (2014). Density dependence or climatic variation? Factors influencing survival, recruitment, and population growth rate of Virginia opossums. *Journal of Mammalogy, 95*, 421-430.

Warren, P. H., & Lawton, J. H. (1987). Invertebrate predator-prey body size relationships: an explanation for upper triangular food webs and patterns in food web structure? *Oecologia*, *74*, 231-235.

Webb, J., Legge, S., Tuft, K., Cremona, T., & Austin, C. (2015). Can we mitigate cane toad impacts on northern quolls? Final report.

Western Australian Herbarium (1998–). FloraBase—the Western Australian Flora. Department of Biodiversity, Conservation and Attractions. Retrieved from https://florabase.dpaw.wa.gov.au/.

White, G. C., & Burnham, K. P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study*, *46*(sup1), S120-S139.

Williams, B. K., Nichols, J. D. & Conroy, M. J. (2002). Analysis and management of animal populations. Academic Press, San Diego, California.

Widdows, C. D., & Downs, C. T. (2015). A genet drive-through: are large spotted genets using urban areas for “fast food”? a dietary analysis. *Urban ecosystems*, *18*, 907-920.

Wolda, H., & Fisk, F. W. (1981). Seasonality of tropical insects. II. Blattaria in Panama. *The Journal of Animal Ecology*, 827-838.

4.7 SUPPLEMENTARY INFORMATION

Supplementary Table S. 1. Percentage frequency of occurrence (%FO) and percentage volume (%VO) for all food types identified in northern quoll scats over the study period (2015 – 2017), grouped by season and habitat type.

	%FO				**%VO**			
	Dry season		Wet season		Dry season		Wet season	
	Native	Anthro	Native	Anthro	Native	Anthro	Native	Anthro
Beetle/ cockroach	56.62	55.81	62.22	76.67	21.79	23.37	27.70	33.01
Caterpillar	0.00	2.33	2.22	1.11	0.00	1.85	2.17	0.11
Centipede	25.74	20.35	24.44	31.11	10.75	8.57	8.30	15.54
Grasshopper/ cricket	16.91	26.74	31.11	31.11	3.32	8.62	6.71	6.88
Ant/ termite	55.15	62.21	64.44	68.89	3.44	4.10	6.39	7.73
Spider	0.74	0.58	2.22	1.11	0.04	0.00	0.22	0.00
Cocoon	1.47	1.74	2.22	1.11	0.41	0.43	0.65	0.34
Crustacean	15.44	1.16	6.67	6.67	11.10	0.17	2.58	2.07
Millipede	0.00	0.00	2.22	0.00	0.00	0.00	0.11	0.00
Unidentified insect	0.74	3.49	2.22	0.00	0.07	0.72	0.43	0.00
Snail	1.47	2.33	26.67	4.44	0.22	0.14	6.58	1.11
Dasyurus hallucatus	2.21	0.00	0.00	0.00	1.36	0.00	0.00	0.00
Zyzomys argurus	2.21	0.58	0.00	1.11	1.24	0.17	0.00	0.78
Pteropus alecto	0.00	0.58	0.00	0.00	0.00	0.41	0.00	0.00
Microbat	0.00	0.58	0.00	0.00	0.00	0.46	0.00	0.00
Bird	2.21	5.81	0.00	5.56	0.96	2.77	0.00	3.74
Skink	27.21	23.84	20.00	13.33	9.82	7.38	3.03	4.09
Snake	2.94	3.49	0.00	2.22	1.22	1.67	0.00	1.46
Gecko	0.00	1.16	0.00	3.33	0.00	0.25	0.00	2.24
Ficus sp.	15.44	9.30	0.00	3.33	8.63	5.77	0.00	2.12
Passiflora foetida	25.74	28.49	15.56	16.67	15.82	19.78	8.75	10.00
Bush tomato	0.74	0.00	0.00	0.00	0.15	0.00	0.00	0.00
Ampelocissus acetosa	5.88	2.86	8.51	0.00	3.58	0.97	7.99	0.00
Seed 2	0.74	1.71	14.89	3.33	0.59	1.04	9.85	1.79
Cassytha filiformis	5.15	8.57	6.38	1.11	2.44	5.67	4.53	1.01
Seed 4	2.94	4.57	6.38	7.78	0.89	2.03	2.92	4.92
Seed 5	0.00	1.14	0.00	0.00	0.00	0.60	0.00	0.00
Seed 6	0.00	0.57	0.00	0.00	0.00	0.58	0.00	0.00
Seed 7	0.74	0.00	0.00	0.00	0.74	0.00	0.00	0.00
Seed 8	0.00	0.57	0.00	0.00	0.00	0.03	0.00	0.00
Vegetation	2.21	4.65	2.22	4.44	0.81	1.97	1.08	0.84
Rubbish	0.74	0.58	0.00	1.11	0.59	0.46	0.00	0.22

Chapter 5: Nursery den site selection by the northern quoll (*Dasyurus hallucatus*)

5.1 ABSTRACT

Shelter and protection is a key habitat element for most mammal species, the specifics of which vary widely contingent upon ecology and physiology. With rapidly accelerating land use and climate change, there is an urgent need to refine our knowledge of species habitat requirements. We examined female den site selection of a rare and declining species, the northern quoll (*Dasyurus hallucatus*), during the period when dependent young are deposited in dens, in a tropical landscape partially modified by mining. We used one-way ANOVAs, GAMMs and logistic regression to investigate the microclimatic and habitat-related variables of den sites, compared to randomly selected available dens and ambient conditions. Dens were found in trees (n = 4), rock crevices (n = 12), and underground (n = 6). No dens were located amongst modified habitat. No difference in mean temperature or humidity measures between used and available dens were detected, although used dens had a more stable temperature and humidity over the entire 24 hour period than available dens. In addition, used dens in rocky substrate had more stable microclimates than both subterranean and tree dens. Aerial cover (canopy cover and rocky overhangs) and number of potential entrances best predicted den site use by females. Northern quolls do not appear to use modified habitat for den sites during this period, which is a key consideration for assessing the potential impacts of future mining operations.

5.2 INTRODUCTION

The effective management of wildlife populations requires a strong understanding of the factors that influence or limit species abundance and distribution (Carter et al. 2012). Spatial distribution of wildlife populations is linked with processes such as predation, competition, availability of resources such as food, water, and shelter (Carter et al. 2012). For species that depend on the availability of shelter sites for denning, the availability of (ecologically or physiologically) suitable den sites can influence survival, breeding success and juvenile recruitment, and therefore may present the greatest limit to population size (Lesmeister et al. 2008). Where mothers deposit young in dens to forage or hunt, the availability of adequate den sites may influence the spatial distribution of females (Lutermann et al. 2010). This is particularly true for species that cannot excavate their own dens and rely on the existence of suitable den sites in their environment (Ross et al. 2010) or where there is an abundance of natural protection.

The structural and habitat attributes of den sites confer protection from the elements and predation risk, and therefore species will select sites based on their physiological and ecological requirements (Lesmeister et al. 2008). For smaller animals, or animals with young that are susceptible to exposure or predation, selecting an appropriate den site is vital to survival. Further, the surrounding environment (e.g. climatic extremes of heat or cold), and a species' life history (e.g. periods of hibernation, parental dependency in the first stage of life) may necessitate an added level of protection from the animal's environment.

Protection from predation can be gained from the selection of dens within particular habitat types or substrate, or in the characteristics of the den that limit predator access or increase the probability of escape. A study of den site selection by Pallas's cat (*Otocolobus manul*) in central Mongolia found that during the maternal period, the species showed a preference for den sites within rocky and ravine habitats and for dens with smaller entrance diameters (Ross et al. 2010). The authors suggest this habitat type provided better protection against access by predators, and that smaller entrances limited interspecific competition and predation risk. The availability of suitable den sites can also limit population change when populations face changing environmental conditions or threats. In an examination of Australian mammal extinctions, the availability of rocky habitat was suggested to buffer island populations from the impacts of feral species (foxes and cats) due to the protection this type of refugia provided against predation (Burbidge and Manly 2002).

If exposure to climatic variables poses a threat to a species, den sites may also need to meet thermoregulatory requirements through protection from adverse weather conditions and changes in ambient temperature and humidity (Frafjord 2003; Benson et al. 2008; Lutermann et al. 2010). This is particularly important for small mammals, or altricial juveniles, with a high surface area to volume ratio and therefore poor temperature regulation capabilities (Lutermann et al. 2010). Microclimatic properties may be influenced by the aspect or number of den openings, thickness of den walls, height above or below ground level, or the substrate or materials comprising the den site (Lutermann et al. 2010; Ross et al. 2010).

The northern quoll (*Dasyurus hallucatus*) is the smallest of four nocturnal quoll species endemic to Australia. As a result of population declines following habitat loss and modification, and the spread of the toxic cane toad *Rhinella marinus*, the species was listed as endangered under IUCN Red List of Threatened Species in 2008 (Oakwood et al. 2008). Before this listing, the species was categorised as lower risk/ near threatened. The northern quoll predominantly occurs in tropical woodland, forest and rocky habitat and has a breeding season that occurs from May to July (Oakwood 2000). During the day the species takes shelter in den sites, which are thought to provide solar protection and a way to avoid diurnal predators, before leaving the den to forage at night (Oakwood 1997).

From the birth of young in late June to August to their becoming independent in November, juveniles are altricial (Braithwaite and Griffiths 1994; Oakwood 1997). At approximately nine weeks of age, juveniles are deposited in den sites by the female (Begg 1981; Schmitt et al. 1989; Oakwood 1997; Oakwood 2000), and left alone at night while the female conducts foraging activities. *D. hallucatus* is partially semelparous, with males undergoing an annual post-mating die-off and females living for 1-2 years on average. As a result, juvenile survival is suggested to exert a significant influence over the population dynamics of this species (Cremona et al. 2017; Thomas et al. 2020). Given the young are altricial for the first three months of life and spend much of this time deposited in dens, den site characteristics may have an important role in juvenile survival. Previous studies have observed northern quolls denning in both naturally occurring (tree hollows, rock crevices, logs, termite mounds, burrows) and anthropogenic (within or around infrastructure, vehicles and equipment) habitats (Oakwood 1997; Pollock 1999; Burnett 2008). However, there have been relatively few studies examining den use by the northern quoll, and none that model macro- and microhabitat characteristics of selected den sites. Further, the microclimatic characteristics of selected den sites, particularly those used by females during the young in den period, has not been explored in detail.

The availability of suitable habitat is an important consideration in the management of threatened species, however objective assessment can be difficult. Habitat modification is encroaching across the northern quoll’s range, leading to a higher likelihood of interaction between *D hallucatus* and novel macro and microhabitat types in the form of anthropogenic infrastructure and equipment. To make reliable assessment of the impact of habitat modification to *D. hallucatus*, conservation managers must understand if or how the species interacts with various artificial habitats. Mining is a classic example and a primary form of habitat modification within *D. hallucatus*’ range, which creates temporary infrastructure, equipment storage areas, mining pits, roads, and artificial landforms created from waste rock material. While the negative impacts of habitat modification on wildlife have been widely studied, there are also known instances of native fauna using novel habitats in a modified environment (Sih et al. 2011; Lowry et al. 2013). This is particularly true if anthropogenic habitats are in some ways analogous to components of native habitat (Lundholm and Richardson 2010). In a study of the rock hyrax (*Procavia capensis*) and its use of artificial dens, Kershenbaum et al. (2011) found that the species actually preferred to den in artificial rock piles over natural rock crevices, hypothesising that artificial rock piles conveyed increased predator protection and social opportunities.

This study uses an island population of *D. hallucatus* in the Kimberley region, Western Australia, to examine den use. We describe the types of dens used by females of this species during the breeding season and identify the drivers of den site selection by *D. hallucatus*, examining macrohabitat, microhabitat and thermal characteristics of 22 used den sites, 24 potential or 'available' (no confirmed use) den sites, and 12 ambient sites. The study area includes both native habitat and modified areas, and thus allows exploration of the use of anthropogenic habitat by females during the breeding season. Our findings are discussed in the context of management challenges currently facing the northern quoll, and its potential to inform innovation in conservation outcomes across the species' range.

5.3 METHODS

5.3.1 Study area

Koolan Island is located in the Buccaneer Archipelago of the Kimberley region, one kilometre off the coast of the north-western corner of Australia (Latitude -16.13, Longitude 123.76; Figure 5.1). The Kimberley region occurs in the wet-dry tropics of Australia and is subject to highly seasonal rainfall, with a wet season that extends from December to April and the majority (75%) of annual rainfall occurring between the months of January and March (BoM 2018). Koolan Island experiences an average annual rainfall of 790 millimetres, and a sub-humid climate with increased humidity from January – March (BoM 2018). While long-term temperature data are not available for the site, nearby Cygnet Bay (85.8km from

Koolan Island) experiences a mean maximum temperature of 32.4°C and mean minimum temperature of 21°C (BoM 2018). During the data collection from September – November 2016 and 2017, mean maximum temperature on Koolan Island was 34.8°C and 33.4°C, respectively, and mean minimum temperature was 23.3°C and 17.9°C, respectively (BoM 2018).

Koolan Island is 2,712 hectares with an underlying lithology of Proterozoic sandstone comprising rugged slopes, ridges and uplands of rock scree and shallow skeletal soils (McKenzie et al. 1995). Five major vegetation communities have been mapped over Koolan Island, the most widespread being *Eucalyptus miniata – Corymbia confertiflora* open woodland generally over *Triodia* hummock grassland and a variable shrub layer (Keighery et al. 1995). Ephemeral creek lines occur across the island, which flow during the wet season. In addition to areas of native habitat, Koolan Island contains an iron ore mine that spans across approximately one third of the island. Mining has occurred since the 1960s, with operations suspended in 1993 and re-commenced in 2006 by Mount Gibson Iron Ltd. The mine footprint includes open mining pits, associated infrastructure, mining accommodation, access tracks, and an air strip.

5.3.2 Study design

To determine if female northern quolls choose den sites based on habitat or microclimatic properties, we used telemetry to locate den sites used by females during the young in den phase. To increase the chances of detecting any den use in modified habitat, we conducted trapping in both native and modified habitat, and tracked females captured in both areas to their den site. Only females who showed physical signs of bearing young that season were used. Each den site was then measured to examine micrcolimatic (temperature, humidity) and habitat characteristics. These measures were also taken for other available den sites in the area, which were not confirmed as used, and ambient sites (microclimate only).

5.3.3 Data collection

Trapping occurred between September – November 2016 and in September 2017 at three locations, with between 10 and 30 collapsible aluminium Elliott traps (9cm x 10cm x 33cm) at each location. Each location was trapped for a maximum of five consecutive nights. Traps were baited using standard universal bait of peanut butter, rolled oats and sardines. Traps were opened at dusk and cleared before midnight to allow females to return to dens before sunrise. Given the study was targeted at locating maternal den site locations, males were immediately released at the point of capture.

A total of 22 females were captured and weighed before being fitted with a telemetry collar containing a Sirtrack Ultimate Lite single stage collar transmitter fitted to a leather band 10mm in width. A weakness was built into the collar using biodegradable polyglycolide suture thread, which breaks down in humid conditions so that if animals could not be recaptured safely the collar would detach. Only animals that weighed over 240 grams were used in this study to ensure that the collar weighed no more than 5% of the animal's body weight.

From September – November 2016 and during September 2017, animals were tracked during daytime hours to locate their den sites. During this period, females deposit young in the den during nocturnal foraging activities. A total of 22 den sites were located, marked using flagging tape and a GPS location recorded. Occupation of a used den was verified by the detection of a signal using the receiver with antenna removed, or the presence of fresh or recent scats at the den entrance. A total of 24 potential (hereafter referred to as available) den sites were selected on Koolan Island for comparison against confirmed used den sites. Available den sites were identified as being within 100 m of a used den site, containing a hollow or crevice of comparable size to used den sites, with exterior access available and no signs (scats etc.) of use by a northern quoll.

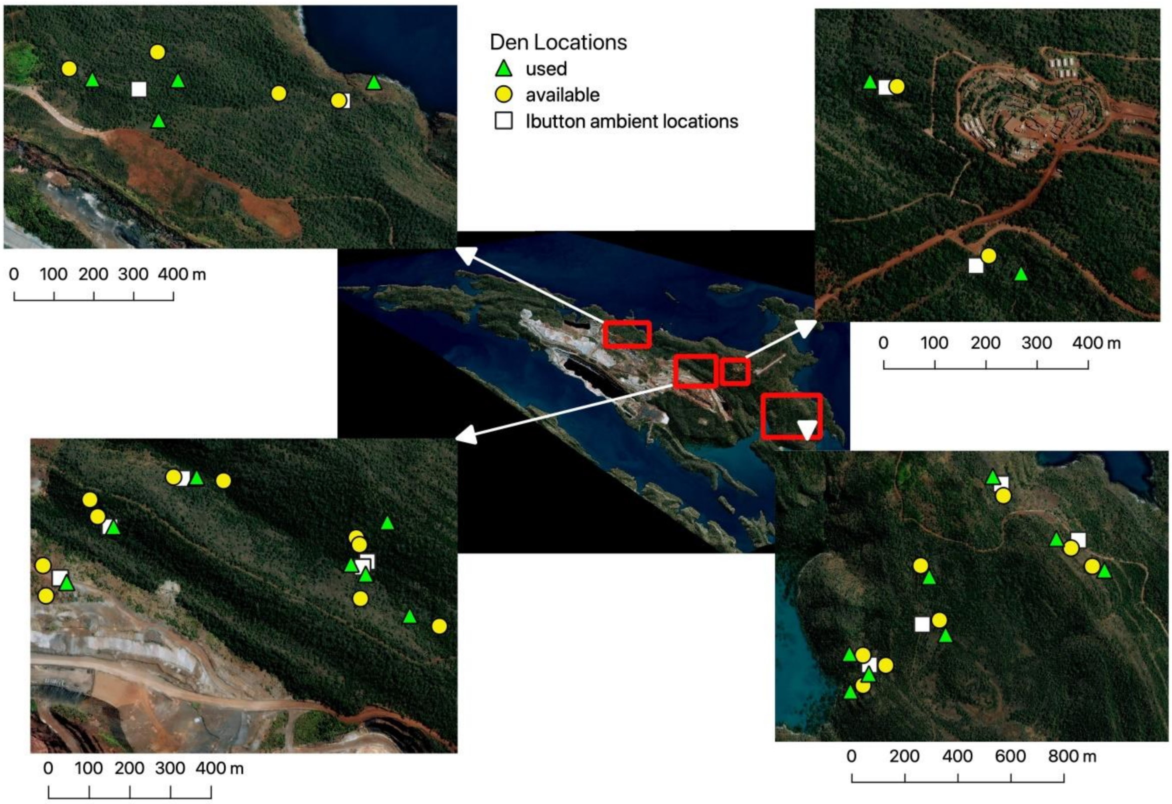


Figure 5.1. Location of Koolan Island showing used dens (triangle), available dens (circle) and ambient sites (square).

Once each animal was located in its den, trapping occurred in the vicinity of the den site to remove the telemetry collar. Trapping was undertaken until all animals were recaptured. Where collars were recovered after becoming detached due to the built-in weakness, trapping was not pursued.

To quantify thermal properties, temperature and humidity data-loggers (Maxim/Dallas Integrated Products, Inc.) (17 mm diameter and 6 mm thick; temperature range, −20 to 85 °C; resolution, 0.0625; humidity range, 0–100 %; resolution, 0.04 %) were deployed at each used and available den site in September 2017. Logistical constraints meant that microclimatic data collection could not occur in 2016, meaning some sites had a 12 month delay between confirmed use and data collection. However, observed fresh scats in 2017 outside some 2016 dens that indicated some sites were used in consecutive years. Impacts of the time-lag were considered to be minimal due to similarity in temperature during this season between 2016 and 2017 (September 2016: 20.4°C - 33.4°C; September 2017: 17.9°C - 33.4°C; BoM 2018), and the stable physical environment at the sites (i.e. no change to the structural attributes of den sites or habitat). For each den site, one data-logger was inserted as deep into the den as possible without preventing use or obstructing access by animals (typically 1-1.5 m), with placement depending on the den structure but usually at the top or side of dens. Twelve data-loggers were placed at random locations on the island within a maximum of 250 m from used and available dens to record ambient temperature. Data-loggers used to record ambient temperate were placed under the shade of a tree 1m from the ground, inside a white upside-down plastic plant pot with holes in the sides to allow air flow but not allow the data-logger to get wet from condensation or rainfall. Each data-logger was left at the site for a period of seven to 45 days (mean = 30) to measure temperature and humidity at 15 minute intervals. All data loggers for a site (used, available and ambient) recorded simultaneously with an overall sampling period of 17 September – 17 November 2017.

Den habitat measurements. Given the available literature on the northern quoll during the young in den period (Oakwood 1997), personal observations of northern quoll denning behaviour, and important den site characteristics identified by similar studies (e.g. Lesmeister et al. 2008; Ross et al. 2010), we recorded nine habitat predictor variables at each used and available den site to encompass local topography, vegetation structure, ground cover and den attributes (Table 5.1). These included measures for ground cover, aerial cover, number of potential entrances, elevation and vegetation structure. Ground cover was recorded at den site locations using four 1 m^2 quadrats located 5 m north, south, east and west of each den site. Four ground cover measurements were estimated by eye: bare soil (sand or gravel), exposed rock, leaf litter and vegetation. The percentage of each quadrat covered by each ground cover type (bare soil, rock, vegetation, leaf litter) was recorded, and then averaged across the four quadrats per den site. Percentage aerial cover recorded by taking a photograph one metre above ground level and visually estimating percentage cover as described in Hnatiuk et al. (2009). Vegetation condition was measured using the vegetation condition scale outlined by the WA Environmental Protection Authority (EPA), whereby vegetation ranges from 'completely degraded' to 'excellent' based on the level of disturbance at each structural layer, and regeneration ability (EPA 2016).

Table 5.1. Habitat variables recorded at each used and available den site.

Variable	Unit	Comment
Bare soil	%	Percent of groundcover that is bare soil
Vegetation	%	Percent of groundcover that is vegetation
Leaf litter	%	Percent of groundcover that is leaf litter
Rocky cover	%	Percent of groundcover that is rocky cover
Elevation	Metres	Elevation of site
Aerial cover	%	Percentage of aerial cover (either canopy cover or rocky cover) above den site
Vegetation condition	Ordinal Scale	Vegetation condition on a scale from 1 to 6, with 1 = completely degraded and 6 = excellent (EPA 2016)
Number of potential entrances	Count	Number of potential entrances to the den site, visually assessed.
Passion vine	Yes/No	Presence or absence of passion vine at the site (within 20 metres)

5.3.4 Statistical analysis

Microclimate

Following data-download of temperature and humidity data from data-loggers, a review of the data indicated spurious humidity readings (i.e. >100%) at one used den, one ambient site and three available dens. These sites were therefore removed from analyses for humidity measures.

To determine whether temperature or humidity was different between used and available dens, and between den sites and ambient conditions (‘site types’), we calculated daily mean, minimum, maximum, range and rate of change of temperature and humidity for each site. Using the data-logger data we calculated overall mean temperature (T_{mean}) using all temperature recordings at each site. We then calculated the mean daily minimum (T_{min}) and maximum temperature (T_{max}) for each site, and mean daily temperature range ($T_{max} - T_{min}$) throughout the day at each site (T_{range}). Rate of change (T_{rate}) was calculated for each day by calculating hourly difference in temperature (hr2 - hr1; hr3 - hr2 etc.) and calculating the daily mean of these values. This process was followed for relative humidity values in generating mean (RH_{mean}), mean daily minimum (RH_{min}), mean daily maximum (RH_{max}), mean daily range (RH_{range}), and rate of change (RH_{rate}) in humidity for each site.

A one-way analysis of variance (ANOVA) was conducted to compare the effect of site type (e.g. used, available, ambient) on measures of temperature and humidity. When a statistically significant difference was observed among factor levels ($P < 0.05$), a Games-Howell post-hoc test was performed using the `userfriendlyscience` package (Peters 2018) to determine which levels differed from one another (Games and Howell 1976). We used the Games-Howell post-hoc test because the sample size between factor levels was unequal and benefited from the conservative pairwise comparison provided by this test (Games and Howell 1976; Sokal and Rohlf 1981). We considered p-values of less than 0.05 to be significant and p-values between 0.05 and 0.1 to be marginally significant. The assumption of homogeneity of variance was tested using Levene’s test for homogeneity, and the assumption of normality of residuals was tested using the Shapiro-Wilkes test.

T_{range} and T_{rate} did not meet the assumption of normality, and so we used the Kruskal-Wallis test followed by Dunn’s multiple comparison test using the `FSA` package (Dunn 1964; Ogle et al. 2018) to compare these variables between site types. We used Dunn's multiple comparison test as it is a non-parametric test and appropriate for groups with an unequal number of observations (Zar 2010), as was the case with our data. Bonferroni's correction was used to control the false discovery rate. Bootstrapping was used to generate medians and percentile confidence intervals for graphing T_{range} and T_{rate} using the `boot` package (Canty and Ripley 2017; Davison and Hinkley 1997).

To explore the daily trends in temperature and humidity between used dens, available dens and ambient conditions, we used generalised additive mixed models (Hastie and Tibshirani 1986) with a Gaussian error distribution. A similar approach was taken in a study by Cowan (2019) that examined the microclimatic conditions of northern quoll den sites in the Pilbara. To take into account dependency resulting from repeated measures, site ID was included in the model as a random effect. To test for a difference between smooths we used the *ordered-factor-smooth interaction* approach with used dens set as the reference level (van Rij 2017). We set the initial number of knots to 24 and used a cyclic penalised regression spline to address the cyclic nature of the data (whereby 12:00 am and 1:00 am are connected). Cross validation was used to estimate the amount of smoothing (see Zuur 2012; Wood 2017). Residuals were assessed to identify outliers and ensure that the model met the assumptions of normality and homogeneity of variance. Restricted maximum likelihood was used to estimate model coefficients and smoothing parameters.

As rock dens were used more often than dens of other substrates, we also sought to determine if daily temperature patterns were different between rock dens and other den substrate types of earth (subterranean dens) or wood (trees). We used the same method as above using only used dens (n = 22; n(rock) = 12; n(earth) = 6; n(wood) = 4). Several r packages were used to plot the results including `ggplot2` (Wickham 2016) and `visreg` (Breheny and Burchett

2017). All GAMMs were fitted using the `mgcv` package (Wood 2004). All analyses were undertaken in the R software environment (version 3.5.0, R Development Core Team 2018).

Habitat selection

Evidence for the importance of habitat variables in predicting den use by female northern quolls was evaluated using generalised linear models (GLMs) with logit link and binomial error structure (logistic regression). The dataset comprised the den sites (22 used, 24 unused) and environmental predictors.

Due to the relatively small sample size ($n = 46$) and to avoid over fitting, we only included a maximum of three predictor variables in each model. Candidate models were compared using Akaike Information Criterion corrected for small sample size (AICc) (Hurvich and Tsai 1993) and associated measures such as △AIC and w_i. Burnham and Anderson (2002) suggest that △AIC values < 2 indicate substantial evidence, values between 4 – 7 suggest considerably less support and values > 10 indicate that the model is highly unlikely. AIC_{wt} is interpreted as the probability that a model is the best among those within the candidate model set, referred to as the model weight (Burnham and Anderson 2002). AICc values and other associated measures were calculated using the `MuMin` package (Barton 2018).

Models were ranked based on their AICc values, with the lowest AICc considered to indicate the best model given the data. Candidate models with a △AICc value < 2 compared to the best model were judged to have considerable support by the data (Burnham & Anderson 2002; Pasinelli et al. 2016). We then calculated unconditional parameter estimates (ß) and 95% confidence intervals for the regression coefficient for each model variable. We considered variables with a 95% confidence interval around ß that did not overlap 0 to have a stronger effect (Burnham and Anderson 2002).

We present all models with < 2 ΔAICc and interpret beta coefficient values that do not overlap 0 to suggest evidence of a relationship between that predictor variable and the use of a den by a female northern quoll during the young in den period. We also calculated odds ratios for each predictor variable in the top model to enable interpretation of the effect of habitat variables on the likelihood of den site use.

Prior to inclusion in models, habitat variables were evaluated for collinearity using pairwise scatterplots, Spearman's rank correlation coefficient, and variance inflation factors (VIF). If any variable pairs had a correlation coefficient of < -0.5 or > 0.5 or a $VIF > 3$, only one variable in the pair was included in subsequent analysis (Zuur et al. 2009). Given the small sample size ($n = 46$), this also minimised overparameterisation. Percentage bare soil and passion vine presence were highly correlated with vegetation condition (bare soil: $r = 0.72$; passion vine: $r = 0.63$). Given that within the woodland habitat of the study site these measures were both indicative of vegetation condition (i.e., both related to disturbance), percentage bare soil and passion vine presence were excluded from further analysis in favour of vegetation condition. Percentage leaf litter was also excluded from analysis as it correlated with percentage rock cover and had a $VIF > 3$ ($r = -0.53$; $VIF = 3.32$).

Based on the results of the goodness of fit tests, there was no evidence of lack of fit of the global model (H-L $\chi^2 = 9.59$, df = 8, $p = 0.30$; Pearson $\chi^2 = 45.14$, df = 39, $p = 0.23$). The examination of h_j and residual-based diagnostics for the global model identified a small number of observations that either did not fit the model or had high leverage. However, no observations met both of these criteria and therefore all data were included in the analysis.

To assess model fit, we used the chi-squared and Hosmer and Lemeshow (Hosmer and Lemeshow 2000) statistical tests for goodness of fit for logistic regression models on the global model. A Hosmer-Lemeshow (H-L) or chi-squared statistic with a p-value > 0.05 is considered to indicate a good fit. The lower the H-L statistic, the less variance in fit, and the greater the p-value. The H-L test was conducted using the `ResourceSelection` package (Subhash et al. 2017).

We calculated hat-values (hat matrix diagonal, h_j), several residual-based diagnostics (delta chi-squared, $\Delta\chi^2_j$; delta deviance, ΔD_j) and the logistic regression analogue of Cook's distance proposed by Priegborn (1981) ($\Delta\beta_j$) to identify outliers and overly influential observations. We constructed plots with these diagnostics against predicted probabilities. In accordance with suggestions by Hosmer, Lemeshow and Sturdivant (2013), observations were defined as 'problematic' if values for one or more of the diagnostic statistics fell well away from the rest of the values.

5.4 RESULTS

The 22 used den sites occurred within dead trees (n = 4), in termite mounds or naturally occurring tunnels below-ground (n = 6), and rocky structures (n = 12). Dens in trees were detected in both basal and trunk hollows. Available dens included seven below-ground, 12 in rocky structures and five in trees/hollow logs.

5.4.1 Microclimate

Daily metrics. T_{mean} values were similar across den types, with used = 31.7°C (se ± 0.28); available = 32.1°C (se ± 0.33), and ambient = 31.1°C (se ± 0.26) (Figure 5.2(a)). RH_{mean} values were marginally different across den types, with used = 66.9% (se ± 2.36), available = 60.7% (se ± 2.17) and ambient = 62.6% (se ± 2.21) (Figure 5.2(b)).

Measures of both temperature and humidity extremes (maximum, minimum) and variation (rate, range) consistently reflected evidence of differences among sites (Figure 5.2). Used den sites recorded a T_{min} of 30.5°C (se ± 0.45) and T_{max} of 33.0°C (se ± 0.45), and an RH_{min} of 56.5% (se ± 2.67) and RH_{max} of 75.5% (se ± 1.77). Available den sites recorded a T_{min} of

30.2°C (se ± 0.43) and T_{max} of 34.6°C (se ± 0.46) and an RH_{min} 49.1% (se ± 2.67) and RH_{max} of 69.1% (se ± 1.77), respectively (Figure 5.2).

Evidence of a difference in T_{mean} between ambient sites, used dens and available dens was marginal (Figure 5.2(a); $F_{2,55} = 2.48$, $P = 0.09$). Similarly, there was marginal difference in H_{mean} between site types (Figure 5.2(b); $F_{2,50} = 2.67$, $P = 0.08$). *Post hoc* comparisons indicated that T_{max} and RH_{max} was higher at ambient sites than either used (T_{max}: $t_{18} = 12.6$, $P = 0.01$; RH_{max}: $t_{29} = 5.4$, $P = 0.01$) or available dens (T_{max}: $t_{25} = 9.3$, $P = 0.01$; RH_{max}: $t_{28} = 8.0$, $P = 0.01$) (Figure 5.2). Additionally, T_{min} and RH_{min} were lower at ambient sites than either used (T_{min}: $t_{29} = 9.36$, $P = 0.01$; RH_{min}: $t_{29} = 6.2$, $P = 0.01$) or available dens (T_{min}: $t_{30} = 8.8$, $P = 0.01$; RH_{min}: $t_{26} = 4.8$, $P = 0.01$) (Figure 5.2).

There was no significant difference in T_{max}, RH_{max}, T_{min} or RH_{min} between used and available dens (T_{max}: $t_{40} = 2.5$, $P = 0.13$; T_{min}: $t_{44} = 0.48$, $P = 1.0$; RH_{max}: $t_{40} = 2.4$, $P = 0.16$; RH_{min}: $t_{39} = 1.9$, $P = 0.50$) (Figure 5.2). *Post hoc* comparisons also indicated that T_{range}, T_{rate}, RH_{range} and RH_{rate} were greater at ambient sites than in used (T_{range}: $z = 5.52$, $P = 0.00$; T_{rate}: $z = 5.54$, $P = 0.00$; RH_{range}: $t_{28} = 14.11$, $P = 0.01$; RH_{rate}: $t_{29} = 14.2$, $P = 0.01$) or available (T_{range}: $z = 4.18$, $P = 0.00$; T_{rate}: $z = 4.16$, $P = 0.00$; RH_{range}: $t_{27} = 14.13$, $P = 0.01$; RH_{rate}: $t_{29} = 13.5$, $P = 0.01$) dens, but not significantly different between used and available dens (T_{range}: $z = 1.70$, $P = 0.27$; T_{rate}: $z = 1.75$, $P = 0.24$; RH_{range}: $t_{40} = 0.35$, $P = 1.0$; RH_{rate}: t_{40} =, $P = 1.0$) (Figure 5.2).

Microclimate over 24-hr cycle. In the GAMM analysis investigating temperature as a function of time and den type (used, available, ambient), approximate p-values of the smooths for available dens ($F_{3.8,\ 1313.9} = 2.27$, $P < 0.001$) and ambient sites ($F_{13.3,\ 1313.9} =116.23$; $P < 0.001$) were found to be significantly different to the smooths for used den sites. Similarly, in the GAMM analysis investigating humidity as a function of time and den type, p-values for the smooths for available dens ($F_{3.8,\ 1218.6} = 2.25$; $P < 0.001$) and ambient sites

($F_{13.4,\ 1218.6}$ = 111.25; $P < 0.001$) were significantly different to used den sites. Both temperature and humidity recorded in used dens appeared to remain more stable (less fluctuation) throughout the day when compared to the other two site types (Figure 5.3).

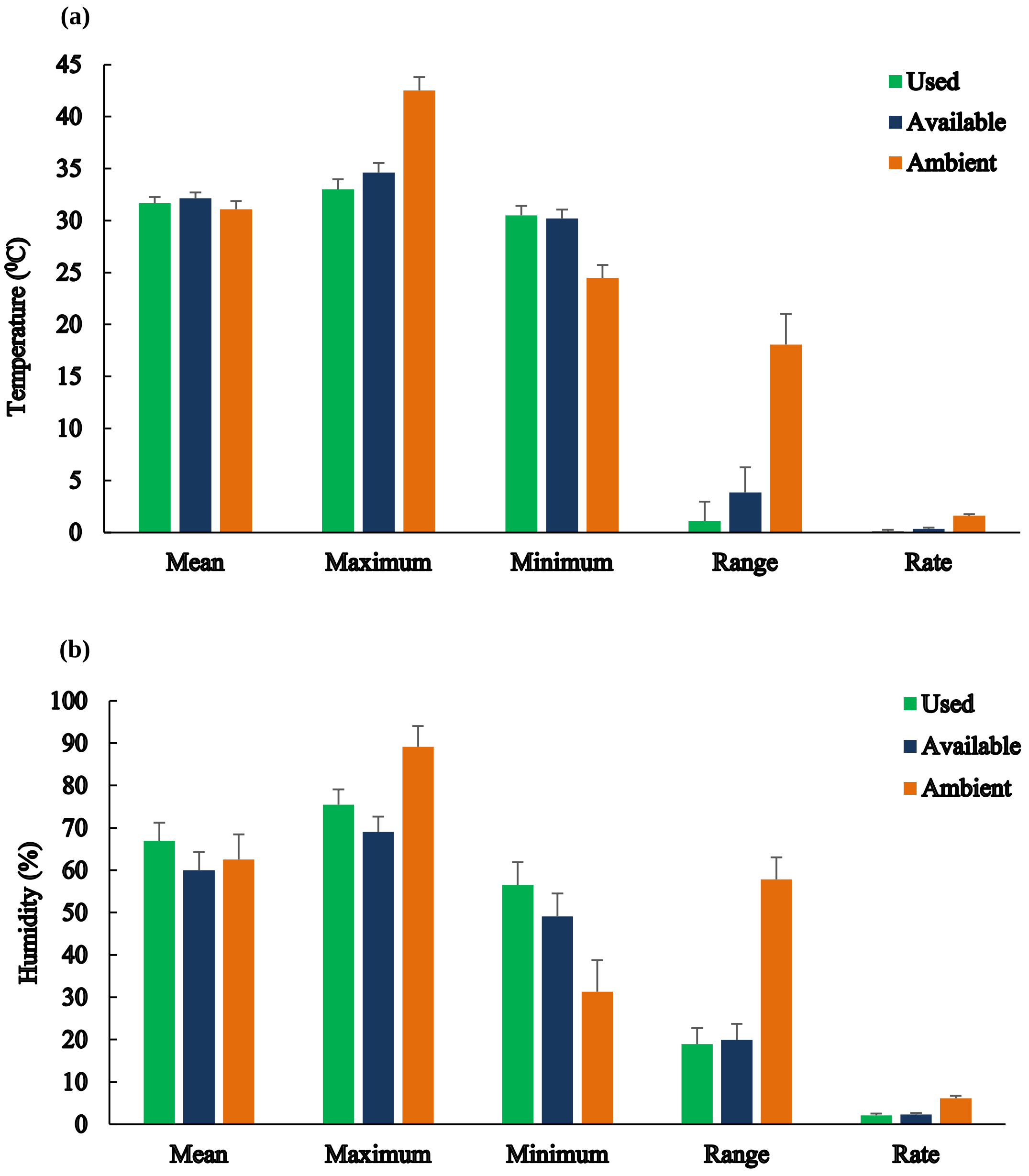


Figure 5.2. Mean estimates and 95% confidence intervals for (a) temperature measures and (b) humidity measures. Note that range and rate represent median values with bootstrapped 95% confidence intervals.

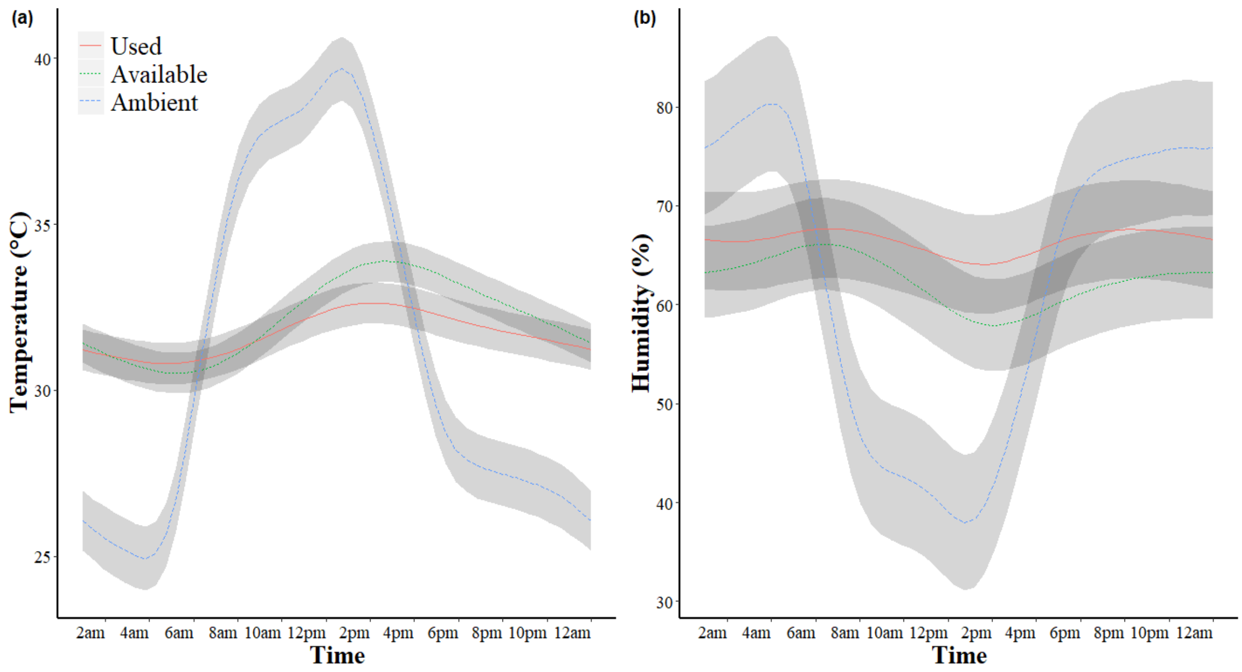


Figure 5.3. Predictions from Generalised Additive Mixed Models of the (a) daily temperature (°C) and (b) daily humidity (%) for used dens, available dens and ambient sites. Blue lines represent ambient sites, red lines represent used dens, and green lines represent available dens. Grey shaded areas indicate 95% confidence intervals.

Used den substrate. In the GAMM analysis investigating temperature as a function of time and used den substrate (rock, earth, wood), approximate p-values of the smooths for earth dens ($F_{4.5,\ 759.3}$ = 3.19, $P < 0.001$) and wood dens ($F_{4.4,\ 759.3}$ =4.76; $P < 0.001$) were found to be significantly different to the smooth for used den sites in rocky substrate. Similarly, in the GAMM analysis investigating humidity as a function of time and den substrate, p-values for the smooths for earth dens ($F_{6.4,\ 706.3}$ = 12.88; $P < 0.001$) and wood dens ($F_{4.8,\ 706.3}$ = 6.18; $P < 0.001$) were significantly different to the smooth for used den sites in rocky substrate. Both temperature and humidity recorded in rocky dens appeared to remain more stable throughout the day when compared to used dens in earth or wood substrate (Figure 5.4).

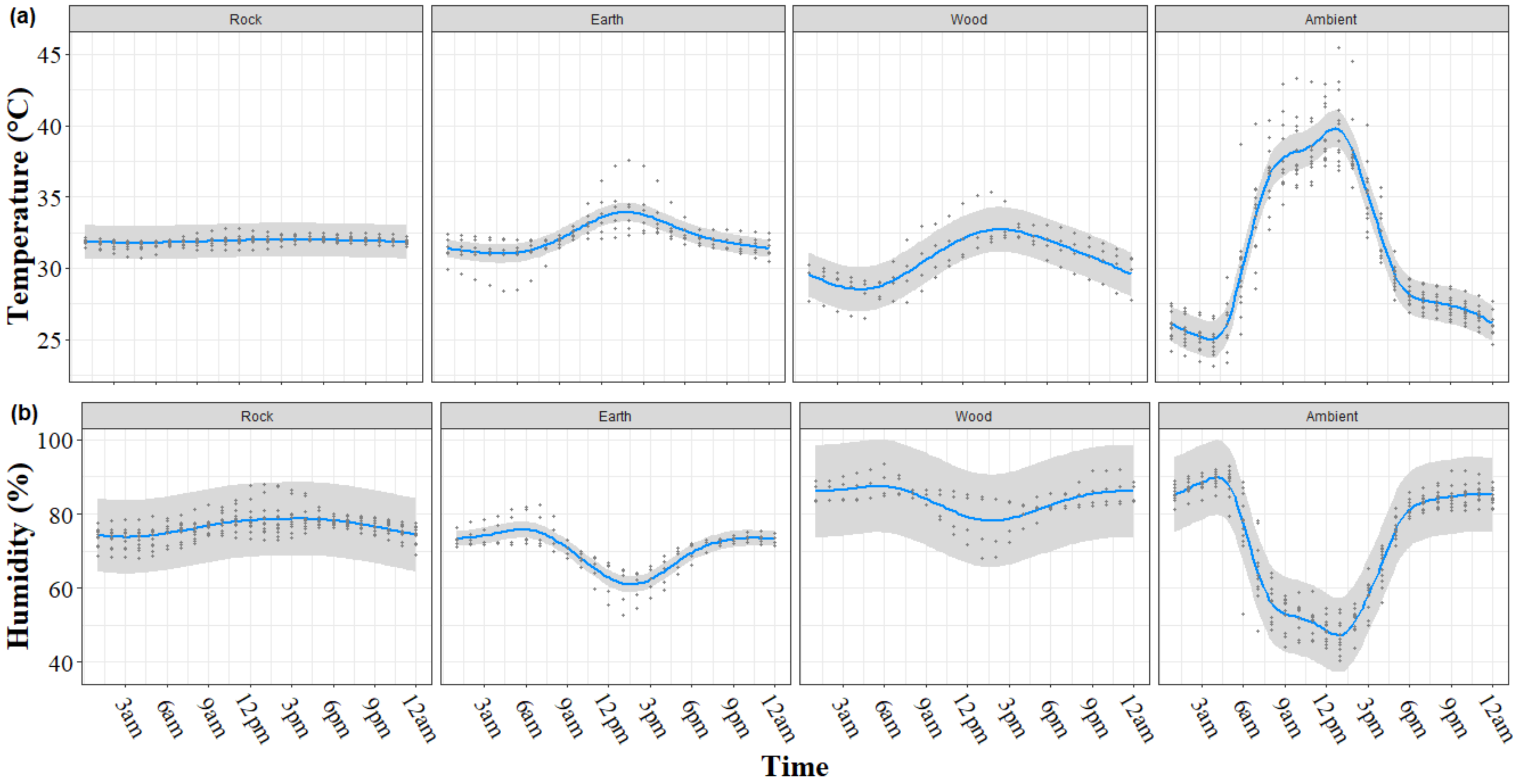


Figure 5.4. Predictions from Generalised Additive Mixed Models of the (a) daily temperature (°C) and (b) daily humidity (%) for used dens in rock, earth and wood substrate. Ambient sites have been included for comparison. Grey dots are observed values. Grey shaded areas indicate 95% confidence intervals.

5.4.2 Habitat

The top model contained aerial cover (both canopy and/or rocky cover above dens) and number of potential entrances (Table 5.2). Although model weight for the top model was low ($AICc_{wt} = 0.17$), an exploration of the ß coefficients for potential entrances and aerial cover in each candidate model with a △AICc value < 2 supported their importance to den selection. The 95% CI for number of potential entrances did not overlap zero in any models it occurred in, and 95% CI for aerial cover did not overlap zero in four of the five models it occurred in. In addition, examination of the log-likelihood values indicated that models with one additional parameter to aerial cover and/or potential entrances did not explain much additional variation in the data (Table 5.2). We take this as strong evidence that the number of potential entrances has influenced den site selection by a female during the young in den period, and moderate evidence that aerial cover influenced den selection by females. There was little evidence that percentage rock cover or elevation, or any other habitat variables measured, influenced den site selection (Figure 5.5).

The odds ratio for percentage aerial cover and number of potential entrances was estimated as 1.033 (95% CI 1.001, 1.075) and 1.644 (95% CI 1.021, 3.102), respectively. Therefore, every one unit increase in percentage aerial cover is associated with a 3% increase in the odds of den use, and every one unit increase in number of potential entrances is associated with a 64% increase in the odds of den use.

Table 5.2. Parameter estimates and AICc values for candidate models within ≤ 2AIC of the top model. Values have been rounded to the nearest 2 decimal points.

df	logLik	AICc	△AICc	AICc wt	elevation	% aerial cover	% rock cover	no. potential entrances
3	-26.52	59.60	0.00	0.17		0.03 (0.001, 0.07)		0.50 (0.02, 1.13)
3	-27.38	61.30	1.73	0.07			0.02 (-0.01, 0.04)	0.56 (0.07, 1.19)
2	-28.54	61.40	1.75	0.07				0.57 (0.12, 1.16)
4	-26.20	61.40	1.76	0.07	0.01 (-0.01, 0.03)	0.04 (0.002, 0.074)		0.57 (0.02, 1.12)
4	-26.21	61.40	1.79	0.07		0.03 (-0.01, 0.07)	0.01 (-0.02, 0.04)	0.57 (0.01, 1.17)
2	-28.64	61.60	1.95	0.06		0.04 (0.01, 0.08)		

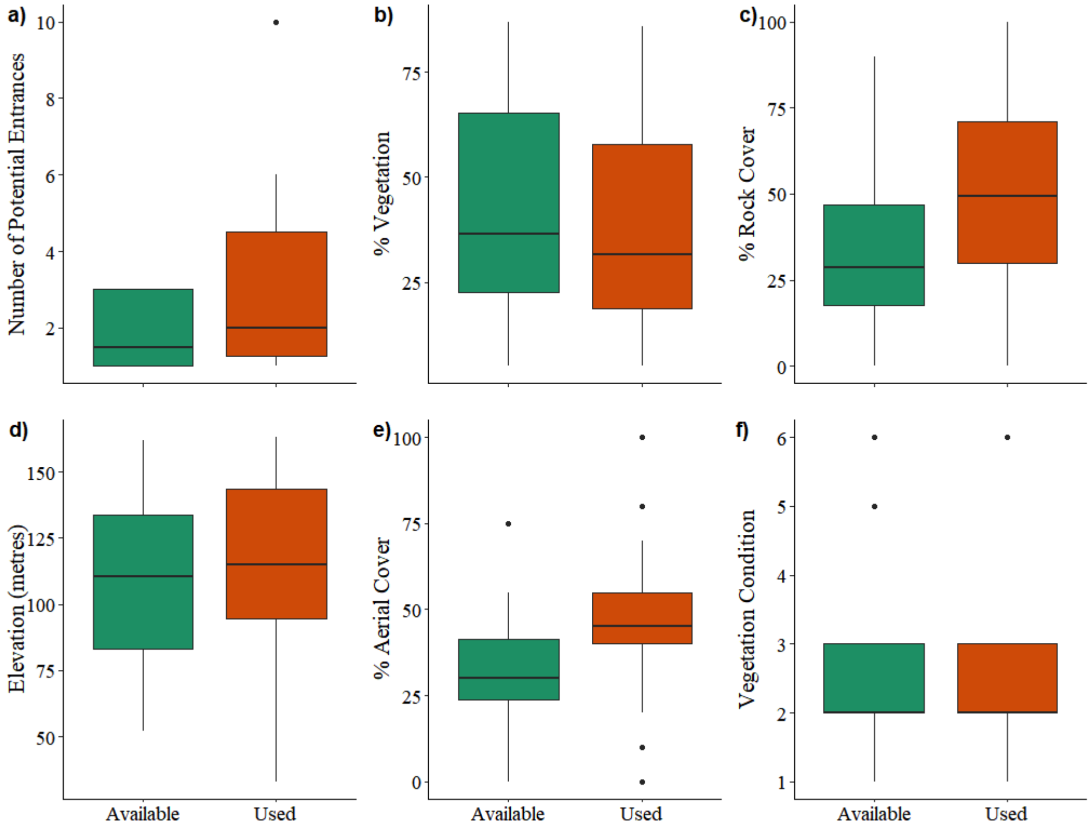


Figure 5.5. Structural and habitat characteristics of used and available northern quoll den sites on Koolan Island, including (a) number of potential entrances, (b) % vegetation cover, (c) % rock cover, (d) elevation (metres), (e) % aerial cover, and (f) vegetation condition using the scale detailed in EPA (2016). Black dots represent suspected outliers.

5.5 DISCUSSION

The northern quoll is a short-lived species, with population dynamics driven by recruitment (Chapter 4; Cremona et al. 2017). We found that used dens, particularly rock dens, provided a more stable microclimate than both available dens and ambient sites and, of the variables measured, den selection during the young in den phase was best predicted by both habitat (aerial cover) and structural (number of entrances) attributes. This is the first study to model the fine-scale characteristics of northern quoll den sites in the wet-dry tropics of northern Australia, and the first study to focus on den use by this species on an island and amongst modified habitat.

Koolan Island has a long (50+ yr) history of mining, with approximately one third of the island modified for mining pits, infrastructure, accommodation and an airstrip. While habitat modification generally results in the loss of important microhabitat features, it may also provide novel shelter resources that may be used by some species (Shine and Fitzgerald 1996; Meier and Garcia 2001). Outside of the breeding season, northern quolls on Koolan Island have been observed denning in anthropogenic habitat such as buildings, vehicles and waste piles. However, despite females being captured and tracked from both within and outside of modified areas, all except one used den sites located within native habitat. The remaining den was a small subterranean tunnel located in an area undergoing rehabilitation. Therefore, the use of modified habitat for maternal dens appears to be limited.

5.5.1 Den substrate and microclimate

During the young in den phase, juvenile northern quolls are completely dependent on their mother and highly susceptible to predation and climatic exposure. Oakwood (1997) observed nests of dry leaves and grass in dens during the first four weeks of young deposition, suggesting that this indicated poor thermoregulation in juveniles.

During our study, females were also observed carrying small bunches of dried grass just before dawn, indicating nesting behaviour on the island.

Temperature and humidity ranged from 30.5 - 33.0°C and 56.5 – 75.5% in used den sites, and 30.2 - 34.6°C and 49.13 – 69.07% in available den sites. We found that both used and available dens provided more stable temperature and humidity than ambient conditions, with less extreme minimum and maximum temperature and humidity, and lower rates of temperature and humidity change per hour. In addition, results from GAMM analyses suggest that used dens have a more stable daily temperature and humidity than both available dens and ambient sites measured.

These findings indicate that microclimate is likely to be an important characteristic of den sites. The findings also demonstrate the importance of using complementary analyses, as while the ANOVA did not detect a significant variation between used and available dens, GAMMs provided a higher resolution of information on the microclimatic characteristics of used and available den sites, and the difference in microclimatic properties of rocky, timber and subterranean dens. In this case, an examination of the cyclical stability of temperature and humidity with time was as, if not more, valuable than an analysis of differences in mean values. It should be noted that the GAMM's used in this study do not account for temporal correlation in observations from individual data loggers (i.e., dens) which may result in overly optimistic precision in smooths, and thus affect the strength of inference being made. However, there were insufficient data to add the required level of complexity to the model to explore this further.

A lack of significant difference between used and available dens as described in our ANOVA results could be further tested by more invasive means. Many of the den sites appeared to be deeper than could be accessed by data loggers without restricting access by animals, and it is also possible that used den sites had even more stable temperature and humidity at greater depths than available den sites. This is supported by a study of den sites within trees, where the authors found that temperature readings were influenced by the depth of data loggers (Isaac et al. 2008). However, in their study depth of data logger was not a significant predictor of microclimate when all other den characteristics were considered, and we believe that the absence of temperature and humidity readings at greater depth does not hinder our findings on the microclimatic characteristics of tree, rock and subterranean den sites on the island.

In our study dens were found in both basal and trunk tree hollows, in tunnels below ground (not excavated by northern quolls), and in fissures in rocky areas. In a study of northern quolls on the mainland, Oakwood (1997) found both males and females to den in live and dead tree hollows, rock crevices, termite mounds, logs and burrows. The majority occurred in live trees, even for dens during the young in den period. Only four den sites in our study occurred within the base or trunk of dead trees, while no dens were recorded in live trees. This is an interesting comparison to Oakwood (1997). Given the superior microclimate stability of rocky dens in our study site, the lower proportion of used dens in trees may reflect a difference in habitat composition between the two study sites, whereby rocky dens are both more available and preferred over tree dens on Koolan Island.

Rocky structures or outcrops were the most common denning substrate, and were found to provide the most stable temperature and humidity throughout the day. Rock substrates alone have not been conclusively identified to be microclimatically superior to other den substrates (such as tree hollows), however the benefits of rocky outcrops may be conferred through the effects of both the substrate and structure combined (Ross et al. 2010). The availability of rocky areas, particularly on Australian islands, is recognised as valuable in providing refugia from predators, to the extent that it may have protected some island populations from extinction by introduced predators (Burbidge and Manly 2002). Despite rocky dens not forming the majority in Oakwood's study, observed predation on northern quolls was lowest in rocky habitats, and attributed to a greater availability of shelters (Oakwood 1997). Given the difficulty in navigating steep, rocky areas, species in other regions have also been shown to prefer dens in rocky habitat, particularly during the maternal period (Ross et al. 2010). Rocky areas are common at the study site, and provide deep fissures with multiple entrance points that may provide better predator protection than other den substrates. Rocky dens may also offer superior protection against fire events, which have been suggested to negatively impact juvenile mortality when timing coincides with this period (Griffiths and Brook 2015). Their availability and conferred protection, combined with the stable temperature and humidity observed within rocky dens selected by females, make rocky dens a high-value denning resource to be considered in impact assessments and rehabilitation planning.

5.5.2 Den habitat characteristics

Previous studies on mammalian den site selection have identified resource selection based on substrate, topography, depth, entrance size and number of entrances, which are generally thought to contribute to either microclimate stability or protection from predators (Zielinski et al. 2004; Isaac et al. 2008; Lesmeister et al. 2008; Trapp et al. 2008; Ross et al. 2010). Of the habitat variables measured to describe topography, vegetation structure and den attributes, we found that aerial cover and the number of potential den entrances best predicted if a den site was used. These findings are similar to other studies of mammals during their maternal period (e.g. Lesmeister et al. 2008, Trapp et al. 2008; Ross et al. 2010). Aerial cover serves to both protect sites against solar radiation and predation from above, such as birds of prey (Lesmeister et al. 2008). Both pressures occur on Koolan Island, with relatively large diurnal and nocturnal birds of prey common in the area, and temperatures that can rise to around 38 – 40ºC during the young in den period from August – November (BoM 2018). The number of potential entrances was positively correlated with used den sites, with a mean of 3 (se ± 0.47) potential entrances in used den sites. A higher number of entrances provides a higher likelihood of escape from predator attacks (Ross et al. 2010) and increases air flow, which may reduce temperature in dens (Clement and Castleberry 2013). Given populations of northern quoll are so heavily influenced by recruitment, these den features most likely serve to minimise predation on juveniles and mortality through overheating.

5.5.3 Conclusion

Given the microclimatic and physical protection that dens provide, den site selection may be one of the most important choices made by small mammals (Zielinski et al. 2004; Lesmeister et al. 2008). With habitat modification encroaching across the range of the northern quoll, a better understanding of the structural, habitat and microclimatic requirements of den sites provides more certainty in assessing the potential impacts of disturbance on populations.

The importance of dens with a number of potential entrances, aerial cover and a stable microclimate throughout the day may complement efforts to recreate denning habitat as part of rehabilitation activities to restore landscape and structural ecosystem components (Drake et al. 2010). While there are a number of studies indicating the importance of introducing logs and coarse woody debris into rehabilitated areas to increase structural complexity (e.g. Koch et al. 2010; Manning et al. 2013), the use of boulders in rehabilitation and the recreation of rocky features is both logistically difficult and poorly studied. In some cases, the use of artificial rocky structures (e.g. concrete) has been used as a substitute for native rock to recreate important habitat features (Webb and Shine 2000; Croak et al. 2013). Further work is required to understand if similar microclimates can be achieved in rocky dens using either salvaged natural rock or artificial materials, and if den structures can be recreated to enable successful use by females in the young in den period.

Part of this work should include further, targeted research on den site characteristics. Amongst our candidate models, the top model with aerial cover and number of potential entrances had a relatively low model weight ($AIC_{wt} = 0.17$). This may indicate that with the collection of more data some of the other predictor variables may prove to also influence den site selection. There has been insufficient research on the drivers of den site selection by dasyurids in Australia, or ground-dwelling mammals in general (further to the overall structure used for denning, such as logs), to identify particular microhabitat characteristics for further study. However, we note that in many cases dens appeared to extend past the maximum depth that data loggers could be placed and suggest that further studies should aim to understand the depth at which northern quolls are denning and the microclimate present at these depths.

Dasyurids, including the northern quoll, are also known to use multiple den sites during the non-breeding and breeding seasons (Serena and Soderquist 1989;

Oakwood 1997; Glen and Dickman 2006). Logistical constraints inhibited the exploration of multiple den use by animals on Koolan Island. However, further information on the number of den sites used by females during the young in den period and the potential reason for using multiple dens may be important if future conservation programs aim to provide denning habitat for the northern quoll.

5.6 REFERENCES

Bartoń, K. (2018). MuMIn: Multi-Model Inference. *R package version 1.42.1.* Retrieved from https://CRAN.R-project.org/package=MuMIn.

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.

Benson, J. F., Lotz, M. A., & Jansen, D. (2008). Natal den selection by Florida panthers. *The Journal of Wildlife Management*, *72*, 405-410.

BOM (Bureau of Meteorology) (2018) Climate Data Online. Retrieved from http://www.bom.gov.au/climate/data/index.shtml?bookmark=136.

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.

Breheny, P. & Burchett, W. (2017). Visualization of Regression Models Using visreg. *The R Journal*, *9*, 56-71.

Burbidge, A. A., & Manly, B. F. (2002). Mammal extinctions on Australian islands: causes and conservation implications. *Journal of Biogeography*, *29*, 465-473.

Burnett, S. (2008). Quolls in the Townsville area: a summary of current knowledge. Progress report to The New Townsville City and BDTNRM.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. Springer Science & Business Media.

Canty, A and Ripley, B. (2017). boot: Bootstrap R (S-Plus) Functions. *R package version 1.3-20.*

Carter, A., Luck, G. W., & Wilson, B. P. (2012). Ecology of the red fox (*Vulpes vulpes*) in an agricultural landscape. 1. Den-site selection. *Australian Mammalogy*, *34*, 145-154.

Clement, M. J., & Castleberry, S. B. (2013). Tree structure and cavity microclimate: implications for bats and birds. *International Journal of Biometeorology*, *57,* 437-450.

Cremona, T., Crowther, M. S., & Webb, J. K. (2017). High mortality and small population size prevent population recovery of a reintroduced mesopredator. *Animal Conservation*, *20*, 555-563.

Croak, B. M., Webb, J. K., & Shine, R. (2013). The benefits of habitat restoration for rock-dwelling velvet geckos *Oedura lesueurii*. *Journal of Applied Ecology*, *50*, 432-439.

Cowan, M. (2019). Denning requirements of the northern quoll (*Dasyurus hallucatus*) and the implications for artificial den construction in the Pilbara, Western Australia. Honours thesis, Charles Sturt University.

Davison, A. C. & Hinkley, D. V. (1997) Bootstrap Methods and Their Applications. Cambridge University Press, Cambridge. ISBN 0-521-57391-2.

Drake, J. A., Greene, R. S. B., Macdonald, B. C. T., Field, J. B., & Pearson, G. L. (2010). *A review of landscape rehabilitation frameworks in ecosystem engineering for mine closure*. International Conference on Mine Closure 2010, ed. Andy Fourie, Mark Tibbett, Jacques Wiertz, Australian Centre for Geomechanics, Perth, 241-249.

Dunn, O.J. (1964). Multiple comparisons using rank sums. *Technometrics, 6*, 241-252.

Environmental Protection Authority (EPA) (2016). Technical Guidance: flora and vegetation surveys for environmental impact assessment. *Environmental Protection Authority, Perth.* Retrieved from http://www.epa.wa.gov.au/policies-guidance/technical-guidance-flora-and-vegetation-surveys-environmental-impact-assessment.

Frafjord, K. (2003). Ecology and use of arctic fox *Alopex lagopus* dens in Norway: tradition overtaken by interspecific competition? *Biological Conservation*, *111*, 445-453.

Games, P. A., & Howell, J. F. (1976). Pairwise multiple comparison procedures with unequal n’s and/or variances: a Monte Carlo study. *Journal of Educational Statistics*, *1*, 113-125.

Glen, A. S., & Dickman, C. R. (2006). Home range, denning behaviour and microhabitat use of the carnivorous marsupial *Dasyurus maculatus* in eastern Australia. *Journal of Zoology*, *268*, 347-354.

Griffiths, A. D., & Brook, B. W. (2015). Fire impacts recruitment more than survival of small-mammals in a tropical savanna. *Ecosphere*, *6*(6), 1-22.

Hastie, T., & Tibshirani, R. (1986). Generalized additive models. *Statistical Science, 1*, 297-310.

Hnatiuk, R.J., Thackway, R. & Walker, J. (2009). Vegetation. In *Australian soil and land survey field handbook* (3rd Ed). National Committee on Soil and Terrain. CSIRO Publishing, Melbourne.

Hosmer Jr, D. W., Lemeshow, S., & Sturdivant, R. X. (2013). *Applied Logistic Regression* (Vol. 398). John Wiley & Sons.

Hosmer, D. W., & Lemeshow, S. (2000). *Applied Logistic Regression* (2nd Ed). Wiley, New York.

Hurvich, C. M., & Tsai, C. L. (1993). A corrected Akaike information criterion for vector autoregressive model selection. *Journal of Time Series Analysis*, *14,* 271-279.

Isaac, J. L., De Gabriel, J. L., & Goodman, B. A. (2008). Microclimate of daytime den sites in a tropical possum: implications for the conservation of tropical arboreal marsupials. *Animal Conservation*, *11*, 281-287.

Keighery, G. J., Gibson, N., Kenneally, K. F., & Mitchell, A. A. (1995). Biological inventory of Koolan Island, Western Australia 1. Flora and vegetation. *Records of the Western Australian Museum*, *17,* 237-248.

Kershenbaum, A., Kershenbaum, A., & Blaustein, L. (2011). Rock hyrax (*Procavia capensis*) den site selection: preference for artificial sites. *Wildlife Research*, *38,* 244-248.

Koch, J. M., Grigg, A. H., Gordon, R. K., & Majer, J. D. (2010). Arthropods in coarse woody debris in jarrah forest and rehabilitated bauxite mines in Western Australia. Annals of *Forest Science*, *67,* 106.

Lesmeister, D. B., Gompper, M. E., & Millspaugh, J. J. (2008). Summer resting and den site selection by eastern spotted skunks (*Spilogale putorius*) in Arkansas. *Journal of Mammalogy*, *89,* 1512-1520.

Lowry, H., Lill, A., & Wong, B. B. (2013). Behavioural responses of wildlife to urban environments. *Biological Reviews*, *88,* 537-549.

Lundholm, J. T., & Richardson, P. J. (2010). Mini-Review: Habitat analogues for reconciliation ecology in urban and industrial environments. *Journal of Applied Ecology*, *47,* 966-975.

Lutermann, H., Verburgt, L., & Rendigs, A. (2010). Resting and nesting in a small mammal: sleeping sites as a limiting resource for female grey mouse lemurs. *Animal Behaviour*, *79,* 1211-1219.

Manning, A. D., Cunningham, R. B., & Lindenmayer, D. B. (2013). Bringing forward the benefits of coarse woody debris in ecosystem recovery under different levels of grazing and vegetation density. *Biological Conservation*, *157,* 204-214.

McKenzie, N. L., Fontanini, L., Lindus, N. V., & Williams, M. R. (1995). Biological inventory of Koolan Island, Western Australia 2. Zoological notes. *Records of the Western Australian Museum*, *17,* 249-266.

Meier, L., and Garcia, J. (2001). Importance of mines for bat conservation. In *Proceedings of bat conservation and mining: a technical interactive forum.* US Department of the Interior, Office of Surface Mining, Alton, Illinois, USA (17-28).

Oakwood, M. (1997). *The ecology of the northern quoll*. Ph.D. thesis, 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., Woinarski, J. & Burnett, S. (2008). *Dasyurus hallucatus. The IUCN Red List of Threatened Species 2008*: e.T6295A12600197. Retrieved from http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T6295A12600197.en.

Ogle, D.H., P. Wheeler, and A. Dinno. (2018). FSA: Fisheries Stock Analysis. R package version 0.8.22. Retrieved from https://github.com/droglenc/FSA.

Pasinelli, G., Grendelmeier, A., Gerber, M., & Arlettaz, R. (2016). Rodent-avoidance, topography and forest structure shape territory selection of a forest bird. *BMC ecology*, *16*, 24.

Peters, G.J.Y. (2018) Userfriendlyscience: Quantitative analysis made accessible. R package version 0.7.2. Retrieved from https://cran.rproject.org/web/packages/userfriendlyscience.

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.

Pregibon, D. (1981). Logistic regression diagnostics. *The Annals of Statistics*, *9*, 705-724.

R Core Team (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from https://www.R-project.org/.

Ross, S., Kamnitzer, R., Munkhtsog, B., & Harris, S. (2010). Den-site selection is critical for Pallas's cats (*Otocolobus manul*). *Canadian Journal of Zoology*, *88,* 905-913.

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.

Serena, M. & Soderquist, T. R. (1989). Nursery dens of *Dasyurus geoffroii* (Marsupialia: Dasyuridae), with notes on nest building behaviour. *Australian Mammal Society*, *12*, 35-36.

Shine, R., & Fitzgerald, M. (1996). Large snakes in a mosaic rural landscape: the ecology of carpet pythons *Morelia spilota* (Serpentes: Pythonidae) in coastal eastern Australia. *Biological Conservation*, *76*, 113-122.

Sih, A., Ferrari, M. C., & Harris, D. J. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, *4*, 367-387.

Sokal, R. R., & Rohlf, F. J. (1981). Biometry WH Freeman and Company. *San Francisco*, 859.

Subhash R. Lele, Jonah L. Keim and Peter Solymos (2017). *ResourceSelection: Resource Selection (Probability) Functions for Use-Availability Data*. R package version 0.3-2. Retrieved from https://CRAN.R-project.org/package=ResourceSelection.

Thomas, J., Fontaine, J., Mills, H. & Spencer, P. (2018). Analysis of mine site monitoring data using spatial and non-spatial capture recapture models reveals the population dynamics of an endangered marsupial. Unpublished manuscript.

Trapp, J. R., Beier, P., Mack, C., Parsons, D. R., & Paquet, P. C. (2008). Wolf, *Canis lupus,* den site selection in the Rocky Mountains. *The Canadian field-naturalist*, *122*, 49-56.

Van Rij, J., Wieling, M., Baayen, R. H., & van Rijn, H. (2015). itsadug: Interpreting time series and autocorrelated data using GAMMs. *R package version*, *1*(1).

Webb, J. K., & Shine, R. (2000). Paving the way for habitat restoration: can artificial rocks restore degraded habitats of endangered reptiles?. *Biological Conservation*, *92*, 93-99.

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. ISBN 978-3-319-24277-4, https://ggplot2.tidyverse.org.

Wood, S.N. (2004) Stable and efficient multiple smoothing parameter estimation for generalized additive models. *Journal of the American Statistical Association, 99*, 673-686.

Wood, S. N. (2017). *Generalized additive models: an introduction with R*. Chapman and Hall/CRC.

Zar, J.H. (2010). *Biostatistical Analysis,* 5th Ed. Pearson Prentice Hall, Upper Saddle River, NJ.

Zielinski, W. J., Truex, R. L., Schmidt, G. A., Schlexer, F. V., Schmidt, K. N., & Barrett, R. H. (2004). Resting habitat selection by fishers in California. *The Journal of wildlife management*, *68*, 475-492.

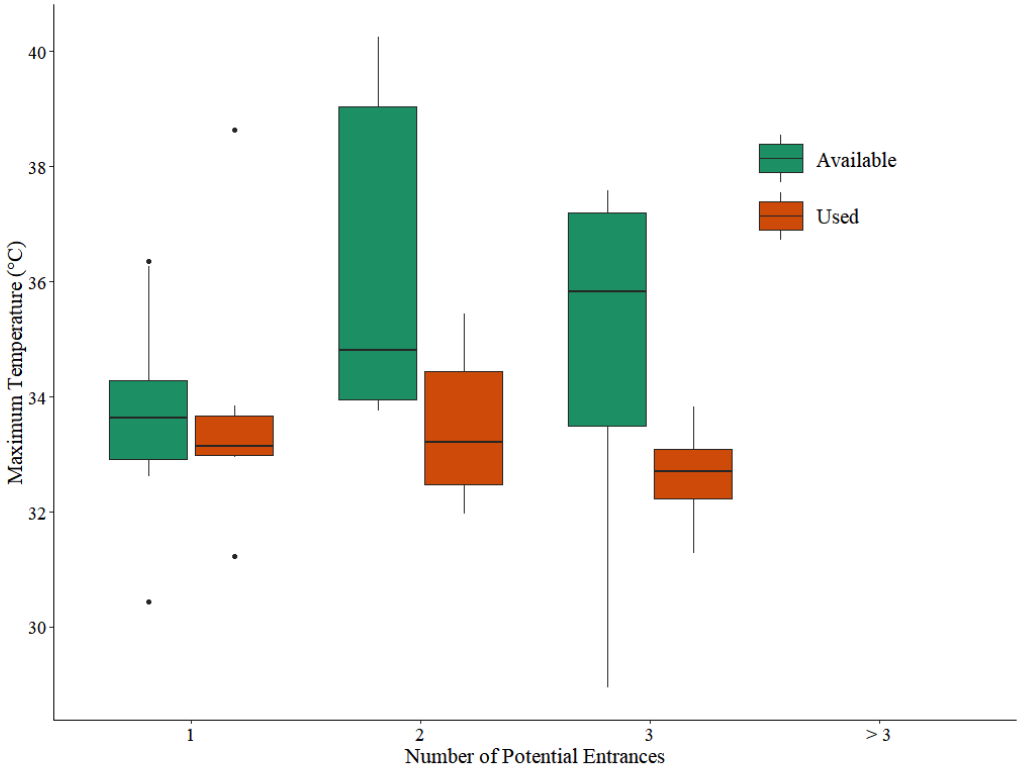
Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). GLM and GAM for count data. In *Mixed effects models and extensions in ecology with R* (pp. 209-243). Springer, New York, NY.

Zuur, A. F. (2012). *A beginner's guide to generalized additive models with R*. Newburgh, NY, USA: Highland Statistics Limited.

5.7 SUPPLEMENTARY INFORMATION

Supplementary Table S. 1. Mean and standard error (se) for each microclimate variable measured across used dens, available dens and ambient sites. Temperature variables are °C, relative humidity measures are %.

	Site Type					
	Used		Available		Ambient	
	Mean	se ±	Mean	se ±	Mean	se ±
T_{mean}	31.66	0.28	32.15	0.33	31.07	0.26
T_{min}	30.50	0.46	30.19	0.46	24.50	0.45
T_{max}	33.01	0.36	34.61	0.53	42.52	0.67
T_{range}	2.503	0.61	4.42	0.75	18.02	0.93
T_{rate}	0.22	0.05	0.38	0.06	1.57	0.08
RH_{mean}	66.91	2.36	62.56	2.21	60.73	2.17
RH_{min}	56.55	3.07	49.13	2.57	31.33	2.69
RH_{max}	75.50	1.92	69.07	1.86	89.16	1.68
RH_{range}	18.95	2.03	19.94	1.93	57.82	1.86
RH_{rate}	2.14	0.21	2.32	0.21	6.15	0.19



Supplementary Figure S. 2. Maximum temperature (°C) of used and available dens by the number of potential entrances.

Chapter 6: General Discussion

6.1 INSULAR POPULATIONS OF NORTHERN QUOLL

In this thesis I examined interrelated topics critical for the long-term conservation of the northern quoll. By using an insular population the conclusions reached in this thesis offer unconfounded insights into the biology of the species and will help conservation actions and future policy towards mining exploration and rehabilitation.

By first characterising population dynamics over the entire island and for 10+ years I was able to understand population level trends and susceptibility to mining activity and annual climate variability. Subsequent chapters exploring diet and den site selection shed light on the most likely drivers underpinning population scale fluctuations (Figure 6.1).

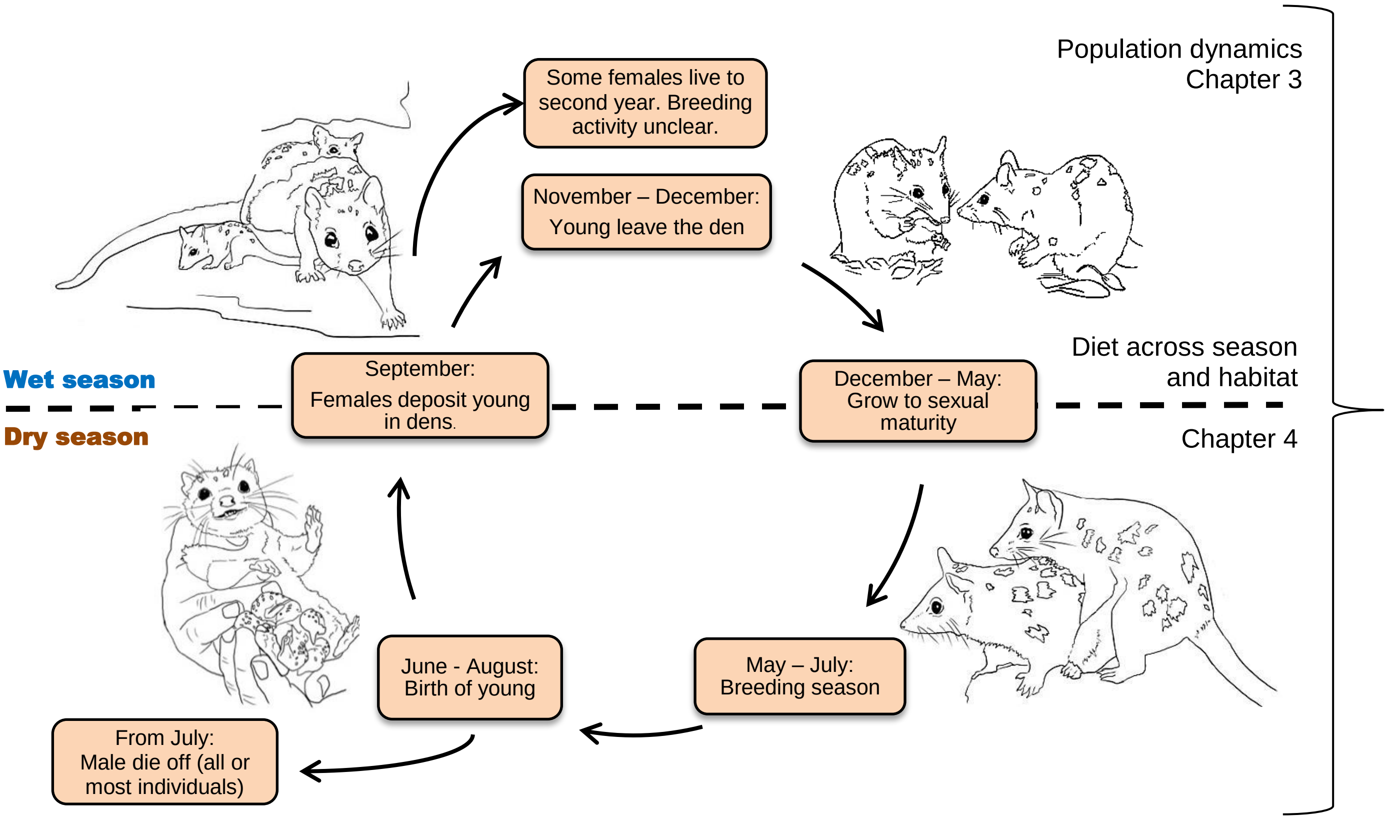


Figure 6.1. Life history of the northern quoll Dasyurus hallucatus, with reference to data chapters in this thesis.

The study population occurs on Koolan Island, which is located one kilometre from the mainland of the west Kimberley region in Western Australia. Given the logistical constraints in accessing these areas, there have been limited studies on island populations of the northern quoll (How et al. 2009; Spencer et al. 2017; Griffiths et al. 2017). However, islands have been recognised as one potential safeguard for the northern quoll while mainland populations decline as a result of ingestion of the toxic cane toad *Rhinella marinus*, which is rapidly spreading from the east to west of northern Australia (Southwell et al. 2017). Therefore, it is important to understand whether island populations of this species behave in a similar way to their mainland counterparts to identify if there are any additional risks or opportunities in conserving insular populations.

Chapter 4 demonstrates that the diet of northern quolls on Koolan Island broadly reflects the diet of studied mainland populations. However, my data revealed that predation on vertebrates occurs less and/or is less preferred than for northern quolls on the mainland. As found by Pollock (1999), Oakwood (1997), and Dunlop et al. (2017), insects were dominant in the diet of the northern quoll, and I found that beetles and cockroaches in particular were consumed the most. However, while Oakwood (1997) and Dunlop et al. (2017) suggested that northern quoll consumption of vertebrates would increase with availability, I found that vertebrates were the lowest consumed food type (after invertebrates and fruit) in each season and habitat type. The data also suggests that skinks, the most commonly consumed vertebrate, were consumed less than what would be expected based on their availability in the environment.

Northern quoll individuals on Koolan Island are some of the smallest observed across the Kimberley, and are certainly smaller than those on the mainland (up to 25 - 30% smaller; How et al. 2009; Spencer et al. 2017). Studies of insectivorous dasyurids have suggested predator size to correlate with prey size (Fisher and Dickman 1993), and my findings may indicate that Koolan Island northern quolls have developed a foraging strategy that suits their size and the food sources available. If this is the case then other fauna on the island are likely to have developed over time accordingly, with most vertebrates (such as *Zyzomys argurus*) not subjected to strong predation pressure from the northern quoll. This should be considered by conservation managers planning reintroduction or translocation programs between island and mainland sites, as mainland individuals may exert a larger predation pressure on the island than prey species are adapted to. There has been one published example of a translocation of mainland northern quolls to two islands off northern Australia (Griffiths et al. 2017). Island sites were selected in part due to the absence of any other conservation values susceptible to predation or competition from translocated northern quolls, and the population grew and stabilised over an 11-year period (Griffiths et al. 2017). An interesting extension to this study may be the examination of population trends of prey items on the islands to assess for any ecosystem-level impacts of the introduced predator, and particularly to the one mammal present (*Hydromys chrysogaster*). However, it is acknowledged that managers must be prepared to weigh the costs and benefits when making conservation management decisions (Moran et al. 2010), and in some cases the decline of local populations is outweighed by the benefit of a persisting population of an endangered species.

Koolan Island is separated from the mainland by a permanent, deep sea channel that impedes gene flow between the island and mainland (How et al. 2009). As a result, the population appears to receive very little to no recruitment via immigration from other populations. From my study on the population dynamics of this species over 13 years, I found that population change is dependent on recruitment. Without recruitment via immigration, juvenile survival and mortality is an extremely important driver of this insular population. The northern quoll is partially (and perhaps in some populations wholly) semelparous (Oakwood et al. 2001). The trapping data analysed in Chapter 3 contained no capture records for males in their second year, suggesting complete or near-complete semelparity on Koolan Island. Additionally, most individuals (including those on Koolan Island) experience a short lifespan of one to two years (Dickman & Braithwaite 1992; Oakwood 2000; Spencer et al. 2010; J. Thomas pers. obs.). As a result, the majority of breeding individuals are likely to be juveniles from the previous season and there is little opportunity to recover from widespread recruitment failure in any given year.

The single large weather event, Cyclone Laurence, in December 2009 coincided with the young-in-den phase period and likely was the cause of poor recruitment that year. The subsequent multi-year recovery of the population to pre-cyclone numbers provides insight into both the sensitivity of the population to a shift in recruitment success as well as the demographic resilience of the species. As a result, recruitment in this year appeared to be poor, and population density estimates dropped the following year. In this case, the following years passed without any significant weather events of this scale or other major disturbances, and the population recovered to pre-cyclone density estimates over approximately two years (Figure 3.3). Theoretically, this would have required two successful reproductive periods following the cyclone, with high juvenile survival. This study therefore demonstrates that in favourable environmental conditions, an isolated population can recover from stochastic events and population decline. However, had a second cyclonic event occurred in following years, or had a second threatening process arrived on the island, it is highly likely that the population would not have had a chance to recover, and instead may have crashed further.

A previous study on gene flow for the northern quoll on the mainland suggests individuals can and do move large distances between populations, particularly across open plains and within high rainfall areas (Hohnen et al. 2016). The importance of recruitment has been demonstrated by reintroduction attempts on the mainland, where a population crash was attributed to low or no immigration to offset mortality (Cremona et al. 2017). Based on the importance of recruitment to population growth, it’s likely that northern quoll populations benefit from a metapopulation dynamic, with populations receiving recruitment in the form of both juvenile survival and immigration. This suggests that populations that are the focus of conservation efforts should be actively managed over time, to facilitate and maintain immigration and emigration between subpopulations if needed. When island populations are considered, ongoing monitoring should be provided to enable an immediate response to population declines, potentially by supplementing the population with more individuals to enhance recruitment. This also means that if islands prone to significant environmental stochasticity (i.e. cyclonic events) or at risk from other threats (i.e. feral predators, cane toads, disease) are chosen, they are less likely to support long-term self-sustaining populations.

6.2 RESPONSE TO HABITAT MODIFICATION

Aside from habitat modification in the form of grazing and altered fire regimes, anthropogenic infrastructure associated with the resources industry is a key form of habitat loss and modification within the current range of the northern quoll (Woinarksi et al. 2014; Cramer et al. 2016). Mining activity is often centralised around landscape features such as mesas and rocky ridges that can provide core habitat for this species (Cramer et al. 2016). Where mining activities have the potential to impact a local population, the mine must implement measures to minimise human-wildlife conflict with this species and conduct ongoing monitoring. To do this effectively, managers need to understand how habitat loss and modification impacts the northern quoll, and how the species interacts with anthropogenic areas (Messmer 2000). This thesis aimed to do this by determining if survival or recruitment differed between anthropogenic and unmodified parts of the island, and then examining diet and den site selection with consideration to the presence of modified habitat and artificial resources.

From the analysis of annual monitoring data, survival and recruitment of the northern quoll did not appear to vary between in and around the mining footprint, and the unmodified western part of the island. Further, population density estimates for the Koolan Island population fluctuated over time, but did not show a continual decreasing trend in the 13 year study period. This indicates that the northern quoll is able to coexist with mining activities on Koolan Island.

For a viable population of northern quolls to coexist on the island alongside mining activities, either sufficient resources must be available in the remaining native habitat on the island, or the northern quoll must be able to utilise food and shelter resources within the mining footprint (Theobald et al. 1997; Messmer 2000). An investigation of northern quoll diet on the island indicated that quolls are taking advantage of food resources that are available due to anthropogenic activity. Northern quolls ate a variety of food types both in native habitat and within the mining footprint, including invertebrates (predominantly beetles and cockroaches), fruits and some vertebrates. Crickets and grasshoppers were more abundant in and around mining infrastructure than in native habitat, and I found that the northern quoll's consumption of this food type increased accordingly within the mining footprint. Similar findings have been demonstrated in other generalist predators such as the spotted genet (*Genetta tigrina*), which takes advantage of the increased invertebrate abundance within residential areas in winter when this food type is less common in its native habitat (Widdows and Downs 2015). Similar to the northern quoll, the spotted genet's diet in urban areas appeared to be consistent with the relative abundance of invertebrate prey items (Widdows and Downs 2015).

I also found that the northern quoll was taking advantage of introduced food resources, such as the weed *Passiflora foetida* (stinking passionflower). Fruits of this plant comprised a significant portion of the northern quoll's diet, occurring in 23% of scats overall. Northern quolls on the mainland have also been found to consume this plant, but not to the extent as on the island (Dunlop et al. 2017). The northern quoll may have adjusted its foraging strategy to compensate for the loss of food resources that were available on the island pre-mining. The northern quoll may also consume the plant because it contains moderate amounts of energy and protein (Hoe and Siong 1999) and can be found and consumed at little energy expense. The use of a weed by an endangered species provides an interesting conundrum in terms of site management during mining operations, and for rehabilitation in mine closure (Section 6.3). *P. foetida* has spread on the island over time from highly disturbed to less- disturbed areas, and staff on the island spend great expense and effort in weed management measures targeting this and other species. If seeds are viable after digestion by the northern quoll, then this endangered species may be contributing in part to weed spread on the island. However, the impact is probably no more so than from the many birds that feed on *P. foetida* on the island (J Thomas pers. obs.), as has also been observed in Hong Kong by Hoe and Siong (1999). Further, if this plant provides an important food source to the northern quoll, then this should be considered alongside any upscaled weed management practices that may greatly decrease the abundance of *P. foetida*, and may necessitate increased monitoring of the northern quoll population.

Species with a generalist diet have greater flexibility in taking advantage of novel food sources, including human food scraps (Newsome et al. 2014). This also appears to be true for the northern quoll, where males may be especially food-oriented prior to the breeding season, and females require sufficient food resources to raise altricial juveniles during the late dry season (Oakwood 1997; 2000). While the island has implemented measures to limit northern quoll access to food waste, they have been observed by the author and staff on the island to obtain human food from stealing scraps from the plates of staff in open mess halls when staff aren’t watching, and by occasionally finding access to rubbish. A small amount of ‘waste’ was detected in scats of the northern quoll (%FO 0.6; %VO 0.4). However, the proportion of anthropogenic food items in the diet of the northern quoll may be underestimated due to the higher digestibility of this food type, making it less likely to be detected in scats (Kapel 1999).

Northern quolls have been observed denning in non-natural structures on the mainland (Pollock 1999), and are known to den in vehicles, equipment, infrastructure and buildings on the island. However, given the importance of juvenile survival to the population growth of the northern quoll, I was interested to examine whether artificial areas were being used by females during the young in den phase. Females were trapped within and around the mining footprint, however none were found to den in mining infrastructure or equipment during this period. One den was located within a rehabilitated area, and the remaining 21 were located in native habitat. However, I did not study juvenile survival from these dens, and therefore could not determine if the den within the rehabilitated area was successful in protecting juveniles from climatic extremes or predation. This indicates that the encroachment of anthropogenic infrastructure may result in a net loss of suitable dens that in turn may impact the breeding success of a population. Should proposed development footprints include suitable denning habitat such as rocky areas and trees with hollows, the net loss of this habitat should be recognised. This should be assessed in the context of the size of the local northern quoll population, and the availability of suitable denning habitat in adjacent areas.

This study’s insight into the importance of recruitment to the population dynamics of the northern quoll can also be used to mitigate the impacts of habitat modification on this species. Land uses that change the landscape, such as the commencement or extension of mining operations, are preceded by vegetation clearing activities. If we identify that the northern quoll population is likely to be particularly vulnerable to impacts during the breeding and young in den period (i.e. June to November), then clearing could be planned to occur outside of this timeframe to reduce the potential for juvenile mortality. This finding is supported by studies on habitat modification by fire, where Griffiths and Brook (2015) suggest that fires in the early dry season would have a lesser impact on northern quoll populations than those in the late dry season.

6.3 REHABILITATION ACTIONS FOR THE NORTHERN QUOLL

Mining development is unique in that most of its footprint is intended to be temporary, and is approved based on commitments to rehabilitate those areas to an agreed final land use. When the final land use is that of native habitat, rehabilitation aims to make areas safe, stable, non-polluting, and create a self-sustaining ecosystem (Department of Mines, Industry Regulation and Safety 2020). Further to these key aims, mines often have specific rehabilitation goals tailored to the bioregion and the vegetation and fauna communities that are present pre-mining (Gould 2011). For mines that occur within northern quoll habitat, many will have completion criteria linked to the return of this endangered species. However, in order to make these completion criteria meaningful, appropriate and effective, criteria need to be based on a thorough understanding of species' habitat requirements. This is a key challenge when developing completion criteria for rare and endangered species, whose often cryptic nature makes it difficult to obtain this information. As a result, fauna outcomes in mine rehabilitation in Australia are often not completely realised (Cristescu et al. 2012). By providing information regarding habitat use and diet within intact vegetation, this thesis generated key knowledge to further refine criteria and provide practical information during rehabilitation.

Understanding resource use is of primary relevance to planning rehabilitation outcomes, and therefore chapters 4 and 5 are the most topical to this subject matter. In my study of diet, I found that northern quolls on Koolan Island have a generalist diet of invertebrates, vertebrates and vegetative material (mostly fruit). Therefore, habitats that support these food sources should be considered in developing rehabilitation completion criteria. The prey items consumed most across seasons were ground-dwelling, such as beetles and cockroaches, crickets and grasshoppers, skinks, and centipedes. Many skinks and invertebrates occur in leaf litter, and northern quolls on the island have been observed foraging in this microhabitat, appearing to use visual and aural cues and vibrissae to detect prey moving amongst the leaf litter. Leaf litter has been suggested to correlate with the richness and abundance of invertebrates including cockroaches, beetles and ants (Sayer 2006; Tarli et al. 2014; Grimbacher et al. 2018). Therefore, both habitat-related parameters to measure leaf litter, and measures of key prey items such as beetles and crickets, may be effective in determining the suitability of rehabilitated areas as foraging habitat for the northern quoll. Further studies on prey item diversity and abundance in native habitat on the island may inform site-specific completion criteria to this effect.

Fruits, predominantly figs (*Ficus* sp.) and the stinking passionflower, were prevalent in the diet of the northern quoll on Koolan Island and may comprise an important part of this species' diet on islands. While I do not suggest that the presence of a weed species is included in completion criteria, the presence of fruits that are collectively available for much of the year may be a valuable consideration in rehabilitation planning. On Koolan Island these findings have informed current and future revegetation activities, where establishing a variety of *Ficus spp.* is now targeted to support northern quoll foraging habitat. Mainland studies of the northern quoll also detected fruit consumption but did not suggest that they were as prevalent in the northern quoll's diet as this study of an island population. The study suggests that the diet of island and mainland northern quolls may differ, and that the diet of the northern quoll varies across its range. The findings of this thesis to rehabilitation of mainland sites should therefore be applied alongside more detailed site-specific information on the diet of northern quolls in that region, and fruit diversity and abundance in the area.

In my study of denning habitat used by females during the young in den phase, I found that rocky structures, trees, and subterranean tunnels were used by northern quolls. Interestingly, one den was located within a newly rehabilitated area in a subterranean tunnel that appeared to have occurred naturally. The area contained little established vegetation, and was very different from the other used den sites that were all located in native vegetation. Nonetheless, it indicates that female northern quolls may be willing to use rehabilitated areas to deposit young in a den site if it meets the required criteria. Rocky areas were the most commonly used as den sites in this study and had the most stable microclimate throughout the day, and I suggest that these should be included in post-rehabilitation landforms (also see Drake et al. 2010). The use of tree hollows by northern quolls also highlights the need for this microhabitat in rehabilitated areas, particularly dead, salvaged logs from cleared areas to account for the significant lag time for hollow creation (McGregor et al. 2014).

Recreating structures that function as effective den sites requires a thorough understanding of both the surrounding habitat and internal structures of selected dens. This study provides a strong basis for understanding the characteristics of den sites during the young in den period, and in directing further targeted research. I found that used den sites provided stable microclimates, with rocky dens providing more stable microclimates than used dens in either tree hollows or below-ground. In terms of den structure, I found that selected dens had multiple potential entrances and higher levels of aerial cover than available dens. Other studies on den site selection by other mammals have identified these and other characteristics based on substrate, topography and structure to be informative for den selection, which are generally considered to provide a stable microclimate and protection from predators (Zielinski et al. 2004; Isaac et al. 2008; Lesmeister et al. 2008; Trapp et al. 2008; Ross et al. 2010).

Stable temperature and humidity and predator protection are also likely to be significant factors in den site selection by female northern quolls. Temperatures in the study area rise to approximately 38ºC to 40ºC during the young in den period (BoM 2018), and humidity fluctuates at a much larger scale than within used or available dens. Further, there are a number of species that may predate on juvenile northern quolls, including pythons (e.g. *Liasis olivaceous*), and numerous diurnal and nocturnal birds of prey (McKenzie et al. 1995). This information provides high-level data that can inform rehabilitation objectives, such as ensuring trees that provide canopy cover are planted in close proximity to landscapes that are intended to provide suitable denning habitat. However, the time lag until trees are established should be considered as a potential factor that may prevent use of otherwise suitable den sites in the immediate years following rehabilitation.

6.4 MANAGEMENT IMPLICATIONS FOR THE CANE TOAD

The cane toad has caused declines in northern quoll populations across northern Australia via toxic ingestion (Oakwood and Foster 2008; Shine 2010; Woinarski et al. 2011) and has spread across north-western Australia over recent years. It is possible that northern quolls on Koolan Island may encounter cane toads within the coming years (Southwell et al. 2017).

The use of a wide range of food resources by the northern quoll on Koolan Island increases the risk that a species will feed on harmful prey if encountered. Three species of frog are known to occur on Koolan Island, *Litoria rubella*, *Litoria coplandi* and *Limnodynastes lignarius* (McKenzie et al. 1995), but no frogs were detected in scats collected in this study. Dunlop et al. (2017) did detect frogs in their study, at low frequencies and volumes. While I did not detect any frogs in the diet of the northern quoll, anurans are known to be difficult to detect in scats due to their high digestibility, and have been more reliably detected by analysing gut contents of the northern quoll (Oakwood 1997). It is likely that, given the propensity of northern quolls on Koolan Island to consume a range of prey items that they would attempt to consume cane toads if encountered.

This study of the population dynamics of the northern quoll, together with evidence of localised declines on the mainland (Braithwate and Griffiths 1994; Shine 2010), highlights how vulnerable this species is to threatening processes such as the cane toad. While I observed the study population recover from a stochastic weather event, more continuous threats such as the invasion of a toxic prey species would pose a genuine challenge to the ongoing management of this species in an area that receives little to no immigration from adjacent areas. Natural waterbodies on Koolan Island are ephemeral, however the presence of anthropogenic infrastructure necessitates a permanent water source that increases the risk of cane toads establishing a population on the island.

There have been a number of management strategies proposed to mitigate the impacts of cane toads on the northern quoll. The scope of this thesis did not extend to an evaluation of the various methods, however it emphasises the value in having a management plan in place to appropriately address the risk of a cane toad invasion in the coming years.

6.5 CHALLENGES AND LEARNINGS FROM THIS STUDY

Conducting a study on an endangered species in the wet-dry tropics and within an active mine site was a case study in navigating various challenges, and this thesis provides valuable insights that may improve the planning, design and implementation of studies in similar environments.

6.5.1 Logistics and safety

Mining companies must adhere to rigorous safety protocols to minimise and mitigate risks to human safety amongst heavy machinery and a rugged environment. The undertaking of an ecological study was no exception to this rule, which required the author to study quolls in difficult to access areas, such as steep rock faces, in isolated areas with no radio coverage. Therefore, the proposal to traverse the island investigating scats and den sites required a level of trust, compromise and practicality between mining staff and the author. A comprehensive approach to logistics was undertaken prior to commencing this study to develop reasonable safety protocols agreed on by all parties to minimise the risk of an accident. This included regular call-ins to a designated contact, and prior agreement to the specific areas that would be traversed.

Due to the strict safety requirements of operating a mine in a remote area, the mining company limits personnel on the island. Volunteers were therefore not an option for fieldwork, necessitating a study design that was manageable for one person to undertake on their own with occasional assistance from one staff member from the island. This particularly limited the number of traps that could be deployed and checked each morning, and the rate of locating and measuring den sites. Further, field work was undertaken outside of the dry season and was carried out wearing full personal protective equipment (PPE) including steel-capped boots, hi-vis clothing and at times a hard hat. These conditions limited the time that could be spent in the field based on the water that could be carried by the author.

Mine sites are a continually-changing landscape, which can make ecological study design and implementation difficult. During the course of the study, the mine was subject to a structural incident that immediately paused mining activity. The mine went into a ‘care and maintenance’ phase while a plan to remediate the incident was developed, and this study was thrown into uncertainty. During this period, personnel on site was extremely limited (<10 staff), and access to the island became less regular. This required the author to renegotiate access to the site and activities undertaken on the island to meet new expectations and requirements. Fortunately, study conditions were successfully renegotiated over the following months and fieldwork continued. However, this highlights the changes that can occur on a mine with little warning, which must be considered and accounted for with appropriate contingencies prior to commencing this type of research.

6.5.2 Equipment

Temperature and humidity also impacted the performance of equipment. During telemetry, my receiver malfunctioned under the weather conditions and I was fortunate to loan a receiver from the Department of Biodiversity, Conservation and

Attractions (DBCA). In hindsight, back-ups for all pieces of equipment were necessary in undertaking fieldwork in such harsh conditions.

The mining company had obtained GPS collars for the northern quoll prior to undertaking this study. However, northern quolls on the island are substantially smaller than their mainland counterparts (How et al. 2009), and on further examination I found that the collars were much too large to use on the study population. They could not be re-fitted, and also didn’t include a VHF component to locate quolls and target recapture trapping areas. Without understanding the recapture probability of these animals, using this equipment was not feasible.

As a result of these constraints, additional VHF-only collars were secured by loan from DBCA, and the study design was revised from its original concept of fine-scale habitat use of the northern quoll to a targeted study of den site selection. However, to meet ethics requirements the size of the animals constrained the size of the transmitters that could be used, and therefore lowered the life and range of transmitters and the scope of inference that could be taken from this study (i.e., the range of time that animals could be tracked over and required proximity from animals to detect a signal). The island contained a rugged and steep topography full of valleys and crests, which was a further constraint on detecting a VHF signal with a transmitter.

6.5.3 Historic datasets

One of the more interesting parts of this thesis is the use of data typical of long-term monitoring programs, and understanding the challenges and opportunities of this dataset. As is typical of long-term monitoring programs, particularly those conducted by industry, the party conducting the monitoring changed over time. Further, the aim of annual monitoring was to satisfy a reporting requirement to regulatory agencies, and was designed to be used with relatively simple statistical analyses of each year in isolation. When combining these data in spatially explicit and non-spatial capture recapture models, I found that trap location, trapping intensity and duration varied between years, thus violating the assumptions for a number of models.

However, by conducting this study and working through these issues I was able to not only identify analyses that could be used to maximise inference for difficult datasets, but also identify clear and simple changes in study design that would greatly improve the robustness of the data and the level of inference that could be made. I would suggest that if more importance was placed on consistency in trap location and duration between years than maintaining a number of ‘trap nights’ across the island, the recapture rate of animals would increase as would the robustness of the analysis. Preliminary information from trapping activities on the island suggests nine days may confer these benefits, however further investigation would be valuable to confirm this estimation. Overall, I expect this to have a direct benefit on northern quoll monitoring on Koolan Island, and note that it may also confer benefits to similar monitoring studies elsewhere.

6.6 DIRECTIONS FOR FUTURE RESEARCH

6.6.1 Population dynamics

This study provides a basis to further improve capture methodology for the purpose of modelling the population dynamics of the northern quoll. Given the rugged landscape that this species often inhabits, it can be difficult to conduct surveys over the spatial and temporal scale needed for reliable estimates. A key challenge for this species is therefore finding the optimum, most efficient way to measure population change. Studies such as Ivan et al. (2013) and Linden et al. (2018) have used novel approaches combining capture-recapture methods with telemetry activities to get more robust estimates of density. This method has also been applied to account for spatial variation in density (Proffitt et al. 2015). Given recent advances in GPS collar technology and the lack of fine-scale habitat use and resource selection information on the northern quoll, this may be a reasonable avenue to explore for this species.

Alternatively, studies such as Soisalo and Cavalcanti (2006) and Molina et al. (2017) use camera traps in capture-recapture studies to estimate density. This approach is logistically easier to undertake than other methods, with minimal interaction with the study species and limited effort required on the part of researchers in the field further to setting up and removing the camera traps. Austin (2016) demonstrated that northern quolls can be identified by their markings from camera traps for capture-recapture methods, and this trapping method may prove more useful in the future for providing long-term data in difficult to access areas or where limited interaction with the study species is desired.

6.6.2 Den site characteristics

The findings of this thesis suggest that stable temperatures (~30°C - 33°C in this study) and humidity (~50% - 75% in this study) are likely to be indicative of a suitable den site during the breeding season. However, I was limited in the depth at which I could measure temperature and humidity without concern that I would impact access to and from the den by northern quolls. Further studies on the internal structure and microclimate of used dens at depth would be valuable in confirming such an important aspect of den selection.

I found that while aerial cover and number of potential entrances were most influential in driving den site selection, their explanatory power was still limited.

Further investigation of structural and habitat characteristics of selected den sites is required to elucidate what makes a viable den. While there have been limited studies on den site selection by Australian dasyurids, similar studies have found characteristics such as aspect, distance to foraging habitat, and height above ground level to be important influencers of den site selection (Lutermann et al. 2010; Ross et al. 2010). However, it is noted that some of these investigations may be better suited to mainland populations within more heterogeneous environments, as Koolan Island is restricted in the habitat types available for comparison.

One potential outcome of confirming the characteristics of a suitable den is the replication of these characteristics in artificial dens. However, studies should also consider the process of den site selection by individuals. In a study of nest and den selection by bats and bird species, Clement and Castleberry (2013) suggested that animals used physical cues as proxy indicators of tree cavity microclimate. This is an important consideration in developing artificial den sites. Although efficient designs may in time be developed that meet the climatic and protective attributes of natural den sites selected by the northern quoll, they will only be effective if they are then actually selected by this species in real-life environments. Therefore, after further exploration on this topic has confirmed the attributes of den sites that allow the protection of northern quolls during the young in den phase, and this can be replicated, trials to confirm their use should be undertaken with multiple design options.

6.6.3 Habitat use

Given the size of the animals and the equipment available, I was not able to examine the fine-scale habitat use by the northern quoll. There are opportunities to use resources such as GPS telemetry to better understand habitat use by this species in order to inform important management decisions. This technology could be used to better quantify the foraging behaviour of the northern quoll, including how far from den sites quolls forage each night, the time spent foraging in different habitat types, how much time they're spending in modified habitat when available, and how this varies across seasons.

Studies such as Oakwood (1997) have suggested that certain denning habitat confers greater protection to northern quolls than other areas, and in particular suggests that mortality is lower in rocky habitat. Based on this information, it would be valuable to understand how both broad-scale habitat use and den site selection impacts survival and recruitment in the northern quoll, to examine whether females selecting certain dens are more likely to parent juveniles with higher survival rates.

6.7 REFERENCES:

Austin, C., Tuft, K., Ramp, D., Cremona, T., & Webb, J. K. (2017). Bait preference for remote camera trap studies of the endangered northern quoll (Dasyurus hallucatus). *Australian Mammalogy*, *39*(1), 72-77.

BOM (Bureau of Meteorology) (2018) Climate Data Online. Retrieved from http://www.bom.gov.au/climate/data/index.shtml?bookmark=136.

Braithwaite, R. W., & Griffiths, A. D. (1994). Demographic variation and range contraction in the northern quoll, Dasyurus hallucatus (Marsupialia: Dasyuridae). *Wildlife Research*, *21*(2), 203-217.

Clement, M. J., & Castleberry, S. B. (2013). Tree structure and cavity microclimate: implications for bats and birds. *International journal of biometeorology*, *57*(3), 437-450.

Cook, G. D., & Goyens, C. M. (2008). The impact of wind on trees in Australian tropical savannas: lessons from Cyclone Monica. *Austral Ecology*, *33*(4), 462-470.

Cramer, V.A., Dunlop, J., Davis, R., 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*(2), 135-148.

Cremona, T., Crowther, M. S., & Webb, J. K. (2017). High mortality and small population size prevent population recovery of a reintroduced mesopredator. *Animal Conservation*, *20*, 555-563.

Cristescu, R. H., Frère, C., & Banks, P. B. (2012). A review of fauna in mine rehabilitation in Australia: current state and future directions. *Biological Conservation*, *149*, 60-72.

Department of Mines, Industry Regulation and Safety (2020). *Statutory Guidelines for Mine Closure Plans.* Department of Mines, Industry Regulation and Safety, Perth. Available at https://www.dmp.wa.gov.au/Documents/Environment/REC-EC-111D.pdf.

Dickman, C. R., & Braithwaite, R. W. (1992). Postmating mortality of males in the dasyurid marsupials, Dasyurus and Parantechinus. *Journal of Mammalogy*, *73*(1), 143-147.

Drake, J. A., Greene, R. S. B., Macdonald, B. C. T., Field, J. B., & Pearson, G. L. (2010). *A review of landscape rehabilitation frameworks in ecosystem engineering for mine closure*. International Conference on Mine Closure 2010, ed. Andy Fourie, Mark Tibbett, Jacques Wiertz, Australian Centre for Geomechanics, Perth, 241-249.

Dunlop, J. A., 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*(3), 858-866.

Fisher, D. O., & Dickman, C. R. (1993). Body Size-Prey Relationships in Insectivorous Marsupials: Tests of Three Hypotheses. *Ecology*, *74*(6), 1871-1883.

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.

Griffiths, A. D., & Brook, B. W. (2015). Fire impacts recruitment more than survival of small-mammals in a tropical savanna. *Ecosphere*, *6*(6), 1-22.

Griffiths, A. D., Rankmore, B., Brennan, K., & Woinarski, J. C. (2017). Demographic evaluation of translocating the threatened northern quoll to two Australian islands. *Wildlife Research*, *44*(3), 238-247.

Grimbacher, P. S., Edwards, W., Liddell, M. J., Nelson, P. N., Nichols, C., Wardhaugh, C. W., & Stork, N. E. (2018). Temporal variation in abundance of leaf litter beetles and ants in an Australian lowland tropical rainforest is driven by climate and litter fall. *Biodiversity and Conservation*, *27*, 2625-2640.

Hoe, V. B., & Siong, K. H. (1999). The nutritional value of indigenous fruits and vegetables in Sarawak. *Asia Pacific Journal of Clinical Nutrition*, *8*, 24-31.

Hohnen, R., Tuft, K.D., Legge, S., Hillyer, M., Spencer, P.B., Radford, I.J., 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.

How, R. A., Spencer, P. B. S., & 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.

Isaac, J. L., De Gabriel, J. L., & Goodman, B. A. (2008). Microclimate of daytime den sites in a tropical possum: implications for the conservation of tropical arboreal marsupials. *Animal Conservation*, *11*, 281-287.

Ivan, J. S., White, G. C., & Shenk, T. M. (2013). Using auxiliary telemetry information to estimate animal density from capture–recapture data. *Ecology*, *94*(4), 809-816.

Kapel, C. M. (1999). Diet of arctic foxes (*Alopex lagopus*) in Greenland. *Arctic*, 289-293.

Lesmeister, D. B., Gompper, M. E., & Millspaugh, J. J. (2008). Summer resting and den site selection by eastern spotted skunks (*Spilogale putorius*) in Arkansas. *Journal of Mammalogy*, *89*, 1512-1520.

Linden, D. W., Sirén, A. P., & Pekins, P. J. (2018). Integrating telemetry data into spatial capture–recapture modifies inferences on multi-scale resource selection. *Ecosphere*, *9*(4), e02203.

Lutermann, H., Verburgt, L., & Rendigs, A. (2010). Resting and nesting in a small mammal: sleeping sites as a limiting resource for female grey mouse lemurs. *Animal Behaviour*, *79*, 1211-1219.

McGregor, R. A., Stokes, V. L., & Craig, M. D. (2014). Does forest restoration in fragmented landscapes provide habitat for a wide-ranging carnivore? *Animal Conservation*, *17*(5), 467-475.

McKenzie, N. L., Fontanini, L., Lindus, N. V., & Williams, M. R. (1995). Biological inventory of Koolan Island, Western Australia 2. Zoological notes. *Records of the Western Australian Museum, 17*, 249-266.

Messmer, T. A. (2000). The emergence of human–wildlife conflict management: turning challenges into opportunities. *International Biodeterioration & Biodegradation, 45*(3-4), 97-102.

Molina, S., Fuller, A. K., Morin, D. J., & Royle, J. A. (2017). Use of spatial capture–recapture to estimate density of Andean bears in northern Ecuador. *Ursus*, *28*(1), 117-127.

Moran, D., Laycock, H., & White, P. C. (2010). The role of cost-effectiveness analysis in conservation decision-making. *Biological Conservation*, *143*(4), 826-827.

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

Oakwood, M. (1997). The ecology of the northern quoll, *Dasyurus hallucatus* (Unpublished doctoral dissertation). The Australian National University, ACT, Australia.

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.

Oakwood, M., Bradley, A. J., & Cockburn, A. (2001). Semelparity in a large marsupial. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1465), 407-411.

Oakwood, M., & Foster, P. (2008). Monitoring extinction of the northern quoll. *Australian Academy of Science Newsletter*, *71*(6).

Pohlman, C. L., Goosem, M., & Turton, S. M. (2008). Effects of Severe Tropical Cyclone Larry on rainforest vegetation and understorey microclimate near a road, powerline and stream. *Austral Ecology*, *33*(4), 503-515.

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*(2), 388-395.

Proffitt, K. M., Goldberg, J. F., Hebblewhite, M., Russell, R., Jimenez, B. S., Robinson, H. S., Pilgrim, K. & Schwartz, M. K. (2015). Integrating resource selection into spatial capture-recapture models for large carnivores. *Ecosphere, 6*(11), 1-15.

Ross, S., Kamnitzer, R., Munkhtsog, B., & Harris, S. (2010). Den-site selection is critical for Pallas's cats (*Otocolobus manul*). *Canadian Journal of Zoology*, *88,* 905-913.

Sayer, E. J. (2006). Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biological Reviews, 81,* 1–31.

Shine, R. (2010). The ecological impact of invasive cane toads (*Bufo marinus*) in Australia. *The Quarterly Review of Biology*, *85*(3), 253-291.

Soisalo, M. K., & Cavalcanti, S. M. (2006). Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. *Biological Conservation*, *129*(4), 487-496.

Southwell, D., Tingley, R., Bode, M., Nicholson, E., & 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.

Spencer, P. B. S., How, R. A., & Schmitt, L. H. (2010). The northern quoll population on Koolan Island: Molecular and demographic analysis. Unpublished report to Mount Gibson Iron Limited, Murdoch University, Perth.

Spencer, P. B., Sandover, S., Nihill, K., Wale, C. H., How, R. A., & 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.

Tarli, V. D., Pequeno, Pedro A. C. L, Franklin, E., Morais, J. W., Souza, J. L. P., Oliveira, A. H. C., & Guilherme, D. R. (2014). Multiple environmental controls on cockroach assemblage structure in a tropical rain forest. *Biotropica, 46*, 598-607.

Theobald, D. M., Miller, J. R., & Hobbs, N. T. (1997). Estimating the cumulative effects of development on wildlife habitat. *Landscape and Urban Planning*, *39*(1), 25-36.

Trapp, Jon R., Paul Beier, Curt Mack, David R. Parsons, & Paquet, P.C. (2008). Wolf, *Canis lupus*, den site selection in the Rocky Mountains. *Canadian Field-Naturalist, 122*(1), 49-56.

Widdows, C. D., & Downs, C. T. (2015). A genet drive-through: are large spotted genets using urban areas for “fast food”? a dietary analysis. *Urban Ecosystems*, *18*, 907-920.

Woinarski, J., Burbidge, A., & Harrison, P. (2014). Action Plan for Australian Mammals 2012. CSIRO Publishing, Melbourne.

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., Johnson, C.N. & McKenzie, N.L. (2011). The disappearing mammal fauna of northern Australia: context, cause, and response. *Conservation Letters*, *4*(3), 192-201.

Zielinski, W. J., Truex, R. L., Schmidt, G. A., Schlexer, F. V., Schmidt, K. N., & Barrett, R. H. (2004). Resting habitat selection by fishers in California. *The Journal of Wildlife Management*, *68*(3), 475-492.

Appendix

Appendix A

Used and available den sites on Koolan Island

Used Dens:

Used den 1

Used den 3

Used den 4

Used den 5

Used den 7

Used den 8

Used den 9

Used den 10

Used den 11

Used den 12

Used den 17

Used den 18

Used den 19

Used den 20

Used den 21

Used den 22

Used den 23

Used den 24

Used den 25

Used den 26

Used den 27

Used den 28

Available dens:

Available den 1

Available den 3

Available den 4

Available den 5

Available den 7

Available den 8

Available den 9

Available den 10

Available den 11

Available den 12

Available den 17

Available den 18_1

Available den_2

Available den 19

Available den 20

Available den 21

Available den 22

Available den 23

Available den 24_1

Available den 24_2

Available den 25

Available den 26

Available den 27

Available den 28