The diet, breeding, and ecological role of Brown Skuas *Stercorarius antarcticus lönnbergi* (Mathews, 1912) on Macquarie Island, following the eradication of invasive prey.

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Declaration of Originality

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text of the thesis, nor does the thesis contain any material that infringes copyright.

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14 February 2021

Statement of Ethical Conduct

The research investigations conducted for this thesis abide by the ethical requirements of the University of Tasmania Animal Ethics Committee. Ethics approval was gained through application A0016085.

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Statement of Co-Authorship

Chapters 2 – 5 of this thesis have been prepared as submissions, have been submitted to or are published in peer-reviewed journals. The design and implementation of surveys and data analysis, interpretation of results and the preparation of manuscripts for submission was the responsibility of the candidate but was carried out in collaboration with supervisors and other co-authors.

The following people and institutions contributed to the publication of work undertaken as part of this thesis:

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Contribution of work by co-authors for each chapter:

Chapter 2. Counting the collateral: inclusion of native predators in eradication planning is vital for success

Toby Travers designed the study, conducted the literature review and data analysis, and wrote the chapter. Justine Shaw contributed to the design of the study. Justine Shaw, Rachael Alderman, Aleks Terauds and Mary-Anne Lea provided comments on the chapter.

Travers, T. 70%, Shaw, J. 21%, Lea, M.-A. 3%, Terauds, A. 3%, Alderman R. 3%

Chapter 3. Bottom-up effect of eradications: The unintended consequences for top-order predators when eradicating invasive prey

Justine Shaw, Aleks Terauds and Rachael Alderman conceived the ideas and designed methodology. Rachael Alderman, Aleks Terauds and Toby Travers contributed to the collection of data. Toby Travers conceived and performed the data analysis. Aleks Terauds and Mary-Anne Lea assisted data analysis. Toby Travers wrote the chapter. Justine Shaw, Rachael Alderman, Aleks Terauds and Mary-Anne Lea provided comments on the chapter.

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Chapter 4. Defining the foraging landscape and breeding success of an island apex predator

Toby Travers, Justine Shaw, Rachael Alderman, Aleks Terauds and Mary-Anne Lea conceived the ideas and designed methodology. Toby Travers performed data collection and analysis. Aleks Terauds and Mary-Anne Lea assisted with data analysis. Toby Travers wrote the chapter. Justine Shaw, Rachael Alderman, Aleks Terauds and Mary-Anne Lea provided comments on the chapter.

Travers, T. 70%, Lea, M.-A. 15%, Shaw, J. 10%, Terauds, A. 10%, Alderman R. 5%

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Melissa Houghton took the photograph. Toby Travers wrote the description. Melissa Houghton provided comments on the description.

Travers, T. 90%, Houghton, M. 10%

Chapter 5. Using distance sampling and predator functional response curves to investigate the influence of Brown Skua predation on recovering petrel populations

Justine Shaw, Jeremy Bird, Aleks Terauds and Toby Travers conceived the ideas and survey design. Toby Travers and Jeremy Bird contributed to data collection. Toby Travers and Jez Bird conceived and performed data analysis. Toby Travers wrote the chapter. Justine Shaw, Rachael Alderman, Aleks Terauds, Mary-Anne Lea and Jeremy Bird provided comments on the chapter.

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We, the undersigned, endorse the above stated contribution of work undertaken for each of the published (or submitted) peer-reviewed manuscripts contributing to this thesis:

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Acknowledgment of Country

Kaya noonakoort. Hello everyone. I grew up on Noongar Boodja (country) on the land of the Yued and Whadjuk people. As a Wedjellah (whitefella) interested in the natural world, it overwhelms me to think of the kaartdijin (knowledge) and culture that has for over 60,000 years shaped and maintained the rich ecosystems found in these places. I acknowledge the Yued and Whadjuk peoples of the Noongar nation as the traditional custodians of the country and waters on which I was raised.

For this thesis I conducted my studies on lutruwita (Tasmania) Aboriginal land, sea and waterways. It has been a privilege to study here in nipaluna (Hobart) and one I do not take lightly. I acknowledge, with deep respect the traditional owners of this land, the muwinina people. They cared and protected Country for thousands of years. They knew this land, they lived on the land and they died on these lands. I honour them and pay my respects to the Tasmanian Aboriginal community that continue to care for Country.

I pay my respects to Noongar and muwinina Elders past and present and to the many Aboriginal people that did not make Elder status.

I recognise a history of truth which acknowledges the impacts of invasion and colonisation upon Aboriginal and Torres Strait Islander peoples resulting in the forcible removal from their lands.

I stand for a future that profoundly respects and acknowledges Aboriginal perspectives, culture, language and history. And a continued effort to fight for Aboriginal justice and rights paving the way for a strong future.

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The work contained within this thesis is my own; however, its disingenuous to think that I contributed more than a small percentage of the effort and sacrifice that went into creating the end product. I cannot begin the rest of my acknowledgements anywhere else than with my partner, Natalie Wren, who has made more sacrifices for this thesis than anyone bar none. For all the late nights I spent writing, Nat spent making a dinner for me when I got home. For all the silent times I spent inside my own head working over and over questions whether related to methods, analysis or theory, Nat spent patiently waiting for me to snap back into reality all the while getting on with everything else that needed doing. For the 5 months I spent in the field, Nat spent living alone and going to work to cover the mortgage. And while I get asked how difficult is it to have a child while completing a PhD, the truth is I would have found it impossible if not for Nat. So thanks Nat for everything you have given me.

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Acknowledgement of Place Name

Sadly, the sting of colonial brutality can even reach a remote sub-Antarctic island with no first nations peoples of its own. Macquarie Island was named in honour of a past Governor of New South Wales, Lachlan Macquarie. Attempting to pillory or pedestal a person on their legacy from 200 years ago will potentially always be contentious. Historians may argue whether Macquarie's instructions to take prisoners during raids or his strong handed approach to assimilation as a Governor can be interpreted as a benign attitude towards aboriginal people or not. However, the events that occurred during raids under Macquarie's command were horrific. During one of these raids on April 17, 1816, at least 14 Aboriginal men, women, children, and the elderly, including Dharawal and Gandangarra peoples, were shot or forced off a cliff and to their deaths by soldiers, in an event now known as the Appin massacre. From observing any number of events over the last two decades we know that, as commander responsibility lands squarely on Macquarie, regardless of his distance from the site of the massacre. Macquarie's instructions to hang the bodies of dead men in trees in a deliberate effort to create "terror" among the Aboriginal communities remain shocking to this day. Bodies were hung upon hilltops and later beheaded.

> *'On any occasion of seeing or falling in with the Natives, either in bodies or singly, they are to be called on, by your friendly Native Guides, to surrender themselves to you as Prisoners of War. If they refuse to do so, make the least show of resistance, or attempt to run away from you, you will fire upon and compell them to surrender, breaking and destroying the spears, clubs, and waddies of all those you take Prisoners. Such Natives as happen to be killed on such occasions, if grown up men, are to be hanged up on trees in conspicuous situations, to strike the Survivors with the greater terror. On all occasions of your being obliged to have recourse to offensive and coercive measures, you will use every possible precaution to save the lives of the Native Women and Children, but taking as many of them as you can Prisoners.'*

> Governor Macquarie's instructions to Captain Schaw of the 46th Regiment

Today his name adorns towns, roads, harbours, universities, and a small remote sub-Antarctic Island. So, while the name Macquarie will be referenced throughout this thesis, I would like to take a moment here to acknowledge the Dharawal, Gandangarra and Dharug peoples and their culture and community that has endured these atrocities. I acknowledge their Elders past and present, and those that that did not make Elder status.

Dedicated to

my darling little boy

Percy Sebastian Wren,
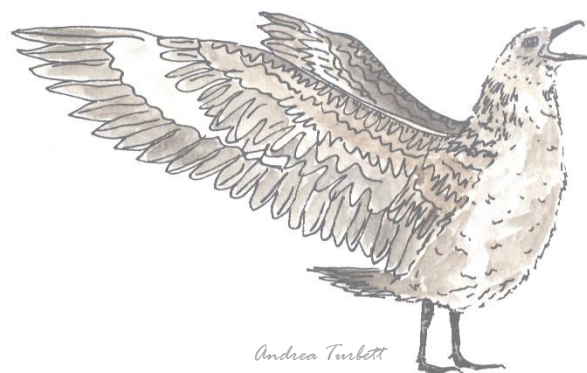
and

Matty Hawkins

a big ole pelican, miss ya

Andrea Turbett

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Abstract

In Foula there is a privileged bird, no man dare shoot it, under the penalty of 16s 8d sterling, nor destroy its eggs: when they meet it at sea, whatever fish they have in the boat Skua always get a share, and all this out of gratitude for beating off the Eagle, who dares not venture to prey on the island during the whole of the breeding season. Skua is not so strong as the Eagle, but much more nimble: strikes out at him without mercy, with such effect that he makes the other scream aloud, and his retreat is so sudden as to avoid all danger from the Eagle.

Rev. Low (1879)

Throughout 2010 and 2011, Macquarie Island underwent a substantial conservation intervention that drastically altered the state of its ecosystem. After 140 years of inhabiting the island, invasive rabbits (*Oryctolagus cuniculus*), black rats (*Rattus rattus*), and house mice (*Mus musculus*) were all eradicated. Brown Skuas (*Stercorarius antarcticus lonnbergi*) are a top-order avian predator and the island's primary terrestrial predator. For skuas, rabbits were an abundant prey species and were heavily relied upon as a food source during the summer breeding season. Prior to the arrival of rabbits, skuas most likely thrived upon vast quantities of seabirds, including burrowing petrels, as a key dietary component. However, as invasive pests severely reduced petrel numbers, rabbits became an important component of skua diet, likely replacing that of burrowing petrels. The rabbit eradication was, therefore, likely to have a negative effect on skuas; however, prior to Macquarie Island, rabbit eradication had never been attempted at this scale.

Apart from the trophic changes brought about by the rabbit eradication, over 500 skuas also died of secondary poisoning after consuming poisoned rabbit carcasses during the eradication. Adaptive management and close monitoring of non-target mortality during the eradication mitigated the degree of poisoning for skuas and other native scavengers to a large extent. Nonetheless, without long-term monitoring the population level impacts would have remained unquantified.

Through this thesis I investigate how the diet, breeding, and ecological role of Brown Skuas changed following rabbit eradication, while considering the contributing effects of prey-loss and secondary poisoning. First, I review the existing research into the effects of invasive prey eradications on native predator populations, focussing on eradications of invasive rabbits and rodents. Second, I assess the effect prey-loss and secondary poisoning had on skua nest density, their breeding success and diet. Third, I investigate the current diet and foraging strategies of Brown Skuas on Macquarie Island and how they influence individual breeding success. Fourth, I examine the role of skua predation in limiting the recovery of burrowing petrel prey species.

Rabbits and rodents have been the target of over 692 successful island eradications. The effects of these eradications on predator populations were underreported in the literature with long-term ecological impacts such as prey loss rarely studied. Native predators were the only group studied that had more reported negative responses to an eradication than positive, highlighting the need for further studies.

Using surveys of skua nest numbers and breeding success, and stable isotope analysis of feathers taken from skua chicks, I found the breeding and diet of Macquarie Island's Brown Skuas were impacted by the eradication of rabbit prey. Both nest numbers and breeding success fell following the eradication of rabbits to their lowest recorded levels on Macquarie Island. Since that time, nest

numbers have slowly recovered. Stable isotope analysis revealed the isotopic niche width of skuas significantly reduced after the eradication suggesting increased competition for remaining prey. Secondary poisoning further lowered skua nest numbers below that expected by prey-loss alone.

I deployed GPS units on breeding adult skuas and surveyed prey remains at the nest to investigate how the diet and foraging decisions of skuas impact their breeding success. Skuas that successfully reared chicks had foraging strategies that allowed for more time spent at the nest site and less energy expenditure. The association between nest proximity to abundant prey and breeding success was highlighted by most birds failing to rear a chick in nesting areas where skuas had historically relied heavily on rabbits in their diet. The current paucity of prey in these areas meant skuas spent longer searching for food far from the nest site and had poorer breeding success.

To investigate the effect of skua predation on the recovery of burrowing petrels on Macquarie Island, I modelled the density-dependent predation rate of Brown Skuas on Antarctic Prions (*Pachyptila desolata*), a burrowing petrel, using burrow density as a proxy for prey density and feather 'sign' (left at the site where a skua had killed a prion) to measure predation rate. I compared this predation rate to Hollings' functional response curves and calculated an annual predation rate of skuas on prions. I found skuas followed a Type III functional response curve with low predation pressure at low prey densities. Comparing the annual predation rate with published growth rates of petrels I found evidence that skua predation, in its current form, could impact the recovery of ~3.5% of burrowing petrel species (those with the lowest growth rates).

My thesis shows the eradication of an abundant rabbit population on Macquarie Island and slow recovery of some native prey species, particularly burrowing petrels, has rapidly reduced food availability for the island's skua population and reshaped their foraging landscape. This has impacts for the native predator and for native prey. I demonstrate that on isolated islands, such as Macquarie Island, where recovery of seabird prey is expected to be slower, the prey deficit left by eradication of invasive prey can have a long-term negative impact for native predators.

Top-order predators are sensitive to changes in food web structure. Quantifying the multiple effects on native predators of eradicating invasive prey is integral to ensuring eradication projects have a net-positive ecosystem outcome. The ecosystem responses documented in my thesis are likely to become increasingly commonplace as eradication projects expand in their scope and scale. My thesis demonstrates the value of strategic monitoring conducted alongside large-scale conservation projects and lends support to the idea of assisted recovery following eradication projects.

During the South Georgia expedition of 1912-13 I became extremely well acquainted with the Brown Skua, which has left, I believe, a more vivid impression in my memory than any other bird I have met. The skuas look and act like miniature eagles. They fear nothing, never seek to avoid being conspicuous, and, by every token of their behaviour, they are the Lords of the far south.

Murphy (1936)

Chapter 1

General Introduction

Predators, their prey, and a changing landscape

Top-order predators maintain ecosystem structure (Ritchie *et al.* 2012; Ripple *et al.* 2014); directly influencing prey and subordinate predator communities through consumption, and sub-lethally by fear and avoidance (Lima 2002; Sivy *et al.* 2018; Cunningham *et al.* 2020). Combined these effects influence the abundance, behaviour, competition dynamics and physiology of prey, mesopredators and scavengers (Phillips *et al.* 1999; Peckarsky *et al.* 2008; Cunningham *et al.* 2018; Sivy *et al.* 2018). Top-order predators shape temporal patterns of prey from daily behavioural cycles (Moreno *et al.* 1996; Mougeot & Bretagnolle 2000) through to multi-year stress-induced physiological cycles that influence prey reproduction (Boonstra *et al.* 1998; Peckarsky *et al.* 2008). Spatially, a fear of predators can shape prey behaviour at a microhabitat (Hollings *et al.* 2015) to landscape scale (Fortin *et al.* 2005). The loss of top-order predators, therefore, can disrupt ecosystem processes and cause trophic cascades that result in dramatic shifts in ecosystem state (Prugh *et al.* 2009; Ferretti *et al.* 2010).

Globally, top-order predators face many threats, several of which are specific to predators (Estes *et al.* 2011). Predators are threatened by persecution, exploitation, habitat loss, prey loss and climate change (Ripple *et al.* 2014). Long-term declines in global top-order predator populations have destabilised a range of aquatic and terrestrial ecosystems (Prugh *et al.* 2009; Ferretti *et al.* 2010). Herbivores, when unconstrained by predators can become overabundant, degrading plant communities, soil health and broader ecosystem processes (Bergstrom *et al.* 2009; Ripple & Beschta 2012; Morris & Letnic 2017). Likewise, mesopredators and scavengers can have a greater influence on biodiversity and ecosystem processes following declines in top-order predators (Prugh *et al.* 2009; Cunningham *et al.* 2018). In extreme cases, mesopredator release (an increase in mesopredators as a result of a decline in top-order predators) can lead to the extinction of prey species (Crooks & Soule 1999).

Predators exert a strong influence on their prey (Peckarsky *et al.* 2008). However, the relationship between predator and prey exists in a fragile balance (Elmhagen *et al.* 2010). Predators are wholly dependent on their prey for survival, as such prey loss can have profound impacts on predators and repercussions for other prey (Wolf & Ripple 2016). Prey loss can cause declines in predator populations and/or increase predation pressure on other prey species (Bode *et al.* 2015; Wolf & Ripple 2016; Cliff *et al.* 2020). Here, I define prey loss as an extreme and unnatural reduction in food availability as opposed to natural prey cycles, which are common in predator-prey relationships (Tyson *et al.* 2010).

To date mammalian predators receive much of the attention in classical predator-prey ecology. Examples include trophic cascades involving gray wolves (*Canis lupus*) in Yellowstone National Park (Fortin *et al.* 2005); predator-prey cycles of Canadian Lynx (*Lynx canadensis*) and snowshoe hares (*Lepus americanus*) in the Yukon (O'Donoghue *et al.* 1998); and mesopredator release involving coyote (*Canis latrans*) in southern California (Crooks & Soule 1999) or feral cats (*Felis catus*) on islands (Rayner *et al.* 2007). Avian predators also play an important yet often understated role in terrestrial ecosystems (Sekercioglu 2006; Tyson *et al.* 2010; Evans 2021). Why birds as predators are absent in many ecological studies is not clear but may be due to the challenges of surveying volant, shy and cryptic species (Krebs *et al.* 2014). The omission of such a diverse and unique group of species from classical ecology studies is limiting and provides an incomplete picture of the mechanisms that drive ecosystem structure and function. Avian predators face the same suite of threats as their mammalian counterparts, however, if they continue to be understudied we risk neglecting the impact these threats can have on top-order avian predators (Ward *et al.* 2019).

Skuas: a polar top-order predator

Skuas (Stercorariidae) are a family of migratory seabirds and top-order predators of high-latitude terrestrial ecosystems (Furness 1987). They are consummate predators, and a defining quality of Stercorariidae is the diverse range of diet and foraging behaviours among and within skua species, including cooperative and nocturnal hunting (Schulz 2004; Votier *et al.* 2006; Perkins *et al.* 2018). In addition to the threats of top-order predators, migratory species and seabirds also face unique stresses (Estes *et al.* 2011; Croxall *et al.* 2012; Bauer & Hoye 2014; Tershy *et al.* 2015). Skuas sit at the intersection of these groups, thereby exposing them to a wide range of threats. Studies from both northern and southern hemisphere field sites have shown skuas face common top-order predators threats including direct persecution, bioaccumulation of heavy metals, competition, climate change and prey loss (Furness 1987; Calle *et al.* 2015; Carneiro *et al.* 2016b). These have led to the decline of some skua species (Catry *et al.* 2011; Dawson *et al.* 2011).

All skua species migrate from their summer breeding grounds to spend most of the winter at sea (Furness 1987; Weimerskirch *et al.* 2015; Schultz *et al.* 2018). They have a range of feeding tactics to exploit marine and terrestrial food webs (Spear *et al.* 1999; Schulz & Gales 2004). One of the smaller skua species, the Pomarine Skua (*Stercorarius pomarinus*), displays the highest degree of dietary specialisation of any skua during its breeding season, relying almost entirely on lemmings as prey and has a nomadic breeding distribution that tracks eruptions of microtine rodent communities across Alaska and the Siberian Tundra (Maher 1970; Wiklund *et al.* 1999). Another of the small skuas, the Arctic or parasitic skua (*Stercorarius parasiticus*), has a highly specialised foraging behaviour, kleptoparasiting the food of other seabirds, a behaviour that it continues throughout the

year (Caldow & Furness 1991; Bélisle & Giroux 1995). While neither of these smaller skuas are true obligate dietary or foraging specialists (Pomarine Skuas do hunt other prey and Arctic Skuas can find their own food) they have a lesser range of feeding tactics when compared with the broad range of foraging behaviours observed in the larger skuas species (Furness 1987).

The larger skuas, sometimes referred to as the genus *Catharacta*, use predation, scavenging and kleptoparasitism to feed on a range of dietary items including small seabirds, the chicks and eggs of seabirds, small mammals, seal and other carrion, fish, squid, marine invertebrates, and anthropogenic food sources such as livestock and waste (Reinhardt *et al.* 2000). The extensive feeding behaviours of larger skua species is linked to their broad distributions across a diverse suite of islands and coastlines (Reinhardt 1997a); however, even on a single island, the individual diets of skuas can vary markedly. At Hermaness in the Shetland Islands, for example, Great Skuas (*Stercorarius skua*) specialise on either seabirds or fish; or have a generalist diet that includes marine invertebrates and rabbits (Votier *et al.* 2004).

Skua phylogeny

The phylogenetic relationships between skua species are yet to be comprehensively resolved (cf. Sangster *et al.* 2004; Carlos 2016). The genus *Catharacta* has been applied to the larger skuas (those breeding in the southern hemisphere, as well as the Great Skua of the northern hemisphere), however, this clade may be a polyphyletic grouping as the Great Skua is more closely related to one of the smaller species, the Pomarine Skua (Cohen *et al.* 1997). This taxonomic uncertainty centres on the unresolved relationship between three fairly well-defined groups: the southern skua clade; the small skua clade containing the Long-tailed Skua (*Stercorarius longicaudus*) and Arctic Skua; and the yet to be placed third group containing the Great Skua and Pomarine Skua (Braun & Brumfield 1998; Andersson 1999; Ritz *et al.* 2008). The small skua clade is generally considered the outgroup to other skuas, however, exactly how the third group links this and the southern skua clade is currently unresolved (Carlos 2016). Some place the third group as a sister group to Southern Skuas or split it between the two other groups (Braun & Brumfield 1998). Another study even suggested the southern skuas could be an outgroup to the third clade (Ritz *et al.* 2008). This composition suggests an ancestor of the Great Skua was a Southern Hemisphere skua that recolonised the North (Ritz *et al.* 2008). To add to the complexity, species within the southern skua clade frequently hybridise and speciation is not considered complete (Ritz *et al.* 2008). Perhaps an ancestor of the Great Skua did recolonise the North and the Pomarine skua is the youngest species or even a hybrid of the Great Skua and one of the smaller skua species, or as recently suggested the Pomarine Skua should just be grouped with *Catharacta* skuas (Carlos 2016). For now however, and out of prudence, I follow

Sangster *et al.* (2004) and refer to all skuas as the genus *Stercorarius* while acknowledging that this is likely to change in the future.

Brown Skuas in the sub-Antarctic

On first appearances Brown Skuas (*Stercorarius antarcticus lonnbergi*) are a drab gull-like bird best known for their brutal assaults on penguins and their young (Young 2008). However, these enigmatic birds are highly social, incredibly cunning, bold creatures, doting parents, and astounding aerial acrobats (Schulz 2004; Schulz & Gales 2004; Ibañez *et al.* 2018; Madani 2020). From an ecological perspective, they are top-order predators with an important role in structuring ecosystems, a role occupied by few other species within their range, sub-Antarctic terrestrial ecosystems (Moncorps *et al.* 1998; Cerfonteyn & Ryan 2015).

Brown Skuas are the most widespread of the southern hemisphere skuas, with breeding populations on nearly all sub-Antarctic archipelagos and a breeding distribution ranging from the Antarctic peninsula to the temperate latitudes of the Chatham Islands (Fig. 1.1). Prey diversity varies greatly across their range and Brown Skuas have developed a variety of diets and foraging behaviours to exploit different prey communities (Reinhardt *et al.* 2000).

Depending on local prey availability their diets can be highly specialised (Hahn & Peter 2003; Ryan *et al.* 2009). Brown Skuas on the Antarctic Peninsula forage primarily on penguin chicks and eggs (Trivelpiece *et al.* 1980), on Iles Kerguelen, diet consists almost entirely of two small petrel species (Mougeot *et al.* 1998), on South Georgia, seal placenta and muscle dominate (Phillips *et al.* 2004; Anderson *et al.* 2009); and on the Chatham Islands, Brown Skua diet includes seabirds and sheep offal where interestingly, in contrast to many other skua colonies, foraging for these two food resources is partitioned between the sexes (Schultz 2019). Due to their dietary plasticity, our understanding of the role of Brown Skuas as top-order predator is highly site specific and incomplete for many islands (Reinhardt *et al.* 2000).

The foraging strategies of Brown Skuas include a wide variety of specialised hunting techniques, some of which are unique to skuas (Johnston 1973). On Heard Island, Brown Skuas have been observed stealing eggs from King Penguins (*Aptenodytes patagonicus*) by making short frequent flights to 'kick' incubating penguins in the chest until they lost balance and dropped their egg, which the attacker then stole (Wienecke 2008). They kleptoparasitise other birds whilst in flight, including Wandering Albatross (*Diomedea exulans*) a bird nearly 6 times their size (Spear *et al.* 1999); they readily steal milk from lactating elephant seals (Johnston 1973); and hunt small petrels on land at night (Mougeot *et al.* 1998). Their ability to recognise individual humans suggests Brown Skuas have high cognitive abilities that may explain their wide range of foraging tactics (Lee *et al.* 2016). On

some islands more than one foraging tactic is required over a breeding season due to seasonal availability of prey (Phillips *et al.* 2004; Carneiro *et al.* 2015). However, despite the fascinating array of foraging behaviours used by skuas, the relationship between foraging strategies and breeding success is not known for many skuas populations (Carneiro *et al.* 2015).

European rabbits (*Oryctolagus cuniculus*) are one of a suite of invasive species that have been introduced to islands across the sub-Antarctic and, where they co-occur, feature in the diet of Brown Skuas (Table 1.1). Rabbits can become an important food source during the skua breeding season (Jones & Skira 1979; Skira 1984; Moncorps *et al.* 1998). Skuas are not the only top-order predator to become dependent on introduced rabbits for food (Lambertucci *et al.* 2009). Top-order predators across a range of ecosystems, consume invasive rabbits, often replacing multiple native prey in predator diet with a single abundant food source (Barbar *et al.* 2016).

Invasive rabbits have devastating impacts on native ecosystems, particularly island environments (Schweizer *et al.* 2016). Of the thirteen sub-Antarctic islands (including the Falkland Islands) that held invasive rabbit populations, seven populations have now been eradicated (DIISE 2015), bringing numerous benefits to the island's native biota (Shaw *et al.* 2011; McGeoch *et al.* 2015). Little is known about how these island eradications impact Brown Skuas *via* secondary poisoning or prey loss. To date there have been no detailed studies quantifying these impacts on Brown skuas, or predators more generally (Ward *et al.* 2019). In this thesis I investigate the diet, breeding, and ecological role of Brown Skuas on Macquarie Island and examine the effect that eradication of an invasive rabbit population had on skua ecology and behaviour (Springer 2016).

The impact of invasive species on islands is widely recognised (Blackburn *et al.* 2004; Towns *et al.* 2006; Tershy *et al.* 2015; Doherty *et al.* 2016; Evans 2021). Ninety-five percent of all extinct bird species were endemic to islands (127 of 129 spp.), and in 50% of all cases (65 spp.) invasive species were the leading cause of extinction (Blackburn *et al.* 2004; Clavero & Garcia-Berthou 2005; Tershy *et al.* 2015). The overwhelming impact invasive species have on ecosystems has led to an increasing number of larger and more complex eradication projects being proposed (Holmes *et al.* 2019). Eradications of invasive species have had immediate benefits for the vast majority of native species (Jones *et al.* 2016; Brooke *et al.* 2018). However, as eradication projects continue to increase in scale and complexity, there is increased potential for unexpected ecosystem responses to eradications that threaten the success of projects (Zavaleta *et al.* 2001). This increased risk has seen managers take a whole-ecosystem view of modern eradications and the adaptive management of projects aimed at minimising ecological uncertainty (Zavaleta 2002; Caut *et al.* 2009).

An invasion history of Macquarie Island

Globally, island ecosystems have been devastated by invasive species and Macquarie Island is no different (Copson & Whinam 2001; Tershy *et al.* 2015). The island's invasion history is a rich and varied one. Humans first discovered the island in 1810 while searching for fertile sealing grounds (Cumpston 1968; Ling 2014). In the first decade of human occupation, sealers introduced feral cats and wild dogs (*Canis lupus familiaris*), which contemporaneous reports describe having an immediate impact on younger seals and on seabird populations (Falla 1937). Cats were feral on the island by 1820 and remained so into the 21st Century. Dogs, however did not persist for long after their arrival (Falla 1937).

During the 1870s, rabbits and weka (*Gallirallus australis*) were introduced to the island as a source of food for sealing parties (Falla 1937; Copson & Whinam 2001). The arrival of rabbits increased cat numbers on the island by providing ample food during winter months when most native prey migrated from the island and food was scarce (Taylor 1979; Courchamp *et al.* 2000). Facilitated by rabbits, cat and weka numbers increased causing rapid declines in native birds (Falla 1937; Taylor 1979). By the end of the 19th Century, at least two native birds, the endemic Macquarie Island Parakeet (*Cyanoramphus erythrotis*) and an endemic subspecies of Buff-banded Rail (*Gallirallus philippensis macquariensis*), and possibly a third undescribed teal, were driven to extinction (Falla 1937; Taylor 1979). Around this time two invasive rodents, the black rat (*Rattus rattus*) and house mouse (*Mus musculus*), had also established on the island (Copson & Whinam 2001).

By the early-1900s, many seabird populations were either extirpated from the island or severely reduced in number by the cumulative impacts of sealers, invasive wekas, cats, rabbits and rodents (Cumpston 1968; Copson & Whinam 2001). However, invasive species continued to arrive during the 1900s. In 1923 after being uninhabited for 5 years, two feral horses (*Equus ferus caballus*) were seen running wild on the island by members of a Norwegian whaling ship, however like dogs their survival was short-lived (Falla 1937). Then by 1930, Common Starlings (*Sturnus vulgaris*) and Common Redpolls (*Carduelis flammea*) had self-introduced from invasive populations on Auckland Islands, New Zealand, over 600km away, and remain on the island to this day (Copson & Whinam 2001; Raymond *et al.* 2011).

The first eradication campaign of the modern era on Macquarie Island began in 1985. It targeted Wekas, which impacted seabirds, vegetation and invertebrates (Brothers 1984; Brothers & Skira 1984). The project was successful and weka were eradicated by 1989 (Copson & Whinam 2001). From the 1970s intermittent programs were then put in place to control cat and rabbit numbers by the land managers, Tasmanian Parks and Wildlife Service (Brothers *et al.* 1982; Raymond *et al.* 2011;

Terauds *et al.* 2011). These programs culminated in the complete eradication of cats in 2001 (Robinson & Copson 2014).

Between 2000 and 2005, following the eradication of cats and cessation of rabbit control programs, the rabbit population increased more than fivefold (Terauds *et al.* 2014), giving further impetus for the eradication of rabbits and rodents from Macquarie Island (Department of the Environment and Heritage 2005a). In what would become the largest multi-species eradication to date rabbits and rodents were eradicated by 2011 making the island free of all invasive mammals, and with the island's seabirds free of invasive predators (Parks and Wildlife Service 2014; DIISE 2015). Two invasive bird species, numerous invasive invertebrates and plants remain on the island (Shaw *et al.* 2010; Raymond *et al.* 2011; Scott & Kirkpatrick 2013; McGeoch *et al.* 2015; Houghton *et al.* 2019).

Predictive challenges of complex eradications

Invasive species negatively impact a wide range of native species (Blackburn *et al.* 2004), in some cases outcompeting and replacing native analogues in occupying ecological roles that other threatened native species depend on, such as a food source or habitat (Lambertucci *et al.* 2009; Lampert *et al.* 2014). In these situations, eradicating the invasive species can also negatively impact dependent native species if native analogues are slow to recover (Buckley & Han 2014). For example, in San Francisco Bay the slow recovery of a native *Spartina* grass after the eradication of an invasive *Spartina* grass negatively affected the California clapper rail (*Rallus longirostris obsoletus*), which used both grasses as nesting and feeding habitat (Lampert *et al.* 2014). Active restoration of the native grass countered habitat loss for the rail and provided an optimal eradication schedule that maintained habitat above a critical threshold (Lampert *et al.* 2014).

Understanding whether ecological roles filled by invasive species are important to the native ecosystem can be difficult as it relies on knowledge of the native ecosystem prior to invasion (Buckley & Han 2014; Lampert *et al.* 2014). If invasive species introduce additional ecological roles into an ecosystem, these roles may be redundant despite benefitting native species (Nur *et al.* 2019). For example, if invasive species act as surplus prey for a native predator then their eradication may not be detrimental to the predator, however, it could increase predation pressure on native prey (Bode *et al.* 2015; Nur *et al.* 2019). Whereas if the invasive species outcompeted native prey and replaced them in predator diet, the eradication of invasive prey may reduce food below a threshold for predator viability, depending on how quickly native prey recover (Brodier *et al.* 2011; Buckley & Han 2014; Kopf *et al.* 2017).

Predicting how an ecosystem will respond to an eradication is confounded by lack of baseline data on direct and indirect ecological interactions involving invasive species (Raymond *et al.* 2011; Bode

et al. 2015; Baker *et al.* 2020; Han *et al.* 2020). This is not uncommon because the data required to inform such predictions are difficult to collect, complex and overwhelmingly large (Montoya *et al.* 2009). Qualitative models are frequently used to predict changes in ecosystem structure and the levels of uncertainty in how native species will respond to an eradication (Raymond *et al.* 2011; Han *et al.* 2020). These models typically address ecological changes (Raymond *et al.* 2011; Han *et al.* 2020). One limitation is the need to incorporate operational impacts such as secondary poisoning, which is rarely if ever performed in these models. However, studies show that secondary poisoning can have a greater impact on native species following an eradication than changes in ecological interactions (Buckelew *et al.* 2011; Ward *et al.* 2019).

Eradicating invasive prey on Macquarie Island

Rabbits, black rats and house mice were eradicated from Macquarie Island using a combination of baiting, virus release and hunting (Springer 2016). Of the risks posed to native wildlife, skuas were identified as a species susceptible to both prey loss and secondary poisoning (Parks and Wildlife Service 2009). Qualitative ecological modelling, (undertaken due to the paucity of empirical data) showed uncertainty when predicting how skuas would respond to prey loss following the eradication (Raymond *et al.* 2011). However, secondary poisoning was expected to reduce skua numbers due to the large number of poisoned rabbit carcasses accessible to skuas during baiting (Parks and Wildlife Service 2009). The deaths of skuas was considered a high risk (Parks and Wildlife Service 2009). However, this risk was acceptable to managers as the skua population was assumed to be inflated by the large number of rabbits on the island (Parks and Wildlife Service 2009). Baiting deaths were only predicted to affect those skuas that specialised on hunting rabbits (Parks and Wildlife Service 2009). Therefore, any death was predicted to lower skua numbers to a level in equilibrium with native prey, a "deflation" of the skua population, and benefit the recovery of burrowing petrel species by lowering predation pressure (Parks and Wildlife Service 2009). However, to understand whether skua food sources on Macquarie Island were "inflated" by rabbits and whether skuas threaten petrel recovery, deeper consideration needs to be given to the species interactions between native and non-native prey, because these ultimately affect the prey base of skuas.

Firstly, burrowing petrels were once an abundant native prey of skuas, however, their numbers plummeted following the introduction of invasive rabbits to Macquarie Island and this was a strong impetus for rabbit eradication (Jones 1980; Brothers 1984; Department of the Environment and Heritage 2005a; Department of the Environment and Heritage 2005b). On other sub-Antarctic islands, burrowing petrels can support the same sized skua breeding populations alone, as when rabbits are present, and with higher breeding success (Brodier *et al.* 2011). This implies the invasion of rabbits replaced petrels as prey, and likely maintained skua numbers rather than inflated them.
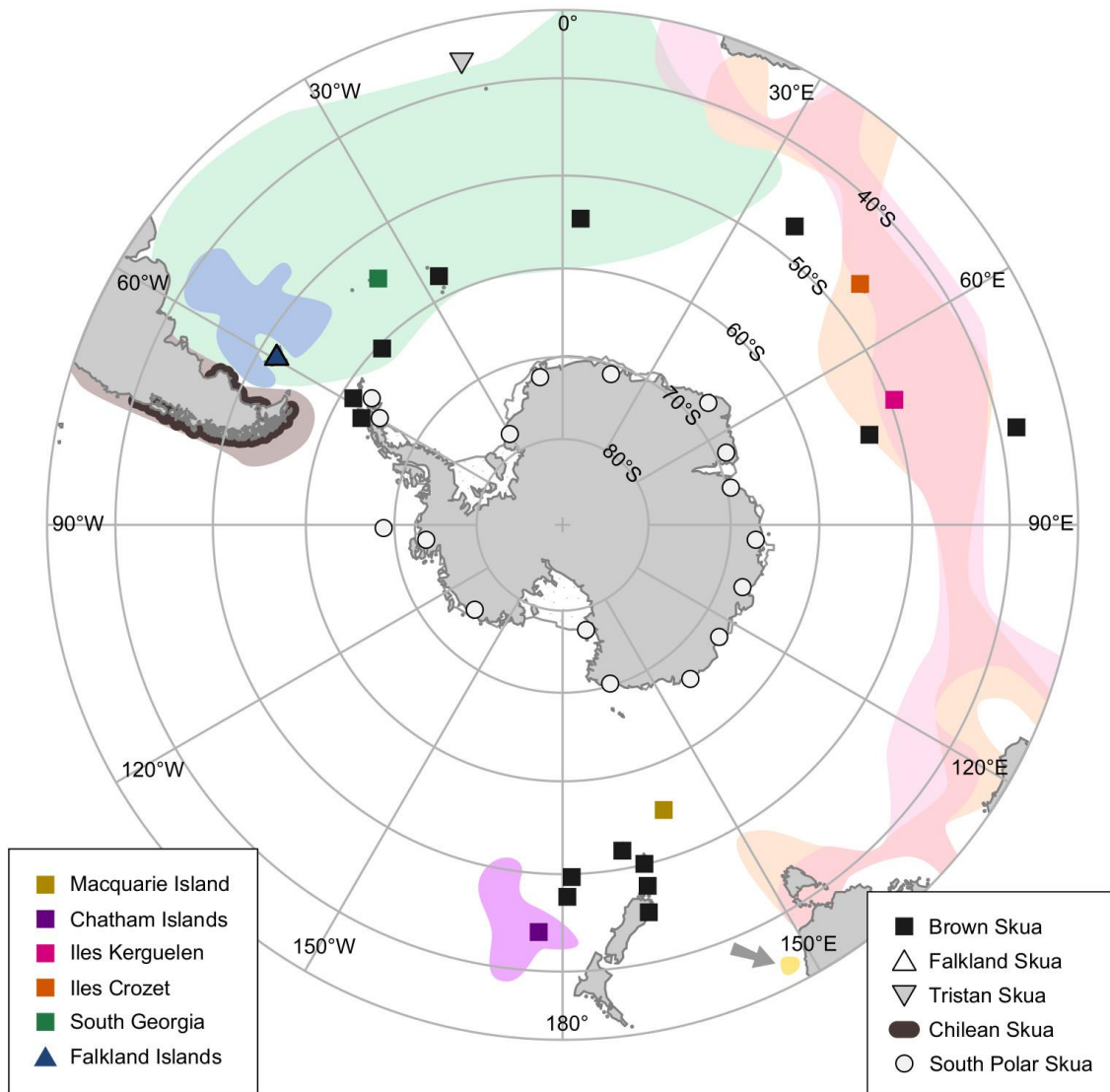
Figure 1.1. Distribution of breeding locations for Southern Skua (*Stercorarius antarcticus*), Chilean Skua (*Stercorarius chilensis*) and South Polar Skua (*Stercorarius maccormicki*) (symbols); and known winter range (shaded areas) of some Brown Skua (*S. a. lonnbergi*), Falkland Skua (*S. a. antarcticus*) and Chilean Skua populations. Breeding locations of Brown, Tristan (*S. a. hamiltoni*), Falkland and South Polar Skuas redrawn from (Carneiro *et al.* 2016b). Winter ranges are redrawn from Phillips *et al.* (2007); Carneiro *et al.* (2016a); Delord *et al.* (2017); Schultz *et al.* (2018); and Furness *et al.* (2020). The only known winter location of Brown Skuas from Macquarie Island (the field site for this study) is highlighted by the arrow and based on a banding record recorded in Carlyon and Cleeland (2014).

Table 1.1. Co-occurrence of Southern Skuas (*Stercorarius antarcticus*) and invasive rabbit and rodent populations. Highlighting contributions of invasive prey to skua diet and if the invasive population has been eradicated.

Archipelago	Island	Invasive Species	Prey	Eradicated	References
Brown Skua *Stercorarius antarcticus lonnbergi*					
Amsterdam and St Paul	Amsterdam	*Mus musculus*			
		Rattus norvegicus			
Antipodes Islands	Antipodes	*Mus musculus*	n [1]	2016	Moors 1980
Auckland Islands	Enderby	*Mus musculus*		1993	Torr 2002; Miskelly *et al.* 2020
		Oryctolagus cuniculus	y [2,3]	1993	
	Rose	*Oryctolagus cuniculus*	y [2,3]	1993	Torr 2002; Miskelly *et al.* 2020
Campbell Island	Campbell	*Rattus norvegicus*		2001	
Chatham Islands	Pitt (Rangiauria)	*Mus musculus*	n [4]		Schultz 2019
Iles Crozet	Possession	*Rattus rattus*	y [5]		Stahl & Mougin 1986
Iles Kerguelen	Cimetiere	*Oryctolagus cuniculus*	y [6]		Moncorps *et al.* 1998
	Cochons	*Oryctolagus cuniculus*	y [6,7]	2002	Moncorps *et al.* 1998; Chapuis *et al.* 2001
	Mayes	*Mus musculus*	y [8]		Mougeot *et al.* 1998
	Verte	*Oryctolagus cuniculus*	y [6]	1994	Moncorps *et al.* 1998
Macquarie Island	Macquarie	*Mus musculus*	n [9]	2011	Jones & Skira 1979
		Oryctolagus cuniculus	y [9]	2011	
		Rattus rattus	n [9]	2011	
Prince Edward Islands	Marion	*Mus musculus*	~ [10]		Schramm 1983
South Georgia	South Georgia	*Mus musculus*	n [11]	2015	Black *et al.* 2012
		Rattus norvegicus	y [11]	2015	
Tristan Skua *S. a. hamiltoni*					
Tristan de Cunha	Gough	*Mus musculus*	y [12]	*planned*	Reinhardt *et al.* 2000
	Tristan de Cunha	*Mus musculus*	y [12]	*planned*	Reinhardt *et al.* 2000
		Rattus rattus	y [13]	*planned*	Brown 2007
Falkland Skua *S. a. antarcticus*					
Falkland Islands	New	*Mus musculus*	n [14]	*planned*	Brown 2013
		Oryctolagus cuniculus	~ [14]	*planned*	
		Rattus rattus	n [14]	*planned*	

Secondly, Brown Skuas are facultative predators of petrels (Ryan *et al.* 2009). Numerous large penguin colonies on the island provide skuas with alternative foraging opportunities that could lessen predation pressure on burrowing petrels (Salton *et al.* 2019). Additionally, skuas selectively hunt abundant petrels over rarer species on some islands (Pacoureau *et al.* 2019), which could further lessen predation pressure on recovering populations. The potential for skuas to prey switch to more abundant prey suggests skuas may not impact the recovery of petrels.

Baiting for rabbits began over winter 2010, partly to avoid exposing the island's native wildlife to secondary poisoning, however was halted due to poor weather after baiting only 10% of the island (Springer & Carmichael 2012). A small number of skuas that since 1999 had begun over-wintering on the island were expected to be exposed to secondary poisoning (Schulz & Gales 2004; Parks and Wildlife Service 2009). This change in skua behaviour began when cats were nearing eradication and rabbit numbers were increasing on the island, and over winter these skuas relied on rabbits as a food source (Schulz & Gales 2004). They were thought to reflect the inflated skua population and so loss of these skuas was not considered to have a significant impact at a population level (Parks and Wildlife Service 2009).

The mortality of a large number of seabirds, including Brown Skuas, from primary, secondary and tertiary poisoning following the 2010 partial baiting prompted a review of the project (Springer & Carmichael 2012; Alderman *et al.* 2019). In response, and to mitigate against further high rates of secondary poisoning, Rabbit Haemorrhagic Disease Virus (RHDV) was released on the island killing an estimated 85% of the rabbit population (Terauds *et al.* 2014). The release of RHDV proved highly successful in reducing secondary poisoning during whole-island baiting, which was completed in winter 2011 (Springer & Carmichael 2012; Cooke *et al.* 2017; Alderman *et al.* 2019).

The assumption that secondary poisoning is restricted to those predators that hunt invasive prey is not uncommon in eradication planning (Daniel *et al.* 2007). However, scavenging poisoned carcasses is fundamentally different to hunting live prey and previous eradications have shown that large numbers of poisoned carcasses lingering in the landscape can create food sinks that alter predator behaviour, attract a large numbers of predators and result in a greater than expected number of secondary poisoning deaths (Salmon *et al.* 2010).

At least 512 skuas died during baiting for rabbits and rodents on Macquarie Island across 129 km^2, however, the population level impact of these deaths was unknown (Springer & Carmichael 2012). Nor was it known how these deaths, combined with the effect of eradicating an abundant invasive prey species of skuas, would affect the broader island ecology and species interactions. My thesis examines and provides insights into these questions.

Despite top-order predators being in decline worldwide (Estes *et al.* 2011), the effect of eradicating invasive prey on predators, has been overlooked in past eradication projects to the detriment of top-order predator populations, and the real and perceived success of eradication projects (Salmon *et al.* 2010). Invasive rabbits on Macquarie Island were an abundant herbivore with an array of complex interactions with native species (Raymond *et al.* 2011). Their rapid eradication could have significant impacts on skua breeding numbers and success through changes to skua diet and foraging. Additionally, the loss of an abundant prey resource could potentially increase predation pressure on sensitive native prey species during their critical recovery period after the eradication of rabbits and rodents.

Addressing how ecological (prey loss) and operational (secondary poisoning) aspects of eradication projects affect top-order predators, their breeding, diet, and foraging, and how eradications alter predation pressure on native prey species is complex and requires a multi-disciplinary approach. For this study I utilised 10 years of data on Brown Skua nest and chick numbers, and collection of skua feather samples. I studied the contemporary diet of skuas through field surveys and laboratory analysis of prey remains. In addition, I deployed GPS trackers on breeding birds. I incorporated data from field reports dating back to the 1970s, and walked island-wide transects to assess changes in predation rates and prey density. I combined empirical data, applied and theoretical ecology. During my PhD I evaluated and undertook novel modern modelling approaches. In quantifying changes to skua ecology during a period of ecological flux following the eradication, I demonstrate the magnitude of monitoring and contemplation required to confirm such large-scale conservation measures are successful and a net gain for the ecosystem. Predator communities scale with habitat size (Crooks 2002; McIntosh *et al.* 2018), and as eradications expand in their scope, complexity and scale, the outcomes I describe herein are likely to be relevant to an increasing number of eradications and predator communities.

Thesis aims

The central aim of this thesis is to quantify changes to the diet, foraging ecology, breeding, and ecological role of skuas on Macquarie Island following the eradication of invasive prey. I use Brown Skuas as a model top-order predator and quantify the impact the eradication of rabbits had on their breeding population to inform predator conservation and improve future eradiation projects. In addressing these issues my thesis is structured around four explicit aims:

i) assess the current level of reporting on the impacts for top-order predators of eradicating invasive prey;

ii)   quantify the effect prey-loss and secondary poisoning stemming from the eradication
        had on skua nest density, breeding success and diet;

iii)   examine the current diet and foraging strategies of Brown Skuas on Macquarie Island
        and how they influence individual breeding success and compare this to historical
        dietary studies; and

iv)   investigate the role of skua predation in limiting the recovery of burrowing petrel prey
        species.

Thesis structure

This thesis is structured around four research chapters written as manuscripts for publication.
Because of this format there is a small amount of text repetition across chapters particularly within
introductions and the study site description. The four research chapters are composed in the plural
pronoun (e.g. "we", "ours") to acknowledge all author contributions suitable for publication. In
contrast, this introduction and the general discussion are in the singular pronoun (e.g. "I", "my").
Published chapters are identified on their respective cover page.

In Chapter 2 I conducted a systematic literature review to determine how top-order predators
respond to eradication of rabbits and rodents on islands. I review the level of reporting on the
response of top-order predators to the eradication of invasive prey. I complemented this review
with case studies to highlight the importance of considering the effects of prey-loss and secondary
poisoning on native predators when eradicating invasive prey. To conclude this chapter, I developed
a decision framework to identify where negative effects on native predators resulting from prey loss
and secondary poisoning can occur and suggest mitigation strategies.

In Chapter 3 I quantified the diet and breeding changes of Brown Skuas following the eradication of
rabbits from Macquarie Island using a 10 year timeseries of breeding surveys and stable isotope
data. I modelled changes in nest density, breeding success and the dietary niche of Brown Skuas
caused by the eradication. To investigate the individual contribution of prey-loss and secondary
poisoning to the overall decline in nest numbers I compared the observed change in nest numbers
caused by the eradication to historical fluctuations in nest numbers, which occurred in response to
changes in rabbit abundance (prey loss) and not secondary poisoning. I used these historical data to
model a hypothetical prey-loss only scenario and found that the effects of prey-loss and secondary
poisoning acted contemporaneously on the breeding population. Skuas are central place foragers
during their breeding season as they are spatially constrained by their nest location. Therefore, the
eradication of rabbits was expected to have a spatially explicit effect on the diets of breeding skuas.
Those skuas nesting near penguin colonies, were expected to have their food supply less altered by

rabbit eradication compared to those nesting in distant areas of the island. We compared the diets of skua chicks grouped based on the distance of their nest to the nearest penguin colony (</> 1km) and used Carbon and Nitrogen stable isotope ratios of feather samples taken from chicks to define their isotopic niches. The monitoring outlined in this chapter highlights the multiple ways eradicating invasive prey can affect native top-order predators, and the importance of this underappreciated relationship.

In Chapter 4 I deployed GPS units on breeding skuas together with surveys of prey remains at the nest to investigate how diet and foraging decisions impacted individual breeding success. The nest location relative to a skua's foraging landscape can influence breeding success and is determined by the costs and benefits of nesting close to food sources including competition for territories and the intrinsic quality of breeding birds (Trivelpiece *et al.* 1980; Anderson *et al.* 2009). I defined individual foraging strategies using ordination of a range of foraging parameters that were selected based on their ecological relevance to skua breeding success taken from a review of previous studies. For this study, diet was assessed using surveys and sorting of prey remains (and pellets) found at the nest – a method commonly used in skua diet studies (Moncorps *et al.* 1998). Finally, differences between the diets and foraging strategies of failed and successful breeders were compared using redundancy analysis and multivariate linear modelling. In this chapter, I show how diet and foraging data can be used to understand many aspects of skua predator-prey ecology including individual fitness, risk of disease transmission, changes in relative abundance of prey, and the legacy effects of eradications for top-order predators.

In my final research chapter, Chapter 5, I investigate the top-down effect skua predation has on the recovery of petrel populations on Macquarie Island. To address this, I modelled the density dependent predation rate of Brown Skuas on Antarctic Prions (*Pachyptila desolata*), a burrowing petrel, and compared this to Holling's functional response curves. By surveying patches of feathers, or 'sign' left where skuas had attacked and killed petrels (termed PPUFs: prion predation undigested feathers) and prion burrow density I modelled the combined numerical and functional response of skuas to changes in prey density. I used the island-wide accumulation of PPUFs over the season as a conservative estimate of the number of petrels killed by skuas *per* season and estimate the maximum daily predation rate. Finally, I used published growth rates of petrels, and the predator functional response curve of skuas to investigate what proportion of petrel species were likely to be exposed to excessive predation under the current skua predation regime.

Understanding the trajectory of predator-prey relationships through periods of drastic change is vital for informing conservation priorities. This thesis presents new and novel work that contributes to

our understanding of how eradications of invasive prey impact top-order predators, and how the diet of top-order predators influences native prey populations, and the breeding fitness of predators. In doing so it informs our broader understanding of the importance of top-order predators in maintaining ecosystem stability on islands, the trophic dynamics of island ecosystems during periods of change and the bottom-up effects of eradications on top-order predators. The majority of modern research into the ecology of Brown Skuas comes from field sites in the South Atlantic and Indian Ocean sectors of the Southern Ocean (e.g. Hahn & Peter 2003; Ryan *et al.* 2009; Carneiro *et al.* 2014). This work builds on our understanding of the ecological role of skuas, their foraging ecology and what drives their breeding success as well as adds to the geographic coverage of modern skua research.

Chapter 2

Counting the collateral: inclusion of native predators in eradication planning is vital for success

The birds of prey and other vertebrate predators are, in a sense, key species in their particular ecosystems. Because they stand at the top of the pyramid of numbers and represent the terminal focus of energy in a wildlife community they are likely to be sensitive to any important changes that may occur in the whole system.

Ratcliffe (1980)

Abstract

Islands ecosystems have low predator diversity. Avian predators occur in many island ecosystems from the tropics to the poles and play an important role in maintaining ecosystem diversity and function. Globally, the introduction of invasive mammals has altered many island ecosystems with devastating consequences for native biodiversity. Invasive rodents and rabbits have caused declines in the abundance of native prey on islands, while at the same time, replacing native prey in predator diet. Eradications of rodents and/or rabbits is often undertaken to facilitate the recovery of threatened native species and ecosystems. As such, it is critical to determine how eradication of invasive prey can impact native predators to avoid unexpected and deleterious ecosystem outcomes.

In this chapter we show the global extent of invasive rodent and rabbit eradications from islands and quantify the level of reporting on top-order native predators during and after eradication projects. We also determine the types of impact studied (either ecological or operational). Using case studies, we illustrate the main ecological and operational mechanisms associated with rodent and rabbit eradications that influence predator populations in the long- and/or short-term. Finally, we highlight the importance of undertaking predator monitoring and conservation during and after the eradication of invasive prey.

Challenges for island eradications

Towards the turn of the 21st Century, the goal for eradicating invasive species shifted from simply invasive species elimination, to viewing invasive species eradication as a step in the path of ecosystem recovery (Myers *et al.* 2000; Zavaleta *et al.* 2001). In this latter scenario, the goal was more typically defined as the recovery of threatened native populations and/or a return to a native-led ecosystem state (Lampert *et al.* 2014; Buxton *et al.* 2016). As knowledge, capabilities and technologies develop, eradication projects move to increasingly larger and more complex ecosystems. As a result, practitioners and ecologists are faced with the dilemma of unintentional negative ecosystem responses to eradication (Zavaleta *et al.* 2001). Unintentional ecological responses such as mesopredator release, where eradication of an invasive apex predator facilitates an increase in the abundance of invasive mesopredators, can result in a greater impact on threatened native species (Courchamp *et al.* 1999). Similar outcomes have also been observed at lower trophic levels (Bergstrom *et al.* 2009). Understanding interactions between target invasive species and the island ecosystem has led to strategic approaches to eradication implementation (Bode *et al.* 2015; Baker *et al.* 2020) and adaptive management of eradication projects informed by monitoring (Springer 2016). Broadly speaking, deleterious outcomes for ecosystems following

eradication occur in two forms (Zavaleta *et al.* 2001). Eradication can benefit other non-native species, such as mesopredator release, with indirect negative effects for native species (Kessler 2002). Or eradication can have a direct cost for native species (Salmon *et al.* 2010; Ward *et al.* 2019). The latter can occur due to invasive species having an ecological role that supports a native species (Lambertucci *et al.* 2009) or from operational impacts such as secondary poisoning that directly harm native species (Eason *et al.* 2002; Ward *et al.* 2019).

Island invasions typically result in the introduction of novel ecological roles that exploit naivety in native species, with often devastating consequences (Blackburn *et al.* 2004). This is common on small oceanic islands where, due to their isolation and discrete size, many ecological niches remain unfilled (Courchamp *et al.* 2003; Mathakutha *et al.* 2019), but can also occur in continental ecosystems (Doherty *et al.* 2016). However, in contrast to small islands, invasive species on larger islands and continental ecosystems are more likely to out-compete native species for an already existing niche due to greater ecosystem complexity (Rodriguez 2006; Lambertucci *et al.* 2009; Barbar *et al.* 2016). For species that depend on a niche occupied by an invasive species, eradicating that invasive species can have a direct negative impact unless there is a reciprocal recovery of the original native occupant (see Box 2.1; Buckley & Han 2014). The speed at which native species recover depends primarily on the proximity of source populations and its intrinsic reproductive rate (Buxton *et al.* 2016; Brooke *et al.* 2018) and for extirpated native species, connectivity to nearby source populations is vital (Buxton *et al.* 2014) without human-assisted reintroduction (Buxton *et al.* 2016).

Historically, island eradications first focused on small islands (Towns & Broome 2003). On small islands invasive species are less likely to provide any facilitative roles due to their distinctive ecological novelty (Ricciardi & Atkinson 2004). Therefore, as eradication targets expand to tackle multiple invasive species on larger islands, the likelihood of eradicating invasive species that fill facilitative ecological roles increases (Lampert *et al.* 2014). Acknowledgement of the facilitative roles invasive species play can be controversial as it lends itself to a sense of valuing invasive species and arguments for their own conservation (Russell & Blackburn 2017; Davis 2020). There is no denying the global biodiversity loss due to invasive
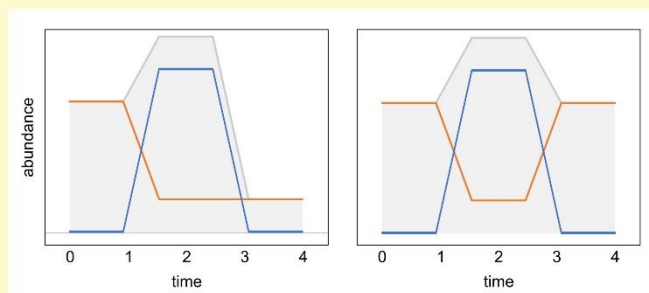
Box 2.1. Prey abundance along a time-line of non-native prey species introduction and eradication (blue line).

Non-native prey are introduced at time period 1 and have a negative effect on the abundance of native prey (orange line). Non-native prey may have a higher abundance than native prey as shown in this example and inflate the overall prey base of the native predator (grey area) when both species are present. After the eradication of non-native prey, native prey may fail to recover (left), recover rapidly (right) or recover to some degree between these two extremes.

Without a rapid recovery of native prey, native predators may be impacted by prey loss. Native predators may suppress the recovery of native prey if native predators compensate for a reduced prey base by increasing predation pressure on native prey.

species (Blackburn *et al.* 2004; Towns *et al.* 2006; Doherty *et al.* 2016), as such their eradication provides significant gains in safeguarding against further extinctions (Towns & Broome 2003; Jones *et al.* 2016). However, failure to appreciate the connectivity of all ecosystem components can be detrimental to project success, and influences public perception of invasive species management and stakeholder buy-in for future eradication campaigns (Salmon *et al.* 2010; Glen *et al.* 2013).

The dependence of native predators on invasive prey

High trophic positions are occupied in larger ecosystems (McIntosh *et al.* 2018), however top-order predators can occur on some of the smallest and most isolated oceanic islands (Ritz *et al.* 2008). The ability of avian predators to rely on migratory life histories that exploit and link disparate ecosystems means their distributions and ecological impact can be ephemeral and difficult to define (Sekercioglu 2006; Bauer & Hoye 2014). As a result, avian predators are often forgotten in ecosystem studies (Sekercioglu 2006).

Invasive species can become important food sources for top-order predators by out-competing and replacing native prey (Corbett & Newsome 1987; Lambertucci *et al.* 2009; Barbar *et al.* 2016). Rodents and lagomorphs have a close association with humans and the ability to disperse and quickly colonise a range of habitats (Capellini *et al.* 2015). Invasive rabbits have replaced a suite of

Figure 2.1. Global area eradicated of invasive rodents and rabbit populations.

Hashed areas represent the largest contribution by a single island to the total area eradicated for each species. These are: Macquarie Island (128km^2) for Black Rat, European Rabbit and House Mouse; Campbell Island (116km^2) for Norway Rat; and Little Barrier Island (32km^2) for Kiore (Polynesian Rat).
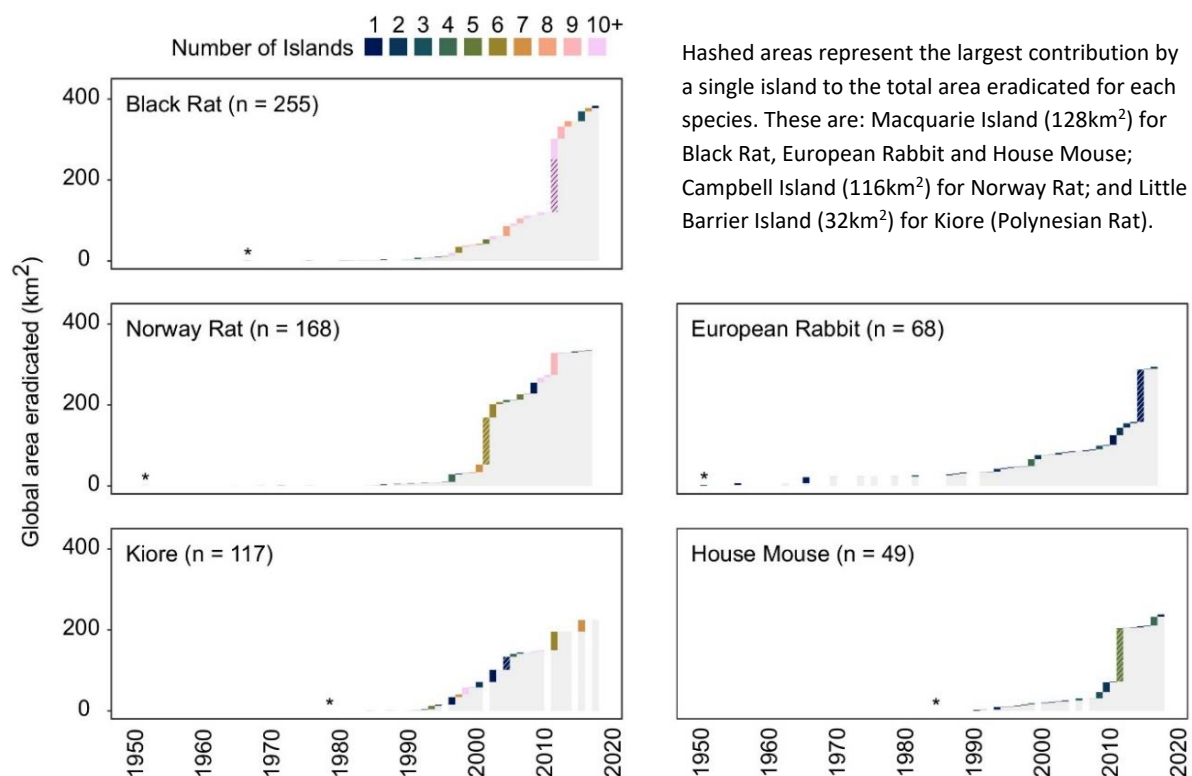
Data taken from DIISE (2015) accessed 23 November 2020

native prey in the diets of predators across a range of ecosystems (Corbett & Newsome 1987; Capellini *et al.* 2015; Barbar *et al.* 2016). Reliance on a single prey species erodes redundancy in the dietary composition of predators, as a stable food web with multiple trophic links is replaced with a single trophic link and high dependence on invasive prey (Barbar *et al.* 2016). Eradicating invasive prey therefore can have a destabilising effect on predator populations by eroding their prey base or on remaining native prey species by forcing a shift in predation pressure (Skira 1984; Bode *et al.* 2015). Here we quantify i) how direct and indirect effects on native predators of eradicating invasive prey are addressed in the literature; ii) how effects on other groups of native and invasive plants and animals are reported in the literature; and iii) assess whether ecological or operational impacts are underreported.

Methods

We conducted a literature review to collate studies that addressed either ecological or operational effects of eradications on any facet of the ecosystem either animals, plants, native or non-native. We searched across Scopus and ISI Web of Science using the search terms [rabbit OR rabbits OR "Oryctolagus cuniculus" OR rat OR rats OR rattus OR mouse OR mice OR mus] AND [eradicat* OR remov* OR control] AND [island OR islands OR isle OR isles OR archipelago] across all years up to the end of May 2018. This search returned 600 papers relevant to eradication literature of which 149 papers reported 173 effects of a successful eradication (with some papers reporting multiple effects). We summarised: i) the number of effects (positive, negative or no change) reported in the literature on native predators, native animals (other), native plants, invasive animals, or invasive plants, ii) whether the effects were a result of ecological outcomes of the eradication (changes to ecosystem structure, either direct or indirect effects) or operational outcomes (effects caused by eradication procedures e.g. secondary poisoning from baiting) and iii) whether responses were observed and/or quantified empirically, or were predicted (predicted including those either implied based on limited observations or derived from mathematical models).

Native predators only included species which included rodents or rabbits in their diet. For example, Bald Eagles (*Haliaeetus leucocephalus*) were considered a *Native predator*, while Common Ravens (*Corvus corax*) and Peregrine Falcons (*Falco peregrinus*) were considered *Native animal (other)* as the former is predominately a scavenger and the latter is predominantly a predator of other birds and not rodents or rabbits (Howald *et al.* 1999). For a full list of all identified studies involving native predators of invasive rabbit and rodent populations see Appendix S2.1.

To describe the global extent of eradication for rodents and rabbits, the Database of Island Invasive Species Eradications (DIISE) was accessed on 23 November 2020. Records of successful whole island

eradications of either Rodents or European rabbits with good or satisfactory data quality and an eradication end date of 1950 or later were included in Figure 2.1 (DIISE 2015).

Results and Discussion

Eradications of invasive prey

Since 1950, there have been over 657 successful eradication campaigns targeting rodents and lagomorphs on over 573 islands (Fig. 2.1; DIISE 2015). Programs to eradicate these species are becoming progressively more ambitious in terms of area covered (Fig. 2.1). The eradication of rabbits from Macquarie Island (128 km²) in 2011 doubled the island area eradicated of rabbits worldwide and remains the largest whole island eradication of rabbits to date (Fig. 2.1). The eradication of Norway rats (*Rattus norvegicus*) from South Georgia was one of the most complex ever undertaken using three phases of baiting over multiple seasons to eradicate several independent sub-populations across large sections of the 3,903 km² island (totalling 1,068 km²) (Martin & Richardson 2019). A number of these 657 eradications have had a range of negative impacts for top-order predators including secondary poisoning and breeding declines driven by reduced food availability (Box 2.2).

Previous studies highlighted that uncertainty in how ecosystems respond to eradications receives little research attention (Zavaleta *et al.* 2001; Buckley & Han 2014; Kopf *et al.* 2017). Qualitative models have been used to better understand species interactions and expected changes caused by eradication projects in complex ecosystems (Bode *et al.* 2015; Baker *et al.* 2020). However these do not always consider operational impacts such as secondary poisoning (Raymond *et al.* 2011; Han *et al.* 2020) potentially due to lack of data available to inform these models (Ward *et al.* 2019). The facilitative roles of invasive vegetation have previously been investigated and used inform eradication schedules (Lampert *et al.* 2014), however bottom-up effects for native predators have been overlooked in past eradications of invasive prey (Salmon *et al.* 2010).

Top-order predators are missing from the eradication literature

Top-order predators maintain ecosystem and food web stability (Estes *et al.* 2011). Human-induced threats that disrupt food chains predators depend upon, including the depletion of prey populations, cause collapses in top-order predators across a range of marine and terrestrial ecosystems (Ripple *et al.* 2014). Such declines can initiate large-scale trophic cascades affecting other native species and ecosystem processes (Estes *et al.* 2011). Given the importance of top-order predators in ecological processes, their response to eradications should be a key component of monitoring programs.
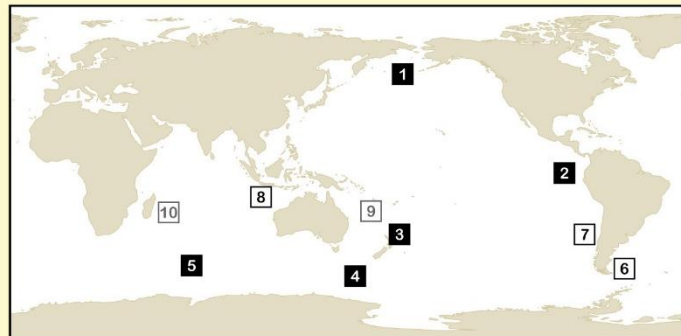
Box 2.2. Eradication of invasive rabbits and rodents, their effect on native predators.

Studies quantifying the effects of eradications on native predators are rare. These examples highlight some of the deficincies in reporting ecological impacts of eradications for predators even from projects where widespread secondary poisoning occured. Native predators can respond negatively to prey loss however this is not always the case and depends on the recovery rate of native prey following an eradication.

Future eradications are planned for a number of islands containing predators. While these predators may not be of conservation concern they often play key functional roles with little redundancy. The isolated nature of islands reduces the likelihood of predators recolonising islands once extirpated. Therefore, the effects of eradication projects on predators should be adequately quantified.

On other islands where control programs targeting invasive rodents are underway these rodents also feature in the diet of conservation significant predators.

See appendix S2.2 for reference material

Prey availability	Secondary poisoning
Increase	None/low death rate
Stable	Moderate death rate
Decline	High death rate

Both	Percentage of diet
Mitigation used	Rabbit
Suggested	Rat
Unreported	Mouse

1. Bald Eagle *Haliaeetus leucocephalus* **(Hawadax Island, Alaska)**

46 bald eagles died of secondary poisoning, a number 4-6 times greater than the island's breeding population[2-4]. The large abundance of rat carcasses during the eradication attracted eagles from nearby islands, which was not anticipated during planning[3,4]. Breeding eagle numbers recovered to 63% of pre-eradication levels 5 years after baiting[2]. Despite rats being the second most frequent prey by species in eagle diet, their eradication was not predicted to adversely impact the diet or foraging strategies of eagles[1,3]. However this was not studied.

2. Galapagos Hawk *Buteo galapagoensis* **(Rábida, Galapagos Islands)**

Secondary poisoning was anticipated and avoided by capturing the hawk population prior to baiting[6]. Hawks were housed for the duration of the eradication and released back in to the wild upon completion[6]. Galapagos Hawks can rely heavily on rats as prey[5] however changes to diet were not studied.

3. Morepork *Ninox novaeseelandiae* **(Mokoia Island, New Zealand)**

An estimated 21-50% of Moreporks died in the months following baiting for mice[8]. A change in diet following eradication was not quantified however, was suggested to have impacted breeding success[8].

4. Brown Skua *Stercorarius antarcticus* **(Macquarie Island, Australia)**

During an initial trial baiting of 10% of the island over 230 skuas died due to secondary poisoning[10,11]. In response to the higher than expected number of deaths, Rabbit Haemorrhagic Disease Virus was released prior to whole island baiting, which killed an estimated 85% of rabbits without exposing skuas and others to a risk of poisoning[11]. Nonetheless, over 500 skuas died during the eradication, despite all baiting be conducted over winter when skuas were largely absent from the island[11]. Seven years after the eradication prey loss still had an impact on skua foraging behaviour, competition and breeding success[12].

5. Brown Skua *Stercorarius antarcticus* **(Ile Verte, Kerguelen Archipelago)**

Baiting was conducted during winter when skuas were absent from the island[14]. Because of this - and the short half-life of the toxin used - no skuas were reported to have died from poisoning during the eradication[14]. After the eradication, native prey rapidly recovered with Blue Petrels (Halobaena caerulea) increasing eightfold in six years[15]. The rapid recovery of native prey was likely facilitated by immigration from source populations on nearby islands. As a result skua breeding success improved[15.]

* up to >50%. Varied with local rabbit density
† data from nearby island

Planned future eradications

6. New Island, Falkland Islands[16]
Striated Caracara *Phalcoboenus australis*
2-9%[17]
Crested Caracara *Caracara plancus*
18%[17]
Red-backed Hawk *Geranoaetus polyosoma*
41%[17]
7%[17]
17%[17]

7. Juan Fernandez Islands[18]
Short-eared Owl *Asio flammeus*
Present in diet[18]
Red-backed Hawk *Geranoaetus polyosoma*
Present in diet[18,19]

8. Christmas Island[20]
Christmas Island Hawk-owl *Ninox natalis*
8-12%[21]
Christmas Island Goshawk *Accipiter fasciatus natalis*
Present in diet[22]

Islands with threatened predators

9. New Caledonia
White-bellied Goshawk *Accipiter haplochrous*
Present in diet[23,24]

10. Reunion Island
Reunion Harrier *Circus maillardi*
50-70%[25]

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In the search of the literature, native predators were the only group for which negative responses to a rodent or rabbit eradication were greater than 50% (Fig. 2.2). Native predators were underrepresented in the literature compared to other groups that often benefitted from eradication projects (Fig. 2.2). No studies documented direct ecological effects such as prey deficits caused by invasive prey removal. Most studies that included a native predator investigated operational impacts. In all studies where negative effects (e.g. population or breeding declines) were reported, it was always due to secondary poisoning.

The omission of predators from ecological studies of eradications could be due to several factors (Fig. 2.2). If predator occurrence was low on the predominantly small islands where eradications have historically taken place (Fig. 2.1), then we would expect few studies on predators in the eradication literature. However, this only holds true for mammalian predators, which are limited in their mobility and are therefore absent from many small islands (Courchamp et al. 2003). We found in this review that across all studies, all native predators were birds (Fig. 2.2). Birds undertake long-distance flight, as such they connect isolated, distant ecosystems and utilise small island ecosystems within a networked distribution (Sekercioglu 2006; Bauer & Hoye 2014; Carneiro et al. 2014). For example, seabirds help plants colonise new islands by transporting their seeds between unconnected landmasses and islands (Magnússon & Magnússon 2000; Nathan 2006; Padilla et al. 2012). Seabirds also transport vast quantities of marine-derived nutrients into terrestrial ecosystems through deposition of guano, which can be an important source of nutrients for vegetation in otherwise nutrient poor landscapes (Selkirk et al. 1990; Jones 2010; Adame et al. 2015). As such birds are keystone species on many islands providing specific ecosystem services with little ecological redundancy (Daily et al. 1993; Sekercioglu 2006). Many birds, such as migratory species, rely on a network of distant ecosystems for their survival, exposing them to a greater range of threats (Saino et al. 2011; Senner et al. 2017). Ecological mismatches between predators and prey availability can occur over long time-scales due to climate change (Senner et al. 2017) or rapidly through the eradication of invasive prey species (Barbar et al. 2016). The absence of predators from the eradication literature may stem from an under-appreciation of the impact eradications have on the ecology of native predators.

Despite the direct threat secondary poisoning has on native species, there have been few studies associated with island eradications (Eason et al. 2002; Ward et al. 2019). In contrast to the expansion of eradication programs worldwide, secondary poisoning reporting is decreasing over time with no data present from up to 78% of baiting operations (Ward et al. 2019). Compared with the few studies on secondary poisoning, there are even fewer studies on the ecological impacts of eradications for native predators (Fig. 2.2).

Native predator-invasive prey relationships

Invasive rodent and lagomorph populations have devastating and far-reaching negative impacts, in part because they reach high population densities (Courchamp *et al.* 2000; Bergstrom *et al.* 2009; Terauds *et al.* 2014). Their abundance also means they are often regarded as inflating prey densities for native predator communities (Daniel *et al.* 2007; Parks and Wildlife Service 2009). In turn the eradication of lagomorphs and rodents is considered as returning inflated native predator populations to a level in equilibrium remaining native prey (Parks and Wildlife Service 2014; Nur *et al.* 2019). This assumption has several limitations. One, it does not account for invasive species often driving declines in native prey abundance following invasion (often the impetus for their eradication) and in doing so replacing native prey in the diet of predators rather than inflating food availability (Box 2.1). Two, it can justify the ameliorating effect of secondary poisoning on reducing an over-abundant native predator population (Parks and Wildlife Service 2009). Implicit in this assumption is
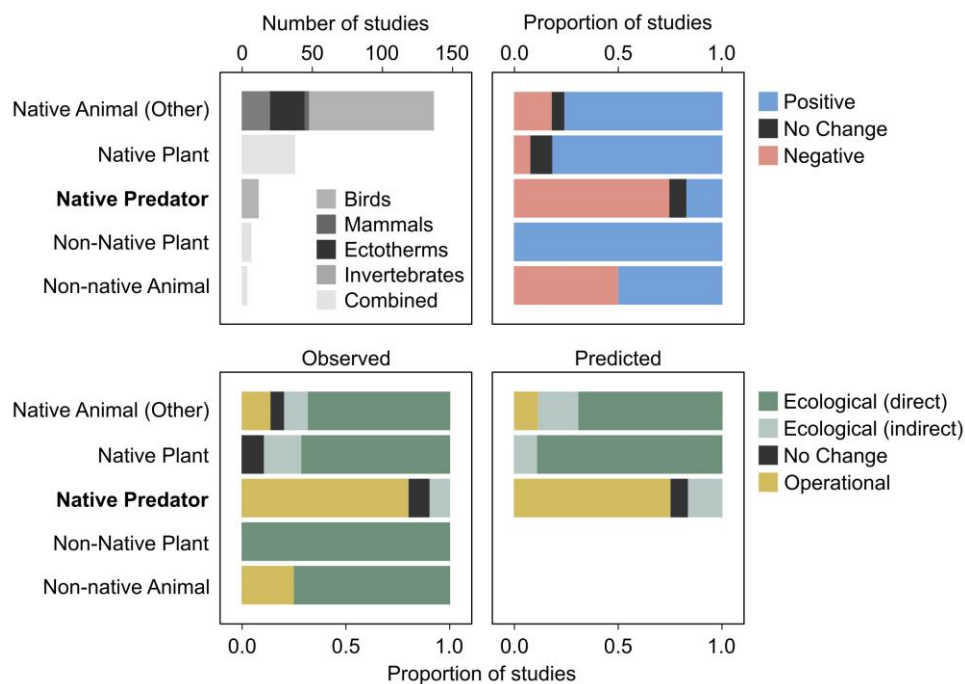
Figure 2.2. The number of studies investigating responses of five functional groups: native predators (of rabbits or rodents), native animals (other), native plants, non-native animals and non-native plants, to the eradication of invasive rodents or rabbits (top left), and the proportion of positive or negative effects (or no change) reported in studies (top right). The effects on functional groups were defined as responses to either ecological outcomes of the eradication (relating to changes in ecosystem structure, either direct or indirect), or operational outcomes (relating to aspects of the eradication procedure e.g. secondary poisoning from baiting). Lower plots are either observed responses (bottom left; observed changes and/or changes empirically quantified) or predicted responses (bottom right; predicted responses including those either suggested as a possibility based on anecdotal observations or derived from mathematical models).

that secondary poisoning is expected to only affect a surplus portion of the predator population, however this is not always the case and is difficult to quantify (Salmon *et al.* 2010; Springer & Carmichael 2012; Alderman *et al.* 2019). Secondary poisoning is commonly a result of scavenging poisoned carcasses rather than hunting live prey (Howald *et al.* 1999). Even when most rabbits and rodents die in areas inaccessible to predators, such as burrows, the remaining carcasses can still expose predators to an unacceptably high risk of poisoning (Howald *et al.* 1999). Furthermore, the surplus of carrion created in a short window of time through eradication programs can create food sinks that attract predators, which exposes the entire predator population to the risk of secondary poisoning (Salmon *et al.* 2010). The dietary flexibility exhibited by native predators should be incorporated into risk assessments when planning eradication projects. Dietary flexibility leads to increased scavenging of poisoned carrion resultant of baiting programs, or increased hunting of sick and dying invasive prey, both of which expose predators to secondary poisoning.

Early explorers were responsible for many island invasions, as a result for most islands the pre-invaded state of ecosystems is poorly understood (Falla 1937). Most ecological studies are implemented well after the arrival of invasive species (Brothers 1984; Copson & Whinam 2001). Nevertheless, the effect of invasive species on native prey abundance is regularly inferred from controlled experiments and field observations (Warham 1969; Simberloff 2009; Stokes *et al.* 2009). For predator conservation, degree of inflation caused by hyper-abundant invasive prey is not as important a consideration as how rapidly native prey can recover to a level that can sustain predators long-term (Box 2.1, Fig. 2.3; Buckley & Han 2014). Estimating a theoretical equilibrium with native prey is problematic and may not guarantee adequate food supply for the long-term sustainment of a predator population. Although some predators are resilient to fluctuations in food availability (Stenseth *et al.* 1997), prey loss can have severe consequences for predators if the effect is long-term (Wolf & Ripple 2016).

The removal of invasive prey not only affects the amount of prey available to predators but also the distribution of prey and foraging landscape for predators (Skira 1984; Lambertucci *et al.* 2009). A reduction in prey distribution can impact a predator's foraging dynamics, competition and breeding behaviour (Phillips *et al.* 2004; Carneiro *et al.* 2015) as well as increasing predation pressure on remaining prey (Bode *et al.* 2015; Nur *et al.* 2019). Increased predation can inhibit the recovery of native prey following an eradication and further impact long-term predator survival (Sinclair *et al.* 1998; Buxton *et al.* 2016; Nur *et al.* 2019).

Native prey can recover rapidly following the eradication of an invasive prey species and benefit native predators (Brodier *et al.* 2011). This depends either on the proximity of source populations for

immigration into the population, or high fecundity; both of which can rapidly replenish a prey deficit cause by an eradication (Buxton *et al.* 2014). These factors are more prevalent in complex ecosystems (e.g. continental ecosystems, larger islands or archipelagos) and can ameliorate negative eradication responses of top-order predators (Covas 2012; Buxton *et al.* 2014). Nevertheless, native prey may not recover if the target species was not acting as a suppressive force on native prey to begin with or if other invasive species also act to inhibit recovery or if it is extinct (Rayner *et al.* 2007; Doherty *et al.* 2016).

Integrating native predators into eradication planning

Eradication projects will continue to have implications for an array of predator communities as projects expand to new locations across diverse ecosystems, including those with mammalian predators (Cypher *et al.* 2014), and those not confined to islands (Russell & Broome 2016). Despite a growing body of knowledge and evidence around eradication outcomes, much uncertainty remains. There are currently few examples of how mammalian predators are impacted by eradication of invasive prey (Fig. 2.2). We can assume the effects will be stronger due to mammals reduced ability
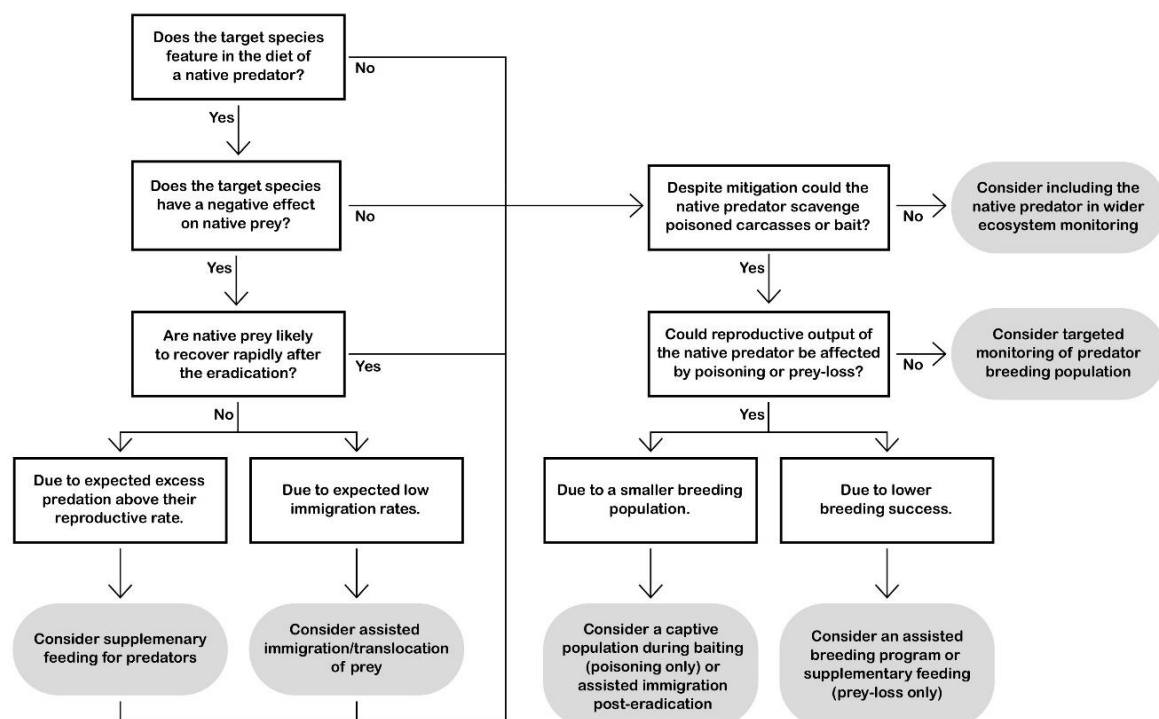
Figure 2.3. A decision framework to consider possible intervention measures to mitigate direct risks posed to native predator from eradicating invasive prey and indirect risks for native prey. The primary considerations in this decision framework are: will native prey recover fast enough to fill the void left by invasive prey in the diet of predators? (left side); and are native predators exposed to secondary poisoning as predators or scavengers? (right side).

to re-colonise from other islands. A precautionary approach for eradication programs could include predictions of potential negative effects during early planning stages and incorporating these into structured decision making (to inform a cost-benefit analysis) and to build adaptive management strategies, prior to an eradication (Fig. 2.3). Figure 2.3 is decision framework that highlights the level of evidence required to make informed decisions on the impact of eradications on predators. Uncertainty can influence the anticipated ecological outcomes of eradication and it is uncommon for managers to have the data required to comprehensively answer every question posed along the decision pathway (Fig. 2.3). Expert advice can fill some knowledge gaps and Figure 2.3 assists in identifying where more information may be needed. For future eradications it is critical to consider: i) Will predators be exposed to poisoned prey carcasses and ii) will the eradication of invasive prey facilitate a rapid recovery of native prey? For ii) recovery is not guaranteed if native prey are: a k-selected species; an isolated population; restricted by another invasive species still present in the ecosystem; or if the native predator increases its predation pressure after the eradication (Rayner *et al.* 2007; Buxton *et al.* 2014; Bode *et al.* 2015).

In light of uncertainties, the importance of assessing potential threats to predator populations from eradications becomes clear, particularly to inform whether mitigation or intervention actions will be needed (see Fig. 2.3). When negative outcomes are identified as a risk prior to an eradication a suite of techniques are available to promote a positive outcome for the entire ecosystem (see Fig. 2.3; Springer 2011; Wilkinson & Priddel 2011; Buxton *et al.* 2016). For example, housing predators during baiting programs can drastically reduce the exposure of predators to secondary poisoning (Wilkinson & Priddel 2011; Nicholls 2013). When risks to native predators are unavoidable, staggered assisted recoveries (where native prey are re-introduced prior to native predators) may be required post-eradication (Buxton *et al.* 2016). If actions are not taken to mitigate impacts on native predators, and an unguided recovery of the ecosystem occurs, the increased risks for native predators and prey may diminish the overall achievements of the eradication, require prolonged remediation, and increased financial costs in the long-term due to additional conservation triage, monitoring and reporting (Salmon *et al.* 2010).

Conclusion

Eradications have had conservation success globally, particularly on islands (Towns & Broome 2003; Jones *et al.* 2016). With every attempt to eradicate an invasive species new challenges arise, whether technical, logistical, social or ecological (Glen *et al.* 2013). As we move from tackling invasive species on uninhabited islands to inhabited ones, new contentions emerge with each new social, political and cultural landscape (Wilkinson & Priddel 2011). These challenges can impact the budget, feasibility, and real and perceived success of an eradication campaign (Gardener *et al.* 2010).

Failure to adequately address these challenges can lead to project setbacks and delays (Salmon *et al.* 2010; Pickrell 2019). Here we emphasize the importance of integrating native predators into the planning and monitoring of eradication projects, and outline ecological considerations for predator populations when eradicating invasive prey.

Predator populations are in decline globally (Ripple *et al.* 2014). This work highlights that avian predators have received little focus in studies associated with eradication projects. Avian predators on islands were negatively affected by eradication of invasive prey in 69% of reported cases. Most studies focussed on secondary poisoning and yet even this has been found to be underreported following eradications (Ward *et al.* 2019). This review highlights the paucity of data on the ecological effects of eradications on native predators and the need for further studies. A bias towards an underappreciation of native predators, likely stems from the fact that native predators can do (or appear to do) quite well in the presence of invasive species, while other lower trophic species are impacted (Lambertucci *et al.* 2009). As such there is need for a greater focus on native predators in the aftermath of an eradication, when they are at a greater risk of decline compared to most other species.

The response of native predators to eradication of invasive prey is driven by the degree to which secondary poisoning directly impacts predator numbers and the pace at which native prey can recover to fill the void left by invasive prey. This has a negative impact on the ecosystem and the success of an eradication in achieving its desired goal. In the long-term, with close monitoring and assistance of ecosystem recovery, native predators (like other native species) will benefit from the eradication of invasive species provided pre-invasion interactions with native species can be restored (Brodier *et al.* 2011). Mitigation measures including assisted recoveries and monitoring to inform when interventions are required will improve the outcomes of future eradications and guarantee the success in achieving a functioning restored ecosystem.

Appendix S2.1: Native predators of invasive rabbit and rodent populations

Predator species	Citation	Notes (relating to predator diet and invasive prey mentioned in the article)	Post-eradication study
American Kestrel (*Falco sparverius*)	Oppel, S. et al. (2015) Important bird areas: Montserrat. British Birds	Rodents known in diet	
Bald Eagle (*Haliaeetus leucocephalus*)	Howald, G.R. et al. (1999) Brodifacoum poisoning of avian scavengers during rat control on a seabird colony. Ecotoxicology	Rats known in diet	
	Taylor, R.H. et al. (2000) Eradication of Norway rats for recovery of seabird habitat on Langara Island, British Columbia. Restoration Ecology	Rats known in diet	Y
	Croll, D.A. et al. (2016) Passive recovery of an island bird community after rodent eradication. Biological Invasions	Rats known in diet	Y
	Myers, JH. (2003) Eradication: Is it ecologically, financially, environmentally, and realistically possible?. Managing For Healthy Ecosystems	Rats known in diet	
Barn owl (*Tyto alba*)	Parrish, R. et al. (2012) Birds of the Aleipata Islands, Samoa. Notornis	Rodents known in diet	
	Le Corre, M. et al. (1997) Ecological significance and conservation priorities of Europa Island (western Indian Ocean), with special reference to seabirds. Revue D'Ecologie (La Terre Et La Vie)	Rodents known in diet	
	Capizzi, D. et al. (2015) Fifteen years of rat eradication on Italian Islands. Problematic Wildlife: A Cross-Disciplinary Approach	Rodents known in diet	
	Ringler, D. et al. (2015) Trophic roles of black rats and seabird impacts on tropical islands: Mesopredator release or hyperpredation?. Biological Conservation	Rats mentioned in diet	
Brown Skua (*Stercorarius antarcticus lonnbergi*)	Chapuis, J.L. et al. (1994) Alien mammals, impact and management in the French subantarctic islands. Biological Conservation	Mentions European rabbits in diet	
	Moncorps, S. et al. (1998) Diet of the brown skua Catharacta skua lonnbergi on the Kerguelen archipelago: Comparisons between techniques and between islands. Polar Biology	Rabbits mentioned in diet	Y
	Taylor, R.H. et al. (1989) Eradication of Norway rats (Rattus norvegicus) from Hawea Island, Fiordland, using brodifacoum. New Zealand Journal Of Ecology	Rodents known in diet	Y
	Ryan, P. et al. (2008) Important bird areas: Tristan da Cunha and Gough Island. British Birds	Rodents known in diet	
	Bergstrom, D.M. et al. (2009) Indirect effects of invasive species removal devastate World Heritage Island. Journal Of Applied Ecology	Rabbits known in diet	
	Springer, K. et al. (2016) Methodology and challenges of a complex multi-species eradication in the sub- Antarctic and immediate effects of invasive species removal. New Zealand Journal Of Ecology	Rabbits known in diet	
	Raymond, B. et al. (2011) Qualitative modelling of invasive species eradication on subantarctic Macquarie Island. Journal Of Applied Ecology	Rabbits known in diet	
	Brodier, S. et al. (2011) Responses of seabirds to the rabbit eradication on Ile Verte, sub-Antarctic Kerguelen Archipelago. Animal Conservation	Rabbits known in diet	Y
	Martin, A.R. et al. (2017) Rodent eradication scaled up: clearing rats and mice from South Georgia. Oryx	Rabbits known in diet	Y
	Bonnaud, E. et al. (2011) Deciphering complex relationships between apparently unrelated species. Animal Conservation	Rabbits known in diet	
Burrowing Owl (*Athene cunicularia*)	Chandler, S.L. et al. (2016) Burrowing owl diet at a migratory stopover site and wintering ground on southeast Farallon Island, California. Journal Of Raptor Research	Mice mentioned in diet	
Buzzard (*Buteo buteo*)	Sumption, K.J. et al. (1985) The ecological effects of the decline in Rabbits Oryctolagus cuniculus L. due to myxomatosis. Mammal Review	Stoat (*Mustela ermineu*) and other predators also mentioned. Rabbits mentioned in diet	
Christmas Island hawk-owl (*Ninox natalis*)	Coddou, A. et al. (2014) Baiting effectiveness for introduced rats (Rattus sp.) on Christmas Island. Raffles Bulletin Of Zoology	Christmas Island goshawk (*Accipiter fasciatus natalis*) also mentioned. Rats known in diet of both	
Culpeo Fox (*Pseudalopex culpaeus*)	Silva, CA. et al. (2008) Knowing for controlling: ecological effects of invasive vertebrates in Tierra del Fuego. Revista Chilena De Historia Natural	Rabbits mention in diet	

Predator species	Citation	Notes (relating to predator diet and invasive prey mentioned in the article)	Post-eradication study
Dibbler (*Parantechinus apicalis*)	Bennison, C. et al. (2016) Potential impacts of poison baiting for introduced house mice on native animals on islands in Jurien Bay, Western Australia. Wildlife Research	Observed eating mice carcass	
Galapagos hawk (*Buteo galapagoensis*)	Rueda, D. et al. (2016) Biologically significant residual persistence of brodifacoum in reptiles following invasive rodent eradication, Galapagos Islands, Ecuador. Conservation Evidence	Rats and lizards (that also ate baits) present in hawk diet	Y
	Phillips, RB. (2016) Comment on "Reporting costs for invasive vertebrate eradications". Biological Invasions	Rats known in hawk diet	
Gough Moorhen (*Gallinula comeri*)	Wanless, R.M. et al. (2007) Predatory behaviour of the Gough Moorhen Gallinula comeri: Conservation implications. Ardea	Mice mentioned in diet	
	Wanless, R.M. et al. (2010) Risk assessment of birds foraging terrestrially at Marion and Gough Islands to primary and secondary poisoning by rodenticides. Wildlife Research	Brown Skua (*Stercorarius antarcticus lonnbergi*) also mentioned. Mice known in diet	
Island Fox (*Urocyon littoralis*)	McChesney, G.J. et al. (1998) History and status of introduced mammals and impacts to breeding seabirds on the California Channel and Northwestern Baja California Islands. Colonial Waterbirds	Rodents known in diet	
	Cypher, B.L. et al. (2014) Multi-population comparison of resource exploitation by island foxes: Implications for conservation. Global Ecology And Conservation	Rodents known in diet	
Másafuera Red-backed Hawks (*Buteo polyosoma exsul*)	Hahn, I. et al. (2006) Population numbers and status of land birds of the Juan Fernández Archipelago, Chile (Aves: Falconiformes, columbiformes, strigiformes, caprimulgiformes, passeriformes). Senckenbergiana Biologica	Short-eared Owls (*Asio flammeus suinda*) also mentioned. Rabbits and rats known in diet	
Morepork (*Ninox novaeseelandiae*)	Galbraith, M. et al. (2010) Bird fauna of Motu Kaikoura, New Zealand. Notornis	Swamp Harrier (Circus approximans) also noted. Rats and mice known in diets of both	
	Stephenson, B.M. et al. (2006) Breeding biology of morepork (Ninox novaeseelandiae) on Mokoia Island, Lake Rotorua, New Zealand. Notornis	Mice mentioned in diet	
	Ogilvie, S.C. et al. (1997) Brodifacoum residue analysis in water, soil, invertebrates, and birds after rat eradication on Lady Alice Island. New Zealand Journal Of Ecology	Rats known in diet	Y
	Murphy, E.C. et al. (1998) Brodifacoum residues in target and non-target animals following large-scale poison operations in New Zealand podocarp-hardwood forests. New Zealand Journal Of Zoology	Rats known in diet	
	Stephenson, B.M. et al. (1999) Fate of moreporks (Ninox novaeseelandiae) during a pest control operation on Mokoia Island, Lake Rotorua, North Island, New Zealand. New Zealand Journal Of Ecology	Mice mentioned in diet	
	Powlesland, R.G. et al. (1999) Impacts of aerial 1080 possum control operations on North Island robins and moreporks at Pureora in 1997 and 1998. Science For Conservation	Rodents known in diet	
	Spurr, E.B. et al. (2005) Residues of brodifacoum and other anticoagulant pesticides in target and non-target species, Nelson Lakes National Park, New Zealand. New Zealand Journal Of Zoology	Rodents known in diet	
	Empson, R.A. et al. (1999) The risks, costs and benefits of using brodifacoum to eradicate rats from Kapiti Island, New Zealand. New Zealand Journal Of Ecology	Rodents known in diet	Y

Predator species	Citation	Notes (relating to predator diet and invasive prey mentioned in the article)	Post-eradication study
Multiple predator species	Donlan, C.J. et al. (2008) Diversity, invasive species and extinctions in insular ecosystems. Journal Of Applied Ecology	Coyote (Canis latrans) and other native mammal and snake predator species mentioned	
	Rattner, BA. et al. (2014) Adverse Outcome Pathway and Risks of Anticoagulant Rodenticides to Predatory Wildlife. Environmental Science & Technology	Bobcats (Lynx rufus) and other native mammal and raptor predator species mentioned	
	Hosea, RC. (2000) Exposure of non-target wildlife to anticoagulant rodenticides in California. Nineteenth Vertebrate Pest Conference, Proceedings	Coyote (Canis latrans) and other native mammal and avian predator species mentioned	
	Bowie, MH. et al. (2006) Identification of weta foraging on brodifacoum bait and the risk of secondary poisoning for birds on Quail Island, Canterbury, New Zealand. New Zealand Journal Of Ecology	Morepork (Ninox novaeseelandiae) and numerous other avian predator species noted.	
	Eason, CT. et al. (1995) Review of the toxicity and impacts of brodifacoum on non-target wildlife in New Zealand. New Zealand Journal Of Zoology	Morepork (Ninox novaeseelandiae) and other avian predator species noted.	
Multiple species of raptors	Lohr, M.T. et al. (2018) Anticoagulant rodenticide use, non-target impacts and regulation: A case study from Australia. Science Of The Total Environment	Includes owls, eagles, skuas and other birds of prey and mentions rodents in diet	
	Ruiz-Suárez, N. et al. (2014) Assessment of anticoagulant rodenticide exposure in six raptor species from the Canary Islands (Spain). Science Of The Total Environment	Includes hawks, falcons, owls and other birds of prey and mentions rodents in diet	
	Howald, G. et al. (2010) Eradication of black rats Rattus rattus from Anacapa Island. Oryx	Includes Burrowing Owl (Athene cunicularia) and American kestrel (Falco sparverius) with rodents known in diet	Y
Swamp Harrier (Circus approximans)	Greene, T.C. et al. (2014) Additional notes on the birds and vegetation of the southern Kermadec Islands, 2002 and 2006. Notornis	Mentions Pacific rats in diet	Y
	Spurr, E.B. et al. (2004) Bird species diversity and abundance before and after eradication of possums and wallabies on Rangitoto Island, Hauraki Gulf, New Zealand. New Zealand Journal Of Ecology	Rats known in diet	
	Veitch, C.R. et al. (2004) Birds of the Kermadec Islands, south-west Pacific. Notornis	Rats known in diet	
	Flux, I.A. et al. (2001) Breeding, survival, and recruitment of Chatham Island pigeon(Hemiphaga chathamensis). Notornis	Rats known in diet	
	Dowding, J.E. et al. (1999) Brodifacoum residues in target and non-target species following an aerial poisoning operation on Motuihe Island, Hauraki Gulf, New Zealand. New Zealand Journal Of Ecology	Morepork (Ninox novaeseelandiae) also noted. Rats known in diets of both	Y
	Ismar, S.M.H. et al. (2012) First breeding report of black-winged petrel (Pterodroma nigripennis) on Burgess Island, Mokohinau Group, Hauraki Gulf. Notornis	Rats known in diet	Y
	Steffens, K.E. et al. (2012) Identification of predators at black-fronted tern chlidonias albostriatus nests, using mtDNA analysis and digital video recorders. New Zealand Journal Of Ecology	Rats known in diet	
	Eason, CT. et al. (2002) Assessment of risks of brodifacoum to non-target birds and mammals in New Zealand. Ecotoxicology	Morepork (Ninox novaeseelandiae) also noted. Rodents known in diets of both	
	Hoare, JM. et al. (2006) The impact of brodifacoum on non-target wildlife: gaps in knowledge. New Zealand Journal Of Ecology	Morepork (Ninox novaeseelandiae) also noted. Rodents known in diets of both	

Appendix S2.2: Reference Material for Box 2.2

Predator responses to invasive prey eradications

Bald Eagle, Hawadax Island (1-4)

Galapagos Hawk, Galapagos Islands (5, 6)

Morepork, Mokoai Island (7, 8)

Brown Skua, Macquarie Island (9-12)

Brown Skua, Kerguelen Islands (13-15)

Planned future eradications

New Island, Falkland Islands (16, 17)

Juan Fernandez Islands (18, 19)

Christmas Island (20-22)

Islands with threatened predators

New Caledonia (23, 24)

Reunion Island (25)

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Chapter 3

Bottom-up effect of eradications: The unintended consequences for top-order predators when eradicating invasive prey
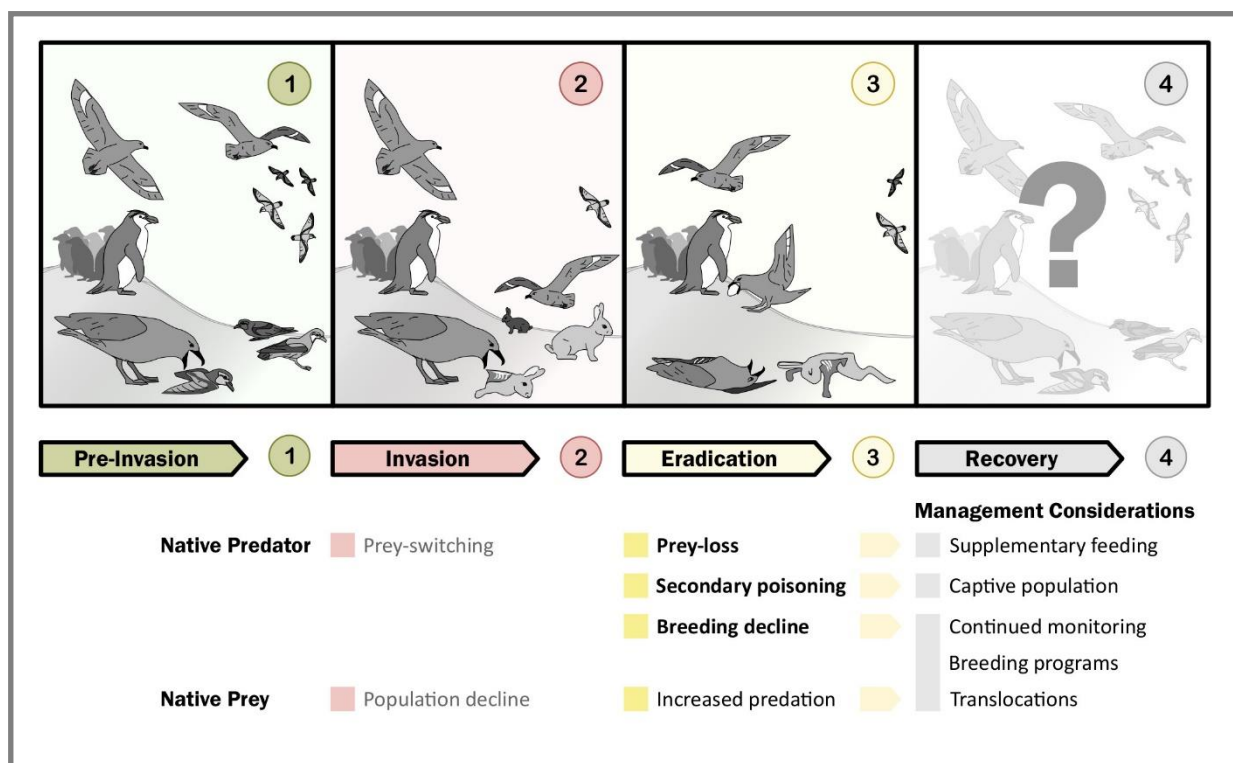
Abstract

The eradication of invasive species from islands yields significant conservation returns. However, novel challenges continue to arise as projects expand in their scope, complexity and scale. Prey-loss and secondary poisoning were historically considered to have limited impact on native top-order predators when planning eradications, but this has rarely been tested quantitatively.

We used a 10-year timeseries of Brown Skua (*Stercorarius antarcticus lonnbergi*) breeding surveys and isotopic dietary analysis on Macquarie Island to investigate how prey-loss and secondary poisoning deaths resulting from the eradication of an abundant invasive prey species, European rabbits (*Oryctolagus cuniculus*), affected a top-order predator.

Skua nest density declined from 7.14 nests/km^2 (95% CI: 6.01-8.27) in the presence of rabbits (pre-eradication) to 3.73 nests/km^2 (95% CI: 2.96-4.51) in the first three years after the eradication of rabbits, before showing signs of recovery in the four years thereafter. However, breeding success dropped from 1.01 chicks/nest (95% CI: 0.76-1.26) to as low as 0.38 chicks/nest (95% CI: 0.23-0.53) with little evidence of recovery.

Secondary poisoning affected a greater number of skuas than anticipated prior to the eradication, including skuas nesting in areas where rabbits were not typically hunted as prey. We highlight that invasive prey often replace native prey in the diet of native predators rather than provide an additional source of food, and rapid eradication of non-native prey can have long-term impacts for predators, particularly when recovery of native prey is slow.

Monitoring programs that complement large-scale eradication projects and address i) trophic driven declines in predator populations and ii) population-level impacts of secondary poisoning are integral to ensuring bottom-up effects of eradications are anticipated and adequately quantified. If prey deficits caused by eradication of invasive prey are expected to be severe but short lived, supplementary feeding programs may buffer against increased predation pressure on native prey and reduced breeding success of native predators. Alternatively, if the rapid recovery of native prey is not expected to occur naturally, breeding programs and translocation of native prey prior to assisted recovery of native predators should be considered to support ecosystem restoration.

Introduction

Invasive species on islands threaten global biodiversity. Sixty-one percent of all global extinctions have occurred on islands, with invasive species being the leading cause (Tershy *et al.* 2015). Furthermore, one-third (37%) of all critically endangered species are only found on islands and many are currently threatened by invasive pests (Blackburn *et al.* 2004; Clavero & Garcia-Berthou 2005; Tershy *et al.* 2015). Removing invasive pests from islands can bring considerable conservation return, and as such, eradication projects have become a central component of global conservation (Jones *et al.* 2016). Invasive lagomorphs and rodents have been eradicated from over 550 islands since 1950 (Towns *et al.* 2006; DIISE 2015). With advances in technology and operational capabilities, conservation efforts have progressed from eradicating an invasive species on small, isolated, uninhabited islands to targeting larger, inhabited islands, and multiple invasive species simultaneously (Kopf *et al.* 2017).

Predicting ecosystem response following an eradication can be difficult (Kopf *et al.* 2017). This is particularly the case in larger complex ecosystems due to the increased number of species interactions, trophic linkages and ecological niches (Zavaleta *et al.* 2001; Kopf *et al.* 2017). Invasive species may perform facilitative roles such as suppressing the abundance of other invasive species, replacing a keystone native species, or occupying a trophic position that benefits native species (Zavaleta *et al.* 2001; Raymond *et al.* 2011; Barbar *et al.* 2016). Invasive lagomorphs, including the European rabbit (*Oryctolagus cuniculus*), readily displace native prey in the diet of native predators, often becoming the predator's preferred prey (Barbar *et al.* 2016). As such, rabbits can be a destabilising force on food webs when native predators become largely dependent on them (Seaton *et al.* 2008; Barbar *et al.* 2016). As a consequence, eradicating invasive prey can lead to bottom-up effects that harm native top-order predator populations (Kopf *et al.* 2017).

Here we quantify the multiple effects of eradicating invasive prey on the breeding and diet of a native top-order predator. In 2011, invasive rabbits and two invasive rodent species – the black rat (*Rattus rattus*) and the house mouse (*Mus musculus*) – were eradicated from a remote oceanic island, Macquarie Island (Springer 2016). With feral cats (*Felis catus*) eradicated a decade prior, Macquarie Island is now free of all mammalian pest species (Parks and Wildlife Service 2014).

For the 140 years that rabbits were on Macquarie Island, they were an abundant prey resource for Brown Skuas (*Stercorarius antarcticus lonnbergi*), a native top-order avian predator (Jones & Skira 1979). Before the eradication of rabbits, the diet of breeding skuas was spatially partitioned across Macquarie Island. Skuas nesting along the coast targeted penguins as prey, while skuas on the interior plateau of the island fed predominantly on rabbits and burrowing petrels (Jones & Skira

1979). With rabbits now eradicated and petrel numbers slowly recovering penguins, which are in abundance, are likely the preferred prey for skuas irrespective of their nest location (Parks and Wildlife Service 2014; Salton *et al.* 2019).

Managers anticipated rabbit eradication would affect the Brown Skua population in two ways. Firstly, brodifacoum, the toxin used to eradicate rabbits and rodents, is known to have lethal effects on birds scavenging poisoned carcasses or the baits themselves, and it was anticipated that a small number of skuas would die from secondary-poisoning (Parks and Wildlife Service 2009). However, following an initial bait drop (covering c. 10% of the island) more seabirds, including skuas, died from poisoning than expected (Springer & Carmichael 2012). In response, rabbit haemorrhagic disease virus (RHDV) was released prior to the final, whole island baiting. RHDV killed an estimated 85% of the rabbit population (Terauds *et al.* 2014), thereby reducing the exposure of native scavengers (e.g. skuas, giant petrels [*Macronectes spp.*] and kelp gulls [*Larus dominicanus*]) to poisoned carcasses. Nevertheless, at least 500 skuas were estimated to have died from secondary poisoning during the entire baiting program (Springer & Carmichael 2012). Secondly, the removal of rabbits was predicted to reduce the prey base of skuas and in turn negatively affect their nest numbers and breeding success (Parks and Wildlife Service 2009).

Managers predicted the reduction in the skua population caused by secondary poisoning would lower their population to a level in equilibrium with remaining native prey abundance (Parks and Wildlife Service 2009). This is a common assumption when eradicating the invasive prey of native predators (Daniel *et al.* 2007). However, it does not account for the possibility that predators may change their foraging behaviour after an eradication in response to the sudden abundance of poisoned carcasses available to them, potentially overexposing the population to secondary poisoning (Salmon *et al.* 2010). Despite the known lethal effects of baiting programs on avian predators, underestimation of secondary poisoning effects at a population level can result in a higher than anticipated fallout for native predators (Eason *et al.* 2002; Buckelew *et al.* 2011). The entire skua population, not just those that hunted rabbits, had access to rabbit carcasses, and therefore all skuas had the potential to be exposed to secondary poisoning. As such, there was a possibility that secondary poisoning could lower the skua population below a hypothetical equilibrium with native prey.

It was assumed that the introduction of rabbits to the island had inflated the skua population and this justified a reduced skua population size post-rabbit eradication (Brothers 1984; Parks and Wildlife Service 2009). However, the introduction of rabbits, feral cats and invasive rodents facilitated a severe decline in the number and diversity of burrowing petrels on the island (Brothers

1984; Copson & Whinam 2001), which were another abundant food source for skuas (Jones 1980; Brothers 1984). On other islands, these petrels can support skua breeding populations as large as those supported by invasive prey and with higher breeding success (Brodier *et al.* 2011). On Macquarie Island, it is likely that rabbits replaced petrels in skua diet, following petrel population declines, and maintained skua numbers at a level that existed pre-invasion, rather than inflating them. Rabbits were then rapidly eradicated, yet there was no reciprocal rapid recovery of burrowing petrels to maintain a stable prey base for skuas (Parks and Wildlife Service 2014). Loss of prey may have a greater effect on island predators than those from continental ecosystems, because the food web energy requirements needed to support viable predator populations are limited by the finite extent of islands (McIntosh *et al.* 2018).

Few studies have quantified the effects of invasive species eradication on native top-order predators (Kopf *et al.* 2017). Brown Skuas on Macquarie Island have never been listed as a threatened species, or been a species of conservation concern (Parks and Wildlife Service 2009). Here, we examine how loss of prey and high number of deaths via secondary poisoning, following a large-scale conservation initiative, impact this native top-order predator. We quantify spatial changes to Brown Skua nest density and breeding success following the eradication of rabbits, and define the isotopic niche of skua chicks to compare how the eradication of rabbits impacted the diets of skuas nesting close to- or far from penguin colonies, the current primary alternative food source for skuas on the island. We also assessed the cumulative effects of prey-loss and secondary poisoning on the skua breeding population size by estimating skua nest density under a hypothetical 'prey-loss only' scenario, to infer the additional impact secondary poisoning had on the breeding population, beyond that solely attributed to prey-loss.

Materials and methods

Study site

This study was undertaken on Macquarie Island (54°30′S, 158°55′E), a remote sub-Antarctic island 1500 km south-east of Australia and a UNESCO World Heritage Site. The oceanic island lies along the Macquarie Fault Zone and is the breeding grounds of numerous migratory seabirds and marine mammals over the Summer months (Selkirk *et al.* 1990).

Four established study areas, Jones and Skira (1979), were resurveyed to determine skua nest numbers and breeding success (Fig. 3.1). The four areas cover around 30% of the island and include both coastal zones and the interior plateau, covering a range of habitats. These areas had previously been used to survey skua breeding intermittently since 1974/75 under various levels of rabbit abundance prior to this study (Appendix S3.1). For our study, surveys commenced prior to rabbit

eradication, in the 2008/09 breeding season, and continued annually until the 2017/18 season, seven years after the last rabbit was seen on Macquarie Island.

Surveys of breeding effort and success

From the 2009/10 breeding season onwards, skua breeding surveys were conducted in two parts following Jones and Skira (1979). First, breeding effort was measured by counting active nests in each study area from November through to early December. Each area was searched by observers walking parallel transects and remaining in visual contact across the entirety of the survey areas. Inaccessible areas were surveyed using binoculars. Occupied nests were identified by the presence of a nest bowl with an adult skua incubating or guarding eggs. Nests were then re-visited during January and early February to count surviving chicks. In the 2008/09 season, only nests were counted.

Stable isotope analysis

Sample collection

Feathers for stable isotope analysis were taken from recently fledged skua chicks before (2008/09 to 2010/11) and after rabbit eradication (2011/12 to 2017/18) (n = 54 for both groups). In addition, muscle tissue was opportunistically collected from dead potential prey sources. These were also included in stable isotope analysis to supplement the interpretation of skua diet. Analysis of prey samples is included in Appendix S3.2.

Sample analysis

Following preparation (Appendix S3.3), samples were combusted using an elemental analyser, and stable isotope ratios assayed *via* a coupled Thermo-Finnigan Delta V Plus Isotope Ratio Mass Spectrometer (IRMS). The global standards
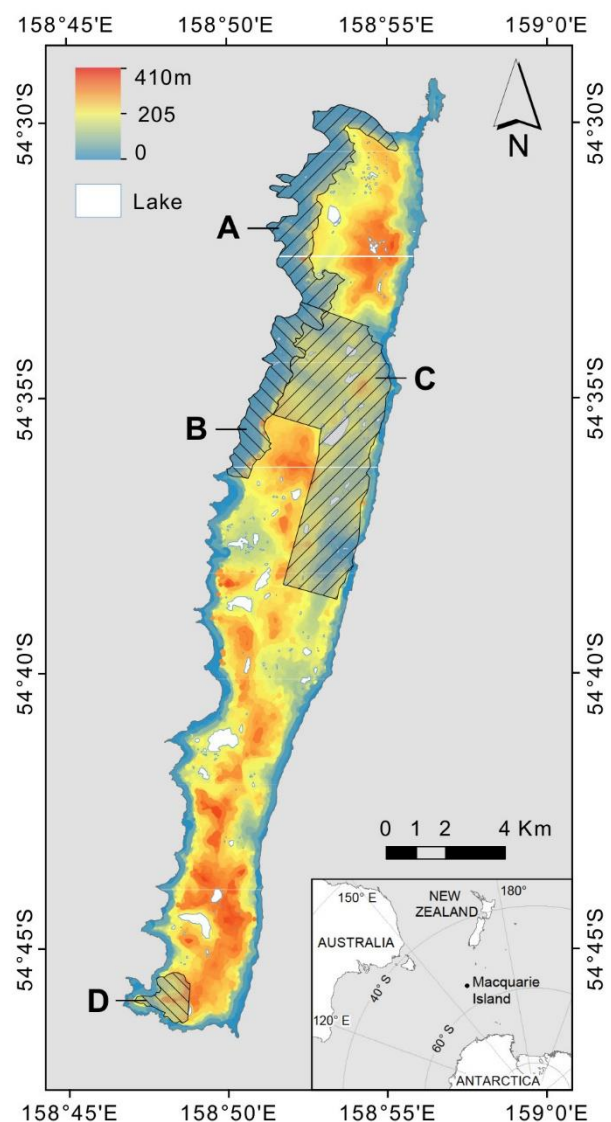

Figure 3.1. Map of Macquarie Island showing the four skua breeding survey areas; two coastal areas (A and B) and two plateau areas (C and D).

used in calculating isotopic ratios of C and N were Pee Dee Belemnite and atmospheric Nitrogen, respectively; and values were presented in standard delta notation following Kimberly and Graham (2006). Precision estimates for $\delta^{13}C$ and $\delta^{15}N$ are 0.1‰ and 0.15‰, respectively.

A correction-factor for comparing across two feather types

Stable isotope ratios can vary between different types of feathers on the same individual due to moult timing, however, this is less common in seabird chicks (Carravieri *et al.* 2014). For this study, the type of feather sampled was either mantle (2008/09 to 2010/11, and 2017/18) or breast feathers (2011/12 to 2016/17) depending on the year of sampling. To account for potential differences between feather types when comparing between years, paired mantle and breast feather samples were taken from a subset of individuals during the 2017/18 season, and the mean difference between paired samples used as a correction-factor to standardise isotopic values between feather types (Carravieri *et al.* 2014; Appendix S3.4).

Data Analysis

Breeding changes

We used Generalised Linear Mixed Models (GLMMs) to test the effect of rabbit eradication on Brown Skua nest density and breeding success (chicks *per* nest; CPN) in each survey area, while accounting for differences between years attributed to environmental variation (Table 3.1). Short-term and long-term responses to eradication were tested by splitting post-eradication years into early post-eradication (2011/12 to 2013/14) and late post-eradication periods (2014/15 to 2017/18).

We used an approximate test of overdispersion on global models to choose model distribution (Lüdecke 2018), then used Likelihood Ratio Tests (LRT) to assess the significance of rabbit eradication as a predictor of skua nest density and breeding success. Results from Tukey's pairwise comparisons between the four survey areas, and conditional and marginal pseduo-R^2 values for both final models were also calculated (Nakagawa *et al.* 2017). Model details, diagnostics and random effect intercepts are provided in Appendix S3.5.

Models were built using the GLMMTMB package 0.2.2.0 (Brooks *et al.* 2017) and plotted with GGPLOT2 3.0.0 (Wickham 2016) in R version 3.5.1 (R Core Team 2018). Analysis and model statistics were calculated using R packages SJSTATS 0.17.0 (Lüdecke 2018) and MULTCOMP 1.4.8 (Hothorn *et al.* 2008). The distribution of skua nests for a subset of years across pre- and post-eradication periods were visualised using kernel densities created in ARCGIS 10.4.

Contributions of prey-loss and secondary poisoning to the overall effect of eradication

To quantify the cumulative effects of prey-loss and death *via* secondary poisoning on the skua breeding population, we compared post-eradication nest density with estimated nest density under a 'prey-loss only' (PLO) scenario. The PLO estimate of skua nest density was calculated by modelling the relationship between skua nest density and rabbit numbers (extracted from Terauds et al. 2014) prior to the baiting program. Historical surveys used to calculate the PLO estimate spanned 1973/74 to 2009/10. With baiting beginning in mid-2010 this relationship was unaffected by the cumulative effect of secondary poisoning. The Generalised Linear Model (GLM) used to model this relationship was built using the R package STATS 3.5.1 (R Core Team 2018). Model details are provided in Appendix S3.6.

Diet changes – isotopic niche analysis

The isotopic niche of skua chicks was compared before and after rabbit eradication following methods in Turner *et al.* (2010) and Jackson *et al.* (2011). For this study we used the isotopic niche as a proxy for dietary variation among skuas, defined in a bivariate space of Carbon (δ^{13}C) and Nitrogen (δ^{15}N) isotope ratios using a mean (M: mean centroid) and a Bayesian estimate of group variance (SEA$_B$: the Bayesian standard ellipse area).

Skua chicks were divided into two spatial groups depending on how close their nest was to the nearest penguin colony: *near*, being nests <1km from a penguin colony; and *far*, being nests >1km from a penguin colony. The isotopic niche of the two groups were then compared between pre-eradication and post-eradication years (n=27 for all four two-way treatment groups). Penguin colonies included King Penguin (*Aptenodytes patagonicus*), Royal Penguin (*Eudyptes schlegeli*) and Southern Rockhopper Penguin (*Eudyptes chrysocome filholi*) colonies but not Gentoo Penguins (*Pygoscelis papua*) because they form small, loose, transient aggregations rather than dense colonies on Macquarie Island.

The distance between mean centroids was used to assess shifts in isotopic niche, while SEA$_B$ was used to assess changes in isotopic niche width. The mean centroids of two groups were considered different from each other if the Euclidian distance between them (ΔM) was significantly greater than zero (Turner *et al.* 2010). To assess differences between the isotopic niche width of two groups, SEA$_B$ and a 95% highest posterior density of SEA$_B$ were calculated using the SIBER 2.1.3 (Jackson *et al.* 2011) and RJAGS 4.6 (Plummer 2016) packages in R version 3.4.0 (R Core Team 2018).

Table 3.1. Comparative analysis to select the final generalised linear mixed models (shown in bold) used in estimating the effect of invasive rabbit eradication on the breeding parameters of brown skuas.

Model	Nest density $N_{ij} \sim log(s_i)_{offset}$			Breeding success $K_{ij} \sim log(m_{ij})_{offset}$		
Fixed effects	a_i	$a_i + f$	**$a_i \times f$**	a_i	$a_i + f$	**$a_i \times f$**
Random effects	c_j	c_j	**c_j**	c_j	c_j	**c_j**
AIC	306	288	**280**	275	263	**249**
$R^2_{GLMM(m)}$	85.9%	96.3%	**96.4%**	11.9%	59.2%	**83.1%**
$R^2_{GLMM(c)}$	96.8%	96.8%	**96.9%**	59.8%	59.2%	**84.7%**
LRT	-	a	$a + f$	-	a	$a + f$
χ^2	-	21.4	20.8	-	16.3	26.2
df	-	2	6	-	2	6
P	-	< 0.001[+]	0.002[+]	-	< 0.001[+]	< 0.001[+]
ODT	χ^2 = 18.08, *P* = 0.90 (Poisson)			χ^2 = 39.52, *P* = 0.012 (quasi-Poisson)		

N_{ij}, Nest count within area *i* in year *j*; s_i, size (km^2) of survey area *i*; K_{ij}, number of fledged chicks within area *i* in year *j*; m_{ij}, number of nests checked for fledged chicks within area *i* in year *j*; a_i, survey area id (*i* = a, b, c or d); *f*, eradication effect (three level: before, early post-eradication and late post-eradication); c_j, *j*th year survey was conducted (2008 to 2017).

AIC: Akaike Information Criterion; $R^2_{GLMM(m)}$: marginal pseudo-R^2 (the variance explained by fixed effects); $R^2_{GLMM(c)}$: conditional pseudo-R^2 (the variance explained by the entire model); LRT: fixed effects of alternative or null model used in the likelihood ratio test; ODT: Overdispersion test (of Poisson distribution); χ^2: Chi-squared value; *df*: degrees of freedom; *P*: p-value ([+] denotes significant values, α = 0.05).

Results

The eradication of rabbits had a significant effect on both skua nesting density and breeding success ($p < 0.001$ both cases, Table 3.1). The effect size of the eradication varied across the island for both models and therefore interaction terms were retained ($p < 0.005$ both cases, Fig. 3.1, Table 3.1). For both nest density and breeding success, pseudo-R^2 values showed most of the model-fit was attributed to the eradication fixed effects, with environmental variation explaining only a small portion of the change in nest numbers between years (Table 3.1).

Nest density

The eradication of invasive prey from Macquarie Island negatively affected skua breeding numbers across the island, however, the strength of the effect varied between regions (Fig. 3.2, Table 3.1). Across all areas surveyed, skua nest density dropped from 7.14 nests/km^2 (95% Confidence Interval [CI]: 6.01-8.27) pre-eradication to 3.73 nests/km^2 (95% CI: 2.96-4.51) in the early post-eradication period, before recovering slightly to 4.46 nests/km^2 (95% CI: 3.65-5.28) in the late post-eradication period. (Fig. 3.2). The pattern of recovery for skua nest numbers post-eradication appears to be related to the distribution of remaining native prey. The most pronounced rates of recovery were centred around large penguin colonies (Fig. 3.3), while recovery was marginal in more distant areas, such as the interior plateau and barren sections of the coast (areas C and A, respectively; Fig. 3.3).
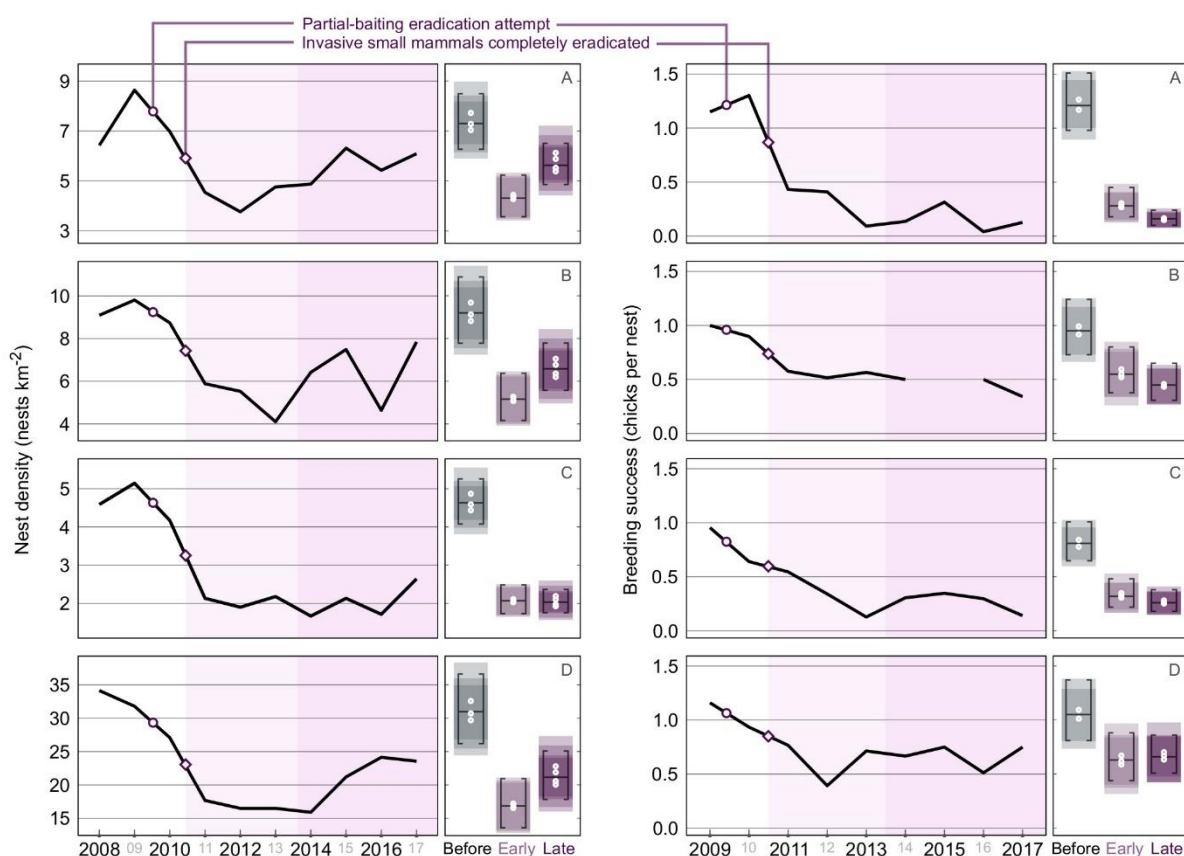
Figure 3.2. Skua nest density (left) and breeding success* (right) in the four survey areas (A, B, C and D; top to bottom) on Macquarie Island before and after rabbit eradication, with light-violet and dark-violet shaded years representing the early and late post-eradication periods, respectively, and pre-eradication years unshaded; and Generalised Linear Mixed Model (GLMM) estimates (black line) with 95% confidence intervals (upper and lower whiskers) for before, early post- and late post-eradication periods, with GLMM estimates for each year (white circles) with 95% confidence intervals (shaded areas) also shown.

 * Note: chicks were not counted in area B during the 2015/16 breeding season.

45
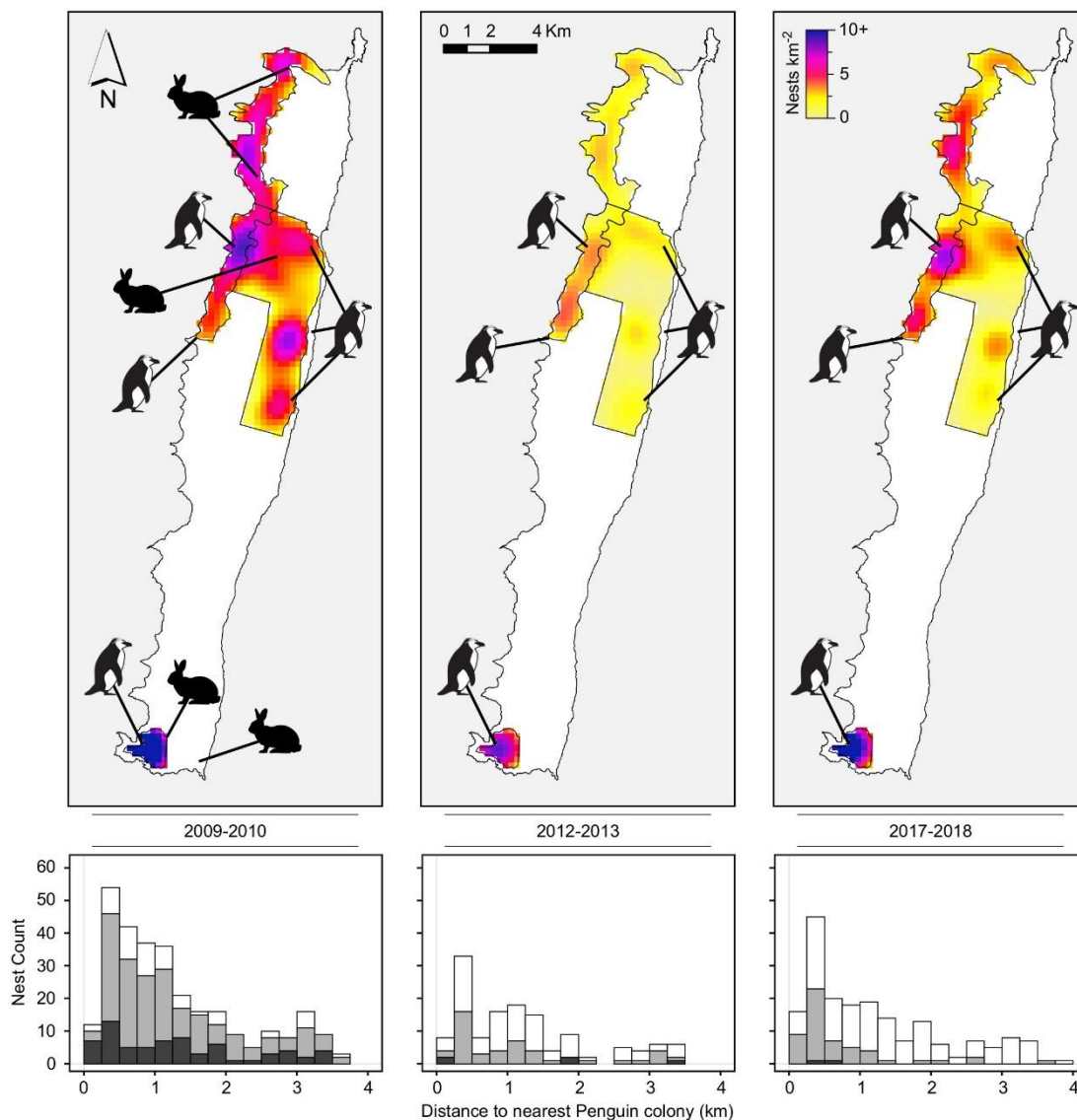
Figure 3.3. Skua nest density[a] and prey aggregations[b] (upper), across representative years for pre-eradication (left), early post-eradication (middle) and late post-eradication (right) periods and histograms of nest counts in the same years (lower) binned by their distance to nearest penguin colony and shaded by breeding success, with nests with two chicks shown in dark grey, one chick shown in light grey and nests that failed left unshaded.

[a] Kernel density estimation of skua nests using a $250m^2$ grid across the four survey areas (estimated using a 1500m search radius).

[b] The broad locations of prey breeding aggregations within or adjacent to survey areas are marked as follows: Penguin icons represent prominent breeding colonies for Rockhopper, Royal and King Penguins taken from https://data.aad.gov.au/aadc/portal/drill_down.cfm?id=15 (date accessed 15/07/2017). Rabbit icons represent areas of high rabbit density in the 2009-2010 season taken from Terauds *et al.* (2014).

Nest numbers in the island's largest survey, area C, had the greatest decline falling to 45% (95% CI: 36-56) of pre-eradication levels in the early post-eradication period and has shown no significant sign of recovery (44% [95% CI: 36-54] in the late post-eradication period; Fig. 3.2). Pairwise comparisons showed the response of skuas to the eradication in area C was distinct from all other survey areas ($p < 0.05$, for all pairwise comparisons involving area C; $p > 0.05$ for all other pairwise comparisons). Nest numbers in the remaining three survey areas also declined but have shown some signs of recovery in the late post-eradication period, peaking at 78% (95% CI: 63-97) of pre-eradication levels in area A during the final survey year (Fig. 3.2).

Figure 3.4. Skua nest density estimates from the early post-eradication period (*E*: the first three years after eradication); late post-eradication period (*L*: 2014/15 onwards) and estimated under a theoretical 'prey-loss only' scenario (*P*: calculated from historic skua nest surveys, inset) shown as a proportion of pre-eradication nest density (2008/09 to 2010/11) in the four survey areas (A, B, C and D) with 95% confidence intervals (shaded area for pre-eradication estimate and lines); and regressions of historic skua nest counts on estimates of rabbit numbers (with 95% confidence intervals) for the four survey areas used to estimate nest numbers when rabbit numbers were zero (hollow red square) for the 'prey-loss only' scenario (inset).

Secondary poisoning and prey-loss as drivers of decline

Secondary poisoning contributed to the decline in skua nest numbers, over and above the decline attributed to prey-loss (Fig. 3.4). Immediately following the eradication, the effect of prey-loss alone could account for decline in nest density in three of the four areas surveyed (A, C and D; Fig. 3.4). However, in area B, secondary poisoning was responsible for up to 95% of the decline in the nest numbers (Fig. 3.4).

In the late post-eradication period, nest numbers in areas A and D recovered to slightly above that estimated in the PLO scenario (Fig. 3.4). Nest densities in areas C and B, however, remained below their respective PLO estimates suggesting a slower recovery from secondary poisoning in these areas (Fig. 3.4).
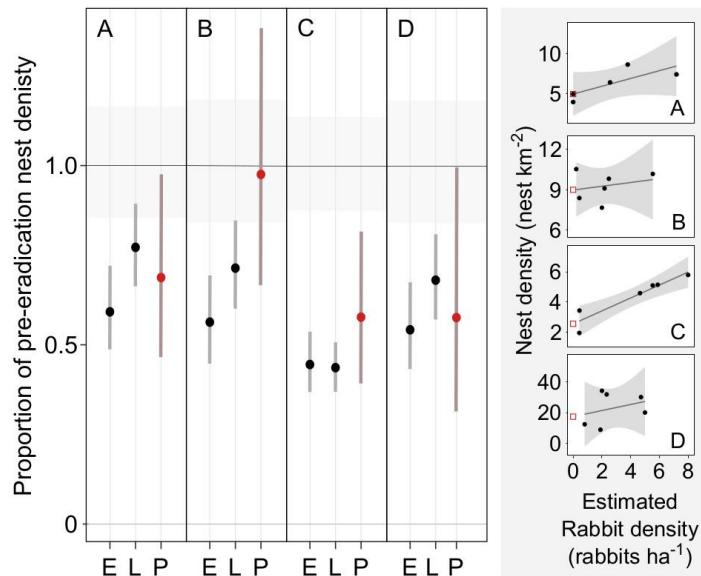
Breeding success

Following the eradication of rabbits from Macquarie Island, breeding success declined across all survey areas and showed no evidence of recovery in the late post-eradication period (Fig. 3.2). Before the eradication, successful breeding occurred across the island; however, like nest density, breeding success became concentrated around penguin colonies after the eradication (Fig 3.2; Fig. 3.3).

Before the eradication, skuas averaged just over one chick per nest (1.01 CPN [95% CI: 0.76-1.26]). However, since the eradication, this has declined to around one chick every 2.5 nests (0.45 CPN [95% CI: 0.25-0.53] in the early post-eradication period, and 0.38 CPN [95% CI: 0.23-0.53] thereafter).

Pairwise comparisons revealed the decline was significantly greater for skuas in area A ($p < 0.05$, for all pairwise comparisons involving area A; $p > 0.05$ for all other pairwise comparisons). Before the eradication, skuas nesting in area A had the highest rate of breeding success (1.21 CPN [95% CI: 0.98-1.51]) but this declined to the lowest rate (0.16 CPN [95% CI: 0.10-0.24]) by the late post-eradication period, representing an 87% drop (95% CI: 79-92; Fig. 3.2).
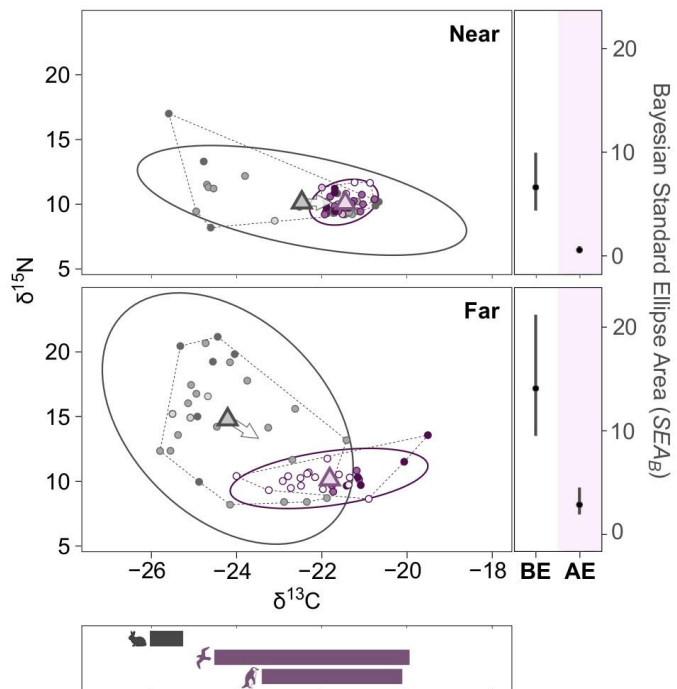
Figure 3.5. Carbon (δ^{13}C) and Nitrogen (δ^{15}N) isotopes ratios of feather samples taken from skua chicks raised *near* penguin colonies (<1km; top) and *far* from penguin colonies (>1km; bottom) either before (grey) or after (violet) the eradication of rabbits from Macquarie Island, with hollow arrows showing the direction of change in mean values after the eradication of rabbits, convex hulls (dashed line), mean centroids (large triangle) and 95% prediction ellipses (solid line) (left), and the median estimate of Bayesian standard ellipse area (SEA$_B$; black points) with 95% highest posterior densities (lines) representing the isotopic niche width of the two spatial groups before rabbit eradication (BE) and after (AE) (right). Inset below, the range of δ^{13}C values for tissue samples of the three main prey of skuas: rabbit (upper), petrels (middle) and penguins (lower) analysed in this study (see Appendix S3.2).

Isotopic niche and diet shifts

The eradication of rabbits from Macquarie Island significantly reduced the isotopic niche width of skuas regardless of whether chicks were raised near or far from penguin colonies (Fig. 3.5). Before the eradication, the isotopic niche widths of *near* and *far* groups were significantly larger than their post-eradication counterparts, paralleling the greater range of diet compositions available to skuas when rabbits were present on the island (Fig. 3.5, Appendix S3.2). Compared with the *near* group, the *far* group had a larger isotopic niche width both before and after the eradication (Fig. 3.5). The *near* group after rabbit eradication had the highest degree of dietary specialisation (smallest isotopic niche width) of any group (Fig. 3.5). In isotopic space, the mean for this group was centred within the isotope values of penguin prey (Fig. 3.5).

In association with a reduced isotopic niche width, the mean diet of the *far* group shifted significantly after the eradication (ΔM_{far} = 5.21, *p* < 0.001); moving away from the isotope values recorded in rabbit muscle tissue, towards that of marine prey, including penguins (Fig. 3.5). However, the eradication had little effect on the average diet of the *near* group (ΔM_{near} = 1.00, *p* = 0.12). After the eradication, *near* and *far* groups converged on enriched $\delta^{13}C$ and lower $\delta^{15}N$ values such that the diets of the two groups were no longer distinguishable from each other (ΔM_{pre} = 4.87, *p* < 0.001; ΔM_{post} = 0.35, *p* = 0.72; Fig. 3.5).

Discussion

The eradication of invasive rabbits from Macquarie Island significantly reduced the breeding population of a top-order predator, the Brown Skua. Our study found an initial 48% decline of the skua breeding population in the first three years following the eradication was compounded further by more than halving of *per capita* chick production. While breeding success of skuas on Macquarie Island remains at its lowest recorded level, breeding numbers recovered to 75% of pre-eradication levels by the final year of this study. The decline was caused by a combination of removing an abundant prey species – an ecological impact of the eradication – and the secondary poisoning of breeding skuas during baiting activities – an operational impact. We found the magnitude of these effects varied across the island, largely in response to the distribution of remaining native prey.

In contrast to historical fluctuations of rabbit numbers on Macquarie Island, which only affected skua nest densities on the interior plateau (Skira 1984), we found the eradication of rabbits impacted nest densities in both coastal and interior sections of the island. This difference in the response of skuas to changes in rabbit abundance is likely due to the additional widespread effect of secondary poisoning during the eradication and its cumulative effect beyond that of prey-loss alone.

At present, skua breeding success is highest in areas near penguin colonies, with nest densities in these areas recovering to near pre-eradication levels. The convergence of isotopic niches of skuas across Macquarie Island, however, suggests skuas nesting near penguin colonies may face increased intraspecific competition for food resources post-eradication. Increased competition for food may explain the generally low skua breeding success across the island (Phillips *et al.* 2004) and result in increased predation pressure for some penguin colonies.

By modelling nest density under a prey-loss only scenario we demonstrate that secondary poisoning reduced the skua breeding population below a level in equilibrium with remaining native prey populations, and that it is still recovering from the larger than expected fallout. A lack of reporting on secondary poisoning from previous eradications (Ward *et al.* 2019), may have led to under-appreciation of its potential impact when planning subsequent eradications (Salmon *et al.* 2010). This has resulted in some projects requiring critical assessment after underestimating the impact of secondary poisoning on native predators (Salmon *et al.* 2010). Future projects should consider stronger mitigation measures when dealing with island predator populations, including the wider use of recognised measures such as creating insurance populations during baiting or assisted re-introductions after baiting, particularly for those species on remote islands where natural immigration is low or populations are of conservation significance (Wilkinson & Priddel 2011; Buxton *et al.* 2014).

On Macquarie Island the eradication of rabbits caused a prey deficit for skuas, which in part reduced the breeding population to an historic low. The recovery of petrel populations to replace rabbits in the diet of skuas is likely to be slow due to the island's extreme isolation from potential source localities (Buxton *et al.* 2014). However, on islands where petrel numbers recover rapidly following rabbit eradication, skua breeding success can benefit from the rapid replacement of invasive prey with native species (Brodier *et al.* 2011). On remote islands, like Macquarie Island, where native prey can take decades to recover after an eradication – if at all – provision of supplementary food sources may be required to maintain a viable native predator population. This may include supplementary feeding programs until native prey can recover or assisted translocations of prey species (Buxton *et al.* 2016).

Conclusions

Across a range of ecosystems, invasive species are significant prey for native predators (Rodriguez 2006; Lambertucci *et al.* 2009; Dijkstra *et al.* 2013; Barbar *et al.* 2016). Our study clearly demonstrates the potential for predators to be susceptible to eradications through changes to food

web dynamics as well as secondary poisoning, and the risk of knock-on effects for prey species through prey-switching and increased predation rates.

It is commonly assumed that the introduction of invasive prey inflates native predator populations by increasing food availability (Daniel *et al.* 2007; Parks and Wildlife Service 2009). However, there is little evidence of this (Salmon *et al.* 2010; Brodier *et al.* 2011) and this assumption may downplay the extent to which secondary poisoning and prey-loss are predicted to impact native predators, post-eradication (Salmon *et al.* 2010; Ward *et al.* 2019). Therefore, it is critical to consider that the native prey base of predators is often reduced by invasive species (e.g. Brothers 1984; Copson & Whinam 2001).

The eradication of invasive mammals from Macquarie Island was an unparalleled conservation success, and has seen the recovery of native vegetation, and the return of threatened seabird species (Shaw *et al.* 2011; Springer 2016). However, this study along with earlier studies from Macquarie Island preceding the eradication (Raymond *et al.* 2011) provide strong incentive for monitoring that specifically investigates changes to bottom-up processes caused by eradications, to inform eradication planning and identify appropriate mitigation strategies (Springer & Carmichael 2012; Alderman *et al.* 2019). Such integrated monitoring, together with a wider consideration of ecosystem impacts, will help to ensure further conservation actions maximise their benefits to the target ecosystems.

Appendix S3.1. Rabbit abundance during historical Brown Skua breeding surveys

Table S3.1. Rabbit abundance during historical Brown Skua breeding surveys, recorded as High (>200,000), Medium (200,000 – 100,000), Low (<100,000) or eradicated (dash), based on population estimates taken from Terauds *et al.* (2014). Presence of feral cats (black dots) is also shown. Pre-eradication years includes breeding seasons between 2008/09 and 2010/11, post-eradication years includes breeding seasons between 2011/12 and 2017/18.

Survey season	Rabbit	Cat
1974-1975	*High*	●
1983-1984	*Medium*	●
1997-1998	*Low*	●
2004-2005	*Medium*	-
Pre-eradication years (this study)	*Medium*	-
Post-eradication years (this study)	-	-

Appendix S3.2: Stable isotope analysis of potential prey in skua diet

Introduction

The use of mixture models with stable isotope analysis in food webs studies can, under the right conditions, provide a detailed insight into the contributions of different sources to the diet of consumers (Phillips *et al.* 2005; Phillips *et al.* 2014). However, the veracity of mixture model estimates in these studies relies on a range of factors including: the method of lipid-extraction used in sample preparation (Logan *et al.* 2008), the choice and reliability of trophic discrimination factor (TDF), and the completeness of the set of source inputs and their geometry in isotopic space (Boecklen *et al.* 2011; Phillips *et al.* 2014; Robinson *et al.* 2017).

Our study design and the mixing space geometry of our source data precluded the use of mixture models for several reasons, particularly because of the difficulty of using only two isotopes (Carbon and Nitrogen) to account for the wide range of potential scavenged and prey sources that could occur in skua diet, being unable to account for variance within source populations based on single samples, and issues with mixing space geometry when including both marine and terrestrial sources in mixture models (Ward *et al.* 2011; Robinson *et al.* 2017). Instead, in future work we plan to use DNA analysis of skua scats and prey remains analysis as more practical solutions to investigate species-level discrimination in skua diet, which will complement this study. These methods allow us to identify the actual components of skua diet without sampling the entire range of possibilities on Macquarie Island (Robinson *et al.* 2017).

Nevertheless, the stable isotope values of dietary source components are provided in this appendix as a supplement to the interpretation of dietary shifts and differences between the four consumer groups identified in the main text (i.e. two-way groups of skuas hatched before/after eradication and nesting near/far from penguin colonies). Source values are compared to the relative positions and dietary niche widths (spread) of each consumer group in isotopic space.

Methods

Sample preparation

Muscle tissue was opportunistically collected from dead specimens of a range of potential skua dietary sources between the 2008-2009 summer to the 2010-2011 summer. Samples were air dried and stored at ambient temperature. Muscle tissue was prepared for stable isotope analysis using the same method as for feather samples. For detailed methods see the main body of text.

Trophic Discrimination Factor

The diet-feather TDFs for Carbon isotope ratios ($\delta^{13}C$: $\Delta^{13}C_{diet-feather}$ = +0.4) and Nitrogen isotope ratios ($\delta^{15}N$: $\Delta^{15}N_{diet-feather}$ = +3.0) were taken from Thompson and Furness (1995). These were added to source isotope values for comparison with the stable isotope values of skua chicks.

Results

Following the eradication of rabbits from Macquarie Island, mean $\delta^{13}C$ of skua chicks in areas far from penguin colonies increased, from moving away from rabbit isotope values towards penguin and other marine prey (Fig. S3.1). Over the same period, the mean $\delta^{13}C$ of skua chicks reared near penguin colonies increased marginally but remained in the region of marine-derived source values (Fig. S3.1).

Discussion

Comparison with values taken from the literature

The mean $\delta^{13}C$ of both groups post-eradication, as well as the *near* group prior to the eradication were similar to those of sub-Antarctic penguin species recorded from another study (-21.5‰ for Macaroni Penguins (*Eudyptes chrysolophus*) and -22.3 ± 0.2‰ for King Penguins) on the Kerguelen Islands when $\Delta^{13}C_{diet-feather}$ is also considered (Yves & Keith 2007). The mean $\delta^{13}C$ of skua chicks in nests far from penguin colonies before rabbit eradication, however, was closer to the $\delta^{13}C$ of terrestrial food webs or fur seal muscle recorded in other studies (Quillfeldt *et al.* 2005; Inger & Bearhop 2008; Anderson *et al.* 2009).

Likewise, mean $\delta^{15}N$ of all skua chicks after the eradication as well as the *near* group prior to eradication were similar to sub-Antarctic penguins species (around 7-10‰) recorded in Yves and Keith (2007) once $\Delta^{15}N_{diet-feather}$ was applied.

The range of $\delta^{15}N$ in the *far* group before rabbit eradication (8.2‰ to 21.2‰) extended beyond the range expected from either penguins or fur seal muscle after the application of $\Delta^{15}N_{diet-feather}$ but remained in the range recorded for plants on Macquarie Island with enriched $\delta^{15}N$ (12.9 ± 4.8‰), particularly when $\Delta^{15}N_{diet-feather}$ plus an additional trophic level of rabbit herbivory between plants and skuas is considered (Erskine *et al.* 1998; Yves & Keith 2007; Anderson *et al.* 2009).

Caveats

When interpreting the contribution of sources to skua diet based on stable isotope values we recognise two things. First, the choice of lipid extraction method on different tissue types (e.g. feathers and muscle) and reliability of trophic discrimination factor can affect stable isotope values

and therefore, the degree to which source values overlay consumer values in isotopic space (Thompson & Furness 1995; Bearhop *et al.* 2002; Logan *et al.* 2008). This means the two datasets could be offset slightly from each other when overlayed. Second, because only one sample of each source species was used it is unlikely that values reflect the extremities of a convex polygon enclosing all possible consumer values in isotopic space (Phillips *et al.* 2014). In addition, the set of source values used is incomplete and other lesser dietary items that were not sampled may also influence some consumer values (Phillips *et al.* 2014). Due to these uncertainties, we use the closeness of association between source values and groups of consumers to inform and guide our interpretation of changes to skua diet following the eradication of rabbits.

Conclusion

After the eradication of rabbits, both consumer groups (skuas nesting both *near* and *far* from penguin colonies) shift from depleted Carbon to enriched Carbon isotope ratios. This is characteristic of a shift in diet from one including terrestrial sources to one solely of marine sources (Inger & Bearhop 2008) and is supported by the source values of this study. The eradication of rabbits in 2011 was absolute and therefore this shift was expected but it does support previous studies that found rabbits were important prey for some breeding skuas on Macquarie Island (Jones & Skira 1979).

Following eradication both groups converge within the middle of penguin isotope values with some outliers closer to seal and petrel isotope values (Fig. S3.1). This suggests that in the aftermath of eradication penguins make up a large portion of the diet of most skuas on Macquarie Island with some utilising other prey and scavenged food in their diets.

Figures
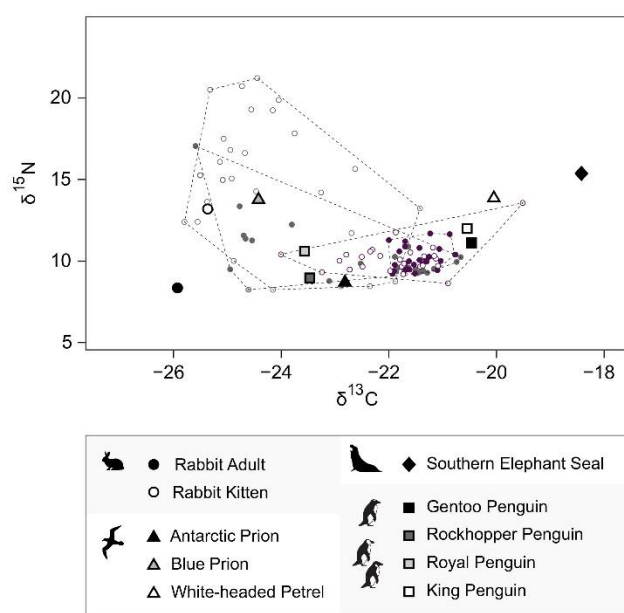
Figure S3.1. Carbon (δ^{13}C) and Nitrogen (δ^{15}N) isotope ratios of muscle tissue taken from animals known to occur in the diet of Brown Skuas, before the eradication of rabbits, with the trophic discrimination factor from Thompson and Furness (1995) applied. Also shown are stable isotope values (points) and convex hulls (dashed line) of the two skua chick consumer groups: chicks reared near penguin colonies (<1km from colony; filled points) and chicks reared far from penguin colonies (>1km from colony; open points) before (grey) and after (violet) eradication of rabbits.

Appendix S3.3: Stable isotope sample preparation

Sample Preparation

To ensure homogenous samples only the distal end of feather vanes were assayed (Bontempo *et al.* 2014). Each sample was stored at ambient temperature then washed with milli-q purified water and left to dry at 60°C in a drying oven. Samples were then placed in a test tube and covered with 10 mL of 2:1 chloroform:methanol solution following (Cherel *et al.* 2005). Whilst in solution, samples were agitated and left to soak for 2 min. This was followed by further rinses in milli-Q purified water and drying at 60°C in a drying oven. After cleaning, the rachis was removed, and samples were finely ground.

Appendix S3.4: Correction factor for feather samples

Introduction

One of the key strengths of this project is the length of the timeseries for skua breeding success and diet surveys, spanning a decade of data collection. Inevitably with such long datasets, and with the best of intentions, sources of variability can occasionally accumulate over time. In the case of this study, data collection was straightforward and so for the most part, methodology was fairly consistent over the ten years of surveys. One source of variability that did enter the data over the years of sampling involved the type of feather sample that was collected for stable isotope analysis. Prior to the 2011-2012 season (and the eradication of rabbits from Macquarie Island), samples consisted of mantle feathers cut from the back of skua chicks. However, after the eradication and with the arrival of a new team of researchers to Macquarie Island, a different sampling regime occurred. From the 2011-2012 season until the 2016-2107 season feather samples were plucked from the breast of skua chicks. Then for the 2017-2018 season the sampling regime returned to the original pre-eradication method.

Stable isotope ratios can vary between different feather types on the same individual due to the timing of moult and feather growth (Carravieri *et al.* 2014). Due to both mantle and breast feathers of skua chicks being grown over a short period during fledging, our hypothesis was that there would not be a large and consistent difference in stable isotope ratios between the two feather types. This was supported by another study that found no variance in stable isotope values between different feather types taken from seabird chicks (Carravieri *et al.* 2014). Nonetheless, in the 2017-2018 the sampling regime reverted to pre-eradication methods for a proper comparison between eradication periods.

To deal with any potential variance between the stable isotope ratios of the two feather types (mantle and breast), both feather types were taken from a subset of individuals (n = 7) during the 2017-2018 season and within-individual differences were compared. For this entire study, only one chick was sampled per nest, meaning another source of variation was the selection of a chick at a nest when there were two chicks to choose from. The difference in stable isotope ratios between feather types was compared with the within-nest difference between two sibling skua chicks to assess the scale of any variation between feathers.

Methods

For stable isotope analysis methods see the main body of text.

The mean difference between the Carbon and Nitrogen stable isotope values of mantle and breast feathers ($\Delta_{mantle-breast}$) was calculated and used as a correction factor to adjust isotope values of breast feathers to those of mantle feathers. This was also visualised using linear regression. During the 2017-2018 season, the second chick was also sampled at a subset of nests (n=2) to compare this potential source of variance with the difference between feather types.

Results

Overall, the isotopic variance between feather types was negligible in comparison to the variance across all samples and was no larger than the difference between two chicks from the same nest (Fig. S3.2; Table S3.2). Between the two feather types there was negligible difference in nitrogen ratios ($\delta^{15}N$: $\Delta_{mantle-breast}$ = 0.0 ± 0.2 S.D.), and only a slight but consistent difference in carbon ratios ($\delta^{13}C$) with mantle feathers being on average 0.4‰ lower than breast feathers (Table S3.2). There was also a greater range in the difference between mantle and breast for $\delta^{13}C$ (mantle feathers ranging 0.0 to 0.7‰ lower than that of breast feathers from the same individual; Fig. S3.2).

Conclusion

Informed by these results, the $\delta^{13}C$ of breast feather samples used in this final study were corrected by -0.4‰ to account for the small but consistent difference between the two feather types and align values with mantle feather samples. $\delta^{15}N$ values were left unadjusted as there was no discernible difference between the two feather types. The correction of $\delta^{13}C$ was minor and only affected the interpretation of one statistic, that being the difference between the two *near* groups (*before* and *after* eradication). The interpretation of all remaining results and the overall findings of the research were unaffected by the $\delta^{13}C$ correction factor.

Tables

Table S3.2. Mean stable isotope ratio values for breast and mantle feathers, the difference between paired (within-individual) samples ($\Delta_{mantle\text{-}breast}$), and the within-nest difference between sibling skua chicks mantle feather samples ($\Delta_{chick\ 1\text{-}chick\ 2}$).

	δ^{13}C	δ^{15}N
within-individual feather comparison		
Mantle feather	-21.4 ± 0.5	10.2 ± 0.9
Breast feather	-21.0 ± 0.5	10.2 ± 1.0
$\Delta_{mantle\text{-}breast}$	**-0.4 ± 0.3**	**0.0 ± 0.2**
within-nest chick comparison		
$\lvert\Delta_{chick\ 1\text{-}chick\ 2}\rvert$	0.4 ± 0.4	0.1 ± 0.2

Figures
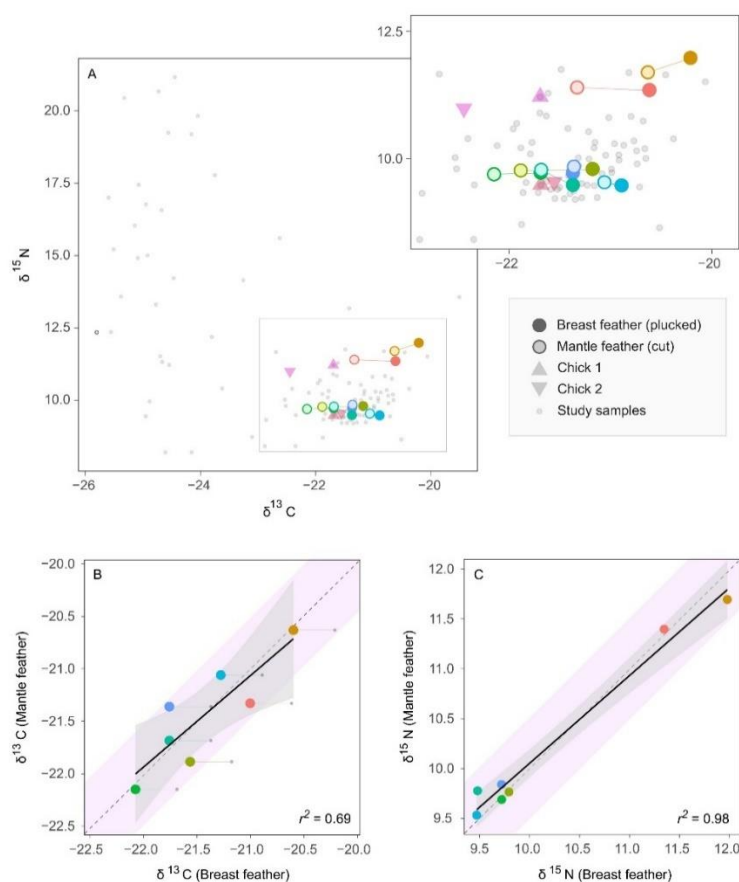
Figure S3.2. A) Nitrogen (δ^{15}N) and Carbon (δ^{13}C) isotope ratios for mantle feathers (open coloured circles) and breast feathers (filled coloured circles). Colours represent individual chicks with pairs of feathers from the same bird linked by a line. Uncorrected samples from the main study are shown in grey. Isotope ratios of two chicks reared at the same nest are shown as triangles for comparison (different nests are coloured separately).

B) Mantle and breast feather δ^{13}C values. Corrected-breast feather values are shown as coloured circles, while grey circles are uncorrected-breast feather values, linked to corresponding corrected values by a line. Linear regression of mantle values on corrected-breast values is shown as black line with a 95% confidence interval shown as a grey shaded area. Adjusted r2 is provided. The identity function is shown as a dashed line, and purple shaded area represents an interval of ±0.5‰ from the identity.

C) Mantle and breast feather δ^{15}N values shown as coloured circles. Linear regression of mantle values on breast values is shown as black line with a 95% confidence interval shown as a grey shaded area. Adjusted r2 is provided. The identity function is shown as a dashed line, and purple shaded area represents an interval of ±0.5‰ from the identity.

Appendix S3.5: GLMM details and diagnostics

Model details

The global model for nest density was:

$$N \sim f + a + f \times a + \log(s)_{offset} + c_{re} \qquad \text{(S1)}$$

Where N is the nest count in a given survey area for a given year, f is a categorical fixed-effect for eradication phase (levels: before eradication, early post-eradication and late post-eradication), a is a categorical fixed effect for survey area (either A, B, C or D), s is the size (km2) of each survey area, and c_{re} is a discrete random effect for the year of each survey (2008 to 2017) to account for changing environmental conditions across years.

The global model for breeding success was:

$$K \sim f + a + f \times a + \log(m)_{offset} + c_{re} \qquad \text{(S2)}$$

Where K is the number of chicks surviving at the end of the breeding season and m is the number of nests re-checked at the end of the breeding season in each survey area.

Model diagnostics and random effect intercepts

Nest density was a good fit with the Poisson distribution (Fig. S3.3). Breeding success showed a good fit to the quasi-Poisson distribution (Fig. S3.4). Random effect intercepts for both models are also provided (Fig. S3.5).

Figures

Figure S3.3. Diagnostics of residuals from final model of nest density. Top left: normal-QQ plot of model residuals showing the data conforms close to a normal distribution. The grey line is the expected alignment if residuals were normally distributed (i.e. a line with intercept 0 and slope 1). Middle left: model residuals plotted against fitted values, showing no linear of curvilinear patterns in model residuals (light grey line has an intercept of 0, dark grey line is a local polynomial regression (LOESS). Bottom left: Square-root of absolute values for model residuals plotted against fitted values. This plot shows residuals were homoscedastic (P = 0.78, r^2 value for linear regression is shown). Top right: Histogram of model residuals, showing residuals are normally distributed. Bottom right: Model residuals plotted against year of survey in each survey area (A, B, C and D) showing no trends in the size of residuals over time. Post eradication is shaded in grey with short term (first three years after eradication) shaded light grey. Filled points show when invasive mammals were eradicated from Macquarie Island in winter 2011, while open points mark the initial partial baiting of the island in winter 2010. Areas A and C have similar trends in residuals over time.

Description of model terms: N, nest count for a given survey area in a given year; a, categorical fixed effect (ID) for survey area (either a, b, c or d); f, three-level eradication fixed effect (either before, 0-3yr or 3+yr); s, offset for size of survey areas (km^2); and c, a discrete random effect for the year of each survey (2008 to 2017). Single terms for interaction components are implied.
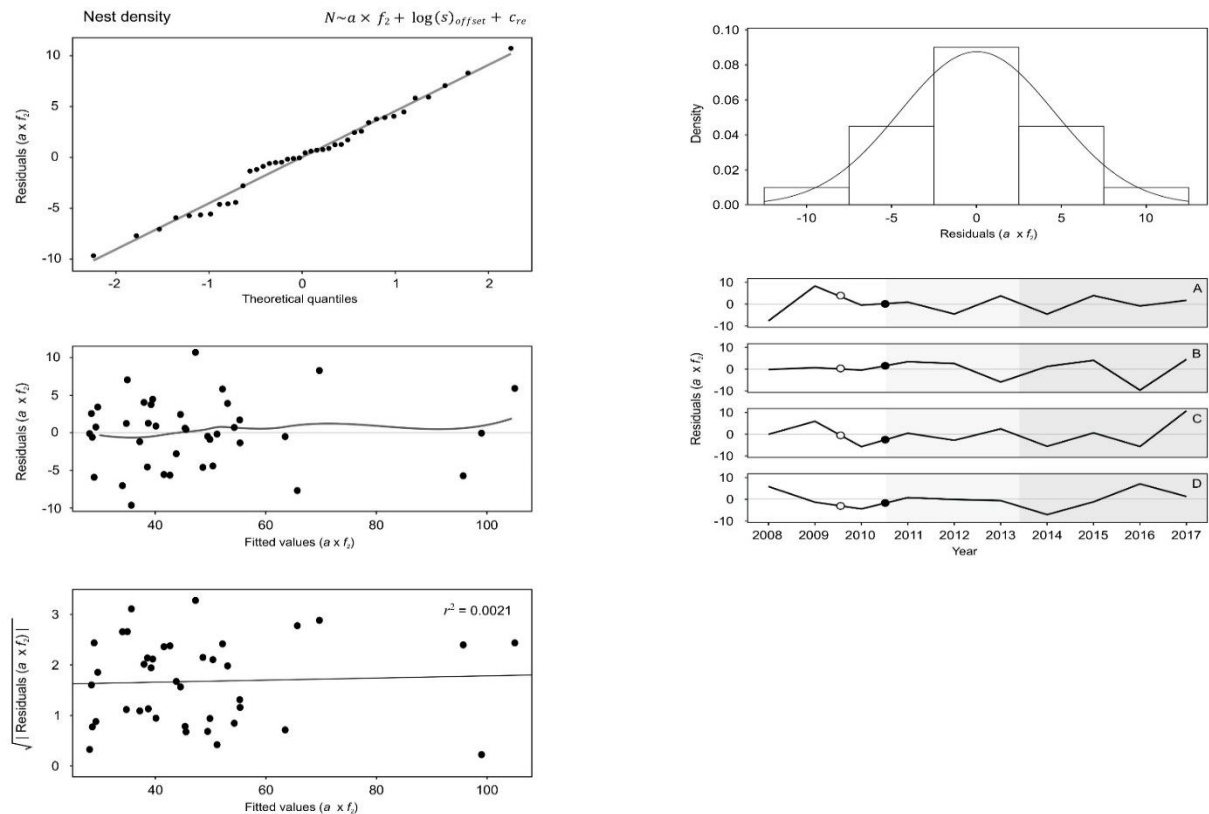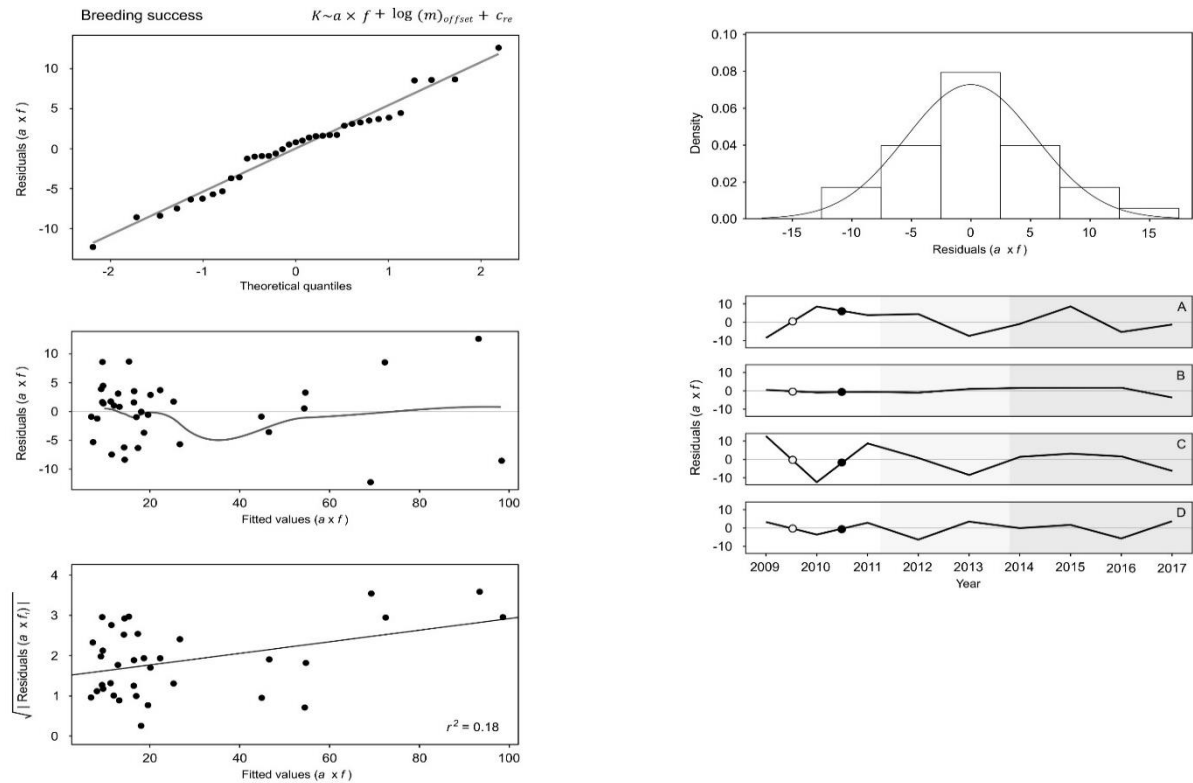
Figure S3.4. Diagnostics of residuals from the final model of breeding success. Top left: normal-QQ plot of model residuals showing the data conforms close to a normal distribution. The grey line is the expected alignment if residuals were normally distributed (i.e. a line with intercept 0 and slope 1). Middle left: model residuals plotted against fitted values, showing no linear of curvilinear patterns in model residuals (light grey line has an intercept of 0, dark grey line is a local polynomial regression (LOESS). Bottom left: Square-root of absolute values for model residuals plotted against fitted values. This plot shows a slight trend towards increasing residual variance as fitted values increase, meaning residuals were marginally heteroscedastic ($P = 0.01$, r^2 value for linear regression is shown). Top right: Histogram of model residuals, showing residuals are normally distributed. Bottom right: Model residuals plotted against year of survey in each survey area (A, B, C and D) showing no trends in the size of residuals over time. Post eradication is shaded in grey with short term (first three years after eradication) shaded light grey. Filled points show when invasive mammals were eradicated from Macquarie Island in winter 2011, while open points mark the initial partial baiting of the island in winter 2010.

Description of model terms: K, number of chicks surviving at the end of the breeding season; a, categorical fixed effect (ID) for survey area (either a, b, c or d); f, three-level eradication fixed effect (either before, 0-3yr or 3+yr); m, offset for number of nests re-checked in each survey area; and c, a discrete random effect for the year of each survey (2008 to 2017). Single terms for interaction components are implied.
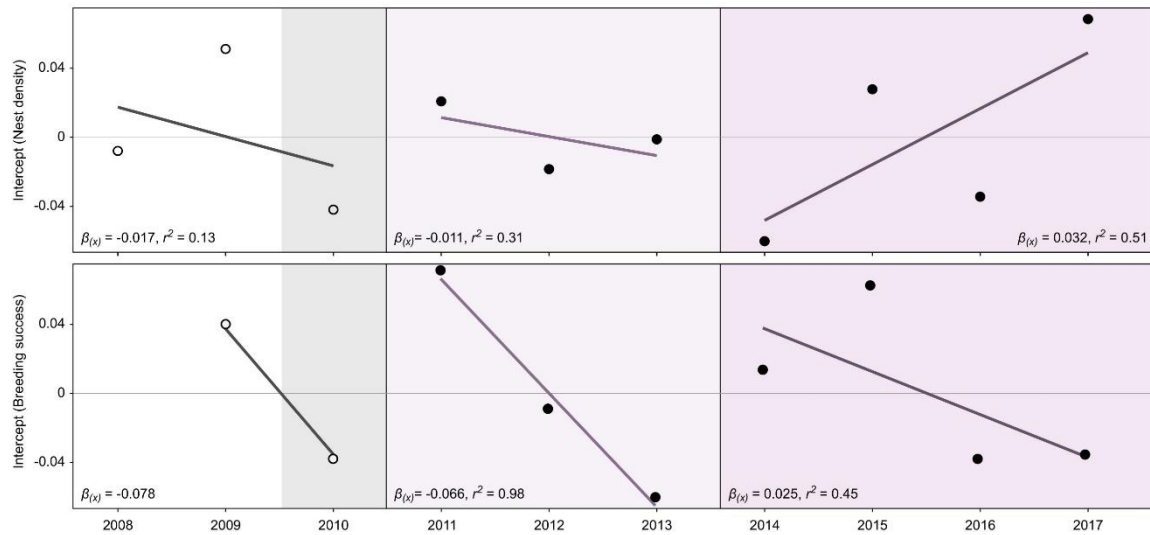
Figure S3.5. Random effect intercepts for each year (variance explained by year) in the nest density model (upper) and breeding success model (lower), shown with linear regression (lines) within each eradication category: before eradication, open markers; early post-eradication, filled markers (light shaded area); and late post-eradication, filled markers (dark shaded area). Slope ($\beta_{(x)}$) and r^2 values for linear regression of intercept values are also shown. The eradication of invasive small mammals occurred during winter 2011 (immediately preceding the 2011 season), however a partial baiting of the island occurred in winter 2010. The grey shaded area highlights the 2010 breeding season, while this year is categorised as *before eradiation*, surveys in this year may have been affected by the partial baiting of parts of the island (note lower intercepts for 2010 in both models relative to other years *before eradication*).

Appendix S3.6: Modelling the PLO scenario

Introduction

The eradication of rabbits affected skua nest numbers in two ways. First, it removed rabbits, an abundant prey species, from the island. Secondly, at least 512 skuas were killed during the baiting campaign by eating poisoned rabbit carcasses (Parks and Wildlife Service 2014). To determine how both these factors contributed to the overall decline in skua nest numbers, we compared the actual decline in nest numbers following the eradication with an estimate of skua nest numbers under a 'prey-loss only' (PLO) scenario. The PLO estimate was calculated by extrapolating skua nest numbers when rabbit abundance was zero from historical skua breeding effort and rabbit surveys (Jones & Skira 1979; Skira 1984).

We included all historical surveys prior to bait being dropped on the island (pre-2010) to solely quantify the effect rabbit abundance (and not secondary poisoning) had on skua nest numbers. Estimating nest numbers in each survey area (A, B, C and D) when rabbit abundance was zero (i.e. the y-intercepts taken from the model of nest density on rabbit abundance) allowed us to determine how many skua nests would be expected under a theoretical PLO scenario.

By comparing the PLO estimate to modelled nest density after the eradication, any additional decrease in nest numbers below the PLO estimate can be attributed to the cumulative effect of secondary poisoning mortality caused by the baiting campaign.

Methods and Results

Calculating historical skua and rabbit densities in survey areas

Prior to the baiting campaign, skua nest numbers had been surveyed in six seasons (1974-1975, 1983-1984, 1997-1998, 2004-2005, 2008-2009, 2009-2010). Although the 2010-2011 season was before the eradication of small mammals from Macquarie Island, a small bait drop had occurred prior to this season and so it was not used in determining nest numbers based solely on prey fluctuations.

This method of approximating contributions of prey loss and non-target mortality required an estimate of rabbit numbers in each survey area for each historical breeding season surveyed. Data on rabbit abundance taken from Terauds *et al.* (2014) for some survey areas in some years existed in the form of 2ha monthly rabbit count plots extending back to the 1974-1975 season, in addition Jones and Skira (1979) mapped rabbit abundance across the island in broad categories. Rabbit counts were conducted monthly at plots across the island. A single count of rabbit abundance was made each month, however occasionally some months were missed. Where rabbit count records

existed, all monthly records from August through to March of that breeding season were averaged to provide a mean for the season (e.g. for the 1974-1975 season, counts from August 1974 through to March 1975 were averaged). Although nest surveys occurred over November and December, rabbit numbers were averaged over the entire summer (beyond December) as the larger sample size of months gave a more accurate mean of rabbit abundance and was less prone to outliers and missing data.

Jones and Skira (1979) contained an island-wide map of rabbit abundance for the 1974-1975 season. An estimated average rabbit abundance for each survey area was taken from that map (estimated as: A: 0, B: 2, C: 8 and D: 5 rabbits per hectare) and this was used in the model for the 1974-1975 season. For this season only areas C and D contained multiple rabbit count plots (six plots in area C and two plots in area D), counts from these plots were divided by the rabbits per hectare estimate of the respective areas taken from Jones and Skira (1979), and the results averaged to provide a single figure with which to standardise all future rabbit counts to the scale used in Jones and Skira (1979). For future seasons, if a rabbit count plot was in a survey area the standardised count for that plot was used as the rabbit density estimate for the area. If an area contained multiple plots, then an average of those counts was standardised. If an area did not contain a plot for a given year then an average rate of change in rabbit density from the previous survey year (based on counts of the other survey areas) was used to extrapolate an estimate for the given area. This was only required for areas A and B in the 1983-1984 and 1997-1998 seasons. Due to the small size of area D, rabbit count plots adjacent the survey area were included (within 2km).

These data provided proxies of rabbit density in each survey area during each season and captured the relative changes in rabbit densities from season to season (Fig. S3.6).

Model details

The equation for regressing nest density on rabbit abundance was:

$$N \sim r + a + r \times a + \log (s)_{offset} \qquad \text{(S3)}$$

Where N is the nest count in a given survey area for a given year, r is estimated rabbit density within each survey area during a given breeding season, a is a categorical fixed effect for survey area (either A, B, C or D), and s is the size (km2) of each survey area. The y-intercept (when rabbit abundance equals zero) from this generalised linear model (GLM) was then used as the PLO estimate. The PLO estimate for each survey area was then compared to the actual change in nest density following rabbit eradication.

Model diagnostics

To test if the model (Eq. S3) had a reliable fit to the Poisson distribution, an overdispersion test in the AER package 1.2.5 (Kleiber & Zeileis 2008) was used. The model was found to be overdispersed ($Z = 2.25$, $P = 0.01$) and thus a quasi-Poisson distribution was used in the final model. Model diagnostics show residuals were slightly heteroscedastic, but the data fit the assumption of normality (Fig. S3.7).

Figures
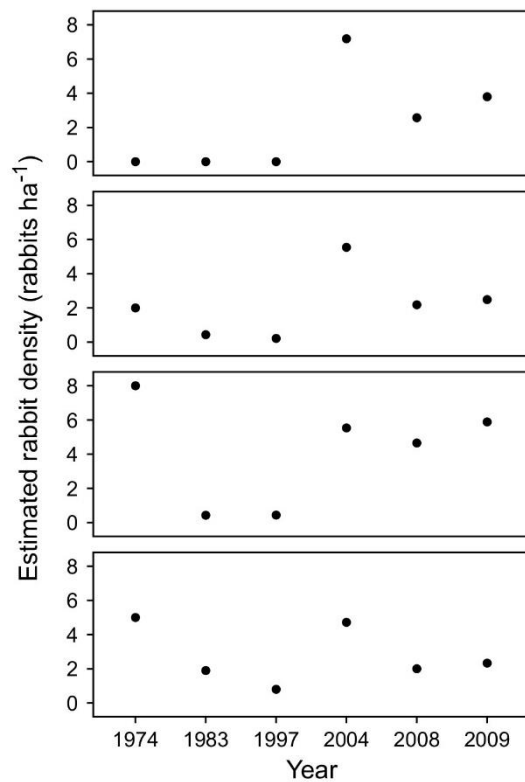
Figure S3.6. Estimated rabbit (*Oryctolagus cuniculus*) density (rabbits per hectare) across the four survey areas (A, B, C and D; top to bottom) during the six seasons Brown Skua (*Stercorarius antarcticus lonnbergi*) breeding effort was surveyed prior to baiting for small mammals on Macquarie Island.
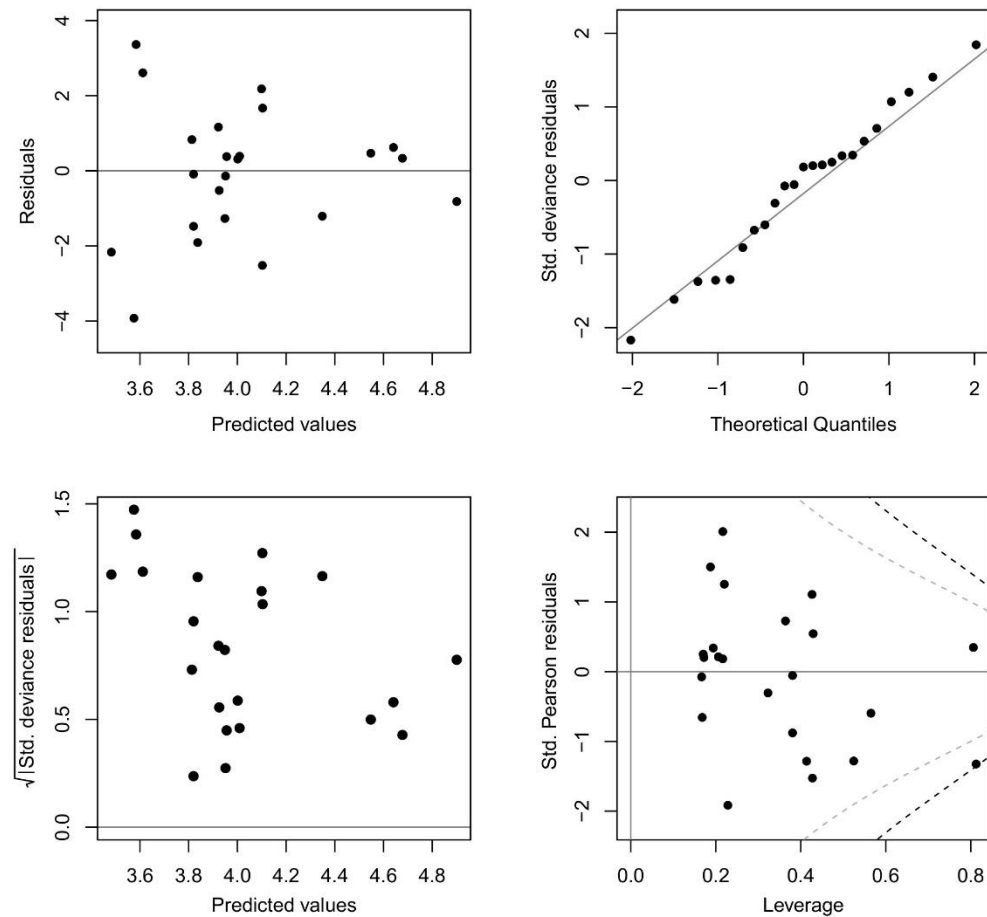
Figure S3.7. Model diagnostics for Eq. 3. Residuals showed no trends across predicted values (top left), were normally distributed (top right), slightly heteroscedastic with lower variance at larger predicted values (bottom left) and with only 1 point falling outside of the 0.5 Cook's distance contour (bottom right). Contours of equal Cook's distance are shown as dashed lines 0.5 (light grey) and 1 (dark grey). Solid grey lines mark x- and y-axes, or in the top-right the expected alignment if residuals were normally distributed (i.e. a line with intercept 0 and slope 1).
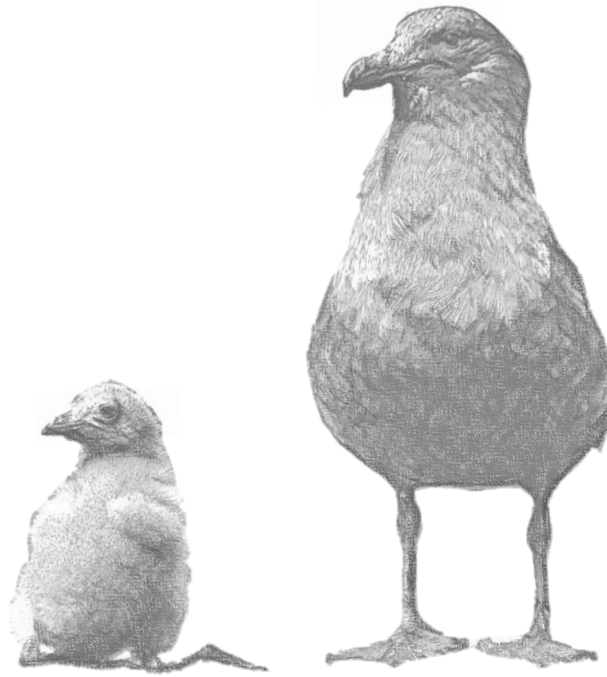
Chapter 4

Defining the foraging landscape and

breeding success of an island apex predator

The Skua in such attacks stoops like many other raptors but, lacking talons, it uses its momentum and weight to knock the rabbit off its feet for long enough to allow it to kill it with its beak. The Skua made several stoops and ensuing ground-flurries before killing the 1,300-g rabbit. If the rabbit had been nearer its burrow, it would have been able to escape after the failure of the first attempt. I have seen less prolonged successful attacks on smaller rabbits.

Johnston (1973)

Abstract

Defining how predators utilise their foraging landscape (the spatial distribution of prey) can be difficult particularly when multiple prey choices are available, or predators employ a variety of foraging tactics to access food. Diet and/or foraging strategies of breeding individuals can influence breeding success and depend on competition with conspecifics and as well as central place foraging constraints for nesting species. Here we quantify how diet and foraging strategies influence the breeding success of Brown Skuas (*Stercorarius antarcticus lonnbergi*), a top-order predator on Macquarie Island. Using animal tracking data to derive a suite of foraging parameters and analysis of prey remains at the nest we illustrate how breeding skuas utilise a diverse foraging landscape and how their choices influence individual breeding fitness. We place our findings in the context of a recent island eradication of an historically abundant invasive prey species, European rabbits (*Oryctolagus cuniculus*), which altered the foraging landscape of skuas.

Diet quality affected overall breeding success, while foraging strategies influenced chick survival. Nearly all skuas focussed their foraging on coastal regions, regardless of their nest location. Skuas that specialised in preying on penguins had better breeding success than skuas with a generalist diet comprised of poor-quality or less reliable foods such as marine molluscs and carrion. Chick survival was higher for skuas with foraging strategies that enabled more time spent at the nest site during chick rearing, less energy expenditure, and less time spent foraging.

The eradication of rabbits has altered the foraging strategies of skuas on Macquarie Island. Prior to eradication, rabbits were an important food source for skuas nesting on the island's interior plateau far from coastal food sources. Since rabbit eradication, skuas nesting on the inland plateau have larger home-ranges to access distant foraging grounds compared with skuas nesting in coastal areas, whose primary food sources were unaffected by the rabbit eradication and remain locally abundant. As a result of longer foraging trips, chick survival was lower for skuas nesting on the inland plateau; however, overall breeding success was similar between skuas nesting on the plateau and the coast.

This work shows how diet specialisation and foraging behaviour affect the breeding fitness of a top-order predator, and how the eradication of rabbits altered the foraging landscape of skuas on Macquarie Island. Changes to foraging behaviour of skuas has potential indirect effects for increased skua competition at native prey colonies and disease transmission by skuas operating as a vector between these colonies. Defining foraging strategies using movement-based parameters that have a close association to aspects of an animal's breeding behaviour and combining these with dietary studies, provide a detailed insight into how the foraging landscape of top-order predators shapes individual breeding fitness and population demographics.

Introduction

The Brown Skua (*Stercorarius antarcticus lonnbergi*) is a top-order predator with a widespread distribution occurring across the sub-Antarctic (Ritz *et al.* 2008). Brown Skuas are adept predator-scavengers with a diverse range of foraging strategies and high dietary plasticity (Spear *et al.* 1999; Reinhardt *et al.* 2000). Across most of their sub-Antarctic range, skua feeding behaviour has been augmented by invasive mammals, and in some cases pest species form a key component of skua diet (Jones & Skira 1979; Reinhardt *et al.* 2000). Breeding behaviour of skuas is closely linked to their diet choice and foraging strategies, and as such, major changes in prey abundance may have long-term effects for their breeding success (Reinhardt *et al.* 2000; Hahn & Peter 2003; Phillips *et al.* 2004; Hahn & Bauer 2008; Anderson *et al.* 2009; Kopf *et al.* 2017).

Depending on local prey diversity and competition for food, the diet of Brown Skuas varies from generalist predation, to scavenging, to specialising on a single species of prey (Moncorps *et al.* 1998; Anderson *et al.* 2009). Diet quality over the breeding season affects several aspects of breeding fitness (Reinhardt 1997a; Phillips *et al.* 2004; Anderson *et al.* 2009). For example, access to a better-quality diet can lead to earlier hatch dates, improved chick development and higher breeding success (Votier *et al.* 2004; Anderson *et al.* 2009; Brodier *et al.* 2011). Equally, the foraging strategies used by skuas can influence breeding success (Trivelpiece *et al.* 1980; Hahn & Peter 2003; Votier *et al.* 2004; Hahn & Bauer 2008). Skuas can reduce the time and energy spent foraging by nesting close to reliable prey aggregations, which benefits chick development and breeding success (Trivelpiece *et al.* 1980; Votier *et al.* 2004). However, nesting close to prey aggregations also comes with an increased risk of conspecific attacks on young, competition for food and inter-specific conflicts at the nest site, which negatively affect chick survival (Hagelin & Miller 1997; Phillips *et al.* 2004). Balancing the costs and benefits to breeding success of different foraging strategies depend on prey abundance, nesting densities and prey choice making overall outcomes equivocal between skua colonies (Furness 1984; Hagelin & Miller 1997; Pezzo *et al.* 2001; Votier *et al.* 2004; Brodier *et al.* 2011). In addition, intrinsic traits such as breeding experience and boldness can also influence foraging decisions and breeding success (Furness 1984; Votier *et al.* 2004; Anderson *et al.* 2009).

A suite of spatial, temporal and state-based models enables detailed analysis of movement data to define foraging strategies of individuals (Calenge 2006; Michelot *et al.* 2016). However, given the multitude of outputs possible from animal tracking data, the utility of any one movement-based parameter in describing an animal's breeding fitness depends on its association with an aspect of the animal's ecology or breeding behaviour (Seidel *et al.* 2018). For example, compare one breeding individual that expends large amounts of energy travelling to a distant foraging ground to access a reliable food source, with another that expends less energy searching multiple nearby locations to

search for an unreliable food source. Using a foraging parameter such as home-range size or average distance of a foraging trip may not detect ecologically important differences between the two foraging strategies or could even result in incorrect inferences about the ecology of the organism, unless combined with a dietary study or additional foraging parameters. Therefore, an informed justification is required when selecting movement-based parameters.

In much the same way, studies of diet quality alone may not inform breeding fitness if individuals use vastly different foraging strategies to access the same food sources. For example, on King George Island skuas that nest near, and defend, foraging territories have higher breeding success than non-territorial skuas that have to steal access to foraging territories despite both having the same diet (Trivelpiece *et al.* 1980). Many complementary methods also exist for defining the diet of predators, including stable isotope and DNA analysis, observational studies, and surveys of stomach contents or prey remains (Barrett *et al.* 2007; McInnes *et al.* 2017). Each method has its own strengths and limitations in regards to ethical constraints, the type of prey and consumer species, and temporal scope of interest (Barrett *et al.* 2007). Therefore, the design of dietary studies and selection of foraging parameters must be closely aligned with the purpose of the study and the ecology of the study species.

Using GPS tracking of breeding individuals during the chick guard phase and surveys of prey remains at the nest we aimed to clarify how diet and foraging strategies influence the individual breeding success of Brown Skuas on Macquarie Island. Based on a review of the relationship between movement ecology and the breeding fitness of Brown Skuas we defined skua foraging strategies using six foraging parameters derived from animal tracking data that were likely to have an impact on the breeding fitness of skuas: time spent either at the nest site, in a resting state, at a lake site away from the nest or in a non-travelling state away from the nest or lake sites, and total and core home-range sizes. We used multivariate analyses to compare diet and foraging strategies between skuas that either successfully reared young or failed in their breeding attempt, and assess which components of diet and foraging influenced breeding fitness.

The introduction, and more recent eradication of invasive mammals to sub-Antarctic islands has altered the foraging landscape of skuas (Jones & Skira 1979; Skira 1984; Brodier *et al.* 2011) yet to date it has not been examined in detail. We use the recent eradication of invasive European rabbits (*Oryctolagus cuniculus*) on a sub-Antarctic island (Terauds et al 2014; Springer et al 2016) to assess the effects of invasive prey removal on the foraging landscape and breeding success of skuas (Skira 1984; Terauds *et al.* 2014).

In the presence of rabbits, distinct prey distributions across the island meant skuas were spatially partitioned in their dietary preferences, with all skuas feeding predominantly on locally available prey (Jones & Skira 1979). Those nesting on the interior plateau of the island relied heavily on rabbits in their diet, while in contrast skuas nesting on the coastal terrace foraged predominantly on penguins, even when large densities of rabbits were nearby (Jones & Skira 1979; Skira 1984). The island-wide preference for locally available prey suggests long distance foraging trips, and frequent visits to coastal foraging grounds were unlikely to have been the norm for plateau nesting skuas, prior to rabbit eradication (Jones & Skira 1979). We compared breeding success, chick survival and home-range sizes of skuas nesting either on the coastal margins of the island or on the interior plateau to investigate any legacy effects of rabbit eradication on breeding and foraging.

Methods

Study site

This study was undertaken on Macquarie Island (54°30'S, 158°55'E), a remote sub-Antarctic island 1500 km south-east of Tasmania, Australia, and a UNESCO World Heritage Site. The remote oceanic island lies along the Macquarie Fault Zone, (Massell *et al.* 2000) and is positioned within the Antarctic Circumpolar Current between the Polar front to the south, and the sub-Antarctic front to the North – in the pacific sector of the Southern Ocean (Hamilton 2006). Over the summer months, Macquarie Island is home to a large number of seabird and marine mammal species which contribute to the diet of Brown Skuas (Jones & Skira 1979). Rabbits were introduced to the island in 1870s and were an important prey item for skuas nesting on the island's interior plateau until their eradication in 2011 (Jones & Skira 1979; Skira 1984; Terauds *et al.* 2014).

Prey remains

The native prey available to skuas on Macquarie Island includes four penguin species, multiple burrowing petrel species, and scavenged carrion predominantly around Southern elephant seal colonies (*Mirounga leonina*) (Jones & Skira 1979). Prey remains are discarded around skua nests during breeding and can include middens of bones, wingsets and shells of prey, as well as regurgitated pellets and hard parts of prey found in scats.

In early November 2017, during the late incubation period, prey remains were cleared from a 10m radius around forty nests across the island (Fig. 4.1). Breeding success of each nest was then monitored over the summer. Once nest sites were found to have either failed or chicks had fledged, prey remains were counted and classified to broad prey type (e.g. petrel bolus, petrel wingset and penguin bone). For wingsets only the right wing was counted to avoid the double-counting of broken wingsets.

Home-range and foraging strategies

GPS logger deployment

A sub-sample of nests was monitored during the late incubation stage. Once a chick was found at a nest, one parent was randomly selected from that nest for GPS deployment. If a nest failed before hatching a chick, an alternative nest was then selected for GPS logger deployment. Twenty-nine GPS loggers (CatLog-S2 GPS loggers, Catnip Technologies Ltd) were deployed on breeding birds during the early chick-rearing period. The GPS devices were attached to the mantle feathers of birds using tesa® 4651 cloth tape and tape ends bonded with Loctite® 401 (Carneiro *et al.* 2015). In total, device and attachment weighed approximately 29g, or 2% bodyweight of the lightest skua tracked during this study (1450g), and roughly 1.5% of the average bodyweight of all tracked birds (1890g). Feather attachment ensured devices that were not retrieved would be shed during the winter moult and no birds would carry GPS loggers for longer than approximately 6-8 months (Graña Grilli & Cherel 2017; Delord *et al.* 2018). GPS loggers were programmed to acquire a fix every five minutes and left on birds for two weeks before retrieval. In some cases, retrieval took longer than two weeks, and in these cases GPS data used in analysis were cropped to a two-week period. On retrieval, feathers attached to the adhesive tape were analysed to determine the sex of tracked birds using molecular methods following Çakmak *et al.* (2016).

On sub-Antarctic islands, the foraging strategies and diets of both skua parents at a nest are typically similar, therefore we assumed the movements of a single parent represented an optimal foraging strategy at that nesting location (Anderson *et al.* 2009; Carneiro *et al.* 2014; Carneiro *et al.* 2015; Jakubas *et al.* 2018). An exception to this has been found in the Chatham Islands where foraging habits are partitioned between the sexes, however being in temperate latitudes the island ecology has less in common with Macquarie Island (e.g. a lack of large penguin and seal colonies) (Schultz 2019). For these reasons, and to reduce disturbance at the nest, we limited tracking to one parent per nest.

Parameters of foraging behaviour

Six foraging parameters that influence breeding success were derived from previous studies on skuas and used to define the foraging strategies of tracked birds in this study (see Table 4.1). Bird movements based on GPS tracks were then used to quantify these parameters. The foraging parameters were designed to have a close relationship with an aspect of skua ecology that informs breeding success. For example, foraging strategies that allow for more time spent at the nest site increase the time parents spend guarding chicks from predation and therefore benefit breeding success (Hahn & Peter 2003). We defined a defendable nest site as a 100m radius around the nest

Table 4.1. Summary of foraging parameters and the threats to chick survival each parameter addresses.

Foraging Parameter	Threat	Effect (+/-) of FP on chick survival (*references*)		FP estimate (*and R package required*)	
N*pt*: Time spent at nest site	Chick predation	Increased time spent guarding chicks	+	*Hahn & Peter 2003; Phillips et al. 2004*	Proportion of GPS fixes at the nest site (within 100m of nest)	
T*hr*: Total home range or area travelled	Increased area covered to find suitable food for chicks	Increased travel to foraging grounds	-	*Carnerio 2010; Hahn & Bauer 2008*	95% utilisation distribution (95%UD)	*adehabitatHR*
C*hr*: Core home range or area utilised	Decreased reliability of foraging grounds	Increased number of foraging grounds visited	-	*Hahn & Bauer 2008*	50% utilisation distribution (50%UD)	*adehabitatHR*
A*pt*: Time spent at lake club sites	Breeding inexperience	A proxy for time spent doing other activities not related to chick rearing*	-	*Furness 1984; Young 1972*	Proportion of GPS fixes at lake club sites (S1 and S2 only)	*moveHMM*
F*pt*: Time spent at foraging grounds and other sites	Excess effort needed to acquire food	A proxy for increased difficulty collecting food for chicks	-	*Votier 2004*	Proportion of GPS fixes outside of nest or lake club sites (S1 and S2 only)	*moveHMM*
E*pt*: Time spent resting	Excess energetic demand	A proxy for the reciprocal of energy used to rear chicks	+	*Schoener 1971; Trivelpiece et al. 1980*	Proportion of fixes in resting state (S1 only)	*moveHMM*

*competing hypothesis: washing at lakes may decrease parasite load and diseases. (+)

and used the proportion of GPS fixes located within the nest site as a proxy for the foraging parameter *time spent at the nest site* (Table 4.1).

In addition, utilisation distributions (UD) were modelled using biased-random-bridges movement-based kernel density estimates to define two foraging parameters: a core home-range (50% UD: C_{hr}); and total home-range (95% UD: T_{hr}) of each skua (Table 4.1). Both were constructed in the ADEHABITATHR 0.4.16 package (Calenge 2006) in R version 3.5.1 (R Core Team 2018).

A state-based hidden Markov movement model with no covariates was used to define the remaining three foraging parameters: energy expenditure (E_{pt}: proportion of time spent in a resting state), time spent foraging (F_{pt}; proportion of time spent in a non-travelling state away from both the nest site and lakes), and time spent undertaking alternative activities (A_{pt}; proportion of time spent in a non-travelling state within 5m of a lake and away from the nest site) (Table 4.1). The state-based movement model was created using the package MOVEHMM 1.6 (Michelot *et al.* 2016) in R version 3.5.1 (R Core Team 2018).

State-based model outputs and location classification of GPS fixes for each skua are included in Appendix S4.1.

Data Analysis

Diet choice and breeding success

To visualise differences in dietary specialisation among nests, percentile rank scores of nests in each prey category were binned into quartiles using DPLYR 0.7.6 in R version 3.5.1 (R Core Team 2018).

Differences in the dietary compositions of successful and failed breeders (classified as nests that fledged at least one chick or nests that failed in their breeding attempt, respectively) were tested using a distance-based redundancy analysis (dbRDA) of log-transformed prey count data. The significance (cut-off α = 0.05) of breeding success as an explanatory variable in dbRDA was tested using a permutational multivariate analysis of variance (PERMANOVA). An assumption for PERMANOVA of equal multivariate dispersion within the two breeding groups was tested using a permutational test of the dispersion (PERMDISP), which tests dispersion of points from group centroids when plotted on principal coordinates axes. All analyses were conducted using VEGAN 2.5.5 (Oksanen *et al.* 2019) in R version 3.5.1 (R Core Team 2018).

Foraging strategies and chick survival

A principal component analysis (PCA) of the six foraging parameters was used to visualise how each parameter contributed to the variation in foraging strategies of skuas. A redundancy analysis (RDA) of standardised foraging data was used to test whether foraging strategies differed between skuas that successfully fledged at least one chick and those that did not, and which foraging parameters covaried with chick survival.

The sex of tracked birds, an estimate of chick age and the date tracking commenced were all tested as potential covariables during model building. A forward-stepwise selection process using PERMANOVA was used to identify a final model with only significant predictors retained (cut-off α = 0.05). Equal multivariate dispersion within the two breeding groups was tested using PERMDISP. In the final model, chick survival was retained as the sole explanatory variable in a partial RDA while other significant variables conditioned as covariables if necessary. All analyses were conducted using VEGAN 2.5.5 (Oksanen *et al.* 2019) in R version 3.5.1 (R Core Team 2018).

Changes to foraging landscape: legacy effects of rabbit eradication

Total and core home-ranges (95% UD and 50% UD, respectively) were compared between skuas nesting on the interior plateau, where skuas historically had a high dependence on rabbits as food, and those nesting in coastal areas, where skuas had historically low rabbit dependence, using one-sided Mann-Whitney-Wilcoxon tests in R version 3.5.1 (R Core Team 2018). To compare diets between the two groups, percentile rank scores were calculated for nests in each prey category and

mean percentiles with standard error calculated for the two areas using DPLYR 0.7.6 in R version 3.5.1 (R Core Team 2018).

The breeding success (at all nests) and chick survival (at nests where GPS units were deployed) were compared between the two groups using Pearson's Chi-squared tests in R version 3.5.1 (R Core Team 2018).

Additional analysis

RDA and other distance-based analysis methods have been critiqued for their coarseness when dealing with multivariate data in reduced dimensions (Warton *et al.* 2012). Given the nature of our data and due to the relatively small sample size of birds tracked in this study nonparametric analysis appeared effective and suitable. Nonetheless, to support distance-based results we also analysed our data with a complementary method, within a multivariate (generalised) linear modelling framework using the MVABUND package (Wang *et al.* 2012) in R version 3.5.1 (R Core Team 2018). The methods and results of this modelling are presented in Appendix S4.2.

Results

Diet choice and breeding success

Nest surveys

Of the 40 nests surveyed, 65% of skuas failed to rear a chick, 33% successfully reared a single chick while only one pair reared two chicks. Prey remains found at skua nests included boluses of penguin, petrel or seal remains, bones of penguins, petrels or seals, penguin eggs, petrel wingsets, mollusc remains, and pebble boluses (Fig. 4.1). Splitting taxa beyond these broad groups was not consistently reliable across nests due to the state of most prey remains. These groupings were used in dietary analysis. Where possible petrel remains were defined to species level and these were reported (see Fig. 4.1), but petrels were kept as a group in analysis. The nutritional purpose of pebble boluses in the diet or behaviour of skuas was not identified, however it is likely they are ingested while parasitising elephant seal milk, a behaviour commonly observed in skuas prior to the weaning of elephant seal pups (Johnston 1973). As such, they were included in dietary analysis.
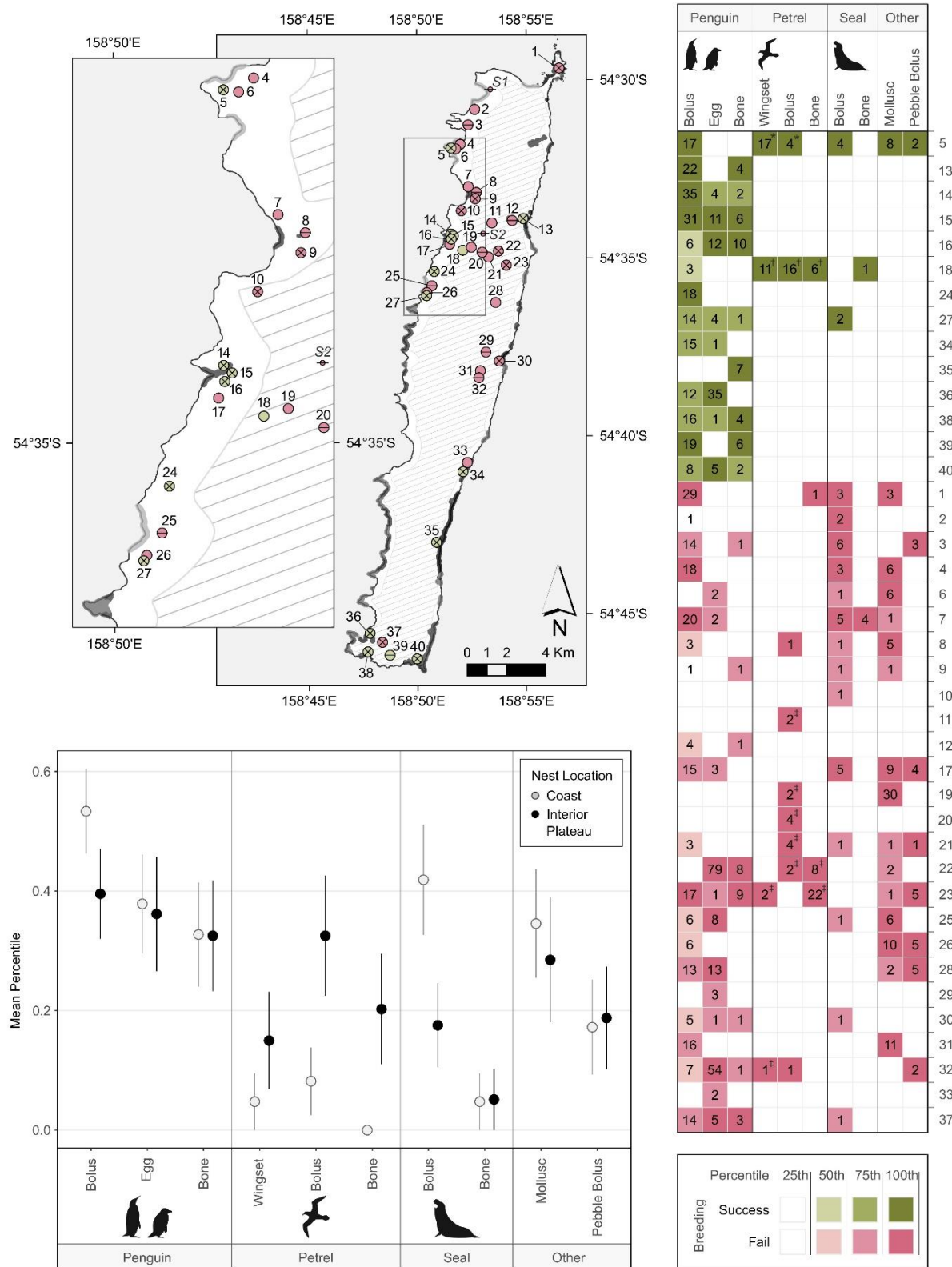
Figure 4.1. Top left: Map of nest locations around the island used in prey remain surveys. Nests that were used in GPS analysis are represented by crossed points on the map. Nests that GPS were deployed but not retrieved or used in analysis are marked by strikethrough lines.

Figure 4.1 (continued). Supplementary nests used in GPS deployment (but not in prey remain surveys) are represented by small points and numbered with the prefix 'S'. Successful breeders (nests that fledged at least one chick) are shown in olive and failed nests (nests that failed to fledge a single chick) shown in rose. The interior plateau is hatched on the map.

Right: Counts of prey remains found at each nest. Counts are shaded by quartiles for each prey remain category and by breeding success. Petrel species where identified are Blue Petrels (*), White-headed Petrels ($\dagger$) and Antarctic Prions ($\ddagger$).

Bottom Left: Mean percentiles, with standard error, in each prey remain category for skuas nesting in areas of historically low rabbit dependence (coast) or high (interior plateau).

Diet quality of breeding skuas

Penguin remains were the most common prey items found at skua nests, occurring at 90% of nests surveyed. 35% of all nests contained only penguin remains and of these 14 nests only three failed in their breeding attempt. Petrel remains were found at 28% of nests, with three species of petrel identified: White-headed Petrel (*Pterodroma lessonii*), Blue Petrel (*Halobaena caerulea*) and Antarctic Prion (*Pachyptila desolata*). Where petrel remains were found at a nest it was always restricted to one species of burrowing petrel. Blue Petrel and White-headed Petrel remains were only found at one nest each, and at both of these nests chicks were successfully fledged (nests: 5 & 18, Fig. 4.1). At all other nests with petrel remains, skuas failed in their breeding attempt. Petrel remains at these nests were comprised of Antarctic Prion, except two where the species of petrel could not be identified. Seal remains were found at 43% of nests (17 nests) and only three of those pairs successfully reared a chick. 45% of nests (18 nests) had either mollusc remains or pebble boluses or both, and only one of those nests successfully reared a chick (Fig. 4.1).

Diet specialisation increases breeding success

Breeding success was a significant variable in the dbRDA of dietary composition ($F_{1,38}$ = 4.65, P = 0.005). PERMDISP showed the failed breeding group had a broader range of diets among its members, while the successful breeders had a comparatively narrower dietary niche, with the difference in multivariate dispersion between the two breeding groups (successful and failed) being significant ($F_{1,38}$ = 6.32, P = 0.016; Appendix S4.3).

Overall, dbRDA showed successful breeding skuas had a greater number of penguin boluses and penguin bones in their prey remains than the failed group (Fig. 4.2). These two prey remain
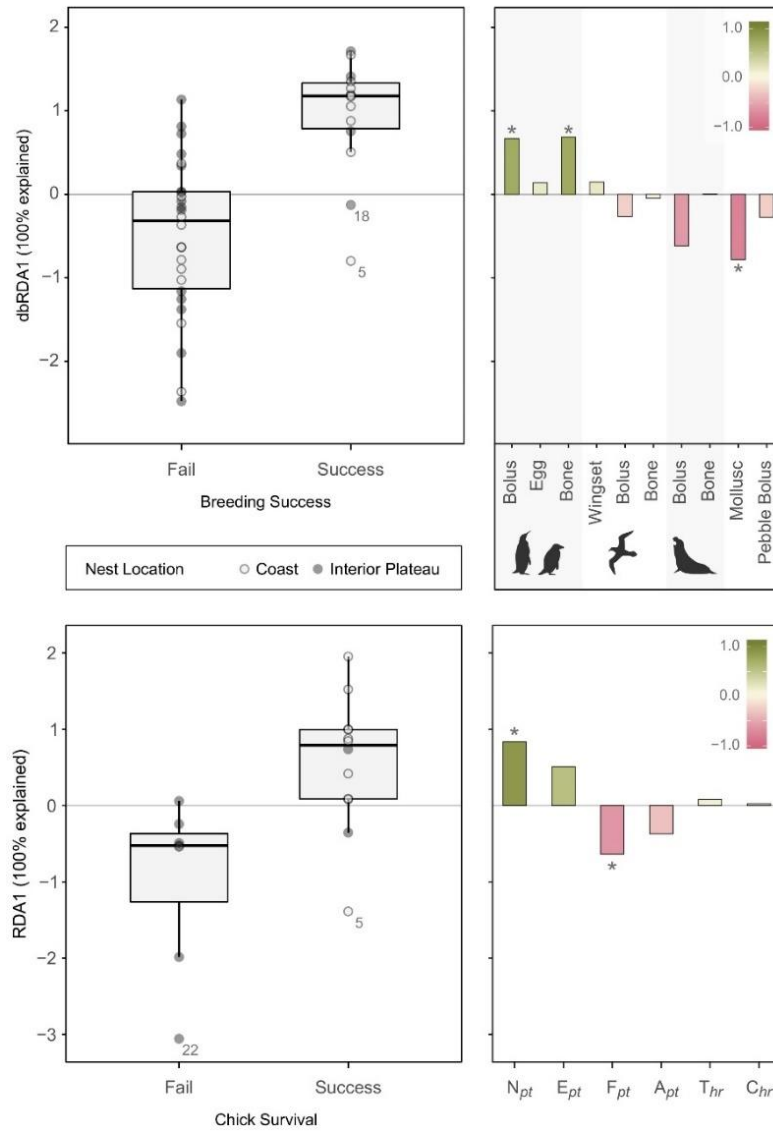
Figure 4.2. Model outputs from (distance-based) Redundancy Analysis comparing diet composition (above) and foraging strategies (below) between successful breeding skuas (fledged one or more chicks) and failed breeders (failed to fledge a chick). Scores along the first redundancy axis for nests (above) and tracked birds (below) are shown to the left, and for prey remains (above) and foraging parameters (below) to the right. Boxplots show median values (black bar); hinges extend from the first to the third quartile, encompassing the interquartile range (IQR) and whiskers extend to samples within 1.5×IQR from the hinges. Outliers are shown with nest IDs provided. * denotes dietary components or foraging parameters that were significantly ($\alpha = 0.05$) associated with breeding success in multivariate (generalised) linear modelling.

Prey remains in top right are classified as either: penguin bolus, egg or bone remains (left); burrowing petrel wingsets, bolus or bone remains (middle left); seal bolus or bone remains (middle right) or mollusc remains, or pebble bolus (right).

Foraging parameters in bottom right are: N_{pt} proportion of time spent at the nest site; E_{pt} proportion of time spent resting; F_{pt} proportion of time spent away from the nest at foraging sites or non-lake sites; A_{pt} proportion of time spent away from the nest at lake sites (non-chick rearing activity); T_{hr} total home range size (95% UD); C_{hr} core home range size (50% UD).

categories were also significantly associated with successful breeding pairs in multivariate generalised linear modelling (Appendix S4.2; Fig. 4.2). Multivariate generalised linear modelling showed seal boluses and mollusc remains were significantly more abundant in the diet of failed breeders, and along with pebble boluses and petrel wingsets were representative of failed breeding attempts in dbRDA (Appendix S4.2; Fig. 4.2).

Along the dbRDA1 axis, nests #5 and #18 were outliers from the rest of the successful breeding group, suggesting these skuas had diets that were considerably different from most successful breeders (Fig. 4.2). These two nest sites were the only two in the successful group where petrel remains were recorded (Fig. 4.1). The failed breeding group spanned a wider range of the dbRDA1 axis than successful breeders, with some failed breeders overlapping with the diet composition of the successful group (Fig. 4.2). The failed breeders with diets similar to the successful breeding group were all skuas nesting on the interior plateau, highlighting the challenges of nesting far from food sources (Fig. 4.1; Fig. 4.2).

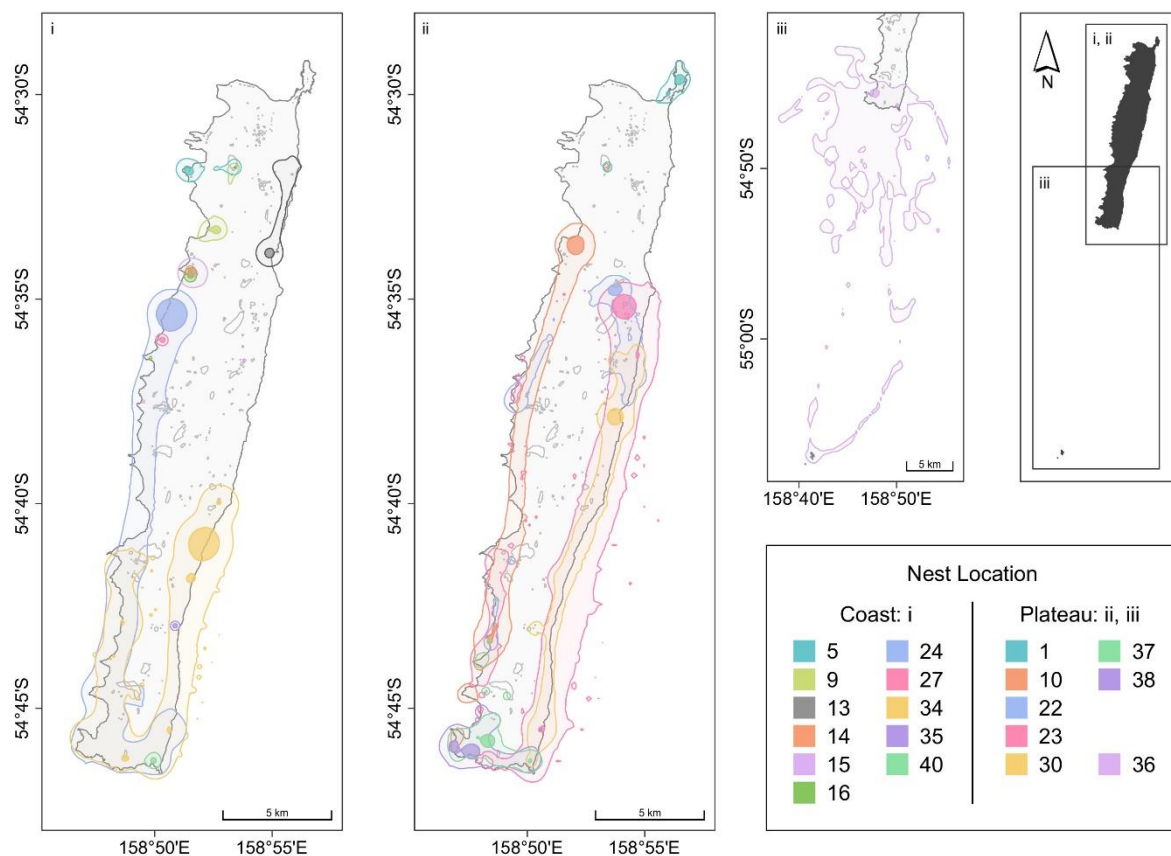**Figure 4.3.** Total home-range (light shaded area) and core home-range (dark shaded area) of GPS tracked breeding skuas represented by 95% and 50% utilisation distributions, respectively. The home-ranges of skuas nesting in areas of historically low rabbit dependence (coast) are shown in plot i. Home-ranges of skuas nesting in areas of historically high rabbit dependence (interior plateau) are shown in plots ii and iii.

Foraging strategies and chick survival

GPS deployment

On average, tracking of skuas began 13 days after chick hatching (range = 5-30 days). Of the 29 GPS units deployed, 22 birds were recaptured and 20 still had their GPS units attached. Of the 20 retrieved, one was omitted from analysis because the nest had failed at an unknown date during GPS tracking, and therefore it could not be guaranteed that tracks represented chick provisioning. This omitted bird was the only bird to forage exclusively at sea. All other birds foraged solely on the island during tracking, with the exception of one bird that made some trips to sea and travelled to the Bishop and Clerk Islets, 33km south of Macquarie Island. All 19 GPS tracked birds were included in the prey remain surveys. King Penguin (*Aptenodytes patagonicus*), Rockhopper Penguin (*Eudyptes chrysocome*) and Royal Penguin (*Eudyptes schlegeli*) colonies were visited by 26%, 42% and 74% of tracked skuas, respectively, while only 1 of the 19 tracked birds foraged at Gentoo Penguin (*Pygoscelis papua*) colonies (Appendix S4.1). Tracking birds over a two-week period allowed for a possible 4032 GPS fixes per bird. No GPS unit recorded all 4032 fixes over that period. The most fixes missed by a unit was 181 (4.5% of fixes or around 1.1hr day^{-1} of tracking).

Chick survival

Of the 19 tracked birds: seven failed to rear a chick, twelve fledged a single chick and one fledged two chicks. The cause of chick death in most cases was unknown, although, one chick (nest 22, Fig. 4.1) was observed being cannibalised by an adult skua. Cannibalism was also observed at another nest that was not part of this study (see Appendix S4.4). A further three failed nests had signs of chick predation, with partially consumed remains of a skua chick found near the nest site (nests 1, 23 & 37; Fig. 4.1). Two nests that successfully fledged one chick also had a second chick die prior to fledging and the partially consumed remains of these chicks were found at their nests, suggesting cannibalisation as a possible cause of death (nests 14 & 40; Fig. 4.1). In addition, conspecific harassment of incubating adult skuas and of chicks was commonly observed in the form of antagonistic flights and defensive displays by breeding adults both during incubation and chick rearing. In most cases, however, cannibalism as the proximal cause of death could not be confirmed based on finding a chick carcass alone due to the possibility of skuas scavenging deceased chicks.

Movement modelling

Total home-ranges varied considerably between individuals from 0.14km^2 (nest 35, Fig. 4.1; Fig. 4.3) to 131.94km^2 (nest 36, Fig. 4.1; Fig. 4.3). Core home-ranges also had a high degree of variability between individual skuas (range: 0.03-1.79km^2).

For state-based movement analysis, a three-state model was selected over a two-state model based on AIC (ΔAIC = 1674). For details on state-based model parameters, classification of GPS fixes and diel activity of Brown Skuas see Appendix S4.1.

More time spent at the nest site increases chick survival

Breeding success ($F_{1,17}$ = 2.89, P = 0.03) was retained in the final RDA of foraging strategies. However, foraging differences based on the sex of birds, chick age and tracking date were not significant at the 0.05 level and were excluded from the final model ($F_{1,16}$ = 1.45, P = 0.200; $F_{1,16}$ = 1.02, P = 0.385; $F_{1,16}$ = 0.77, P = 0.59; respectively). Multivariate linear modelling also found no significant difference in the foraging strategies of birds based on the latter three variables (Appendix S4.2). PERMDISP showed there was no significant difference in the multivariate dispersion of foraging strategies of the two breeding groups ($F_{1,17}$ = 0.305, P = 0.59; Appendix S4.3).
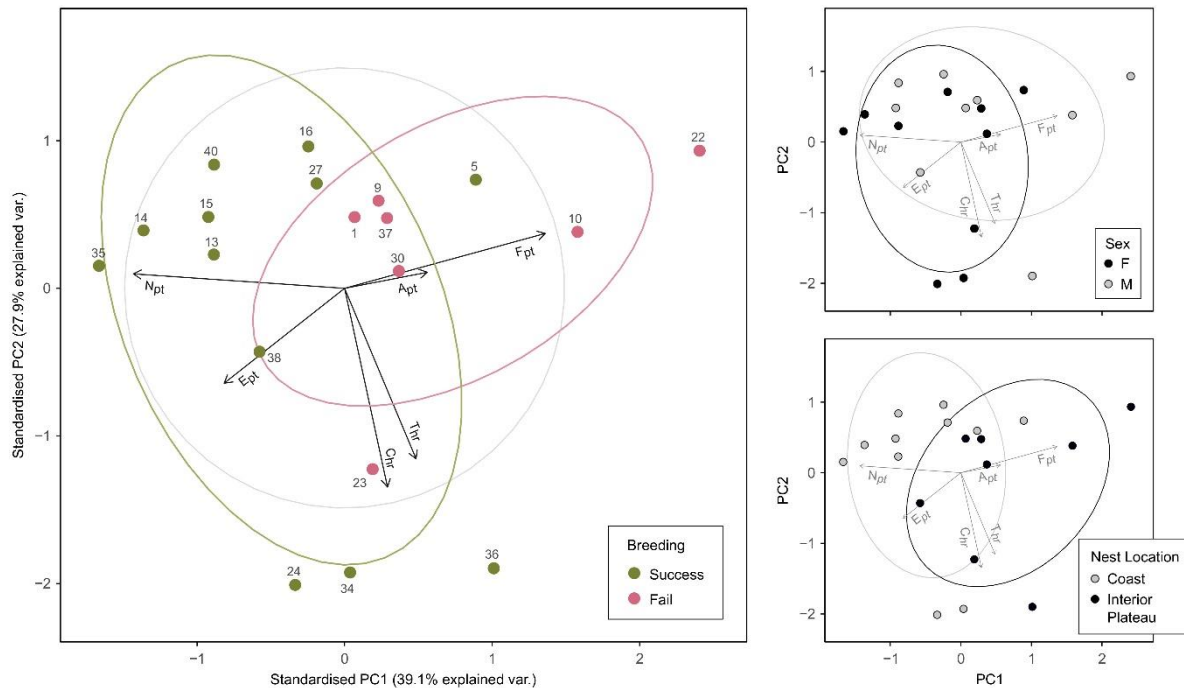
Figure 4.4. Principal component analysis of the foraging parameters used to describe foraging strategies of tracked birds. Foraging strategies are group by breeding success (left), sex (top right; M: Male, F: Female) or nest location (bottom right), with normal ellipses shown for groups. Vectors from the origin show the correlation of each foraging parameter with the first two PCs, and a correlation circle of maximum extent (cos^2 = 1) is provided in the main plot (left). Nest IDs shown in grey relate to those in Figure 4.1.

Foraging parameters are: **N$_{pt}$** proportion of time spent at the nest site; **E$_{pt}$** proportion of time spent resting; **F$_{pt}$** proportion of time spent away from the nest at foraging sites or non-lake sites; **A$_{pt}$** proportion of time spent away from the nest at lake sites (non-chick rearing activity); **T$_{hr}$** total home range size (95% UD); **C$_{hr}$** core home range size (50% UD).

RDA showed successful breeders spent more time at their nest territory, less time foraging away from the nest site and expended less energy than failed breeders (Fig. 4.2). Linear modelling confirmed that successful breeders spent significantly more time at the nest and less time foraging (Appendix S4.2; Fig. 4.2). Along the RDA1 axis as well as in PCA, the foraging strategy of the skua from nest #5 differed from the other successful breeders and was behaviourally more aligned with failed breeders (Fig. 4.2; Fig. 4.4). This skua was unique from all other tracked birds as it was from the only nest where Blue Petrels were found in prey remains and spent greater periods at lake sites than all other skuas (Appendix S4.1). Skuas were clearly separated along the first two PCA axes by nesting region (either interior plateau or coastal areas), with coastal nesting skuas spending more time at their nest site and having smaller home-ranges (Fig. 4.4).

Changes to foraging landscape: legacy effects of rabbit eradication

Skuas nesting on the interior plateau had wide-ranging foraging strategies, a diet that included coastal prey as well as burrowing petrels, and largely visited coastal areas when not at their nest site (Fig. 4.1; Fig. 4.3). In contrast, coastal nesting skuas, foraged predominantly on penguins and seal carrion often close to their nest site (Fig. 4.1; Fig. 4.3), as was observed in historic surveys (Jones & Skira 1979). Skuas nesting on the interior plateau, where historically skua diet had a high dependence on rabbits as prey, travelled a wider area, and visited more locations compared to skuas
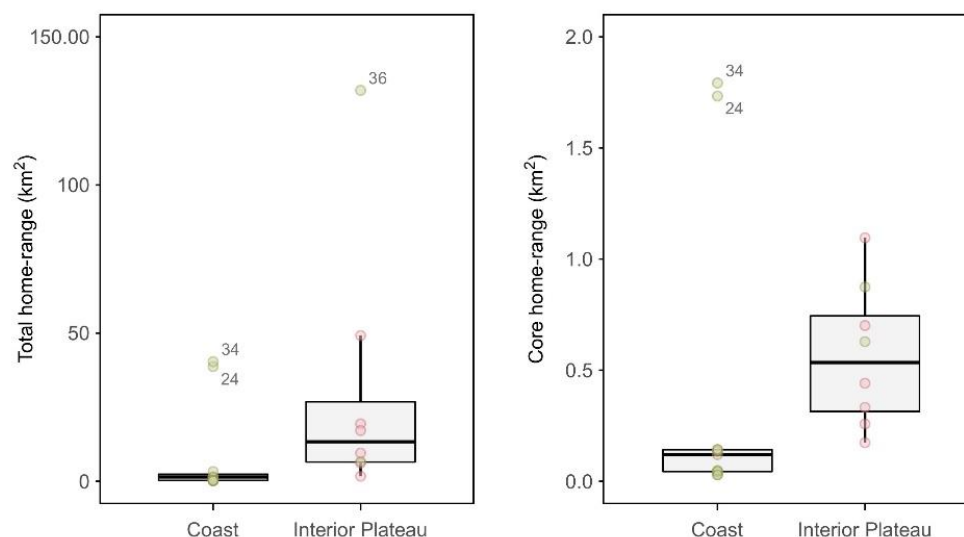
Figure 4.5. Total home-range (95% utilisation distribution (UD); left) and core home-range size (50% UD; right) of skuas nesting in areas of historically low rabbit dependence (coast) or areas of historically high rabbit dependence (interior plateau). Boxplots show median values (black bar); hinges extend from the first to the third quartile, encompassing the interquartile range (IQR) and whiskers extend to samples within 1.5×IQR from the hinges. Outliers are shown with nest IDs provided. Points are coloured by chick survival, with successful breeders (those that fledged one or more chicks) in olive and failed breeders in rose.

nesting in coastal areas. This resulted in skuas on the interior plateau having significantly larger mean total home-range (U = 13, P = 0.005) and mean core home-range sizes (U = 16, P = 0.01) compared to skuas nesting on the coast (Fig. 4.3; Fig. 4.5).

There was a significant correlation between nesting region and chick survival ($\chi^2_{1,n=29}$ = 4.30, P = 0.038), but not with overall breeding success ($\chi^2_{1,n=40}$ = 2.04, P = 0.154). Skuas nesting on the interior plateau had lower chick survival than those nesting on the coast, however both had similar overall breeding success. Of the 15 birds nesting on the coast and used in GPS deployment only five failed to rear at least one chick to fledging, while of the 14 birds nesting on the plateau 11 failed.

Despite plateau nesting skuas having lower chick survival and a larger mean home-range size, skuas with some of the largest home-range sizes successfully reared at least one chick to fledging in both coastal and plateau areas (Fig. 4.5).

Discussion

The diet and foraging strategies of Brown Skuas, a top-order predator on Macquarie Island, affect their reproductive fitness. Skuas that successfully fledged chicks had specialised diets primarily targeting penguin prey, their diet did not include poorer quality, less abundant or ephemeral food sources such as Antarctic Prions, seal carrion, and molluscs. In a few cases, skuas specialising on petrels were successful in rearing their young, however this depended on the species of petrel targeted. In contrast to successful breeders, skuas that failed in their breeding attempt had generalist diets over the late incubation and chick rearing periods, comprised of seal carrion, molluscs and pebbles (possibly reflecting parasitism of seal milk in their diet).

In addition to diet, the foraging strategies of breeding skuas also affected their reproductive fitness. Skuas that undertook longer foraging trips away from the nest site and expended greater energy during chick rearing had poorer chick survival than those that spent more time at their nest site when raising their young.

Diet specialisation and breeding success

Diet quality influenced the overall breeding success of skuas. Penguin prey remains were the most frequently recorded dietary component for skuas regardless of whether their nest was located on the coast or interior plateau. On Macquarie Island, large penguin colonies are a reliable, abundant, and high-quality food source for skuas, with the eggs and chicks of Rockhopper, Royal and King Penguins available throughout most of the skua's chick rearing period (Jones & Skira 1979; Hindell *et al.* 1995). The breeding colonies of these three penguin species have a strong effect on the distribution and density of skua nests across Macquarie Island (Chapter 3). Penguins are important

prey for skuas and likewise, skua predation has a strong negative impact on penguin breeding success, in some cases accounting for a third (37%) of breeding failures at Rockhopper Penguin colonies (Hull *et al.* 2004).

Specialisation on a single food resource often benefits breeding success of skuas (Votier *et al.* 2004), however, the diets of skuas on Macquarie Island do differ from the diets of Brown Skuas at Hope Bay on the Antarctic Peninsula (Borghello *et al.* 2019). Here breeding skuas had a higher proportion of penguin eggs, fish and molluscs in their prey remains (boluses) compared with non-breeders, which had higher proportions of penguin bones and eggs (Borghello *et al.* 2019). This difference may be due to differences in timing of surveying, as penguin eggs appeared to be an important food source for breeding skuas on Macquarie Island during the early incubation stage, however, this could not be quantified during our study. Prevalence of molluscs and fish however, likely reflect differences in local prey availability and represent less reliable food sources on Macquarie Island compared to the abundance of seabird prey.

Dietary specialisation on penguins is common among Brown Skuas on many sub-Antarctic Islands (Reinhardt *et al.* 2000; Graña Grilli & Montalti 2012; Graña Grilli *et al.* 2014; Graña Grilli & Montalti 2015). On Macquarie Island, penguins are the most ubiquitous prey of skuas, including over 1.5 million Royal Penguins (*Eudyptes schlegeli*); however, availability of penguin prey is spatially and temporally limited across the island (Salton *et al.* 2019; Pascoe *et al.* 2020). The abundance of penguin feather boluses at Brown Skuas nests has been attributed to a gut-cleaning function as well as diet, leading to a suggestion diet studies using this method over-represent adult penguins in skua diet (Graña Grilli & Montalti 2015). This may be the case for South Polar Skuas, which often specialise on a fish-based diet (Trivelpiece & Volkman 1982; Reinhardt 1997b; Santos *et al.* 2012), however, this interpretation is not directly transferable to Brown Skuas that frequently specialise on penguin eggs, chicks and adults (Trivelpiece *et al.* 1980; Hahn & Bauer 2008). The predominance of penguin remains in the stomach contents of Brown Skua chicks, further supports that penguin feather boluses reflect a penguin-based diet for Brown Skuas (Reinhardt 1997b; Graña Grilli *et al.* 2014).

Only one of the birds tracked during this study (nest #5) visited a Gentoo Penguin colony. This nest was located close to one of the largest Gentoo colonies on the island and penguin remains were found at the nest. Gentoo Penguin eggs on Macquarie Island hatch prior to the chick guard phase of skuas (Hindell *et al.* 1995). As a result, their eggs are available as food during the skua's incubation period, but Gentoo chicks are only available as prey for chick provisioning at the start of the skua chick rearing period for some skuas. This mismatch in timing of breeding phenologies combined with

their small population size (~2,500 breeding pairs island wide) relative to the other three penguin species found on Macquarie Island may explain the lack of skua activity recorded around Gentoo Penguin colonies in this study (see also:Hindell *et al.* 1995; Pascoe *et al.* 2020).

All methodologies used for dietary analysis contain biases and as such there are caveats to any particular method (Barrett *et al.* 2007). For our study, prey remain searches were limited to around the nest, which specifically documented the hard parts of food processed back at the nest (Santos *et al.* 2012). This method is biased against soft prey items (e.g. animal tissue and seal milk), and food that was processed away from the nest. Additionally, at failed nest sites this method only includes prey remains up until the point of nest abandonment. Because failed nest sites are typically occupied for a shorter length of time compared with successful nest sites (Carneiro *et al.* 2016a), we would expect a greater diversity of prey and higher counts of prey items to accumulate over time at successful nests. Yet failed nests had higher counts for poor quality or less reliable diet components (mollusc remains, pebble boluses and carrion), and a tendency towards a greater diversity in dietary composition. These trends away from expected biases in the data support our interpretation that successful breeders feed mainly on higher-quality prey, predominantly penguins, and failed breeders typically have lower-quality generalist diets. Dietary specialisation has been found to benefit breeding fitness of Brown Skuas on South Georgia as well as other skua species (Votier *et al.* 2004; Anderson *et al.* 2009).

Foraging and chick survival

Foraging strategies influenced chick survival, with some aspects of foraging behaviour having a greater effect than others. In general, the home-range size of skuas didn't affect chick survival, provided time spent away from the nest site was kept to a minimum. This highlights the importance of efficient foraging practices when nesting far from foraging sites. On Macquarie Island skuas largely converged on coastal penguin colonies making foraging efficiency a premium for skuas nesting on the interior plateau.

Despite plateau nesting skuas having lower chick survival compared to coastal nesting skuas, overall breeding success was comparable between the two. This suggests coastal skuas had lower hatch success. The relationship between nest proximity to foraging grounds and these two components of breeding success (hatch success and chick survival) mirrors that of skuas on South Shetland Island. Hahn and Peter (2003) compared breeding success between skuas that defended feeding territories around penguin colonies on the South Shetland Islands and those that intruded territories for access to food. Similar to our study they found intruding skuas had better hatch success, poorer chick

survival and equivalent overall breeding success compared to skuas that defended feeding territories (Hahn & Peter 2003).

Impact of rabbit eradication

Prior to the eradication of rabbits, the diets of breeding skuas were spatially partitioned between coastal and plateau nesting regions, with nests across the island focussing on locally available prey (Jones & Skira 1979). For coastal skuas this was primarily penguin prey and seal carrion, while on the plateau, skuas also targeted rabbits and petrel prey. Similar spatial partitioning of diets based on local prey has also been observed on Antipodes Island where coastal nesting skuas targeted penguin colonies and inland nesting skuas targeted petrels (Moors 1980).

The current foraging landscape for skuas on Macquarie Island is dominated by abundant coastal prey, namely penguin colonies. Because of the current focus on coastal prey, foraging movements are now spatially segregated between skuas nesting on the plateau and those nesting on the coast. Long distance foraging strategies now dominate the habits of plateau nesting skuas, while most coastal nesting skuas still forage locally. The differences in foraging strategies between the two areas have implications for the amount of time skuas can partition between the nest site and foraging areas and as a result plateau nesting skuas had lower chick survival compared with their coastal counterparts.

The legacy of rabbit eradication on skua foraging strategies has resulted in plateau nesting birds having lower chick survival than their coastal counterparts. Plateau nesting skuas now spend more time undertaking foraging trips, use more energy searching for food and as a result spend less time at the nest site guarding chicks.

Implications for disease transmission

Due to their wide-ranging migratory movements and catholic foraging behaviours, skuas have been implicated in the transmission of diseases for several marine mammals and seabirds (Miller *et al.* 2008; Hurt *et al.* 2014; Pinpimai *et al.* 2018; Gamble *et al.* 2020). The eradication of rabbits from Macquarie Island led to some skuas travelling further and accessing a greater number of prey colonies in search of food. These larger searches increase the risk of skuas transmitting diseases of conservation significance including avian influenza A viruses, avian cholera bacterium and Klebsiella pneumoniae, between spatially isolated colonies of many native prey species, particularly the endemic Royal Penguin, as their colonies were visited frequently by skuas (Miller *et al.* 2008; Pinpimai *et al.* 2018; Gamble *et al.* 2020). The risk of increased diseased transmission among prey

communities due to changes in the foraging behaviour of predators and scavengers should be a consideration when planning future pest eradications or pest control measures.

Skuas as sentinels of recoveries

As top-order predators, skuas are useful sentinel species for monitoring changes in the abundance of threatened or cryptic prey species (Jones 1980; Cerfonteyn & Ryan 2015; Pacoureau *et al.* 2019). Studies of skua diet have revealed declines in the abundance of burrowing petrel species at Mayes Island in the Kerguelen Archipelago (Pacoureau *et al.* 2019).

Currently, burrowing petrels are targeted by a small number of breeding skuas on Macquarie Island. For skuas that did consume burrowing petrels, their breeding success was linked to the species of petrel targeted and the degree of specialisation on that target species. Whether specialising on a particular petrel species is a successful foraging strategy for breeding skuas may depend on the overall abundance, distribution, density and/or burrow-occupancy of the petrel species (Ryan *et al.* 2009; Cerfonteyn & Ryan 2015; Pacoureau *et al.* 2019). Monitoring for future increases in the number of breeding skuas targeting petrels and trends in their breeding performance would be useful indicators of species-specific petrel recovery across the island.

Blue Petrels have been recorded in the middens at skua nests on Macquarie Island from as far back as 1967 at the same location as the pair in this study (nest 5, Fig. 4.1), Langdon Point (Merilees 1971; Jones 1980; Brothers 1984). Interestingly, a lone nest occupied by a pair of skuas targeting Blue Petrels has been recorded in a similar location to the nest used in this study adjacent the Langdon Point Blue Petrel colony since at least 1993 (Brothers & Bone 2008). White-headed Petrels and Antarctic Prions have been recorded in skua diet on Macquarie Island since 1974 (Jones 1980). The distribution of prey remains of these two species found at nests broadly followed the distributions and relative densities of these petrels (Brothers 1984; Bird *et al.* 2021).

Currently, skua diet and breeding success suggest Blue Petrel and White-headed Petrel populations on the island are patchy but with locally dense colonies. While only a small proportion of the skua population consumed these petrels, both nests successfully fledged chicks. Antarctic Prions on the other hand, appear to be widespread but have either lower burrow occupancy or burrow density, or are more difficult to access than Blue Petrels and White-headed Petrels; because although many skua middens contained prion remains, most of these skuas had generalist diets and all failed in their breeding attempt. Brothers (1984) reported mean burrow densities of White-headed Petrels and Blue Petrels 2.5 and 50 times higher than that of Antarctic Prions, respectively; however, Antarctic Prions had by far the largest distribution, and overall abundance on the island. These differences in

burrow density and distribution of petrels support our observations of predation rates on petrels and their association with skua breeding success.

Conclusion

The diet and foraging strategies of Brown Skuas on Macquarie Island impact individual breeding fitness and are closely linked to nest location within the island's foraging landscape. Here we demonstrate how examining diet and foraging strategies can quantify the feeding actions of individuals within a complex foraging landscape. Our results also highlight how the use of ecologically informed foraging parameters in constrained ordination can reveal aspects of foraging decisions that influence an individual's breeding success.

Six years since the eradication of rabbits from Macquarie Island foraging movements and chick survival of breeding skuas continues to be impacted. These changes in skua behaviour on Macquarie Island, underpin their lower breeding success in the years since rabbit eradication (Chapter 3). Changes to the foraging landscape of top-order predators not only affects their own diet and breeding behaviour but has knock-on effects for native prey species, through changes to predation rates and the role of predators in disease transmission.

Appendix S4.1: State-based Modelling and Classification of GPS Fixes.

Methods

The number of states, either two or three, in the state-based model used to inform foraging parameters was selected based on AIC.

The location of GPS fixes used to inform foraging parameters were classified based on histograms (with 5m intervals) of the distance of GPS fixes to the nearest lake or penguin colony after excluding GPS fixes at the nest site (within 100m of the nest).

In addition, GPS fixes by location classification were split by the diel cycle to compare activity of coastal and inland nesting skuas over dawn, dusk, night, and day.

Results

Based on a comparison of AIC values of state-based models a 3-state model (resting, short flight and long flight) with no covariates was selected to inform foraging parameters (Table S4.1).

Histograms of GPS fixes all had peaks within 5m of lakes and penguin colonies of all species (Fig. S4.1; Fig. S4.2). As such a 5m cut-off was used in conjunction with the activity state of a GPS fix (either resting or short-flight, excluding GPS fixes modelled as the long flight state) to define whether a skua's position was classed as being at a lake (or penguin colony) or not.

All GPS fixes outside the nest site, not within 5m of a lake and in a resting or short flight activity state were defined as foraging when defining foraging parameters (including those within 5m of penguin colonies). GPS fixes at penguin colonies (in either a resting or short flight state) are shown here for detail, however, because all other potential foraging locations are unmapped, penguin foraging was not separated from other foraging activity when defining foraging parameters. Only 1 of the 19 tracked skuas was recorded foraging at Gentoo Penguin colonies (Table S4.2). In contrast, 14 of these visited Royal Penguin colonies (Table S4.2).

Coastal nesting skuas spent a greater portion of their time at the nest site, while skuas nesting on the inland plateau spent a greater portion of time in the long-flight state, implying greater reliance on travelling (Fig. S4.3). Time spent at lakes was minimal for all skuas (Fig. S4.3). Compared with coastal nesting skuas, plateau nesting skuas conducted more long flights at dawn and during the day and overnighted at sites away from the nest site more often (Fig. S4.4).

Tables

Table S4.2. Mean parameters of step length and turning angle, AIC and delta AIC of two state-based models of GPS locations.

Model	Step Length		Turning Angle		Max Log-Likelihood	AIC	ΔAIC
	Mean (m)	S.D.	Mean	Conc.			
2-State					30966.7	-61907.41	16744.00
State 1	*15.49*	*14.09*	*-180°*	*0.59*			
State 2	*710.97*	*1054.34*	*-177°*	*0.03*			
3-State					39348.7	-78651.41	0.00
State 1	*9.36*	*6.96*	*-179°*	*0.54*			
State 2	*52.50*	*49.11*	*179°*	*0.62*			
State 3	*1262.42*	*1595.46*	*-2°*	*0.35*			

Table S4.3. The number of GPS fixes recorded within 5m of a penguin colony by species for each tracked skua. Only GPS fixes classified as short flight or resting state were counted.

Nest ID	Gentoo	King	Rockhopper	Royal	Number of species visited
1	0	0	0	0	0
5	444	0	0	0	1
9	0	57	0	0	1
10	0	0	9	7	2
13	0	22	0	73	2
14	0	0	0	725	1
15	0	0	0	164	1
16	0	0	12	232	2
21	0	0	0	105	1
22	0	0	0	133	1
23	0	0	10	84	2
26	0	0	0	0	0
29	0	4	6	137	3
33	0	1	14	104	3
34	0	2771	0	0	1
35	0	0	135	196	2
36	0	0	4	233	2
37	0	0	4	120	2
39	0	0	0	2630	1
Number of tracked skuas	1	5	8	14	

Figures
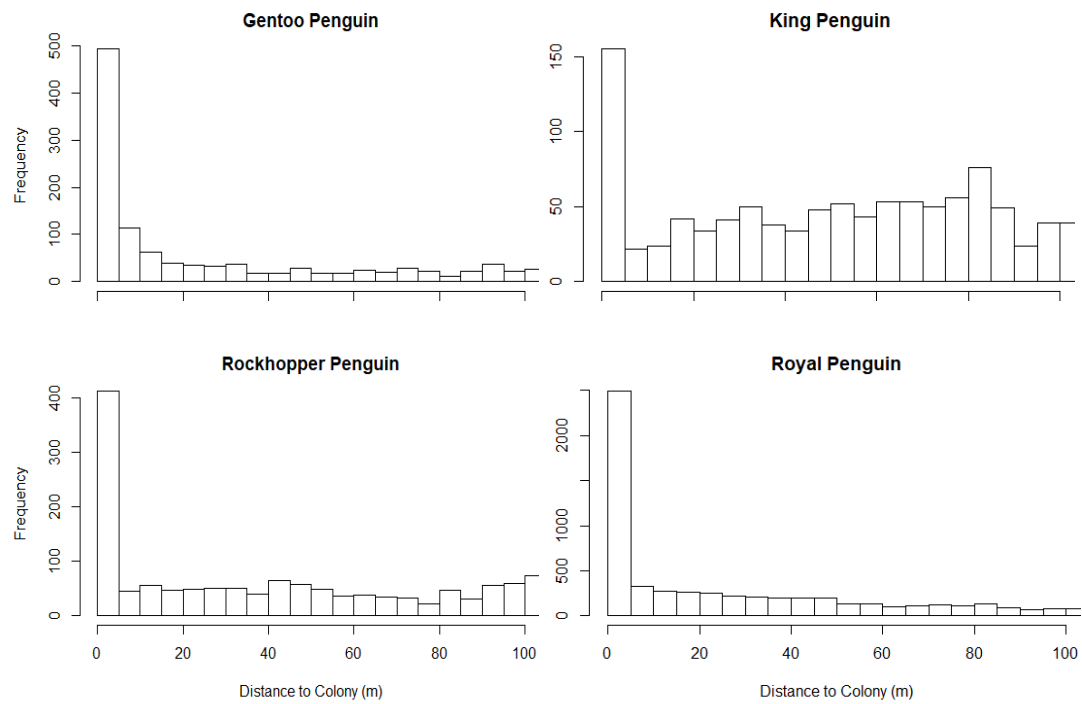
Figure S4.1. Histogram of distance to penguin colonies for all GPS fixes outside nest sites (100m radius of nests).
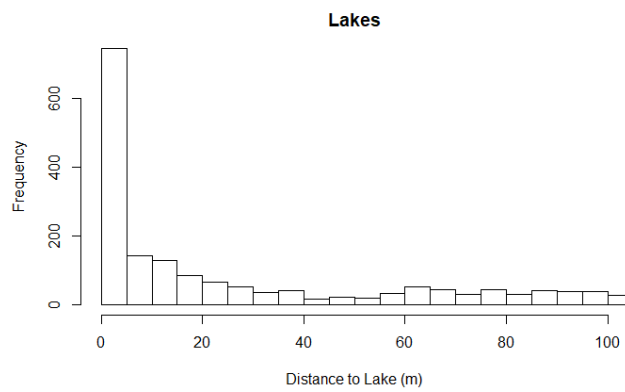
Figure S4.2. Histogram of distance to lake for all GPS fixes outside nest sites (100m radius of nests).
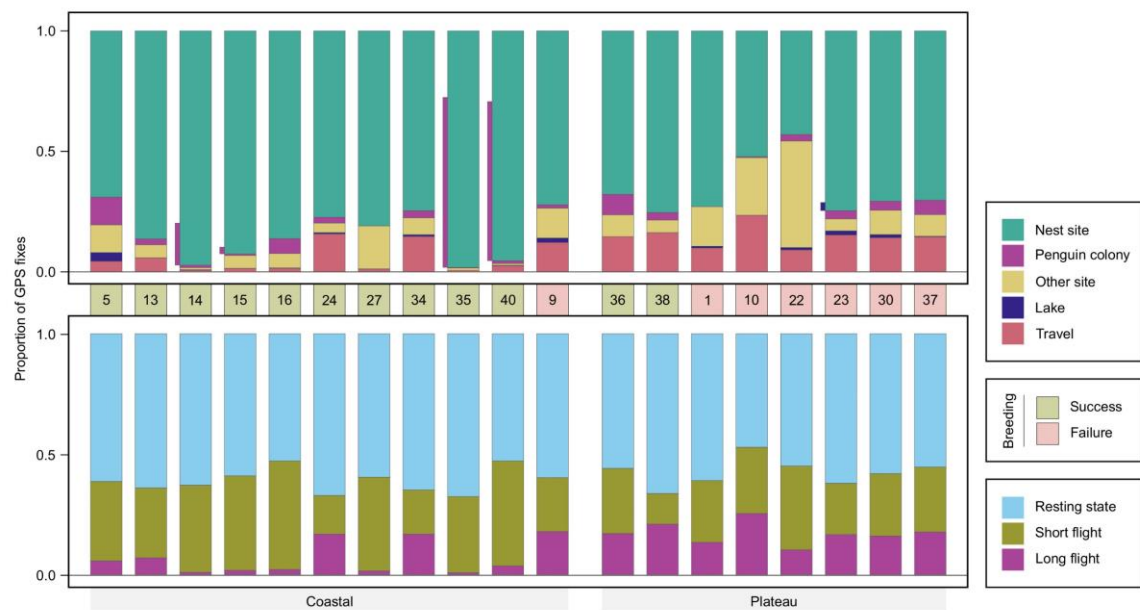
Figure S4.3. Proportion of GPS fixes for each Brown Skua classed by location (upper) and movement state (lower). Nest number and breeding success are shown (middle).
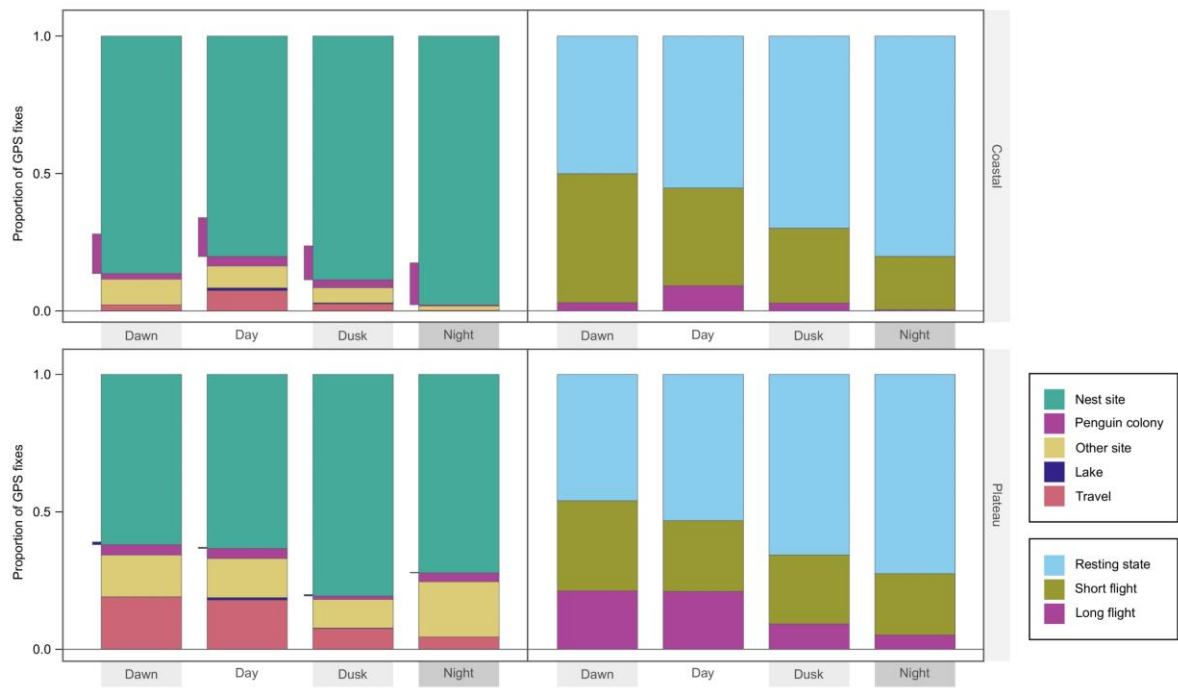
Figure S4.4. Proportion of GPS fixes for Brown Skua nesting on coastal areas (upper) and the interior plateau (lower) classed by location (left) and movement state (right).

Appendix S4.2: Multiple (Generalised) Linear Modelling for multivariate analysis

Methods

For both diet composition and foraging strategy, the significance of all explanatory variables (cut-off α = 0.05) was tested by comparing single variable models for each explanatory variable against the null model using Likelihood-ratio tests (LRT). The sole explanatory variable tested in dietary analysis was breeding success (two-level variable: failed breeders, nests that did not rear a chick; and successful breeders, nests that reared one or more chicks). For foraging strategies four explanatory variables were tested: chick survival (two-level variable: chick death, nests where the chick did not survive to fledging; and chick fledging, nests that reared one or more chicks to fledging) as well as the sex of tracked birds, an estimate of chick age at the start of tracking and the start date of tracking.

For analysis of the relationship between individual response variables and explanatory variables in the best model, a final model for analysis was selected based on lowest sum Akaike's Information Criterion (ΣAIC) for both dietary and foraging analysis. The ΣAIC is the sum of all AIC values of the multiple linear sub-models (one for each response variable) in multivariate analysis. If necessary, the marginal effect of breeding success and chick survival in final models was tested after accounting for any other significant variables.

Results

Diet composition

Compared to the null model, the model including breeding success as the sole explanatory variable had a (marginally) lower ΣAIC and was therefore retained for analysis (Table S4.3). The difference between the diets of the two breeding categories was also marginally significant based on LRT (P = 0.054; Table S4.3). Diets of successful and failed breeders were separated by successful breeders having more penguin boluses and bones, and less mollusc remains in their prey middens than failed breeders (Table S4.4).

Foraging strategies

Based on LRT comparisons with the null model, chick survival was the only significant explanatory variable for foraging strategies (P < 0.05; Table S4.5). The model containing only chick survival also had the lowest ΣAIC of all the models tested and was therefore used in analysis (Table S4.5). The foraging strategies of skuas that either successful reared at least one chick to fledging or lost all their chicks prior to fledging were separated by successful breeders spending more time at home and less time foraging than failed breeders (Table S4.6).

Tables

Table S4.3. Multiple-generalised linear models of diet composition used in multivariate model selection. Statistics shown are: sum Akaike's Information Criterion (ΣAIC); the difference in ΣAIC from lowest ΣAIC (ΔAIC); the alternative model used in Likelihood-ratio Testing (with degrees of freedom and residual degrees of freedom in test); Likelihood-ratio test statistic (LRT) and P-value of LRT. The final model used in analysis, based on lowest ΣAIC, is highlighted in bold. For full details of explanatory variables see methods.

Model	Σ AIC	ΔAIC	Alternative model ($_{df, res. df}$)		LRT (P-value)
Success	**1152.2**	**0**	***null***	$_{(1,38)}$	**20.9 (0.054)**
null	1153.1	0.9	-	-	

Table S4.4. Likelihood-ratio Tests (LRT) of individual diet components between breeding groups (successful and failed breeders). Dietary components that were significantly different between successful and failed breeders are highlighted in bold.

Dietary Component		LRT (P-value)
Penguin	**Bolus**	**3.53 (0.02)**
	Egg	0.10 (0.79)
	Bone	**3.44 (0.05)**
Petrel	Wingset	2.76 (0.14)
	Bolus	0.75 (0.41)
	Bone	0.25 (0.63)
Seal	Bolus	2.67 (0.09)
	Bone	0.13 (0.76)
Mollusc		**4.61 (0.03)**
Pebble Bolus		2.66 (0.09)

Table S4.5. Multiple-linear models of foraging strategies used in multivariate model selection. Statistics shown are: sum Akaike's Information Criterion (ΣAIC); the difference in ΣAIC from lowest ΣAIC (ΔAIC); the alternative model used in Likelihood-ratio Testing (with degrees of freedom and residual degrees of freedom in test); Likelihood-ratio test statistic (LRT) and P-value of LRT. The final model used in analysis, based on lowest ΣAIC and model significance, is highlighted in bold. For full details of explanatory variables see methods.

Model	Σ AIC	ΔAIC	Alternative model ($_{df, res. df}$)		LRT (P-value)
Survival	**345.2**	**0**	***null***	*(1,17)*	**19.6 (0.02)**
Age	352.9	7.7	*null*	*(1,17)*	11.9 (0.14)
Sex	353.7	8.5	*null*	*(1,17)*	11.1 (0.18)
Date	357.4	12.2	*null*	*(1,17)*	7.4 (0.39)
Survival + age + date + sex	355.1	9.9	*null*	*(4,14)*	45.7 (0.09)
null	352.8	7.6	-	-	
Sex + survival	346.7	1.5	*success*	*(1,16)*	10.54 (0.19)
Age + survival	349.5	4.3	*success*	*(1,17)*	7.362 (0.38)

Table S4.6. Likelihood-ratio Tests (LRT) of individual foraging parameters between breeding groups (successful and failed breeders). Foraging parameters that were significantly different between successful and failed breeders are highlighted in bold.

Foraging Parameter	LRT (P-value)
N_{pt}	**9.78 (0.003)**
E_{pt}	3.09 (0.12)
F_{pt}	**5.09 (0.03)**
A_{pt}	1.56 (0.27)
T_{hr}	0.07 (0.89)
C_{hr}	0.01 (0.94)

Foraging parameters are: N_{pt} proportion of time spent at the nest site; E_{pt} proportion of time spent resting; F_{pt} proportion of time spent away from the nest at foraging sites or non-lake sites; A_{pt} proportion of time spent away from the nest at lake sites (non-chick rearing activity); T_{hr} total home range size (95% Utilisation Distribution (UD)); C_{hr} core home range size (50% UD).

Appendix S4.3: Plots of multivariate dispersion on principal coordinates axes.

Figure S4.5. Principal coordinate analyses used in dispersion tests comparing diets of successful and failed breeding skuas.
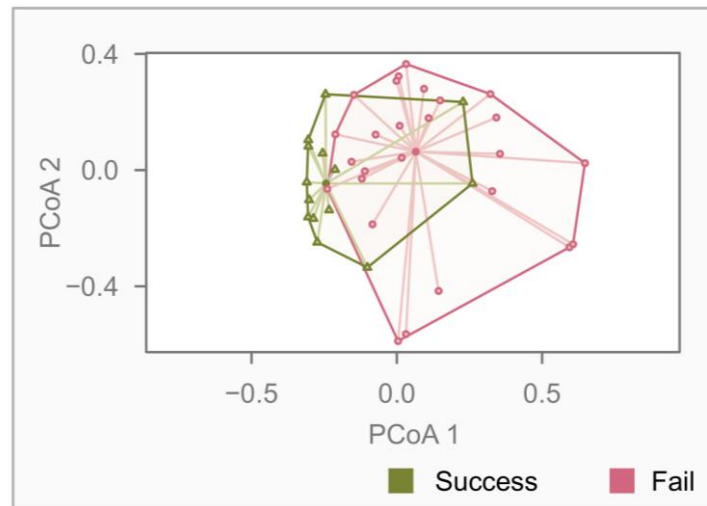
Figure S4.6. Principal coordinate analyses used in dispersion tests comparing foraging strategies of successful and failed breeding skuas.
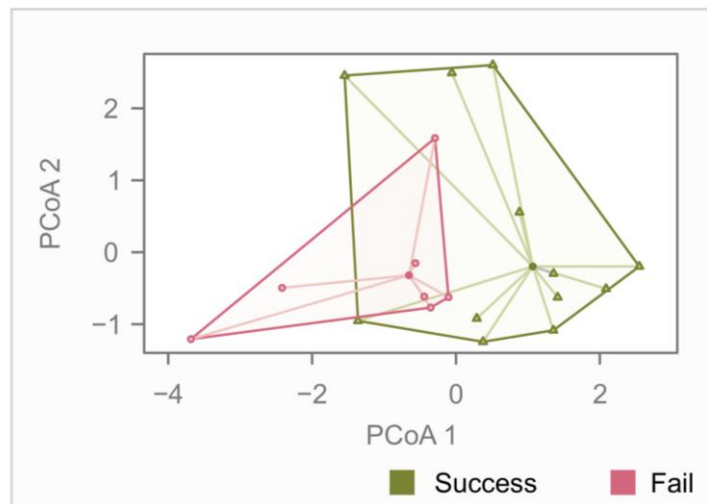
Appendix S4.4: Observation of chick cannibalism at skua nest (23/01/2018)

Cannibalism is not unknown in Brown Skuas (*Stercorarius antarcticus lonnbergi*), but recorded observations are rare. During the 2017-2018 breeding season on Macquarie Island, cannibalism of skua chicks by adults was directly observed twice, with five additional carcasses and two skua eggs found in the prey middens of other nests. Multiple instances of skuas harassing conspecifics during incubation and chick rearing were also observed. Cannibalisation of chicks has a direct impact on the breeding success of skuas and may be a manifestation of prey scarcity on the island following a recent eradication of invasive prey.

In 2011, Europeans rabbits (*Oryctolagus cuniculus*) and all mammalian pests were eradicated from Macquarie Island to the benefit of many threatened plant and animal species. However, Brown Skuas, the island's top-order predator, once preyed upon rabbits. Since the eradication, skuas returning from their annual migration to breed each summer arrive to an altered foraging landscape on Macquarie Island.

The introduction and ultimate eradication of rabbits both caused rapid disruptions to food web interactions on Macquarie Island. The consequences of both are long-lasting and while most responses to the eradication have been positive, our photo highlights how eradications might not always return systems to a historical norm.

Chapter 5

The influence of Brown Skua predation pressure

on recovering petrel populations

Tristan Skuas can also get at petrels by digging through the soft peaty ground to open up burrows if they hear a petrel. I was surprised to discover that a hunting skuas would often ignore my torch beam and allow me to watch as it walked from burrow entrance to burrow entrance, putting its head into each in turn, until it found one where it could hear a petrel moving inside. It would then start to pull the burrow open with its bill, twisting and turning and tugging at the old plants roots until it could pluck the petrel from the burrow.

Furness (1987)

Abstract

Mechanistic and structural changes to ecosystems can be difficult to quantify following invasive species eradication. Prior to their eradication in 2011, invasive European rabbits (*Oryctolagus cuniculus*) impacted the habitat of burrowing petrel species on Macquarie Island through extensive grazing and burrowing. The eradication of rabbits was anticipated to facilitate a recovery in burrowing petrels. However, both rabbits and petrels were prey for a native predator the Brown Skua (*Stercorarius antarcticus lonnbergi*). It was not known if the removal of rabbits would lead to increased predation pressure on petrels, and thereby inhibit their recovery. We modelled the density-dependent predation rate of skuas on Antarctic Prions (*Pachyptila desolata*) to assess the risk skua predation poses to the recovery of burrowing petrels on Macquarie Island.

We model changes in skua predation pressure in response to changes in prion density in a space-for-time sampling design on Macquarie Island using field surveys of burrow density and 'sign' of skua-prion predation events. We then used this to estimate the number of prions killed by skuas in a season and generalise this relationship to assess what percentage of petrel populations may be impacted by the current levels of skua predation pressure on Macquarie Island.

Skuas consumed an estimated 27096 prions (95% CI: 16,124-195,628) in a season, which represents 11% (95% CI: 7-82%) of the breeding population, noting this includes non-breeding birds and chicks.

We found skua predation on prions resembled Holling's Type III functional response curve. This means at low prey densities prions were spared from excessive predation pressure. Applying this relationship to all burrowing petrel species using published growth rates of petrels, we found skuas could restrict the recovery of around 1 in every 28 petrel species to low densities (3.6% of species, 95% Confidence Interval: 0.5-31.2) but are unlikely to inhibit recovery altogether. Of the species restricted to low densities by skuas, over three quarters (86%) were trapped in a 'predator pit' meaning their population could potentially reach higher numbers if predation pressure was reduced.

We quantify the risk to petrel recovery posed by Brown Skua predation on Macquarie Island in response to the eradication of rabbits. These findings suggest that the risk posed to Antarctic Prion recovery on Macquarie Island by Brown Skuas is relatively low. Skua predation would be insufficient to prevent the re-establishment and/or recovery of species that have populations already above the threshold of a predator pit or high intrinsic growth rates. However, skuas could limit full recovery of petrel species that have low intrinsic growth rates. In these cases, assisted recovery may help petrels recover to historic numbers. Our approach is relevant and applicable to future eradication projects where there maybe uncertainty regarding the role of native predators in supressing the recovery of native prey.

Introduction

Eradicating invasive species has had significant success globally. Through eradication, ecosystems can restructure in unexpected ways and in some instances reach an undesired or unrestored state (Zavaleta *et al.* 2001; Kopf *et al.* 2017). Eradicating an invasive yet significant prey species can increase predation pressure on native prey populations and potentially cause greater harm to the conservation species intended for protection (Bode *et al.* 2015; Nur *et al.* 2019). Novel predation on native species is often the impetus for eradication programs, therefore, quantifying any potential deleterious outcomes for native prey is important for ensuring project success and ecosystem recovery (Doherty *et al.* 2016; Nur *et al.* 2019; Baker *et al.* 2020). Methods for mitigating increased predation by invasive predators are well established and involve controlling predator numbers, creating predator exclusion areas, or eradicating the predator prior to eradicating invasive prey (Bode *et al.* 2015; Baker *et al.* 2020). However, these approaches may not be appropriate when the predator is a native species.

Eradicating (or controlling) invasive prey can alter predation pressure on remaining native prey *via* a numerical response of predators (changes in number of predators eating prey) and/or functional response (number of prey eaten *per-capita*), with consequences for the desired aim of the conservation action (Cliff *et al.* 2020). In New Zealand, the control of rabbit numbers reduced the abundance of an invasive predator the ferret (*Mustela putorius furo*), a numerical response, however remaining ferrets increased their *per-capita* consumption of native lizards and invertebrates, a functional response (Cliff *et al.* 2020). The total response of ferrets to rabbit control resulted in increased predation pressure on lizards, and decreased predation pressure on invertebrates (Cliff *et al.* 2020).

Here we use empirical data and fundamental theoretical ecology to estimate how predation by a native predator is likely to impact the recovery of native prey following the eradication of invasive prey.

Brown Skua predation on petrels

Brown Skuas (*Stercorarius antarcticus lonnbergi*) are a native top-order predator that breed across the sub-Antarctic and have a generalist diet that includes predation, scavenging and kleptoparasitism (Reinhardt *et al.* 2000). Brown Skuas have high dietary plasticity and individual skuas may specialise on one or two prey resources over their breeding season depending on spatiotemporal availability of prey and competition with other skuas (Mougeot *et al.* 1998; Votier *et al.* 2004; Ibañez *et al.* 2018).

Skuas hunt petrels and co-exist with abundant petrel populations across the sub-Antarctic islands (Mougeot *et al.* 1998; Phillips *et al.* 2004; Ryan *et al.* 2009; Brodier *et al.* 2011). On islands with recovering or re-colonising petrel populations, skuas may inhibit recovery if their predation pressure exceeds the petrels' own intrinsic population growth rate at lower establishing petrel densities (Sinclair *et al.* 1998). On islands where skuas do target burrowing petrels as prey, common species can be selectively targeted over rarer species, lessening predation pressure on recovering populations (Pacoureau *et al.* 2019), although this is not always the case (Hahn & Quillfeldt 1998).

Skua prey selectivity varies with prey density (Cerfonteyn & Ryan 2015; Pacoureau *et al.* 2019). We propose that this could ease predation pressure on recovering prey populations. In addition, burrowing petrels are cryptic prey species, with behavioural adaptations to reduce skua predation including returning from sea to islands at night and breeding in burrows (Mougeot & Bretagnolle 2000). These cryptic behaviours may reduce skua predation at recovering petrel colonies where prey is at low density and the energetic demands of detecting and capturing prey overcome the energetic benefits of consuming prey (Mougeot *et al.* 1998).
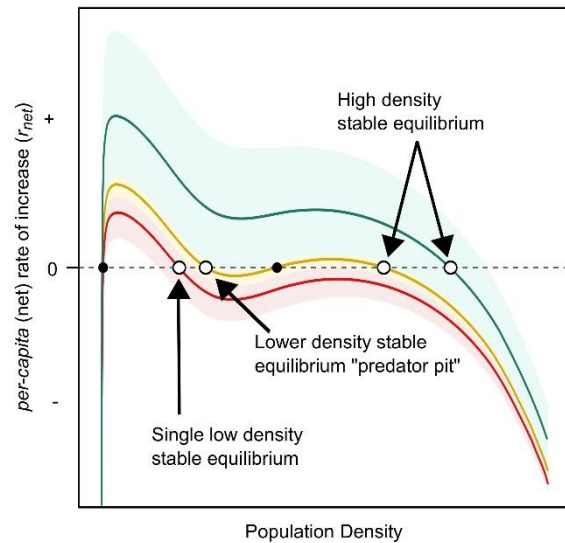
Figure 5.1. The *per-capita* (net) rate of increase for prey populations (r_{net}) as a function of population density. Curves are the sum of the prey's intrinsic density-dependent rate of increase and density-dependent mortality rate from predation. Curves reach zero at equilibrium points. If the slope of the line is inverse to population density then the equilibrium state is stable, because as the population density increases, the rate of increase becomes negative (thereby lowering the population density) and *vice-versa.* The bottom line, and shaded area (red), only has one stable equilibrium at low prey density, the upper line and shaded area (green) only has one stable equilibrium at high density, the middle line and shaded area (yellow) has two stable equilibria: one at low and one at high prey density. In the yellow example, recovering populations are likely to become stuck at lower population densities in a "predator pit". Stable equilibria are shown by white circles, unstable equilibria or "thresholds" are shown as black circles. The black circle at lower prey density represents a threshold for allee effects.

Theoretical ecology

Predators can vary their predation pressure according to changes in prey density, either through a functional or numerical response (Sinclair *et al.* 1998). A functional response is used to describe how the *per-capita* predation rate changes with changing prey density, while a numerical response is a change in the number of predators consuming prey as prey density changes (Holling 1959). In sum, the total response is the *per-capita* rate of consumption multiplied by the number of predators consuming prey and defines the predation pressure placed on a prey population (or proportion of prey eaten) at a given density (Holling 1959; Sinclair *et al.* 1998). The Holling's Type II predator functional response defines a predation rate that has an initial linear increase as prey density increases before it asymptotes to a plateau at a point where the predator population is satiated (Holling 1959). The Holling's Type III predator functional response is similar to Type II, however, resembles a sigmoidal curve, where few if any prey are consumed at low prey density, then predation rate begins to increase at moderate prey density before again reaching a plateau at the point where the predator population is satiated.

The predation rate of skuas may inhibit the recovery of petrels in two ways. First, if burrowing petrels were easily consumed at low density i.e., a Type II functional response, then predation pressure on petrel populations would be greatest at low prey densities thereby having a negative effect on recovering species. However, due to the availability of alternative prey options for skuas and the crypsis of petrels we predict the predation rate on petrels is lowest at low prey density resembling the Holling's Type III functional response curve. Second, the Holling's Type III functional response can also inhibit prey from recovering to their highest potential when the predator population is excessively large or when prey have a low intrinsic growth rate (Sinclair *et al.* 1998). Due to the curvilinear shape of the proportional predation rate of both Holling's curves two stable equilibria can exist for prey populations (see Fig. 5.1; Liermann & Hilborn 2001). In these cases, recovering prey populations can become trapped at intermediate to low densities in what is known as a 'predator pit' despite a potential higher stable equilibrium being attainable if prey densities are allowed to exceed the lower limiting equilibrium (Sinclair *et al.* 1998). Other prey with lower growth rates may simply coexist with predators at lower density (Sinclair *et al.* 1998). Predator pits can expose recovering populations to an increased risk of stochastic extinction events and require management interventions to assist prey recovery (Clark *et al.;* Sinclair *et al.* 1998).

Macquarie Island

On Macquarie Island, European rabbits (*Oryctolagus cuniculus*) were an abundant food source for breeding skuas nesting on the island's interior plateau (Jones & Skira 1979). However, rabbits also

caused extensive damage to many aspects of the island's ecosystem (Costin & Moore 1960; Copson & Whinam 2001; Bergstrom *et al.* 2009; Marchant *et al.* 2011; Saunders *et al.* 2013) and were eradicated in 2011, 140 years after their release on the island (Springer 2016). Along with the simultaneous eradication of black rats (*Rattus rattus*) and house mice (*Mus musculus*) and eradication of feral cats (*Felis catus*) a decade prior (Robinson & Copson 2014), Macquarie Island is now free of invasive mammals (Parks and Wildlife Service 2014). With the eradication of rabbits, skuas lost an abundant prey species, affecting their diet, breeding and behaviour (see Chapter 3 and Chapter 4).

Rabbit grazing, burrowing and digging severely impacted the breeding activity and habitat of burrowing petrel species on Macquarie Island, this coupled with predation by cats and rats led to the extirpation of some species and reduction in populations of other species (Schulz *et al.* 2005; Brothers & Bone 2008). Invasive mammal eradication was implemented to remove this pressure from burrowing petrel populations (Department of the Environment and Heritage 2005b; Parks and Wildlife Service 2007).

Figure 5.2. Macquarie Island showing coverage of transects walked for this survey in 2018.

Eleven species of ground and burrow nesting petrels, prions, storm-petrels and shearwaters are known to breed on Macquarie Island and surrounding islets (Clarke & Schulz 2005). These species are currently recovering from the impacts of invasive species; however, their intrinsic growth rates are not known (Bird *et al.* 2021). Burrowing petrels are also hunted by skuas and uncertainty remained whether the eradication of rabbits would result in increased predation pressure on burrowing petrels, in turn limiting or delaying the recovery of some species.

To investigate whether skua predation is likely to limit the recovery of petrel populations on Macquarie Island, we measured skua predation rates on Antarctic Prions (*Pachyptila desolata*) across a range of burrow densities. We used Antarctic Prions as our model burrowing petrel prey species, as their breeding grounds are widespread across the island and they occur at a broad range of burrow densities across their distribution. The density-dependent predation rate on Antarctic

Prions by skuas was compared with the forms of Holling's functional response curves; and used to estimate the minimum number killed by skuas *per* breeding season. The estimated annual predation rate was modelled using the intrinsic growth rates of a range of petrel species taken from Brooke *et al.* (2018) to predict the percentage of petrel species that are likely to be trapped in a predator pit under the current levels of skua predation.

Methods

Study site

This study was undertaken on Macquarie Island (54°30'S, 158°55'E), a remote sub-Antarctic island 1,100 km south-west of New Zealand and a UNESCO World Heritage Site. The remote oceanic island lies along the Macquarie Fault Zone, (Massell *et al.* 2000) and is positioned within the Antarctic Circumpolar Current between the Polar front to the south, and the sub-Antarctic front to the North – in the pacific sector of the Southern Ocean (Hamilton 2006). The eradication of invasive vertebrates on Macquarie Island began in 1989 with the eradication of the Weka (*Gallirallus australis scotti*), a predatory rail (Copson & Whinam 2001). This was followed by the eradication of feral cats in 2001, and rabbits, rats and mice in 2011. The island is now free of mammalian pests (Parks and Wildlife Service 2014).
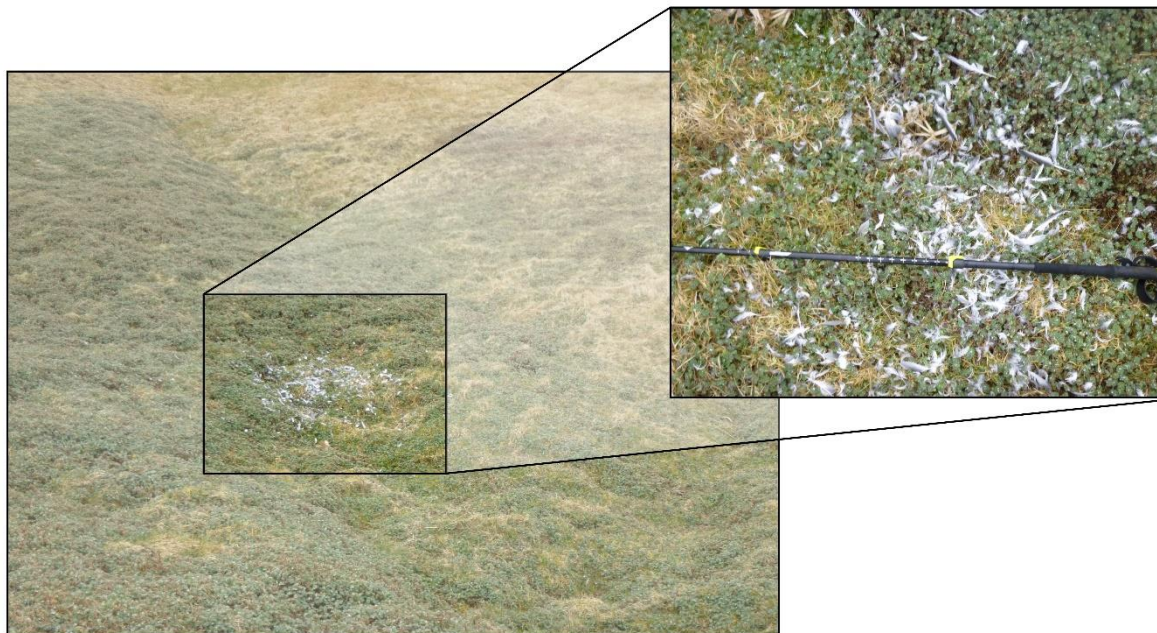
Figure 5.3. An example of a PPUF (prion predation undigested feathers). Feather 'sign' left at the site where a prion was attacked by a skua.

Data Collection

Transects were walked during the late austral summer of 2018 between early January and late March (Fig. 5.2). Transects were not systematic but stratified to cover all broad habitat types occupied by burrowing petrels on the island. Transects were randomized within strata, consisting of straight line transects walked between two end points, and totalled 155.8km in length. Along each transect, 'sign' of a prion predation event was recorded with location and distance from the transect. For this study, sign of petrel predation by skuas was a discrete patch of feathers left on the ground marking where a skua had captured, brought to ground, plucked and killed petrel prey, termed 'Prion Predation Undigested Feathers' or PPUFs (Fig. 5.3). Skuas were observed using this hunting technique and the creation of a PPUF was observed by skuas killing an Antarctic Prion. This has been documented on other islands where skuas hunt petrels (see Appendix S5.1; Osborne 1985).

It is possible that not all PPUFs were independent samples and therefore not directly resultant of discrete predation events, as multiple PPUFs could be created by a single predation event. For example, if a skua moved to multiple locations whilst plucking prey, or if the prion survived the encounter after a PPUF was created. However, the number of feathers found at each site indicates PPUFs were often left *in situ* and the predator-prey interaction recorded at these sites would have been fatal for the prion. Based on the discrete nature of most PPUFs throughout the landscape, we used PPUFs as an index of predation rate to mark the location where a single prion had been killed by skuas (Fig. 5.3; see Appendix S5.1). The estimates of prion burrow density used in this study, were recorded along these same transects. For further details on transects and prion burrow density estimates used in this study see Bird *et al.* (2021).

Functional response curves

Burrow density estimates, taken from Bird *et al.* (2021), were used as an index of prion density, assuming high and density-independent burrow occupancy (Brothers & Bone 2008; Bird *et al.* 2021). Therefore, by modelling PPUF density at different burrow densities along transects we were able to investigate the functional response of skua predation to different levels of prey density, and the degree of predation pressure placed on burrowing petrels by skuas at low densities, which would include recovering sites.

Functional response curves typically calculate *per capita* predation rates, which was not necessary for this study as our aim was to quantify the total response (i.e. the population level function response) (Sinclair *et al.* 1998). Because we focus on a single population in a single season, a *per capita* rate could in theory be calculated by dividing this consumption rate by an estimate of skua population size, however, for our study this was not necessary.

Data Analysis

PPUF density using distance sampling

Transects were split into 30 x 30 m segments based on a truncation distance of 15m that removed the furthest 5% of PPUF observations. These segments were then used as sample units for modelling predation rate as a function of prion burrow density. Prion burrow density was estimated for each segment using a density surface model of the whole island taken from Bird *et al.* (2021).

A detection probability function and a generalised additive model (GAM) of PPUF density as a function of burrow density were produced in the DSM 2.3 package (Miller D. L. *et al.* 2020) in R version 3.6.3 (R Core Team 2018). The best detection function from all possible key functions and adjustment terms up to the fourth order was selected based on QAIC and goodness-of-fit using a two-step selection process following Howe *et al.* (2019). Covariates of observer and vegetation height (either tall or short) were added to the best model to see if fit was improved using the same two-step selection process.

To account for seasonal changes in predation rate, the date of transect surveys was included as a term in a global GAM, while a spatial smoothed term of segment coordinates was included to account for spatial autocorrelation. The covariates kept in the final GAM were selected using shrinkage *via* a double penalty approach (Marra & Wood 2011). Those terms for which smoothing parameters were shrunk to zero were removed from the final model. Model selection for the detection function and model diagnostics for both the detection function and GAM are provided in Appendix S5.2.

Estimating a minimum number of prions killed per breeding season

The density of PPUFs in a given area reflects the skua-prion predation rate over a finite period (i.e. the length of time that sign of a PPUF persists in the environment). The feathers that mark PPUF sites decay over time. Therefore, on any given day the number of distinguishable PPUFs across the island represented the number of prions killed up to that point minus the number of sites that had perished. As both prions and skua migrate away from the island over winter, we have assumed that all PPUFs detected during this study were from the same season. While we were not able to estimate the average length of time a PPUF persisted in the environment, monitored sites suggested the lifetime of sites varied from around one month to longer than two months. This wide variation is probably due to several factors that may disturb a site including weather conditions and vegetation growth.

We predicted the number of PPUFs across the island for each day of the study period. We used the peak in predicted daily PPUF counts island-wide as a minimum estimate of the number of prions killed by skuas over the breeding season up to that day (minus any sites that had perished). After this peak the number of PPUFs decaying per day began to outnumber the daily predation rate suggesting predation rates after this peak were minimal. Likewise, the daily rate of change in PPUFs across the island would represent the number of prions

Table 5.1. All subset generalised additive models for PPUF density, Akaike's Information Criterion (AIC), proportion of null deviance explained by each model and difference in AIC from the top model. Predictors are: Burrow Density (Burrow); Date of survey (Day) and the spatial coordinates of each transect segment (Location).

Model Predictors	AIC	Deviance explained	ΔAIC
Burrow + Day	1081	44.7%	0
Global model	1085	44.9%	4
Burrow + Location	1103	43.9%	22
Burrow	1104	42.2%	23
Location + Day	1233	34.4%	152
Location	1244	32.3%	163
Day	1334	17.5%	253
null	1423	0.0%	342

killed in the past 24 hours minus any PPUFs that had ceased to be detectable over that time. We used the peak estimated daily rate of change in PPUF counts across the island to provide a minimum estimate of the peak daily consumption of prions by skuas over the season and to identify the peak period of predation pressure on prions.

Predicting the effect of skua predation on petrel recovery

We modelled the range of possible recovery trajectories for burrowing petrels on Macquarie Island under current skua predation pressure, using growth rates of recolonising petrel species (in the order Procellariiformes) taken from Brooke *et al.* (2018) and the predation rate on Antarctic Prions from this study following Sinclair *et al.* (1998). Growth rates of recolonising petrel populations from Brooke *et al.* (2018) ($n = 10$) were converted to initial intrinsic rates of increase (r_i) and resampled 10,000 times under a normal distribution to generate our samples of r_i used in density-dependent models (Appendix S5.3). These samples were used because no similar data was available for Macquarie Island. Density-dependent rates of increase (r_d) were modelled as a linear decay from initial values (r_i: when density is zero) down to equilibrium at the carrying capacity of Antarctic Prions (a zero rate of increase), which was estimated as the maximum density recorded in Bird *et al.* (2021). These models were summed with the density-dependent mortality rate inflicted by skuas predation (m_d: a negative rate of increase) to give a net rate of increase for petrels (r_{net}) under the current skua predation regime. The highest density-dependent predation rate on petrels by skuas

Table 5.2. Maximum values for the number of accumulated PPUFs estimated across the island and the daily rate of change in estimated PPUFs, with 95% confidence intervals.

			95% CI	
	Date	**Estimate**	**Lower**	**Upper**
Maximum Number of PPUFs (Island Wide)	12 February	27096	16124	195628
Maximum Daily Rate of Change	26 January	842	455	6268

Table 5.3. Percentage of petrel species that current skua predation rates could impede or inhibit recovery. Those with two stable equilibria under current levels of skua predation pressure could be trapped in a predator pit by current predation pressure, inhibiting them from reaching their potential higher stable equilibrium. Those with only one lower equilibrium would remain at lower densities under current skua predation pressure.

	Initial rate of increase (r_i)	**Percentage of species**
Trapped in Predator Pit (two stable equilibria)	0.18 (0.13 - 0.26)	3.1% (0.5 - 19.3)
Held at Lower Density (one stable equilibrium)	0.13 (0.07 - 0.23)	0.5% (0.03 - 11.9)
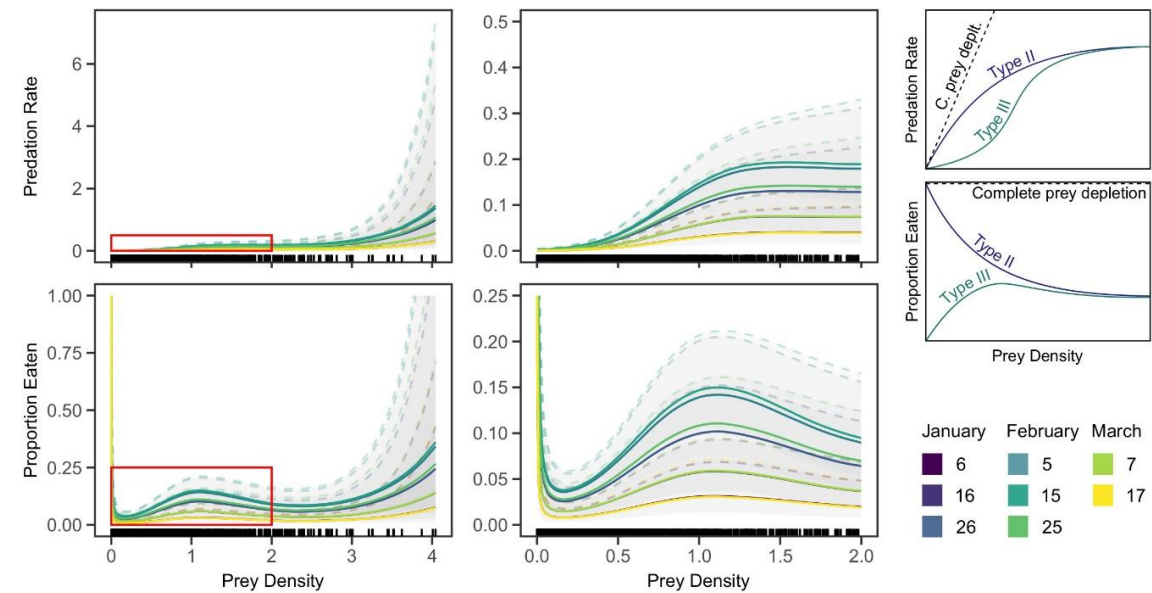
Figure 5.4. Predation rate (kill site density 100m^{-2}) and proportion eaten (predation rate/prey density) as a function of prey density (burrows 100m^{-2}) modelled at eight time points over the study period. Inset shows theoretical Hollings curves to demonstrate the close approximation of skua-prion predation to a Hollings Type III predator functional response curve. Red boxes mark the extent of exploded plots on the right, shaded areas indicate the 95% confidence interval with the upper confidence limit shown as a dashed line, rug plots mark the prey density of each transect segment.

(including 95% Confidence Interval [95%CI]) (taken from the day of peak PPUF counts; see Table 5.2) was used as m_d as this was our best estimate of the annual skua predation rate on prions. For equations and further details on model methods see Appendix S5.3.

In scenarios where r_{net} was reduced below zero at low population density by skua predation, petrels were at risk of being trapped in a predator pit or maintained at low density (Fig. 5.1). These were scored as a percentage of all petrel samples using percentile ranks scores.
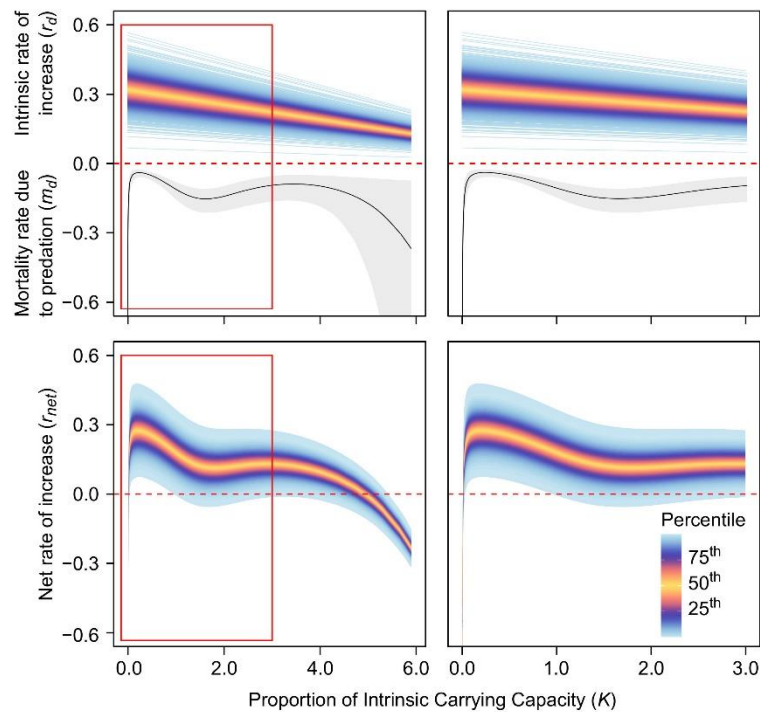
Figure 5.5. The density-dependent intrinsic rate of increase of Procellariiformes (r_d) modelled from 10,000 resamples taken from a normal distribution (top half of upper plot), and the annual density-dependent mortality rate for Antarctic Prions inflicted by skuas (m_d), taken as the peak daily estimate of accumulated kills over the study period (bottom half of upper plot: black line shows the estimate 95% confidence intervals are shaded). Net rate of increase (r_{net}: lower) is the sum of the density-dependent intrinsic rate of increase and mortality rate ($r_{net} = r_d + m_d$; only r_{net} using mean m_d are shown). The x-axis shows prey density as a proportion of the intrinsic carrying capacity of Antarctic Prions (K: the potential carrying capacity in the absence of predators), which was estimated as the highest Antarctic Prion burrow density modelled on Macquarie Island in Bird *et al.* (2021). Where r_{net} is zero and has an inverse slope are stable equilibria. Where r_{net} has two stable equilibria the lower equilibrium point is referred to as a predator pit. Red boxes mark the extent of exploded plots on the right.

Results

PPUF counts

A total of 176 PPUFs were counted over an area of 4.67km^2 or 3.6% of the island (after truncation) during 4 months of surveying. The best detection function for PPUFs based on the QAIC two-step selection process was hazard-rate with no adjustment terms and no covariates and this was used in GAM (Appendix S5.2). Burrow density and the date of survey were retained as covariates in the final GAM based on shrinkage and supported by AIC. No other model was within 3 ≥ ΔAIC of the best model (Table 5.1).

Functional response of skuas to changes in Antarctic Prion density

Estimates of predation rate at the highest prey densities were not reliable due to small sample size (Fig. 5.4). However, this did not affect our interpretations of the functional response of skuas and recovering petrel populations, as we were interested in low prey densities areas. Burrow density observations were zero-inflated. Only 5% of observations had burrow densities higher than 0.01 m^{-2} (n = 267) and only 52 observations (less than 1% of records) beyond 0.02 burrows m^{-2}.

At low to moderate prey density (below 0.02 burrows m^{-2}), the model estimates of predation rate resembled the sigmoidal Holling's Type III functional response with lowest predation rate and predation pressure (proportion eaten) at lower prey density (Fig. 5.4). Predation pressure peaked at a burrow density of 0.01 burrows m^{-2}, roughly a quarter of the mean burrow density of 0.04 burrows m^{-2} (± 0.006 SE) of established colonies previously recorded by Brothers (1984) or 16% of the peak estimated from the island-wide density surface model of Bird *et al.* (2021) (0.068 burrows m^{-2}).

The approximation of the Holling's equation using GAM was imperfect at very small prey densities. This is reflected in the proportion eaten (Fig. 5.4), as prey density approaches zero faster than the predation rate, the proportion of prey consumed rapidly increases to beyond 100% (Fig. 5.4). As there is no ecological basis for predation pressure to suddenly increase as prey density approached zero, this is attributed to a marginally spurious approximation by the GAM as values approach zero, and does not affect the conclusions drawn in this study.

Estimates of seasonal Antarctic Prion consumption

The maximum daily PPUF count occurred toward the end of the season in mid-February (Appendix S5.4). This count suggests at least 27,096 prions were killed by skuas *per* breeding season by mid-February (Table 5.2). Most prions were killed in late January (Appendix S5.4), with at least 842 prions estimated to have been killed across the island on 27 January (Table 5.2). This occurred during the

chick rearing period of both skuas and prions. However, both values had wide confidence intervals and should be interpreted cautiously (Table 5.2).

Predicting the effect of skua predation on petrel recovery

Modelling r_i of petrels (i.e. the rate of increase when population density and predation rate is assumed to be zero) under a normal distribution had a mean value of 0.32 (95%CI: 0.15 - 0.59). Model residuals showed a normal distribution was a reasonable fit to the data (see Appendix S5.5). The r_{net} of Procellariiformes suggested 3.1% (95%CI: 0.5-19.3) of petrels or those with an r_i of less than 0.18 had two stable equilibria and were likely to be trapped in a predator pit under current skua predation pressure, impeding recovery (Table 5.3; Fig. 5.5). A further 0.5% (95CI: 0.03-11.9) of petrels or those with r$_i$ values less than 0.13 had only one lower equilibrium point suggesting current skua predation pressure would hold these populations at a lower level (Table 5.3; Fig. 5.5).

Discussion

Like many top-order predators, skuas have an important role in shaping prey abundance, demography, and behaviour (Mougeot & Bretagnolle 2000; Lima 2002; Ripple & Beschta 2006; Votier *et al.* 2006). Throughout their range Brown Skuas co-occur with, and prey upon, many threatened burrowing petrel populations (Reinhardt *et al.* 2000). Findings from this study suggest that their current predation pressure on burrowing petrels on Macquarie Island is unlikely to inhibit recovery for most petrel species. However, under the current level of skua predation pressure even petrels with the highest population growth rates had realised carrying capacities that were an estimated 55% (95%CI: 45-81) of their potential intrinsic carrying capacity, highlighting the role skua predation plays in structuring prey populations.

Skuas had their lowest predation pressure on Antarctic Prions at low prey density, with a functional response curve following a Holling's Type III form. This relationship concurs with observed trends in the diets of breeding skuas on Macquarie Island, with nests of breeding skuas that consumed petrels all located close to established petrel colonies (Chapter 4). Despite lower predation pressure at low prey densities, we found current skua predation rates could restrict the recovery of petrels with population growth rates in the lowest 3.6% of all petrel species to densities at or below a predator pit. Assuming growth rates are constant for each species this represents 4 of the 104 petrel species globally (Hamer 2001). 14% of the petrels held at or below a predator pit by current skua predation (~1 species) had only one stable equilibrium point, meaning this species may naturally occur at low density in the presence of skuas. The remaining 86% of petrel species held at or below a predator pit (~3 spp.) had two stable equilibria (see Figs. 5.1 & 5.4) meaning, historically, they may have existed

at higher densities when co-existing with skuas but may require additional conservation assistance to reattain their higher stable state.

The actual impact of skua predation on the recovery rates of burrowing petrels, however, is likely to be less than that reported for two reasons. First, when hunting petrels, Brown Skuas often target non-breeding individuals and chicks (Mougeot *et al.* 1998; Mougeot & Bretagnolle 2000; Votier *et al.* 2006; Miles *et al.* 2013). Deaths of these individuals are less likely to impact population growth rates and as such the effect of skua predation on petrel recovery may be lower than that estimated in this study (Votier *et al.* 2006). Second, with rabbits now absent and vegetation rapidly recovering, increased crypsis of petrels and their burrows provided by dense vegetation may further reduce the effects of predation pressure on recovering populations (Brothers 1984; Schulz *et al.* 2005; Shaw *et al.* 2011).

This study illustrates how skuas, as top-order predators, currently structure petrel populations on Macquarie Island and could explain low densities of some petrel species at other locations (Hahn & Quillfeldt 1998). On King George Island, predation pressure from skuas is 7.4 times higher on Black-Bellied Storm-petrels (*Fregetta tropica*) than on Wilson's Storm-petrel (*Oceanites oceanicus*) and the former is 4.4 times less abundant (Hahn & Quillfeldt 1998). Neither of these species are abundant on Macquarie Island (Clarke & Schulz 2005). On Macquarie Island, we estimate skuas consumed around 11% (95%CI: 7-82%) of the Antarctic Prion breeding population, based on the mean population estimate and burrow occupancy for Antarctic Prions in Bird *et al.* (2021). However, those consumed are likely to include large numbers of non-breeding birds and chicks (Mougeot *et al.* 1998).

The peak predation recorded in this study occurred over the hatching period for prions (Brothers 1984), a period of heightened activity around burrowing petrel colonies by non-breeding individuals (Mougeot *et al.* 1998; Mougeot & Bretagnolle 2000; Votier *et al.* 2006; Miles *et al.* 2013). Peak predation by skuas on prions has been observed over this same period on other islands prior to a rapid slowing in capture rates, similar to that observed in our study (Mougeot *et al.* 1998). Comparison with Mougeot *et al.* (1998) suggests our study captured the majority of skua predation on prions however, they recorded other shorter periods of heightened skua predation during prenuptial return of petrels to their breeding grounds, egg laying, and chick fledging. Our study began at the end of egg laying and finished prior to fledging. Due to the persistence of PPUFs in the environment we likely captured all predation except that associated with chick fledging and possibly those prions killed during their prenuptial return.

Eradication of invasive species leads to substantial ecosystem restructuring (Kopf *et al.* 2017). Native species may be slow to recover, or indeed never fully recover to their pre-invasion state. Their

response is driven by multiple factors; distance to source populations, exclusion by native competitors or suppression by native predators (Brodier *et al.* 2011; Buxton *et al.* 2014; Nur *et al.* 2019). The role of predators in supressing the recovery or recolonisation of prey relies on predators detecting and consuming prey at marginal densities before they become established. Despite some species being held at low density, the Type III functional response of skuas to petrel prey density suggests all petrel species should have the opportunity to colonise Macquarie Island to some degree. In addition, petrel species re-colonising islands following the eradication of invasive mammals typically have higher growth rates than those species already present and recovering (Brooke *et al.* 2018). This comparison between the growth rates of recolonising and pre-existing petrel colonies in Brooke *et al.* (2018) supports a density-dependent growth rate of petrels, such as the one used in our study. While the relationship between r_d and population density may not be linear, our models are likely a conservative estimate of this relationship (Clark *et al.;* Sinclair *et al.* 1998).

Brown Skuas co-exist with healthy and recovering petrel populations on other islands (Moncorps *et al.* 1998; Brodier *et al.* 2011). On Ile Verte, Blue Petrels (*Halobaena caerulea*) increased eightfold in six years following the eradication of invasive rabbits despite being the preferred prey of Brown Skuas (Brodier *et al.* 2011). However, foraging behaviour of Brown Skuas is notoriously site specific between and within islands (Ryan *et al.* 2009) and the functional response of skuas reported here and observations from Ile Verte may not apply to all other sub-Antarctic Islands during periods of recovery (Jones & Skira 1979; Reinhardt *et al.* 2000).

Small islands that have high densities of Brown Skuas may inhibit petrel re-colonisation due to excess predation pressure from a large number of predators (Sinclair *et al.* 1998). For example, the abundant carrion at New Zealand Sea Lion (*Phocarctos hookeri*) colonies on Enderby Island attracts large numbers of skuas to the island's coast (Miskelly *et al.* 2020). High skua densities caused by this abundance of food may have a seasonal hyperpredation effect on prospecting petrels along the island's shoreline (Courchamp *et al.* 2000; Madani 2020). A similar effect has been observed on the South Farallon Islands, where abundant introduced house mice support Burrowing Owls (*Athene cunicularia*) on the island for longer periods of the year than otherwise normal, which subsequently increases their predation on Ashy Storm-petrels (*Oceanodroma homochroa*) when mice populations die off over winter (Nur *et al.* 2019). On larger islands, abundant prey with less seasonal fluctuations may have the opposite effect. The numerous penguin colonies on Macquarie Island, including over 750,000 breeding pairs of the endemic Royal Penguin (*Eudyptes schlegeli*), may lessen predation pressure on recovering burrowing petrel populations by providing alternative foraging grounds for skuas (Chapter 4; Salton *et al.* 2019; Pascoe *et al.* 2020).

Conclusions

The goal of eradicating invasive species from islands is the recovery of the native species that were constrained by presence of invasive species, without causing subsequent damage to other aspects of the natural ecosystem (Zavaleta *et al.* 2001). At Macquarie Island, a primary concern that led to the eradication of rabbits and rodents was their impact on the island's burrowing seabird community (Department of the Environment and Heritage 2005b). A widely recognised consideration for island eradications is the potential for unplanned changes to ecosystem structure and function that have negative impacts for native species (Chapter 3; Zavaleta *et al.* 2001; Kopf *et al.* 2017). Our study has shown that when eradications remove a native predator's major invasive prey resource and prey switching occurs, there is the possibility predators could limit recovery of native prey populations. This is an important finding potentially influencing the outcomes of eradication and control programs (Cliff *et al.* 2020). These considerations are highly pertinent for decision makers regarding restoration targets and perceived management success (Buxton *et al.* 2016).

This study was conducted as the island continues to recover from the impacts of invasive species. In consequence, the relationship between skuas and petrels reported here will continue to change as vegetation cover, petrel numbers and the skua breeding population all increase. Our study utilises fundamental theoretical ecology coupled with empirical field data to quantify uncertainty in the recovery of species of conservation significance in response to invasive species eradication. Our approach is relevant to future eradication projects to assess whether they achieve their desired goals and if further interventions for assisted recovery of native species are needed.

Appendix S5.1: Sign of a skua-prion predation event

Prior to walking transects, four skuas were observed in the aerial hunt of a prion, which had been flushed from its burrow by the skuas. In flight the four skuas maintained a constant web of action around the prion, effectively surrounding the bird and blocking its attempts to escape. The prion had been flushed from its burrow into broad daylight and was erratic in flight, making quick changes in direction as the skuas took successive attempts to attack it and bring it to ground. On a successful attack, one skua pinned the prey to the ground and was immediately joined by its partner. The two birds claimed their quarry by performing a territorial long-call, which signalled for the other two skuas to leave and they did. The two birds then consumed the prion in a matter of seconds using a well described cooperative feeding behaviour. The prion was held between the beaks of the two skuas and torn into smaller digestible pieces. Upon consuming the entire bird, all that remained was the prion's wingset and a discrete patch of prion feathers from where the prey was initially brought to ground. The patch of feathers termed Prion Predation Undigested Feathers (PPUF) occurred when the prion was initially pinned down and torn into by the first skua. Unlike wingsets, which can be carried away if skuas are disturbed whilst feeding or to feed their chicks, PPUFs are a passive sign of the predation event that are fixed at a location. In this way, PPUFs were a spatially explicit sign of prion predation that could be used to record the distribution of prion predation events by skuas across the island. No other extant predators on Macquarie Island are known to consume prions in this manner and so all PPUFs were likely attributable to skua predation.

Appendix S5.2: Model selection and diagnostics for detection probability function and generalised additive modelling of PPUFs

Detection probability function

Methods

Transects were split into segments based on a truncation distance of 15m that removed the furthest 5% of observations (30x30m) and these segments were used as sample units for modelling predation rate as a function of prion burrow density. Uniform, half-normal and hazard-rate key detection functions with cosine, polynomial and Hermite adjustments up to the fourth order of each adjustment term (beginning at no adjustment term) were all tested for goodness-of fit to the data.

The best detection function from all possible key functions and adjustment terms was selected based on QAIC and goodness-of-fit using a two-step selection process following Howe *et al.* (2019). Covariates of observer and vegetation height (either tall or short) were added to the best model to see if fit was improved based on the same selection process.

Results

A right-truncation distance of 15m resulted in a total survey area of 4.67km^2 or 3.6% of island area. The best detection function based on the QAIC two-step selection process was hazard-rate with no adjustment terms and no covariates (Table S5.1). Model diagnostics showed a good fit to the data (Fig. S5.1).

PPUF density modelling

Methods

Model distribution was selected from quasi-Poisson, Tweedie and negative binomial based on model diagnostic plots of residuals and goodness-of-fit of the global model (Fig. S5.2). Partial regression smooth plots from the best model are also provided (Fig. S5.3).

Tables

Table S5.1. The best detection functions for each key function based on QAIC used to select a final detection function for modelling PPUFs in a two-step process (the overall best model based on goodness-of-fit is highlighted in bold). The addition of covariates to improve the best model was tested using the same process with the final model highlighted in bold.

Key Function	Adjustment term	Orders	AIC	log L(ϑ-hat)	K	c-hat	QAIC	χ^2 / df
Uniform	Cosine	1,2,3	800	-397	3	4.95	166	1.49
Half-normal	Cosine	2	799	-397	2	1.85	434	1.16
Hazard rate	-	-	792	-394	2	1.30	612	**0.75***
Covariate selection (using Hazard rate detection function)								
none	-	-	792	-394.2	2	1.04	**762.8***	0.75
Observer	-	-	793	-393.5	3	1.04	763.4	0.83
Veg height	-	-	794	-393.1	4	1.04	764.6	0.90
Obs + Veg	-	-	795	-392.3	5	1.04	765.2	1.04

Figures
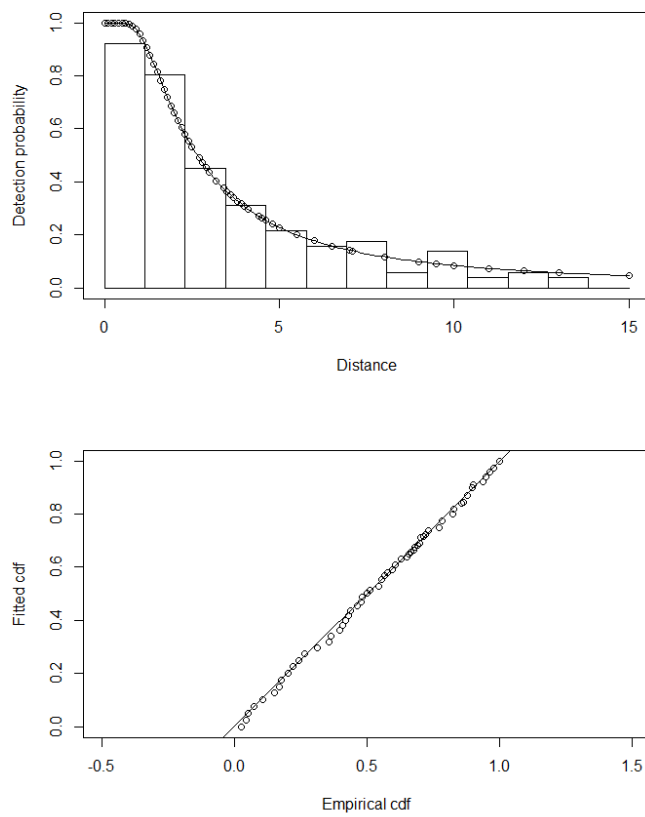
Figure S5.1. The best detection function (hazard-rate with no adjustment terms and no covariates) fit to a histogram of distance sampled kill site data (upper) and normal probability plot of residuals (lower) showing a good fit to the data.
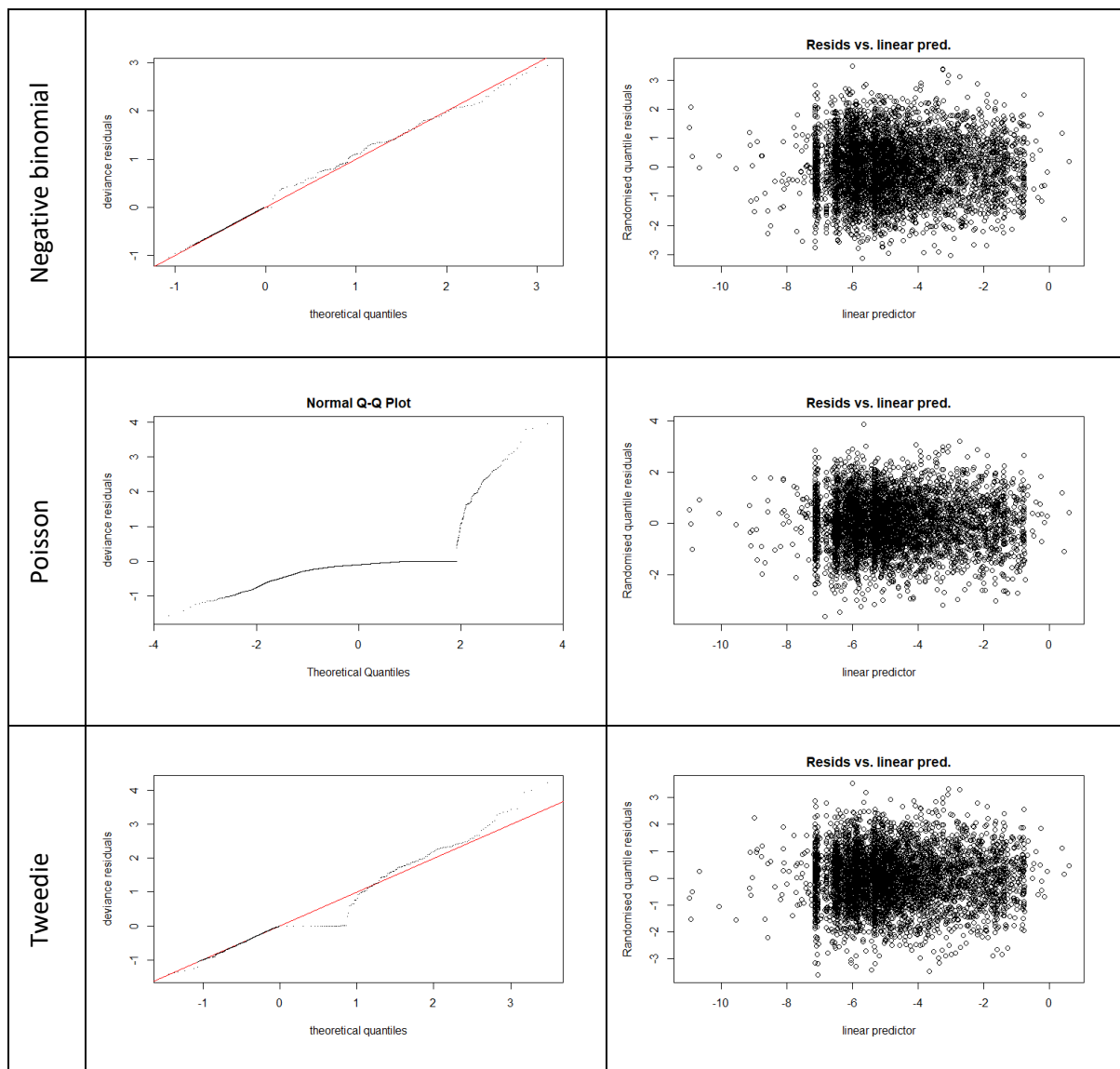
Figure S5.2. Normal probability residual plots of global model for PPUF density (left) and Dunn and Smyth (randomised quantile) residuals vs the linear predictor (right) under three distributions.
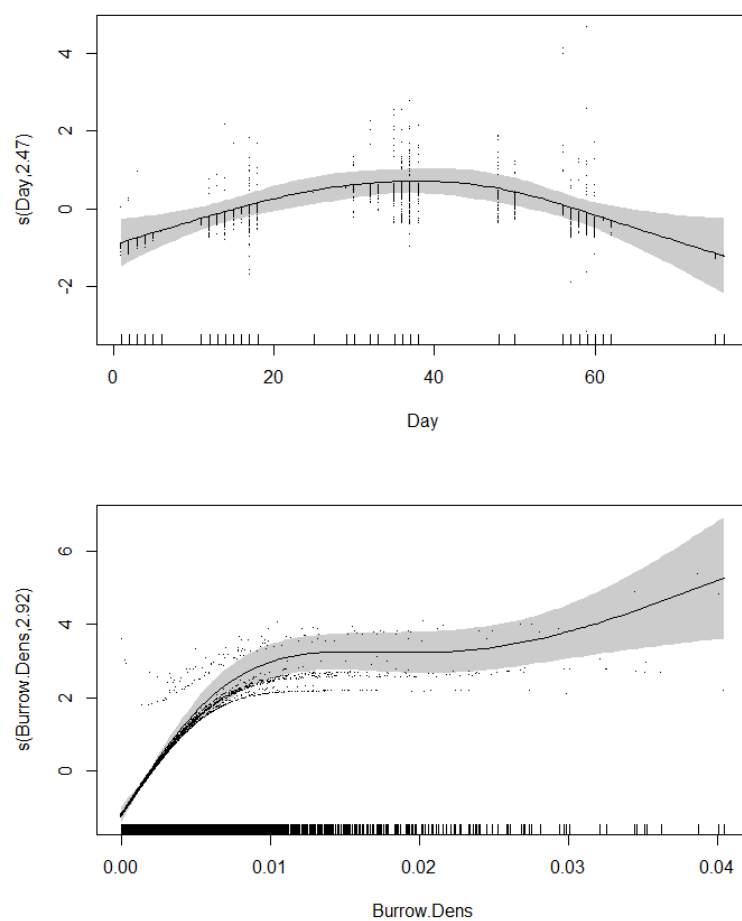
Figure S5.3. Partial regression smooth plots from the best model for kill site density. Note smooths are shown on the scale of the linear predictor and not the response.

Appendix S5.3: Modelling the net effect of predation rate and intrinsic population growth on the recovery of petrel populations.

Methods

Following Sinclair $et\ al.$ (1998) the density-dependent intrinsic rate of increase for petrel populations (r_d) was modelled as a linear decay rate starting at an initial intrinsic rate of increase (r_i) and declining to 0 at the population's carrying capacity (K), in this case defined as the highest burrow density estimated by Bird $et\ al.$ (2021) in their island-wide density surface model. This was calculated as:

$$r_d = r_i \times (1 - D/K)$$

Where D is burrow density. Starting values of r_i for petrel populations were calculated from population growth rates reported in Brooke $et\ al.$ (2018). Population growth rates of seabirds following predator eradication are higher for re-colonising species compared with the growth rates of recovering extant species (Brooke $et\ al.$ 2018). As re-colonising populations are likely to have intrinsic rates of increase similar to initial values, only the range of growth rates reported for re-colonising populations were used to determine the range and distribution of r_i values in our study. As D increases in eq. 1, r_d would come to resemble the slower growth rates of extant populations at higher burrow densities. Population growth rates (λ) of recolonising petrel species from Brooke $et\ al.$ (2018) were converted to r_i by:

$$r_i = \ln(\lambda)$$

A sample of 1000 starting r_i values were generated by resampling within the model distribution for growth rates of recolonising petrel species taken from Brooke $et\ al.$ (2018) and used to calculate a range of possible r_d values.

The density-dependent mortality rate due to skua predation (m_d) is the proportion of petrels killed annually by skuas at a given prey density. We estimated m_d using the density model for highest daily estimate of accumulated prion kills during the study period (Table 5.3; Appendix S5.4). The additive inverse of this estimate, as a proportion of D, was used to approximate m_d.

To calculate the percentage of petrel populations that are likely to be impacted by skua predation, m_d and r_d were summed to calculate a net rate of increase (r_{net}) for each value of r_d.

Appendix S5.4: Peak island-wide daily PPUF count and rate of change in PPUF accumulation
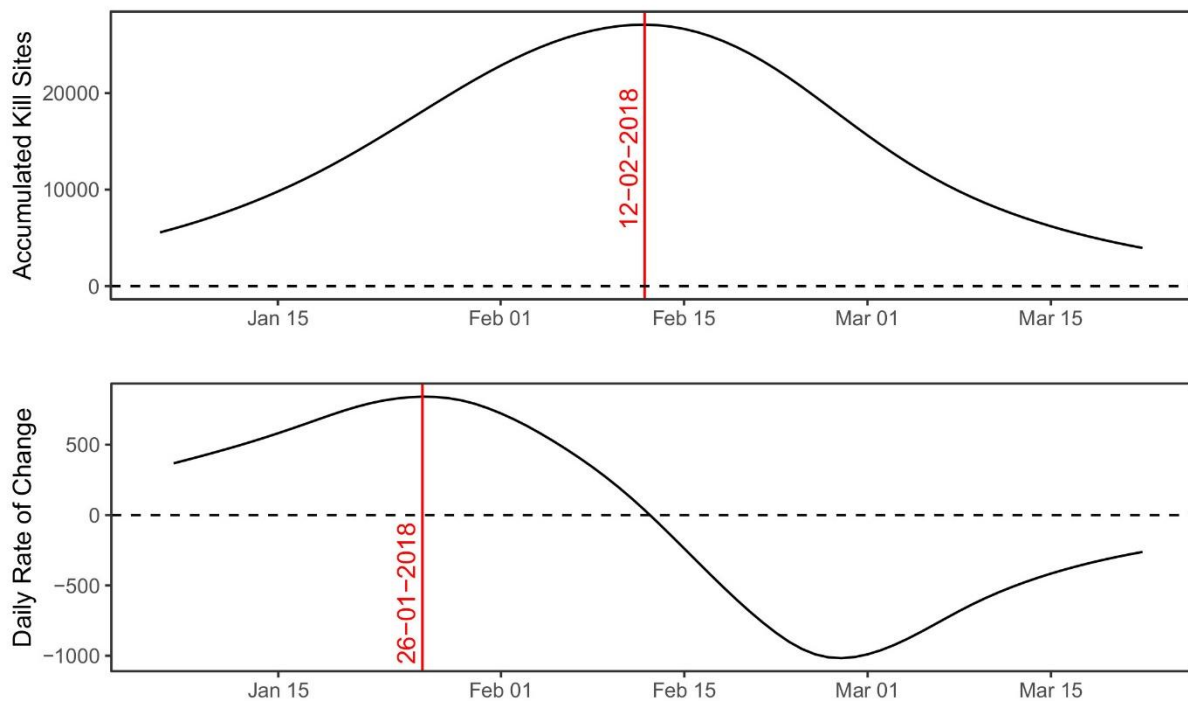
Figure S5.4. The island-wide daily accumulation of PPUFs estimated over the survey period (upper), showing the date of maximum PPUF count (red line) and daily rate of change in PPUF accumulation (lower) showing the date of the highest rate of change (red line).

Appendix S5.5: Model diagnostics for intrinsic growth rates of Procellariiformes
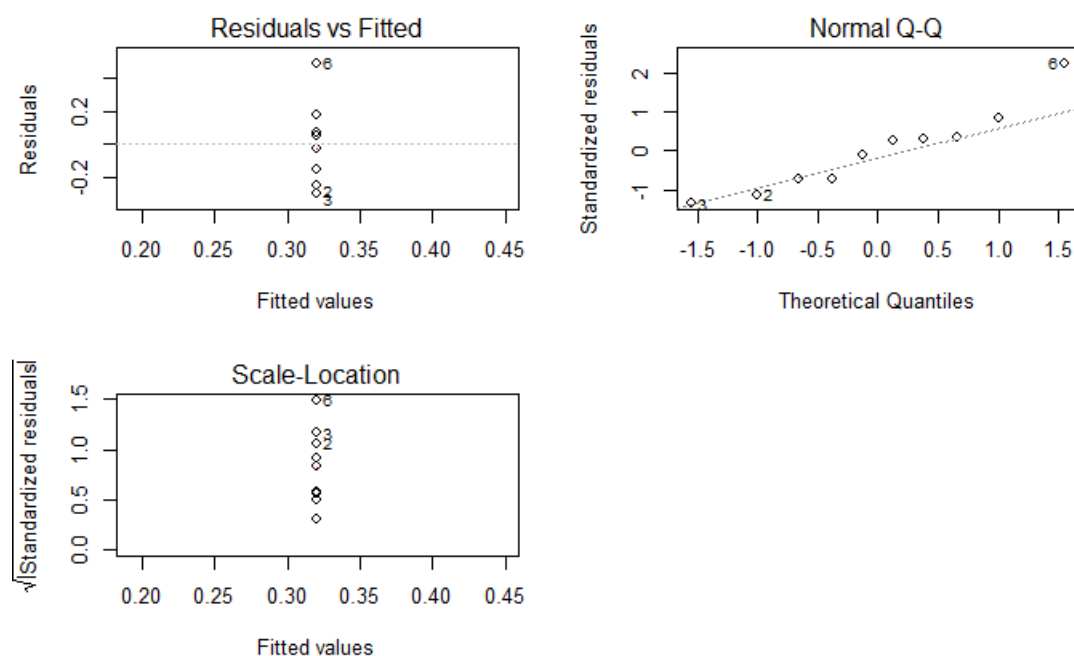
Figure S5.5. Residuals of intrinsic growth rates of re-colonising Procellariiformes taken from Brooke *et al.* (2018) modelled under a normal distribution.

Chapter 6

General Discussion

The key to their [Brown Skua's] character may perhaps be found in Murphy's description of them as "… gulls which have turned into hawks". Their remarkable curved talons, aerial agility, advantage in size and power, and capacity for individual behaviour fit them well to a life of predation, scavenging, and piracy ; on the occasions when they compete against Black Backed Gulls for food or nesting space, it is the gulls which inevitably find themselves at both physical and mental disadvantage.

Stonehouse (1956)

In this thesis I investigated how native predators are regarded and integrated in eradication studies (Chapter 2) and quantified how eradication of invasive prey impacts a top-order predator (Chapter 3). As a basis for this research, I assessed changes in top-order predator demography, diet and behaviour following a multi-species eradication on a remote, world heritage island, devoid of other confounding anthropogenic processes such as habitat loss, hunting and over-exploitation (Selkirk *et al.* 1990; Tershy *et al.* 2015). These findings reveal some of the bottom-up impacts that eradication projects have on native predators as well as increase our understanding of Brown Skua ecology. My work also extends our understanding of how to set and evaluate conservation targets for future eradications.

I provide novel insights into how Brown Skuas (*Stercorarius antarcticus lonnbergi*), as a top-order predator, structure prey communities in island ecosystems (Chapter 5) and utilise a diverse foraging landscape (Chapter 4). As predators, skuas potentially affect a range of broader ecosystem processes, including nutrient cycles and disease transmission (Jones 2010; Gamble *et al.* 2020), which will influence the trajectory of the island ecosystem recovery. I examined how prey distribution influences skua diet, habitat use, foraging behaviour and ultimately breeding success (Chapter 4). To achieve this, I collated historic data and undertook 5 months of field work that built on a decade of monitoring. I drew on theoretical, applied, field and movement ecology, and broadened my skills base by integrating laboratory, modelling, spatial, and isotope analysis through this thesis.

Brown Skuas and their prey in a changing landscape

My thesis unpacks the many ways Brown Skuas are vital to a functioning ecosystem on Macquarie Island (Chapter 5). I quantified the multiple ways eradicating invasive prey affects the diet of skuas, breeding success, competition dynamics and predation pressure on native prey (Chapter 3 ; Chapter 4 and Chapter 5). Invasive prey are prevalent in the diet of many predators (Barbar *et al.* 2016), yet despite the myriad of threats facing top-order predators globally (Estes *et al.* 2011), the impact on predators of eradicating invasive prey are rarely studied (Chapter 2).

Changes to skua breeding

The eradication was an important conservation intervention on an island ecosystem that was under significant stress (Bergstrom *et al.* 2009). It was also an extensive ecological perturbation. In the final year of this study, breeding success of skuas on Macquarie Island remained at around 0.38 chicks *per* nest (Chapter 3). This is low for Brown Skuas and close to minimum estimates reported from declining populations elsewhere (Hahn & Peter 2003; Catry *et al.* 2011; Krietsch *et al.* 2016). Similar to that on Macquarie Island, reductions in Brown Skua breeding success of this magnitude recorded

elsewhere have been linked to periods of food scarcity (Reinhardt 1997a; Krietsch *et al.* 2016). In this thesis I outline the proximal causes of the breeding decline as prey-loss and secondary poisoning; however, multiple potential mechanisms exist to explain how these led ultimately to a decline in skua nest numbers and breeding success.

Possible mechanisms of decline in skua nest numbers

In Chapter 3 I recorded an initial large and sudden decline in skua nest numbers island-wide following the eradication of rabbits from Macquarie Island. Prior to the eradication, the majority of skuas breeding on the interior plateau either specialised or relied heavily on rabbits for chick provisioning (Skira 1984). Therefore, along with secondary poisoning deaths, the loss of local rabbit prey may have reduced the skua breeding population in these areas by forcing pairs to move to other areas of the island with better foraging opportunities or to abandon breeding altogether. The lack of any reciprocal increase in nest numbers in other parts of the island during the early post-eradication period (Chapter 3), suggests breeding abandonment and secondary poisoning, not intra-island migration, contributed largely to the initial decline in the skua breeding population. Promisingly, through my work we now know, the breeding population on Macquarie Island is slowly increasing in size (Chapter 3).

Possible mechanisms of decline in skua breeding success

The breeding success of skuas may have been impacted by prey-loss and secondary poisoning in multiple ways. First, the poisoning deaths of one or both partners in a breeding pair could have affected skua breeding success. The majority of skuas form monogamous partnerships, and the death of a single bird from a breeding partnership may lower breeding success by forcing the remaining partner to try and establish a new, potentially less successful breeding bond (Ainley *et al.* 1990; Naves *et al.* 2007). Breeding success also increases with age and breeding experience (Furness 1984). Therefore, the death of an experienced breeding pair could fast-track new, inexperienced recruits into the breeding population and thereby lower breeding success (Furness 1984). The recruitment of inexperienced birds into the breeding population may explain why breeding success remained low in the late post-eradication period despite a recovery in skua nest numbers (Chapter 3).

Second, breeding pairs that depended on rabbits as prey before their eradication would have had to either prey-switch to a sub-optimal diet or travel further from the nest for food, or both. For these skuas, the decline in breeding success could be explained by less reliable prey resources (resulting in poorer chick condition) or longer foraging trips resulting in chicks being left unguarded for longer periods and an increased risk of cannibalism by other skuas (Phillips *et al.* 2004). Both diet and

foraging factors were studied in Chapter 4, where I found poorer diet and foraging strategies contributed to lower breeding success of skuas.

Third, in Chapter 3 I found the eradication also impacted the breeding success of skuas that did not historically include rabbits in their diet. For these skuas, prey remained consistent before and after the eradication, and centred around marine species (namely those skuas nesting near penguin colonies; see Chapter 3). For pairs breeding in areas where rabbits were not a major prey item, the decline in breeding success could be explained by increased competition around remaining prey hotspots. This mechanism for decline is supported by the island-wide convergence of isotopic niches of skua chicks after the eradication (Chapter 3). On Bird Island in South Georgia, increased competition for prey among breeding skuas reduced the likelihood of chicks surviving to fledging (Phillips *et al.* 2004). On Macquarie Island, the reduction in breeding success for skuas nesting near prevailing prey hotspots could be explained by either exploitative competition (increased competition for prey resources) or interference competition (chicks killed in conflict by visiting skuas).

The future recovery of skua breeding success on Macquarie Island will likely depend on the degree of breeding experience within the population, competition for current prey hotspots and the recovery of burrowing petrels (Furness 1984; Ainley *et al.* 1990; Phillips *et al.* 2004; Naves *et al.* 2007).

Changes to skua foraging landscape of skuas

Often diet and foraging strategies are not clearly delineated when comparing feeding behaviour with breeding success (Phillips *et al.* 2004; Carneiro *et al.* 2014). On Macquarie Island, the wide range of prey and foraging strategies available to skuas enabled me to present a clear picture of how diet and behaviour affect individual breeding fitness (Chapter 4). My study is a snapshot of diet during a period of recovery for numerous prey, particularly the island's burrowing petrel community. As prey populations on Macquarie Island recover from the impacts of invasive mammals, the Brown Skua breeding population will continue to undergo a realignment of diet, foraging strategies and population size (Chapters 3 & 4).

Skuas that once relied on rabbits as prey over the breeding season now return to the island, to a dramatically altered foraging landscape (Chapter 4). Rabbits and burrowing petrels utilised the same inland areas of Macquarie Island (Jones & Skira 1979; Brothers 1984). For skuas nesting in these areas, the current low levels of prey caused by an absence of rabbits and recovering petrel numbers has altered foraging behaviour (Chapter 4). However, the foraging dynamics I defined in Chapter 4

are likely to evolve as petrels continue to recover on Macquarie Island. We can anticipate that the patterns in foraging, diet and breeding success, I describe in this thesis will change into the future.

I predict that as petrel density increases a greater number of skuas will be able to specialise on petrel prey and successfully raise young. The proportion of skuas successfully utilising this specialist strategy is currently low (5% of diets studied; Chapter 4). In the future, the greatest changes to foraging strategies are likely to be shaped by the densities of recovering petrel populations, which will support local foraging by skuas nesting on the interior of the island (Ryan *et al.* 2009; Brodier *et al.* 2011).

Eradicating invasive prey and ecosystem complexity

Eradication projects are increasing in complexity, becoming more likely to impact a greater number of native predators (Terborgh *et al.* 2001). I have shown that while native predators are more likely to respond negatively to eradications, relative to other species these impacts are rarely studied (Chapter 2). Greater consideration needs to be given to native predators when planning future eradications.

To date most eradications have been undertaken on small islands, which are isolated, simple ecosystems (Tershy *et al.* 2015). This leads me to propose – to what extent do the issues addressed in this thesis scale-up to larger ecosystems and continental environments?

The rapid recovery of native prey following eradication of invasive prey can improve conditions for top-order predators (Buckley & Han 2014). The speed at which native prey recover depends on the number of nearby source populations (Buxton *et al.* 2014; Brooke *et al.* 2018), their reproductive rate (Buxton *et al.* 2014), and the capacity of a potentially deteriorated ecosystem to hold more prey (Terborgh *et al.* 2001). All three of these factors scale positively with ecosystem size, reduced insularity, and habitat connectivity (Covas 2012; Buxton *et al.* 2014; McIntosh *et al.* 2018). This suggests that the negative effects of prey loss may be ameliorated in larger complex ecosystems. However, globally invasive species in continental ecosystems have contributed to the extinction of at least 18 native prey species and impacted a further 118 threatened native prey species (Doherty *et al.* 2016). Due to the severity of these impacts and the additional pressures currently facing continental ecosystems (Tershy *et al.* 2015) a rapid recovery of prey should not be taken for granted in larger ecosystems.

Furthermore, operational impacts of eradications such as secondary poisoning can impact a larger number of predators in continental ecosystems due to their greater predator diversity (Terborgh *et*

al. 2001; Christensen *et al.* 2012). For these reasons, I suggest the mechanisms of decline outlined in Chapter 3 will remain an issue for future eradication projects in large ecosystems.

Avian predators as keystone species

Avian predators make substantial contributions to ecosystem function (Moreno *et al.* 1996; Sekercioglu 2006; Salo *et al.* 2008), suffer the same persecution as their mammalian counterparts (Ritchie & Johnson 2009), and are just as prominent in continental ecosystems (Sergio *et al.* 2008; Ritchie *et al.* 2012). Yet they are under-represented in ecological studies (Chapter 2; Sekercioglu 2006; Terraube & Bretagnolle 2018; Evans 2021). Continuing to overlook avian predators, their ecological role and the effects we have on their populations, hinders our understanding of ecological interactions, and leads to catastrophic outcomes for birds and ecosystems more generally (Salmon *et al.* 2010; Terraube & Bretagnolle 2018).

Avian predators and scavengers provide ecosystem functions that mammalian and other terrestrial predators cannot deliver (Sekercioglu 2006). Birds are the only vertebrate obligate scavengers, an important ecosystem service across many continents (Graña Grilli *et al.* 2019). Flying enables these birds to overcome the large energy constraints of searching for carrion (Ruxton & Houston 2004).

In Chapter 2 I show that very few studies have quantified the impact of eradicating rabbits and rodents from island ecosystems on native predators, and that all native predators studied to date have been birds. The prevalence of birds as predators on islands is not particularly surprising given flight allows birds to readily colonise islands or utilise islands as part of a migratory lifestyle (Magnússon & Magnússon 2000; Schulz & Gales 2004). I quantified the paucity of studies on avian predators in the eradication literature compared with those focussed on recovering species (Chapter 2). Further research into avian predators is required as part of eradication monitoring programs (Chapter 2). I recommend this research focuses on developing ways to anticipate and quantify the population-level impacts of secondary poisoning and the minimum amounts of prey required to sustain predators (Chapter 2).

The majority of ecology paradigms on top-order predators such as trophic cascades, mesopredator release, and predator-prey relationships focus on mammalian predators in continental ecosystems (Crooks & Soule 1999; Krebs *et al.* 2001; Fortin *et al.* 2005; Sekercioglu 2006). Avian predators in continental ecosystems have analogous roles in trophic cascades and influencing prey behaviour (Salo *et al.* 2008; Ritchie *et al.* 2012; Terraube & Bretagnolle 2018). Yet they are not common in apex predator literature (Wallach *et al.* 2015; Terraube & Bretagnolle 2018). A search of ISI Web of Science (conducted on February 2 2021) using the term "mesopredator release" shows the most frequently cited study of mesopredator release and mammalian predators is Crooks and Soule

(1999), cited 972 times to date (44 citations *per* year, ranked 1st), while the most frequently cited study involving avian predators is Sergio and Hiraldo (2008), cited 96 times to date (4 citations *per* year, ranked 24th). Closer attention on the ecological function of birds will progress our knowledge towards a comprehensive understanding of ecosystem processes.

Birds are frequently used as passive end-members in ecology studies, particularly regarding mesopredator release (Crooks & Soule 1999; Rayner *et al.* 2007; Russell *et al.* 2009). Perhaps, the overarching focus on mammalian predators in predator-prey ecology stems from emotive rationales such as a human fear of mammalian predators (Conforti & de Azevedo 2003); or due to birds being elusive and difficult to study (Krebs *et al.* 2014). Or perhaps the perception of birds as passive players is a legacy of birds dominating island ecosystems where naivety to introduced predators threatens many populations (Blackburn *et al.* 2004). However, naivety is a syndrome of island ecology rather than avian ecology (Jolly *et al.* 2018), and island-endemic mammals can equally be threatened by novel avian predation (Roemer *et al.* 2002). Avian predators highlight the active role birds have in structuring ecosystems, and due to their keystone role on islands need to be considered when planning eradications including targeting invasive avian predators (Evans 2021).

Conservation status and management considerations

Informing and prioritising management based on species conservation status has risks (Possingham *et al.* 2002). During eradication projects, the large quantities of prey carcasses produced during baiting can alter predator and scavenger feeding behaviour and illicit mass feeding events that expose all predators to secondary poisoning (Salmon *et al.* 2010). Regardless of their conservation status, this can have significant impacts on island predator populations with no guarantee of recovery (Buckelew *et al.* 2011).

This is even more of an issue when the predator has an important role in ecosystem function and little ecological redundancy, as is the case for Brown Skuas on Macquarie Island. Brown Skuas not only influence prey populations as apex predators (Chapter 5) but also have important roles as scavengers at seal colonies, acting as the island's "clean-up crew" during birthing and deaths (Phillips *et al.* 2004; Anderson *et al.* 2009).

Brown Skuas are not listed as a threatened species, at a global or national level (Parks and Wildlife Service 2007; IUCN 2020). As a non-listed species and the belief that skua numbers on the island were inflated, the perceived risks of the eradication of rabbits and rodents on Macquarie Island was deemed acceptable for Brown Skuas (Parks and Wildlife Service 2009).

In Chapter 3 I show that the reduction in skua nest numbers caused by the eradication was greater than that estimated from prey-loss alone, suggesting secondary poisoning impacted more skuas than just those that hunted rabbits as prey (Chapter 3). This impact on skuas was greater than predicted (Parks and Wildlife Service 2009) and occurred despite the use of mitigation measures (Springer & Carmichael 2012). The release of Rabbit Haemorrhagic Disease Virus (RHDV) killed an estimated 85% of the rabbit population (Terauds *et al.* 2014) and was arguably the strongest mitigation measure used (Springer & Carmichael 2012). Without the release of RHDV it is highly likely the outcomes for Brown Skuas would have been much worse. However, RHDV was not released to protect Brown Skuas specifically, but two conservation significant species the Northern Giant Petrel (*Macronectes halli*) and Southern Giant Petrel (*M. giganteus*) (Alderman *et al.* 2019).

It was the high number of carcasses found of these two conservation significant species from secondary poisoning (306 Northern Giant Petrels and 17 Southern Giant Petrels were found dead) during the first round of baiting that prompted the release of RHDV (Springer & Carmichael 2012; Cooke *et al.* 2017; Alderman *et al.* 2019). Equally large numbers of Brown Skuas were also found dead after initial baiting (230 skuas; Springer & Carmichael 2012) but these deaths did not trigger a management response (Alderman *et al.* 2019).

Brown Skuas are not listed as threatened but they were still susceptible to unmitigated island-wide impacts of the eradication. Despite the nearest neighbouring colony of skuas being only 600 km away in the Auckland Islands, the closest genetically related populations of Brown Skuas with those on Macquarie Islands are found in the South Atlantic, 7,000 km away, suggesting immigration and interaction with other populations are rare events (Ritz *et al.* 2008). Additionally, mixing between sub-populations of Browns Skuas is not likely to occur during winter migration as sub-populations from different regions migrate to separate sections of southern hemisphere ocean basins (see Fig. 1.1, Chapter 1; Phillips *et al.* 2007; Carneiro *et al.* 2016a; Delord *et al.* 2017; Schultz *et al.* 2018).

Other insular seabird species with sub-Antarctic distributions similar to Brown Skuas are listed as regionally endangered due to local population-level impacts, despite being globally common (Department of the Environment and Heritage 2005a; Threatened Species Section 2021). This discrepancy between the conservation status of Brown Skuas and other insular species relates to the current threats facing each species and not their capacity to recover from additional pressures (Possingham *et al.* 2002), such as the negative impacts of eradication projects. When predicting population-level impacts from eradications, species conservation status, population connectivity/insularity, thresholds of functional extinction, and the likely scale of the impact all need to be considered (Epstein *et al.* 2016).

Monitoring to quantify success of eradication projects

Eradication monitoring typically focuses on the recovery of threatened species or in many cases there is no monitoring at all (Jones *et al.* 2016; Bird *et al.* 2019; Ward *et al.* 2019). This thesis is underpinned by historical data spanning five decades, and targeted monitoring of skuas before and after the eradication. Monitoring must be well funded and framed to address uncertainty, whether informing ecological questions or adaptive management of conservation projects, or it risks becoming a costly and futile exercise (Bird *et al.* 2019; Buxton *et al.* 2020).

The risks posed by eradication of rabbits and rodents to skuas on Macquarie Island was unknown (Raymond *et al.* 2011). The foresight of managers and scientists at the time enabled this thesis to be viable. In Chapter 3 I used a decade of research – spanning three years prior to eradication of rabbits and rodents and seven years post-eradication – combined with additional historical data dating back to the 1970s, to quantify ecological uncertainty surrounding the impact of the eradication on skuas. These data allowed me to quantify a decline in nest numbers and breeding success of skuas following the eradication (Chapter 3). In later years, this monitoring also revealed signs of skua nest numbers recovering on Macquarie Island although with continued low breeding success (Chapter 3). In addition, incidental monitoring of bird deaths during the eradication led to adaptive mitigation measures that proved highly valuable and prevented greater levels of secondary poisoning (Springer & Carmichael 2012; Alderman *et al.* 2019).

Arguably the species that are incidentally put at risk during ecosystem-wide conservation actions, like eradication projects, deserve greater attention than the species that are set to benefit from our actions. Negative impacts on native species from management actions, could have further indirect impacts on other species, such as loss of prey causing increased predation pressure on native prey (Nur *et al.* 2019). The potential for increased predation pressure on recovering petrel populations was the driver for monitoring the current predation pressure of skuas on recovering petrel species, which I quantified in Chapter 4. Without these monitoring programs, unintended negative consequences can never be truly quantified and used to inform future eradication projects, which will only limit the development and progress of such actions (Ward *et al.* 2019).

Assessment of modelling approaches for predator-prey analysis

Application of functional response curves and empirical data to understand predator-prey relationships has utility for a range of conservation actions (Cliff *et al.* 2020) and potential to inform assisted recovery (Sinclair *et al.* 1998). In Chapter 5 I used Antarctic Prions as a model species to compare skua predation pressure to changes in prey density. I then expanded this relationship to the wider petrel family. However, skua predation on other petrel species could have different functional

response curves to that of prions due to a range of factors. Differences in mean burrow density, occupancy rates, burrow lengths, habitat preferences, or the size and behaviour of other petrels could make them easier or more difficult prey for Brown Skuas and alter functional response relationships (Hahn & Quillfeldt 1998; Mougeot *et al.* 1998; Pacoureau *et al.* 2019). For example Blue Petrels on Macquarie Island have patchy discrete colonies with higher mean burrow density than widespread low density Antarctic Prions (Brothers 1984). As a result, the high burrow densities reported in our modelling may represent low density recovering populations for Blue Petrels. There is no available data on growth rates for Macquarie Island petrels, instead I was able to apply data for the entire Procellariiform family (Brooke *et al.* 2018). While this may add uncertainty as to how well these growth rates represent the growth rates of burrowing petrels on Macquarie Island, all growth rates were from either shearwater, storm-petrel or petrel species. All these groups represent species that are currently recovering on Macquarie Island or may do so in the future (Clarke & Schulz 2005; Bird *et al.* 2021).

Despite these limitations the conclusions in Chapter 5 can be generalised to the wider petrel population. Future work focusing explicitly on functional relationships between skuas and other petrels on Macquarie Island would be beneficial. An analogous relationship to the Hollling's Type III relationship between Brown Skuas and petrels was observed in another skua, the Pomarine Skua (*Stercorarius pomarinus*), whose nest density had a sigmoidal relationship with the density of their prey, Brown Lemmings (*Lemmus trimucronatus*) (Maher 1970). With skuas being largely opportunistic predators and facultative specialists this relationship could potentially hold for many other prey species (Reinhardt *et al.* 2000).

Future Directions

Ecosystem monitoring on remote islands is often under budget, logistical and time constraints (Bird *et al.* 2019). Trying to cover the breeding cycle of skuas across a 128km^2 island becomes a marathon for one researcher and a few enthusiastic volunteers as skuas arrive on the island, court, mate, incubate eggs, rear young and depart. Many aspects of skua ecology on Macquarie Island remain unknown and the aspects covered in this thesis are inevitably set to change as the island ecosystem continues to recover and change. Constrained by shipping schedules, I was not able to study the arrival, mating, pre-laying exodus, egg-laying or early incubation period of skuas. This leaves much for the future skua researcher to uncover.

Refining the predator-prey cycles of skuas and petrels

The methods outlined in Chapter 5 could now be applied to other petrel species to gain a deeper and more accurate picture of the ecological role of skuas in structuring the island's burrowing

seabird community. Greater accuracy of absolute numbers of petrels killed over a season could be gathered by clearing transects of feather 'sign' (PPUFs: Prion Predation Undigested Feathers) prior to subsequent repeat counts throughout the entire season. Repeat sampling would also assist our understanding of how predation pressure varies with stages in predator and prey breeding phenologies. Ongoing monitoring of PPUFs would capture how the skua-petrel predator-prey relationship will progress into the future as the ecosystem continues to recover.

Repeating the diet and foraging sampling from Chapter 4 in intervals of 3 to 10 years will reveal how skua diet, foraging and breeding success progress with the recovery of petrel prey and the ongoing effects of climate change.

Restoration, monitoring and eradication projects

For future eradications I suggest, from a predator perspective the key questions should be: How fast will native prey recover and replace invasive prey? And, is exposure of the entire population to the expected rate of secondary poisoning acceptable? Any decline in prey numbers post-eradication should be compared with estimates of prey abundance in the pre-invaded state not the invaded state. Assuming that invasive prey boost the amount of prey for predators often overlooks the impact invasive prey have had on native prey abundance.

Finally, as eradication projects become increasingly complex, an ever-widening array of possible ecosystem responses arise (Kopf *et al.* 2017). The emergence of complex recovery trajectories means recovery should not be left to chance and assisted restoration projects will become necessary for project success (Buxton *et al.* 2016).

Eradication projects targeting invasive mammals are currently being considered for several large islands containing native predators; Amsterdam, Auckland, Christmas, Gough, Tristan de Cunha, and Marion Island (Brown 2007; Algar & Johnston 2010; Holmes *et al.* 2019). These islands contain multiple conservation significant species including the New Zealand Falcon (*Falco novaeseelandiae*) on Auckland Island and the Christmas Island Goshawk (*Accipiter fasciatus natalis*) and Christmas Island Hawk-Owl (*Ninox natalis*) on Christmas Island. These predators eat invasive mammals (Reinhardt *et al.* 2000; Hill & Lill 2001; Hill 2004; Miskelly *et al.* 2020). It is imperative native predators are monitored to inform island eradication programs, particularly if recovery of alternative native prey is slow, the predator is highly dependent on the invasive prey or eradication techniques pose a threat to predators.

Concluding remarks

My thesis has shown eradications can have severe negative effects on top-order predators. My work also revealed signs of recovery and continuity in the Brown Skua population on Macquarie Island, following the eradication of invasive prey. It could be questioned if the threats to native predators resulting from eradication projects are short-term, do they matter when overall the eradication benefits the whole island ecosystem? Indeed, they do still matter. Any negative impact we have on native species through our management actions should be quantified, and where the scale of the effect is uncontrolled or unknown *a priori* the impact should be mitigated against, residual risk should be closely monitored, and contingencies should be planned. The short-term nature of impacts will not be guaranteed in all cases going forward as it is partly driven by the choice of mitigation measures to be used and partly by the predator's own ecology. Impacts on native predators identified *a priori* should not be treated as static threats that pose a risk to a small portion of the population but as ecological perturbations that will alter predator behaviour, demography, diet and ecological role. The goal of my thesis is not to prohibit future eradications but improve our understanding of how they impact species, their interactions and ultimately shape ecosystems. I aim to ensure future eradications can be more robust to adverse outcomes. While the magnitude of impacts recorded during the eradication of rabbits and rodents from Macquarie Island does not appear to have threatened the long-term viability of Brown Skuas; without ongoing monitoring, quantification of these risks, and adaptive management and mitigation, the outcomes could have been poorer for skuas and what is worse, we would not have known.

Monitoring the unanticipated or negative impacts from an eradication may seem an unattractive proposal compared with the alternative focus of monitoring the recovery of threatened species back from the brink due to eradication. As monitoring budgets are finite and often inadequate, there can be a tension between monitoring that highlights the success stories of an eradication and adequately quantifying the collateral damage that occurred (Possingham *et al.* 2012; Bird *et al.* 2019). Documenting success stories is important for securing public support and funding for future projects (Bird *et al.* 2019). However, this must be balanced with studies that address the unintended negative consequences of eradications (Chapter 2). Studies addressing negative consequences should be prioritised not only on the basis of the conservation status of the species impacted, but its ecological role and the scale of the impact relative to the capacity for recovery. Without developing our understanding of these negative impacts, we are unable to refine and improve eradication methods, provide sufficient assistance to species incidentally harmed and risk compromising the success of future eradication projects (Salmon *et al.* 2010; Ward *et al.* 2019). All these outcomes influence decision makers, threaten public perception and social capital of eradication projects and

our ability to secure funds for future projects. Public support will be of vital importance in the future as larger inhabited islands become the focus of eradications (Glen *et al.* 2013).

On most sub-Antarctic Islands, Brown Skuas along with the two other *Stercorarius antarcticus* subspecies, the Falkland (*S. a. antarcticus)* and Tristan Skua (*S. a. hamiltoni*), continue to co-exist with invasive rabbit and rodent populations or have co-existed them in the past (Table 1.1 & Fig. 1.1; Chapter 1). In over half of reported cases the invasive species featured in the diet of Southern Skuas (Table 1.1 & Fig. 1.1; Chapter 1). Some of these islands have plans for eradicating invasive rabbits and rodents or have recently done so (Brown 2007; Black *et al.* 2012; Brown 2013). Managers for these projects have acknowledged that secondary poisoning and prey loss will impact skuas, however few recommend mitigation measures even for those islands where the entire skua population is under threat (Brown 2007). Avian predators are unique ecological actors that make substantial contributions to the maintenance of healthy ecosystems. My thesis provides methods and insights that if incorporated into future island management and conservation actions will help to ensure the roles they serve in ecosystems are not diminished and that these species are appreciated and protected.

Preparing to blow the tops off fourteen empty drums, Bob Dovers, who was resting in camp, ran a long trail of cortex explosive. The fuse passed near the garbage cans, where the skuas gathered. Bob left the gelignite at the end of the fuse, returning to the drums to supervise the final arrangements.

When he turned to walk back to the gelignite, the skuas were pecking at the wrapping paper. Before he could reach them, they had pecked through the paper, swallowing the gelignite. According to all the rules, several dozen skua bodies should have been found round the garbage pile next morning. No such thing! The birds were still there, none the worse for their explosive meal.

Scholes (1951)

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There is a skua on the wing,

Bringing death to everything,

Goodbye to darling petrels,

Goodbye my little ones,

Goodbye to penguin young,

Whose time had just begun.

There is a skua rising on the wind,

Returning home to a hungry nestling.