

The population status, breeding success and diet of Subantarctic Skuas two decades after the feral cat eradication on Marion Island

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ABSTRACT

Prey availability is often the driver behind predator population trends, diet and breeding success. Changes in predator abundance and breeding success represent numerical responses to changes in prey abundance, whereas dietary shifts can be classified as functional responses. Invasive mammals introduced to island ecosystems can have detrimental impacts on endemic bird populations and thus disrupt predator-prey relationships. In cases where a predator is dependent on a certain prey species, the distribution, abundance, breeding success and diet of a predator can reveal disruptions in their prey abundance and density.

Marion and Prince Edward Islands form the Prince Edward Islands group and are situated 20 km apart in the Subantarctic Indian Ocean, 2300 km southwest of Africa. These two young volcanic islands display similar fauna and flora, with the exception of two invasive mammals which were introduced to Marion Island. Domestic cats *Felis catus* were introduced to the meteorological station in the late 1940s to control House Mouse *Mus musculus*, which were accidentally introduced by sealers in the 19th century. Unfortunately the cats turned feral and formed a large population which had disastrous effects on the local burrowing petrel (Procellariidae) populations. The Subantarctic Skua, an opportunistic predator endemic to Marion Island, mainly predated on burrowing petrels and penguins while breeding on the islands. Skuas were assumed to be in direct competition with the cats for food resources, especially burrowing petrels. After the cats were eradicated in the early 1990s, the skuas were expected to increase in abundance and extend their distribution inland as burrowing petrel colonies recovered. However, the numbers of skuas decreased after cats were eradicated, with the 2008 count suggesting that their population had more than halved in the two decades since the eradication of their main competitor.

This unexpected and perturbing finding motivated my study. The skua breeding population on Prince Edward Island appears to have remained stable, whereas numbers on Marion Island are dwindling. I studied the distribution, abundance, diet and breeding success of Subantarctic Skuas on Marion Island to confirm whether their population has indeed decreased in size, and to detect functional and numerical responses possibly caused by an insufficient availability of burrowing petrel prey. Data collected included a whole island census of breeding pairs and non-breeding clubs in 2010/11, mapping the nest distribution in relation to major prey sources, collecting pellets and midden items for diet analysis and monitoring nests to calculate breeding success.

The comprehensive breeding survey found that skua abundance was roughly half that found 23 years ago, confirming that the population at Marion Island has decreased significantly in the two decades since cats were eradicated. A low ratio of non-breeders to breeding pairs were found, less than half of that on Prince Edward Island, suggesting a history of either poor recruitment or a high turnover rate of breeding territories. The distribution of breeding territories remained largely clustered around penguin colonies, and the diet of skuas remained similar to what it was more than two decades ago, with no marked increase in burrowing petrel consumption. Penguins still formed the major part of their diet and their concentration around penguin colonies suggests that most skuas remain largely dependent on penguins at Marion Island.

Skua breeding success was similar to, and in some cases slightly higher, to that found on Marion Island 20-30 years ago and in other healthy skua populations. This suggests that either this breeding season was unusually successful or that poor breeding success is not the driver behind the reduction in skua population numbers. Skua breeding pairs mainly preying on penguins had a lower incubation success, but significantly higher fledging success than those preying mostly on burrowing petrels. This could be attributed to high predator traffic in breeding territories close to penguin colonies resulting in more egg losses and available burrowing petrel prey becoming more scarce as the breeding season progresses. Overall breeding success and egg volume, however, was not significantly affected by the diet.

Overall my results suggest that there has been little if any recovery of the burrowing petrel breeding population on Marion Island since the eradication of feral cats. The last mammalian invasive left on the island, the House Mouse, has been found to be a significant predator of several burrowing petrel chicks on Gough Island. Further studies are needed to assess whether burrowing petrel chicks on Marion Island also are preyed upon by mice, and whether this has slowed or possibly even prevented the recovery of burrowing petrel populations since the eradication of cats. If mice are found to be significant predators of petrel chicks, it will strengthen calls for an attempt to be made to eradicate mice from the island and thus to prevent further disruption of the endemic bird populations and predator-prey relationships on Marion Island.

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CHAPTER 1

General Introduction: Predator-prey relationships and the detrimental effects of invasive mammals on island ecologies

Avian predator–prey relationships

Prey availability plays a major role in the population regulation of predators (Lack 1966, Newton 1998). Avian predators have better breeding success and breed at higher densities when their preferred prey species are abundant, and may refrain from breeding when their prey species are rare (Andersson 1976, Lundberg 1981). An example of this is the breeding success of the Golden Eagle *Aquila chrysaetos* which is positively correlated to the availability of its major prey species (Tjernberg 1983). The adjustment of breeding effort or adapting population numbers through emigration due to poor prey availability are known as numerical responses (Andersson and Erlinge 1977). Avian predators can also show a functional response by adjusting their behaviour when faced with scarce food sources, i.e. by exploiting alternative prey sources (Andersson and Erlinge 1977, Miller et al. 2006, Gilg et al. 2006). Dietary generalists usually show a functional response whereas dietary specialists respond numerically (review in Newton 1979), although some avian predators can show both responses (Korpimäki and Norrdahl 1989, 1991). For example, Long-tailed Jaegers *Stercorarius longicaudus* respond numerically to low lemming abundance by not breeding or failing to fledge chicks (Wiley and Lee 1998). Gilg et al. (2006) found that Long-tailed Jaegers also showed a functional response when confronted by low Collared Lemming *Dicrostonyx groenlandicus* densities by shifting to alternate foods such as berries and insects. However, the potential for a functional response is limited when no alternative prey source is available, or if the avian predator lacks plasticity in its diet.

Predator diet or breeding success as an indicator of prey availability

Prey availability can sometimes be inferred from the diet and breeding success of a highly dependent predator (Croxall 1989, Montevecchi and Meyers 1995). A change in the availability of the prey species may result in either a change in the predator's reproductive success (a numerical response) or by switching to an alternative prey source (a functional response), or both. The Montagu's Harrier *Circus pygargus* in France showed a significant

relationship between the abundance of the Common Vole *Microtus arvalis* and the vole biomass in its regurgitated pellets (Salamolard et al 2000), and the harrier's breeding success was tightly linked with local vole abundance (Salamolard et al. 2000).

Skuas are dietary generalists, but show individual specialization within populations through adapted foraging behaviour (Votier et al. 2004). The Great Skua *Catharacta skua* colony on Foula, Shetland, provides a good example of these responses. The skua's preferred prey are Lesser Sandeels *Ammodytes marinus* found in the surrounding waters, but there has been a steady decline in sandeel availability since the 1970s (Wanless et al. 2004). A reduction in sandeel availability was directly correlated with decreased skua breeding success and a dietary shift towards bird prey (Hamer et al. 1991, Ratcliffe et al. 1998). In this case, studying the diet and breeding success of the Great Skuas on Foula can give a good indication of the population density of sandeels in the surrounding waters.

Subantarctic skuas and petrels

Skuas are opportunistic predators that use a variety of foraging methods to target a wide diversity of prey types. They actively predate on seabirds (Young 1978, Furness and Hislop 1981), scavenge dead animals (Zipan and Norman 1993) and feed by kleptoparasitism (Furness 1987), as well as feeding at sea. Subantarctic Skuas *Catharacta antarctica lönnerbergi* spend their summers on the breeding colonies which falls on most of the Southern Ocean islands found from Chatham Island to the Antarctic Peninsula (Furness 1987). Subantarctic islands offer skuas a diverse range of potential prey, but their main prey are penguins and/or petrels during the skua breeding season (Young 1978; Moors 1980; Sinclair 1980; Adams 1982; Osborne 1985; Pietz 1987, Hunter 1990, Ryan et al. 2009). Skuas breeding on Inaccessible Island are very dependent on the burrowing petrel (Procellariidae) populations (Ryan and Moloney 1991), a situation which is similar to that found on the Prince Edward Islands (Adams 1982, Schramm 1983, Ryan et al. 2009) and Kerguelen Island (Moncrops et al. 1997, Mougeot et al. 1998).

Skuas can catch burrowing petrels in flight (Sinclair 1980), but most are captured on the ground, and they are especially vulnerable during courtship behaviour (Mougeot et al. 1998) when skuas can catch burrowing petrels outside of their burrows (Young 1978, Fraser 1984, Furness 1987), avoiding the energy expenditure of excavation. Courtship behaviour forces

burrowing petrels to vocally display outside of their burrows, making them conspicuous and susceptible to capture (Mougeot et al. 1998).

The petrels, like many seabird species, are long lived with high adult survival and low fecundity (Warham 1996). It has been suggested that skua predation can be a significant selective pressure for petrel populations (Mougeot et al. 1998). Some studies have shown that the presence of petrel prey in skua diets can indicate their relative availability (Adams 1982, Schramm 1983, Zipan and Norman 1993). However, these results need to be explored with caution as factors other than prey density have been suggested to play a significant role in prey selections, e.g. quality of prey and capture effort (Ryan and Moloney 1991).

Invasive species on islands

The introduction of invasive species often leads to a significant reduction in biodiversity (Vitousek et al. 1997). Islands ecosystems are especially vulnerable to the introduction of mammalian predators as the indigenous fauna and flora never evolved defences against these animals (Brown 1997, Kress 1998, Atkinson 2001). A quarter of the world's threatened bird species are exposed to invasive predators (Stattersfield and Capper 2000) and 92% of the extinct bird species in the past four centuries were found on islands (Kress 1998). Island nesting seabirds are particularly vulnerable due to their long life times and low fecundity (Weimerskirch 2002) and their exposure to mammalian predators usually lead to a drastic decrease in population size (Moors and Atkinson 1984).

Marion and Prince Edward Island form the Prince Edward Island group, situated in the southwest Indian Ocean, 2 300 km southeast of Cape Town, South Africa. These two islands have a tundra biome and are key breeding grounds for 29 bird species, including 12 burrowing petrel species (Williams et al. 1979, Crawford et al. 2003, Ryan et al. 2003, Ryan and Bester 2008). Marion Island (46°50'S, 37°45'E) is the larger of these two volcanic islands, with an area of about 290 km², whereas Prince Edward Island, 20 km away, is only 45 km² in extent.

In 1949 three domestic cats *Felis catus* were introduced to Marion Island to manage the invasive House Mice *Mus musculus* around the meteorological station (van Aarde 1977). Unfortunately these individuals, plus another two which were later added, formed a feral cat population, which had grown to more than 2000 individuals by 1975 (van Aarde 1980).

Prince Edward Island was kept free from any mammalian introductions. It was estimated that the cats on Marion consumed almost half a million burrowing petrels each year during the 1970s, driving the local Common Diving Petrel *Pelecanoides urinatrix* breeding population to local extinction (van Aarde 1980, Brooke 1984, Williams 1984). Cats are very destructive mammalian invasives as they can predate on the chicks and adults of many of seabird species (Moors and Atkinson 1984). On Chatham Island, feral cats pose the greatest threat to the Magenta Petrel *Pterodroma magentae* (Johnston et al. 2003).

Previous studies have shown that the removal of cats from islands can have a positive effect on the local seabirds by improving their breeding success (Cooper et al. 1995), reducing their mortality rates (Keit and Tershy 2003, Rodriguez et al 2006, Peck et al. 2008) and promoting the recovery of nesting habitats (Hanel and Chown 1998, Wolf 2002, Ratcliffe et al. 2010). Lavers et al. (2010) found that most predator eradications led to an increase in bird fecundity.

A cat eradication program was initiated on Marion Island in 1977 with the primary purpose of allowing the seabird populations on the island to recover (van Aarde 1979, Bester et al. 2002). The feline panleucopaenia virus was used to infect the cats, causing the population to decrease by roughly half (Erasmus 1979, van Aarde 1979), but the cat population then stabilized around 1983 with no more significant declines due to the virus (van Rensburg et al. 1987). From 1986 to 1989, cats were shot and the remainder were caught with gin traps or poisoned (Bester et al. 2002). The last cat was trapped in 1991 and the eradication programme was deemed successful (Bester et al. 2002). There have been no further sightings or evidence of the presence of cats on the island in the last 20 years.

Initial studies in cat free enclosures indicated that the breeding success of burrowing petrels significantly increased in the absence of cats (van Rensburg and Bester 1988). Great-winged Petrels *Pterodroma macroptera* increased their breeding success from 0% to 64% and that of the Blue Petrels *Halobaena caerulea* increased from 24% to 64% when the cat numbers decreased markedly on Marion Island (Cooper and Fourie 1991, Cooper et al. 1995). With this significant increase in burrowing petrel breeding success in the absence of cats, the population recovery of the affected bird species was expected after the cat eradication (Bester et al. 2002).

Van Aarde (1980) found that the diet of the feral cats on Marion Island contained 63% Salvin's Prions *Pachyptila salvini*. This burrowing petrel was one of the main species found in the diet of the Subantarctic Skuas breeding on Marion Island by Hunter (1990), which

suggests that skuas and cats competed for the same prey. Hunter (1990) predicted that the predator-prey relationship between the skuas and the petrels was disturbed by the invasive cats and that the cat eradication would result in burrowing petrel populations recovering and skua nests becoming more abundant inland around petrel colonies (away from coastal penguin colonies).

However, after the eradication of feral cats in 1991 the Subantarctic Skua population on Marion Island apparently has declined from 878 pairs in 1987/1988 to only 282 pairs in 2008/09 (Hunter 1990, Ryan et al. 2009). Ryan et al. (2009) calculated the rate of decline to be 5% per year, with the tempo speeding up in the last decade. The skua breeding population on the neighbouring Prince Edward Island appears to be stable and the island supports a density of breeding skuas five times greater than that on Marion Island (Ryan et al. 2009).

If the abundance, distribution and diet of skua breeding pairs could indicate the relative density and distribution of burrowing petrels (Adams 1982, Schramm 1983, Ryan and Moloney 1991) then the studies of Hunter (1990) and Ryan et al. (2009) could provide some insight into the effects the cats had on the predator-prey relationship of the Subantarctic Skua on Marion Island. Hunter (1990) showed that the diet of skuas on Marion Island nearing the end of the cat eradication period consisted of 22% burrowing petrels. By comparison, the diet on Prince Edward Island was found to be 96% petrels in 2008 (Ryan et al. 2009). Such a drastic difference between two very similar islands could almost certainly be attributed to the presence of a mammalian invasive on the one and the absence of it on the other. We do not know whether the diet of the skuas on Marion Island has changed since the cat eradication, but we do know that their numbers appear to have declined whereas the population of skuas feeding predominantly on burrowing petrels on Prince Edward Island have remained roughly stable (Ryan et al. 2009). This suggests that the recovery of the burrowing petrel population on Marion Island after the cat eradication has been less than expected (Hunter 1990). If Marion Island was able to support 1500 skua breeding pairs prior to the cat invasion, as suggested by Ryan et al. (2009), then the estimated population of 282 pairs two decades after the cat eradication suggests that the Subantarctic Skua population has not at all recovered as expected on Marion Island.

Objective and aims

This study was motivated by the sparse population and diet data of Subantarctic Skuas on Marion Island following the eradication of cats from the island as well as indications of an ongoing decline in skua numbers. I investigated the abundance and distribution, diet and breeding success of the Subantarctic Skuas in the 2010/11 breeding season, 20 years after the eradication of cats from Marion Island. I conducted a detailed count of the skua nests on the island and mapped their distribution and I monitored 102 skua pairs in the area previously studied by Steve Hunter (1990) to assess changes in their diet and breeding success.

The abundance and distribution of Subantarctic Skuas typically reflects the availability and distribution of their prey (Adams 1982, Schramm 1983, Ryan and Moloney 1991). Subantarctic Skuas on Marion Island breed in open territories and are conspicuous due to their extremely defensive behaviour. Thus it is possible to conduct a relatively accurate census of breeding pairs on the island. Chapter 2 is based on an intensive survey of the abundance and distribution of skua nests and non-breeder clubs. Non-breeding skuas are sexually mature birds that have not established a breeding territory. They form a pool of potential recruits for open breeding territories (Klomp and Furness 1992). A low ratio of non-breeders to breeders suggests that either experienced breeding pairs are not returning to the island to breed or that previous breeding success has been so low that there are fewer young adults returning to their natal island (Klomp and Furness 1992). All the nests and clubs were counted and their GPS locations were taken to construct a map of their distribution. With these data the severity in decline of skua numbers could be assessed as well as the change in their distribution in relation to prey sources and the ratio of non-breeders to breeders.

The diet of predators typically reflects the density of their prey (Adams 1982, Schramm 1983, Ryan and Moloney 1991). The diets of breeding skuas can be inferred by inspecting the undigested prey remains in the pellets they regurgitate as well as their middens which consist of prey remains carried to the nest site. Subantarctic Skua diet on Marion Island in 1987/88 showed a predominance of penguins whereas the skuas on Prince Edward Island, a mere 20 km away, predominantly predate on burrowing petrels (Adams 1982, Hunter 1990, Ryan et al. 2009). Marion Island has a penguin population ten times larger (Crawford et al. 2009), and a burrowing petrel population much smaller than that of Prince Edward Island (Schramm 1986), so it is to be expected that the Marion Island skuas will have more penguin remains in their diet than those on Prince Edward Island. However, the last diet analysis of skuas done

on Marion Island was in 1987/88 which was just before the cats were completely eradicated and 20 years later the burrowing petrel populations should have recovered. This would in turn be reflected in diet of the skuas on Marion Island which is why another diet assessment of the skuas is necessary. In Chapter 3 I examine the pellets and midden contents from 102 Subantarctic Skua nests on Marion Island. The proportion of burrowing petrel remains and penguin remains was focussed on to see if a prey shift had occurred since the cat eradication.

Breeding success of some skua species have been found to depend on prey availability (Furness and Hilsop 1981, Hamer et al. 1991, Phillips et al. 1996). It is assumed that the cause for decline in Subantarctic Skua numbers is restricted to Marion Island, because the numbers on Prince Edward Island have stayed stable (Ryan et al. 2009). Thus it must be something that affects the skuas during the breeding season, which should then be reflected in their breeding success. Also, prey availability is not the only factor which motivates prey choice; prey quality as well as energy expenditure during capture should also be taken into account (Ryan and Moloney 1991). This can be measured by comparing the breeding success of skua parents mainly preying on different prey types. I monitored 102 skua nests from incubation to fledging to assess their breeding success (Chapter 4). This was compared to the breeding success found on Marion Island in 1987/88 (Hunter et al. 1990) and that of other healthy skua populations. As the diets of these pairs were analyzed in Chapter 3, I could use these data to compare the breeding success of skua breeding pairs targeting different prey. I could also find out whether poor breeding success is the driving factor behind the decline of skua numbers on Marion Island.

CHAPTER 2

Subantarctic Skua abundance and distribution two decades after the feral cat eradication on Marion Island

Abstract

The Prince Edwards Islands in the south Indian Ocean comprise two islands with similar fauna and flora, Marion and Prince Edward. An invasive mammalian predator, the feral cat, was successfully eradicated from Marion Island in 1991 after having detrimental impacts on the local burrowing petrel population. Prince Edward Island has had no introductions of invasive mammals. The population of Subantarctic Skuas was impacted by the reduction in burrowing petrels, a key prey species for breeding skuas, and the population recovery of both the petrels and the skuas was expected after cats were eradicated. However, there is evidence of a steady decrease in skua numbers over the last two decades on Marion Island, whereas the numbers of Subantarctic Skuas on Prince Edward Island have remained constant. I investigated the abundance and distribution of skuas on Marion Island in 2010/11, repeating a detailed survey conducted in 1987/88. The number of skua nests has halved since 1987/88 and their distribution remains concentrated around penguin colonies. The ratio of non-breeders to breeding pairs is much lower than found on Prince Edward Island, indicating either high adult/juvenile mortality confined to Marion Island or poor breeding success in recent years. If skua abundance and distribution reflects their prey availability and distribution, my results suggest that there has been little if any recovery in burrowing petrel numbers since the cat eradication two decades ago.

Introduction

Human contact with oceanic islands often leads to accidental or purposeful invasive predator introductions, which have detrimental consequences for the local bird populations (Moors, Atkinson 1984, Frenot et al. 2005). Domestic cats were introduced to Subantarctic Marion Island in 1949 to control the established invasive House Mouse at the island's weather station (Cooper 2008, Jansen van Vuuren and Chown 2007). By 1975 the original five cats had increased to a feral population of roughly 2 000 individuals (van Aarde 1979), mainly

preying on the local burrowing petrels (Procellariidae) (van Aarde 1980). The cats were estimated to consume more than 450 000 burrowing petrels annually in the mid 1970s (van Aarde 1980), resulting in calls for a multi-faceted eradication programme. The cats were finally eradicated by 1991 (Bester et al. 2002). The destructive effects the cats had on the burrowing petrel population apparently impacted the breeding population of their main predator on Marion Island, the Subantarctic Skua (Hunter 1990).

Subantarctic Skuas are opportunistic predators, scavengers and kleptoparasites, which predominantly feed on penguins and/or petrels when breeding (Young 1978, Moors 1980, Sinclair 1980, Adams 1982, Osborne 1985, Pietz 1987). Marion Island supports 11% of the global Subantarctic Skua population (Crawford and Cooper 2003). Most Subantarctic Skua pairs on Marion Island feed at penguin colonies (van Aarde 1980, Hunter 1990, Ryan et al. 2009), whereas burrowing petrels constitute most of their diet on neighbouring Prince Edward Island (20 km away), which has no introduced mammals (Adams 1982, Ryan et al. 2009). Hunter (1990) argued that the decrease in burrowing petrel numbers on Marion Island, due to intense cat predation, caused inland Subantarctic Skua breeding pairs, dependent on petrels for food, to shift to coastal penguin colonies on Marion Island. He predicted that the long-term recovery of burrowing petrel breeding populations after cat eradication should result in an increase in the numbers of Subantarctic Skua pairs breeding at inland territories.

Subantarctic Skuas return to their natal colony 3-4 years after fledging where they join the non-breeders (immature birds and mature birds without breeding territories) at club sites (Burton 1968), and usually do not breed before they are 8 years old (Hemmings 1989). In the 1970s there were estimated to be about 400 skua pairs breeding on Marion Island (Siegfried et al. 1978, Williams et al. 1979) but this was a gross estimate, not based on a formal survey. Given the difficulty of getting around the island at this time (there were no field huts, and field workers seldom ventured far from the base), it is quite likely that a large proportion of skua nests were overlooked. A more intensive survey of the avian scavenger-predators of Marion Island in 1987/88 reported 878 breeding territories (Hunter 1990).

After 20 years of recovery time from the invasive cats, we would expect some indication that the breeding populations of both affected burrowing petrels and Subantarctic Skuas have recovered (Hunter 1990). However, Ryan et al. (2009) reported that skua numbers on Marion Island appeared to have decreased since 1987, with 749 breeding pairs in 1997/98, 546 in

2001/02 and only 282 pairs in 2008 (Crawford et al. 2003a, b, Ryan et al. 2009). The latter two counts were made as part of general surveys of surface-nesting birds on Marion Island, and thus were not directly comparable to Hunter's (1990) estimate. Yet even when taking into account differences in counting methods and effort (Ryan et al. 2009), the apparent downward trend in skua numbers at around 5% per year suggests that the breeding population has not recovered and continues to decrease after the eradication of feral cats. The aim of this chapter is to find whether skua numbers have in fact decreased on Marion Island and whether the distribution of breeding pairs over the island has at all changed since 1987.

Methods

Marion Island (46°52' S; 37°51' E), one of two islands in the Prince Edward Island group, is situated in the southwestern Indian Ocean, some 1 800 km southeast of South Africa. It is an active volcanic island of 290 km² that rises up to 1 230 m above sea level. This study was conducted from August 2010 to February 2011, with a census of breeders and non-breeders in December 2010 to January 2011 when most of the Subantarctic Skua pairs were breeding. Breeding pairs can be tracked by their characteristic alarm calls at nest sites (Ryan et al. 2009), however most nests in this study were found by visual identification and alarm calls were only given after the territories were found and entered. The coastal area of Marion Island was intensively searched for skua nests, such as in Hunter (1990), and more inland areas were less intensively searched on scouting trips (Figure 1). The discrepancy between the areas searched in this study and in Hunter (1990) was due to time limitations, harsh territory and poor weather conditions. The Global Positioning System (GPS) location of all nest sites was noted and used to map all the nest positions. Hunter (1990) mapped skua nest density and distribution in half-minute grid squares, so half-minute gridlines were added to my map to generate comparable numbers of skua nests within each half-minute grid square (0.58 km²). During the survey, the number of territories which were defended by pairs without nests were separately noted. This number was only noted for the area from Goney Plain to Devil's Footprint and the percentage of defended territories without nests out of the total number of defended territories (with and without nests) could then be extrapolated for the whole island count. A portion (57) of the 2010 nests were only counted in February 2011, and if this number of nests is corrected for by percentage failure (16%) of the monitoring colony (n=102) then I can add another 9 possibly failed nests to that total count.

Non-breeding skuas congregate at club sites which breeders rarely visit (Klomp and Furness 1990), and Ryan et al. (2009) reported seven club sites on Marion Island. All the skua clubs found were counted one to four times during the 2010/11 breeding season. The overwintering skuas were also counted three times over the winter season for comparison with counts found by Williams et al. (1979) to assess whether a change in overwintering numbers has occurred since the 1970s.

Data analyses

The GPS points of all the nests and non-breeder clubs were plotted. I used the counts of skua nests found in the half minute squares for my study and that of Hunter (1990) as directly comparable data, which could be analyzed in Statistica (v. 10). To find changes in nest distribution from 1987 to 2010, nest densities were compared at specific locations using the nests found per half-minute square in 1987 (Hunter 1990) and comparing it to that found in the corresponding half-minute square in 2010. For the sake of density comparisons, the number of nests in half-minute squares in which only a portion of coastline is covered (and the rest falls over the ocean) was multiplied by the number needed to make a whole square (e.g. only a quarter of the square covers land, in which two nests were found, thus the density is two times four nests per square). The nests found in the 2010/11 breeding season's half-minute squares were plotted against that found in 1987/88 and the relationship analyzed using a linear regression.

The distance from each skua nest in the study colony to the nearest large King *Aptenodytes patagonicus* (more than 200 individuals) or Macaroni Penguin *Eudyptes chrysolophus* colony (more than 500 individuals) was calculated from penguin distribution data (Crawford et al. 2003a; Crawford et al. 2003b; Crawford et al. 2009). Southern Rockhopper Penguin *Eudyptes chrysocome* breeding territories were omitted from this analysis as these penguins do not form distinct colonies and occur mostly spread out along the coastal area. The distance was also measured from the mid-points of the half minute squares to the nearest major penguin as well as distance to the coast. Altitude was measured in the middle of each half-minute square. The data were then analyzed using a general linear model (GLM) to find the variable (distance from penguin colonies, altitude or distance from coast) with the strongest impact on nest density in both breeding seasons and to find the nature of the relationship between the variable and nest density. For the final GLM analysis only one variable was chosen, distance

to major penguin colonies, as it had the highest F-statistic in the previous analyses for both 1987/88 and 2010/11. The other two variables, altitude and distance to coast, were excluded as they were both correlated with each other (Pearson's $r = 0.78$, $p < 0.05$) as well as distance to penguin colonies (Pearson's r for altitude and distance to penguin colonies = 0.23 , $p < 0.05$; r for distance to coast and distance to penguin colonies = 0.29 , $p < 0.05$) probably due to Marion Island's conical shape and the fact that penguins breed close to the coast.

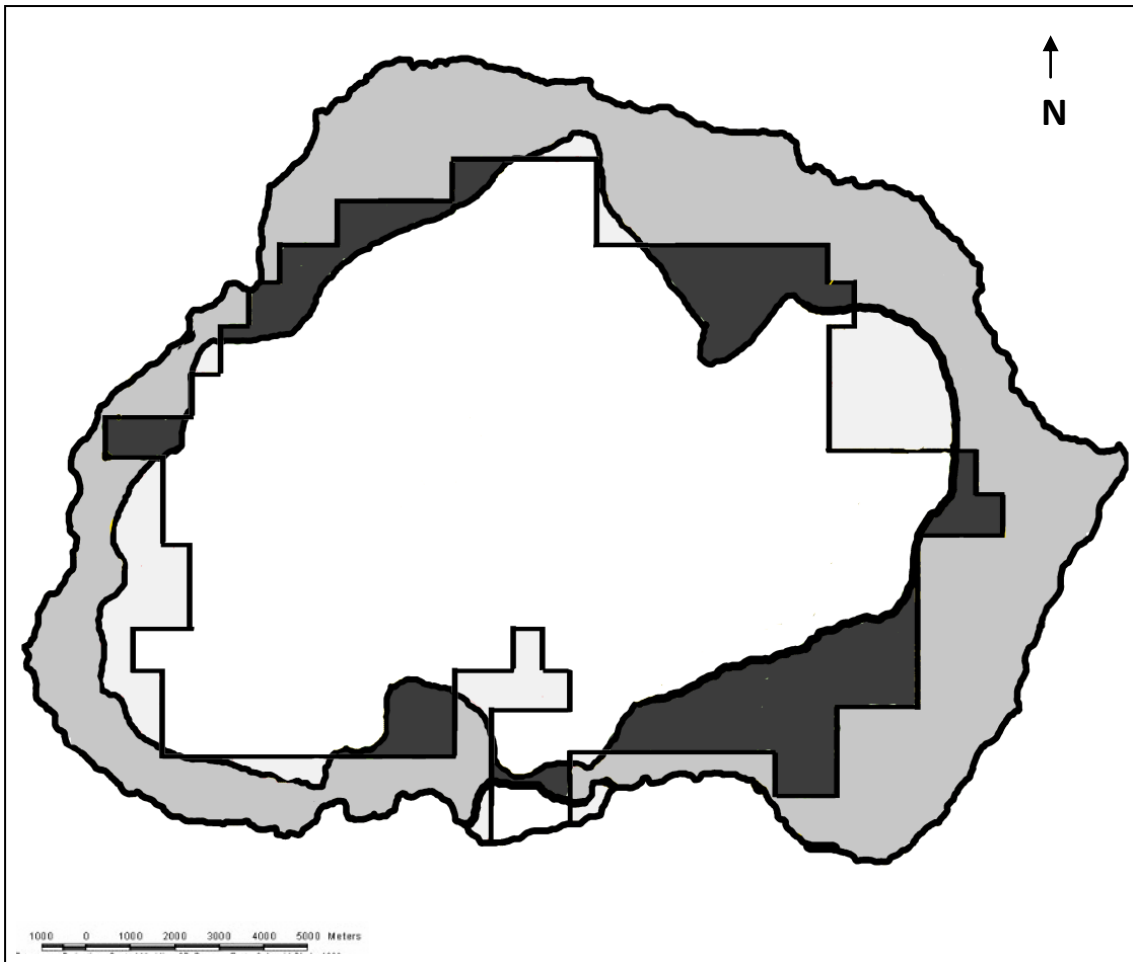


Figure 1: A map of Marion Island depicting the areas searched in 1987/1988 by Hunter (1990, mid-grey and pale grey) and in this study (2010/2011, mid-grey and dark grey).

Results

A total of 441 Subantarctic Skua nests were found on Marion Island in the 2010/2011 breeding season (Figure 2) and when I add the 9 possibly failed nests, it totals to 450 nests. An area with 214 breeding territories contained 91 territories that were defended by pairs but

contained no nests. Extrapolation of these data results in 188 non-breeder territories of the total 629 defended skua territories on Marion Island (with and without nests). The areas that were not searched in this study, but in Hunter (1990), contained 3% of the whole island count in 1987. If that percentage is applied to this study, it means that approximately 12 nests could have been missed.

General linear model results showed that the distance from skua nests to the nearest major penguin colony had a significant negative relationship with nest density in 1987/88 and 2010/11 (Table 2). Figure 3 shows with this study's Subantarctic Skua abundance data the rate of decrease in skua numbers averages 3% per year, less than the 5% estimated by Ryan et al. (2009). The pattern of nest distribution in 1987 and 2010 showed a significant linear correlation ($R^2=0.43$, $p<0.00$).

Non-breeder counts from 13 club sites totaled at 377 individuals, with the largest club at Swartkops Point containing 72 individuals (Table 1). All large clubs were close to major penguin colonies, except for small clubs next to a small inland lake near Mesrug and at an inland site on Long Ridge (Figure 1). An average of 11 overwintering individuals (range 9-13 birds) was found.

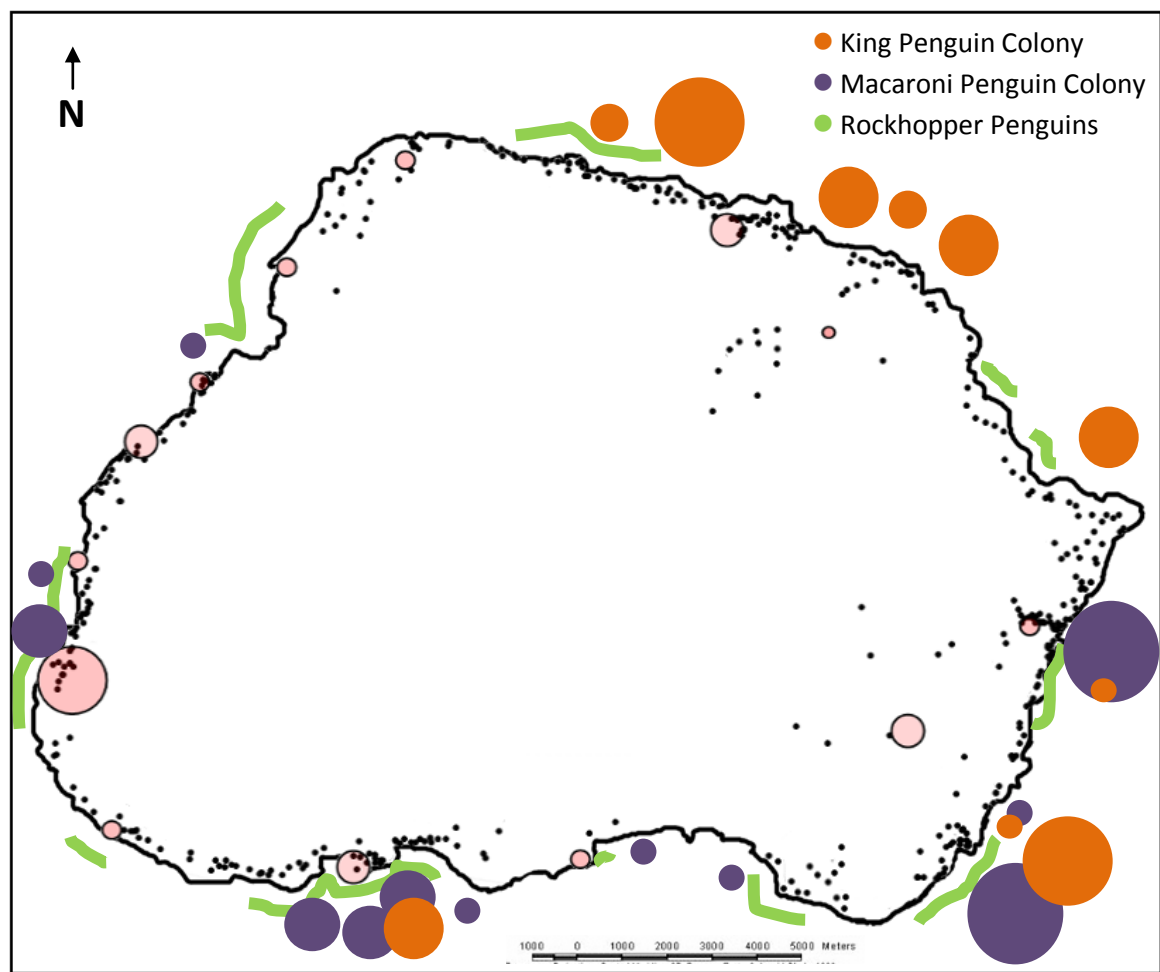


Figure 2: The distribution of Subantarctic Skua nests on Marion Island in the 2010/2011 breeding season. Each of the 441 black dots represents a skua nest, whereas the pink filled circles represent skua non-breeding clubs. The circles of increasing sizes represent skua clubs with more than 5 ($n=1$), 10 ($n=6$), 30 ($n=2$) and 70 ($n=1$) individuals, respectively. Major penguin colonies are indicated by circles indicating colonies of different sizes: purple = Macaroni Penguin colonies (500-1 000, 1 000-10 000, 10 000-100 000 and >100 000 breeding pairs); orange = King Penguin colonies (200-500, 500-1 000, 1 000-10 000 and >10 000 breeding pairs). The data are from previous penguin abundance and distribution studies (Crawford et al. 2003a; Crawford et al. 2003b; Crawford et al. 2009). The green lines indicate areas of high Rockhopper Penguin densities as found in Hunter (1990).

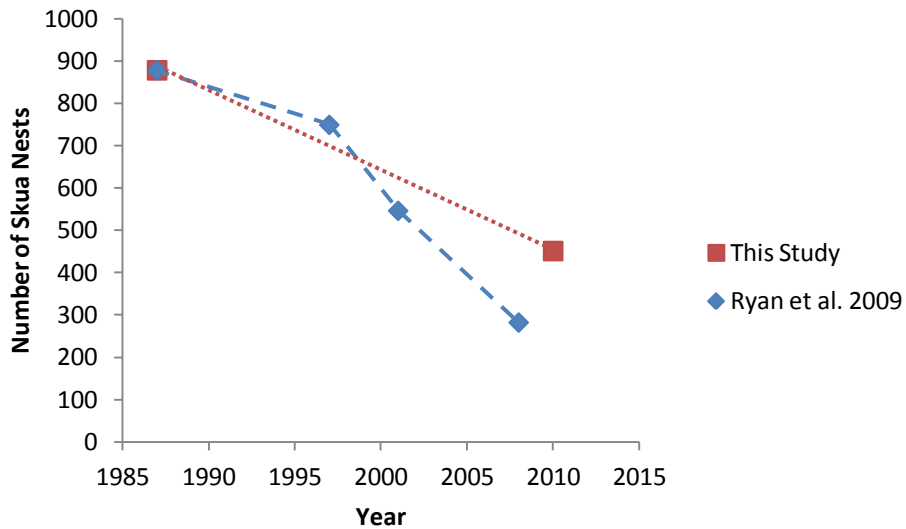


Figure 3: Comparison of the Subantarctic Skua population sizes found in 1987 and 2008 or 2010 by Ryan et al. (2009) and in this study. The results in this study show a less marked decline (3% per year) than inferred by Ryan et al. (2009) (5% per year).

Table 1: The position and sizes of the 13 clubs of non-breeding Subantarctic Skuas on Marion Island during summer 2010/11 (October to February).

Clubs	Longitude	Latitude	Average	Counts
Cape Davis	37.69265	-46.82942	6	1
Kampkoppie	37.61552	-46.88492	35	1
Le Grange	37.59710	-46.90847	14	1
Third Sister	37.81642	-46.86348	12 (4-20)	4
Bullard Beach	37.87514	-46.92138	20 (18-22)	2
Gazella Plain	37.74384	-46.96725	45 (24-60)	3
Mesrug	37.83975	-46.94185	50	1
Prinslooemeer	37.78679	-46.84326	38 (29-54)	3
Rookes Peninsula	37.67753	-46.96865	38 (35-41)	2
Swartkop Point	37.60306	-46.90144	72 (65-78)	3
Toffee Lava	37.60682	-46.96150	10	1
Mixed Pickle	37.63262	-46.87310	22	1
Devil's Footprint	37.65813	-46.85045	15	1
TOTAL			377	

Table 2: The influence of the distance to the nearest major penguin colony on nest density in the 1987/88 and 2010/11 Subantarctic Skua breeding seasons on Marion Island calculated with a GLM. The slope (b*-value) of this relationship shows that skua nest density significantly decreases as distance to major penguin colonies increases.

Variable	1987/88			2010/11		
	b*-value	F-value	p-value	b*-value	F-value	p-value
Distance from major penguin colonies	-0.38	31.0	0.00	-0.32	27.8	0.00

Discussion

Although the number of Subantarctic Skua pairs on Marion Island during this dedicated survey in 2010/11 was more than the estimate of 282 nests in 2008 (Ryan et al. 2009), it is less than the three other surveys conducted from 1987/88 to 2001/02. The most comparable survey is the 878 territories counted in 1987/88 (Hunter 1990), which suggests that skua numbers on Marion have decreased by at least a third over the last two decades. The small number of nests found in 2007/8 is likely due to this survey, and the 2001/02 survey, having been conducted by observers with little experience of the island, and the survey not being restricted to skuas. Thus the last really comparable count was the 749 nests found during in 1997/98 (Ryan et al. 2009). This suggests that the decrease in skua numbers at Marion Island has been most rapid since the late 1990s, with roughly 4% per annum decrease to 2010/11 ($\lambda=0.962$). Ryan et al. (2009) compared the Marion Island Subantarctic Skua population trends to neighbouring Prince Edward Island. Although the count data are even more scant for Prince Edward Island, the skua breeding population appears stable over the last decade.

The lack of population structure and demographic data prior to 2010 makes it difficult to understand what has driven the reduction in skua numbers on Marion Island over the past 20 years. The health of skua populations can be inferred from the ratio of non-breeders to

breeders (Klomp, Furness 1990, 1992). A decrease in the proportion of non-breeders is a warning sign that breeder numbers are only superficially constant, as non-breeder recruitment into vacated breeding territories will conceal a decline in the number of breeding pairs (Porter 1988). Similar to the findings of Ryan et al. (2009), this study also found less than one non-breeder per breeding pair (377 non-breeders to 450 breeding pairs). Compared to the two non-breeders per breeding pair on Prince Edward Island, which has a stable breeding population (Ryan et al. 2009), the low non-breeder counts on Marion Island could provide further evidence that the Marion population is declining. It must be noted that if the skua population on Marion Island was recovering the ratio of non-breeders to breeders would be the last variable to reflect this as returning skuas would fill up newly available territories before joining non-breeder clubs. However, in conjunction with the evidence of declining breeder numbers, the low non-breeder to breeder ratio can be seen as further evidence indicating poor population health on Marion Island. Due to the large difference in the non-breeder ratio between Marion Island and Prince Edward Island, it appears that the reason for this is restricted to the islands and not a common cause at sea. Small numbers of non-breeders could indicate either high adult mortality rate and thus depletion of the non-breeder pool into vacated breeding territories, or periods of low breeding success or low juvenile survival rate resulting in few young returning birds (Klomp and Furness 1992). Low breeding success or breeders not attempting to breed at all due to environmental factors (however, non-breeding is not common in adult skuas, Catry et al. 1998) is more likely to be the reason for the dwindling numbers on Marion island, rather than high mortality at sea. No non-breeders were associated with a rapidly decreasing Falkland Island skua breeding colony, emphasizing the importance of non-breeders as indicators of population health (Catry et al. 2011). The 9-13 overwintering individuals recorded during the 2010 winter on Marion Island falls within the lower range of 10 to 25 individuals reported by Williams et al. (1979).

The close relationship between skua density and the distance to the nearest penguin colony suggests that there is still a heavy reliance on penguin colonies as was the case in 1987/88. This is further supported by the diet data reported in Chapter 3. Subantarctic Skuas have not moved more inland to nest as predicted by Hunter (1990) once the burrowing petrel populations start to recover. Breeding success of some burrowing petrel species increased after the cats were eradicated (Cooper et al. 1995, Ryan, Bester 2008), but there is no direct evidence that burrowing petrel populations have increased. The similarity in the pattern of distribution in 1987 and 2010 indicates that the decrease in skua numbers occurred over the

whole island and was not restricted to certain areas.

Recent population trends indicate that there is some negative factor on Marion Island that is not on Prince Edward. The breeding success data in 1987/88 indicates that the skua population was still in disequilibrium due to the reduction in burrowing petrel numbers, as breeding success further away from major prey colonies was much lower than the breeding success of skua nests close to prey colonies (Hunter 1990). This suggests that the negative effects of cat predation were still persisting during this time, due to a lag in recovering burrowing petrel population numbers as well as the skua population numbers, and that the skua population counted in 1987 was probably still decreasing. My breeding success data in Chapter 4, however, shows a smaller difference between the breeding success of skua territories closer and further away from prey colonies, which suggests that the Subantarctic Skua population on Marion Island might be reaching an equilibrium.

In conclusion, the Subantarctic Skua breeding population has continued to decrease since the cat eradication in 1991. The distribution data indicates that the decrease in numbers took place over the whole island, and the Subantarctic Skuas breeding territories still compact around penguin colonies as they did in 1987/88 (Hunter 1990).

CHAPTER 3

Have burrowing petrels recovered on Marion Island two decades after cats were eradicated? Evidence from changes in Subantarctic Skua diet

Abstract

In the 1980s, Subantarctic Skuas breeding on Marion Island preyed mainly on penguins, whereas on Prince Edward Island, only 20 km away, they mainly targeted burrowing petrels. This difference probably resulted at least in part from the destructive effects of feral cats on the populations of burrowing petrels on Marion Island. Cats were introduced to Marion Island in 1949, and prior to their eradication in the early 1990s they killed up to 450 000 petrels each year, greatly reducing the densities of petrels breeding on the island. Penguins still dominated the diet of breeding Subantarctic Skuas on Marion Island in 2010/11, two decades after cats were eradicated from the island. No significant change was found in the proportions of burrowing petrels and penguins in skua diets compared to 1987/88. The proportion of penguins decreased and the proportion of burrowing petrels increased slightly, but this tendency might be expected given the reduction in penguin numbers at Marion Island over the last few decades. Coupled with the decrease in skua numbers at the island reported in Chapter 2, my results suggest that there has been little if any recovery of the burrowing petrel population since cats were eradicated from Marion Island.

Introduction

Skuas are opportunistic predators (Furness 1987) and those that breed on Subantarctic islands mostly predate on burrowing petrels and/or penguins during their breeding season (Ryan and Moloney 1991, Zipan and Norman 1993, Mund and Miller 1995). The Prince Edward Islands in the southwest Indian Ocean consist of two islands, Marion and Prince Edward, which support very similar biotas (Gremmen and Smith 2008; Ryan and Bester 2008). They are home to 11% of the global Subantarctic Skua population (Crawford and Cooper 2003), but the recent population trends of skuas differ between the two islands (Ryan et al. 2009). Numbers of skuas breeding on Marion Island have decreased over the past 20 years, whereas the Prince Edward Island population appears to be stable (Ryan et al. 2009, Chapter 2). There is a significant relationship between food availability and reproductive success in skuas

(Furness and Hislop 1981; Hamer et al. 1991; Phillips et al. 1996), which makes diet important to assess when studying population trends.

Based on diet data from Marion Island in the 1980s, skua populations show distinct differences in diet between the two islands, with burrowing petrels comprising a much greater proportion of prey on Prince Edward Island (96%, Ryan et al. 2009) than on Marion Island (22%, Hunter 1990). These differences in diet result in part from the greater abundance of penguins on Marion Island (Ryan and Bester 2008), but mainly from the marked reduction in burrowing petrel numbers on Marion Island caused by feral cats, which have never occurred on Prince Edward Island. Cats were introduced to the newly-established weather station on Marion Island in 1949 to help to control populations of House Mice (which were introduced by sealers in the 19th century). However, the cats soon turned feral and started to eat large numbers of native birds, especially nocturnal, burrow-nesting petrels (Rand 1954). By the 1970s, some 2 000 cats were estimated to eat 450 000 petrels each year, resulting in the local extirpation of some species (van Aarde 1980). By the late 1970s the density of burrowing petrel nests on Marion Island was estimated to be roughly 100 times lower than on Prince Edward (Schramm 1986). A programme was initiated to control cats, and they were eventually eradicated from Marion Island in the early 1990s (Bester et al. 2002).

Hunter (1990) predicted that once cats were eradicated the recovery of Marion Island's burrowing petrel populations would increase the numbers of skuas breeding inland, away from penguin colonies. The breeding success of at least some burrowing petrels increased soon after cat eradication (Cooper et al. 1995), suggesting that the removal of cats should result in an increase in petrel populations. Elsewhere, burrowing petrel populations have increased by roughly 7% per year following the removal of introduced predators (e.g. Ryan et al. 2006), and up to 20% per year where there is an adjacent, predator-free island that can provide a source of immigrants (Harper 1983). These rates of increase suggest that burrowing petrel populations could increase 4-40 fold over the 20 years since cats were removed from Marion Island. Such marked increases in burrowing petrel abundance should be reflected in the diets of Subantarctic Skuas breeding on Marion Island. Even though skua prey items are not an accurate depiction of relative prey abundance (Young 1978; Moncorps et al. 1997; Mougeot et al. 1998), they should detect gross changes in burrowing petrel population abundance at Marion Island. I studied the diet of breeding skuas on Marion Island in 2010/11, two decades after cats were eradicated, and compared it to their diet in 1987/88 (Hunter

1990). In addition to assessing whether burrowing petrel populations have recovered, my findings could provide useful insights into the reasons for the decrease in skua numbers at Marion Island over the past two decades (Ryan et al. 2009, Chapter 2).

Methods

Breeding skuas bring large prey back to their nesting territory, forming middens, and regurgitate indigestible prey remains in pellets. I collected skua prey remains and regurgitated pellets at 102 nests along 18 km of coastline from Prinsloo Meer to Bullard Beach (Figure 1). Nest locations were recorded with a hand-held GPS unit. Hunter (1990) failed to define his study area, but it is likely that it overlaps with my study area, which is centered on the research station. Prey remains and pellets were collected during the chick-rearing period from mid-December 2010 to mid-February 2011. Four checks were made of each nest: immediately post-hatching (mid- to end December), chicks 2-4 weeks old (early to mid-January), pre-fledging (mid- to end January), and post-fledging (early to mid-February).

All prey remains and pellets were collected within a 10 m radius of nests, as this was where most pellets were found and it reduced the chances of including pellets from other Subantarctic Skuas or giant petrel *Macronectes* spp. Most burrowing petrel prey remains were wings. Wing length was used to discriminate between Blue Petrels *Halobaena caerulea* (>220 mm) and Salvin's Prions *Pachyptila salvini* (<205 mm). Kerguelen *Lugensa brevirostris* and the Soft-Plumaged *Pterodroma mollis* petrels were grouped together as their wings could not be discriminated with confidence. Pellet contents were analyzed by identifying bones, fur and feathers to the lowest taxon possible and then the pellet was classified according to the predominant prey items. Egg shell fragments found in pellets were identified as belonging to penguins or petrel based on their thickness; penguin eggs have distinctly thicker shells than those of burrowing petrels. Prey remains were then grouped into three categories, burrowing petrels, penguins or other prey types (e.g. mice, seal remains, etc.), for comparison with Hunter (1990).

Goodness-of-fit tests (chi-squared, with Yates's correction for continuity where appropriate, G tests or exact binomial probabilities) were used to compare the observed prey composition of each nest with the population mean for both midden and pellet data. Specialization on a particular prey type was inferred where the prey remains or pellets from a given nest deviated

significantly from the population mean.

To assess the diet around the entire island, middens were checked at all skua nests found during a complete island census of breeding skuas conducted in December 2010 (Chapter 2). The position of each skua nest was recorded with GPS, and the nest classified according to the most abundant prey items (penguins, burrowing petrels or other prey) after Hunter (1990). Additional nests found in January-February 2011 were not included because their middens were not sampled. The distance from each skua nest to the nearest penguin colony was regressed against the proportion of penguin pellets found for each nest. Statistical analyses were conducted in Excel (2007) and Statistica (v. 10).

The ratio of penguins to burrowing petrel biomass was calculated for Prince Edward Island and Marion Island using population estimates from Ryan and Bester (2008) and Ryan et al. (2012), but modifying penguin numbers following Crawford et al. (2009). Gentoo Penguin *Pygoscelis papua* numbers were taken from Ryan and Bester (2008) as the count in Crawford et al. (2009) was done too late in the breeding season. As skuas mostly predate on the chicks and eggs of penguins, only the biomass of these were calculated:

$$\text{Available penguin prey biomass} = (\text{egg weight})(\text{clutch size})(\text{number of breeding pairs}) + (\text{chick weight at two weeks of age})(\text{hatching success})(\text{number of breeding pairs})$$

Hatching success values were found in Crawford et al. (2009). King Penguin egg mass and clutch size values were found in Handrich (1989) and chick weights in De Margerie et al. (2004). Gentoo Penguin egg weight and clutch size values were used from Williams (1990a) and chick weight from Cobley and Shears (1999). The egg weight, clutch size and chick weight of Macaroni Penguins were found in Williams (1990b) and that of the Rockhopper Penguin were found in Poisbleau et al. (2008). Available burrowing petrel prey was calculated as the number of breeding adults estimated in Ryan and Bester (2008) and Ryan et al. (2012) multiplied by their weights (Ryan and Bester 2008). These ratios were then compared with the ratios of petrels to penguins in skua middens of each island (Ryan et al. 2009; this study). The biomass densities of available burrowing petrel prey on Marion Island and on Prince Edward Island were calculated by dividing the burrowing petrel biomass by the area of land found below the elevation of 850 m (as Prince Edward Island is only 850 m high) for each island. The biomass densities of available penguin prey was calculated as the

biomass of penguin prey divided by the area below 100 m elevation (as this is approximately where most penguin colonies occur) for Marion Island and Prince Edward Island, respectively. The areas of the altitudinal zones of Marion Island were estimated using a Digital Elevation Model supplied by KI Meikeljohn, Department of Geography, Geoinformatics and Meteorology, University of Pretoria. The area data for Prince Edward Island were used from values published in Ryan et al (2009).

Results

Based on the midden and pellet data, breeding Subantarctic Skuas in the monitoring area on Marion Island mainly preyed upon penguins (67.3% of pellets and 70.6% of midden remains, Table 1), followed by burrowing petrels (27.2% of pellets and 27.6% of midden remains, Table 1). Most penguin items in middens were either eggs (60.5% of all penguin remains, Table 1) or chick carcasses (4.5%, Table 1). Only roughly half of skua pairs in the monitoring area specialized on one type of prey (41% and 57%, in pellet and midden remains respectively, Table 2), with only one instance of conflict in the type of prey specialization between midden and pellet data (Table 2). The proportion of skua diet comprised of burrowing petrels was similar to that found by Hunter (1990) in 1987/88 (Table 3).

Table 1: The total numbers and percentages of Subantarctic Skua prey remains and pellets (classified to their main prey item) found in the monitoring area during 2010/11. Note that no penguin remains found in the pellets could be identified down to the species.

Main prey	Number of pellets	Percentage	Number of prey remains	Percentage
All burrowing petrels	407	27.2%	379	27.6%
Blue Petrel	49	3.3%	34	2.5%
<i>Halobaena caerulea</i>				
Salvin's Prion	252	16.8%	197	14.4%
<i>Pachyptila salvini</i>				
Black-bellied Storm Petrel			1	0.1%
<i>Fregetta tropica</i>				
White-chinned Petrel			14	1.0%
<i>Procellaria aequinoctialis</i>				
Gadfly petrels*	6	0.4%	14	1.0%
Unidentified Petrels	100	6.7%	119	8.7%
All penguins	1 008	67.3%	964	70.6%
Eggs			826	60.5%
Chicks	495	33.1%	61	4.5%
King Penguin			14	1.0%
<i>Aptenodytes patagonicus</i>				
Gentoo Penguin			4	0.4%
<i>Pygoscelis papua</i>				
Macaroni Penguin			704	51.6%
<i>Eudyptes chrysolophus</i>				
Rockhopper Penguin			1	0.1%
<i>Eudyptes chrysocome</i>				
Unidentified penguins	1 008	67.3%	241	17.7%
Seal	20	1.3%	0	0%
Mice <i>Mus musculus</i>	7	0.4%	0	0%
Limpets	1	0.1%	6	0.4%
Squid beaks	5	0.3%	12	0.9%
Other**	49	3.3%		
TOTAL	1497		1364	

*Soft-plumaged *Pterodroma mollis* and Kerguelen Petrels *Lugensa brevirostris*

** Grass and unidentified bones and feathers.

Table 2: A 3x3 matrix with the number of nests that showed similar or different diet specialization combinations as inferred from pellet and midden data.

		Pellet data		
		Generalist	Penguin	Burrowing petrel
Midden data	Generalist	22	12	2
	Penguin	16	9	0
	Burrowing petrel	10	1	14

Table 3: The percentage of Subantarctic Skua prey remains comprising burrowing petrels or in 1987/88 (Hunter 1990) and this study for regularly sampled nests and whole island surveys.

Prey remains	1987/88		2010/11		
	Monitoring area (136 nests)	Whole island (370 nests)	Monitoring area (102 nests)		Whole island (166 nests)
	Middens	Middens	Pellets	Middens	Middens
Petrels	22%	27%	27%	28%	38%
Penguins	78%	72%	67%	71%	61%
Other	0%	1%	6%	1%	1%

Of all skua nests on Marion Island, 69% were found within 500 m of Macaroni and King Penguin colonies (Fig. 1), and of the remaining 31% of nests, 76% were within 500 m of the coast. Skua pairs breeding close to major penguin colonies tended to consume mostly penguin prey (Fig. 1). There was a significant decrease in penguin remains in pellets as distance to nearest Macaroni or King Penguin colony increased ($R^2=0.16$; $p < 0.001$). No relationship was found between skua diet and distance to the coast (a proxy for distance to the nearest Rockhopper Penguin colony as their breeding territories are generally spread out along the coast; $R^2=0.01$, $p > 0.05$). The overall proportions of burrowing petrels ($\chi^2=0.1$; $df=1$; $p > 0.05$) and penguins ($\chi^2=2.36$; $df=1$; $p > 0.05$) were similar in the midden and pellet

data, although the proportion of pellets containing mainly penguin remains decreased as the breeding season progressed (Figure 2, $\chi^2=233.94$; $df=3$; $p<0.001$).

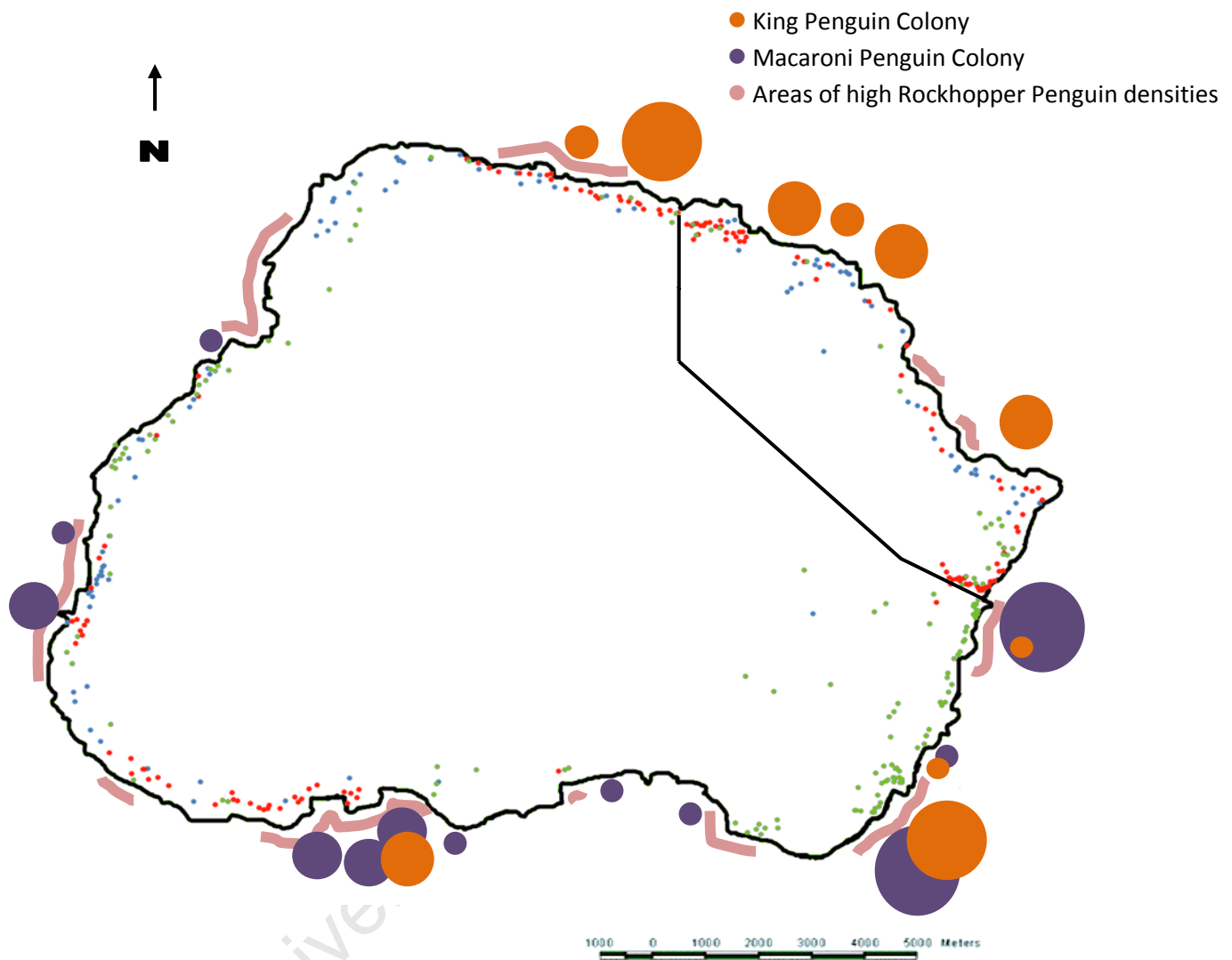


Figure 1: Marion Island showing Subantarctic Skua nests of known diet according to midden analyses: red = predominantly penguins; blue = burrowing petrels; green = diet not recorded. The monitoring area boundary is indicated by a solid black line. Major penguin colonies are indicated by circles indicating colonies of different sizes: purple = Macaroni Penguin colonies (500-1000, 1 000-10 000, 10 000-100 000 and >100 000 breeding pairs); orange = King Penguin colonies (200-500, 500-1 000, 1 000-10 000 and >10 000 breeding pairs). Data from previous penguin abundance and distribution studies (Crawford et al. 2003a; Crawford et al. 2003b; Crawford et al. 2009). The pink lines indicate areas of high Rockhopper Penguin densities as found in Hunter (1990).

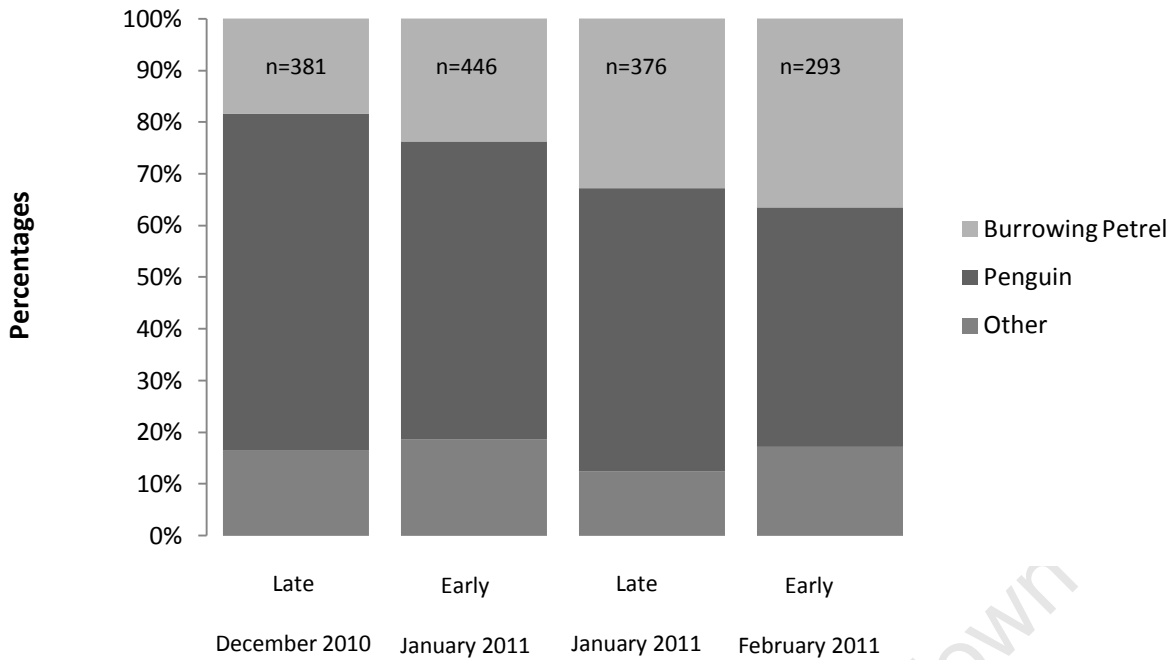


Figure 2: Seasonal changes in prey composition among skua pellets at 102 nests in the main study area on Marion Island. The penguin content of the diet steadily decreases while the burrowing petrel content increases as the breeding season progresses.

Discussion

Most Subantarctic Skuas breeding on Marion Island still depend mainly on penguins as a food source two decades after the cat eradication. Due to the lack of recent burrowing petrel abundance data on Marion Island, it is difficult to say whether their current prey choice simply reflects the relative abundance of the different prey types. Hunter (1990) predicted that after the cat eradication, the skuas would take advantage of the recovering burrowing petrel populations as a prey source. My study shows that this has not happened, or has occurred only marginally, even after two decades of cat-free recovery time.

The best estimates of burrowing petrel and penguin available prey biomass on Marion Island and Prince Edward Island closely correlate with the diet content of Subantarctic Skuas breeding on the two islands (Table 4). The ratio of burrowing petrels are very similar in biomass and skua diet on Prince Edward Island, whereas on Marion Island the dietary content of skuas reflects less than the estimated availability of burrowing petrels (Table 4). This suggests that relative prey availability could be the main factor regarding skua diet on both

islands and that the burrowing petrel abundance on Marion Island might be lower than previously estimated (Ryan and Bester 2008). The relative densities of burrowing petrels and penguins on Marion and Prince Edward Island show that Marion has a burrowing petrel density almost ten times smaller than that of Prince Edward, and has a penguin density roughly three times larger than Prince Edward Island. With a Macaroni Penguin breeding population more than 20 times the size of that found on Prince Edward Island (Crawford et al. 2003b; Ryan et al. 2003), these birds are probably the most abundant food source available for skuas on Marion Island and midden data indicates that they are the penguin most preyed upon (Table 1). The main burrowing petrels found in the skua diet, Salvin's Prions and Blue Petrels, are the same as found by Hunter (1990) and Grindley (1981).

Table 4: The percentages of penguins and burrowing petrel biomass for both Prince Edward Island and Marion Island (Ryan and Bester 2008) and the percentages of penguins and burrowing petrels found in the middens of Subantarctic Skuas on Marion Island (this study) and Prince Edward Island (Ryan et al. 2009). Also, the relative densities of penguins found below 100m elevation and burrowing petrels found below 850m elevation for both Marion and Prince Edward Island are shown.

	Marion Island		Prince Edward Island	
	Penguin	Burrowing petrel	Penguin	Burrowing petrel
Island Biomass (%)	54.2	45.8	6.5	93.5
Skua midden (%)	70.6	27.6	<4	96
Biomass/Area (kg/km ²)	3 650	782	1 393	7 524

Large skuas often specialize on certain prey types (Bayes et al. 1964; Green 1986; Ryan and Moloney 1991; Zipan and Norman 1993, Votier et al. 2004), which is also shown by my results. Midden and pellet data rarely conflicted in indicating the type of prey on which a breeding pair specializes at Marion Island. Pellets fail to show carcass scavenging where no indigestible items were ingested or predation of soft bodied prey items such as certain fish (Bearhop et al. 2001) or seal placenta (Anderson et al. 2009). This bias should be minimal however, because few soft-bodied prey species are eaten by skuas breeding on Marion Island (Hunter 1990). I found that roughly half of the skua breeding pairs studied on Marion Island are specialists on either burrowing petrels or penguins. Penguin predation decreased over the

breeding season, whereas burrowing petrel predation increased. This could be due to a decrease in penguin chick vulnerability as they grow larger, an increase in burrowing petrel chick vulnerability as they start to exit their burrows nearing the end of their breeding season, or both.

Rockhopper Penguin numbers decreased by roughly two thirds and Macaroni Penguins by one third since 1994, whereas the King Penguin numbers have stayed relatively constant (Crawford et al. 2009). This equals an overall decrease of one third in these three penguin numbers combined. If this decrease is directly reflected in skua diet, the 72% penguin content of the whole island skua diets found in Hunter (1990) would have dropped down to 49%, and burrowing petrel content would then have increased by 89%. The slight increase in the burrowing petrel proportion and decrease in the penguin proportion of the skua diet since 1987 could be caused by the reduction in penguin numbers. However, I would have expected a greater difference if the burrowing petrel population had recovered whilst the penguin numbers were decreasing on Marion Island.

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CHAPTER 4

The breeding success of the Subantarctic Skua two decades after the eradication of feral cats from Marion Island

Abstract

Subantarctic Skuas on Marion Island competed with feral cats for burrowing petrels as a food source before the cats were eradicated in 1991. Two decades after the cats were removed; the burrowing petrel population on Marion Island should have recovered substantially, increasing food availability for breeding skuas. However, the skua population breeding on Marion Island halved during this period. I assess whether skua breeding success has changed since the cat eradication, and whether diet affects their breeding success. Skua pairs that did not predominantly feed on burrowing petrels suffered a higher probability of egg loss, possibly due to high predator traffic close to penguin colonies. However, chicks of skuas feeding mainly on burrowing petrels had a significantly lower probability of survival. The overall survival probability for the breeding season did not differ between the diet groups. Skua breeding success overall was similar, if not slightly higher, to that found before the cat eradication and is typical of healthy breeding populations of large skuas. This suggests that low breeding success was not the driver for the reduction in the skua breeding population on Marion Island, or that the breeding population has stabilized recently.

Introduction

The Prince Edward Islands, comprising Marion and Prince Edward Island, host some 11% of the global population of Subantarctic Skuas (Crawford and Cooper 2003). Two invasive mammals were introduced to Marion Island, the House Mouse and the feral cat, whereas Prince Edward Island has remained free of introduced mammals. Cats were eradicated from Marion Island in 1991 (Bester et al. 2002) after drastically reducing populations of burrowing petrels (Procellariidae), an important prey of breeding skuas on adjacent Prince Edward Island (Adams 1982, Ryan et al. 2009). The breeding success of burrowing petrels on Marion Island increased shortly after the cats were removed (Cooper et al. 1995), but it is unknown whether the breeding success of their main predator followed suit (Ryan et al. 2009, Chapter 2).

In 1974/75 and 1976/77, Williams (1980) reported 0.96 chicks fledged per Subantarctic Skua breeding pair and in 1987/88, 1.02 chicks were fledged per skua breeding pair on Marion Island (Hunter 1990), which is similar to that of healthy skua populations (Davis 1976, Furness 1984). However, since the cat eradication, when food resources should have increased as burrowing petrel numbers recovered, skua numbers have declined, roughly halving by 2010 (Ryan et al. 2009, Chapter 2). The reason for this decline might be limited food sources on Marion Island, due to the failure of the burrowing petrel populations to recover (Chapter 3) and penguin numbers dropping by 32% since 1994 (Crawford et al. 2009).

Food availability is often the main factor responsible for variation in breeding success (Mitchell et al. 2004) because seabirds are more restricted in their feeding range during the breeding season (Ashmole 1971). Food availability has significant effects on egg size and the proportion of chicks fledged (Monaghan et al. 1992). Egg size represents the initial reproductive investment of a female and is strongly linked with a female's protein reserves (Houston et al. 1983), giving an indication of parental quality as well as access to resources. Egg size is also positively linked with the survival and growth of chicks soon after hatching (Bolton 1991; Furness 1983) thus playing an important role in overall breeding success. Skua breeding pairs that have access to abundant, high quality prey would be expected to invest their extra nutrient reserves into egg size (Ratcliffe et al. 1998). Skua chick mortality is often caused by conspecific predation rather than low food supply (Ratcliffe et al. 1998), which makes egg size a good indicator of nutrient availability to breeding skuas.

Changes in seabird breeding populations are typically driven by changes in adult mortality rather than breeding success, unless changes in breeding success are sustained for long periods (Gaillard et al. 1989, Saether and Bakke 2000). Marion Island's population of skuas has decreased over the last two decades while Prince Edward Island's population has stayed constant (Ryan et al. 2009, Chapter 2). The ratio of non-breeders (i.e. potential recruits for nesting sites) to breeding pairs on Marion Island is much lower than on Prince Edward Island (Ryan et al. 2009), which could be an indication of either high recruitment rates due to high breeding adult turnover or less potential recruits due to high juvenile mortality or previous years of low breeding success. Juvenile and adult mortality would most probably take place at sea during winter due to long-line fisheries or low food supply. However, if high mortality rates occurred at sea this is likely to be reflected in the skua numbers at Prince Edward Island as well. As the decline in numbers has taken place only on Marion Island, the causative factor

is likely restricted to that island. Subantarctic Skua numbers at New Island, the Falklands, have decreased markedly, and this change was explained by their extremely low breeding success (Catry et al. 2011). Low breeding success due to limited food sources might explain the consistent decline in skua numbers on Marion Island.

I tested whether skua breeding success has changed since cats were eradicated from Marion Island by comparing their breeding success in 2010/11 to data from 1987/88 (Hunter 1990). I also compared the average egg volume and survival probabilities of the eggs and chicks between skuas feeding mainly on burrowing petrels or penguins as well as dietary generalists.

Methods

Some 450 pairs of Subantarctic Skuas bred around the periphery of Marion Island in 2010/11 (Chapter 2). Egg laying takes place during a 6-week period, but in 2010 most pairs had laid by 16 November. The laying interval between the first and second egg is about 3 days, incubation lasts about 30 days and chick rearing takes roughly 55 days (Williams 1980b). I checked 102 skua nests every 5, 10 or 14 days along 18 km of coastline from Prinsloo Meer to Bullard Beach (Fig. 1; Chapter 3). Nests were checked from the first day found, which was usually after both eggs had been laid, and 18 nests were only found after the chicks hatched. The length and maximum width of the eggs were measured to the nearest 0.1 mm with Vernier callipers and the formula: $\text{length} \times \text{breadth}^2 \times 0.00048$ (shape constant K_v , Coulson 1963, Votier et al. 2004) was used to estimate egg volume in cm^3 . I controlled for clutch size by calculating the average egg volume for each clutch. Differences in average egg volume between the three diet groups (burrowing petrel specialists, penguin specialists and generalists, Chapter 3) were tested with an ANOVA in Statistica (v. 10).

Mayfield (1975) calculations were used to estimate incubation daily survival rate $\{1 - (\text{number of eggs lost} / \text{egg days until last active egg seen})\}$ and the daily survival rate (DSR) from hatching until fledging $\{1 - (\text{number of chicks lost} / \text{chick days until fledging})\}$. The presence of egg shells within or around the nest during the hatching phase was grouped within egg losses. Chick losses were only noted after the first chick was seen or if a chick carcass was found around the nest. The probability of a nest surviving the incubation or fledging phase was calculated as the appropriate DSR raised to the power of the number of days it takes that phase to complete (incubation phase = 30 days, hatching to fledging = 55 days; Williams 1980b). The overall survival probability of a nest from laying until fledging was calculated as incubation survival probability multiplied by fledging survival probability. The diets of the

pairs (Chapter 3) were used to group the skua pairs in the breeding success analyses to compare the effects of diet on breeding success probabilities. Unless a chick carcass was found near the nest site, the absence of a skua chick aged 30 days or older was not scored as a failure because few chicks die after this age (Catry and Furness 1997). The variance (var) of the daily survival rates (DSR) and t-test for significance were calculated according to Johnson (1979):

$$\text{variance} = \{(\text{exposure} - \text{losses}) \times \text{losses}\} / (\text{exposure})^3 \quad \text{and} \quad t = \frac{DSR_1 - DSR_2}{\sqrt{\text{var}_1 + \text{var}_2}}$$

Breeding success was also calculated as the number of chicks fledged per skua breeding territory to compare to the breeding success found in Hunter (1990) and as the percentage of chicks fledged per egg laid to compare to other studies (Burton 1968; Furness and Aitken 1992; Hemmings 1984; Neilson 1983).

The average breeding success (chicks fledged per skua breeding pair) was calculated for breeding pairs nesting within a half-minute (0.76 km) of major prey colonies (major penguin colonies as described in Chapter 2) and breeding pairs nesting further away. These values were then compared with the breeding success values found in Hunter (1990) for skua breeding pairs found within the same half-minute square as a major prey colonies (large penguin colonies and Blue Petrel breeding colonies) and the breeding success of skua pairs nesting outside of these areas. This data were used to find if an equilibrium had been reached in the breeding success of skuas nesting close and far away from major prey colonies since 1987.

Results

The distribution of nesting territories for dietary specialists was clustered within the study area (Figure 1), with 12 of the 19 burrowing petrel specialists (63%) found in one cluster (Blue Petrel Bay) and 25 of the 34 penguin specialists (73%) found in either one of two clusters (Goney Plain and Bullard Beach). The difference in average egg volume was not significant between the three diet groups (ANOVA, $F=0.33$, $p>0.05$). Average egg volume (101.75 cm^3) was similar to previously published estimates from Marion Island: 101.7 cm^3 (Rand 1954) and 101.8 cm^3 (Williams 1980a).

Mayfield results (Figure 2) showed that burrowing petrel specialists had the highest egg survival probability of the three diet groups, but a significantly lower chick survival

probability than breeding pairs predominantly feeding on penguins or showing a generalist diet ($t=68.2$, $p<0.0167$; $t=46.5$, $p<0.0167$, Bonferroni correction, respectively). Overall survival probability was very similar between the three groups (Figure 2). The percentage of chicks fledged from eggs laid was 56%, and the number of chicks fledged per nest was 1.16.

The difference in breeding success between breeding pairs nesting close or further away from major prey colonies was found to be smaller in 2010/11 (difference was 0.14) than in 1987/88 (0.39, Table 1).

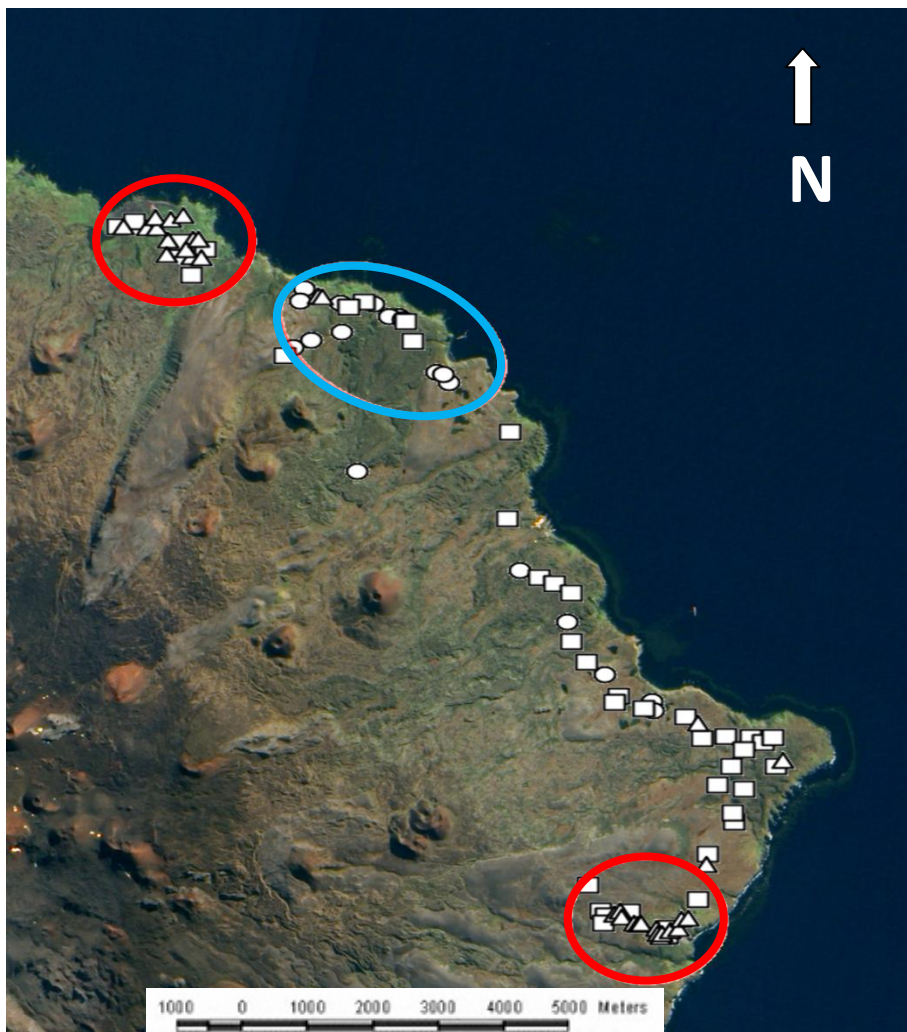


Figure 1: Distribution of the regularly checked Subantarctic Skua nests with the different symbols representing different foraging strategies. Triangles = penguin diet; circles = burrowing petrel diet and squares = generalist diet. The ovals indicate clusters of nests with similar foraging strategies with blue indicating skua breeding pairs mainly predated on burrowing petrels and red

for penguins. From top to bottom there is a penguin diet cluster adjacent to the large King Penguin colonies at Goney Plain, a burrowing petrel diet cluster at Blue Petrel Bay and another penguin cluster adjacent to the Macaroni Penguin colony at Bullard Beach. Image from <http://earthobservatory.nasa.gov>.

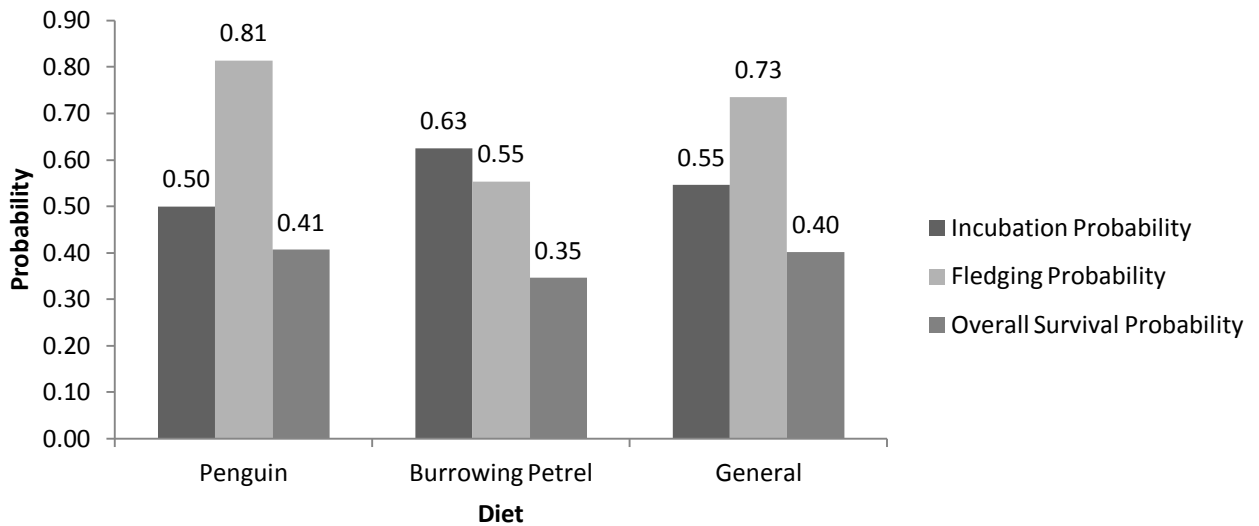


Figure 2: A graph depicting the incubation (30 days), fledging (55 days) and overall survival probabilities for nests with parents mainly predated on penguins, burrowing petrels or following a generalist diet. Pairs predated mainly on burrowing petrels had a significantly lower fledging probability than pairs mainly predated on penguins ($t=68.8$, $p<0.0167$, Bonferroni correction) and lower than breeding pairs following a generalist diet ($t=46.5$, $p<0.0167$, Bonferroni correction).

Table 1: The average number of Subantarctic Skua chicks fledged per nest for breeding territories found within a half-minute of major prey colonies and for territories found further away in 1987/88 (Hunter 1990) and in 2010/2011.

	Average number of chicks reared per skua breeding pair	
	1987/88	2010/2011
Territories close to major penguin colonies	1.19	1.29
Territories away from major penguin colonies	0.8	1.15

Discussion

Egg volume is an indication of available prey quality and quantity (Gill et al. 2002). Diet had no significant effect on egg volume of Subantarctic Skuas. These results suggest that during the pre-laying period either diet is sufficient for the female skua to acquire the necessary nutrients before laying. One reason for specializing on a certain prey is having an easily accessible prey source close to the skua breeding territory (Mougeot et al. 1998). Within the study area 63-73% of specialist pairs were in distinct clusters indicating a prey source in the close vicinity (Figure 1). Skuas preying partly (generalists) or mainly on penguins had a lower incubation survival probability than those preying mainly on burrowing petrels, which might be linked to their close vicinity to penguin colonies. Large penguin colonies attract many non-breeding skuas as well as other predators, such as Northern *Macronectes halli* and Southern *M. giganteus* giant petrels, which results in high predator traffic. Skuas specializing on burrowing petrels nest at lower densities, usually well away from penguin colonies (Figure 1), and are thus not as vulnerable to high predator traffic. However, skuas preying predominantly on petrels had a significantly lower probability of survival during the chick rearing phase.

Subantarctic Skuas tend to predate on the adults of burrowing petrels during their breeding seasons (Mougeot et al. 1998) rather than the chicks and eggs as they do in penguin colonies. Burrowing petrel predation is easiest before and during laying, when a large number of breeding and non-breeding adults court and call outside their burrows (Mougeot et al. 1998), and when young birds fledge. This occurs in October-November (pre-laying) and January-February (fledging) for Salvin's Prions and Blue Petrels (Berruti and Hunter 1986, Fugler et al. 1987), the main burrowing petrel prey species of skuas breeding between Prinsloomeer and Bullard Beach on Marion Island (Chapter 3). The phase where breeding and non-breeding burrowing petrel adults are most active outside of their burrows coincides with the incubation period of the Subantarctic skuas, but the fledging phase of burrowing petrels may be slightly too late to influence the fledging success of skuas. This and the lack of high predator traffic could be the reason why skuas preying mainly on burrowing petrels had the highest incubation success, but the lowest survival probability during the chick rearing phase when most burrowing petrel courtship behaviour has passed. However, the lower survival probability post hatching could also be attributed to inexperience if the burrowing petrel predators were mostly newly recruited skua breeding pairs.

The overall survival probabilities from laying until fledging were the same for skua predating mainly on penguins or burrowing petrels as well as for skuas following a generalist diet. This suggests that the skua breeding pair's diet choice does not play a major role in their final breeding success. Breeding success values were also much more similar between skua breeding territories found close and further away from major prey colonies in 2010/11 than in 1987/1988, which could mean that the skua population on Marion Island is reaching an equilibrium. The overall breeding success (1.16 chicks fledged per breeding pair) is slightly higher than that recorded by Hunter (1990, 1.02 chicks fledged per breeding pair), but this could also be attributed to the large difference in sample sizes (in 1987/88 the $n = 878$ nests, Hunter 1990, and in 2010/11 the $n = 102$ nests). The percentage of chicks fledged per egg laid (56%) in 2010 is typical of healthy skua populations (Burton 1968; Furness and Aitken 1992; Hemmings 1984; Neilson 1983). There is a 23 year period between the two breeding success data points of Hunter (1990) and this study, so it is impossible to say that this has been the case for that whole period of time. If poor breeding success was the driver for the reduction in skua numbers on Marion Island, then our findings could mean that the population has recently stabilized at a lower number which can be maintained by the limited food sources. This could be substantiated by the fact that differences in breeding success related to prey availability is smaller than it was in 1987/88 and the overall breeding success is slightly higher. Future counts on Marion Island will show whether the skua population has stabilized, starts increasing or whether it continues to decrease due to reasons other than low breeding success.

In conclusion, dietary differences appear to affect daily survival rates of eggs and chicks, but not overall breeding success or average egg volume. Skuas that rely mainly on burrowing petrels may struggle to obtain enough prey during the chick rearing phase, whereas skuas that feed mainly on penguins have a better chance to fledge chicks. The overall breeding success of skuas on Marion Island has not changed much since cats were eradicated and is not unusually low for large skuas. This could mean that the population has either stabilized or breeding success was not the driver for the decreased population of Subantarctic Skuas on Marion Island.

CHAPTER 5

Synthesis and conclusions

This study was motivated by recent findings which showed that the Subantarctic Skua breeding population on Marion Island declined in the last 20 years, despite the eradication of feral cats from the island (Ryan et al. 2009). The skua population on neighbouring Prince Edward Island, which was never invaded by mammals, and where most breeding pairs depend on burrowing petrels for food, has remained stable. The fact that the feral cats had detrimental effects on the burrowing petrel population of Marion Island before the 1990s suggests that the cause for decline in skua numbers on could be an unrecovered burrowing petrel population on Marion Island. Initial studies showed an increase in burrowing petrel breeding success on Marion Island following the removal of cats, but there is no data on whether their numbers have increased. As a result, the marked decrease in skua numbers is a strong indicator that the burrowing petrel population has not yet recovered. Because burrowing petrel populations are hard to census, a study on the abundance, distribution and diet of their main predator, the Subantarctic Skua, could give an indication of population status of burrowing petrels 20 years after the cat eradication.

The purpose of this study was to confirm whether skua numbers had indeed decreased on Marion Island since Steve Hunter's study in 1987/88, and to attempt to determine the cause(s) of the decrease. To assess whether the apparent decrease in skua numbers on Marion Island was due to unrecovered burrowing petrel populations, I assumed that prey abundance and distribution are the main factors determining predator abundance, distribution, diet and breeding success. Indications that petrel prey availability remain depressed include low skua abundance, distribution of nests still centred around penguin colonies and no increase in burrowing petrels in their diet. If the decline in skua numbers is not related to low burrowing petrel numbers, more skua breeding territories should have moved inland and their diet should have a higher portion of burrowing petrels than that found in 1987/88.

By assessing the distribution, abundance and diet of the skuas I could make deductions about changes in skua relative abundance and distribution since 1987/88 using the data from Hunter (1990). Breeding success of the skuas was investigated to assess whether low breeding success is driving the decline in numbers. As breeding success is correlated with prey availability (Mitchell et al. 2004), it could also be used to assess prey quality when comparing the breeding success of skuas preying mainly on penguins vs. those pairs mainly

targeting burrowing petrels. Since the breeding success of only one year was investigated and there being no other data for Subantarctic Skuas since 1987/88, I used the ratio of non-breeding skuas to breeding skuas to get an idea of the breeding success in previous years. A low ratio of non-breeders to breeders could indicate previous years of low breeding success, high juvenile mortality rate at sea (possibly caused by poor body condition) or high recruitment rate into breeding territories deserted by breeders due to poor resource availability.

Summary of findings

The abundance of Subantarctic Skuas on Marion Island was almost half of the 878 breeding pairs found in 1987. However, it was still 59% more nests found than in 2008 (Ryan et al. 2009). This indicates that even though skua nests are conspicuous, a dedicated survey is crucial for accurate censuses. The pattern of nest distribution stayed relatively similar from 1987/88 to 2010/11, indicating that the decline in skua numbers occurred over the whole island. Distance to major penguin colonies was the major variable in determining nest density in both 1987/88 and 2010/11. This suggests that the concentration of skua nests around penguin colonies has not changed in the last 20 years.

The non-breeder to breeding pair ratio was less than one, which is much less than on Prince Edward Island (two non-breeders to each breeding pair; Ryan et al. 2009). As Prince Edward Island represents a stable and healthy Subantarctic Skua population, the low ratio on Marion Island could indicate high adult or juvenile mortality, a low number of returning breeders or previous years of low breeding success as on New Island in the Falklands (Catry et al. 2011). The drastic decline in breeding pairs on Marion Island and the dwindling supply of non-breeders suggests that the factors impacting the Subantarctic Skua breeding population are of a local nature.

Most Subantarctic Skuas breeding on Marion Island still depend mainly on penguins for food two decades after the cat eradication. The percentage of burrowing petrels eaten was slightly higher than that found in Hunter 1990, but this could be due to the 32% reduction in local penguin numbers. Skuas apparently have not taken advantage of a recovering burrowing petrel populations as predicted by Hunter (1990). By comparison, the diets of skuas on Prince Edward Island continue to be dominated by burrowing petrels.

Although the decreasing breeding population and low ratio of non-breeders to breeders indicate an unhealthy population of Subantarctic Skuas on Marion Island, their breeding success and egg volume was similar to that reported by Hunter (1990) and Williams (1980), and is similar to that of healthy populations at other Subantarctic islands (Burton 1968; Furness and Aitken 1992; Hemmings 1984; Neilson 1983). A diet of mostly burrowing petrels enabled the skuas to have a very high chance of nest survival during incubation, whilst a penguin diet resulted in a lower nest survival during the incubation phase presumably linked to high predator traffic close to penguin colonies. However, birds targeting burrowing petrels raised fewer chicks possibly due to limited prey availability. Overall breeding success did not differ between skuas preying mainly on penguins or burrowing petrels, or those following a generalist diet. The overall high breeding success could be due to an unusually successful season, or that the skua population on Marion Island is stabilizing and their numbers will increase in the coming years, or that low breeding success is not the driving factor underpinning the decline in skua numbers over the last two decades.

Limitations of methods

This study only covers one breeding season and it is compared to a single breeding season in 1987/88. For inferring what has happened in the past 20 years, this is a low resolution study. More regular monitoring of skua breeding pairs on Marion Island will ensure that more accurate data are available for deducing the Subantarctic Skua population trends and the possible reasons therefore. The lack of accurate skua census data prior to 1987/88 means that there is no concrete evidence that the skua population on Marion Island suffered whilst cat predation on burrowing petrels took place. The rough estimate of 400 nests made in the 1970s (Siegfried et al. 1978) is less than half that found in 1987/88 (Hunter 1990), but I excluded this estimate due to the extreme differences in methodology (i.e. a rough estimate compared to an intensive survey). Skua nests are widely dispersed and relatively cryptic, making an accurate population estimate problematic without a systematic survey. As a result, no accurate deductions about population trends can be made from the apparent difference in estimates from the 1970s to 1980s.

Two conventional methods of diet analysis were used in this study and each comes with its own limitation. Regurgitated pellets only represent undigested prey remains and thus soft bodied prey are not represented (Bearhop et al. 2001, Votier et al. 2001). Also, some prey

types result in more pellets than others (Votier et al. 2001) which makes it difficult to infer the amount of prey consumed, e.g. pellets mostly consisting of burrowing petrel bones with only a few penguin feathers do not necessarily indicate a diet consisting mostly of burrowing petrels. Midden content analysis compensates for this to some extent by representing prey remains dragged back to the nest that was not swallowed whole. However, these remains tend to be biased towards larger prey items. Thus where pellet contents may under represent penguin remains, midden contents may over represent them. A third diet analysis, stable isotope analysis, would increase the resolution of the diet study by representing soft bodied prey ingested, e.g. seal placentae, which have been found to form a larger part of the skua diet than indicated only by the pellet and midden analyses (Anderson et al. 2009).

During the whole island census, not all inland areas were searched intensively, which means that I could have under-reported inland breeding skuas. I found 450 skua nests compared to the 280 found in 2008 which is probably due to more detailed observer effort rather than an actual increase in population numbers. Thus I am confident that most skua nests were found and that the few missed inland nests were negligible for assessing the large scale population trend. Inland nest locations will be important information for later studies, as the lack of this data in Hunter 1990 (also motivated by no sighting during scouting trips) would have made it impossible to detect slight changes in inland skua nest distribution in this study.

Implications of findings and suggestions for future research

The Subantarctic Skua population on Marion Island is half of what it was in the late 1980s (Hunter 1990). This result, in conjunction with the distribution and diet data, points to a burrowing petrel population which has not recovered since the cat eradication in the early 1990s. This implies that some factor other than the cats is negatively affecting the burrowing petrel breeding populations and the House Mouse seems a likely culprit. It has been suggested that when invasive mammalian prey and predators are found on the same island, care needs to be taken when only eradicating the predator as it could result in population increase of the prey (Quillfeldt et al. 2008). The loss of their main predator in conjunction with global warming could be causing the House Mouse population on Marion Island to increase (Smith and Steenkamp 1990, Smith 1993, Chown and Smith 1993). Invasive mice are significant predators of seabird chicks, especially burrowing petrels, on Gough Island (Wanless et al. 2007, Cuthbert et al. 2013) and the same situation could be found on Marion

Island (Jones and Ryan 2010).

On Gough Island the invasive House Mouse is responsible for the critically endangered status of the Tristan Albatross *Diomedea dabbenena* and the Gough Bunting *Rowettia goughensis* and the endangered status of the Atlantic Petrel *Pterodroma incerta* (IUCN 2010). Invasive mice are the suggested culprits for the drastic declines in burrowing petrel population numbers on Gough Island and their low breeding (Ryan 2010, Cuthbert et al. 2013). Above ground mouse predation on Marion Island is still negligible in terms of affecting albatross population numbers (Jones & Ryan 2010); however it is still to be shown whether mouse predation occurs on burrowing petrel chicks below ground as on Gough Island (Wanless et al. 2012). Preparations for House Mouse eradication on Gough Island is already under way on Gough Island (Cuthbert et al. 2011) due to their detrimental effects on the local bird populations. The question whether mouse predation of burrowing petrel chicks significantly affects petrel breeding success, or if predation takes place at all, remains to be answered. Further studies need to investigate whether mouse predation on burrowing petrel chicks and eggs occurs on Marion Island which could motivate an eradication program.

A census of the burrowing petrels as well as a study of their breeding success is needed to ascertain their population status 20 years after the cat eradication. The population of Subantarctic Skuas on Marion Island needs to be monitored to assess whether their numbers are still decreasing, and whether their diet and breeding success are stable. Specifically, inland nests should be mapped annually to note any change in distribution or numbers which could indicate recovering burrowing petrel populations. This information is critical for understanding the reason for the deteriorating Subantarctic Skua breeding population on Marion Island as well as tracking the recovery of burrowing petrel populations. When we have this information conservation efforts can be put into place to prevent the further decline of these important breeding populations on Marion Island.

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