Impacts of the introduced house mouse on the seabirds of Gough Island

by

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Frontispiece: A house mouse *Mus musculus* atop the carcass of an Atlantic Petrel *Pterodroma incerta* chick which it has attacked and killed, Gough Island, 2004.

DECLARATION

This thesis reports the results of original research I conducted under the auspices of the DST/NRF Centre of Excellence at the Percy FitzPatrick Institute, University of Cape Town and the Royal Society for the Protection of Birds, UK. All assistance that I have received has been fully acknowledged. This work has not been submitted for a degree at any other university.

Signed by candidate

Ross M. Wanless

To John Cooper, on whose vision much of this work rests, and whose legacy in ensuring the conservation of Gough and its magnificent seabirds will, with a little luck, endure beyond both of our lifetimes

To Andrea, without whom none of this would have been possible

To Alén Angel Wanless, mi hijo, El Porotito, El Frijolito, my son, whose only night-time companion is, appropriately enough, a fluffy toy in the form of a Tristan Albatross. I hope with all my being that one day you will share my passion for the real thing: those majestic animals and their indescribably beautiful island

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I have appended a paper to this thesis which is cited several times. I am the lead author and the paper details some of the key findings of this research. Andrea and I conducted essentially all the field work that is presented (which has not already been published). I wrote all drafts and considered inputs from the co-authors, formatted and submitted the paper, dealt with reviewers' comments and resubmitted for final publication. The full citation is: Wanless, R. M., A. Angel, R. J. Cuthbert, G.M. Hilton, and P. G. Ryan. 2007. Can predation by invasive mice drive seabird extinctions? Biology Letters 3:241-244.

SHORT ABSTRACT

Introduced house mice *Mus musculus* on Gough Island were suspected of widespread predation of Atlantic Petrel *Pterodroma incerta* and Tristan Albatross *Diomedea dabbenena* chicks in 2000/01. Video cameras recorded six fatal attacks by mice on live, healthy Atlantic Petrel chicks in 2004. Crude estimates of annual breeding success were 47%, 7% and 7% in 2003, 2004 and 2006, respectively. Mouse attacks were responsible for most chick failures.

Mice were largely responsible for high numbers of Tristan Albatross chick failures in 2004-2006. Total failures were significantly related to total attempts but breeding success and total attempts were not correlated. There was little spatio-temporal consistency in total failures or breeding success. No environmental or biological variables examined explained the pattern. Proximity to a failed nest was a significant predictor of failure, suggesting a localised effect possibly due to a few predatory mice. Fledgling production has decreased by 1% annually since 1979-1982. Annual adult Tristan Albatross survival and breeding success averages are extremely low (91% and 32%, respectively) and modelled population growth using these parameters was -2.85% p.a. Either parameter will drive decreases so reversing negative trends requires improving both.

Stomach content and stable isotope analyses implied predation on Atlantic Petrel chicks in late-winter was important for lowland mouse survival. In the highlands I compared sites with severe and minimal albatross predation but found little evidence that seabird consumption is important to highland mice.

Variable reproductive effort and reproductive seasons for mice suggests moderate inter-annual fluctuations in densities, but confirmed no reproduction from May-August. Average body condition in lowland mice decreased significantly in late-winter. Monthly density estimates were relatively static from February-June and decreased from July-September. These results suggest that June-August would be the most appropriate time of year for an attempted eradication. The highlands appear sub-optimal for mice and they should readily accept toxic bait.

The Gough mice do prey on seabird chicks at levels sufficient to drive population decreases. Globally, in view of this research, similar predatory behaviour may have been overlooked or could evolve elsewhere. Mouse eradications should receive a high priority in island restoration projects.

GENERAL ABSTRACT

Introduced house mice *Mus musculus* on Gough Island were suspected of having caused widespread breeding failures of Atlantic Petrel *Pterodroma incerta* and Tristan Albatross *Diomedea dabbenena* chicks in 2000/01. However, prior to this study no unequivocal evidence existed for significant predation of seabird chicks by mice. This thesis reports another three years of breeding success data for both seabird species and defines the role of predation by mice in the observed patterns of failure.

In 2003 mice killed at most one of 41 Atlantic Petrel chicks monitored. Breeding success (number of chicks fledged per nesting attempt) for the period of study in 2003 (part of chick-rearing) was 93% and a crude estimate of annual success was 46.5%. Video recordings in August-September 2004 captured six fatal attacks by mice on live, healthy chicks. From June-September 2004, 40 of 60 monitored nests failed and from September-November 2006, 14 of 19 monitored chicks died; the majority of chick failures were ascribed to mouse attacks. Overall, breeding success estimates were *ca* 7% for both 2004 and 2006; incomplete seasons means actual success could have been higher (maximum 33% in 2004 and 26% in 2006). Roughly the same nest period was studied in 2003 and 2006, but 2006 experienced significantly lower success than 2003. Chick mortality in 2003 prior to October is unknown, however, and may have been higher than the breeding success estimate of 46.5% suggests. The 2004 and 2006 breeding success estimates are probably insufficient to maintain the Atlantic Petrel population.

Mice also attacked live, healthy Tristan Albatross chicks in 2004. Video showed mice attacking more-or-less constantly at night, with up to 10 mice at the nest simultaneously and 4-7 mice competing aggressively for access to an open wound. Breeding success from four seasons averaged at most 32%. Total failures were significantly related to total attempts but breeding success and number of attempts were not correlated. One sub-colony experienced consistently low predation and high annual breeding success. There was little temporal consistency in total failures or breeding success in other sub-colonies, with sites varying in opposite directions within and between years. Despite strong and consistent differences in breeding success between sites, no environmental or biological variables examined explained the pattern. Nests that failed in a given month were significantly closer to the nearest nest that failed the previous month than predicted by chance, suggesting a localised effect possibly due to a few predatory individuals. Mean total fledglings have decreased by *ca* 1% per year since 1979-1982. A reassessment of the 1956 population estimate suggests a negative trend of *ca* 1% per year over 50 years. Annual adult survival is *ca* 91%. Population models and consecutive

annual incubator counts allow the first estimates of adult and total Tristan Albatross populations (5400 and 11300 individuals, respectively). Modelled population growth based on current estimates of adult survival and breeding success was -2.85% per year and annual breeding attempts are likely to decrease to *ca* 500 in 30 years. Modelling additive (vs proportional) adult mortality and chick failures predicted a catastrophic decrease, with extinction occurring in *ca* 25 years. An historical account from the 1880s describes high levels of chick failures suggesting significant predation levels for >100 years. Reversing negative Tristan Albatross population trends requires mitigating both longline mortality and mouse predation, else breeding success must exceed 100% or adult survival must exceed 97%.

I used stomach content and stable isotope analyses to investigate the importance of seabirds to mice. Plant $\delta^{15}N$ values were significantly negatively correlated with altitude, reflecting altitudinal differences in marine nitrogen input due to higher seabird densities in the lowlands. Mouse isotope signatures differed significantly with altitude (for both $\delta^{15}N$ and $\delta^{13}C$). GLMs showed a strong, significant enrichment of both isotopes for lowland mice in August-September, implying significant levels of seabird consumption. Seabird remains in lowland mouse stomachs were low through winter, but peaked in August, supporting the isotope findings. These changes coincided with the timing of Atlantic Petrel chick hatching and very high observed predation rates in 2004. Using $\delta^{13}C$ only, a rough estimate suggests seabird consumption contributes 40-60% to mouse diets at this time. Collectively these findings support the hypothesis that seabirds are an important part of mouse diets in late winter in the lowlands. In the highlands I compared a site with severe predation on albatross chicks (Green Hill) to one with minimal predation (Gonydale). GLMs revealed no effect of site on plant $\delta^{15}N$ or $\delta^{13}C$. Surprisingly, despite strong differences in albatross chick predation rates between sites, mice did not differ in $\delta^{13}C$ values, implying no differences in the relative importance of seabird consumption. Stomach content analysis from mice collected in May revealed virtually no seabird remains in Gonydale but a mean for Green Hill >30% by volume. Nevertheless, no seabird consumption in Gonydale, and no differences in seabird contribution to mouse stable isotope signatures between sites implies that seabird consumption is also a negligible component of mouse diets in Green Hill. The fertilizing effect of seabirds means that terrestrial productivity will decrease in tandem with seabird population decreases at all altitudes. This could drive down mouse numbers, ameliorating predation levels, or it could cause increased reliance on seabird predation by mice, setting up a positive feedback and exacerbating predation. This should be a conservation research priority.

Mice ended breeding in April 2000 vs February 2004 and proportions of reproductively active mice were lower in the latter season, suggesting density-dependent effects, possibly due to inter-annual fluctuations in winter survival rates and spring densities of mice. In 2004, lowland males weighed an average of 45% more ($p<0.001$), had 9.5% longer tails ($p<0.001$) and higher body condition ($p<0.001$) than highland males. Average lowland tail length increased significantly at the end of winter, showing that survival during the critical late-winter period is biased towards larger individuals. Average body condition in lowland mice was low in February, increased in autumn after the cessation of breeding and decreased significantly from June-September. Monthly density estimates from a mark-recapture study in 2005/06 showed that apparent densities were relatively static from February-June and decreased from July-September. These congruent results suggest that June-August would be the most appropriate time of year for an attempted eradication, as mice were not breeding, showed the clearest signs of food-deprivation but densities had not yet equilibrated to their lowest levels. The highlands appear sub-optimal for mice and they should readily accept toxic bait.

The introduced house mice on Gough Island prey on seabird chicks at levels sufficient to drive population decreases. Mouse impacts elsewhere, while requiring verification, suggest that when mice are the only introduced mammal on islands, they can become significant predators of seabird chicks. From a global perspective, this research suggests that mouse impacts may have been overlooked or could evolve elsewhere. Further, it is highly desirable to eradicate mice from Gough and other islands, and mouse eradications should receive a high priority in island restoration projects.

GENERAL INTRODUCTION

The study of islands and insular organisms has been and remains a central theme in biology, evolution and conservation (Williamson 1996). The study of insular ecosystems has become increasingly important in understanding ecosystem and species responses to major drivers of biodiversity loss such as habitat fragmentation and invasive species (Case 1996; Terborgh et al. 1999; Terborgh et al. 2001). But islands are worthy of study and conservation in their own right, not only as models for more complex systems, because relative to their land area, they are repositories of a disproportionate store of earth's biodiversity (Diamond 1989; Steadman 1995; Quammen 1996). The need for research and conservation action is clearly demonstrated by the abysmal state of conservation of insular fauna. This is borne out by the historical avian extinction record, in which island birds dominate continental birds overwhelmingly (Diamond 1989; Steadman 1995; Quammen 1996; Simberloff 2000), and insular birds, and especially seabirds, have higher proportions of threatened species than any other groups (BirdLife International 2004).

Gough Island has not (yet) suffered an avian extinction in recorded history. It is a UNESCO World Heritage Site and rightly considered one of the greatest seabird colonies in the world (Angel & Cooper 2006). Its climate, geography and political status have conspired to keep it from being a better-researched system. It has two procellariiform seabirds that are, to all intents and purposes, endemic following catastrophic decreases in populations at Tristan da Cunha (Richardson 1984; Ryan et al. 2001): the Tristan Albatross *Diomedea dabbenena* (Red-list status: Endangered) and the Atlantic Petrel (Red-list status: Threatened). The discovery in 2001 that large numbers of chicks of both species were dying, possibly due to unprecedented levels of predation from the introduced house mouse *Mus musculus*, led to the research that I present in this thesis

In Chapter 1 I review the impacts that introduced house mice have had on islands. Due to a preponderance of literature relating to their effects on islands in the Southern Ocean, the review is regional in details, but I extrapolate the consequences of introductions globally. I discuss the general perception, even amongst island conservationists, that mouse impacts are minor relative to those of other invasive mammals (e.g. Atkinson 1978; Moors & Atkinson 1984; Atkinson 1985, 2001). I review evidence of mouse attacks on seabirds elsewhere and address the question of why the attacks happen on Gough, and virtually nowhere else, despite the fact that mice and seabirds co-exist on hundreds of islands and reviews.

Chapter 2 describes the nature and impacts of predation by house mice on chicks of Atlantic Petrels and other burrowing petrels. I present three (incomplete) seasons of breeding success for the Atlantic Petrel. The role that mice played in creating the patterns is explored, with the use of video cameras providing crucial evidence. Based on a rough population model for the Atlantic Petrels (Cuthbert 2004), I speculate on the likelihood that mouse attacks are causing a population decrease. Finally I consider the risks of predation faced by other seabird species breeding on Gough which have not been studied.

Prior to this study, only a single year of breeding success for the Tristan Albatross population on Gough Island was known (Cuthbert et al. 2004). I describe spatio-temporal patterns of Tristan Albatross chick deaths in Chapter 3 and consider the role of predation by mice in creating those patterns. I use video recordings and analyses of breeding success within and between sites, and within and between years to address these issues. I also compare sites with strong differences in annual breeding success, to investigate possible mechanisms or correlates that could explain the patterns. Lastly, the video evidence is used to examine the behaviour of mice at a wounded albatross. The description of patterns and processes leads on to Chapter 4, where I explore the consequences of predation for the Tristan Albatross population using a population model and various scenarios of some key parameters. I update Cuthbert et al. (2004) with more robust estimates of parameters using longer sequences of data. The model and consecutive counts of incubating birds allows the first estimate of the Gough population. I use these estimates to compare to historical data, exploring evidence of a long-term Tristan Albatross population decrease. The relative importance of adult survival (impacted by longlining) and annual chick production (impacted by predation by house mice) is considered, and the levels of these parameters required for a stable or growing population are estimated.

In Chapter 5 I turn attention to the mice. A key question of the thesis is the importance of seabirds as a food resource for the mice on Gough Island. This is important because it helps understand or predict the consequences of continued predation for the affected seabird populations. If seabirds are important, then as their populations decrease, so might predation rates. However, if seabird consumption is a relatively minor component of average mouse diets, then predation rates might increase as the populations decrease and spiral towards extinction. Traditional stomach content analysis is used, but primary inference about the contribution of seabird protein to mouse diets is made using natural chemical tracers in the form of stable isotope ratios. Three key subsidiary questions are addressed in this chapter. First, what factors could cause mice to attack seabird chicks in certain times of the year and not at others, or to attack more in some areas than in others? Second, is evidence of attacks apparently opportunistic (i.e. normally distributed in the population), or is there evidence of seabird specialists? Third, do factors such as size, sex or condition correlate with predation?

The last data chapter (Chapter 6) is devoted to the biology, population dynamics and survival of the house mice on Gough Island. A specific goal for understanding their biology is to inform a potential eradication operation about periods of vulnerability and potential obstacles to success. These include seasonal changes in breeding status, annual cycles in population density and seasonal changes in body condition, which may determine when 100% of mice will accept toxic bait.

The final chapter synthesises key results and proposes directions for future research. I also draw together some of the more intriguing patterns that were left unexplained in data chapters.

The timing of field work on Gough is dictated by the South African National Antarctic Programme's annual relief voyage in September-October. This timing was unfortunate for the study of winter-breeding species, because hatching success and failure of small chicks prior to October 2003 was missed. Thus my fieldwork commenced when Atlantic Petrel and Tristan Albatross chicks from 2003 were already well-developed and apparently immune or no longer subject to predation. This placed some obvious constraints on analysing data and interpreting results, particularly for the Atlantic Petrels.

Each chapter is written as a stand-alone piece, to ease the passage to publication. This has necessitated a certain amount of repetition (with separate reference lists for each chapter), but I have endeavoured to keep this to a minimum. Explicitly, where two chapters draw on the same data I have cross-referenced rather than repeat methods and results sections. Also, all acknowledgments are dealt with in the Acknowledgement section of the thesis, and are not repeated in each chapter. I have followed the convention of not capitalising common names of mammals, but all other common names are capitalised.

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CHAPTER 1

Review of impacts of the introduced house mouse on islands in the Southern Ocean: regional details, global relevance

Abstract

Research on the impacts of house mice *Mus musculus* introduced to islands is patchy across most of the species' global range. However, the islands of the Southern Ocean have been unusually well studied. Here I review mouse impacts on Southern Ocean islands' plants, invertebrates, land birds and seabirds, and describe the kinds of effects that can be expected in other island systems where similar studies are few or lacking. A key finding is that where mice occur as part of a complex of invasive mammals, especially other rodents, their densities appear to be suppressed and rat-like impacts have not been reported. Where mice are the only introduced mammal, a greater range of native biota is impacted and the impacts are most severe, and include the only examples of predation on seabird eggs and chicks. Thus mice can have devastating, irreversible and ecosystem-changing effects on islands, impacts typically associated with introduced rats *Rattus* spp. Island restoration projects should routinely include mouse eradication or manage mouse impacts.

Introduction

The impacts of invasive mammals are most profound on insular fauna, flora and ecosystems (Diamond 1989; Williamson 1996); in particular, the predatory impacts of rats *Rattus rattus*, *R. norvegicus* and *R. exulans*, cats *Felis catus* and pigs *Sus scrofa* on on insular ecology and charismatic fauna such as seabirds are such that their eradication from islands has progressed apace (Veitch & Clout 2002; Courchamp et al. 2003; Towns & Broome 2003; Nogales et al. 2004). House mice *Mus musculus* are one of the most widespread invasive mammals on islands and amongst vertebrates the breadth of their global distribution is second only to humans (Bronson 1979). Despite this, there has been little conservation action devoted to mice, relative to other mammals (Wanless et al. 2007). Why has the world's most widespread invasive mammal been so widely ignored by island conservation programmes? Two reasons are suggested. First is the relative paucity of described impacts on charismatic fauna (cf. Brooke 1995; Fritts & Rodda 1998), or lack of devastating herbivory, e.g. by goats Capra hircus (Campbell & Donlan 2005), especially relative to the impacts of other introduced mammals. Second, a higher percentage of mouse eradications has failed compared to *Rattus* spp. eradications (38% vs 5-10%, Howald et al. 2007; MacKay et al. in press), although the reasons for the higher rate of failed mouse campaigns remain unclear (MacKay et al. in press). These factors have probably contributed to the slow development of technology for successful mouse eradications, and the patchy coverage of eradication attempts, relative to rat eradications

Purpose of this review

The impacts of introduced mice on seabirds have only recently been assessed critically, in contrast to studies of their impacts on other biota from Southern Ocean islands; here we review all their described impacts. The impacts of mice preying on island-endemic invertebrates and causing extinctions, e.g. on Antipodes Island (Marris 2001) and Marion Island (Chown et al. 2002) or precipitating potentially irreversible changes to ecosystem functioning, e.g. Marion Island (Smith et al. 2002), have, to the best of our knowledge, failed to generate wide scientific, popular or conservation interest. By contrast, descriptions of conclusive proof that mice were preying on Gough Island's seabirds (Angel et al. 2005; Wanless et al. 2005) led to substantial media interest (e.g. Marris 2005; Dangerfield 2006), an unsolicited offer of support for eradication from the New Zealand Department of Conservation (G.M. Hilton pers. comm.) and the establishment of an advisory group to raise funds for and oversee a process aimed at eradicating mice (Angel & Cooper 2006). The subsequent publication describing those impacts in a peer-reviewed, international journal (Wanless et al. 2007) led to renewed media interest (e.g. Millius 2007). The relative importance of conserving endemic invertebrates or plants is, in theory, the same as conserving charismatic fauna such as albatrosses. However, the evidence suggests that in reality, less visible fauna and flora tend not to generate sympathetic responses or to drive island conservation actions. It is my belief that negative impacts of mice on any insular systems, either direct or indirect (such as through changing nutrient cycles, synergy with other invasive species or changes to other major ecosystem processes) are sufficient grounds to merit remedial action as a high conservation priority. Demonstrating negative impacts on charismatic species such as seabirds should not be a pre-requisite for planning island conservation and restoration projects or securing funding for such projects.

The regional focus is chosen because various national Antarctic research programmes have facilitated the publishing of a substantive body of relevant research within the biogeographic setting. Special focus is given to those islands where mice are currently the only invasive mammal, some of which have been particularly well studied, and these studies describe the kinds of impacts that could be expected elsewhere, in more temperate and tropical systems where such studies are lacking. The aim of this review is to describe the distribution of introduced house mice on islands in the Southern Ocean and to draw attention to the importance of mouse impacts on island ecosystems, impacts that may be overlooked or (more probably) suppressed on islands where mice occur together with other introduced mammals. The long-term consequences of the impacts, both direct and indirect, of invasive house mice are as important to consider as the impacts of more widely studied invasive mammals on islands. Finally, I point to the importance of including the management of mouse impacts in island restoration programmes.

Regional distribution of mice

For the purposes of this review, I have defined the Southern Ocean to include islands slightly to the north of the summer position of the Subtropical Convergence (such as Tristan da Cunha, Amsterdam and St Paul) and islands well south of the winter position of the Antarctic Convergence (Heard and McDonald) (Figure 1). Only oceanic islands are considered.

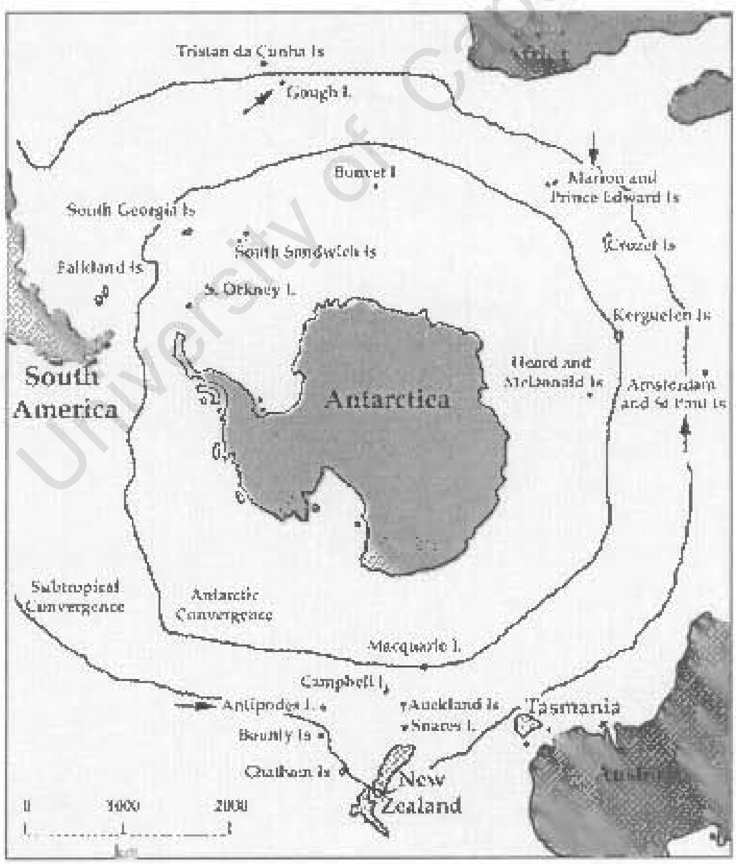

Figure 1. Islands of the Southern Ocean. Islands with house mice as the only introduced mammal currently present are indicated with arrows.

Table 1. Invasive mammal taxa extant and recently (since the start of large-scale eradications, *ca* mid-1970s) eradicated/died out from oceanic islands of the Southern Ocean. Islands where mice are now the only introduced mammal are in bold. Only associated islands ≥4 km^2 are reported.

Main island - associated islands	Area (km^2)	Extant introduced mammals	Eradicated or died out in last 30 years	Refs
Tristan da Cunha	94	Rats, house mice, sheep, cattle	Cats	1
- Nightingale	4	None		2
- Inaccessible	14	None		3
Gough	64	House mice		1
Bouvet	47	None		4
Marion	290	House mice	Cats	5
Prince Edward	45	None		6
Crozet	352			
- Possession	150	Rats		7
- Cochons	67	House mice, cats, rabbits		8
- Est	130	Rabbits		8
Kerguelen (>20 large islands)	7200	Rats, house mice, cats, mouflon, sheep, reindeer, rabbits	Rats, rabbits from some islands	7
- **Australie**	21	House mice	Rats, rabbits	7
Amsterdam	55	Rats, house mice, cats, cattle		8
St Paul	6	House mice	Rats, rabbits(?)	8
Heard	386	None		7
- McDonald	25	None		7
Macquarie	128	Rats, house mice, rabbits	Cats	9
Auckland	510	House mice, cats, pigs	Goats	10
- Enderby	7	None	Rabbits, house mice, cattle	10
- Adams	100	None		10
- Disappointment	5	None		10
Antipodes	60	House mice		11
Bounty (various)	1.3	None		10
Campbell	130	None	Rats, sheep, cats, cattle	12

[1]Richardson 1984; Angel & Cooper 2006, [2]Holdgate 1969, [3]Ryan & Glass 2001; Ryan 2005, [4] Pers. obs., [5]Bester et al. 2000; Jansen van Vuuren & Chown 2007, [6]Crafford & Scholtz 1987; Anon. 2006, [7]Chapuis et al. 1994; Frenot et al. 2004, [8]Chapuis et al. 1994; Micol & Jouventin 2002, [9]Copson 1986; Copson & Whinam 1998; Pye et al. 1999; Frenot et al. 2004; Anon. 2005, [10]Clark & Dingwall 1985; Shirihai 2002, [11]McIntosh 2001, [12]Towns & Broome 2003

Although the house mouse is one of the most widely introduced mammals on oceanic islands it is seldom the only one (Berry et al. 1978; Bronson 1979; Brooke et al. 2007). Thus, across most of their non-native range, the impacts of mice on island biota appear to be difficult to separate from those of other introduced mammal species. Antipodes and Gough islands have mice as the only introduced mammal (King 1990; Jones et al. 2003a; Angel & Cooper 2006). On Marion Island, mice have been present since the 1800s (Jansen van Vuuren & Chown 2007), whereas the domestic cat was introduced in the 1950s and eradicated in the early 1990s (Bester et al. 2000). On the French islands of St Paul and Australie (Kerguelen Archipelago), mice remain after successful eradications of rats and rabbits *Oryctolagus cuniculus*, in both cases the only other introduced mammals (Micol & Jouventin 2002; Micol in litt). All other Southern Ocean islands/island groups either lack mice or also have other introduced mammals (Table 1).

Impacts on flora

On Antipodes Island sedge species, in particular the native *Carex appressa* (Cyperaceae), attract large concentrations of mice that feed extensively of the inflorescences and seeds (Godley 1989). A more recent diet study found a large percentage of mouse diet on the Antipodes to consist of native sedges and plants in general (McIntosh 2001). On Gough Island at least 15 species of endemic or native as well as seven introduced plant species are consumed by mice (Jones et al. 2003a). The flower heads and fruiting bodies of the native tussock grasses *Spartina arundinacea* and *Paridocloa flabellata* (both Poaceae) are extensively chewed by mice as are the seeds of the native *Acaena sarmentosa* (Roseaceae), and endemic sedges *Carex* spp. and *Scirpus* spp. (Wace 1986; Jones et al. 2003a). On Macquarie Island mice consume a range of native plant species, some of which are available throughout the year (Copson 1986). Comparative studies between mouse-free Prince Edward Island and Marion Island are to date the most comprehensive with regards to the possible impacts that mice have on Southern Ocean Islands flora. The mice on Marion feed on the seeds and young shoots of at least five native and one introduced plant species. In the late 1960s the native sedge *Uncinia compacta* (Cyperaceae) was abundant in mire vegetation (Huntley 1971) but has now almost been extirpated from this habitat on Marion due to seed harvesting by mice (Smith & Steenkamp 1990). Mice remove up to 75% of all the seed heads of this native plant, significantly reducing the population compared to the neighbouring mouse-free island of Prince Edward (Chown & Smith 1993). Mice are also thought to be having a similar impact on *Acaena magellanica* (Avenant 1999) and damage the peat-forming *Azorella selago* (Araliaceae), a disturbance-sensitive cushion plant, by burrowing into it (Chown & Cooper 1995). On Guillou Island (Kerguelen group), the seeds and flowers of the indigenous *Acaena magellanica* were among the main plant items consumed during summer (Le Roux et al. 2002). These studies all suggest a preference for native plants over introduced species, possibly related to the lack of defensive traits such as secondary compounds, commonly lost among native island plants (Bowen & van Vuren 1997). There is, however, no evidence of plant species having gone extinct on any of these islands due to mice (Wace & Dickson 1965; Godley 1989; Copson & Whinam 1998). Excluding Marion Island, there are no studies on the possible population-level impacts that mouse predation has on the plants on any of these islands, possibly reflecting a paucity of data rather than a lack of effect. The importance of plant material compared to invertebrates in mouse diet on Marion Island has increased over time, from occurring on average in 36% of stomachs in the late 1970s to 59% in the 1990s, particularly during mid to late-summer (Avenant 1999; Smith et al. 2002). The seasonal pattern may reflect prey-switching from invertebrates to seeds as invertebrate densities decrease, (Avenant & Smith 2004), but could also be due to optimal foraging in the presence of abundant seed loads. Similar patterns of seasonal changes in the importance of dietary groups have been found on Guillou and Gough islands (Le Roux et al. 2002; Jones et al. 2003b).

Impacts on invertebrate fauna

Although mice are omnivorous they can also be highly selective and may prefer invertebrate prey. This has been documented for Subantarctic islands such as Guillou, Antipodes and Macquarie (Gleeson 1981; Copson 1986; McIntosh 2001; Le Roux et al. 2002). Comparative studies of island pairs where one is mouse-free and one has mice (Bollons-Antipodes and Prince Edward-Marion) strongly suggest that mice have a major impact on invertebrates at three levels: species composition, relative abundances and size distributions. Predation by mice is considered responsible for local extinctions of several invertebrate species on Antipodes Island (Marris 2000) and also for the absence of the flightless moth *Pringelophaga kerguelensis* on Marion (Vari 1971). Differences in invertebrate abundances between Bollons Island and Antipodes Island are dramatic and have been attributed to mouse predation on Antipodes (Marris 2000). Mice on Marion are strongly size-selective feeders, preferring the larger individuals of moth larvae and weevils (Crafford & Scholtz 1987). This has resulted in quantitative differences in invertebrate body size and biomass between the two islands (Crafford & Scholtz 1987; Chown & Smith 1993). Further quantitative and robust analyses of population trends of moth larvae and weevil larvae on Marion Island showed that densities decreased significantly, by approximately an order of magnitude, between 1976/77 and 1996/97 (Chown et al. 2002). Flightless island species are particularly vulnerable to introduced predators (Quammen 1996), and the flightless Lepidoptera on Antipodes and Gough islands are heavily impacted by mouse predation (Patrick 1994; Jones et al. 2002); indigenous moths are major prey items wherever mouse diets have been studied in the Subantarctic (Gleeson & Van Rensburg 1982; Copson 1986; Le Roux et al. 2002). Inter-decadal comparisons from Marion Island showed that the relative importance of the main invertebrate species in mouse diet has changed since the late 1970s (Chown & Smith 1993). By the 1990s, endemic moth larvae had been replaced by native weevil adults, in particular *Ectemorrhinus similis* and *Bothrometopus randi*, as the main prey. This prey shift suggests a marked impact on their previously preferred prey (Chown & Smith 1993).

Strong preferences by mice for large, slow-growing invertebrate species has serious consequences, given the life-history traits of some species (Peters 1983; Brown et al. 1993). For example, the flightless moth *Pringelophaga marioni* adults are short-lived (10-14 days) and have very low dispersal abilities (Rowe-Rowe et al. 1989) and larvae take 2-3 years to mature (Crafford 1990). The decreased abundance of this species in mouse diets on Marion suggests over-harvesting, and unless remedial action is taken, local extinction is possible. *P. marioni* plays a critical role in Marion Island's nutrient cycle; where invertebrate species are also keystone species, predation can have deleterious effects for the whole ecosystem (Smith 1978; Smith & Steenkamp 1992; Smith & Steenkamp 1993).

Impacts on terrestrial birds

Relatively few reliable studies have shown any direct impacts of mice on native terrestrial birds. On Gough Island, direct nest predation and competition are believed to explain the reduced abundance of the endemic Gough Bunting *Rowettia goughensis* in the lowlands, but there are few quantitative data to support this contention. During the 2000/01 breeding season, four of 15 monitored Gough Bunting nests (27%) were apparently depredated by mice, one during incubation, and three during the chick stage (Cuthbert & Hilton 2004). A study using artificial nests and eggs found evidence of mouse predation, although such studies are difficult to interpret (Faaborg 2004; Thompson & Burhans 2004).

Mouse predation on invertebrates may have an indirect influence on several island bird species. Lesser Sheathbill *Chionis alba* numbers on Prince Edward Island have remained relatively constant since the 1970s but have decreased on Marion Island by 20% over the same period (Burger 1978; Huyser et al. 2000). Observations on Marion over the last 20 years indicate that Lesser Sheathbills now forage mostly on the coast during winter and not inland as they did previously and still do on Prince Edward (Huyser et al. 2000). The change in foraging behaviour is thought to be due to mouse predation reducing invertebrate densities (Crafford & Scholtz 1987; Rowe-Rowe et al. 1989). The sheathbill population relies heavily on invertebrates during the winter when other, preferred food resources in penguin or seal colonies are not available (Burger 1982). Nowadays sheathbills on Marion commence breeding at a lower body mass and lay smaller clutches (Huyser et al. 2000). Kelp Gulls *Larus dominicanus* also forage more on invertebrates during winter (Burger 1978). Mouse predation on invertebrates may thus impact this species in a similar manner as it does the Lesser Sheathbill.

A comparative study of Antipodes Island Snipes *Coenocorypha aucklandica meinertzhagena* and Auckland Island Snipes *C. a. aucklandica* found that Antipodes Island Snipes were much less abundant than expected, and they are probably affected by mice consuming invertebrates in a similar manner to the Lesser Sheathbills on Marion Island (Miskelly et al. 2006). Mice on Antipodes Island are probably also in direct competition with the Antipodes Parakeet *Cyanoramphus unicolor* as scavengers of Subantarctic Skua *Catharacta antarctica* and Northern Giant-Petrel *Macronectes halli* kills (Imber et al. 2005).

Impacts on seabirds

In this section I draw on all available data, not just from Southern Ocean islands. The direct impact of house mice on seabird populations was until recently considered negligible (Moors & Atkinson 1984; Atkinson 2001). Reported impacts were restricted to predation of eggs and young chicks of very small seabirds, such as storm-petrels (of which newly hatched chicks may weigh only 10 g). Only four credible examples are known to me, excluding Gough Island. Mice were suspected of depredating eggs of the Grey-backed Storm-Petrel *Garrodia nereis* on Antipodes Island (Burger & Gochfeld 1994), eggs and chicks of the White-faced Storm-Petrel *Pelagodroma marina* on Selvagem Grande Island, Madeiran archipelago, eastern North Atlantic Ocean (Campos & Granadeiro 1999), eggs and small chicks of the Ashy Storm-Petrel *Oceanodroma homochroa* on the Farallon Islands, coastal eastern North Pacific Ocean (Ainley et al. 1990) and Blue Petrel *Halobaena caerulea* chicks (*ca* 30 g) on Marion Island (Fugler et al. 1987), where a chick was found with deep wounds on its back and neck. I have disregarded an unsupported statement of depredation of nests of the Polynesian Storm-Petrel *Nesofregetta fuliginosa* (BirdLife International 2004) and other unsubstantiated reports in the grey literature. Bird remains in mouse stomach samples is a possible indication of mouse predation, e.g. on Macquarie and Antipodes islands, although these could derive from scavenging (Copson 1986; McIntosh 2001).

Also on Antipodes Island, the abundance of species such as Black-bellied Storm-Petrels *Fregatta tropica* on mouse-free offshore islets, but their extremely low density on Antipodes, has been speculatively attributed to predation by mice (Imber et al. 2005). To date there has been no direct evidence of mice predation on Antipodes Albatross *Diomedea [exulans]*, but predation may have been overlooked (K. Walker in litt.).

All of the above reported incidents of predation are incidental, inferred or based on *post hoc* observations of gnawed egg shells, wounded chicks and mice eating dead chicks. Without direct observations of mice depredating nests or killing live chicks, the possibility that mice were only scavenging abandoned eggs and moribund or dead chicks cannot be excluded. Recent events on Marion Island suggest that mouse predation on Wandering Albatross *Diomedea exulans* chicks may be evolving there. House mice on Marion became the sole introduced mammal following the eradication of cats in the 1990s (Bester et al. 2000). Since 2004, several Wandering Albatross chicks have succumbed to wounds consistent with mouse attacks (pers. obs.). These are the first records of wounded chicks in over 20 years of intensive study (P.G. Ryan pers. comm.). A key observation is that to date, the only records of mouse predation on seabird eggs and chicks are from islands on which mice are the only introduced mammal. On islands where the mice are part of a complex of invasive mammals, the effects of dominance, competition and predation by larger species may render them less of a threat to native vertebrates (Courchamp et al. 1999; Wanless et al. 2007).

The dynamics of seabird—invertebrate—nutrient cycle interactions have been well studied in the Subantarctic (Smith 1978, 1979; Smith & Steenkamp 1990, 1992; Smith & Steenkamp 1993). The transport of nutrients from marine to terrestrial systems is a critical determinant of terrestrial productivity on Subantarctic and other seabird-dominated islands (Smith 1978, 1979; Smith & Steenkamp 1993; Erskine et al. 1998; Croll et al. 2005; Fukami et al. 2006; Maron et al. 2006). In Chapter 5 I argue that predation on seabird chicks on Gough Island will ultimately reduce nitrogenous fertilisation, leading to lower primary productivity (e.g. (Croll et al. 2005; Fukami et al. 2006). This could cause mice to prey more heavily on seabirds, setting up a positive feedback and precipitating a rapid decreases in seabird numbers.

Effects of climate change on mouse impacts

Climatic change is expected to be marked in the Southern Ocean, and empirical evidence of change already has been reported from Macquarie, Kerguelen, Marion, Heard and South Georgia

(Allison & Keague 1986; Bergstrom & Chown 1999; van Aarde & Jackson 2006). There is now abundant evidence that temperatures and hours of sunshine are increasing and rainfall regimes are changing at several islands (Allison & Keague 1986; Smith & Steenkamp 1990; Smith 2002). The actual causes for these changes are unknown, but they may reflect atmospheric changes associated with changes in the oceanic circulation patterns (Smith & Steenkamp 1990).

The impacts of climate change may affect mouse populations directly in two ways. First, if mice are temperature-stressed and experience thermally-induced die-offs during winter (e.g. at Marion Island, Crafford & Scholtz 1987; Crafford 1990), then ameliorating conditions could facilitate higher survivorship in winter, leading to higher densities at the start of the breeding season and potentially higher average or peak densities (Rowe et al. 1964; King 1982; Singleton et al. 2001; Ruscoe et al. 2005; Singleton et al. 2005; Ferreira et al. 2006). Second, climate change has the potential to enhance terrestrial productivity, through lengthened growing seasons for plants or longer breeding seasons for mice and invertebrates. However, these effects may be self-regulating or off-set because of deleterious effects of higher mouse densities on ecosystem functioning. On Marion Island, an increasing mouse population is likely to place enhanced predation pressure on soil invertebrates. This will decrease rates of nutrient cycling (nutrient availability and mineralization) with a negative effect on primary productivity (Crafford 1990; Chown & Smith 1993; Smith et al. 2002).

Global consequences

The impacts of introduced mice on island ecosystems and species are poorly described across most of their range. However, the islands of the Southern Ocean represent an exception to this pattern. Mice are the only introduced mammal on three of these islands (Gough, Marion and Antipodes), and it is on these islands that their impacts appear to be the most significant, although this may reflect relative research effort to some extent. Where mice co-occur on islands with other introduced mammals, their densities are suppressed (e.g. Miller & Miller 1995; Russell & Clout 2004; Witmer et al. 2007). It is probable that their (visible?) impacts are diminished as a consequence. However, eradications of other introduced mammals from islands are leaving increasing numbers of islands with mice as the only introduced mammal e.g. on Marion, St Paul and Australie (Kerguelen group) islands in the Southern Ocean (Bester et al. 2000; Micol & Jouventin 2002; T. Micol in litt). Far more islands have had rats *Rattus* sp. eradicated than mice, and the total island area cleared of rats globally dwarfs that cleared of mice (Figure 2). Ironically, the largest island cleared of house mice is Enderby (700 ha), but the operation was targeted at rabbits and the successful eradication of mice was incidental (Torr 2002). Several attempts to eradicate mice and rats simultaneously have failed (e.g. St Paul and Île Australie, Micol & Jouventin 2002; T. Micol in litt.), although the reasons for this are unclear (Brown 2005).

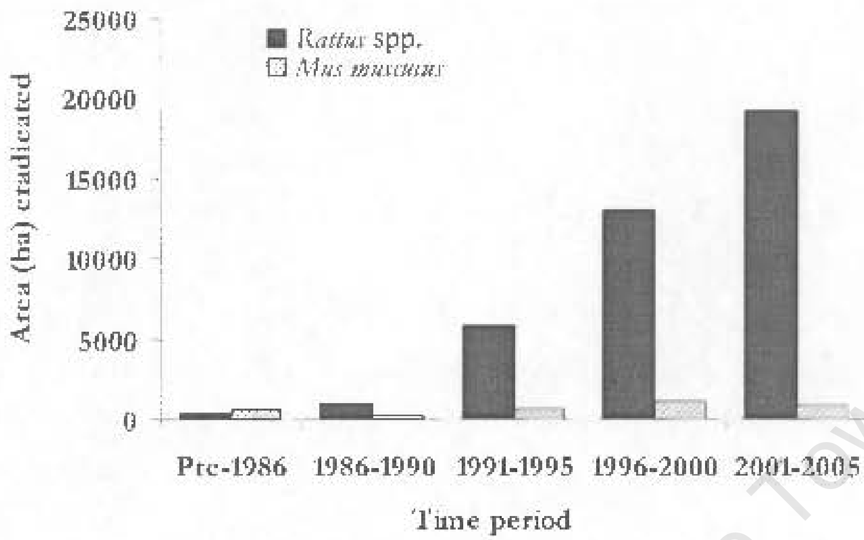

Figure 2. Island area cleared of rats (*Rattus* spp.) and mice (*Mus musculus*). All known efforts prior to 1986 are summed. Modified from (Wanless et al. 2007)

The incidence and impacts of rat predation on island biota vary widely and depend on factors such as the physical environment of the island, seasonal availability of food, the size, behaviour and population density of the rats and the presence of other rat species and/or other predators or competitors (Woodward 1972; Atkinson 1978; Taylor 1979; Moors & Atkinson 1984). Although the effects of these factors have been studied principally for rats, there is evidence that the impacts of mice vary according to similar factors (Chown & Smith 1993; Smith et al. 2002; Wanless et al. 2007). The evidence of significant impacts by mice on birds of the Southern Ocean islands is limited. What little evidence we found was mostly indirect, due to competition for food. Wanless et al. (2007) have, however, shown significant effects of mouse predation on the chicks of seabirds as large as albatrosses. Outside the Southern Ocean, especially on islands where small passerines or ground-nesting birds occur that do not have strong nest-defence or predator-avoidance instincts, the impacts of mouse predation could be/become significant. Small rodents have been shown to be significantly more motivated to attack chicks and depredate eggs when denied food (i.e. food-stressed), in contrast to when provided with alternatives *ad libitum* (Bradley & Marzluff 2003). I predict that where house mice are or become the only introduced mammal, including on temperate or tropical islands, nest predation is likely to occur during times of severe food-stress, such as winter seasons or dry monsoons.

Mouse impacts have probably been overlooked to some extent, but this review shows that rat-like behaviour and impacts can be expected, especially on islands where mice are the only introduced mammal. Predation by introduced mice on seeds, invertebrates and the eggs and chicks of birds is causing significant changes to species distributions, densities and persistence on islands in the Southern Ocean. Some of these impacts are likely to result in extinction of impacted taxa and irreversible effects on ecosystem functioning and similar effects are likely to occur on islands outside the Southern Ocean. There is thus a strong case for eradicating introduced mice from islands. It may be important to eradicate mice and other species simultaneously, or to give careful consideration to the best order of a staged, multi-species eradication programme, for three reasons. First, if toxic baits are applied to eradicate mice, primary or secondary poisoning of 'non-target' species could achieve eradication or substantial knockdown of numbers (e.g. of cats), making subsequent operations for other species cheaper and more efficient. Second, higher densities of mice following release from competition or predation could conceivably accelerate extinction of prey sources (e.g. endemic invertebrates) (Courchamp et al. 1999; Caut et al. in press); thus eradication of one invasive species could lead indirectly to the extinction of a native or endemic species (Zavaleta 2002). Third, a rebounding mouse population or rejuvenating island ecology (e.g. higher seed loads after release from herbivory) might compromise the susceptibility of mice to eradication for an unknown period of time, while exacerbating their negative biodiversity impacts.

Island ecosystems are beguilingly simple, but should nevertheless be treated as a whole (Poiani et al. 2000; Zavaleta et al. 2001). Where several invasive mammals coexist, eradicating one could have profound and perhaps unpredictable effects on the interactions between native species and other invasive species. I recommend that mice be included in island restoration plans while taking due cognisance of the difficulties of eradicating multiple species from an island, such as is being planned for Subantarctic Macquarie Island (Anon. 2005). Methods that result in the simultaneous eradication of mice and rats should be a high priority for island conservation research. In addition, changes in the diet and behaviour of mice on Marion, St Paul and Australie should be studied, as these provide excellent and immediate 'natural' experiments on the effects of competitive release or meso-predator release and could give insights into causal mechanisms for the evolution, or the lack of evolution, of predatory behaviour in house mice.

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CHAPTER 2

The nature and impacts of predation by house mice on chicks of Atlantic Petrels and other burrowing petrels on Gough Island

Abstract

I studied Atlantic Petrel *Pterodroma incerta* nests over three incomplete seasons: October 2003-January 2004, June-September 2004 and September-November 2006. In 2003 introduced house mice *Mus musculus* visited all burrows studied, and thus all chicks were exposed to mouse predation, but they killed at most one of 41 chicks monitored. Breeding success (number of chicks fledged per nesting attempt) for the period of study in 2003 (part of the chick-rearing stage) was 93% and estimated annual success was 46.5%; however, the failure rate prior to October is unknown and may have been higher than suggested by the estimates of success. Video recordings in August-September 2004 captured six attacks by mice on live, healthy Atlantic Petrel chicks. In 2004, 40 of 60 nests had failed by late September and in 2006, 14 of 19 chicks failed from September-November. The majority of chick deaths in 2004 and 2006 were ascribed to mouse attacks. Overall, breeding success estimates for 2004 and 2006 were *ca* 7%, but seasons were incomplete so actual success could have been higher (maximum 33% and 26%, respectively). The rate of failure in 2004 was significantly higher in August than in September. Smaller chicks were also more likely to be attacked than larger chicks. Thus the effects of size and time of year cannot be separated, but both may be important. The upper estimates of breeding success for 2004 and 2006 are probably insufficient to maintain the population, and the lower estimates, if typical for Gough, will cause the population to decrease. The high breeding success of 2003 appears to be exceptional, but the failure rate during early chick-rearing may have been high.

Introduction

The impacts of invasive mammals are most acutely experienced on islands, where the poor dispersal abilities of terrestrial, non-volant mammals has meant that the vast majority of insular fauna have evolved in the absence of terrestrial mammalian predators (BirdLife International 2004). Oceanic islands hold a disproportionate percentage of global avian biodiversity and an even more disproportionate percentage of known avian extinctions

(Atkinson 1985; Steadman 1995; Blackburn et al. 2004). Virtually no island of significant size in the world has escaped invasion by mammals, which have caused the vast majority of known island-endemic avian extinctions (Atkinson 1985; Steadman 1995; Blackburn et al. 2004). This is partly why seabirds and island-endemic landbirds are among the most globally threatened groups of birds (BirdLife International 2004). House mice *Mus musculus* have successfully colonised an impressively broad range of continental and insular habitats, including most Subantarctic islands (Pye 1993; Angel & Cooper 2006), Chapter 1). This suggests that house mice are highly adaptable, have naturally broad niches and are adept at exploiting novel resources. Despite this, some 20 years ago and with no significant evidence to the contrary, house mice were deemed to pose no serious threats to seabirds (Atkinson 1978; Moors & Atkinson 1984; Atkinson 1985). Indeed, even the mice on Gough were dismissively described as being 'probably harmless' (Elliott 1953).

Approximately 1.8 million pairs of Atlantic Petrels *Pterodroma incerta*, a species of gadfly petrel, breed at lower elevations on Gough Island (Swales 1965; Cooper & Ryan 1994; Cuthbert 2004; Angel & Cooper 2006). The species is practically endemic to the island, as the only other population is a small relict colony on Tristan da Cunha, last estimated at 100-200 pairs (Richardson 1984). There has been no conclusive evidence of them breeding on Tristan da Cunha since the 1970s (Angel & Cooper 2006). The species' IUCN conservation status is currently 'Vulnerable' (BirdLife International 2004), although Cuthbert (2004) argued that it might merit upgrading to 'Endangered'.

Atlantic Petrels are one of three burrowing petrel species that breed on Gough in winter. They have a chick-rearing period of *ca* 138 days, extraordinarily long even by other winter-breeding *Pterodroma* standards (Warham 1990; Cuthbert 2004). Breeding success from the 2000 and 2001 seasons was around 20%, probably insufficient to maintain a stable population of gadfly petrels (Brooke 1995; Cuthbert 2004). Circumstantial evidence suggested that predation by house mice was driving the low success (Cuthbert 2004; Cuthbert & Hilton 2004). However, alternatives for the low observed fledging success, *viz* disease and predation by species besides mice, couldn't be excluded. A candidate nest predator is the endemic Gough Moorhen *Gallinula comeri*. It regularly enters burrows and depredates nests, like insular rallids elsewhere (Watkins & Furness 1986; Taylor & van Perlo 1998; Bester et al. in press; Wanless & Wilson in press).

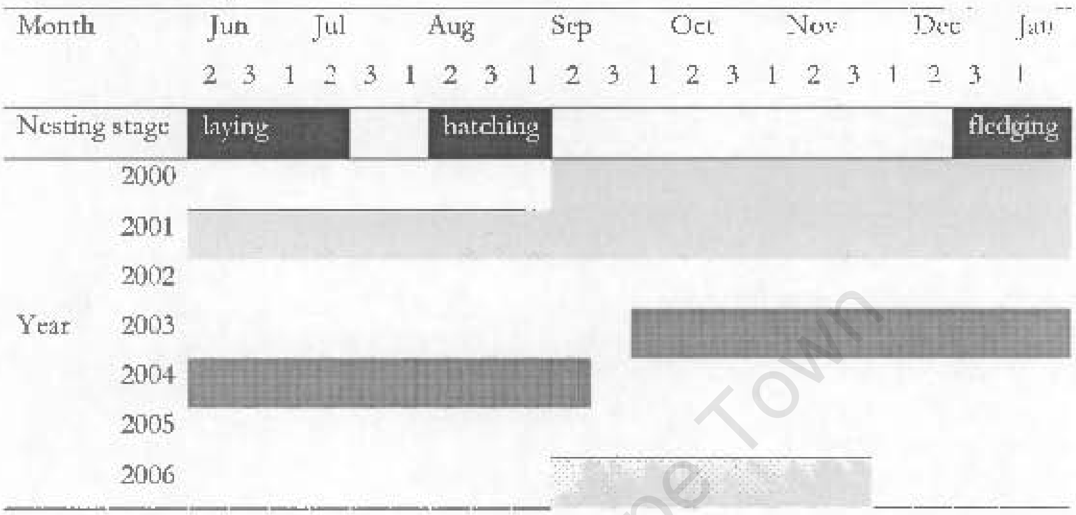
In this study I set out to investigate the possibility that mice prey on healthy Atlantic Petrel chicks (weighing 75-750 g) at levels sufficient to drive negative population trends. I also examine whether the low fledging success observed in 2000 and 2001 is consistent among years and present another three seasons' data for breeding success. The results of video recordings made in burrows of Atlantic Petrels and Great Shearwaters *Puffinus gravis* are used to define the causes of chick mortality and describe the characteristics of mouse activity and behaviour in burrows. I then consider the implications of low fledging success on Atlantic Petrel population trends and assess the risk of mouse predation faced by other procellariiform species breeding on Gough.

Methods

Study site and design

Atlantic Petrel nests were monitored on Gough Island over three seasons, from October-December 2003, May-September 2004 and September-November 2006 (Table 1). I searched in the fern-bush habitat (in the SE coastal plain) for burrows containing chicks in 2003 (41 burrows) and 2006 (21 burrows), and for occupied nests in 2004 (70 burrows). A flexible metal rod (*ca* 1 m long) was inserted up to an arms length into burrows to detect the presence of an incubating adult or chick; burrows where the chamber could not be reached (too deep or curved too tightly) were not excavated. If a bird was encountered an inspection hole was excavated into the nest chamber. A 5 l plastic ice-cream container with the bottom removed was fitted into the hole and pegged through the sides of the container into the peat walls, and I ensured that soil was packed tightly down the sides of the container. A sod of (vegetated) soil was placed on the lid of the container to further insulate the chamber, darken the interior and disguise the inspection hole from predatory Subantarctic Skuas *Catharacta antarctica*. Birds could then be easily visually inspected or removed from the chamber, without causing further changes to the burrow entrance or chamber, simply by removing the container lid.

Table 1. Breeding schedule and study periods for Atlantic Petrels on Gough Island. Each month is divided into thirds (~10 days). Study periods are shaded grey and study periods with video recordings are hatched.



Upon excavating a burrow, standard measurements were taken and each chick was weighed to the nearest 1 g with a Pesola spring balance; thereafter chicks were weighed every 10-15 days. For estimates of breeding success it was important to know approximate chick age. Chick age was determined by solving for age the wing growth-curve equation: wing (mm)=$31.5e^{(0.021 \times age)}$ (Cuthbert 2004). Mean chick age at excavation of the observation hatch was 65 days (range 28-98 days) in October 2003 and 26 days (range <7-59 days) in September 2006. In 2004 the study commenced at laying/during incubation and the mean chick age of surviving chicks at the end of the study period was 32 days (range 20-44 days).

The effect of time-of-year on survival was assessed by dividing data (in 2004) into week-long periods. Weekly hatching and failure counts were summed and the resulting rates correlated with time. I tested the effect of age on the probability of dying, to see if young chicks were more susceptible to attacks than older chicks. For each chick that was alive at the start of the week, I calculated the age it was/would have been at the end of the week (to prevent a bias towards increasing age of survivors versus chicks that died before the end of the week), and coded each individual as having survived or died that week. A t-test was used to test for differences in the mean age of survivors versus failures.

Chick weights were used to check for colony-wide evidence of under-feeding or starvation as a reason for mortality. A healthy colony is when, on average, chicks did not differ significantly from the expected weight for a given (known or estimated) age. Expected weight was determined by Cuthbert (2004) to be mass (g)=4 × age + 146.2. However, a close examination of the relationship between weight and age (Cuthbert 2004, Fig. 3, pg. 224) shows that the linear regression has a poor fit for small chicks (indeed, most chicks hatch at well under 100 g, so the addition of a constant of 142.6 is guaranteed to create a poor fit), and I therefore considered only chicks older than 10 days. The weights of all surviving chicks >10 days old on 1 and 10 September 2004 were compared to their expected weights, using paired t-tests: an average significantly lower than predicted from the growth curve would imply that chicks were underweight, suggesting a systematic effect, probably related to at-sea foraging conditions negatively impacting parents' provisioning of chicks. Chicks were also inspected for wounds every 2-5 days, except after September 2006, when B. Bowie, based at the meteorological station, checked nests every ~15 days.

The mean chick-rearing periods under study in 2003 and 2006 were 59 and 71 days, respectively. Mean estimated time to fledging for the remaining five chicks at the end of November 2006 was 23 days (SD=6.7 days, n=5 nests), assuming a chick period of 138 days.

Video evidence of mouse attacks

Three infra-red cameras were deployed in randomly-selected Atlantic Petrel burrows in 2003 and 2004 and in Great Shearwater burrows in 2004. Between four and ten infra-red LEDs were used to illuminate each burrow. Activities were recorded 24 hours/day on time-lapse recorders, recording at one frame per second (f.p.s.) onto VHS video cassettes. Nests were filmed until the nest failed, the chick fledged, or I left the island. When a nest failed, the camera was redeployed. Four Atlantic Petrel nests were filmed in 2003, nine in 2004 and three Great Shearwater nests were filmed in 2004.

Characteristics of mouse attacks

The primary objective of making the recordings was to determine the role of mice in chick mortality, and for this the recording system was adequate. However, a subsidiary objective, to quantify the nature of attacks, was thwarted for several reasons. First, the time-lapse interval (1 f.p.s.) was too long to sensibly assess chick and mouse behaviour; this was compounded by an unresolved issue on all three recording devices, resulting in no recordings *ca* every fifth minute. Second, the LEDs used emitted a strong but narrow beam, resulting in the field of view of wide-angled images not being fully illuminated. Third, adult birds frequently obscured chick and mouse activities, chicks moved themselves or were dragged by mice out of the field of view. Lastly, mice were not individually identifiable, preventing me from determining the number of mice involved in an attack or other individual-specific data.

Visit rates by mice to all active study burrows in 2003 were checked using 'smoke plates' (see Cocucci & Sersic 1998). Smoke plates were made from white plastic discs, held over burning cotton soaked in vegetable oil, which left a sooty deposit on the plastic disc. The soot comes off easily when rubbed with skin, fur or feathers, showing clear white tracks against the sooty background, but is waterproof. Plates were pegged to burrow entrances in the evening and checked the following day for signs of mouse footprints, indicating that mice had visited the burrow. Effort amounted to 440 burrow-nights at 40 burrows, with a maximum of 29 burrow-nights per burrow.

Survival estimates

Breeding success is defined as the number of fledglings per pair that laid an egg. Nests were discarded from analysis if the study may have caused their failure. This included deserted or temporarily abandoned eggs that were then depredated in 2004. I performed a Kaplan-Meier survival function analysis (which calculates the cumulative proportion of nests surviving over time, Kaplan & Meier 1958) of chick survival rates in 2004 and 2006. Chick survival data for 2004 were divided into two groups. All chicks were included in the first group but were censored (i.e. the analysis was truncated) at chick-age 10 days; chicks that survived beyond 10 days were assigned to the second group, with survival censored at chick-age 20 days (the age of the youngest surviving chick at the end of the study period) (e.g. Anders et al. 1997; Swinnerton et al. 2005). I compared survival in the two groups using a log-rank test (Johnson 1979; Nur et al. 2004). In 2006, nests were censored at chick-age 90 days (the approximate age of the youngest surviving chick at the end of the study period).

I used the Mayfield Method (Mayfield 1975) to estimate breeding success. Daily mortality (*DM*) is equivalent to $\frac{losses}{e}$, where *e* is exposure, the total number of active nest days, and *losses* is the number of failures in the period under consideration (Mayfield 1975). Success $= (1 - DM)^{np}$, where *np* is the nesting period being considered; for each season I estimated the success for the study period (using the mean age of chicks that survived to the end of the study) and for the whole period. The standard error (SE) of Mayfield's estimator is derived from the expression $\sqrt{\frac{(e - losses) \times losses}{e^3}}$ (Johnson 1979). Statistical comparisons of daily mortality rates were effected by calculating the *Z*-statistic as the ratio of the difference between two mortality rates to the sum of the standard errors (Johnson 1979). Rate differences were tested between 2003 and 2006 and between incubation and chick stages in 2004.

I combined incubation and chick mortality rates to estimate breeding success, defined as the number of fledglings per pair that laid an egg, using Johnson's (1979) equation: $S_I^{\ I} \times S_N^{\ N}$, where S_I and S_N are the daily survival rate (=1- *DM*) during incubation and nestling stages, respectively, I is the length of the incubation period (in days) and N is the length of the nestling period (in days) (Johnson 1979). To estimate breeding success for 2003 and 2006 required two assumptions. First was that incubation success was the same as 2004. Second was that daily mortality did not vary across the nestling period. The observed chick daily mortality rates for the respective seasons were used to generate rough estimates of breeding success. This procedure rests on the assumption that survival rates are constant over the course of the respective periods, but results of the Kaplan-Meier analysis showed that this was not the case even during brief nesting period studied in 2004. An additional complication for this season is that the ultimate fate of many nests in 2004 is unknown, Consequently, I divided the chick period into early (August) and late (September) periods (equivalent to the two groups used in the Kaplan-Meier analysis) and calculated *DM* separately. Johnson's (1979) method was modified to include the two chick survival rate estimates accordingly: $S_I^{\ I} \times S_{EN}^{\ EN} \times S_{LN}^{\ LN}$, where EN and LN are the early and late nestling periods

Results

Video evidence of mouse attacks

Video recordings amounted to *ca* 850 days of footage at 16 nests and resulted in seven mouse attacks being filmed (Table 2). None of the four Atlantic Petrel chicks filmed in 2003 was attacked, whereas six of nine Atlantic Petrel chicks and one of three Great Shearwater chicks filmed in 2004 were attacked and killed by mice. Video evidence showed chicks to be well-fed and apparently in good health when they were attacked and killed. Of six Atlantic Petrel attacks, one chick was still being brooded and parents were in attendance at two others. There was no evidence that mice depredated eggs and one video sequence showed mice repeatedly attempting and failing to gnaw into an unattended egg. Mice were recorded in all filmed burrows and were the only cause of mortality amongst videoed chicks. Moorhens entered a burrow once on camera (and scavenged an unattended egg). At other times they were frequently observed entering burrows and scavenging carcasses.

Table 2. Camera deployment dates, deployment effort and number of attacks captured on video.

Timing	Species	Nests filmed	Days filmed	Total attacks
Oct-Dec 2003	Atlantic petrel	4	255	0
Jan-Apr 2004	Great shearwater	3	348	1
Jul-Sep 2004	Atlantic petrel	9	234	6

Characteristics of mouse attacks and attacked chicks

Out of seven attacks captured on video, only one lasted more than 24 hours, and this was because the attack stopped when a parent arrived in the late evening (to feed the chick) and stayed until the following morning. The attack resumed at twilight (*ca* 18:30) the following day and within four hours the chick was dead. All other attacks continued more-or-less without pause until the chick was dead. The actual attacks by mice were quite sporadic, with mice attacking (always singly) for a few seconds before moving away. The duration of attacks, duration of breaks and the time of chick death could not be quantified. Inasmuch as it could be determined, it appeared that all attacks were initiated by single mice, but more mice joined in as the attack progressed. A maximum of five mice was recorded at a dying chick/carcass at one time. Scavenging of carcasses by mice and Moorhens was near-complete, regardless of the cause of death.

Research effort amounted to 522 nest checks in 2003, 626 in 2004 and 240 in 2006; no checks were made after a nest failed or a chick fledged. In all these checks, only three chicks were found alive but wounded, two of which died shortly after they were discovered with wounds and one (in 2003) recovered. At the colony level there was no evidence that chicks >10 days old in Sept 2004 were systematically underweight compared to expected weights (paired t-tests, 1 September: $T_{18}=0.87$, $p=0.40$ and 10 September: $T_{35}=1.24$, $p=0.22$). With no plausible alternatives, mice were assumed to be responsible for the majority of chick failures.

Smoke plates were deployed on 439 burrow-nights in 36 burrows. Mice visited every burrow that had smoke plates for more than five nights and a total of 178 deployments (40.5%) had definite mouse tracks leading into and/or out of the burrow. Only two nests did not get visited, but effort was <5 nights in both cases (Figure 1). Some burrows may have had resident mice that used the burrow entrance as a major access route to their own burrows (and hence were detected frequently), whereas other burrows may have been visited only occasionally. None of the nests monitored in this way failed due to mouse attacks.

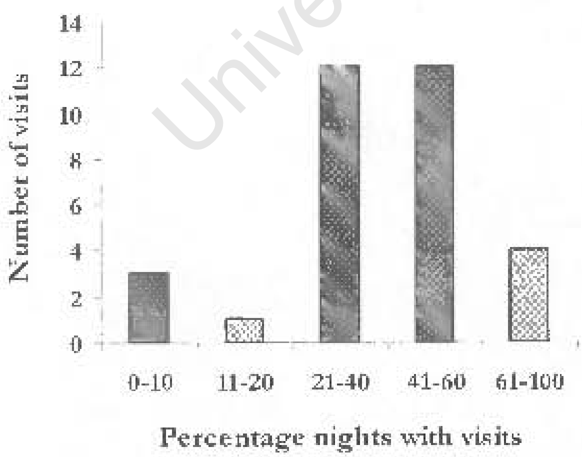


Figure 1. Mouse visit rates in 36 Atlantic Petrel burrows in 2003.

Survival estimates

One out of 41 chicks in 2003 died with wounds consistent with mouse attacks, although the cause of death is uncertain. A second chick sustained wounds consistent with mouse attacks, but it recovered and subsequently fledged. The other two losses in that year were found dead in burrows without wounds. Three other chicks (one in 2004, two in 2006) were also found dead or moribund but without wounds. Attacks on Atlantic Petrel chicks commenced at hatching in late July 2004 and by the time I left the island only 20 of the 60 monitored nests (33%) were still active. In 2006, failures began within a day of nests being excavated and continued until the last check, on 30 November.

The relatively close hatching synchrony meant that chick age and time of year were closely correlated, making it difficult to separate these parameters in analysing the timing of predation. The timing of hatching and the rate of failures were very closely matched in 2004 (Figure 2). The weekly timing of these events were significantly correlated (R^2=0.659, p=0.014) although weeks 3 and 4 departed quite widely from the pattern. Thus mouse predation in 2004 was concentrated in August and early September.

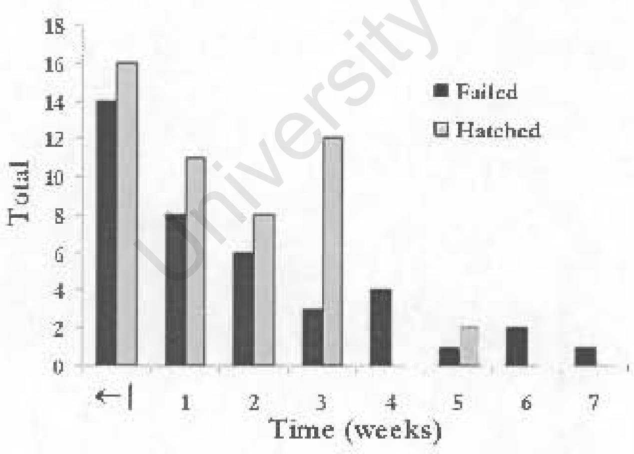


Figure 2. Weekly hatchings and failures of Atlantic Petrel nests in 2004. All events prior to 9 August were pooled (denoted ←|), weeks 1-7 run from 9 August to 25 September.

A t-test for the differences in age between chicks that survived a given week versus chicks that failed (Table 3) showed a significant difference, with older chicks (mean age = 16.9 days) showing significantly better survivorship than younger birds (mean age = 9.5 days) (T_{134}=2.98, p=0.003). A visual inspection of Table 3 suggests that mice preferentially targeted younger chicks, but once all chicks were at least 10 days old that preference fell away.

Table 3. Mean age of chicks that survived and failed each week (starting 9 August). Sample sizes are in parentheses.

Week	1	2	3	4	5	6
Mean age of survivors	5.2 (13)	8.2 (14)	11.0 (22)	18.2 (21)	22.4 (22)	29.7 (20)
Mean age of failures	5.6 (8)	10.7 (6)	6.7 (3)	5.1 (4)	24.0 (1)	27.0 (2)

Incubation success for 2004 was 56% (Table 4); this value was used to estimate annual breeding success for all three years. Breeding success for the whole study period in 2003 (October-January) was 93% (Table 4), significantly higher than the estimated 33% in 2006 (Z=25.6, p<0.05), although the nesting periods under study were roughly the same. Annual breeding success was 46.5% for 2003 and 7% for 2006. In 2004, survival for chicks aged 0-10 days was significantly lower than for chicks aged 10-20 days (Figure 3, Log-rank test statistic=2.95, p=0.003). The estimate of breeding success for the whole year (from laying to fledging) in 2004 therefore included separate estimates for incubation (56%), chick survival for 0-10 days old and chick survival from 10-138 days old (i.e. assuming a constant survival rate from 10 days old until fledging). The result was an estimated breeding success of *ca* 7%.

Incubation vs chick mortality rates did not differ significantly in 2004 (Z=0.33, p>0.25). However, the estimated incubation success is probably an under-estimate, an artefact of my inability to detect all failures due to mouse attacks at hatching. Where on the previous visit the egg was still being incubated, and on the subsequent visit the nest was empty, I ascribed it to an incubation failure; however, some of these failures probably occurred just after hatching. This assumption did not affect the estimate of annual success.

Table 4. Mayfield estimates of daily mortality and nest success for Atlantic Petrels on Gough Island over three seasons. Values in parentheses indicate numbers of failures definitely not due to mouse predation. Incubation period = 55 days and whole chick period = 138 days (Cuthbert 2004)

Year	Study period	Nests	Losses	Daily mortality	Success
2003	Chick-rearing to fledging (Oct-Jan)	39	3 (2)	0.0013	0.925
2004	Incubation (Jun-Aug)	60	17 (2)	0.0104	0.560
2004	Chick-rearing (Aug)†	43	23 (4)	0.070	0.372
	Chick-rearing (Sep)‡			0.0116	0.690
2006	Chick-rearing (Sep-Nov)	19	14 (0)	0.0155	0.331

†Mean age of surviving chicks at end of period = 13.6 days

‡Mean age of surviving chicks at end of period = 31.7 days

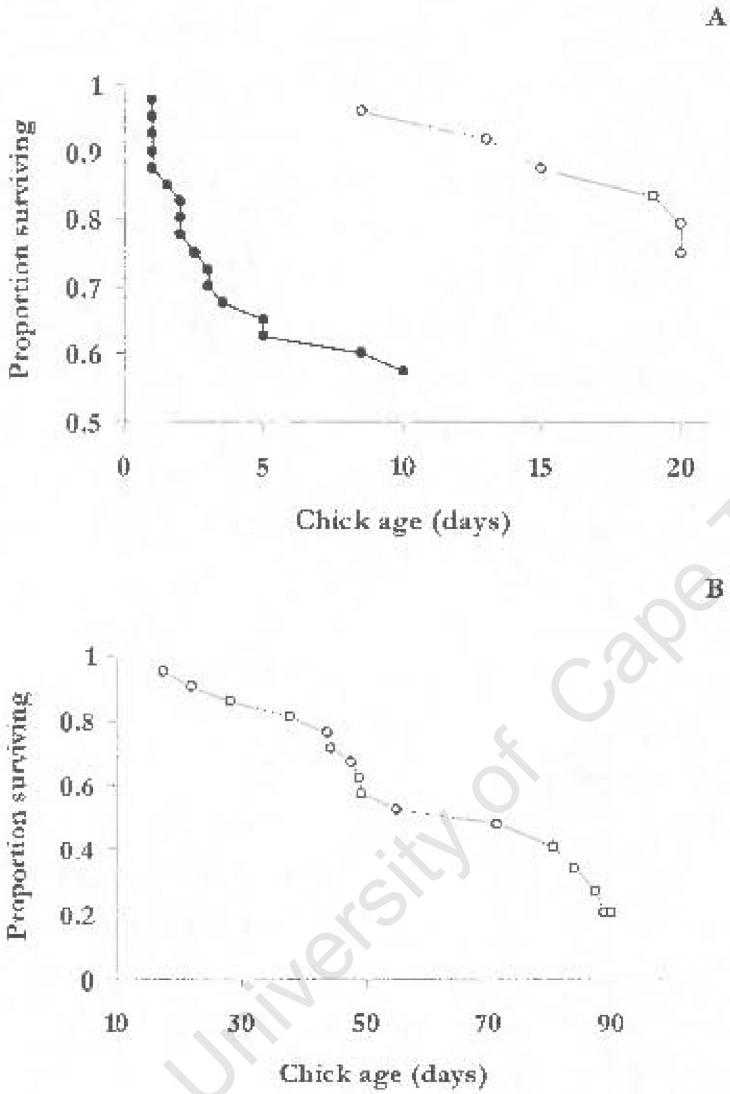


Figure 3. Kaplan-Meier survival probabilities for Atlantic Petrel chicks on Gough Island in 2004 (A) and 2006 (B). In 2004 separate survival functions were plotted for all nests, censored at 10 days (filled circles), and for chicks surviving >10 days, censored at 20 days (open circles).

Discussion

Cuthbert (2004) surmised that house mice were responsible for the low fledging success of Atlantic Petrels observed on Gough Island in 2000 and 2001. Here I have shown that predation by mice is indeed causing very severe failure rates. All failures at filmed nests were due to mice; predation of chicks by moorhens or failure due to disease or starvation appears to be negligible. This is the first incontrovertible evidence that mice are capable of preying on burrowing petrels. Probable mouse predation on burrowing petrels has been reported from Blue Petrel chicks *Halobaena caerulea* on Marion Island (Fugler et al. 1987), Ashy Storm-Petrel *Oceanodroma homochroa* eggs and chicks on the Farallon islands (Ainley et al. 1990), Grey-backed Storm-Petrel *Garrodia nereis* chicks on Antipodes Island (Burger & Gochfeld 1994) and White-faced Storm-Petrel *Pelagodroma marina* eggs and chicks on Selvagem Grande Island (North Atlantic) (Campos & Granadeiro 1999). However, none of these studies showed conclusively that mice were responsible for the observed failures—they could have been scavenging abandoned eggs or dead/moribund chicks. In light of my findings, the probability that these other researchers (as well as Cuthbert 2004) were correct in assigning failures to mouse predation is strengthened.

The apparent preference for attacking smaller chicks in 2004 is surprising, given that mice in the highlands successfully attack Tristan Albatross *Diomedea dabbenena* chicks (Chapter 3), showing that size is no insurance against attacks. It is possible that the developmental stage of chicks influences decisions about whether or not to attack. Alternatively, bigger chicks may take longer to kill, requiring a greater initial investment by mice. Mice may thus attack the easiest targets first, rather than the biggest meals. These alternatives are not mutually exclusive and both allow for the possibility that mice learn.

The estimates of breeding success for 2004 and 2006 were derived using incomplete datasets. However, there were significant differences between years, so pooling data to estimate success is of little value as it obscures the interesting fact of inter-annual variation. The worst-case breeding success estimate for the whole of the 2004 season is premised on the assumption that failure rates in the *ca* 100 days of chick-rearing after the end of the study were the same as those during September. This is more reasonable than assuming no further mortality, given the results from the 2000, 2001 and 2006 seasons, which all showed chick mortality throughout the study periods (Cuthbert 2004). Nevertheless, assuming no further mortality gives an upper estimate of breeding success of 33% in 2004. The actual breeding success for 2004 thus probably lies somewhere between 7% and 33%. In 2006, the study commenced about a month after peak hatching and ended shortly before fledging, so failure rates for the incubation, early chick-rearing and very late chick-rearing phases had to be estimated based on 2004 data (incubation) and the assumption of constant mortality across the whole chick-rearing phase. Incubation success in 2004 (56%) is virtually identical to that reported in 2001 (57%); it is likely that both studies under-estimated incubation success, due to the infrequent nest-checks and the fact that when failures occurred at hatching but between checks, they were assigned to incubation failures. Nevertheless, for the purposes of the analysis the similarity of these results lends some degree of confidence to the use of 56% incubation success in estimates of breeding success for 2003 and 2006. Further, apportioning failures to incubation or early nestling periods makes no difference to the estimate of annual breeding success. If the lower estimates of breeding success for 2004 and 2006 are accurate, out of ~1.8 million pairs of nesting Atlantic Petrels, approximately 1 million failed during incubation (but note caveat above) and 666 000 chicks died, with only 126 000 chicks fledging per year.

Results from the 2003 season appear more optimistic than all other years studied, because the daily mortality rate over the bulk of the chick-rearing period was much lower than in other years, and differed significantly from the same period in 2006. An estimated success for the entire chick-rearing period of around 82% is at the upper end of the spectrum for petrels (Simons 1984; Cruz & Cruz 1990; Warham 1990; Chastel et al. 1993; Brooke 1995; Keitt et al. 2003; Cuthbert 2004; Cuthbert 2005). This raises the possibility that in some years, predation rates are low, and reproductive output is in the normal range for petrels breeding on predator-free islands. Three key questions arise from this result. First, given that the 2003 data do not cover the whole breeding season, is it possible that there had already been high mortality before the study commenced, so that 2003 wasn't in fact a year of high reproductive output? Second, if predation levels were low and reproductive output was high, how frequent are such years? Third, why did mice not attack large numbers of chicks in 2003, unlike in all other years studied.

While the data are as yet too sparse to comment definitively, there is little cause for optimism for this IUCN Red-listed species. The population-level consequences of predation are likely to be strongly negative. Breeding success estimates for 2004 and 2006 (both *ca* 7%) are extremely low compared to the range of breeding success estimates for *Pterodroma* petrels on predator-free islands, typically 50-80% (Warham 1990). A demographic model developed for this population by Cuthbert (2004) suggests that, even with the most optimistic estimates of some surrogate parameters (such as adult survival), breeding success would have to average >30% for the population to remain stable. It is possible that one of the three years of this study (2003), and one out of five for which we have any data, exceeded this theoretical threshold, whereas 2004 and 2006 appear to have fallen far below. Although both this and the previous study were performed in roughly the same area on Gough, it is unlikely that the mouse-induced mortality is a geographically localised phenomenon, because similar attacks occur in all Tristan Albatross *Diomedea dabbenena* colonies on Gough (Chapter 3) and their range does not overlap with Atlantic Petrels, suggesting instead that attacks are spatially ubiquitous. Nevertheless, there is substantial variation in the incidence of attacks in different albatross sub-colonies both within and between years and the variability in annual Atlantic Petrel breeding success possibly reflects similar processes of predation, although this requires further research.

It is likely that the Atlantic Petrel population on Gough is decreasing. If they do breed still breed on Tristan da Cunha, the impact of predation by black rats *Rattus rattus*, which are aggressive nest predators, is likely to be extreme and the viability of the population (if it still exists) is in serious doubt (Angel & Cooper 2006). Thus Gough probably houses the only viable population of Atlantic Petrels. It is therefore imperative that remedial action is taken to prevent (further?) population decreases as a result of predation of chicks by house mice.

What of the possibility that other factors, such as poor at-sea conditions could explain the failures. I seldom found carcasses, and when I did, they were usually partially consumed. This meant that I couldn't test for the 'health status' of chicks that died. Weighing chicks at intervals shorter than 10-15 days would have facilitated analysis of mouse attacks relative to 'chick health', but this was not done because chicks regurgitated frequently (unlike in 2000/01, Cuthbert 2004). Each regurgitated meal increased the likelihood that my investigations would have an impact on chick survival through under-nourishment. Further, and of possibly greater significance, the presence of regurgitated food in the nest chamber and on down/feathers may have encouraged mice to attack. Cuthbert (2004) found no evidence that chicks were underweight when they died; similarly, I found no evidence of systematic under-feeding or starvation in the study colony in 2004, so the high chick failure rates were not due to abandonment or under-nourishment due to poor foraging conditions for adults. Attacked chicks were apparently all healthy when attacked, whereas five dead or moribund chicks were found in the three seasons, none of which had wounds. Thus mice do not preferentially target weak or sick individuals. They even attacked successfully chicks that were being brooded or attended by parents, showing that parents were unable to defend their chicks. Further, all chick deaths captured on video were the direct result of mouse attacks. On one occasion a study chick was found at the surface being attacked by a moorhen. The recovered chick was very weak, having been attacked by mice the previous night: I assume that the Moorhen was able to carry the chick out of its burrow due to its already weakened condition, and consider mouse attack to be the indirect cause of death (Wanless & Wilson in press). I conclude that most of the unusually high chick mortality in Atlantic Petrel chicks in 2004 and 2006 can be ascribed to mouse attacks.

The rapid, lethal nature of attacks is attested by the video evidence. Also, out of 104 chicks monitored and almost 1400 nest checks in three seasons, only three chicks were found wounded but alive. This result is not surprising, because the mice on Gough are primarily nocturnal (pers. obs.) and all the videoed attacks were initiated at night. It was relatively unusual to even find remains of smaller chicks that had died – they simply disappeared between checks. A second cause of carcasses disappearing from the burrows is scavenging by Gough Moorhens.

Both winter-breeding seabird species that have been studied on Gough, the Tristan Albatross and Atlantic Petrel, sustain severe mouse predation on their chicks. It is probable that chicks of the two remaining winter-breeding, burrowing petrel species which have not been studied on Gough, the Grey Petrel *Procellaria cinerea* and Great-winged Petrel *Pterodroma macroptera* also are attacked by mice.

Table 5. Phenology of procellariiform seabirds of Gough Island, with an estimation of the risk that house mice pose to them. Breeding months are shaded. L = Laying, H = hatching, F = Fledging. Information based on Angel & Cooper (2006).

Common name	Months												Risk factor
	J	F	M	A	M	J	J	A	S	O	N	D	
Tristan Albatross	L		H								F	F	Confirmed
Atlantic Yellow nosed Alb.				F					L		H		Unlikely
Sooty Albatross					F					L		H	Unlikely
Southern Giant-Petrel			F						L		H		Unlikely
Great-winged Petrel						L		H				F	Probable
Atlantic Petrel						L		H				F	Confirmed
Soft-plumaged Petrel	H			F							L		Probable
Kerguelen Petrel		F								L		H	No evidence
Grey Petrel					L		H				F		Probable
Great Shearwater				F						L		H	Confirmed
Little Shearwater		F							L		H		No evidence
Broad-billed Prion								L		H		F	Probable
Grey-backed Storm-Petrel			F?							L		H	No evidence
White-faced Storm-Petrel			F							L		H	No evidence
White-bellied Storm-Petrel	L		H			F							Probable
Common Diving-Petrel		F								L		H	No evidence

The discovery that mice also attack Great Shearwater chicks was surprising for two reasons. First, a study of Great Shearwater breeding biology in 2001 reported high breeding success and no unusual mortality (Cuthbert 2005). Either there is substantial spatial and/or temporal variation in the extent of attacks on Great Shearwater chicks, such that none were detected in 2001, or else attacks are unusual, and the 2004 camera deployment in Great Shearwater burrows was fortuitous. Second, none of the summer-breeding species (Subantarctic Skua, Yellow-nosed Albatross *Thalassarche chlororhynchos* and Sooty Albatross *Phoebetria fusca*) studied to date on Gough Island have been subject to mouse attacks (Cuthbert & Sommer 2004; Angel & Cooper 2006). In Chapter 3 I present evidence that mice successfully attack Tristan Albatross chicks, which weigh up to 8 kg when attacked. Thus size offers no absolute protection against attacks. However, attacks on Tristan

Albatross chicks ended in October, in contrast to attacks on Atlantic Petrels which in 2000, 2001 and 2006 continued until at least November. This discovery raises the possibility that other summer-breeding seabirds are also attacked. Table 5 summarises the phenology of procellariiform seabirds breeding on Gough. If I assume (conservatively) that chicks are safe between December (apparently when attacks on Atlantic Petrels end) and March (before attacks on Tristan Albatrosses begin), and accept the available evidence that chicks of summer-breeding, surface-nesting species are not vulnerable, then the chicks of the following species are at high risk: Great-winged and Grey petrels, because their phenology is virtually identical to that of Atlantic Petrels; Soft-plumaged Petrels *P. mollis* because their phenology is virtually identical to Great Shearwaters, and Broad-billed Prion *Pachyptilla vittata* and White-bellied Storm-Petrel *Fregetta grallaria* because they have chicks in October-November and April-May, respectively.

Directions for future research

Seabirds offer an extraordinarily good food resource for mice, representing multiple meals that are high in proteins and lipids but not packaged in indigestible material such as cellulose or chitin. There appear to be few risks associated with accessing the resource, with the possible exception of aggressive scramble competition with other mice (Chapter 3). Feeding on chicks in burrows provides a dry environment in which predatory skuas cannot access either mice or carcasses. Yet several results are surprising. Two videoed chicks in 2004 were visited by mice, which even attempted to eat spilled food from the down of one chick, yet the chicks were not attacked. Why not, when several attacks were happening simultaneously within 100 m? Why does virtually every single Atlantic Petrel burrow get visited, if not used as a home, by mice, but only some chicks are attacked? Why was there a maximum of two attacks on study chicks in 2003, in opposition to predation rates in the other seasons for which data exist? This result is even more enigmatic when considering the high mouse visit rates at all burrows. Why did attacks on one of the two wounded chicks in 2003 cease before significant damage was inflicted, allowing the chick to survive and fledge? Why did one of three Great Shearwater chicks under observation get attacked in April 2004, when no attacks were recorded from >60 study nests in 2001 (Cuthbert 2005)? There are no obvious answers to these questions. It is clear that we are only starting to understand the patterns and consequences of the remarkable predatory behaviour of the house mice on Gough Island, but are some way from understanding the processes driving those patterns.

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CHAPTER 3

The role of predation by mice in spatio-temporal patterns of Tristan Albatross chick deaths

Abstract

Here I describe the first unequivocal evidence that mice are capable of attacking live, healthy Tristan Albatross *Diomedea dabbenena* chicks, and in so doing are responsible for very low Tristan Albatross breeding success relative to congeners on islands free of introduced predators. I describe spatio-temporal patterns of breeding failure at three levels: whole island, sub colony and individual, and infer processes where strong patterns occur. Overall, inter-annual patterns of breeding success (number of chicks fledged per nesting attempt) were similar (up to 27-29%) in three of four years and averaged 32% for 2001-2006. Despite the relatively constant breeding success, the number of nesting attempts varied annually and total number of failures was significantly related to the total number of attempts per year, for the whole island over the four years (2001 2006) of breeding success data and for the Tafelkop sub-colony with 16 years of data. This was opposite to the expectation that the number of failures would be relatively constant across years, and thus that fewer attempts would result in a higher proportion of failures. At the level of sub-colonies, Gonydale was the only site to experience consistently high annual breeding success (i.e. expected without predation), although predation occurred there. There was little temporal consistency in total failures or breeding success in other sub-colonies and different sites varied in opposite directions between years. The onset of attacks differed by a month between sites and there was little consistency in the numbers of failures per month within or between sites. The Green Hill sub-colony contrasts most strongly with Gonydale in having consistently amongst the lowest breeding success of all sites. However I could find no environmental or biological variables to explain the different predation rates. At the individual level, the site of wounds appeared to be random, with the head, the least likely part of the body to be attacked, having the second-highest frequency of wounds. This and other descriptive data suggest that attacks are not optimal at delivering energetic returns for mice. Nests that failed in a given month were significantly closer to the nearest nest that failed the previous month

than predicted by chance, suggesting a localised effect possibly due to a few predatory individuals. For the mice, analysis of a videoed attack showed that mice attacked more-or-less constantly, with up to 10 mice around the nest at a time and 4-7 mice competing aggressively for access to an open wound. Of mice that participated in attacks, 60% of their time was spent feeding, whereas 32% of all visits to the nest ended in mice leaving the nest having consumed nothing. There was a significant negative relationship between mouse startle reaction-strength and time, and mice returned to the nest sooner after each startle as the attack progressed, suggesting either that mice became more accustomed to chick movements, or were increasingly motivated to feed from the wounds.

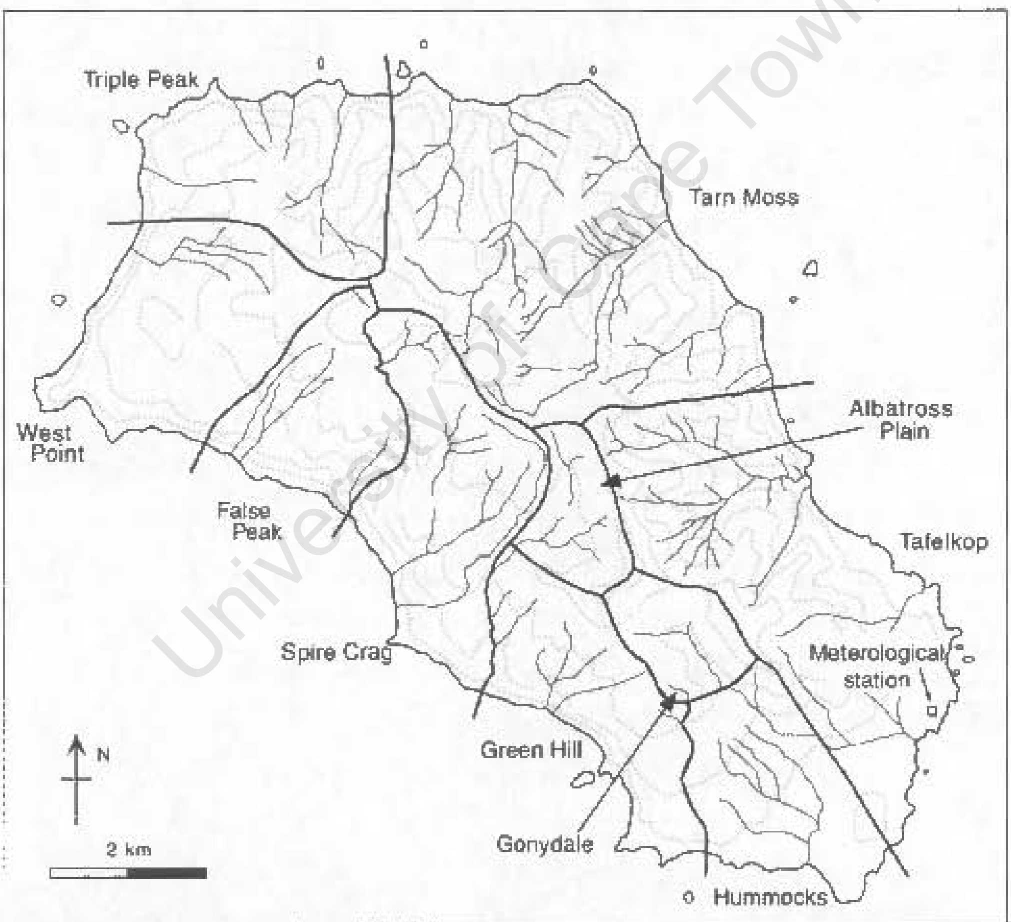

Figure 1. Topographical map of Gough Island showing sub-colonies for breeding Tristan Albatrosses (dark solid lines) superimposed on 200 m contour lines (dotted) and major watercourses (light solid lines).

Introduction

Invasive species frequently show novel and completely unpredictable responses to new ecosystems (Peterson & Vieglais 2001). Nevertheless, it is surprising that major discoveries can still be made about the behaviour of the house mouse after a history of invasion spanning several centuries. House mice are the only alien mammals on Gough, and were introduced there some time before 1888 (Verrill 1895). In 2000/2001, unexpectedly low breeding success and widespread evidence of chick mortality of the Tristan Albatross *Diomedea dabbenena* was reported from Gough Island, and the possibility that mice were responsible was mooted (Cuthbert & Hilton 2004; Cuthbert et al. 2004). This mooted the possibility that, contrary to conventional wisdom, mice could pose a threat to seabirds, and could be significant predators of chicks as large as albatrosses.

In this chapter I describe the nature, timing and extent of mouse attacks on Tristan Albatross chicks. For the albatrosses, I define the role of mice in creating patterns of failure at three levels: the whole island, sub-colony and the individual. At the island level, four years of incubator counts and breeding success estimates are in hand. I use these and long-term data from a small sub-colony to test the hypothesis that lower densities of breeding birds will result in lower breeding success, because proportionally more chicks are attacked. If this hypothesis is correct, the implications for a decreasing Tristan Albatross population (Chapter 4) are profound. Understanding spatio-temporal patterns may shed light on why predation occurs and possibly suggest management options. The former is relevant for predicting possible predatory behaviour in mice on other islands. At the sub-colony level, Cuthbert et al. (2004) showed that there was significant inter-colony variation in chick survival in 2001, a result which merited further investigation. I describe four years of spatio-temporal patterns of chick mortality and consider variables that could explain large differences. At the individual level, a question underlying the presentation of data is why do some chicks survive and others not? I address several questions to understand the value that mice in general, and some mice in particular, might gain from attacking chicks. First, how many mice are involved in an attack? Second, how much competition is there between mice for access to albatross chicks? Third, are some mice better than others at attacking (and so do some mice gain more from attending an attack than others)? These questions are designed to further understanding the evolution of the remarkable predatory behaviour of the mice on Gough.

Methods

Study site and period

Gough Island (40° 21'S, 9° 53'W, *ca* 6400 ha) lies about 3 000 km WSW of South Africa and about 400 km SSE of Tristan da Cunha. It has a wet, cold-temperate climate with strong prevailing westerly winds (Cooper & Ryan 1994). It has an undulating plateau (hereafter referred to as highland) that rises to about 900 m. The SE of the island has an extensive coastal plateau (hereafter referred to as lowland) which rises steeply to the interior. Lowland habitat is dominated by fernbush, characterised by relatively tall, dense vegetation dominated by ferns, sedges and *Phylica arborea* trees. The highland plateau is dominated by wet heath, characterised by stunted vegetation and comprised principally of mosses, grasses and sedges and *Empetrum rubrum*, a low-growing, woody perennial (Wace 1961).

Albatross counts

Tristan Albatrosses breed in the highlands on Gough, mostly above 400 m. Peak laying occurs in January, hatching in March and fledging in November. Gough is divided into discrete counting areas for Tristan Albatross monitoring (Figure 1), with set routes and count methodologies (Ryan et al. 2001). Complete counts of incubating adults (January-March) and large chicks (September) were completed in 2001, 2004 and 2006, following Ryan et al. (2001). Missing values from partial counts in 2005 were imputed (see Chapter 4 for details). Incubator counts are a measure of annual reproductive attempts. Large chick counts are equivalent to the maximum number of fledglings, because early incubation and post-September chick failures missed counts of fledglings (Cuthbert & Sommer 2004) and are implicitly treated as fledgling counts throughout. Breeding success is defined as the percentage of nests that fledged a chick. From 5-9 October 2003, approximately 200 chicks in Tarn Moss, Albatross Plain, Gonydale and Tafelkop were physically examined for wounds. I also examined 378 chicks for wounds from 28-30 April 2004. Time constraints did not permit all chicks in each area to be investigated, but I examined at least some chicks from every sub-colony. The location of wounds was recorded according to gross morphological features (e.g. head, wing, rump, etc.). In 2004, around 300 Tristan Albatross nests (ca 16% of the island total at the start of incubation) from Gonydale, Green Hill, Albatross Plain and Tafelkop sub-colonies were monitored. Chicks were examined for wounds 1-3 times per month from hatching (around March) until the end of September.

A shortcoming of the data in this chapter is the fact that natural (or background) failure rates (of eggs and chicks) cannot be separated from mortality caused by mice or other unnatural/unusual causes *per se*. No attempt is made to compensate for this, but I have implicitly assumed throughout that natural failure rates are roughly constant across areas and years, and are similar to those recorded elsewhere for congenerics breeding on islands free of mammalian predators, typically 25-40% (Weimerskirch & Jouventin 1987; Croxall et al. 1990; Weimerskirch et al. 1997; Elliott & Walker 2005; Walker & Elliott 2005). Thus although inferences are made about the role of mice by comparing breeding success, all the reported figures include some level of natural mortality too. Wherever possible I have used the largest sub-colonies for comparative purposes, to minimise the influence of stochastic variation in natural mortality on the results.

Spatio-temporal patterns of chick mortality

WHOLE ISLAND LEVEL

I expected that the pattern of predation by mice would conform approximately to the dictates of supply and demand. From this expectation, two alternative predictions arise – supply-side drivers and demand-side drivers. The simpler option is that supply dictates predation rates: mice prey on chicks in proportion to their availability, resulting in a significant relationship between total nesting attempts and total failures, and a relatively constant annual breeding success but with a wide range of actual failures per year. The second is that failures are demand-driven: mice require albatross chicks in order to satisfy nutritional requirements that change annually according to fluctuations in mouse densities, availability of alternative resources and/or other environmental factors (e.g. a harsh winter). These other factors are unknown at present, but if they are important the pattern of failure with respect to the total number of attempts should either be random (if these factors vary widely between years) or a relatively constant number (if the environment is relatively predictable and follows the same annual patterns with low variance). A corollary to the latter expectation is that albatrosses meet a significant proportion of the energetic demands of mice. Total failures were regressed against incubator counts for the whole island for 2001, 2004-2006 and from the Tafelkop study colony, from 1989-2006; no incubator counts were done in 1997 or 2003 and these years were excluded.

SUB-COLONY LEVEL

Using data from study nests in 2004, I performed a Kaplan-Meier survival function analysis (which calculates the cumulative proportion of nests surviving over time) of chick survival rates in Albatross Plain, Green Hill, Gonydale and Tafelkop, and tested for differences in survival over time between areas using a log-rank test (Johnson 1979; Nur et al. 2004).

I investigated the importance of environmental variables in explaining the differing extent of mouse attacks in 2004 at Green Hill and Gonydale. Plant community composition was compared on 5 June 2004, to test for gross differences in food availability for mice. At each location I ran a 200 m baseline roughly perpendicular to the contours and spanning the bulk of the altitudinal range of Tristan Albatross nests in each area. The baselines were on well-drained, west-facing slopes. The starting point for each baseline was chosen arbitrarily, somewhere near the lower end of a slope. Ten transects were laid out at 20 m intervals at right angles to the baseline. Each transect was 20 m long and sampling was done in 1 m^2 quadrats at 2 m intervals. Sampling effort amounted to 100×1 m^2 plots at each site. In each plot I estimated percentage cover of mosses and ferns (dominant groups but not food resources), grasses, sedges and other angiosperms. For the latter group I estimated separately the percentage cover of the berry-bearing *Empetrum rubrum* and *Nertera depressa,* because these are potentially important food species for mice (Jones et al. 2003). Differences in mean cover between the two sites were tested using a Kruskall-Wallis ANOVA.

INDIVIDUAL LEVEL

Schematic maps of relative nest positions and inter-nest distances were made for study nests at Green Hill. At each visit, nests were classed as either active, failed since the last check, or failed prior to the previous check. Status changes are displayed at monthly intervals. I tested whether the probability of a nest failure at Green Hill was random with respect to distance to nearest failed nest. For each chick I measured the distance to the nearest nest that had failed at the previous check and recorded the status of the nest (active or failed) and tested for differences between the groups with a t-test.

Analysis of video attack

I found a severely wounded Tristan Albatross chick at Green Hill on 7 May 2004. It had a large, fresh wound on its right upper wing, parts of which had been eaten down to the bone. There was a second large, bloody wound on its right rump, between the cloaca and right leg (Figure 9). Examination of subsequent mouse behaviour suggests that a third wound was located under the right wing. I used a hand-held Panasonic NV-DS30 digital video camera and a custom-made infra-red lamp to record mouse-chick interactions. Filming started at 19h00 on 7 May, before complete darkness, and ended at 21h45 pm, when rain prevented further recording. Data collection was interrupted by rain and the chick's frequent shuffling of position, which obscured the wounds and mouse behaviour. Slow-motion replay was used to quantify chick and mouse behaviour. A mouse was defined as attending the attack/nest if it came to the rim of the nest cup, but attendance was recorded from the time it could be detected on camera. Although mice were not individually identifiable, individuals could be followed for periods from 2-135 seconds.

I quantified the proportion of time that individual mice at the nest spent attacking. When a mouse approached an open wound and appeared to feed from it, I defined this activity as an attack. Time spent feeding was quantified; all other activities (washing, interacting with other mice, investigating the chick, etc.) were treated as 'non-attacking time' and lumped. Forty-nine time budgets were constructed for mice (the actual number of mice involved is unknown) that could be accurately observed around the bird, including mice that appeared to do no more than arrive and then depart the nest immediately. Individual mice were followed under continuous observation for as long as possible and the proportion of time at the nest that was spent feeding from wounds was quantified. However, because individual mice could not be repeatedly identified, all analyses may be vulnerable to some level of pseudoreplication, and caution is urged in interpreting the results. I compared the mean time that 1, 2, 3 and >3 mice spent feeding per 1 minute period, and tested for differences using a one-way ANOVA. I also measured the intensity of attacks by summing the total time all mice spent feeding in each 1 minute period and dividing that by the maximum number of mice feeding per period, and correlated this with time (in minutes, from the start of the first attack).

I counted the frequency and scored the intensity of the chick's behavioural responses to being attacked, referred to as reactions, and related these reactions to the relative intensity of the attack over the same time period. I divided the recording into 1 minute periods in which accurate budgets of attack time at the main wound (on the rump) could be constructed. The sum of all mouse attack times in each of the 36 1 minute periods was used as a measure of the intensity of the attack during that period. Attack intensity was correlated with time to investigate the temporal pattern of attack intensity. I then scored the chick's reactions over the same 1 minute periods. A reaction is defined as a movement by the bird that it was unlikely to have made if mice had not been attacking it. The summed scores per minute gave an index of reaction intensity and these were plotted against attack intensity for the same period. Reaction intensity was scored from 1 to 4:

Slight movement (e.g. twitching muscles) = 1

Definite movement of the affected area (e.g. shuffling leg or wing) = 2

Sits upright = 3

Shakes vigorously or shuffles = 4.

For each chick reaction, the startle response of each mouse was scored as follows:

No startle = 1

Reacts slightly but remains at/near wound = 2

Moves away from chick but remains at nest = 3

Moves away from nest = 4

Runs or jumps as if startled and leaves nest = 5

Data were collected from 19h25–20h00 pm and 20h35–21h10 pm (hereafter referred to as 'Early' and 'Late' periods, respectively). Startle responses in the two periods were correlated separately with time to look for temporal trends in the strength of startle responses. I then calculated the mean startle score per chick reaction and correlated this with chick reaction, to see if the strength of startle reactions was related to the strength of the chick's movements.

To give an indication of the degree of competition at the wound during a period of acute competition, I counted the number of mice that were in physical contact with each other. Counts were made at 5 second intervals for 70 seconds. I also counted the frequency with which mice aggressively replaced each other at wounds in 10-second intervals over a 130 second period.

Results

The key result for this chapter and the thesis is that mice are responsible for widespread chick mortality on Gough Island. I checked the Green Hill sub-colony on 20 April 2004 and recorded eight fresh Tristan Albatross chick carcasses and 10 wounded chicks (five of which were still being brooded or guarded by adults). The wounds on brooded or guarded chicks could not have derived from attacks by predatory seabirds and disease was an improbable cause of the lesions, as the chicks were otherwise asymptomatic (no half-closed nictitating eyelids, drooping wings or hanging heads). The only plausible explanation was that the wounds were the result of attacks by mice, leading to the obvious conclusion that the recent carcasses were the result of fatal attacks. A round-island check of 375 chicks on 28-30 April revealed fresh carcasses and/or wounded chicks from all sub-colonies except Gonydale and Hummocks, confirming that mouse attacks were happening across the island. Video footage of a wounded chick at Green Hill in May and observations of mice at a wounded chick in Gonydale in August confirmed that mice were attacking and ultimately killing live, healthy Tristan Albatross chicks.

Spatio-temporal patterns of chick mortality

WHOLE ISLAND LEVEL

Inter-annual breeding success was relatively constant in 2001, 2004 and 2005 (all 27-29%). The year with highest breeding success (2006, *ca* 45%) is also the year with the fewest nesting attempts (Table 1). Figure 2 shows regressions of total failures against total incubating pairs were significantly positive for both the whole-island and for the 16-year data-set from Tafelkop (adjusted R^2=0.968, p=0.011 and adjusted R^2=0.618, p<0.001, respectively).

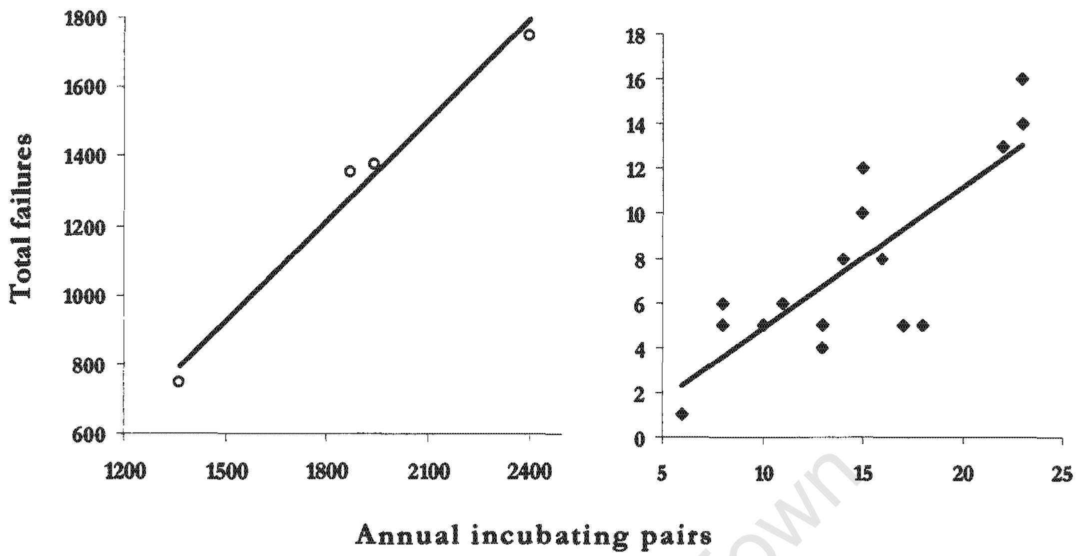

Figure 2. Regressions of incubation pairs with total nest failures of Tristan Albatrosses from 2001 and 2004-2006 for the whole island (○), and from 1989-2006 (n=16 years) for the Tafelkop sub-colony (◆).

SUB-COLONY LEVEL

Breeding success was very variable among sub-colonies both within and between years (Table 1). Only Gonydale showed a relatively consistent, high breeding success. Tafelkop was counted on 29 August 2004, and actual fledging success may have been lower than reported, especially as one of the birds counted in August had open wounds from a recent mouse attack, and fatal attacks were initiated in other areas after this date. Examination of breeding success alone masks considerable variation in the actual number of failures between years. For example, breeding success in Albatross Plain was 9% lower in 2004 than in 2001 but there were only six more failures in 2004. Also, breeding success in West Point in 2004 and 2006 was similar (28% vs 33%) but there were 201 fewer failures in 2006. Although whole-island breeding success is closely correlated with the number of incubating pairs, these data average out inter-area differences and there is little inter-annual consistency in absolute mortality or breeding success between sites.

Table 1. Annual counts of incubating pairs (IP), minimum number of failures (F) and % breeding success (BS) of Tristan Albatrosses on Gough Island. Imputed values for missing counts are given in parenthesis (see Chapter 4).

Area	**2001**			**2004**			**2005**			**2006**		
	IP	F	BS	IP	F	BS	IP	F	BS	IP	F	BS
Albatross Plain	325	236	27	294	242	18	283	153	46	213	55	74
False Peak	129	94	27	74	54	27	(90)	(42)	47	59	26	56
Gonydale	125	40	68	154	43	72	116	17	85	145	71	51
Green Hill	310	241	22	164	131	20	(238)	(178)	25	(135)	(95)	30
Hummocks	51	23	55	45	10	78	(47)	(37)	21	(32)	(7)	78
Spire Crag	338	210	38	210	175	17	(252)	(181)	28	187	134	28
Tarn Moss	35	22	37	45	29	36	(42)	(10)	76	41	10	76
Tafelkop	16	8	50	23	16	30	17	5	71	15	10	33
Triple Peak	153	126	18	166	154	7	130	109	16	96	40	58
West Point	918	744	19	694	499	28	724	639	12	443	298	33
Total	**2400**	**1744**	**27.3**	**1869**	**1353**	**27.6**	**(1939)**	**(1389)**	**29.0**	**1366**	**746**	**45.4**

Summary statistics show that variation in breeding success from 2001-2006 was high in most sub-colonies (Table 2). Annual breeding success was consistently <40% at Green Hill, Spire Crag and West Point, and Gonydale was the only site with breeding success consistently >50%. Green Hill and Gonydale had the lowest coefficient of variation (CV), a result that suggests the differences between these areas are relatively consistent. Sub-colonies averaging <50 pairs/year had high variability in annual breeding success, although Albatross Plain, with the second-highest mean incubator count, had the highest overall variability in breeding success.

Table 2. Sub-colony size and summary statistics on breeding success for Tristan Albatrosses on Gough Island in 2001, 2004-2006.

	Mean	Maximum breeding success (%)		
Sub-colony	incubating pairs	Mean (SD)	Range	CV
Albatross Plain	278.8	41.3 (24.9)	74-18	1.20
False Peak	88.0	39.2 (14.5)	56-27	0.74
Gonydale	135.0	69.1 (14.1)	85-51	0.41
Green Hill	210.3	24.7 (4.9)	31-20	0.40
Hummocks	45.3	54.4 (23.4)	78-22	0.86
Spire Crag	246.8	27.8 (8.7)	38-17	0.62
Tafelkop	17.8	46.1 (18.5)	71-30	0.80
Tarn Moss	40.8	56.1 (22.8)	76-36	0.81
Triple Peak	136.3	24.8 (22.8)	58-7	1.84
West Point	694.8	22.9 (9.4)	33-12	0.82

Breeding success and incubator and chick counts for each year (2001, 2004-2006) were plotted separately for Gonydale, Albatross Plain, West Point and Triple Peak. These sites were chosen because actual (rather than imputed) count data exist for all years and the mean number of nests in each area is >100 annually. There is relatively little correlation between the number of breeding attempts and breeding success within a site across years (Figure 3). However, a general pattern in West Point, Albatross Plain and Triple Peak, but not Gonydale, is the trend of fewer breeding attempts over time.

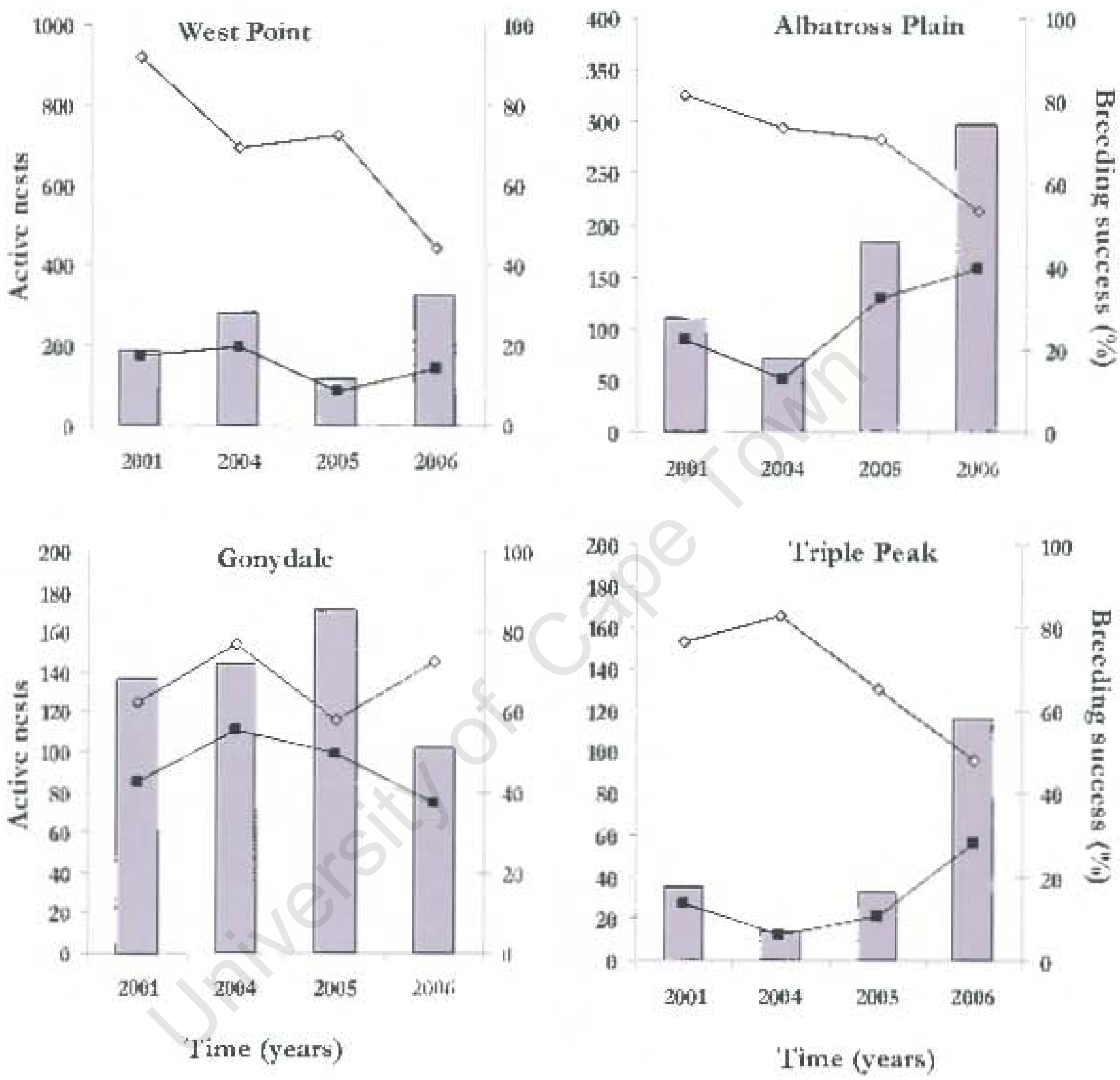

Figure 3. Numbers of active nests of Tristan Albatrosses at the incubation (◇) and fledging (■) stages from four sub-colonies on Gough Island. Vertical bars denote breeding success. Note the different scales on the primary ordinates.

The Kaplan-Meier survival function showed that there were significant differences (Log-rank test, χ^2_3=63.9, p<0.001) in the temporal pattern of chick mortality rates in the four sub-colonies that were regularly monitored in 2004 (Figure 4). Gonydale is clearly the exception, as it had virtually no failures (and none attributable to mouse attacks) between April and mid-June. Although the slight increase in failure rate towards the end of the season was due largely/entirely, to mice, the final breeding success for the whole sub-colony was relatively high (Table 3). The patterns of failure at Green Hill, Albatross Plain and Tafelkop are characterised by a sudden onset of attacks, which were sustained at a spatially and temporally similar rate. The slowed rate of failure at Green Hill after July was probably due to there being large areas with no chicks left—only five chicks survived out of an original 43 nests (Table 3). Although the general pattern of failure is similar in the four areas, the timing of the onset was not, with the first chick failures in the subset of chicks being studied in Albatross Plain being recorded in May, versus in April for Green Hill and Tafelkop. However, this result should be viewed with caution, because on 28 April I found fresh carcasses and one wounded chick out of 30 chicks checked in Albatross Plain, although they were not near the study nests. When the actual numbers of failures per month are examined (Figure 5), however, the trends in the different areas are quite divergent. Green Hill experienced a very high number of failures initially and, for reasons explained above, was the only area that did not show an increase in the numbers of failures in August/September.

There were no failures during incubation in Tafelkop, and although Table 3 does not show it, I found no abandoned nests amongst the study nests in Albatross Plain, indicating zero failures during incubation there too. Thus the bulk of failures in Albatross Plain, Green Hill and Tafelkop occurred during the chick stage.

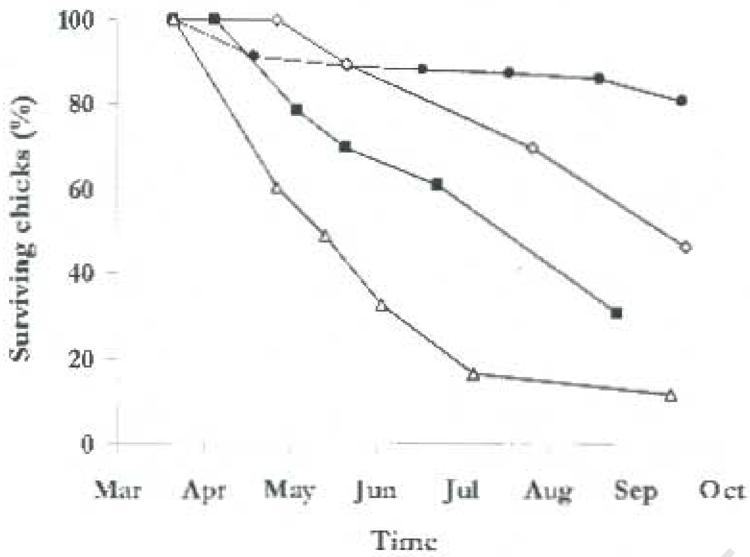

Figure 4. Kaplan-Meier survival probabilities for Tristan Albatross chicks over time. Data are from entire sub-colonies of Gonydale (●) and Tafelkop (■) and sub-samples of Green Hill (△) and Albatross Plain (◇).

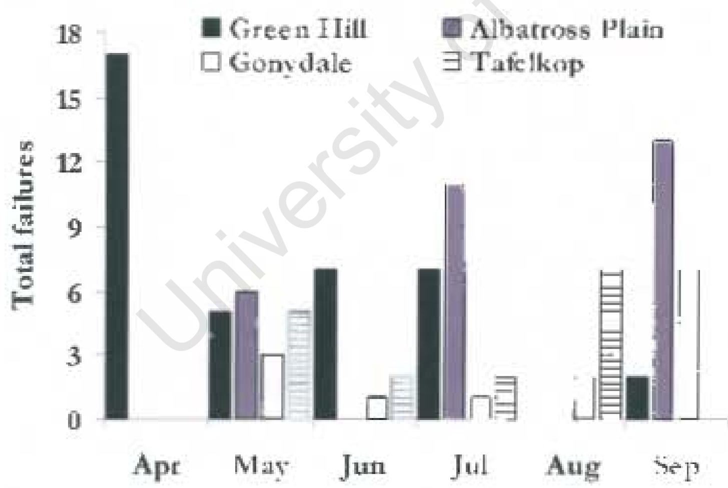

Figure 5. Temporal patterns of numbers of Tristan Albatross chick failures from four sub-colonies on Gough Island in 2004. Data are from entire sub-colonies of Gonydale and Tafelkop and sub-samples of Green Hill and Albatross Plain.

Table 3. Tristan Albatross breeding success data from four sub-colonies in 2004 on Gough Island. Hatching success is not shown for Albatross Plain or Green Hill because only a portion of the nests were individually monitored, from chick stage onwards. Breeding success is for the entire sub-colony.

	Incubator count	Chicks monitored	Fledglings	Hatching success	Fledging success	Breeding success
Gonydale	154	134	111	87.0	82.8	72.1
Albatross Plain	294	56	26	-	46.4	18.4
Green Hill	164	43	5	-	11.6	20.1
Tafelkop	23	23	7	100	30.4	30.4

The differences in relative cover of the major plant groups or significant food species between Green Hill and Gonydale were remarkably minor (Figure 6). Of the plants that produce macroscopic, edible seeds (grasses, sedges and 'other angiosperms') and fruits, the maximum difference in relative cover between sites was 1.1%. The frequency of occurrence (percentage of plots in which each category of plant occurred) gives an indication of spatial heterogeneity. This measure matched fairly closely the relative abundance, meaning that few transects lacked any one category of plant. The only significant differences between Green Hill and Gonydale were in relative abundances of *E. rubrum* and 'other' angiosperms ($H_{(1,200)}$=4.35, p=0.037 and $H_{(1,200)}$=30.82, p<0.001, respectively). In both cases, but particularly for *E. rubrum*, the difference was largely due to the differences in heterogeneity of the distributions, with *E. rubrum* being more clumped (occurring in fewer plots) at Green Hill than in Gonydale.

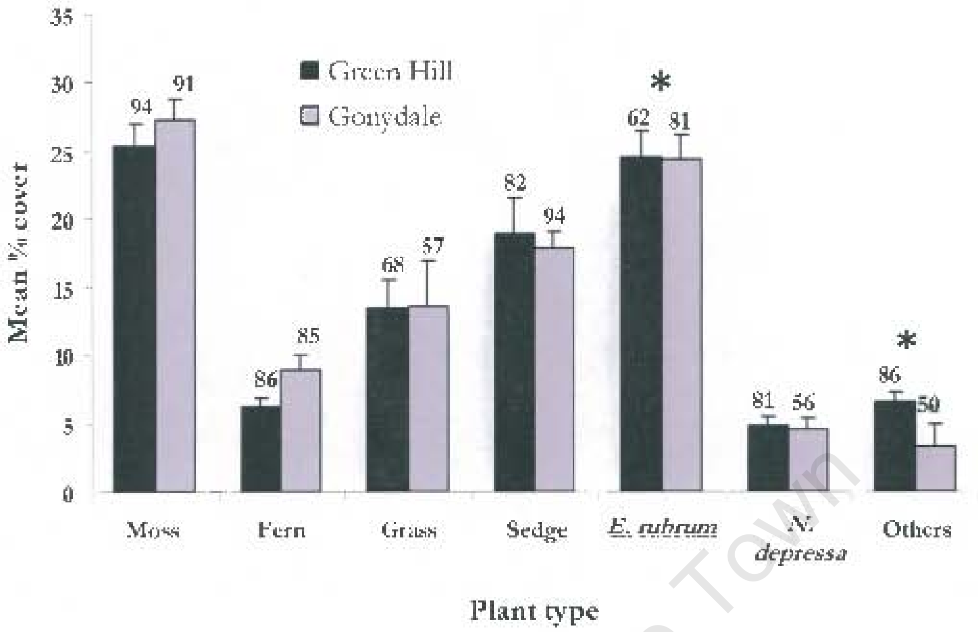

Figure 6. Relative abundances of major plant groups/species at Green Hill and Gonydale sub-colonies. Percentage cover of each category was estimated in 1 m^2 plots (n=100 per area) and the mean calculated for each area. Error bars denote SE, data labels denote percentage of plots in which a category occurred and * denotes significant differences between sites.

INDIVIDUAL LEVEL

The frequency of 38 observed wound sites on 30 chicks is shown in Figure 7. I expected that the parts of chicks most accessible to mice (such as the rump and undersides) would be targeted most frequently, and this was the case. However, the most unlikely area of a chick to be targeted—the head—was the second most frequently wounded area; the category 'other' included throat/neck, breast, under-wing and feet. One chick was not included in Figure 7, because it was discovered with a large number of individual bite marks all over its body. Besides this individual, two chicks were found with patches of down removed from their bodies but without visible wounds. Six individuals recovered from their wounds, although four of these died subsequently.

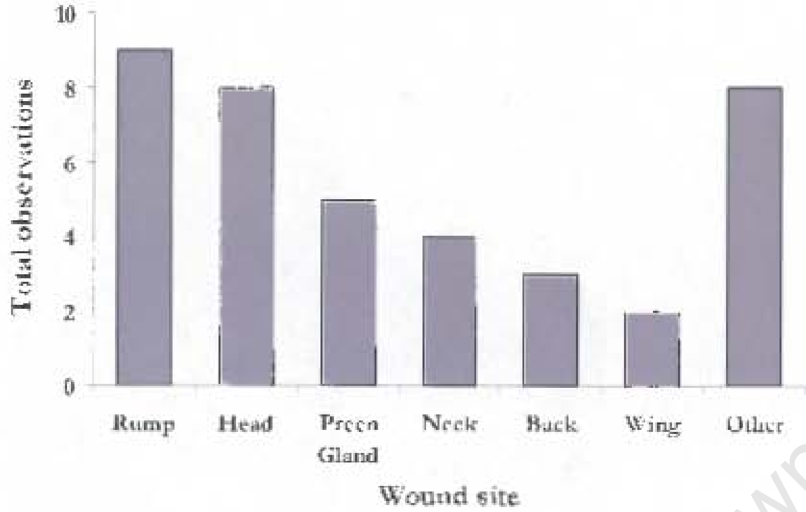

Figure 7. Frequency of wounds (n=38) on different body-parts of albatross chicks (n=30 chicks). Chicks with multiple wound sites contributed to multiple categories.

The starting date of attacks was variable between sub-colonies in 2004, with the earliest attacks recorded on chicks (many still being brooded) at Green Hill on 20 April; several carcasses were observed at this check, suggesting that attacks had commenced earlier (possibly as much as 7-10 days). Only Gonydale had no definite records of wounded chicks by 30 April; the first record of a mouse attack there was on 20 June. Examination of large chicks in October 2003 suggested that attacks had ceased by then: four wounded chicks were discovered on 7-9 October, but all the wounds were scabbed and healing and ultimately the wounded chicks all fledged. The latest date for a fresh carcass is 21 September (found in 2006). Although some inter-annual variability in the seasonal timing of the cessation of attacks is expected, the fact that only healing wounds were found in October 2003 suggests that there is a seasonal or chick age limit beyond which attacks stop.

Only one dead Tristan Albatross chick was found unwounded. A second chick was discovered in a weakened state on 8 July: it didn't regurgitate oil when handled or respond aggressively to me. However, it died between 29 July and 17 September. These observations suggest that, as for the lowlands (Chapter 2), mice do not preferentially select weak or moribund chicks to attack. The majority of chicks that died were not found wounded first; they either disappeared or were reduced to stripped carcasses between checks. However, 19 chicks in the study areas were found alive but wounded. Of these, 13 (68%) had died when next checked, four died later and two fledged.

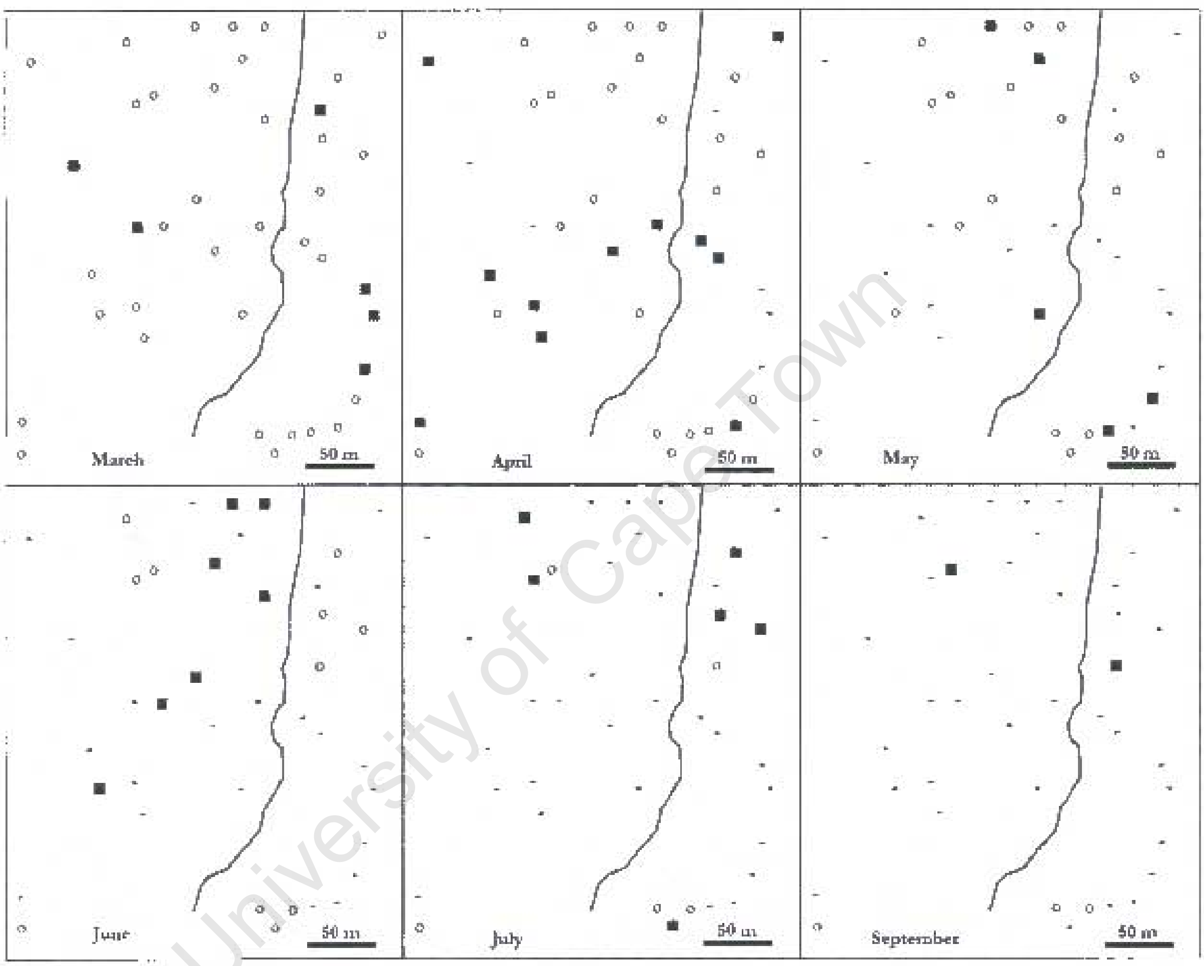

Figure 8. Spatio temporal patterns of chick deaths at Green Hill (35 nests). **o** = active nests, ■ = failed since last check and - = failed before last check. Solid lines indicate water-courses (possible barriers to significant mouse movement). Failures in March were not due to mice. Schematic not to scale, but distance bars indicate approximate scale.

Proximity of nests to others that failed was a strong predictor of failure probability: nests that failed in a given month were significantly closer to the nearest nest that failed the previous month than predicted by chance (T_{30}=2.9, p<0.002). The widespread incidence of attacks is best illustrated in the Green Hill colony in which only three of the 35 study nests depicted in Figure 8 did not fail. This implies that nests in high density areas (i.e. in close proximity to several other nests) are no more likely to be attacked than nests that are at low densities.

Analysis of video attacks

MOUSE BEHAVIOUR

Mouse attacks on albatross chicks appear to be exclusively nocturnal, in keeping with the primarily nocturnal habits of the house mouse (pers. obs.). At the filmed attack, the first mouse appeared at the nest at 19h13 (sunset was at 17h38) and within three minutes it began to attack an existing wound. By 19h32 there were at least five mice present. Attacks from that point onward occurred almost continuously until videoing ended, with only brief intermissions caused by the bird's movements scaring mice from the area. Mice were constantly approaching the nest and leaving again, often without even touching the albatross chick or without attacking it. The maximum number of mice recorded at the nest at any one time was 10 individuals (Figure 9A). Close-up footage at the wound showed mice apparently licking blood-soaked feathers around the wound (Figure 9B). Other footage showed a mouse repeatedly inserting its head through a hole into the body cavity and biting and pulling at internal organs that were clearly visible through the wound.


A


B

Figure 9. Images captured from infra-red video recording showing 10 house mice attacking a Tristan Albatross chick (A), and mice feeding at a hole eaten through the rump of the chick (B). The chick was dead the following morning.

The frequency distribution of the proportion of time at the nest that was actually spent attacking is tri modal, with many mice doing no attacking, most doing some attacking and some doing nothing but attacking (Figure 10). Caution is urged in interpreting these data, as the level of independence of each observation is unknown because some mice contributed several observations to the data-set. However, out of 49 mouse time-budgets at the nest, cumulatively totalling almost 2000 'mouse-seconds', 16 observations (32% of the total and cumulatively 215 seconds) were of mice that ate nothing and then left the nest (Figure 10). Nevertheless they seemed to be very interested in the chick, with some investigating it at length, but either they failed to find the existing wounds or they decided not to compete and did not open up any new wounds. The mean proportion of time mice spent at the nest actually eating was 41%. If the mice that ate nothing are excluded, however, the mean increases to 61%. Several mice were observed attacking uninterrupted for more than 60 seconds.

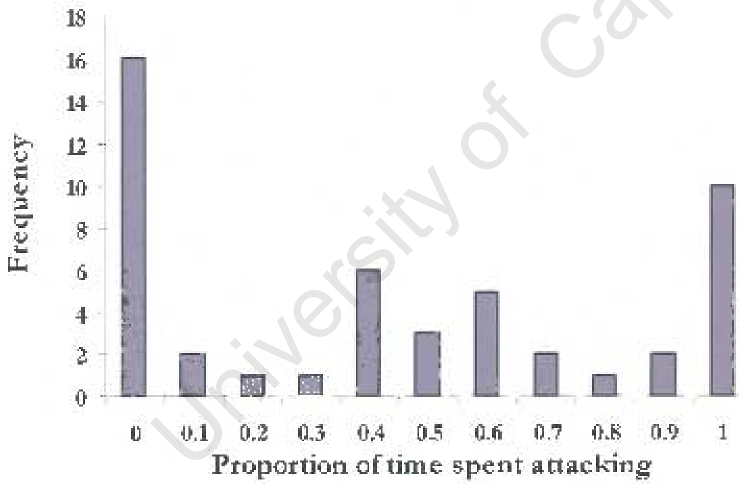

Figure 10. Frequency distribution showing proportion of total observation time that mice spent attacking a wounded Tristan Albatross chick.

The startle responses of mice, ranked on a scale of 1 (no response) to 5 (fleeing from the nest) showed that mice differed in their individual responses to chick movements. In *ca* 24% of observations mice showed no startle response at all. They only stopped feeding when they were dislodged by the chick's movements or displaced by other mice. The mean score for startle response in the early period was 3.4, versus 2.2 for the late period. A partial correlation of mouse startle strength with time (in minutes from the start of attacks) which controlled for the chick movement (scaled 1-4) that caused mice to startle, showed there was a significant negative relationship ($R=-0.42$, $p<0.001$, $n=95$ observations), suggesting that mice became accustomed to the chick's movements. Figure 11 shows that startle responses were positively correlated with the strength of chick reactions, but the differences were not significant ($R^2=0.683$, $p=0.476$, $n=95$ observations). Thus although the mean startle response diminished over time, the range did not. There was, however, a significant decrease over time in the average time that it took for the first mouse to return to the wound after each chick movement. During the early period the mean return time was 12.6 seconds ($n=8$ events) versus 2.1 seconds ($n=22$) in the late period (Mann-Whitney U, adjusted $Z=2.0$, $p=0.045$). Thus early in the evening, mice startled easily, strongly and took longer to return, but this response decreased substantially over time.

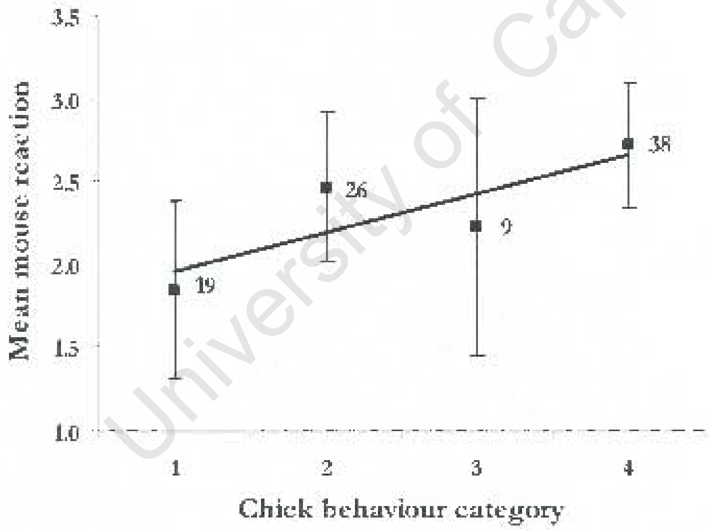

Figure 11. Correlation of chick behaviour (in reaction to being attacked) and corresponding startle response of mice to the chick movement.

At peak times there were 4-7 mice competing for access to a single wound. Aggressive interactions (where one mouse forced another away from the wound) occurred on average 2.9 times per 10 seconds (max = 7, min = 0). Although there were probably fewer than 10 individuals competing during this time, the rapid turnover gives an indication both of the degree of competition as well as the determination of the mice. As the number of mice feeding increased, up to three mice, so the mean proportion of the time that each mouse spent feeding increased (Figure 12): mice attacked with greater intensity when others were also doing so. However, when more than three mice were feeding simultaneously, the proportion of time spent feeding by individual mice decreased. The effect of increasing numbers of mice on mean feeding time per mouse approached significance ($F_{3,32}$=2.76, p=0.059), but power was hampered by small sample sizes. Figure 13A shows that attack intensity was positively correlated with time (R^2=0.63, p<0.001, n=36 1 minute observations).

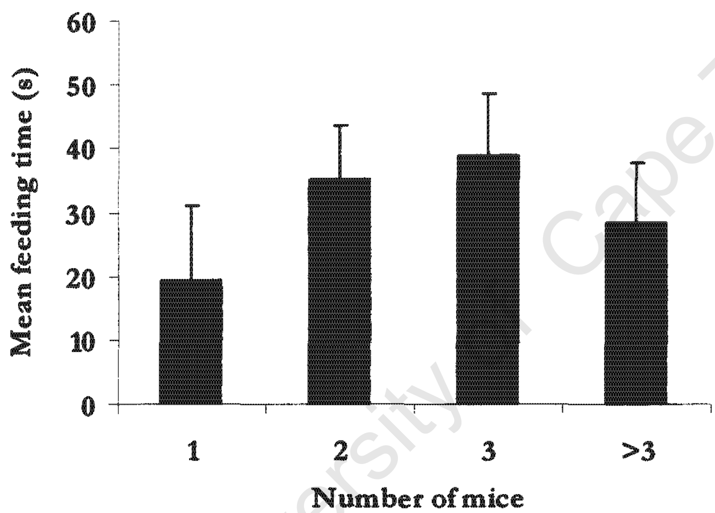

Figure 12. Mean duration (in seconds, per mouse) of feeding by mice at a single wound on a Tristan Albatross chick during 36 1 minute periods. Error bars denote 95% CI.

CHICK BEHAVIOUR

The response of the filmed chick to a fatal attack was remarkably minimal. In essence, it sat on its nest and occasionally made soft vocalisations, shuffled, shook or otherwise moved its body but for the most part appeared impassive, allowing the mice to consume its internal organs at will (Figure 9). It appeared completely unable to see the mice and only twice snapped at (but missed) mice that touched its bill; on >10 other occasions mice were observed touching its bill without the chick reacting significantly. Out of 36 discrete, 1 minute observations when attacks were underway, the chick did not react at all in 10 of these and in 13 observations reacted only once. The chick's reaction to being attacked showed no temporal trend (Figure 13B; R=-0.001), despite the fact that the attacks increased in intensity over the same period (Figure 13A). Only once throughout the entire filming did the chick appear to deliberately dislodge a mouse. This mouse was eating from the wound on its wing, and it remained *in situ* despite several mild shakes by the chick. It was only removed when the chick sat upright and shook its wings quite vigorously. The chick was dead and its carcass stripped clean (by scavenging Subantarctic Skuas *Catharacta antarctica* and Giant-Petrels *Macronectes* spp.) the following morning.

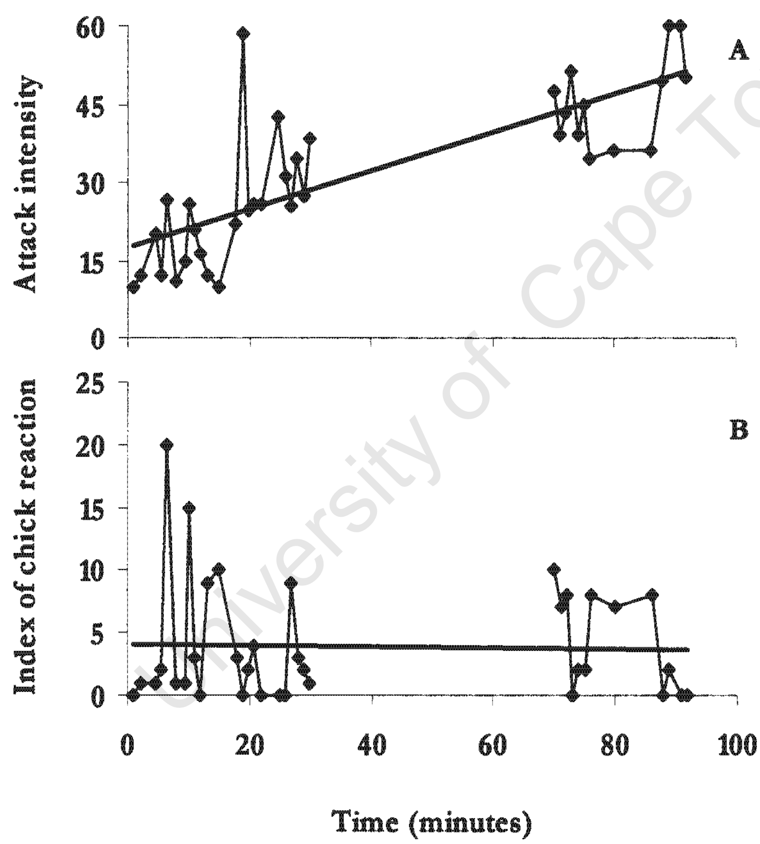

Figure 13. Temporal behavioural patterns during an attack by mice on a Tristan Albatross chick. Attack intensity is the total time all mice spent attacking the chick (during 36 × 1 minute periods) divided by the maximum number of mice feeding from a single wound per period (A). Index of chick reaction is the sum of the behavioural responses of the chick

(scored 1-4) to being attacked per 1 minute period (B). Time is in minutes from when attacks began, starting at 19h16.

Discussion

Mice attacked and killed healthy Tristan Albatross chicks on Gough Island in 2004. How can we be certain that they are responsible for the widespread reproductive failures observed from 2001-2006? First, aside from exceptionally high failure rates on Gough, the timing of failures (Table 3), which was heavily biased towards the chick stage in all years, is unprecedented among *Diomedea* albatrosses, which fail mostly in the incubation or early chick stages (Croxall et al. 1990; Weimerskirch 1992). Thus something very unusual was happening on Gough. Second, chicks with wounds from mouse attacks were found in all sub-colonies. Third, mouse attacks were directly observed, 68% of wounded chicks in study areas (13 of 17) had died at the next check, and ultimately only two wounded chicks survived. Fourth, there was no evidence of any other cause of systematic chick mortality. Chicks with otherwise asymptomatic for disease (no drooping wings, hanging heads or half-closed nictitating membranes, Weimerskirch 2004) and only one chick appeared to be weak from starvation. Exactly 100 chicks of the 256 nests that were monitored closely died: in every case for which there was any evidence of the cause of death (n=13), mice were the only discernable contributing factor. Last, attacks on burrowing petrels (Chapter 2) are almost identical to those filmed and observed on Tristan Albatross chicks, and continuous sequences of video at multiple petrel nests show that mouse attacks are the direct cause of chick deaths. It is thus with confidence that I ascribe most of the unusual chick mortality in the Tristan Albatrosses (in all years in which their breeding success has been studied) to mouse attacks.

A standard explanation for the vulnerability of island birds to attacks from novel predators is that island species lack appropriate behavioural responses (Kepler 1967; Atkinson 1985). The video evidence supports this, as does the widespread and frequent nature of the attacks. The videoed chick appeared to be almost completely night-blind and ineffectual at fending off attacking mice. Additionally, from the onset of attacks on albatross chicks it often took several days for them to die, during which time mice would have fed repeatedly on them, sometimes opening multiple wounds. This is reminiscent of parasitism rather than predation, analogous to finches in Galapagos pecking at tail feathers of Booby *Sula* sp. chicks and drinking their blood (Grant 1986), although in that case the chick seldom dies as a consequence.

Spatio-temporal patterns of chick mortality

Whole-island counts and long-term data from the Tafelkop colony show that the number of incubating pairs has a strong positive effect on the number of failures. This result lends support to the hypothesis that mice depredate chicks according to their relative abundance and does not support the hypothesis that other factor(s), such as annual fluctuations in numbers of mice in winter, or availability of alternative food resources for mice during winter, contribute significantly to the observed patterns. Further, this result means that albatrosses do not necessarily constitute an important part of mouse diets. This latter point is taken forward in Chapter 6.

At the scale of the sub-colony, Gonydale is clearly different to other areas. Breeding success there averaged 70.2±7.8% over five years (1979-2001), consistently within the range expected without mouse predation (Cuthbert et al. 2004). This broad pattern continued, although with higher variability, up to 2006. In contrast to this are all other sub-colonies, which have experienced low breeding success indicative of significant mouse predation in some or all years from 2001-2006 (Table 1,2). The strongest contrast to Gonydale breeding success was at Green Hill, which has experienced amongst the most consistently low breeding success of all sub-colonies (Table 1). Why is there such strong contrast between adjacent sub-colonies? They are contiguous and the sites examined within each area have almost identical orientation, slope, aspect and altitude. Annually they have similar starting densities of nesting albatrosses. A stable isotope study of marine nitrogen input to the two areas (reported in more detail in Chapter 5) showed no significant differences. This confirms that at a landscape level there are no systematic, long-term differences in the amount of seabird-derived nitrogen, and thus no differences in mean densities of nesting seabirds of all species, between Green Hill and Gonydale. The similarity in plant community composition between Green Hill and Gonydale (Figure 6) is not especially surprising, as the sites were chosen to minimise environmental differences and maximise climatic similarity. Crucially, mouse densities were similar between these sites (see Chapter 6). Thus the base of the food chain (plant composition) is the same, micro-climatic differences are unlikely to drive big differences in plant productivity, availability of seabirds appears to be broadly similar and mice occur at very similar densities. The environmental variables considered do not explain the differences in breeding success, yet in all years mice inflicted huge mortality on the Green Hill chicks, whereas in Gonydale mouse predation barely affected breeding success.

The absolute number of failures varied substantially between years and between sub-colonies. Although the patterns conformed broadly to the predictions based on the number of incubating pairs, individual sub-colonies did not vary systematically. Why did the number of failures in some sub-colonies decrease relative to the previous year, and increase in others? Consider, for example, the apparently random changes in the total failures for each sub-colony between 2004 and 2005 (Table 1). It is probable that variable rates of 'natural'/background mortality contribute to the patterns of absolute numbers of failures and breeding success. However, the role of variable predation rates, and what drives those to vary, must also be considered a probable driving factor. This is most apparent in areas such as West Point and Albatross Plain, with large (>100) numbers of incubating pairs annually (that will buffer the impact of background mortality), in which the number of failures varies widely between years.

Mice are widely recognised as being highly adaptive and capable of existing in an impressive diversity of habitats around the world (Bronson 1979; Pye 1993). However they are generally not aggressive predators of other vertebrates. On Subantarctic islands, including Gough Island, their diet consists largely of plant and invertebrate matter (Le Roux et al. 2002; Smith et al. 2002; Jones et al. 2003; Chapter 1). On Gough, several features of the way in which mice attack albatross chicks suggest that the predatory behaviour is not an efficient foraging behaviour for all the mice attending a wounded chick, i.e. it could be done with less effort and yield greater returns. First, mice get only a small benefit from albatross chicks, relative to the nutritional content of a chick. Although many mice may get one or more meals, it is highly probable that skuas and giant-petrels actually kill most wounded chicks, scavenge all carcasses and thus consume the overwhelming bulk of the flesh. Second, Figure 7 shows the intriguing result that the head was the second most frequently wounded part of the body. This is surprising because it is probably the most mobile and (with the possible exception of the belly) the least accessible part of a chick. Furthermore, in order to access the head mice must climb onto the chick's back and up its neck, yet only two chicks had wounds on their backs. Third, six chicks had wounds that healed (but four ultimately died before fledging, presumably from subsequent attacks). Why did mice desist, allowing the wounds to heal, when in most cases the attacks appeared to continue until the chick died? Fourth, at least one chick had multiple bites but no significant wound and it is doubtful that the mouse/mice responsible for that attack gained any energetic return. Fifth, a single chick died without being attacked and a second chick was found in a very weakened state, at Green Hill, showing that mice did not specifically target weak or sick individuals (although this may be because these situations are relatively rare). Collectively, these observations suggest that mice are not pre-adapted to attack seabird chicks, mooting the possibility that this behaviour is learned, rather than instinctive.

The spatial pattern of attacks at Green Hill in 2004, where nests were significantly more likely to fail if they were close to a recently failed nest, suggests that there was a systematic nature to the attacks. However, attacks appeared to originate at multiple loci (i.e. occurred in the same month over large distances, thus at a minimum, several mice must have initiated attacks). Also, the spread of failures in time was not even. The fact that some chicks did not get attacked, or were attacked but survived, raises the possibility that some individuals behave differently to most others and may able to deter attacking mice.

Analysis of video attacks

The intensity of the videoed mouse attack on the Tristan Albatross, and the severely weakened or moribund state of other wounded chicks leaves little doubt as to the ultimate cause of those particular chick deaths. However, in the majority of cases, mice are probably not the proximal cause of death, particularly because they are seldom active during the day and almost never in full daylight where they are exposed to predatory skuas. Instead, repeated nocturnal mouse attacks probably render chicks defenceless against skuas and Giant-Petrels, through exhaustion, loss of blood or massive infection.

Figure 14. Remains of a Tristan Albatross chick the morning after a nocturnal attack by mice was captured on video.

The video footage showing mice successfully attacking albatross chicks is the first of its kind. Gough mice are relatively large compared to natural populations elsewhere (Berry et al. 1979; Angel & Cooper 2006). Nevertheless, they are much smaller than rats and it is astonishing that they can successfully attack chicks of one of the largest seabirds in the world, the Tristan albatross, weighing >300 times more than mice. Healthy Tristan Albatross chicks thwart avian predators such as skuas and giant-petrels, but appear incapable of defending themselves against diminutive mammalian predators such as mice.

Analysis of the videoed attack shows that for mice that visited the nest and participated in attacks, the majority of the time was spent feeding. This suggests that for those mice that know how to, high feeding rates and the highly nutritious, energy-rich food source that is not packaged in indigestible cellulose or chitin, makes attacking a rewarding activity. The intensity of the competition for access to the wound further suggests that the motivation was strong, which supports the suggestion that rewards were high. There appeared to be some kind of synergistic effect or shared vigilance which caused the intensity of attacks to increase over time (Figure 13). Figure 12 shows this even more clearly, with feeding rate of individual mice being higher when more mice were at the wound. The decrease in intensity with >3 mice is probably due to limited access and increased competition at the wound. Despite this, mice were observed investigating the wounded chick but not joining in the attack surprisingly often (Figure 10). This suggests that some mice have not learned how to access the wounds or are unable to compete for a space at a wound. The data showing mouse startle responses and the temporal decrease in return-time after a chick moved can be interpreted in one of two ways. It could be argued that mice generally became increasingly acclimatised to the disturbance events as time progressed, and their perception of the associated risk went down. Motivation to feed may also have increased with time as the wounds were enlarged, bled more and food thus became easier to access. However, although the frequency of startle responses of mice changed over time, the range did not. Strong startle responses continued throughout the recording (Figure 12), possibly due to the arrival of 'naive' mice throughout the recording. Another explanation is that mice least prone to startle spent the most time attacking, got the most benefit from the wounded albatross and thus were most motivated to stay and feed.

In conclusion, this is some of the first unequivocal evidence that mice can successfully attack seabird chicks, including those of albatrosses. The failure rates of Tristan Albatross chicks were unusually high in all years for which breeding success has been studied, and the evidence for mice causing this unusual mortality is overwhelming. Attacks appear to be uncoordinated, with scramble-competition at wound sites, yet some mice appear attracted to wounds but do not participate in attacks (and thus apparently derive no direct benefits from the attack). The patterns of attacks in time and space are predictable at the coarse scale, but are locally stochastic with no discernible reasons for this. In some sites most chicks died yet, somewhat enigmatically, some survive despite being very close to chicks that were attacked and killed (and thus presumably within the home range of attacking mice), and despite attacks continuing elsewhere. In chapter 7 I present some more speculative ideas that could explain some of these patterns.

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CHAPTER 4

Population dynamics and trends of Tristan Albatrosses on Gough Island: causes and consequences

Abstract

Previous research suggested negative population trends for Tristan Albatrosses *Diomedea dabbenena* on Gough Island, citing low adult survival and low breeding success as causal factors. Here I update and reassess trends with new data. Breeding success from four season averages at most 32%, but in three of those years it was at most 27-29%. The number of fledglings produced has decreased at a rate of *ca* 1% per year since 1979-1982. The 1956 population estimate appears to be unduly conservative, and a reassessment using the most reliable data suggests a negative trend of *ca* 1% per year over 50 years. The estimate of annual adult survival is revised downwards to *ca* 91%. Population models are used explore likely demographic trends under scenarios of proportional and additive adult and juvenile survival, using combinations of optimistic vs observed estimates for adult survival and breeding success. Consecutive incubator counts and the model suggest present-day adult and total Tristan Albatross populations are approximately 5400 and 11300 individuals, respectively. The most optimistic model based on current estimates of adult survival and breeding success suggest an annual growth rate of -2.85%, with the number of breeding attempts likely to decrease to *ca* 500 per year in 30 years. A stable population would require breeding success >100% or annual survival >97%. A worst-case scenario of additive (vs proportional) adult mortality and chick failures from mouse predation predict a catastrophic decrease, with extinction occurring in *ca* 25 years. The models were most sensitive to adult survival, but observed levels of breeding success are alone sufficient to drive population decreases. Thus if the conservation status of the Tristan Albatross is to be improved, the impacts of fishery mortality and mouse predation must both be addressed. An historical account from the 1880s describes high levels of chick failures, and this is interpreted as evidence that mouse attacks have occurred at significant levels for >120 years.

Introduction

Albatrosses are iconic examples of K-selected animals, with high adult survival, low fecundity and delayed sexual maturity. As a consequence, their demographic resilience to lowered adult survival is poor (Weimerskirch & Jouventin 1987; Croxall et al. 1990; Weimerskirch et al. 1997; Cuthbert et al. 2004). The impact of longlining on seabird populations was first described in the late 1980s (Brothers 1991). Thereafter albatross mortality from fishery interactions has been invoked to explain decreases in virtually every population of *Diomedea* (*sensu stricto*) albatrosses (as well as for many mollymawk albatross species), and is considered the most important conservation threat to albatrosses (Weimerskirch & Jouventin 1987; Croxall et al. 1990; de la Mare & Kerry 1994; Weimerskirch et al. 1997; Nel et al. 2002a, b; Cuthbert et al. 2004). The only other significant, human-vectored cause of mortality reported for Southern Ocean albatrosses is disease, recorded in Indian Yellow-nosed Albatrosses *Thalassarche carteri* on Amsterdam Island (Weimerskirch 2004).

Island-endemic bird species are amongst the most threatened groups of birds in the world (BirdLife International 2004). Several factors underlie this pattern. First, mammalian predators have become invasive on the vast majority of islands around the world (Blackburn et al. 2004; Martins et al. 2006). Second, insular faunas (and particularly seabirds) are famously ill-equipped to defend themselves against invasive predators (Moors & Atkinson 1984; Atkinson 1985). Third, small population sizes are typical of single-island endemics, which are therefore inherently susceptible to extinction (Ebenman et al. 1995; Simberloff 2000). Thus, from a conservation perspective, it is dangerous to be a single-island-endemic seabird species. The Tristan Albatross *Diomedea dabbenena* historically bred on Tristan da Cunha, Inaccessible and Gough islands, but humans and their commensal invasive species drove the Tristan da Cunha population extinct (Angel & Cooper 2006). The Inaccessible Island population has numbered <5 pairs since 1950. The estimated maximum productivity for this population in nine years of monitoring since 1982 is 0.78 chicks per year, including three years in which zero chicks were fledged (Ryan 2005); it cannot be considered viable. Thus Gough Island now supports >99% of the global population, making the Tristan Albatross *de facto* a single-island endemic. Prior to this study, there was no unequivocal evidence that mice posed a threat to seabirds (reviewed in Chapter 1), and little attention was given to the potential impacts of invasive species on the Tristan Albatross, since mice are the only introduced mammal on Gough.

Although Weimerskirch et al. (1997) argued correctly that a 5% decrease in Wandering Albatross *Diomedea exulans* breeding success would have a negligible impact on population growth, a population model by Cuthbert et al. (2004) showed that a decrease >20% was sufficient to cause negative population growth for Tristan Albatrosses. Chapter 3 presents conclusive evidence that mice are causing widespread mortality of Tristan Albatross chicks on Gough Island, and that this has occurred in all four seasons studied. In this chapter I update Cuthbert et al. (2004) with another three years of breeding success data, four years of incubator counts and mark-recapture data, and five years of chick counts. I re-estimate recruitment age and adult survival, the latter being a critical parameter in albatross demographics (Weimerskirch et al. 1997; Cuthbert et al. 2004), and estimate for the first time the mean annual breeding success, the adult population size and the total population size. The new data allow me to develop a more realistic and robust population model than Cuthbert et al. (2004) were able to achieve, affording greater potential for exploring demographic scenarios. Reinterpretation of historical data in the light of these findings allows a revision of Cuthbert et al.'s (2004) estimate of the annual decrease in the population.

Methods

Study area

Tristan Albatrosses breed in sheltered areas and on the slopes of valleys above the 350 m contour on Gough Island. Peak laying occurs in January, hatching peaks in March, and fledging occurs from November onwards (Cuthbert et al. 2004).

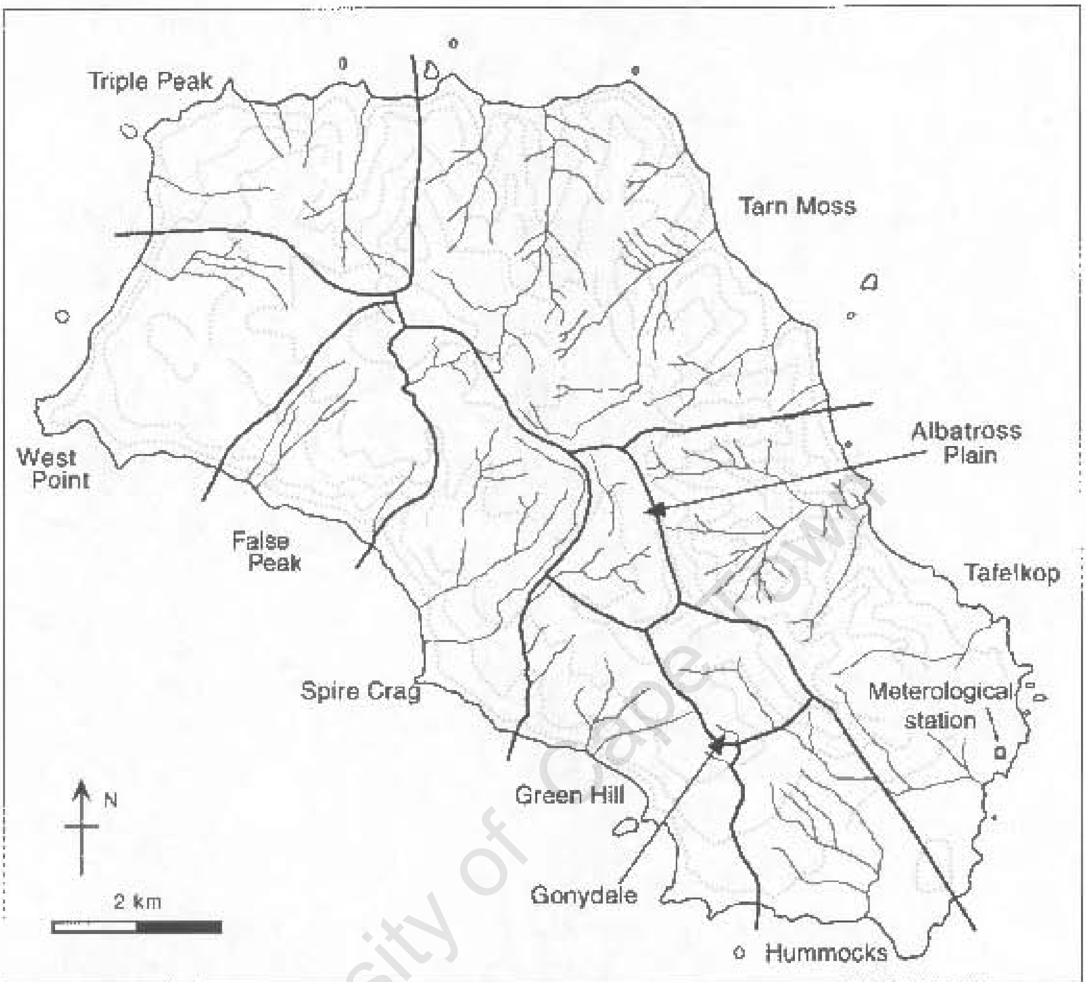

Figure 1. Count areas for Tristan Albatrosses on Gough Island. Dotted lines indicate 200 m contours, thin solid lines represent major water courses and thick solid lines delineate count areas.

Demography

Tristan Albatrosses on Gough Island are counted using scan counts, done from ridge-tops or vantage points using binoculars, following Ryan et al. (2001), who showed the reliability of scan counts versus ground counts to be very high. Ground counts involve walking through an area and counting. Complete scan counts of incubating adults (January-March) were done in 2001, 2004, 2006 and 2007 and a partial count in 2005. Counts of near-fledging chicks have been conducted between September-November, sporadically since 1979 and annually since 1999. These counts are equivalent to a maximum estimate of fledglings

(Cuthbert & Sommer 2004) and are implicitly treated as such hereafter. Limited evidence suggests that mouse attacks cease in October (Chapter 3). Incubator and chick counts from the same breeding season allow crude estimates of the total annual breeding population and maximum breeding success. These counts represent maximum estimates because early egg failures will be missed, although late-laid eggs compensate to some unknown extent because they will also be missed but if successful will be included in the subsequent chick count. Crude breeding success was calculated by dividing the number of large chicks by the number of incubating birds. A mean present-day value of breeding success was calculated from the mean of these four years.

The number of incomplete annual counts (three of 11 (27%) chick counts and one of five (20%) incubator counts) made it necessary to impute missing values. I tested two TRIM models (Pannekoek et al. 2006) but they achieved very poor fits to the data ($p<0.001$ in both models) and were rejected; TRIM estimates are neither used nor presented. An alternative technique was employed, referred to as the Underhill method, which uses a multiplicative model and Maximum Likelihood estimates, including correction for overdispersion (Underhill & Prŷs-Jones 1994). This method imputes expected counts in two-way (site and time) contingency tables (Underhill & Prŷs-Jones 1994). The accuracy of the Underhill method was assessed by deleting five actual data from count areas across years with complete counts, and inserting 'estimates'. The procedure was then run and the 'missing data' imputed. The percentage difference between imputed values and actual counts was <1%, lending confidence to the use of imputed values in further analysis.

I estimated population trends by comparing the 1956 incubator counts from Green Hill, Gonydale (including the Hummocks area) and Albatross Plain, believed to have been most reliably counted (Cuthbert et al. 2004), with the incubator counts in 2004-2007. Chick counts from 1979-2006 were correlated with time to investigate trends. Differences between early (1979-1982) and recent (1999-2006) periods were tested with a Mann-Whitney U test. I then hindcast from the chick counts to estimate the number of annual breeding pairs using modal observed breeding success and expected breeding success (based on breeding success from other *Diomedea* albatrosses, see below). To assess which level of breeding success was more likely, I estimated the population growth rate required to achieve observed counts from 2001-2006. Averages were used to minimise potential bias from the demi-population fluctuations inherent in a biennially breeding species, and change was calculated over the period from the midpoints of each time group (23 years).

All analyses were performed in Statistica (StatSoft 2004). Where appropriate, means are reported with standard deviations (SD). SE denotes standard error and CI denotes 95% confidence intervals.

Population model: parameters

I developed a model of the female albatross population to explore the consequences of various scenarios on the mean population growth rate. The following input parameters were estimated: annual juvenile, immature and adult survival, annual breeding success and mean recruitment age. Where parameters could not be reliably estimated because data for Gough Island are either absent or from too few years to be reliable, I used published estimates from sibling species as surrogates (e.g. (Keitt et al. 2003; Cuthbert 2004; Cuthbert et al. 2004).

Adult survival, recruitment age and breeding site fidelity were estimated from banding and recovery data from Tafelkop, where adults and chicks have been banded annually since 1985. Adult survival was estimated using the program MARK (White & Burnham 1999). Only birds that bred at least once between 1985 and 2006 were used in the analysis; retraps of non-breeding birds were ignored. There was zero retrap effort in 2005, so this year was excluded from all analyses. Two models were tested with constant vs variable survival (denoted $\varphi(.)$ and $\varphi(t)$, respectively). Retrap probabilities (denoted p) were variable in both models because of variable retrap effort between years. Model fits were assessed using Akaike's Information Criterion (AIC). I then modelled trends in adult survival over time, first for the whole period and then mean survival over four time periods (initially six years, then three five-year periods). Two alternatives for annual survival were used in the population model. First, expected annual survival was fixed at 0.956, the value used by Cuthbert et al. (2004) and derived from Wandering Albatrosses without fishery-related mortality. Second, observed adult survival, taken from the MARK model with the lowest AIC, was 0.9096% (SE±0.013). Annual survival was a fixed value, not a stochastic variable.

Average recruitment age was estimated from all 40 birds banded as chicks that bred in the Tafelkop colony. There are, however, two sources of error in this estimate. First, there are too few years of data to analyse only cohorts older than 20 years (the maximum age at first breeding). Thus some birds >10 years old may yet recruit but are not accounted for, underestimating recruitment age. On the other hand, retrap effort was variable over the 22 years, and it is probable that some breeders were not retrapped in their first year, causing an over-estimate. The magnitude of these opposing errors is unknown and thus I cannot control for them. However, the resultant estimate is similar to that of sibling taxa. Fidelity to breeding site was checked from records of birds that bred at least once in Tafelkop and subsequently were recorded breeding elsewhere.

Juvenile and immature survival is unknown for Tristan Albatrosses. Cuthbert et al. (2004) used data from the Wandering Albatross population on the Crozets, where survival of juvenile birds (aged 0-5) was 75.6%, (Weimerskirch et al. 1997). However, juvenile survival on South Georgia up to the 1980s was 81-86% (Croxall et al. 1990), so I used 80%, the mid-point between the means of the Crozet and South Georgia estimates. Immature survival was assumed to be the same as adult survival (Croxall et al. 1990; Weimerskirch et al. 1997).

Expected breeding success ranged from 60-80% of the number of breeding attempts, approximating success reported for sister taxa on islands free of alien albatross nest-predators (Weimerskirch & Jouventin 1987; Croxall et al. 1990; Weimerskirch et al. 1997; Elliott & Walker 2005; Walker & Elliott 2005). Observed annual breeding success for the population model used the same variable as for expected breeding success, but from the range of observed annual values (27-45%).

The percentage of successful breeders that take a single sabbatical year and the percentage of failed breeders that return to breed the following year (estimated from sister taxa) ranged from 72-85% and 68-78%, respectively (Croxall et al. 1990; Weimerskirch 1992). Thus in the model the proportion of non-breeders returning to the breeder pool and the proportion of failed breeders returning to the non-breeder pool each year were strings of evenly distributed random numbers from 0.72-0.85 and 0.68-0.78, respectively. I performed a sensitivity analysis on the effect that the rate of interchange between the two pools had on population growth. For these analyses, random variables were made to be repeatable, enabling direct comparisons between simulations.

Population model: design

The model was run over 30 years with each iteration being one year. The starting point was taken from the 2001 incubator count, thus the model runs from 2001-2031. All values were rounded to the nearest integer during calculations. The model consisted of 13 pools of individuals: two for adults (breeding and non-breeding stocks), chicks, five juvenile stocks (age-classes 1-5 years) and five immature stocks (age-classes 6-10 years). The model assumed an equal sex ratio and no intrinsic, density-dependent effects on survival or breeding success. The initial value for breeder stock was 2400, the 2001 incubator census. Although it is probable that unusually high numbers of pairs bred in 2001, this estimate was used to facilitate direct comparisons with Cuthbert et al. (2004). Values of other stocks were generated using a stable-age distribution derived from a Leslie matrix model with the same parameters. The model was not critically sensitive to any surrogate parameters, and it is unlikely that any of the surrogate estimates differ widely between different *Diomedea* populations.

The stock of breeding females increased and decreased in each of two ways. Breeders increased when immature birds recruited into the adult population and when non-breeders returned from sabbatical. Breeders decreased as a result of annual mortality (representing a loss to the system) or, if successful, to become non-breeders. Approximately 25% of breeders that fail will re-attempt the following year (Weimerskirch 1992); the remainder also take a sabbatical and move to the non-breeding stock. This is probably an optimistic estimate for Gough, because that estimate is derived from a population where most failures occur during incubation. On Gough, most of the failures were at the chick-rearing stage, and adults whose attempts fail probably do not have sufficient time to regain condition; thus the actual movement out of the breeder stock may be higher than has been modelled. The breeder stock B at time t can be expressed as:

$$B_t = B_{(t-1)} \times S + R + W_t - X_t$$

where $B_{t=0}$ was 2400 females, R is recruitment (of immature birds of age-class 10), W is the number of non-breeding birds returning to breed, X is the number of breeders that take a sabbatical year and S is annual survival. The non-breeder stock N at time t was governed by a simpler subset of conditions, being mortality, gain from X and loss from W, expressed as

$$N_t = N_{(t-1)} \times S + X_t - W_t$$

where $N_{t=0}$ was 1800 females. W_t is the movement of females at time t from N to B, equivalent to the number of non-breeders multiplied by a factor representing the estimated proportion of birds that take a single sabbatical year (72-85%, Weimerskirch 1992), expressed as

$$W_t = (N_{t-1} \times S) \times Y$$

where Y is a random number with a uniform distribution between 0.72-0.85. X_t is the number of females moving from B to N at time t (i.e. the number taking a sabbatical). This was a function of breeding success (all successful breeders, less those that died, exit B) and the proportion of failed breeders that take a sabbatical year (*ca* 0.25, Weimerskirch 1992), expressed as

$$X_t = B_{t-1} \times S \times P_{t-1} + B_{t-1} \times (1 - P_{t-1}) \times 0.25$$

where P is productivity (i.e. breeding success), a variable that produced a uniformly distributed string of random numbers from 0.6-0.8 or from 0.27-0.45, depending on the estimate of breeding success being modelled. The distribution of the random numbers for the lower breeding success estimate was skewed using a graphical function to produce a mean of 32%, the mean observed breeding success. The initial values for chick, juvenile and immature stocks were adjusted downwards accordingly when lower breeding success was used. Chick production C at time t was purely a function of breeding success and the number of breeding attempts, expressed as

$$C_t = B_t \times P_t$$

The juvenile J and immature I populations consisted of 10 age-class stocks Y_n, where n_{1-5} = juveniles and n_{6-10} = immatures. The progression of individuals from one age-class to the next of was as follows. At each iteration, each age-class Y_n (for n_{2-10}) at time t was simply Y_{n-1} at time $t - 1$ (the previous year's stock), less a mortality factor (S) and the entire C_{t-1} stock became Y_1. Y_{10} stock (less a mortality factor) exited I to become the recruits R into the breeder stock. Juvenile (Y_{1-5}) survival is lower than immature or adult survival (Cuthbert et al. 2004) so for these stocks I multiplied S by a correction factor of 0.837 to achieve the estimated 80% annual survival. The stocks Y_n at time t are described by the following expressions:

$$Y_1 = C_{t-1}$$

$$Y_n = Y_{n-1} - (Y_{n-1} \times S \times 0.837) \qquad [1<n<6]$$

$$Y_n = Y_{n-1} - (Y_{n-1} \times S) \qquad [5<n<11]$$

and

$$J_{t=0} = \sum_{t=0} Y_{1-5} = 2222$$

and

$$I_{t=0} = \sum_{t=0} Y_{6-10} = 1145$$

To determine the importance of fishery interactions (affecting adult survival) and mouse predation (affecting productivity) on population viability, four scenarios were simulated using combinations of low (observed) vs high (expected) values for these two parameters:

Scenario A: expected adult survival and expected breeding success

Scenario B: expected adult survival and observed breeding success

Scenario C: observed adult survival and expected breeding success

Scenario D: observed adult survival and observed breeding success

The model was simulated 50 times under each scenario and the mean for each iteration calculated. The use of random variables and the stochastic nature of the interchange between breeding and non-breeding stocks meant that to estimate population growth rates, I had to pool these stocks. Trends, however, are illustrated using means of simulations for the breeder stock only.

Scenario D employs proportional adult mortality and proportional breeding success, which includes a percentage of natural/intrinsic mortality (e.g. senescence or infertility, respectively) as well as mortality due (most probably) to fishery interactions or mouse predation, respectively. However, the numbers of fishing vessels and longline hooks available to albatrosses is independent of albatross numbers. Also, breeding success (from four years for the whole island and from 16 years in Tafelkop) was independent of the number of breeding pairs (Chapter 3). I explored the population-level consequences of density-independence of fishery-induced mortality and mouse-induced chick mortality (cf. Ryan et al. 2006). First I modelled constant, density-independent adult mortality (to mimic severe, additive fishery-related mortality) using both breeding success alternatives. Adult survival was 0.956, accounting for intrinsic mortality, and the impact of mortality from fishery interactions (LM), which affected all stocks except chicks, was set at Low, Medium and High; the number of individuals removed per year was 100, 200 and 300, respectively. LM removed individuals at random, which over 30 iterations approximated relative abundances in the different stocks. Second, for density-independent mouse predation, I reduced the total number of failed nesting attempts in 2001 (1744) by 30% (to account for intrinsic/expected failures) the remainder (1221) being roughly the failures due to mice. Half of this (610, females only) was then used as a fixed annual loss of chicks. A final, worst-case model was developed with fixed, density-independent mortality (200 individuals per year) and fixed, density-independent mouse predation.

Results

Demography

Whole-island breeding success was at most 27-29% in 2001, 2004 and 2005 but was 45% in 2006, resulting in a mean success for the period 2001-2006 of up to 32.3% (Table 2).

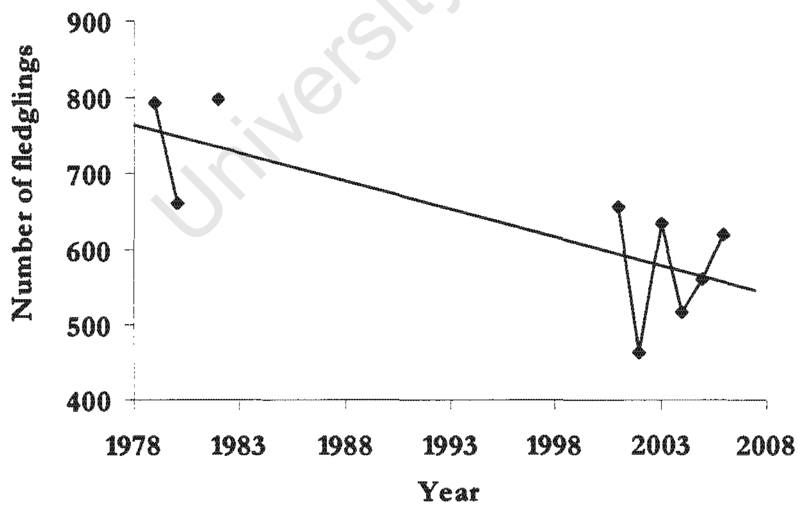

Figure 2. Trends in the numbers of Tristan Albatross fledglings on Gough Island.

Table 1. Actual chick counts and extrapolated breeding pairs based on modal observed (27%) and expected (70%) annual breeding success. Values in parentheses represent imputed values for missing counts. Only total counts are available for 1979 and 1980.

Sub-colony	1979	1980	1982	1999	2000	2001	2002	2003	2004	2005	2006
Albatross Plain			168	160	74	89	110	117	52	130	158
Green Hill & Gonydale			84	265	89	182	85	138	179	169	139
False Peak			55	107	22	35	59	(48)	20	(42)	33
Spire Crag			113	224	19	128	(68)	120	35	71	53
Tafelkop			13	6	5	8	9	9	7	12	5
Tarn Moss			37	42	15	13	12	(24)	16	32	31
Triple Peak			68	70	15	27	6	(31)	12	21	56
West Point			260	255	79	174	(114)	(159)	195	85	145
Total	792	661	798	1129	318	656	463	634	516	562	620
Extrapolation											
at 27%	2933	2448	2956	4181	1178	2430	1715	2348	1911	2081	2296
at 70%	1131	944	1140	1613	454	937	661	906	737	803	886
Actual incubators						2400			1869	(1939)	1366

Although more fledglings were produced annually between 1979-1982 than 1999-2006 (Table 1), there was no significant correlation with time (R^2=0.126, p=0.283). However, there was a strong inter-annual oscillation in production in 1999-2000, which damped by 2003-04. When the 'outlier' years of 1999 and 2000 were excluded from analysis, a significant negative relationship was found (Figure 2, R^2=0.557, p=0.017). A Mann-Whitney U test confirmed that a significant difference exists between the two periods (adjusted *Z*=2.32, p=0.02). Mean annual productivity for 1979-82 (n=3 counts) was 750 chicks, compared to 575 during 2001-2006 (n=6 counts), corresponding to a mean decrease of 7.6 fledglings (1.0%) per year over 23 years.

Table 2. Tristan Albatross incubator counts from Gough Island. Values in parentheses are imputed (see text for method details).

Count Area	1956	2001	2004	2005	2006	2007
Tafelkop	0	16	23	17	12	13
Green Hill & Gonydale	700	486	363	(401)	337	293
Albatross Plain	430	325	294	283	229	226
Spire Crag	35	338	210	(252)	197	142
False Peak	10	129	74	(90)	63	48
West Point	35	918	694	724	473	422
Triple Peak	16	153	166	130	103	89
Tarn Moss	0	35	45	(42)	44	38
Total	1226	2400	1869	(1939)	1458	1271

The mean present-day (2004-2007) contribution that Albatross Plain, Green Hill and Gonydale incubator counts make to the total is 37.5 ±2.9%, compared to 92% in 1956 (Table 2). The incubator counts in these areas have decreased from 1130 pairs in 1956 to a mean of 607 ±77 pairs (2004-2007), a mean decrease of 46.3% over 50 years, equivalent to an annual decrease of 0.93 ±0.136%.

The best-fit MARK model had constant adult survival and variable recapture probability (φ(.) p(t), AIC=908.6 vs φ(t) p(t), AIC=909.7). Mean adult survival was estimated at 0.9096 per annum (SE±0.013, 95% CI=0.882-0.932) and this was used as the observed adult survival in the population model. Although the models of trends in adult survival had similar AICs to the constant survival model, they produced survival estimates with wide confidence limits. Further, due to poor retrap effort in several years, and good effort in others, the models were not robust, i.e. a few, well separated years with good retrap effort and with strong differences could produce a spurious trend. Thus I present the results of these analyses for interest, but they should be treated with caution. Annual adult survival appeared to decreased from 94.2% (95% CI=86.7-97.6%) in 1985 to 86.8% (95% CI=75.5-93.3%) in 2006 (Figure 3). When adult survival was averaged over four periods, the model showed survival was lowest between 1996 and 2001 (survival=87.9%, SE=3.1%, 95% CI=80.4-92.8%), but with survival over the last five years increasing (survival=92.9%, SE=5.1%, 95% CI=74.1-98.3%). There is little evidence of inter-area movements by breeding birds, as only 3 of 239 birds that bred in Tafelkop between 1976 and 2006 have been retrapped breeding in other count areas. Thus no adjustments were made to account for emigration, and the resultant estimate of adult survival may be slightly pessimistic.

The mean recruitment age was 10.1±2.7 years (mode 10 years, range 6-20 years, n=40 recruits). However, in 2004 a three-year-old bird and a four-year-old bird were retrapped while incubating. These data were not included in the estimate because both were banded and recruited outside the Tafelkop study colony.

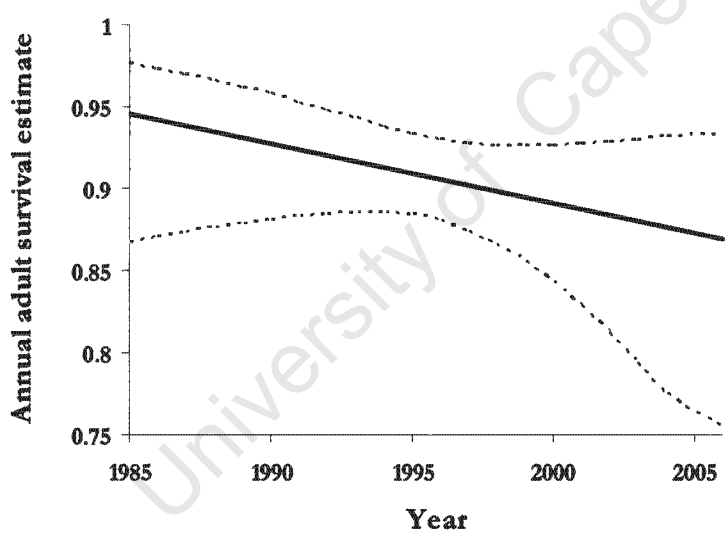

Figure 3. Modelled temporal trend in estimated adult survival of Tristan Albatrosses from Gough Island from 1985-2006, based on a mark-recapture model with variable annual retrap probabilities ($\varphi(t)$ $p(t)$). Dashed lines represent CI

Population model

The different scenarios modelled all produced estimates of annual growth comparable to other *Diomedea* populations where adult survival, breeding success and population growth rates are known (Table 4). The sensitivity analysis showed the model was relatively robust to changes in the rate at which birds moved between the breeder and non-breeder pools: e.g. when the rate at which non-breeders moved to the breeder pool each year was fixed at 65% and then at 95%, the annual growth rates were -0.08% and 0.24%, respectively. Scenario A is the most optimistic result for the Tristan Albatross, predicting a stable adult population (annual growth rate = 0.09%, Figure 4). This scenario is what could be expected from a population with low levels of mortality from fishery interactions and with breeding success typical of other *Diomedea* populations. Scenarios B-D, in contrast to Scenario A, all predict population decreases. Scenario B modelled the observed (low) breeding success as a proportion of the number of incubators, but used a high annual survival value. The result was a decreasing population (annual growth = -1.26%), thus even if adult mortality from fishery interactions (and other extrinsic sources) is completely mitigated, low productivity due to mouse predation is alone sufficient to drive a negative trend. The negative growth rate predicted is close to the estimated annual decrease of 1% since 1956. When the observed adult survival rate was used in the model with high productivity (Scenario C), the negative annual growth predicted (-2.51%) was more severe than Scenario B. This implies that the low observed adult survival is having a stronger effect on the Gough population than low productivity. However, both survival and breeding success need to improve in order to reverse the model's negative trend (Scenario B: survival >0.97, Scenario C: annual breeding success >100%). Unsurprisingly, Scenario D, which used the lowest values for adult survival and annual productivity, predicted the lowest annual growth rate (-2.85%). The Gough population under this scenario was reduced to *ca* 500 breeding attempts per year within 30 years. This scenario, however, used the current best estimates of both adult survival and breeding success, and modelled their impacts as conservatively as possible (i.e. assumed proportional adult and chick mortality).

Table 3. Input parameters and mean estimated annual growth rate (%) from a 30-year population model for Tristan Albatrosses. *S*=Adult Survival, *P*=Productivity (mean annual breeding success), LM=Longline Mortality and DI=Density independent chick mortality; simulations with LM included additional mortality of 100 (Low), 200 (Medium) and 300 (High) birds (taken at random from all stocks except chicks). Values in brackets represent the frequency with which simulations predicted the earliest time to extinction.

Scenario	Input parameters		% growth rate n=50 simulations			Earliest time (in years) to extinction
	S (%)	*P* (%)	Mean	min	max	
Scenario A	95.6	70	0.16	-0.30	0.66	-
Scenario B	95.6	32	-1.09	-1.32	-1.19	-
Scenario C	91.0	70	-2.50	-2.52	-2.50	-
Scenario D	91.0	32	-2.80	-2.86	-2.83	-
Low LM	95.6	70	-1.08	-1.14	-1.03	-
Medium LM	95.6	70	-2.40	-2.46	-2.34	-
High LM	95.6	70	-3.39	-3.44	-3.34	29 [8]
Low LM	95.6	32	-1.60	-1.65	-1.54	-
Medium LM	95.6	32	-3.54	-3.57	-3.50	28 [30]
High LM	95.6	32	-5.20	-5.30	-5.09	19 [5]
DI *P*, High *S*	95.6	70	-1.41	-1.46	-1.37	-
DI *P*, Low *S*	91.0	70	-3.00	-3.01	-2.99	-
DI *P*, High LM	95.6	70	-4.27	-4.33	-4.21	23 [1]

Table 4. Adult survival, breeding success and population growth rates for *Diomedea exulans* (*sensu lata*) albatrosses. All data are percentages and degree of accuracy is presented as reported.

Species	Location	Study period	Adult survival	Breeding success	Growth rate (%)
D. amsterdamensis[1]	Amsterdam	1983–1994	95.7	71.6	+1.0*
D. [e.] antipodensis[2]	Antipodes	1994–2004	95.7	74	+1.0
D. dabbenena	Gough	1985–2006	91.0	32.3	-2.8*
D. exulans[1]	Crozet	1986–1994	95.6	72.0	+1.0
D. exulans[3]	Macquarie	1966–1981	90.5	–	-8.1
D. exulans[4]	Marion	1984–1999	94.2	74.6	+5.0
D. exulans[5]	South Georgia	1961–1988	94	64	-1.0
D. [e.] gibsoni[2]	Auckland	1991–2004	96.1	63	+1.0

[1]Weimerskirch et al. 1997, [2]Elliott & Walker 2005, [3]de la Mare & Kerry 1994, [4]Nel et al. 2003, [5]Croxall et al. 1990

*Modelled estimate

If annual adult survival in the absence of fishery mortality is 0.956 (as used in these models) then the observed survival (0.9096) means that up to 5% of adults die as a result of fishery interactions each year. The mean number of pairs attempting to breed from 2004-2007 was 1612. The closest value to this in the population model under Scenario D was 1514 breeding pairs (in 2008). In this year the mean (n=50 simulations) total female population was 5749 birds and the total adult female population was 2748 birds. Total population and total adult population (rounded to nearest 100) were 11300 and 5400 birds, respectively. Thus the mean number that died annually due to fishery interactions under Scenario D was 128 adult females and 267 females in all age-classes. The impact of additive mortality on adult survival is shown in Figure 5. Initial survival values were better than the current estimate (0.9096), but after seven years survival fell below the current estimate. This suggests that quite large population decreases could occur well before an equivalent decrease in survival rate is detectable.

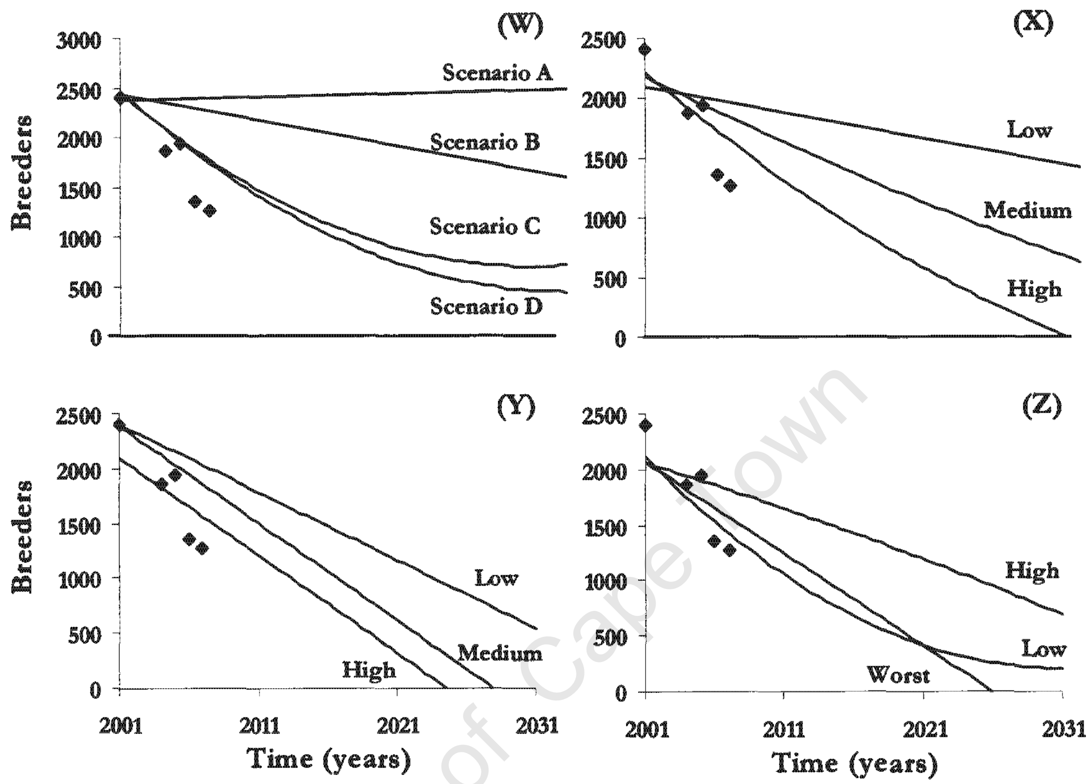

Figure 4. Predicted growth rates from a model of the Tristan Albatross population on Gough Island. Trend lines are means of 50 simulations per scenario; note different ordinate scale for (W). ♦=actual incubator counts. Scenario A=high survival and high annual productivity, Scenario B=high survival and low annual productivity, Scenario C=low survival and high annual productivity and Scenario D=low survival and low annual productivity (W). Scenarios of additive mortality from fishery interactions affecting all post-fledging stages modelled Low, Medium and High mortality, removing 100, 200 and 300 birds annually from the population, respectively, and using high (X) and low (Y) estimates of breeding success. Three scenarios modelled density-independent chick mortality (Z), using both survival alternatives (High and Low) and, for the worst case, high survival but Medium mortality from fisheries.

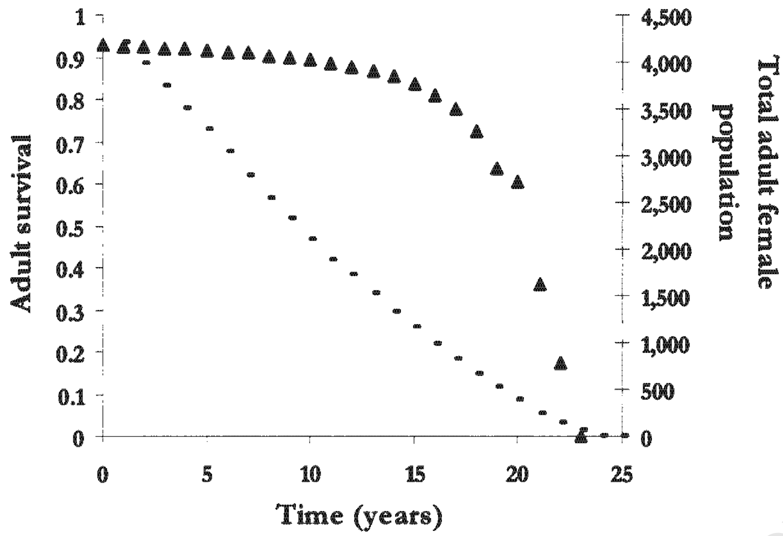

Figure 5. Changing annual adult survival rates (▲) and female population size (-) under a modelled scenario of additive (density independent) mortality from fisheries or Tristan Albatrosses. Intrinsic survival was set at 0.956, extrinsic mortality (due to fishery interactions) was set at 300 birds per year and mean annual productivity was 32%.

Figure 4 shows that when significant, density-independent juvenile, immature and adult mortality (from fishery interactions in this case) was modelled, the population underwent very rapid decreases. The most extreme scenario (Figure 4y) predicts extinction as early as 19 years, with a mean annual growth rate of -5.2% and mean time-to-extinction *ca* 25 years (Table 3). Thus if mortality from fisheries is indeed density-independent and occurs annually at modelled rates, time to extinction of 30-50 years should be considered a fairly realistic estimate. To estimate the effect of density-independent mouse predation, I assumed an annual mean of 30% of nest failures were not due to mice. Thus predation in 2001 accounted for *ca* 1220 chicks. Using half this value (female chicks only), the model with high annual survival (0.956) showed a relatively sharp decrease (-1.41% per year, Figure 4z), comparable to estimates of annual growth at low levels of fishery-related mortality (Figure 4x,y, Table 3). This suggests that density-independent chick mortality will cause a strong population decrease. However, with low adult survival (0.9096), the annual decrease in the population was sharp (-3.0%) and when additive adult and chick mortality were combined as a worst-case scenario, the population underwent a catastrophic decrease (-4.27% per year) and reached zero in 23-30 years, a similar result to the simulations with high mortality from fishery interactions and low, density-dependent breeding success.

Discussion

The paper by Cuthbert et al. (2004) presented the first whole-island count of incubating birds since 1956 and the first data on breeding success for the whole of Gough Island. The conservation implications of the paper were notable, because breeding success in 2001 was much lower than expected. However, the paper relied on a single year of data for some key parameters, and several important findings could only be suggested, or were reported with a relatively low degree of confidence. For example, mean annual breeding success could not be estimated. The incubator count represented a single datum which could not be used to estimate either the annual breeding population or the population as a whole, because the Tristan Albatross is a biennial breeder and there was no way to estimate reliably the other part of the demi-population. This problem was exacerbated by the fact that the demi-population became strongly asymmetric from 1999-2002, making inference particularly difficult. Biennially breeding albatrosses typically return to breed after a sabbatical year if successful, but may return the following year if they fail within the first half of the year, which is also when most failures ordinarily occur (Weimerskirch 1992). Therefore the actual ratio of breeders:non-breeders usually departs from parity. Cuthbert et al. (2004) estimated mean breeding frequency from a small number of birds over several years to account for this in their model. Instead, I used published data from sister taxa to estimate percentage failed breeders that return the following year and percentage successful breeders that take one or more sabbatical years (but see Ryan et al. (2007) for intra-specific variations in this parameter). This allowed a model that reflected annual variations in breeding success in the fluctuating numbers of breeding and non-breeding adults, rather than a single, fixed percentage or random variable that was unrelated to breeding success. Table 5 summarises the key findings of this study relative to those reported (and omitted) in 2004. In all but two parameters the consequences of the updated information are more pessimistic for the species' demography.

Table 5. Key findings about Tristan Albatross demographic parameters from this study compared to those reported from a study using data up to 2001 (Cuthbert et al. 2004). NE=No Estimate. Values in parentheses indicate number of years of data

Parameter	2001	This study
Modeled annual adult survival (%)	92.6 (16)	90.96 (21)
Mean breeding success (%)	27 (1)	32 (4)
Mean recruitment age (years)	9.7 (17)	10.1 (21)
Total adult population (2004-2006)	NE	5 400
Total population (2004-2006)	NE	11 300
Modeled population growth (%)	+0.3 to -5.3	-2.8
Estimated annual growth rate since 1956 (%)	-0.62	-0.92

All the available evidence points towards a decreasing Tristan Albatross population since at least the 1980s. First, estimates of breeding success from all recent years are much lower than has been reported for sister taxa breeding on predator-free islands (Weimerskirch & Jouventin 1987; Croxall et al. 1990; Weimerskirch et al. 1997; Elliott & Walker 2005; Walker & Elliott 2005) and are sufficiently low to cause a long-term decrease due to low recruitment. Second, the number of fledglings produced each year in 2001-2006 is significantly lower than it was in 1979-1982. Third, the trend in the five incubator counts this decade is downward, with ca 1200 (50%) fewer incubators counted in 2007 than in 2001 (Table 2), although the 2001 count was probably high due to demographic fluctuation. Fourth, demographic models, using reliable estimates of certain parameters, confirm that a population decrease is highly probable.

The first count of incubating Tristan Albatrosses on Gough Island was done in 1956, as part of the ornithological studies conducted by Michael Swales on the Cambridge Gough Island expedition (Swales 1965). Swales' estimate for the whole-island population of just over 1200 pairs is, in retrospect, almost certainly a significant underestimate of the true population at that time. How this came about is uncertain, although the effects of demi-population dynamics may have played a role. Albatrosses are susceptible to climatic or other events that can discourage large numbers of birds from attempting to breed in a given year (Nel et al. 2002a); in a biennially breeding species this can result in large swings in the numbers of breeding attempts in subsequent years (this may partially explain the huge change in productivity between 1999 and 2000). 1956 may have been a year of low breeding effort, resulting in an underestimate of the average number of pairs per year at that time. However, there is a serious anomaly to the 1956 count that cannot be this easily resolved. Swales' counts concentrate over 90% of the Gough population in just three areas: Albatross Plain, Green Hill and Gonydale, whereas in 2001-2007 these same areas account for a mean of only 36.8% of the island's total incubators. The diminution of pairs in these areas contrasts with an ostensible increase in pairs in other areas of the island. Treating the distribution of birds from the 1956 data as accurate would require a widespread shuffling of preferred breeding areas. The relative proportions of chicks counted in 1982 is similar to present day proportions and contrasts with the 1956 count (Table 2). If redistribution did occur, it took place in the space of 27 years, marginally more than one generation length (Cuthbert et al. 2004), and includes the establishment of two new sub-colonies (Tafelkop and Tarn Moss). This is unprecedented for any *Diomedea* albatross, a group characterised by high natal philopatry and even stronger breeding site fidelity (Croxall 1979; Weimerskirch et al. 1987; Croxall et al. 1990; Elliott & Walker 2005; Terauds et al. 2006). Even though there is significant dispersal of young birds away from the natal site in other *Diomedea* populations (Inchausti & Weimerskirch 2002), the rates of movement, once a breeding site is selected, are negligible from a sub-colony perspective (Inchausti & Weimerskirch 2002; Cooper & Weimerskirch 2003). These data make the redistribution of breeding birds between sub-colonies on Gough an unlikely explanation for the anomalous 1956 count. Furthermore, Wilkins' (1923) account of the island includes the following statement, which strongly suggests a large percentage of the population bred in the West Point area at that time: "...possible that [Tristan Albatrosses] nest at the extreme western point...[where they] were observed in great numbers." (Wilkins 1923, pg 509). The limited data from the Tafelkop and Gonydale study colonies support this general pattern, with *ca* 1% of breeding birds from Tafelkop (3 of 239) having been retrapped breeding in Gonydale over 31 years. There are good reasons to trust the accuracy of the 1956 counts in Albatross Plain, Green Hill and Gonydale, primarily because Swales spent considerable time working (and banded almost 200 albatrosses) there (Swales 1965). However, his estimates from other areas are difficult to reconcile with recent data, especially when viewed in the light of our understanding of the species' biology and I argue that they are unduly conservative.

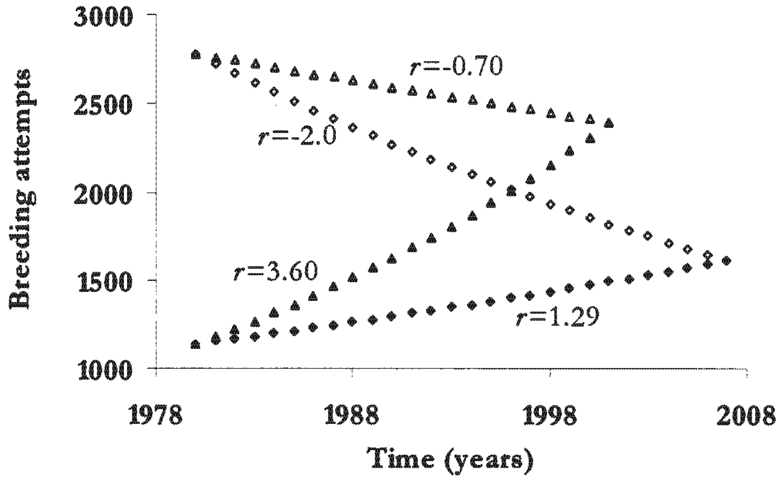

Figure 6. Effects of breeding success estimates of 27% (open symbols) and 70% (filled symbols) on estimates of the mean number of breeding pairs of Tristan Albatrosses on Gough Island in 1979-1982, and forecasted percent annual population growth (r) required to achieve observed numbers of breeding pairs in 2001 (diamond symbols) and the 2004-2007 mean (triangle symbols).

How long have mice been attacking albatross chicks and causing widespread reproductive failure? If one assumes 70% breeding success in 1979-1982, the resultant mean is 1140 breeding pairs per year. In order for that to increase to 2400 pairs (2001) or 1612 pairs (mean 2004-2007) requires annual growth rates of *ca* 3% and *ca* 1%, respectively (Figure 6). However, for a positive population growth rate to be achieved with the observed adult survival estimate for 1985-2006 (0.9096, Scenario C), the model requires an annual breeding success in excess of 100%; thus breeding success even close to 70% in these years is improbable. Mean annual breeding success of 27% in 1979-1982 yields an estimated annual breeding population of 2780 pairs. Forecasting to the present, if the population changed to 2400 (2001 incubator count), annual growth would have been -0.6%, or -1.82% if it changed to 1612 (mean of 2004-2007 incubator counts). If I accept that the 1956 whole-island census was an underestimate and assume an annual population growth rate of -1% for 1956-2007, then taking the mean incubator counts for 2004-2007 and hindcasting at 1% to 1979 yields 2109 incubating pairs. The equivalent breeding success is 37%, within the observed range on Gough. Thus it is likely that breeding success has been low since the late 1970s.

There is intriguing circumstantial evidence that mice have caused widespread and large-scale reproductive failure from at least the 1880s. Mice were probably introduced by early sealing parties who remained ashore, probably the 1810/1811 visit (Wace 1961). The earliest biological reports of Gough come from George Comer, who stayed on Gough Island in 1888/89 as part of a sealing party (Verrill 1895). He noted that mice were already abundant on the island. Subsequent visitors in 1919 (Green 1960) and 1922 (Wild 1923) also had cause to comment on the large numbers of mice. Comer made the first detailed biological observations (including Tristan Albatross breeding behaviour and phenology) and specimen collections on Gough (Verrill 1895). His diary includes the startling comment that "not more than five out of a hundred [Tristan Albatross chicks] live to leave their nests. They are killed by [Subantarctic Skuas *Catharacta antarctica*] and [giant-petrels *Macronectes* spp.]." (G. Comer, as cited by Verrill 1895, p 437). The reliability of many of Comer's other observations lend confidence to this observation. While it is a crude guess (and was presented as such) and is surely something of an exaggeration, it seems highly likely that he was observing very low chick survival. Comer also visited South Georgia and the Kerguelen islands, but his Gough Island observation must have been both unique and a significant occurrence for him to have commented on it. However, his assertion that the majority of chicks are killed by skuas and giant-petrels is completely at odds with more recent understanding of albatross chick defensive behaviour and their vulnerability to these predators, which co-occur with all *Diomedea* albatross populations and are not known to cause low breeding success anywhere. Comer most likely observed skuas and giant-petrels scavenging carcasses or attacking moribund or fatally wounded chicks by daylight (he had no opportunities to observe nocturnal mouse attacks), or assumed they were responsible because there were no alternative predators. Thus he predictably deduced that the predatory/scavenging birds were responsible for the widespread chick mortality. Hatchling survival of congeners on other islands is typically around 85% (Croxall et al. 1990; Weimerskirch et al. 1997), and I observed only one non-mouse related Tristan Albatross chick death in 2004. Reinterpretation of Comer's observation suggests that mice have been preying upon Tristan Albatross chicks at levels that would have had measurable effects on population growth rates for more than a century.

Hindcasting using estimates of annual growth from the different models to estimate the original population size before the advents of fishery mortality and mouse mortality is relatively straightforward, but the results are entirely dependent on some fairly significant assumptions and are therefore purely illustrative. I assumed that fisheries had a constant, density-dependent negative effect on adult survival (since 1970) and that mice have had a constant, density-dependent negative effect on annual productivity. Thus I used annual growth rate of -2.8% (from Scenario D – low adult survival and low productivity) for 35 years (2005-1970) and then -1.09% (from Scenario B – high adult survival and low productivity). The initial breeding stock was set at 1612 pairs. Under these conditions, the number of pairs breeding was *ca* 3000 in 1970 and *ca* 7000 in 1850.

Biennially breeding species are prone to fluctuations in the number of breeding attempts each year. Variable annual breeding success will affect return rates of failed breeders and will thus have a strong impact on demi-population dynamics, as seen in the data for productivity between 1999 and 2000 (Figure 2; see also Cuthbert et al. 2004). However, the magnitude of the oscillation between 1999 and 2000 (Figure 2), where the number of chicks differed by a factor of almost four, requires additional explanation. A significant demographic event (such as a climatic event that could have affected either adult albatrosses' ability to achieve breeding condition or the predatory impact of mice) in or before 1999 would cause increased reproductive effort and/or high breeding success in that year. 1997/98 was a strong El Niño Southern Oscillation (ENSO) event, and may be causally related to the observed fluctuations; other Southern Ocean seabirds also show strong (but varied) responses to ENSOs (Guinet et al. 1998; Croxall et al. 2002; Nel et al. 2003; Weimerskirch et al. 2003). Because of the above-average number of birds that attempted to breed and/or fledged a chick in 1999, many pairs would have taken a sabbatical year in 2000, resulting in relatively few breeding attempts, possibly reflected in the extremely low chick count in 2000. If mouse predation was particularly severe in 2000, this could cause still lower breeding success. The incubator counts post-2001 suggest that 2001 was a somewhat anomalous year too, probably experiencing above-average breeding attempts as a result of the low effort/success in 2000.

The results of the population modelling impacts confirm broadly what Cuthbert et al. (2004) found, which is that current estimates of adult survival and annual productivity for the

Tristan Albatross population cannot sustain a stable or growing population on Gough. However, data in the current model (Scenario D) are the best available estimates of population parameters, drawn from four years of whole-island breeding success, and 21 years of mark-recapture, whereas Cuthbert et al. (2004) used only one and 16 years, respectively. The new estimate of adult survival is even lower than was estimated for 2001. Furthermore, it is quite possible that the recent observations of acutely low productivity, despite showing some inter-annual variability, are probably typical on Gough. The implications of this are significant. First, both low adult survival and low annual productivity are driving negative population trends, and positive growth can only be achieved if both of these improve. Second, unless ameliorative action is taken, Scenario D suggests that the mean annual Tristan Albatross population on Gough could fall to *ca* 500 annual breeding attempts within 30 years.

Scenario D could be construed as slightly optimistic, because it assumed adult survival and mouse-induced mortality were proportional. However, mice may continue to kill large numbers of chicks each year, and thus as the population decreases, the relative impact of mouse predation will increase, resulting in an accelerated population decrease. The same applies to the effects of density-independent adult mortality from fishery interactions. Most scenarios using various combinations of additive annual survival and annual chick mortality suggest far more rapid decreases than Scenario D; the most extreme model results in extinction by 2020 (annual growth rate *ca* -5%). I predict that the causes and extent of the Tristan Albatross decrease lie somewhere between Scenario D and the more extreme models. Several facts support this. First, the apparent adult survival estimate from the Tafelkop colony (<91%) is as low as the estimate for the disappearing Macquarie Island Wandering Albatross population (Table 4), whose decline has been ascribed as almost completely due to longlining (de la Mare & Kerry 1994; Terauds et al. 2006). Second, Tristan Albatrosses are killed during fishing operations (Cooper 1994; Glass et al. 2000; Ryan et al. 2001). Third, I note with concern that the decrease in numbers of incubators between 2001 and 2007 amounts to a decrease of 188 pairs per year. This result, however, should be treated with caution because inter-annual variability make estimates of population changes using short sequences of data unreliable.

The apparent annual rate of decrease from 1956 to the present (0.93%) is very similar to the rate of decrease in annual chick production from 1979-1982 to the present (1.0%). These contrast with the modelled rate of decrease under Scenario D (2.8%), the most conservative model that uses present-day estimates of adult survival and annual breeding success. This discrepancy is probably due to the fact that the model uses a mean of the current estimates of adult survival and breeding success, which may well have changed from 10 or 50 years ago. Also, fisheries are unlikely to have had a significant effect on adult survival before the 1970s, and probably had the most severe effect in association with the rise of longline fishing in the Southern Ocean in the 1990s, possibly extending into this millennium (Tuck et al. 2003). A second source of error in the estimates relates to the uncertainties surrounding the earlier counts: the 1956 count represents a single datum – thus there may well have been a demi-population effect. If the 1956 counts in Albatross Plain, Gonydale and Green Hill were below average for the period, then the actual rate of annual decrease would have been steeper than 0.93%, and vice versa. The chick counts from 1979-1982 tell nothing of breeding success, the number of breeding attempts or demi-population dynamics, and thus estimates and the crude extrapolations using those counts are purely illustrative.

There appears to have been no real change in mean recruitment age in recent years (Table 5). However, the Tafelkop dataset is small, with limited power and the young breeders in 2004 were not from Tafelkop. The mean recruitment age of Wandering Albatrosses decreased during periods of low adult survival in two studies (Weimerskirch & Jouventin 1987; Croxall et al. 1990). Nevertheless, recruitment of birds as young as 3 and 4 years-old is exceptional for *Diomedea* albatrosses. One possible mechanism driving earlier breeding in populations with low survival is through sex-biased adult mortality, such as has been demonstrated for several seabird species drowned on longlines (Nel et al. 2002a, b). Unpaired older birds, lacking experienced partners with which to form new pair bonds, could become more forceful in courtship, coercing into breeding young birds that have returned to Gough to court. Also, high numbers of serially unsuccessful pairs could increase the divorce rate, driving experienced birds to coerce young birds into breeding earlier than usual. Alternatively, if adult numbers have decreased significantly or subsidies from fishery discards are significant, young Tristan Albatrosses may be able to forage more successfully and thus achieve breeding condition much earlier. These hypotheses are not mutually exclusive.

Conclusions

If the benchmark 1956 count was indeed an underestimate, it has had an ironic negative consequence for albatross conservation on Gough Island. First, the two- to four-week annual relief voyage to Gough Island takes place between August and November each year. Until recently, researchers were forced to visit Gough Island for either an entire year or else their visits were confined to the relief period. From 1957-2000, no ornithologist spent a summer on Gough and all albatross censuses for that period were chick counts. Second, Table 1 reveals a perverse coincidence: assumptions of normal breeding success before 2001 meant that hindcasting from chick counts to numbers of pairs match closely the 1956 (under)estimate of breeding pairs. Third, counting Tristan Albatrosses with binoculars from vantage points is extremely unlikely to result in observers detecting wounds on chicks. As a consequence, widespread and devastating mouse attacks on Tristan Albatross chicks have, until now, gone unnoticed (Ryan et al. 2001) or unconfirmed (Cuthbert & Hilton 2004; Cuthbert et al. 2004). These attacks have probably been happening since at least the 1970s and quite likely since before 1888 (Verrill 1895), have probably contributed significantly to an estimated 50% decrease in the breeding population over 50 years, and are one of the most pressing conservation issues affecting an albatross species since the impacts of fishery interactions were described (Brothers 1991). The timing of reduced adult survival is likely to have coincided with the increase in fishing effort in the waters of the Atlantic and Indian oceans that began in the 1970s and continues to the present (Cooper 1994; Glass et al. 2000; Ryan et al. 2001; Tuck et al. 2003). A time-dependent adult survival model might be able to link periods of lower survival to changes in fishing effort (Terauds et al. 2006), although the nature and extent of fishing, reporting and mitigation measures used have changed substantially, and the present data are ill-suited to this type of analysis (Ryan & Watkins 2002; Tuck et al. 2003). The population models presented here, however, agree with those of Cuthbert et al. (2004) in showing that observed low adult survival may have an even stronger negative effect on population growth than observed low productivity levels. Irrespective of the relative impacts, the Tristan Albatross population on Gough, the last viable population of this species in the world, will continue its apparent trend towards extinction unless the impacts of both fishery interactions and mouse attacks are ameliorated.

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CHAPTER 5

The importance of seabirds as a food resource for the mice on Gough Island

Abstract

I use stomach content and stable isotope analyses to address the question of how important seabird consumption is to introduced house mice *Mus musculus* on Gough Island. There are significant differences between highland and lowland sites in terms of demographic parameters and densities of mice, densities and species of breeding seabirds, climate and general ecology. $\delta^{15}N$ values of the abundant and ubiquitous sedge *Scirpus* spp. were significantly negatively correlated with altitude ($p=0.008$), reflecting altitudinal differences in marine nitrogen input, with higher manuring rates from seabirds in the lowlands. Mouse isotope signatures (both $\delta^{15}N$ and $\delta^{13}C$) confirm that highlands and lowlands are functionally different and should be treated separately. In the lowlands, GLMs showed a strong, significant enrichment of both isotopes for mice in August-September (late austral winter) relative to other times. Seabird remains in mouse stomachs were low through winter, but peaked in August, providing strong empirical support for the isotope findings. The onset of these increases in apparent seabird consumption coincided with the hatching of Atlantic Petrel *Pterodroma incerta* eggs and very high predation rates by mice on petrel chicks. Using $\delta^{13}C$ only, a rough estimate suggests seabird consumption contributes 40-60% to mouse diets at this time. These findings support the hypothesis that seabirds are an important part of mouse diets in late winter in the lowlands. Intriguingly, seabird remains in mouse stomachs also peaked in March (austral autumn). This suggests mouse predation of seabird chicks in autumn may be more than incidental. In opposition to this result, the corresponding $\delta^{13}C$ mouse values did not reflect seabird consumption; these results merit further research. In the highlands I compared a site with severe predation on Tristan Albatross *Diomedea dabbenena* chicks (Green Hill) to one with low predation (Gonydale). GLMs revealed no effect of site on plant $\delta^{15}N$ or $\delta^{13}C$. Surprisingly, despite strong differences in albatross chick predation rates between sites, mice did not differ in $\delta^{13}C$ values, strong evidence for no differences in the relative importance of seabird consumption between sites.

Stomach content analysis from mice collected in May revealed virtually no seabird remains in Gonydale but a mean for Green Hill >30% by volume. Nevertheless, no seabird consumption in Gonydale, and no differences in seabird contribution to mouse stable isotope signatures between sites implies that seabird consumption is also a negligible component of mouse diets at Green Hill. The fertilising effect of seabirds means that terrestrial productivity could decrease in tandem with their decreases at all altitudes. This effect could drive down mouse numbers, ameliorating predation levels, or it could cause increased reliance on seabirds, setting up a positive feedback and exacerbating an already dire situation for the seabirds and the whole ecology of Gough Island. This should be a conservation research priority.

Introduction

A variety of techniques exists to assess the importance of different food resources to a consumer. Behavioural observations and analysis of stomach contents, despite some inherent weaknesses as analytical tools (e.g. pseudo-replication and differential retention times of dietary items), can provide broadly reliable information about diet, at a minimum indicating presence/absence of major prey types. The diet of Gough mice was studied in 1999/2000 using stomach content analysis, and suggested that the importance of different dietary items for mice in the lowlands changed seasonally (Jones et al. 2003a,b). A point of interest from that study was the prominence of avian remains in mouse stomach samples during the winter months. In Chapters 2, 3 and 4 I show that introduced house mice *Mus musculus* prey upon chicks of Atlantic Petrels *Pterodroma incerta* and Tristan Albatrosses *Diomedea dabbenena*, and that this has significant, negative consequences for the seabird species' populations. However, what has not been shown is whether seabird consumption is important in mouse population dynamics. Is it a key or an incidental food resource for mice? What are the spatio-temporal patterns in seabird consumption? Is it a rare specialism or a general behaviour? A key unknown is the importance of seabird consumption in sustaining the mouse population.

The use of stable isotopes has added a new dimension to ecological studies of diet. Body tissues are constantly broken down and rebuilt (referred to as 'tissue turnover'), and the differential (and generally systematic) enrichment of tissues with heavier carbon and nitrogen isotopic elements during metabolic processes (known as fractionation) has made possible studies of consumer diets that overcome many of the problems common to traditional approaches to diet analysis (DeNiro & Epstein 1978, 1981; Kelly 2000; Phillips & Gregg 2001; Phillips & Koch 2002; Dalerum & Angerbjörn 2005). The component chemicals of a consumer's tissues consist of a mix of its dietary sources, i.e. you are what you eat (DeNiro & Epstein 1978). Stable isotope analysis of prey types (or 'sources') with distinct isotopic values ('signatures') can be used as natural chemical tracers (Kelly 2000; Phillips & Gregg 2001; Phillips & Koch 2002). The rate of tissue turnover will determine how long it takes for new dietary items to be reflected in a consumer's tissues (MacAvoy et al. 2005; MacAvoy et al. 2006). Thus the strength of a source's signature will depend on its relative contribution to the diet and, if the diet changes, the time that the sampled tissue takes to equilibrate. The analysis of isotopes from lean muscle tissue will reflect the relative contributions of different protein sources (lipids have alternative metabolic pathways and are essentially independent of proteins) (Arneson & MacAvoy 2005). Thus if a dietary switch occurs to a hypothetical source with distinct $\delta^{13}C$ and $\delta^{15}N$ values, the new source's signature must be reflected in changes of both $\delta^{13}C$ and $\delta^{15}N$ values of the consumer's tissues. A change in one isotope, but not the other, reflects something other than the inclusion of the new source.

With n stable isotope variables it is possible to estimate the relative contribution of n+1 dietary sources to a consumer's tissue. Given this condition, proportional contributions can be determined by use of linear mass balance mixing models, once the source values have been adjusted to account for trophic fractionation (DeNiro & Epstein 1978, 1981; Hobson 1999). Thus for a two-isotope system, the relative contributions of up to three sources can be determined precisely. This can be visualised using a bivariate plot of two isotopes (Figure 1): the plot of the mixture must fall between the connecting lines of the three dietary sources, referred to as the mixing space (Phillips & Koch 2002). However, if the potential sources exceed n+1, possible contributions can still be estimated using mixing models, for example using the software Isosource (Phillips & Gregg 2003). Briefly, this method estimates all possible combinations of each source contribution (in user-defined increments). If the mixture lies outside the mixing space, it indicates that either an important dietary source has been omitted, the number of samples is too few to adequately describe the source's variability, an incorrect fractionation value has been used or an assumption of the mixing model has been violated, such as that the consumer's tissue is in equilibrium with sources (Phillips & Koch 2002; Carleton & del Rio 2005).

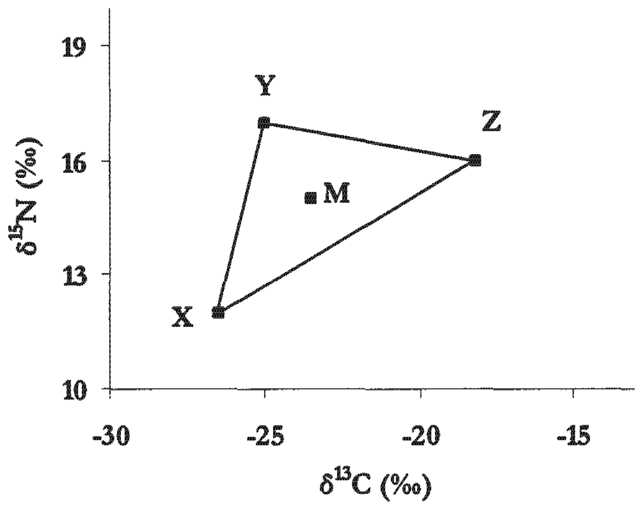

Figure 1. Hypothetical example of a two-isotope mixing triangle, with three dietary sources (X, Y and Z) after adjusting for fractionation and a consumer mixture (M).

In this chapter I compare the Jones et al. (2003a) data from 1999/2000 to a second season of stomach samples from lowland mice. However, given the problems associated with this kind of data, primary inference of seabird consumption by mice is based on stable isotope analyses. I also describe patterns of variation in plant isotope signatures. For plants, I predict that $\delta^{15}N$ will differ significantly with altitude, because lowlands have far higher densities of nesting seabirds (Swales 1965; Cuthbert & Sommer 2004), and should therefore have a much stronger marine $\delta^{15}N$ signature (Hobson et al. 1999; Stapp et al. 1999; Drever et al. 2000). These differences also should be reflected in invertebrate and mouse $\delta^{15}N$ signatures. The pattern of attacks on seabird chicks is described in detail in Chapters 2 and 3 (on Atlantic Petrel chicks in the lowlands and Tristan Albatross chicks in the highlands, respectively). In the lowlands, attacks on Atlantic Petrel chicks commenced at hatching in July/August 2004. The timing of Atlantic Petrel chick hatching coincides with decreasing mouse body condition (Chapter 6) and the birds therefore represent an opportunity for mice to suddenly include significant quantities of highly nutritious seabird in their diet at what is ostensibly a critical juncture in their annual survival. I compare the isotope signatures of highland plants and mice from sites with and without attacks. In the highlands, attacks on albatross chicks commenced in April and continued into September. I use stable isotope data to address two main questions. First, do all mice eat some seabirds, is there a normal distribution along a continuum or are some mice 'seabird specialists'? Second, if the consumption is significant, do sex, body size or body condition predict whether an animal will be a seabird specialist? The overarching objective of this chapter is to quantify the importance of seabirds as a food resource to highland and lowland populations of mice.

Methods

Sample collection

For a full description of mouse trapping regimes see Chapter 6. In brief, mice were trapped at monthly intervals from November 2003-September 2004 in the lowlands and from December 2003-September 2004 (excluding February and April) in the highlands. Additional trapping in the highlands was conducted at Green Hill (May and July) and Albatross Plain (May). Hearts were dissected and analysed for isotopes from all highland mice and a sub-sample of 20 mice/month from the lowlands. I harvested fresh muscle tissue from six Atlantic Petrel chicks that were attacked and killed by mice the previous night. Invertebrates were collected from each lowland mouse-trapping plot by pitfall traps and dedicated searches for Lumbricid worms (hereafter earthworms), but extremely low success of pitfall traps meant that very few non-earthworm samples were collected. In the highlands, similarly poor success with pitfall traps meant that invertebrates were collected opportunistically. Feathers were collected randomly from adult Tristan Albatrosses; differences between adult feather and chick muscle signatures are expected to be negligible relative to differences of either to other sources (Cherel et al. 2000; Cherel et al. 2002; Cherel et al. 2005; Dalerum & Angerbjörn 2005; Podlesak et al. 2005; Cherel et al. 2006).

Plant samples for stable isotope analysis were collected in lowland and highland sites, as well as along an elevational gradient at 50 m contour intervals from 100-450 m (totalling eight stations) between the lowlands and the highlands. Plant samples were collected from five stations in all nine mouse trapping grids (see Chapter 6). Stations were at each corner and the centre of grids. In the highlands, sampling grids were established at Green Hill and Gonydale, in the same locations in which relative abundance of plant groups was estimated (Chapter 3). In Gonydale a 5 x 6 grid was laid; five lines running parallel with elevation contours and separated by 50 m, and six stations on each line, each station separated by 25 m, totalling 30 stations and covering 7.5 ha. This included a mouse-trapping site. The design at Green Hill was the same, except that it was a 4 x 8 grid, totalling 32 stations and covering 8 ha; in addition I collected 14 plant samples from a Green Hill mouse-trapping grid. I collected only *Scirpus* spp. (Cyperaceae) along the elevational gradient, because aside from it being an important food resource for mice (Jones et al. 2003a) it was the most widespread genus and was abundant in all locations and elevations, and thus most appropriate for large-scale comparisons. Altitude was determined using a Garmin GPS with a minimum of 10 m coordinate accuracy and after the altitude reading had not changed by >5 m in a minute. Target genera were chosen because they were a) common, and thus likely to occur in most sampling stations, and/or b) known or likely food plants for mice (Jones et al. 2003a). Target genera in the lowlands were *Scirpus* sp., *Acaena sarmentosa* (Rosaceae), and *Histiopteris incisa* (fern) and in the highlands *Apium australe* (Apiaceae), *Empetrum rubrum* (Empetraceae), *Nertera depressa* (Rubiaceae) and *Acaena* sp. and *Scirpus* sp. At each sampling station only those target species that were within a 1 m radius were collected, thus not all species were present in each station. This method was chosen to circumvent any species-specific biases, such as growing only where there is strong nitrogen input from seabirds.

Stable isotope analysis

All samples were rinsed in distilled water to remove surface contaminants and then oven-dried at 70° C (plants and feathers) or freeze-dried (all other tissues) before being processed. Seabird muscle was defatted in a mixture of methanol, chloroform and water (2:1:0.8) and placed in a demineralizing solution of 0.1N HCl for 24-36 hrs. They were then rinsed repeatedly in distilled water and freeze-dried. Samples were weighed to an accuracy of 1 μg on a Sartorius micro balance and enclosed in tin cups before being combusted. Carbon and nitrogen isotopes were determined in a Finnigan Flash EA 1112 series elemental analyser coupled to a Delta^{Plus} XP isotope ratio mass spectrometer via a Finnigan Conflo III gas control unit. Results are presented in conventional δ notation in units of parts per thousand (‰), relative to Pee Dee Belemnite and atmospheric nitrogen international standards for $\delta^{13}C$ and $\delta^{15}N$, respectively, derived from the expression:

$$\delta = \left(\frac{R_{Sample} - R_{standard}}{R_{standard}}\right) \times 1000 ,$$

where R_{sample} is the isotopic ratio of the sample and $R_{standard}$ is the isotopic ratio of the relevant international standard. Analyses included three in-house standards every 20 samples. Standard deviations for repeated measurements of laboratory standards were less than 0.1‰ for $\delta^{13}C$ and 0.3‰ for $\delta^{15}N$.

Data analysis

I plotted $\delta^{15}N$ against $\delta^{13}C$ values for mice from the lowlands in August and for all mice from the highlands, together with likely dietary items. Means were calculated by pooling data except for plants, where I calculated the mean of the genus- or species-specific means. I used the lower estimate of $\delta^{15}N$ fractionation (3.8‰) estimated by Arneson & MacAvoy (2005) for house mice under experimental conditions and a fractionation of 1‰ for $\delta^{13}C$, typical of most dietary studies and within the range for house mice (Arneson & MacAvoy 2005). A variety of techniques, such as Isosource (Phillips & Gregg 2003) and variations that account for differences in C:N ratios, CIs, SEs and sample sizes of sources (Phillips & Gregg 2001; Koch & Phillips 2002; Phillips et al. 2005) were used to estimate relative source contributions.

I tested for the effect of altitude on $\delta^{15}N$ and $\delta^{13}C$ values, so that subsequent analyses would use only appropriate datasets. For mice, differences in stable isotope values between highlands and lowlands were tested using a t-test. For plant isotopes, all *Scirpus* $\delta^{15}N$ and $\delta^{13}C$ data (using means for the lowlands and highlands) were regressed against elevation. Note that only seven mid-altitude *Scirpus* samples were available for the nitrogen analysis because repeated machine failures consumed all material from the 300 m contour. I checked for spatial homogeneity of lowland plant stable isotope values both within and between plots using ANOVAs, because mice trapped in plots that differed in average isotope signatures would most likely be consuming plants (and other organisms higher up the food-chain) with differing stable isotope signatures, and would not be strictly comparable. First, fine-scale, within-plot differences were tested with main effects ANOVAs, using all plant samples collected from a single 8×8 m grid, with species and station (the point of collection within the grid, each station being *ca* 5 m apart) as categorical predictors and $\delta^{15}N$ and $\delta^{13}C$ as respective response variables. Only one grid was analysed because of prohibitive costs of stable isotope analyses; the grid chosen had all target species present in all stations. Second, variance at the meso-scale (between plots) was tested with one-way ANOVAs, using only *Scirpus* sp. (to control for potential inter-specific differences), with plot as a categorical predictor and $\delta^{15}N$ and $\delta^{13}C$ as respective response variables. For the highlands, General Linear Models (GLMs) were performed, to test for differences between Green Hill and Gonydale in stable isotope values of *Scirpus, Acaena,* and *Empetrum*, the main food plants for which I had >10 samples per site. $\delta^{15}N$ and $\delta^{13}C$ were response variables in respective models, and species and site (plus a two-way interaction) were categorical explanatory variables. Non-significant interactions and then terms were removed sequentially to produce minimum adequate models.

A potential source of error in plant isotope analyses is differences between vegetative and reproductive tissues. Plant samples were collected in September, and I was only able to collect reproductive parts from *Empetrum* plants in the highlands. I tested for differences between leaves (vegetative) and flowers (reproductive) parts in this species using a paired t-test.

Measures of mouse body condition and tail length (a surrogate for body size), used as explanatory variables in some analyses, are the same as those described in Chapter 6. Stable isotope data from the lowlands were divided into four seasons (based on biological and environmental considerations), designated summer (Nov-Feb), autumn (Mar-Apr), early-winter (May-Jul) and late-winter (Aug-Sep). GLMs were performed with isotopic ratios as response variables and season, sex, body condition and size as explanatory variables, plus all possible 2-way interactions, to test for seasonal trends in isotopic values of mice in the lowlands. Body weight was not included as a variable because it is highly correlated with skeletal body size, and is already accounted for in body condition. Non-significant interactions and then terms were deleted sequentially to produce minimum adequate models. For the highlands, I compared mice trapped at Green Hill (with numerous attacks on albatross chicks) with Gonydale (with very few attacks). GLMs were performed as for the lowland data, except site replaced season as an explanatory variable. Interpretation of results is premised on the fact that seabirds are isotopically enriched for both nitrogen and carbon relative to all other sources (see Figure 4). Thus for seabird consumption to be indicated, both $\delta^{15}N$ and $\delta^{13}C$ signatures should change.

I analysed the frequency distributions of $\delta^{15}N$ and $\delta^{13}C$ by season for the lowlands and by site for the highlands. Frequencies were determined in 0.5‰ steps. Data for highland sites are presented as proportional frequencies because of large differences in sample sizes. For clarity of presentation, distributions are presented as frequency polygons rather than histograms (Zar 1999).

All statistical analyses were performed in Statistica (StatSoft 2004). Significance is reported at the 0.05 level and to three significant figures. SD, SE and CI denote standard deviation, standard error and 95% confidence intervals, respectively.

Stomach contents

Stomachs were dissected out from 20 mice/month trapped from the lowlands (November-August) and all mice snap-trapped in the highlands in May. Stomachs were preserved in 70% ethanol. Lowland samples from July went missing and September mice were live-trapped, so diet data from these months are absent as a consequence. Stomachs were opened, flushed with ethanol and the contents examined under a Kowa SDZ-PL optical light microscope, using 7-45 times magnification. Identifiable remains were grouped according to the following categories: plants, flightless moths (*Dimorphinoctua goughensis* and *Peridroma goughi*), earthworms, other invertebrates, birds and mice. The bird and mouse remains were identified principally on the basis of feathers and hair, respectively, although flesh was found occasionally with hair or feathers still attached. For each stomach, the percentage volume (PV) that each dietary group made to the total stomach content was estimated. The highly digested state of most mouse stomach contents made detailed analyses and comparisons with other work difficult. Furthermore, from February-August, it is probable that many mice were trapped after they had scavenged carcasses of mice already trapped that night. This is likely to have had a strong bias on an estimate of levels of cannibalism, and the mouse remains were not analysed further.

Differential retention times for hard and soft parts and the high visibility and good diagnostic features for certain prey types can bias estimates of PV. Earthworms and moths were easily detected, because I was able to identify highly characteristic, banded pattern (the body segments) and scaly thoraxes or larval integuments, respectively, and could estimate quite accurately the PV that those items comprised. In contrast, bird and mouse flesh were extremely difficult to identify and impossible to discriminate between them in the absence of either feathers or hairs. However, feathers and hairs are indigestible and probably remain in stomachs for longer than soft-tissues. Thus the volume of seabird remains (for example) may be underestimated if it is a recent addition to the diet (because soft tissues are difficult to identify), but if consumed over a period of days or weeks, may be overestimated as feathers accumulate in the gut. The mean PV of seabird remains in mouse stomachs was calculated for all samples per month in the lowlands. These were compared to monthly seabird PVs from 1999/2000 (data courtesy of A. Jones). I tested for differences in the proportions that seabird remains contributed to monthly stomach contents between years with a Chi-square test, the null hypothesis being that 2003/04 did not differ from 1999/2000.

A problem common to both stable isotope and stomach content analyses is the inability to distinguish between seabird consumption derived from scavenging carcasses from Subantarctic Skua *Catharacta antarctica* kills as opposed to from mice preying on seabird chicks. To compensate, I also made weekly counts of skua numbers at a communal roost near the research station (lowlands), to give a rough indication of seasonal changes in skuas at Gough, and concomitant numbers of seabird carcasses provided by these predatory seabirds, typically 1-2 birds per night per skua (Furness 1987); pers. obs.). I compared PVs from mice trapped in three separate areas the highlands (Green Hill, Albatross Plain and Gonydale) in the month of May 2004.

Results

Stable isotopes

$\delta^{15}N$ and $\delta^{13}C$ signatures were analysed from 117 highland mice and 201 lowland mice trapped in 2003/04. Sample sizes of lowland mice were 68 (summer), 40 (autumn), 58 (early-winter) and 35 (late-winter), and in the highlands, 98 mice were analysed from Gonydale (including 60 from May-July) and 19 from Green Hill (all from May-July). Male:female sex ratios were 0.703:1 (lowlands) and 0.705:1 (highlands), virtually identical to the ratio for all trapped mice for the year (0.708:1, Chapter 6). I analysed 14 highland and 30 lowland invertebrate samples, six Atlantic Petrel chick muscle samples, four Tristan Albatross feather samples and 246 plant samples, including 58 lowland samples and 180 highland samples. Raw isotope data for all sources are in Appendix 1.

Highland mice were substantially depleted for $\delta^{15}N$ (mean=6.98‰, SE=0.179) relative to lowland mice (mean=14.59‰, SE=0.010) and slightly depleted for $\delta^{13}C$ (mean=-23.54‰, SE=0.060) relative to the lowlands (mean=-22.13‰, SE=0.061). A dual-isotope plot of mouse data showed a clear difference between highland and lowland mice (Figure 2) with significant differences for both $\delta^{15}N$ (T_{186}=23.2, $p<0.001$) and $\delta^{13}C$ (T_{186}=11.6, $p<0.001$). Using data from *Scirpus*, there was a highly significant negative relationship between $\delta^{15}N$ and altitude (R^2=0.66, $F_{1,7}$=13.7, p=0.008, highlands mean=5.08‰, SE=0.317, lowlands mean=11.41‰, SE=0.432), but there was no effect of altitude on $\delta^{13}C$ ($R^2<0.01$, $F_{1,8}$=0.035, p=0.86, highlands mean=-26.68‰, SE=0.144, lowlands mean=-27.08‰, SE=0.272, Figure 3). Thus both plants and mice showed strong, consistent altitudinal differences in $\delta^{15}N$ signatures. This confirmed my hypothesis, that the highlands and lowlands were isotopically very different systems, and subsequent analyses treated them separately. In addition, a visual inspection of Figure 2 shows that there were no strong dual-isotope outliers or clusters of individuals from either site. This implies a single statistical population with random variation at each altitude, with no genuine seabird specialists or seabird-avoiders. Finally, the altitudinal differences in mouse $\delta^{13}C$ suggest quite different diets, because there were no altitudinal differences in plants for this isotope.

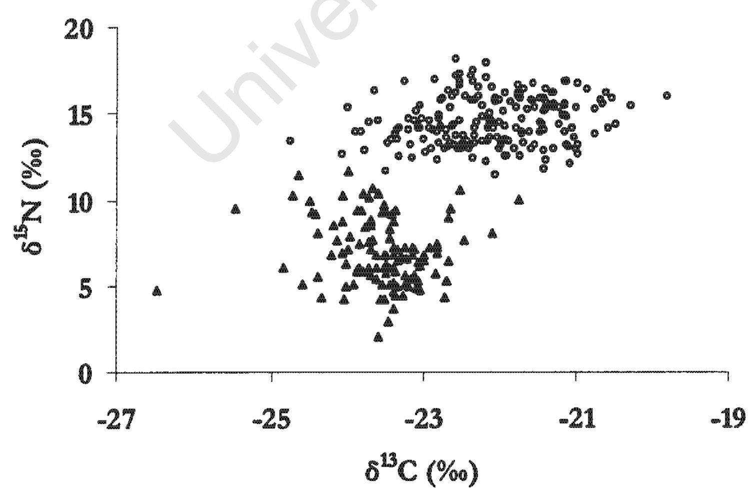

Figure 2. Dual isotope plot of all stable isotope data from highland mice (▲, n=117) and lowland mice (○, n=201) trapped on Gough Island in 2003/04.

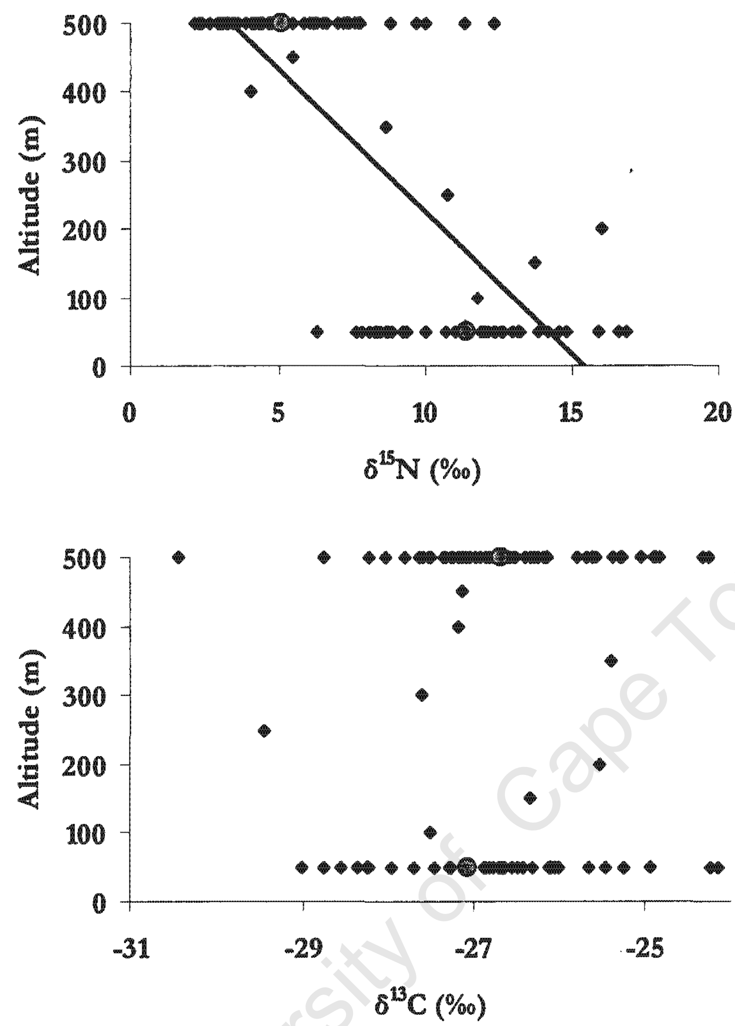

Figure 3. Relationship between altitude and $\delta^{15}N$ and $\delta^{13}C$ values for *Scirpus* spp. sedges on Gough Island. Lowland and highland data were set at 50 m and 500 m, respectively, and means were used for regression analyses (indicated by shaded circles). Regression line for $\delta^{13}C$ is not shown because it was non-significant and had a very low R^2.

ANOVA tests for fine-scale, intra-plot variation in $\delta^{15}N$ and $\delta^{13}C$ in the lowlands revealed no systematic effect of station on either $\delta^{15}N$ ($F_{4,8}$=1.6, p=0.26) or $\delta^{13}C$ ($F_{4,8}$=1.7, p=0.50). $\delta^{15}N$ signatures for the three species examined (n=5 samples per species) did not differ significantly ($F_{2,8}$=3.2, p=0.098) but $\delta^{13}C$ signatures did ($F_{2,8}$=7.3, p=0.016). Thus at the scale of a plot, $\delta^{15}N$ did not appear to vary significantly and $\delta^{13}C$ varied systematically between species but not spatially. At the meso-scale, the ANOVA tests for differences between plots were non-significant for

$\delta^{13}C$ values ($F_{8,29}$=1.13, p=0.373) but were significant for $\delta^{15}N$ values ($F_{8,29}$=4.39, p=0.002), indicating substantial heterogeneity between plots within similar altitudes and habitats. A Tukey post-hoc comparison for unequal sample sizes showed that the only significant differences were between plots B1 and A1 (p=0.05) and B1 and C2 (p=0.008). I took a conservative approach and excluded mouse samples from B1 in subsequent stable isotope analyses.

For the highlands, the final GLM showed a significant effect of species on $\delta^{15}N$ ($F_{2,123}$=22.2, p<0.001) as well as a significant species × site interaction ($F_{2,123}$=50.7, p<0.001), but no site effect (although this was retained in the final model). Parameter estimates are presented in Table 1. The model indicates that *Scirpus* was significantly enriched relative to *Acaena* and *Empetrum*, and *Empetrum* significantly depleted relative to *Acaena*. The interaction effect showed that in Gonydale (relative to Green Hill) *Scirpus—Acaena* differences were smaller but also that *Empetrum* was more enriched relative to *Acaena*. For $\delta^{13}C$ there was also a significant species effect ($F_{2,126}$=35.1, p<0.001), with *Scirpus* significantly enriched relative to *Acaena*. There were no site or interaction effects. Because neither model showed significant site-effects, differences between Green Hill and Gonydale mouse signatures are not likely to be due to differences at the base of the food-chain. There were no significant differences between vegetative and reproductive tissues for *Empetrum* samples (T_{22}=-0.3, p=0.8).

Dual-isotope plots of mice from both the lowlands (Figure 4) and highlands (Figure 5) and likely dietary sources (Table 2) show that the mean mouse values do not fall within their respectively delineated mixing spaces. This suggests a significant violation of some assumption(s) and meant that none of the techniques for estimating source contributions from two isotopes could be used, without first making arbitrary changes to $\delta^{15}N$ values for sources, or their fractionation. Alternatively, a new source is required with a much lower $\delta^{15}N$ value but a relatively high $\delta^{13}C$ (lowlands) or a low $\delta^{13}C$ (highlands). Note that mice were included as a putative source despite the probability that levels of cannibalism were overestimated.

Table 1. GLM relationships between stable isotope values, species and site, from plants collected in the highlands of Gough Island. All models were tested against Green Hill (site effect) and *Acaena* (species effect) as reference values (as appropriate).

	Comparison	DF	Parameter estimate (SE)	p
Response variable: $\delta^{15}N$				
Intercept		1	3.13 (0.22)	<0.001
Species	*Empetrum*	2	-1.47 (0.32)	<0.001
Species	*Scirpus*	2	1.81 (0.29)	
Site	Gonydale	1	-0.10 (0.22)	0.64
Species × Site	*Empetrum*	2	1.24 (0.32)	<0.001
Species × Site	*Scirpus*	2	-0.90 (0.29)	
Response variable: $\delta^{13}C$				
Intercept			-27.41 (0.09)	<0.001
Species	*Empetrum*	2	0.23 (0.13)	<0.001
Species	*Scirpus*	2	0.73 (0.11)	

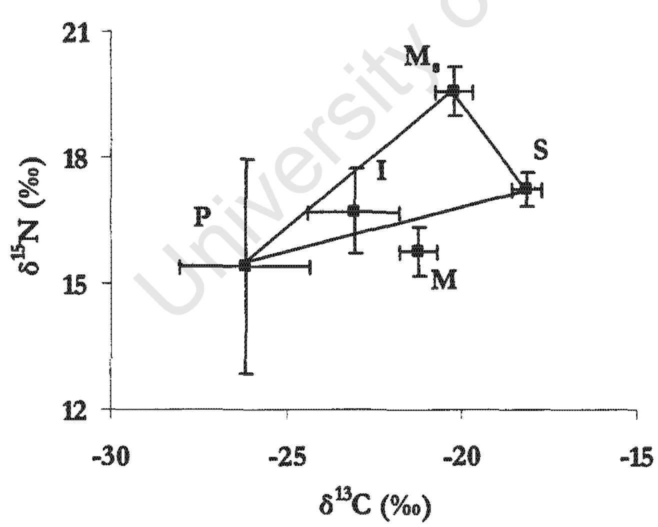

Figure 4. Mixing space on a plot of dual isotopic compositions of lowland mice and putative lowland food sources (after adjustment for trophic fractionation, estimated at 3.8‰ ($\delta^{15}N$) and 1‰ ($\delta^{13}C$)) on Gough Island. P=edible plants, M=mice, M_s=mice as a source, I=invertebrates and S=seabirds. Error bars denote one SD.

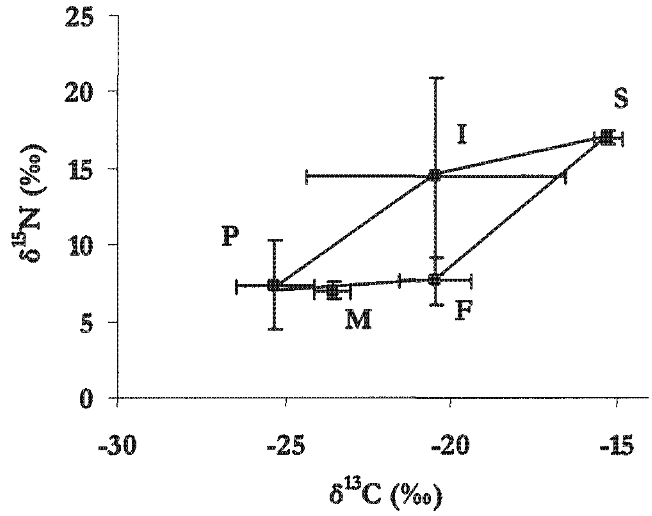

Figure 5. Mixing space on a plot of dual isotopic compositions of all highland mice and putative food sources (after adjustment for trophic fractionation, estimated at 3.8‰ ($\delta^{15}N$) and 1‰ ($\delta^{13}C$)) P=edible plants, M=mice, M_s=mice as a source, I=invertebrates, F=flightless moths and S=seabirds. Error bars denote one SD.

Table 2. Summary isotope data for dietary sources used in analysis of the diets of mice on Gough Island. Raw data in Appendix 1.

Sources		$\delta^{15}N$			$\delta^{13}C$	
Highland	n	Mean	(SD)	Range	Mean (SD)	Range
Moth	6	3.82	(1.52)	2.06-6.198	-26.45 (1.08)	-28.34 to -25.56
Earthworm	1	3.71			-24.08	
Other invert.	7	10.90	(5.36)	5.73-18.98	-21.86 (3.90)	-24.69 to -16.45
Tristan Albatross	4	13.20	(0.31)	12.92-13.48	-16.24 (0.31)	-16.41 to -15.77
Plant	129	3.54	(2.92)	-3.77-12.35	-27.29 (1.18)	-24.26 to -30.44
Lowland						
Earthworm	10	12.95	(0.73)	11.65-13.82	-24.26 (0.94)	-25.83 to –22.72
Other invert.	20	12.72	(1.28)	10.51-15.17	-24.37 (1.65)	-27.46 to -20.57
Atlantic Petrel	6	13.43	(0.41)	13.01-14.18	-19.15 (0.44)	-19.79 to -18.53
Plant	58	11.59	(2.56)	6.31-18.25	-27.17 (1.83)	-32.38 to -23.62

The minimum adequate model for differences in $\delta^{15}N$ signatures from mice in the lowlands had a strongly significant seasonal effect ($p=0.001$). The effect of size was non-significant ($p=0.58$), but this effect was retained in the model because there was a significant size × season interaction ($p<0.001$). Parameter estimates and test statistics are presented in Table 3. The effect of size varied between seasons, although the magnitude of the effect was relatively minor. The model predicted a negative relationship between size and $\delta^{15}N$ in summer (i.e. larger mice were slightly depleted relative to smaller mice) but predicted a positive relationship in autumn. In testing for differences in lowland mouse $\delta^{13}C$ signatures, the final GLM included no significant interaction terms and season ($p<0.001$), body condition ($p=0.02$) and size ($p<0.001$) as explanatory variables. Relative to late-winter (the reference for analyses), all other seasonal values were depleted, with summer and autumn values significantly depleted. Size had a significant positive effect on $\delta^{13}C$, meaning that the expected $\delta^{13}C$ signatures from the heaviest mice (>40 g) were approximately 1.1‰ enriched compared to the smallest mice (10 g). The effect of body condition was also positive: the model estimated that mice varied by as much as *ca* 2‰ within the observed range of body condition.

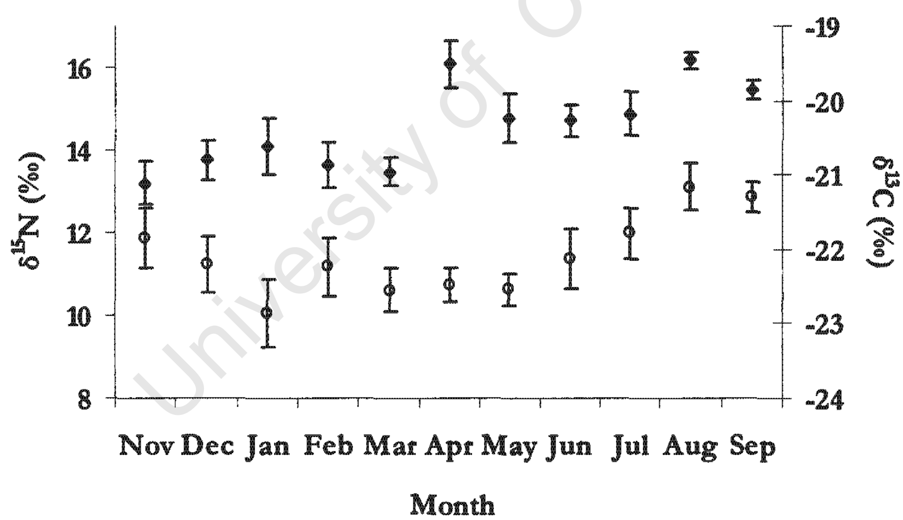

Figure 6. Temporal changes in $\delta^{15}N$ (♦) and $\delta^{13}C$ (○) ratios of mice trapped in the lowlands of Gough Island. Vertical bars denote CI.

Table 3. GLM effects of season, body size and body condition on stable isotope values from house mice in the lowlands of Gough Island. All seasonal parameter estimates are modelled relative to late-winter. Only significant terms and interactions are presented.

	Comparison	DF	Parameter estimate (SE)	F	p
Response variable: $\delta^{15}N$					
Season	Summer	3,183	3.112 (1.673)		
Season	Autumn	3,183	-6.765 (1.797)	5.67	0.001
Season	Early-winter	3,183	0.543 (2.188)		
Size		1,183	0.007 (0.013)	0.31	0.580
Season × size	Summer	3,183	-0.047 (0.018)		
Season × size	Autumn	3,183	0.077 (0.020)	6.53	<0.001
Season × size	Early-winter	3,183	-0.007 (0.023)		
Response variable: $\delta^{13}C$					
Intercept			-26.645 (1.105)		<0.001
Season	Summer	3,188	-0.220 (0.086)		
Season	Autumn	3,188	-0.330 (0.105)	11.26	<0.001
Season	Early-winter	3,188	-0.116 (0.087)		
Size		1,188	0.027 (0.007)	14.19	<0.001
Body condition		1,188	2.041 (0.854)	5.71	0.018

The effect of season on the distribution of isotopic ratios of lowland mice is illustrated in Figure 7. The shift in $\delta^{15}N$ values from lowest values in summer to highest values in late-winter is obvious. However, the autumn distribution included a relatively high proportion of enriched values, reflecting the contribution from April (Figure 6). The distributions of $\delta^{15}N$ values were essentially uni-modal in summer, early-winter and late-winter. Summer and early-winter distributions had strong single peaks clustered around 13.5-14.5‰ and long tails to the right. The autumn distribution was dissimilar to other seasons in being less well-defined and showing almost no central tendency, with the strongest pattern being a near-absence of values from 15-16‰. The range of values in late-winter was mostly between 15.5-16.5‰. Seasonal $\delta^{13}C$ distributions were approximately uni-modal. The biggest seasonal difference was between early-winter, when the modal range centred on -22.5, compared to -21 in late-winter. Also, as for $\delta^{15}N$, the range of $\delta^{13}C$ values in late-winter was noticeably narrower than at any other time, although variance ratio tests found that late-winter differed significantly only from autumn ($F_{15}=3.7$, $p<0.05$) for $\delta^{15}N$ and there were no seasonal differences for $\delta^{13}C$. This suggests that feeding niche was broader in autumn than in late-winter.

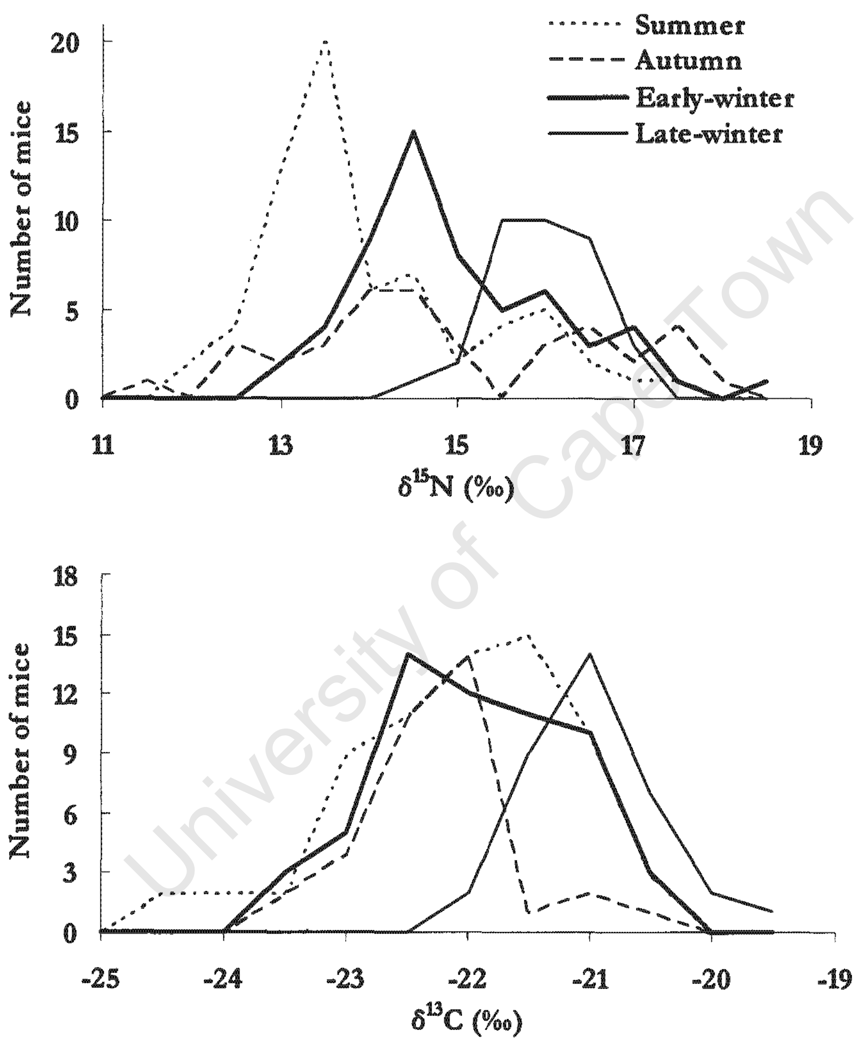

Figure 7. Frequency polygons of seasonal $\delta^{15}N$ and $\delta^{13}C$ values of mice trapped in the lowlands of Gough Island, 2003/04.

I could not determine the importance of seabird consumption to lowland mice without an estimate of the percentage contribution from stable isotopes. I therefore attempted an estimate for late-winter mice using Isosource, disregarding nitrogen and using $\delta^{13}C$ values from Table 2 and the mean late-winter mouse $\delta^{13}C$ value (-21.25‰). The initial estimates were relatively unconstrained, as expected for an analysis with a single isotope and four sources (plants, invertebrates, seabirds and mice), one of which is both source and mixture. Nonetheless, possible contributions were Plants: range 0-33%, mode=1%, Invertebrates: range 0-62%, mode=0%; Seabirds: range=0-70%, mode=38% and Mice: 0-100%, mode=0%. If mice are assumed to be a minor source and are removed, the contribution of seabirds becomes more defined: range=40-60%, median=54% (there was no defined mode). This represents a very rough estimate of the likely contribution that seabirds make to the diet of lowland mice in August-September.

The GLMs testing for differences in highland mouse signatures between Green Hill (with attacks on albatross chicks) and Gonydale (with few attacks on albatross chicks) showed significant effects of site ($p<0.001$), size ($F_{1,70}=10.26$, $p=0.002$) and body condition ($p=0.008$) on $\delta^{15}N$ values, and no interaction effects. On average Gonydale mice were $\delta^{15}N$-depleted relative to Green Hill by 1.03‰ (SE±0.22‰). Bigger mice were enriched for $\delta^{15}N$ and across the range of observed sizes (tail lengths: 72-107 mm), the model estimated enrichment differed by *ca* 3.1‰ (SE±1.1‰). The model estimated an even stronger positive effect of body condition, implying that the $\delta^{15}N$ signatures of mice in best condition were massively enriched by *ca* 9.2‰ (SE±3.33‰) relative to the mice in poorest condition. However, the model fit was relatively poor (whole-model $R^2=0.32$), suggesting that these results be treated with caution. The minimum adequate model for the equivalent $\delta^{13}C$ test had a very poor fit to the data (whole-model $R^2=0.13$) and results are not presented. A variance ratio test found no significant differences between the sites for $\delta^{13}C$ ($F_{19,30}=1.54$, $p>0.20$), but Gonydale mice were marginally enriched for $\delta^{13}C$ (mean=-23.52, SE=0.10) relative to Green Hill (-23.83, SE=0.155), and a t-test for site differences approached significance ($T_{58}=2.0$, $p=0.052$). I conclude that differences in $\delta^{13}C$ appear minor.

Frequency distributions of both isotopes for highland mice (Figure 8) corroborated the GLM results, showing a range of higher values for $\delta^{15}N$ and a lower peak for $\delta^{13}C$ at Green Hill vs Gonydale. This is a key result for the highlands, because there were no significant differences in plant isotopes between Green Hill and Gonydale, and thus the seabirds, with highly enriched $\delta^{15}N$ and $\delta^{13}C$ values (Figure 5), were not being consumed at levels detectable with stable isotope analysis. An intriguing result is the effect of size and body condition on $\delta^{15}N$. The frequency distribution of $\delta^{15}N$ for Green Hill clearly shows two 'populations', feeding on different sources.

Table 4. Effects of site, body size and body condition on $\delta^{15}N$ values from house mice in the highlands of Gough Island. Site parameter estimates are modelled relative to Green Hill, based on General Linear Models. Only significant terms are presented.

	Comparison	DF	Parameter estimate (SE)	F	p
Response variable: $\delta^{15}N$					
Intercept			-9.011 (4.20)		0.035
Site	Gonydale	1,70	-1.076 (0.232)	21.45	<0.001
Size		1,70	0.088 (0.028)	10.26	0.002
Body condition		1,70	9.168 (3.328)	7.59	0.007

Stomach contents

Stomach samples were analysed from 170 lowland mice and from 114 highland mice. Summary data are presented in Figure 9 (lowland mice, November-August) and Figure 10 (highland mice, May-September). Of those samples, 79 and 22, respectively, contained virtually no (≤5% by volume) identifiable remains. These poor results limited my capacity to make comparisons with Jones et al. (2003), which I confine to seabird remains.

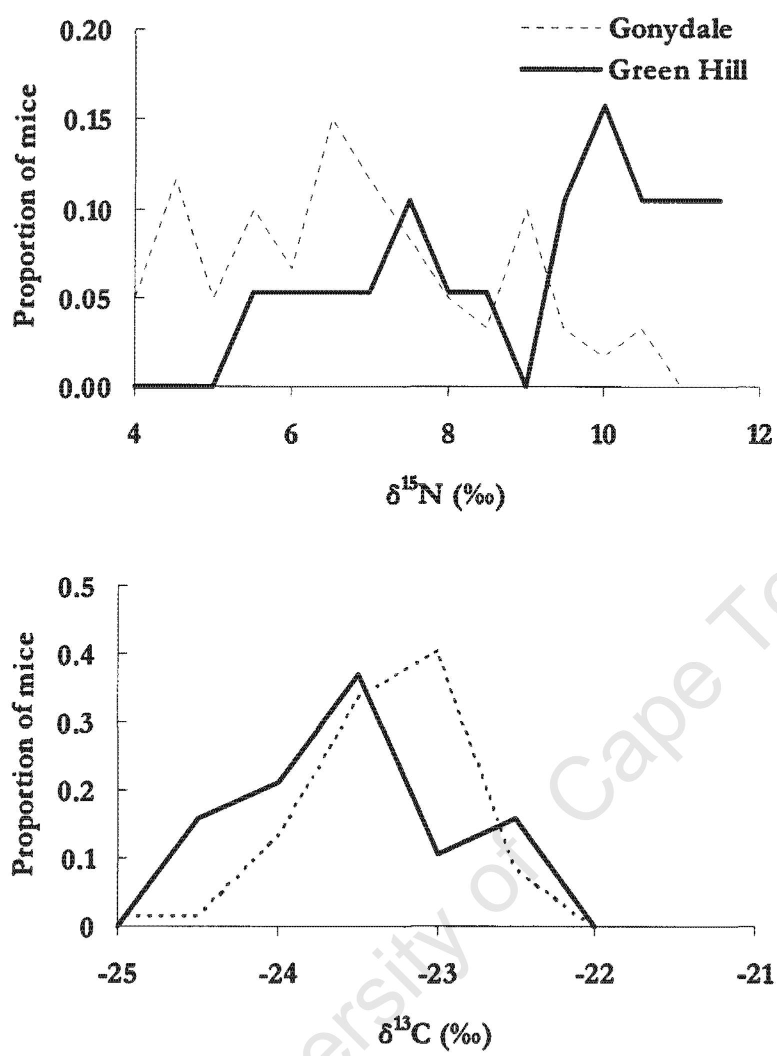

Figure 8. Proportional frequency polygons of $\delta^{15}N$ and $\delta^{13}C$ values of mice trapped in May-July 2004 in Gonydale (few albatross attacks) and Green Hill (numerous attacks).

Seabird remains were evident in lowland mouse stomachs throughout the year in both 2003/04 and 1999/2000 (Figure 11), but proportions differed significantly between seasons (χ^2_5=389.9, p<0.001). PVs were relatively high in all winter months in 2000, whereas in 2004, seabird remains peaked in March and August but were lowest from April-June. The skua count data do not co-vary with monthly seabird PVs in either field season.

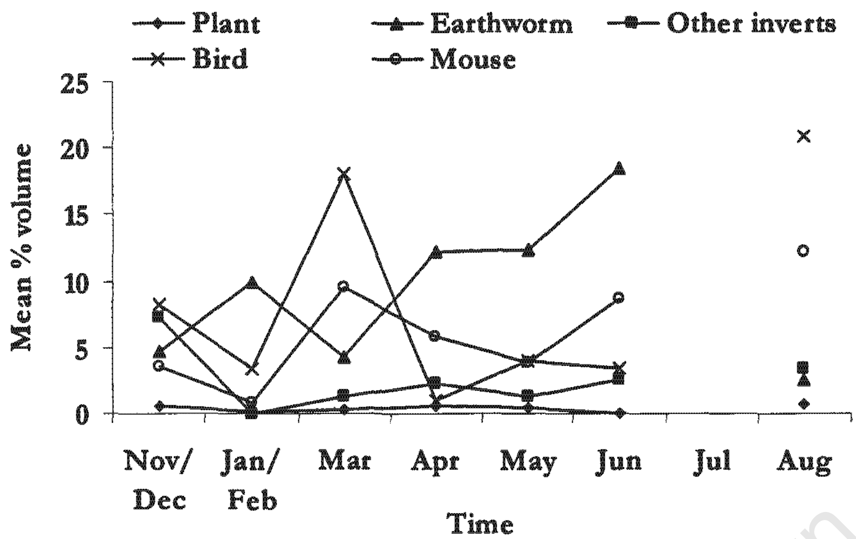

Figure 9. Mean monthly percentage volumes of different dietary items from house mouse stomachs in the lowlands of Gough Island in 2003/04. Data from austral summer months were pooled due to low numbers of stomachs with >5% by volume of identifiable remains.

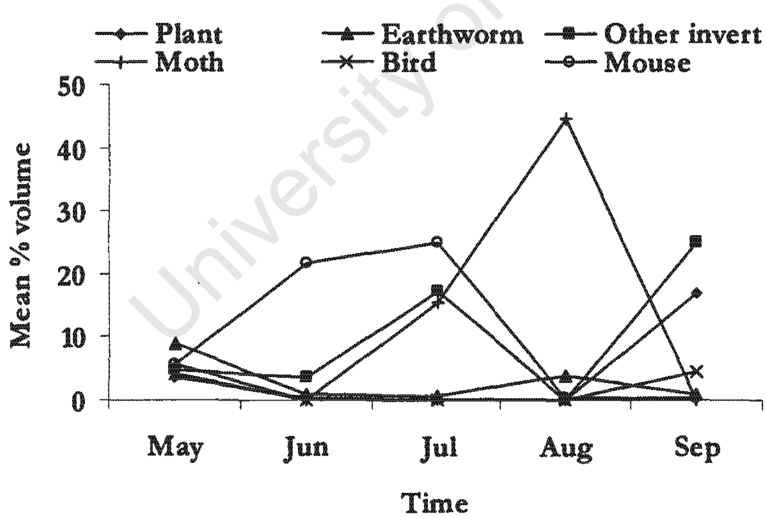

Figure 10. Mean monthly percentage volume of different dietary items from house mouse stomachs in the highlands of Gough Island in 2004.

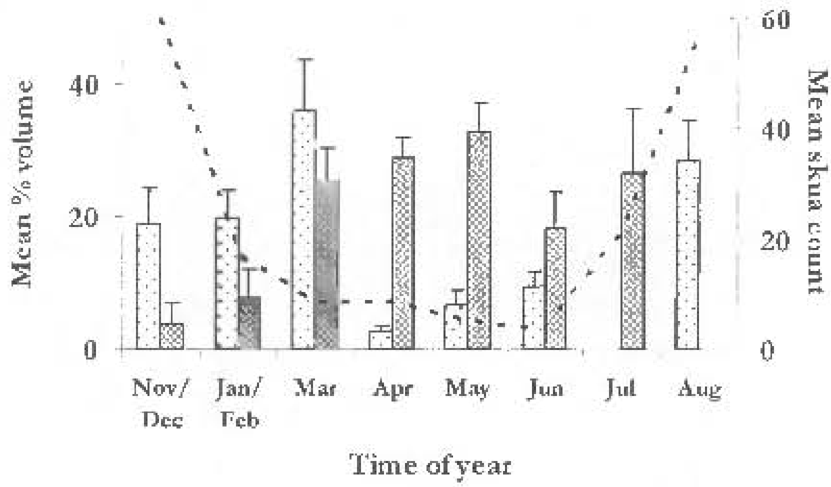

Figure 11. Mean monthly percentage volume of seabird remains in mouse stomach samples from the lowlands of Gough Island in 2003/04 (stippled bars) and 1999/2000 (shaded bars). Error bars denote SE. The dashed line indicates mean Subantarctic Skua abundance at a communal roost near the SE coast.

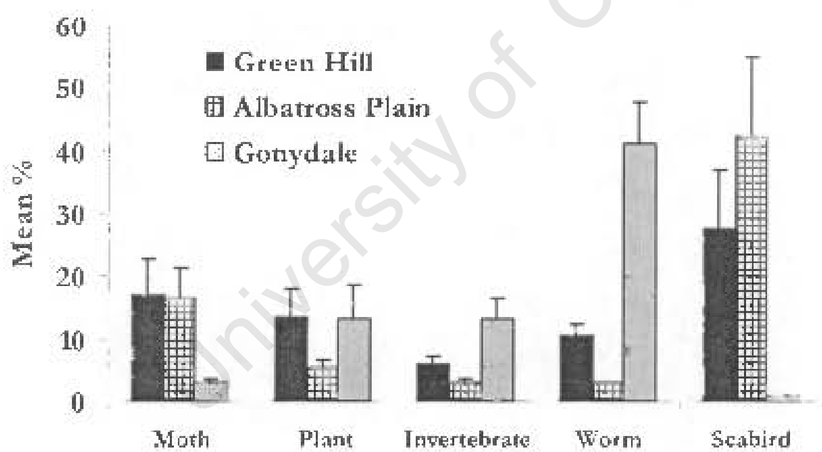

Figure 12. Mean monthly percentage stomach volume of dietary items from the stomachs of mice trapped at Green Hill (n=25), Albatross Plain (n=14) and Gonydale (n=24) in the highlands of Gough Island in May 2004. Error bars denote SE.

The diets of mice in different areas of the highlands in May (Figure 12) differ principally in the proportional contributions of earthworms and seabirds. Mouse attacks on albatross chicks were confirmed at Green Hill, had just begun in Albatross Plain but had not yet occurred in Gonydale (Chapter 3), and this is reflected in the near absence of bird remains in diet samples from Gonydale, whereas bird remains were, on average, the most important dietary item for Green Hill and Albatross Plain mice.

Discussion

Gough Island is justifiably considered one of the greatest seabird colonies in the world, playing host to several million breeding seabirds of 20 species, including two functionally endemic procellariiforms (Swales 1965; Cuthbert & Sommer 2004; Angel & Cooper 2006). Extraordinarily high densities of seabirds have a profound effect on the terrestrial nutrient cycle: seabird-derived $\delta^{15}N$ values from Gough plants (Table 2) are similar to other Subantarctic islands, where they play a major role in driving terrestrial productivity (e.g. Smith 1979; Erskine et al. 1998). The significant inverse relationship between plant $\delta^{15}N$ and altitude is likely to be a direct consequence of densities of breeding seabirds, which are lower in the highlands (Swales 1965; Cuthbert & Sommer 2004) and these differences are reflected through the food chain to mice, which also show significantly different altitudinal $\delta^{15}N$ signatures. Thus, in contrast to many ecological studies tracing isotopic signatures through food-chains, the pervasiveness of marine-derived $\delta^{15}N$ signatures on Gough makes this isotope relatively poor at distinguishing marine (=seabird) versus terrestrial contributions to mouse diets or discriminating trophic levels (cf. Hobson et al. 1999; Drever et al. 2000; Stapp 2002). By contrast, the $\delta^{13}C$ signature of seabirds is very different from other sources, because plants sequester atmospheric carbon and are thus unaffected by seabird-derived organic carbon in soils.

The degree of fractionation varies according to the metabolic rate of the tissue and of the species (or population) being considered, the state of nutrition and feeding rates (Kelly 2000; Olive et al. 2003; Vanderklift & Ponsard 2003; MacAvoy et al. 2005; MacAvoy et al. 2006). Furthermore, state of nutrition can affect carbon and nitrogen enrichment differently, because mobilisation of endogenous lipid stores during nutritional stress will happen before catabolism of skeletal muscles (Zuercher et al. 1999). Assimilated lipids may be catabolised into new, non-lipid tissues, enriching the carbon signature of that tissue without affecting the nitrogen signature (Hobson & Stirling 1997; Phillips & Koch 2002; Dalerum & Angerbjörn 2005). Metabolic rate is an important determinant of tissue turnover rate (and thus of equilibration time after diet switch to a new source with a different isotopic signature) (MacAvoy et al. 2005; MacAvoy et al. 2006). However, it has also been shown that fractionation values correlate with metabolic rate, because more active tissues accumulate more heavy isotopes and are thus enriched relative to less active tissues (Arneson & MacAvoy 2005). Last, metabolic rate correlates negatively with body size (Nagy 1987) and variably in response to temperature and food availability (e.g. Mueller & Diamond 2001; McKechnie et al. 2007).

MacAvoy et al. (2005) showed that the equilibration time for carbon and nitrogen isotopic values in muscle tissue after a diet switch in house mice under laboratory conditions was 85 days (half-life=24 days) and 112 days (half-life=25 days), respectively. Arneson & MacAvoy (2005) demonstrated a wide range of heart muscle tissue fractionation for house mice under experimental diets, from 1.0 to -2.3‰ for $\delta^{13}C$, and more predictable but high fractionation values (3.8-4.4‰) for $\delta^{15}N$, due to the relatively high metabolic rate of heart muscle. Uncertainty in determining actual tissue-fractionation values of wild-caught animals arises from the unknown magnitude of influence that variables such as field metabolic rate, temperature and nutritional status have. These issues represent something of a problem for apportioning diet with stable-isotope analysis. Of particular concern is the analysis of mouse diet in the lowlands during late-winter (August-September), the period of greatest interest from a conservation perspective. This is the period when Atlantic Petrel chicks hatch and become available in large numbers to predatory mice (Cuthbert 2004), and when there was an increase in the importance of 'avian material' in mouse stomachs (Figure 11) and enrichment of mouse $\delta^{15}N$ and $\delta^{13}C$ values. This suggests a diet switch and thus a potentially serious violation of the assumption of equilibrium, and any analysis will likely underestimate the contribution that seabirds make to mouse diets at this time. Further, many mice exhibited significantly lowered body condition in these months (Chapter 6), implying that they experienced varying degrees of starvation, with potentially confounding effects on fractionation values. Although the factors affecting direction and magnitude of this effect are still debated, it appears to generally cause enrichment (Hobson et al. 1993; Oelbermann & Scheu 2002; Olive et al. 2003; Haubert et al. 2005; Kempster et al. 2007). An additional complication is the fact that Gough mice are larger than other house mouse populations (Berry et al. 1978), and both equilibration time with diet and fractionation values are negatively correlated with body size (Arneson & MacAvoy 2005; MacAvoy et al. 2006).

The average $\delta^{15}N$ signatures of mice were substantially lower than expected when compared to source signatures. The reasons for this conundrum can only be speculated upon at this point, but probably include one or more of the reasons outlined above. Isotopic fractionation values vary between taxa and between tissues within taxa (McCutchan et al. 2003; Arneson & MacAvoy 2005). The results illustrated in Figure 4-Figure 5 show that the $\delta^{15}N$ fractionation value used may have been too high, creating uncertainty about a key step in analysis of diet (Dalerum & Angerbjörn 2005). Alternatively, source signatures may vary seasonally, implying that this analysis may have used incorrect sources values. A third alternative is that a key resource, with much lower $\delta^{15}N$ values, was missed. However, the overwhelming dominance of seabird-derived nitrogen in the trophic ecology of Gough makes the existence of such a source quite unlikely. There are several potential sources of sampling error that may also have contributed to this problem. Although there were no consistent differences between vegetative and reproductive $\delta^{15}N$ signatures for *Empetrum* in the highlands, it is possible that such differences exist for other plant species. Detritivorous invertebrates (e.g. earthworms) could also become seasonally enriched or depleted for either isotope (Ponsard & Arditi 2000). Thus if stable isotopes are to be used to estimate more accurately the relative contributions of dietary sources for mice on Gough, an extensive source sampling regime is required, and should ideally be coupled to direct studies of tissue fractionation values for Gough mice across seasonal changes in both diet and nutritional status of individuals. This could be done with mark-recapture and repeated harvesting of blood, from which plasma and cell fractions can be analysed for short-term (<1 week) and medium-term (*ca* 1 month) changes, respectively (Hobson & Clarke 1993; Hobson 1999). Such a study would facilitate a robust reanalysis of these results.

Despite these concerns, the analyses of isotope signatures reveal a high likelihood that seabird consumption plays an important role in some mouse diets. In the lowlands, mice had very strong seasonal variations for both isotopes, with enrichment occurring in late-winter (Figure 6). This result is in agreement with observations of the timing of attacks on Atlantic Petrels (Chapter 2) and suggests that predation on seabird chicks is predominantly a late-winter phenomenon in the lowlands. The Isosource estimate for the percentage contribution that seabird consumption makes to lowland mice (excluding mice as a dietary source) indicated that seabirds constitute an average of at least 40% of mouse diets in August-September. These lines of evidence suggest that Atlantic Petrel chicks may represent an important winter resource for lowland mice. The timing of the hatching of Atlantic Petrel eggs coincides with a significant drop in mouse body condition, and mice are probably highly motivated to attack chicks when under-nourished (Bradley & Marzluff 2003). The patterns of isotopic variation were random with respect to body condition, sex and size in the lowlands, although size interacted with season. Size and body condition had positive effects on $\delta^{13}C$, with bigger and better-condition mice $\delta^{13}C$-enriched. Thus, while controlling for season and other factors, there is a suggestion that bigger mice consume more seabirds, but the effect is open to alternative explanations. The dual-isotope plot (Figure 2) and the frequency distributions (Figure 7) show a lack of 'specialist' mice with very strong seabird signals. The latter figure also showed a narrower range of values in late-winter compared to other seasons, which implies that diets of mice were converging to include a smaller range of dietary items. This, and the relatively low degree of variance explained by the other factors implies that amongst mice that survived to be trapped in late winter, seabird consumption was widespread, if not ubiquitous. From stomach content analysis, seabirds constituted a mean of up to 30% of mouse diets in August-September. In a very similar study, of predation on seabird chicks by Norway rats *Rattus norvegicus*, stomach content analysis underestimated the contribution of seabirds to diet relative to estimates based on stable isotope analysis (Hobson et al. 1999).

In the highlands, mouse predation had a devastating impact on Tristan Albatross chicks at Green Hill, whereas before August there were virtually no attacks in Gonydale (Chapter 3). The GLM testing for differences in plant signatures showed significant inter-species and inter-site differences but no significant overall differences between the sites for either isotope. In Chapter 3 I show that there are no differences in the relative abundances of the major plant groups, thus the base of the food-chain in the two sites appears to be very similar. Three results are of interest. First and most importantly, although mice were significantly $\delta^{15}N$-enriched at Green Hill vs Gonydale, they didn't differ between sites in $\delta^{13}C$, ruling out seabird consumption as an explanation for the higher mouse $\delta^{15}N$ at Green Hill. *Scirpus*, however, was enriched for $\delta^{15}N$ at Green Hill. Second, larger mice and mice in better condition were $\delta^{15}N$ enriched in both sites. Third, there was quite a wide range of $\delta^{15}N$ values for plants and invertebrates (Figure 5). I speculate that effects of site, size and condition on $\delta^{15}N$ are because larger mice dominate more productive micro-habitats with high marine nitrogen inputs, in both Green Hill and Gonydale. Albatross nests are the most obvious sites of high, localised enrichment. Further, if *Scirpus* is an important resource (which it probably is), then if larger mice dominate enriched, productive patches of this resource (or some other source not measured but similarly $\delta^{15}N$-enriched at Green Hill) this would explain the observed differences in $\delta^{15}N$ enrichment for mice from the two sites. If mouse $\delta^{13}C$ values are the same between sites, and I accept the strong evidence that seabird consumption in Gonydale is negligible, it follows that seabird consumption is an insignificant component of mouse diets at Green Hill.

Traditional dietary studies that investigate stomach contents have acknowledged flaws and biases. Despite the caveats already mentioned, Jones et al (2003) were able to show quite convincing seasonal changes in the relative importance of major dietary groups in lowland mice in 1999/2000. However, the high seabird PVs during the period May-July 2000 (not presented in their publication) is anomalous for two reasons. First, skua abundances, and consequently their prey remains, are at their lowest levels during these months. Second, the phenology of seabirds is such that there are essentially no petrel chicks present in the lowlands in these months (Swales 1965; Angel & Cooper 2006). Consequently, mice are without seabird resources at this time. In strong contrast is the monthly pattern through the winter of 2004, which matched expectations more closely: low mean PVs coincided with periods of low seabird availability, and the highest value (in August) coincided with the period when mice were depredating Atlantic Petrel burrows heavily (Chapter 2).

The strong peak in bird PVs in March 2004 was unexpected. Again, skua kills cannot be invoked as the source because they depart *en masse* in January/February. This result, when considered with the stable isotope frequency distributions for lowland mice, raises the possibility mice attack seabird chicks in autumn (March-April). There was, however, no support from the seasonal $\delta^{13}C$ distributions. In Chapter 2 I describe a fatal mouse attack on a Great Shearwater *Puffinus griseus* chick, on 9 April 2004. However, this was only one of three chicks of this species under observation, making wider inference highly speculative. Nevertheless, together these observations provide circumstantial, but equivocal evidence that mice may (at least in some years) attack chicks of burrowing petrels still present in March and April (cf. Cuthbert 2005). Further research in to the timing and frequency of possible mouse predation in autumn is merited, particularly for species whose chicks fledge in April-May (Great Shearwaters, Soft-plumaged Petrels *Pterodroma mollis* and White-bellied Storm-Petrel *Fregetta grallaria*). Seabird phenology and associated predation risks are considered in more detail in Chapter 6.

Cumulatively, skuas kill large numbers of petrels each night. However, any significant effect of mice scavenging from skua kills should be reflected by a closer covariation between apparent mouse diet and skua abundance on the island (Figure 11), and the lack of fit implies that skua kills do not represent a significant resource for mice. Although no data were collected on skua numbers in the highlands, personal observations suggest that their densities are a lot lower than the lowlands, and fresh carcasses also appeared to be far less abundant. Thus the pattern is likely to hold for the highlands too.

The relative quantities of bird remains in stomach contents from mice trapped in May from three areas of the highlands matches quite closely to what would be predicted based on the observed mortality of Tristan Albatross chicks. There was virtually no avian material in mouse stomachs in Gonydale, which was more intensively studied than any other highland area in 2004, and in May had not yet had a chick failure due to mouse attacks. However, the ostensibly high importance albatross chicks is not actually that clear-cut. At Green Hill it appears straightforward, with several attacks on albatross chicks in May within 50 m of the trapping grid. However there were no chick failures in May within 100 m of the Albatross Plain trapping grid, yet the stomach contents data indicate high seabird consumption. Albatrosses probably contributed to some of the avian material in mouse stomachs from both areas, but I presume that burrowing seabirds were also significant contributors. The virtual absence of seabird remains from Gonydale mouse stomachs implies that either there is a lower density of seabird burrows in Gonydale than at Green Hill (and Albatross

Plain), or that Gonydale mice consume few seabird chicks relative to their availability. Seabird colonies have an overwhelming enriching effect on the $\delta^{15}N$ of surrounding systems (Smith 1978; Erskine et al. 1998; Hobson et al. 1999; Stapp et al. 1999; Drever et al. 2000). The lack of significant differences in $\delta^{15}N$ ratios of plants between Gonydale and Green Hill suggests that there are not significantly different densities of nesting seabirds. Thus the reasons for lower levels of seabird predation by mice in Gonydale (relative to elsewhere) is probably not because of lower availability. These strong differences in apparent seabird consumption between Green Hill and Gonydale contrast with the findings from the stable isotope analyses, in which seabird consumption was virtually undetectable. The long retention time of indigestible material such as feathers may mean that the relationship between seabird consumption and estimates of avian PV is relatively shallow (Kelly 2000, but cf. Hobson et al. 1999).

A key objective of this chapter was to investigate the importance of seabirds as a food resource for mice. A rationale underlying this objective is to predict likely consequences of continued predation of chicks by mice. Mice on Gough turn to seabird chicks as winter food resources in both highland and lowland sites. The impact of predation averaged across the seabird populations is strongly negative: it is an important factor driving a decrease in the Tristan Albatross population, and is probably also causing a decrease in Atlantic Petrels. It does not necessarily follow that the relationship is symmetrical: predation by mice may be a very important factor for certain seabird species' population dynamics, but those species may constitute a negligible benefit to the mice. If seabirds are an important resource for mice, enhancing mouse survival through the lean Subantarctic winter, then, all else being equal, decreasing seabird populations will have a negative effect on mouse survival. In line with standard ecological theory, I expect that predation rates will either remain roughly constant or, more optimistically, decrease proportionally (Begon et al. 2003). However, if seabirds are not a significant resource for mice, i.e. the relationship between mice and seabirds is strongly asymmetric, then a decreasing seabird population may have no significant effect on mouse survival. Proportional predation rates could increase over time, creating positive feedback with dire consequences for the survival prospects of impacted seabird species. The results from the lowlands suggest that seabirds may well be an important late-winter resource for mice. In the highlands, the opposite is true: seabirds were a negligible component of mouse diets.

Aside from direct predator—prey interactions, there is a second, indirect effect of predation and decreasing seabird densities. The dynamics of seabird—nutrient cycle interactions have been well studied on Subantarctic Marion Island (Smith 1978, 1979; Smith & Steenkamp 1990, 1992; Smith & Steenkamp 1993). The transport of nutrients from marine to terrestrial systems is a critical determinant of terrestrial productivity on Subantarctic islands (Smith 1978, 1979; Smith & Steenkamp 1993; Erskine et al. 1998) and other seabird-dominated islands (Croll et al. 2005; Fukami et al. 2006). Reduced densities of breeding seabirds will reduce this nitrogenous fertilisation effect, with a strongly negative effect on terrestrial productivity. The timing of the reduction in fertilisation is crucial. If it is roughly simultaneous with seabird decreases, then reduced seabird densities will have an immediate effect of lowered plant productivity. This would likely cascade to lower invertebrate productivity (Smith & Steenkamp 1992; Smith & Steenkamp 1993). Lower overall productivity could have one of two effects on mouse—seabird interactions. Either it would cause lower mouse productivity, resulting in lower densities and perhaps lower predation levels. Alternatively, mice might rely increasingly on seabirds for their survival, setting up a positive feedback. These scenarios are not mutually exclusive, because either could eventuate in the functionally discrete highland and lowland ecosystems. However, if nitrogen depletion lags behind seabird decreases appreciably, then productivity could remain high, supporting high densities of mice throughout seabird decreases. The conservation consequences of these scenarios for the seabirds, and the general ecology of the island make understanding these possibilities and predicting outcomes a significant priority.

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CHAPTER 6

Biology, population dynamics and survival of the house mice on Gough Island: key periods of vulnerability for eradication

Abstract

The introduced house mice *Mus musculus* on Gough Island represent a significant threat to the native biota (plants, invertebrates and seabirds) of the island, and eradication by means of aerial broadcast of toxic baits is widely considered the best management option to mitigate rodent threats on islands. Here I report seasonal and inter-annual demographic patterns of the mice on Gough, to inform the viability of a toxic baiting operation, as well as to suggest the most appropriate timing, such that the highest probability of 100% acceptance of bait is achieved. In the two seasons studied (1999/2000 and 2003/04) breeding started in September, in keeping with other Subantarctic house mouse populations, but there were pronounced inter-annual differences in the cessation of breeding, which occurred in April 2000 vs February 2004. Proportions of reproductively active mice differed between 1999/2000 and 2003/04, with a lower proportion of individuals reproductively active in most months of the latter season. Nevertheless, no reproduction occurred between May and August. Sex ratios switched from male-biased in 1999/2000 to female-biased in 2003/04 ($p<0.001$) and were consistent between months for each season. Sexual dimorphism has not been reported from other feral populations, but on Gough males averaged 8.2% (2.2 g) heavier than females and had tails 2.3% (2.1 mm) longer than females' tails. There were significant altitudinal differences in size, with male mice being on average 45% heavier ($p<0.001$) in the lowlands and having tails 9.5% longer ($p<0.001$) than males from the highland. Highland mice also had significantly lower body condition than lowland mice ($p<0.001$). Average tail length increased significantly at the end of winter ($p<0.001$), suggesting that survival during the critical late-winter period is strongly biased towards larger individuals. Seasonal changes in body condition were broadly similar across altitude; condition in mice from the lowlands was low in February, also the month in which breeding ended in 2004. Mice were able to increase body condition immediately after the cessation of breeding, but condition decreased from June-September. Monthly density estimates from a mark-recapture study in 2005/06 showed that densities

remained relatively static from February-June and decreased from July-September. These congruent results suggest that June-August is the most appropriate time of year for an attempted eradication, as the mice were not breeding and showed the clearest signs of food-deprivation, but densities had not yet equilibrated to their lowest levels. Further, highland conditions were obviously suboptimal for mice and they should accept bait at least as readily as mice at lower altitudes.

Introduction

Detailed studies have been conducted on introduced house mice *Mus musculus* on several Subantarctic islands (Berry et al. 1978; Gleeson & Van Rensburg 1982; Pye 1993; Matthewson et al. 1994; Le Roux et al. 2002, reviewed in Chapter 1). However, relatively little is known about the biology of mice on Gough Island (Hill 1959; Breytenbach 1986; Rowe-Rowe & Crafford 1992; Jones et al. 2003a). They are unusual in that they are the largest-bodied insular house mice in the world, and in contrast to most other island populations, are also the only introduced mammal on the island (Berry et al. 1979; Brooke & Hilton 2002; Angel & Cooper 2006; Brooke et al. 2007). House mouse populations at similar or higher latitudes undergo relatively predictable annual cycles of increasing density through summer and decreasing density, often with high rates of mortality, occurring during winter (Berry 1968; Ferreira et al. 2006). The impact of mice on the native fauna of Gough has been shown to be severe, particularly on the winter breeding seabird species, and eradication would achieve significant conservation goals (Jones et al. 2002; Jones et al. 2003a; Cuthbert & Hilton 2004; Angel et al. 2005; Wanless et al. 2005; Angel & Cooper 2006; Wanless et al. 2007).

An attempted eradication of mice on Gough would, in some respects, be entering uncharted territory: to date the largest island to have been cleared of mice is Enderby Island, which at 700 ha is an order of magnitude smaller than 6400 ha Gough Island (Torr 2002). Several mouse eradication attempts have failed, and the reasons for these failures (or for the 18 successes to 2005) are not well understood (Howald et al. 2005). Before management action is undertaken on Gough it is imperative to understand the biology and demography of the mice there in relation to mice elsewhere. This will inform decision-makers about the chances of successfully eradicating mice, and possibly point out areas of concern for which an eradication operation should take special precautions. Key amongst the biological issues related to an eradication is determining the time of year when all mice are most likely to accept toxic bait. This is assumed to be the time when mouse numbers are decreasing, but before the population stabilises at its minimum size. It is also important to know when mice reproduce, because pregnant or lactating females and their pups may not exhibit normal foraging behaviour (e.g. they may subsist off cached or body reserves) or may be neophobic and thus avoid baits (J. Parkes pers. comm.).

The Island Syndrome (Thiollay 1993; Adler & Levins 1994) describes a suite of life history and demographic characteristics that vary systematically between insular and mainland populations, especially in rodents (Lomolino 1985; Stamps & Buechner 1985; Adler & Levins 1994; Dayan & Simberloff 1998; Lomolino 2005). Insular rodent traits include high population densities, gigantism, lower fecundity and greater life expectancy. A key prediction of the Island Syndrome is that population density decreases with increasing island area (Adler & Levins 1994). The inverse relationship between density and island size is not an effect of area *per se*, but rather an effect of competition and predation (Michaux et al. 2002; Lambert et al. 2003). As island area increases, the complexity of its ecological character approaches that of a mainland, there tend to be more predators and competitors of rodents and the insular effect (of high density) diminishes accordingly. Gough, with no predators of rodents, should have high mouse densities relative to mouse populations on larger land masses and similar-sized islands with predators. After more than 120 years on Gough Island (Verrill 1895), the mouse population is presumably relatively stable. They have a discrete breeding season that coincides with the austral summer (Jones et al. 2003a), and must therefore experience an annual cycle in numbers. Rowe-Rowe & Crafford (1992) reported densities of 224 mice/ha in the lowlands of Gough in September (early spring), a density classified as a "minor plague" in Australia (Singleton et al. 2005). Gough mice are thus exemplars of two Island Syndrome characters, gigantism and high population density.

This study examines morphological, demographic and reproductive data from mice collected on Gough Island and makes comparisons to similar data collected previously from Gough, as well as with other published studies. I describe inter-annual and seasonal patterns of reproduction, seasonal changes in body condition and seasonal density fluctuations and make inferences about the underlying mechanisms. I use these data to test: (1) if there is a selective pressure for larger body size; (2) if the population is regulated by density-dependent factors; (3) the influence of altitude on demographic parameters of the mice. I use these results to identify the time of year when a toxic baiting operation is most likely to be successful.

Methods

Study site

Gough Island (40° 21'S, 9° 53'W) lies in the mid South Atlantic Ocean some 3 000 km west-south-west of South Africa and 400 km south-south-east of Tristan da Cunha. It has a wet, cold-temperate climate with strong prevailing westerly winds (Angel & Cooper 2006). It is predominantly surrounded by steep coastal cliffs and has an undulating plateau (hereafter referred to as highland) from 450-900 m The south-eastern part of the island has an extensive coastal plateau from 40-90 m (hereafter referred to as lowland) which rises steeply to the interior (le Maitre 1960). Lowland habitat is dominated by fernbush, characterised by relatively tall, dense vegetation of mostly ferns, sedges and *Phylica arborea* trees (Wace 1961). The highland plateau is covered with wet heath, characterised by stunted vegetation and dominated by moss, grasses and sedges and *Empetrum rubrum*, a low-growing, woody perennial (Wace 1961).

Snap-trapping

Mice in the lowlands were snap-trapped at monthly intervals between November 2003 and September 2004. Trapping was done on the south-eastern coastal plateau near the meteorological station. In the highlands trapping took place monthly between December 2003 and September 2004, excluding February and April, and was done principally in Gonydale and Green Hill. Nine plots were set up in both highland and lowland areas, and monthly trapping grids (of 25 and 50-75 traps per grid, respectively) were rotated such that no area was trapped more than once every three months. Trapped mice were sexed, weighed and measured, except I discarded carcasses that had been scavenged significantly.

Reproduction

The reproductive status of a subset of 20 mice from the lowlands was determined through dissection each month. Female mice were defined as reproductively active if they were either pregnant or lactating, whereas males were deemed to be active if they exhibited scrotal testes (Jones et al. 2003a). Because some males exhibit scrotal testes in almost all months, the breeding season was defined in terms of reproductively active females only. Reproductive data from this study were compared to data from 1999/2000 (Jones et al. 2003a), using the same definitions. I confine inter-annual comparisons to mice caught in the same area of lowland habitat using comparable trapping methods. Litter size refers to the number of foetuses *in utero*. Litter size data from 2003/04 were compared to published data from mainland populations, although no statistical testing was possible. I tested for temporal trends in lowland litter sizes using a Kruskal-Wallis ANOVA, but grouped January and February (n=4 and n=1 pregnant females, respectively). A difference in the sex ratio between 1999/2000 and 2003/04 was tested using a Chi-squared contingency table with Yates' correction. I tested for seasonal consistency in bias in each year by comparing observed monthly sex ratios against the expected ratio (the sex ratio for the whole year pooled).

Size

Several standard morphometric measurements were taken. Intact mice were weighed to the nearest 0.5 g using a 100 g Pesola spring balance. Tail length (from tip to start of curvature at junction with body) and total body length were measured to the nearest mm by flattening and straightening bodies on a stopped metal rule. Tail length was subtracted from total body length to get body length. Head width (measured at the widest part of the skull) was measured to the nearest 0.1 mm using vernier callipers. Relevant measurements were not taken in cases where carcasses had been partially scavenged, had docked tails or crushed skulls. Snap-traps frequently damaged skulls and spines (>30%), thereby limiting the utility of head width or body length measures. To compensate, I correlated head width, tail length and body length measurements to check that these covaried, and used tail length as a representative measure of skeletal size. I checked for consistency in the relationship between tail length and other skeletal measures between sexes and size-classes. Lowland mice were divided into four tail-length size-classes (classes 1-4 respectively: <81 mm, 81-90 mm, 91-100 mm and >100 mm), but due to insufficient data on body length, only the tail vs. head width correlations were analysed. Simultaneous-inference tests such as this run a cumulative risk of Type-1 errors, and a sequential Bonferroni test was used to control for this (Rice 1989).

I tested for altitudinal differences (males only) and differences in sexual dimorphism (lowland mice only) in tail length and body mass using t-tests. Analyses were confined to mice caught from May-Sept (to control for possible confounding effects of breeding season or juvenile mice) and analysis of sexual dimorphism was further confined to lowland samples. I then tested the hypothesis that there was selection during winter for larger mice by examining the differences in mean monthly tail lengths (a surrogate for body size) on mice trapped in the lowlands from May to September (August and September data were combined). Because mean monthly tail length increased through autumn and winter (presumably due to young mice growing through the winter), a simple analysis of the difference in mean tail lengths would have produced a spurious result. I sought to determine whether there was a period when the mean monthly increase in tail length was greater than expected. For each record in a given month I subtracted the mean from the previous month, calculated the monthly mean and then tested for differences in the monthly rate of change in tail length using a one-way ANOVA with a Tukey post-hoc test. A significant increase in the mean of the remainders from any one month would indicate that either there were significantly more large mice in the population or that tail growth rates changed.

Body condition

Indices of body condition in house mice and other small mammals have been criticized (for a review see (Hayes & Shonkwiler 2001), in part because there is little or no relation between body condition and fat reserves, militating against the use of body condition as a measure of energy reserves (Krebs & Singleton 1993; Virgl & Messier 1993; Schulte-Hostedde et al. 2001). However, body condition can explain variation in whole body composition (fat, skeletal muscle, water and other body-parts, Schulte-Hostedde et al. 2005). Furthermore, small mammals can catabolise protein during periods of low food abundance (Zuercher et al. 1999). I calculated a body condition index by regressing log weight against log tail length. Transformations were used to account for the dimensional differences (volumetric versus linear measures) and to permit comparisons of straight lines (Hayes & Shonkwiler 2001). The regression line was used to calculate the expected weight for a given tail length. The actual weight divided by the predicted weight provides an index that is independent of size (Hayes & Shonkwiler 2001). I corroborated this by correlating body condition with tail length. Data were then divided into nine (lowland) and five (highland) groups of a month or two months, depending on sample sizes. Pregnant females were excluded from the analyses. I tested for intra-altitudinal differences in seasonal changes in body condition and body mass using one-way ANOVAs with Tukey post-hoc comparisons for both highland and lowland populations. Altitudinal differences in body condition were tested with a two-way ANOVA using altitude and month as explanatory variables. I also tested for significant trends in monthly changes in actual body mass from mice in the lowlands using a one-way ANOVA with a Tukey post-hoc comparison.

Density estimates

Repeated live-trapping sessions took place at two locations in both the lowlands and the highlands between October 2005 and September 2006. Small metal live traps were set at 8 m intervals on 80 x 80 m grids (totalling 100 stations per grid). Traps were set out after sunset and mice were retrieved the following morning, individually marked by toe-clipping and released. For each session, mice were trapped over 3-5 consecutive nights, although inclement weather caused minor deviations from this protocol. Sessions were conducted at approximately 6-week intervals on the same grids. This allowed marked mice to be captured on the first night of a new session. However, each trapping session was treated as a new study (this was possible because marked mice were individually identifiable). For the purposes of estimating density, all mice were recorded as new captures the first time they were captured in a particular session, regardless of their previous retrap history from earlier sessions. The second retrap in a session was used but subsequent retraps within the same session were disregarded (i.e. mice were only 'trapped' once and 'retrapped' once per session). I used the Schnabel method for estimating densities, as it is the most appropriate measure for multiple retrap sessions (Krebs 1999).

Statistical tests

All tests were performed using Statistica (StatSoft 2004) and significance values quoted at the 0.05 level. Where data were not normally distributed, appropriate non-parametric analyses were performed and are mentioned accordingly. Where appropriate, standard deviation 95% confidence intervals are presented, denoted SD and CI respectively.

Results

In 2003/04 I set >1500 snap-traps, and 770 trapped mice were sufficiently intact to have some demographic data collected. Each lowland plot was trapped on average 2.4 times (max=3) in the year, and there were 22 trapping sessions in total. In Gonydale, each plot was trapped 2.2 times (max=3) and there were 18 trapping sessions in total. The overall rate of trap failure (traps that triggered but caught nothing, or that failed to trigger but lost bait) ranged from 12-48% (mean 27%).

Reproduction

In 2000 the reproductive season of females ended in April, whereas in 2004 it ended two months earlier, in February (Figure 1). The proportions of reproductively active females and males were consistently higher in 2000 than in 2004 (until all reproductive activity ceased).

In 2003/04 the mean litter size (all foetuses) was 7.67 (range=2-12, SD=2.51, n=24). Mean litter sizes were higher in November (8.8, n=5) and December (8.4, n=7) than in January-February (7.0, n=5), but differences were not significant (K-W ANOVA, $H_{2,17}=3.66$, p=0.16). The sex ratio of animals trapped in the lowlands was male biased (1.57:1, n=398) in 1999/2000 and female biased in 2003/04 (0.72:1, n=621 mice) and this difference was highly significant ($\chi^2_1=37.34$, $p<0.001$). The monthly sex ratios did not differ significantly from the annual values in either 1999/2000 or 2003/04 ($\chi^2_{10}=1.16$, p=0.99; $\chi^2_{10}=0.53$, p=0.99, respectively).

Table 1. Correlations of body measures of 770 Gough house mice trapped in 2003/04.

Variables	Correlation	r^2	P	n
	Grouped	0.559	<0.001	387
	Females	0.584	<0.001	232
	Males	0.509	<0.001	155
Head width vs Tail	Size class 1	0.242	0.011	26
	Size class 2	0.081	0.004	101
	Size class 3	0.072	0.008	98
	Size class 4	0.131	0.036	34
	Grouped	0.494	<0.001	87
Head width vs Total Body	Females	0.885	<0.001	57
	Males	0.446	0.012	31
	Grouped	0.837	<0.001	88
Tail vs Total Body	Females	0.539	<0.001	55
	Males	0.387	<0.001	30

Size

The various measures of body size were all highly significantly correlated to one another (Table 1). Furthermore, there were no differences in the correlations of the different measures between sexes or size-classes, and the sequential Bonferroni test confirmed no Type-1 errors. This allowed the use tail length, the measure for which I had most data, as a surrogate for body size in all subsequent analyses.

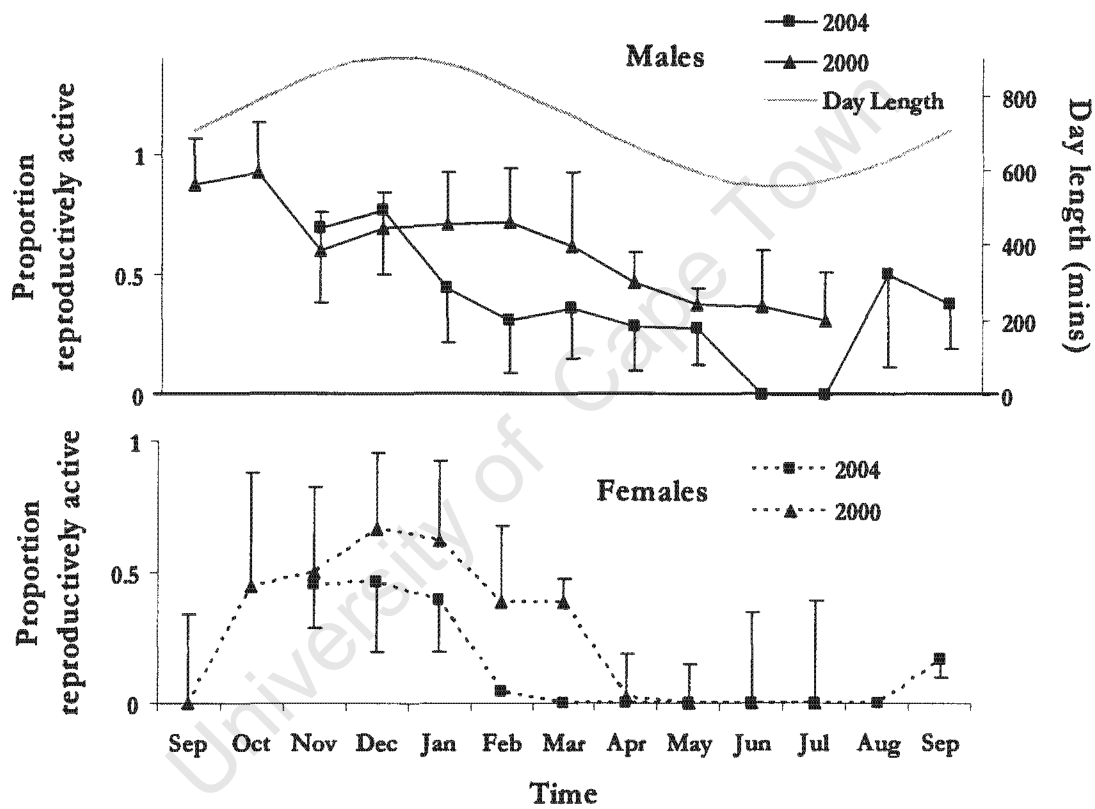

Figure 1. Seasonal changes in proportions of reproductively active mice in from Gough Island. Vertical bars denote CI but only half-bars are shown for readability; and season is indicated by day length (total minutes between sunrise and sunset). Data from 1999/2000 from Jones et al. (2003).

The tests for altitudinal differences in size revealed that mice in the highlands were, on average, significantly smaller than mice in the lowlands (Table 2), with male mice being on average 45% heavier in the lowlands and having tails 9.5% longer. I therefore used only lowland samples to test for sexual dimorphism (Table 2). Males were on average 8.2% (2.2 g) heavier than females and had tails that were 2.3% (2.1 mm) longer than females' tails.

Table 2. Altitudinal and sexual dimorphism in house mice from Gough Island in 2003/04. Only lowland data from May-September were used to test for sexual differences and only males were used in altitudinal tests.

		Mean (SD)	T	df	p
Weight (g)	Lowland (n=97)	28.6 (5.4)	-9.19	142	<0.001
	Highland (n=47)	19.7 (5.6)			
Tail (mm)	Lowland (n=95)	96.7 (6.2)	-7.3	141	<0.001
	Highland (n=48)	88.3 (7.1)			
Weight (g)	Female (n=151)	26.4 (7.7)	3.13	246	0.002
	Male (n=97)	28.6 (7.6)			
Tail (mm)	Female (n=149)	94.6 (8.3)	2.5	242	0.013
	Male (n=95)	96.7 (8.5)			

The test for differences in the rate of increase in mean monthly tail lengths was highly significant ($F_{3,\ 233}$=5.33, p=0.001). Figure 2 shows that mean monthly tail lengths in August/September (mean=99.5 mm) differed significantly from May, June and July (means=92.2, 94.3 and 95.0 mm, respectively).

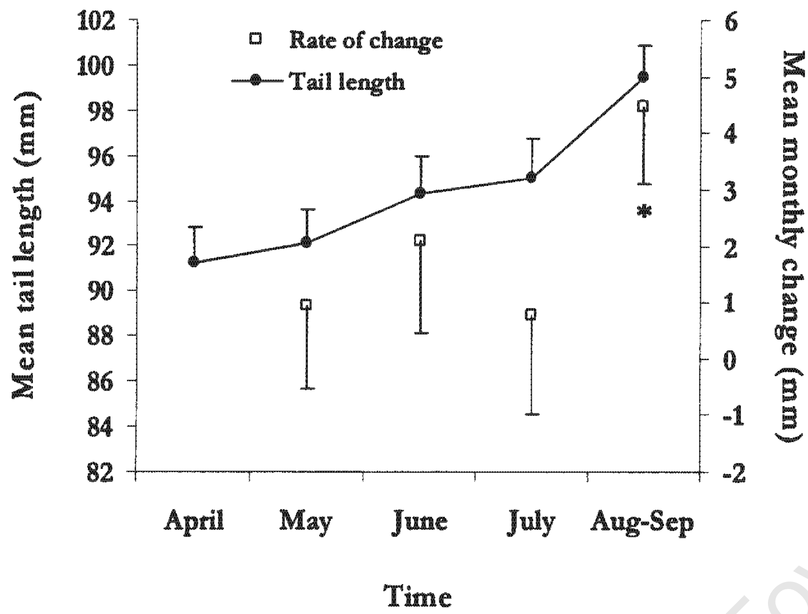

Figure 2. Monthly increases and rate of change (between months) in mean tail length of mice from the lowlands during the austral winter of Gough Island. Vertical bars denote CI but only half-bars are shown for readability; * indicates a significant difference from other months in the rate of change.

Body condition and body mass

There was no correlation between body condition and tail length (R^2=0.004, p=0.9, n=597). Therefore the body condition index is truly independent of size. The utility of examining body condition in conjunction with body mass is clearly shown in the divergence of these two measures after May. Condition and mean body mass of lowland mice covaried from December to May, but body mass shows a single annual cycle, with mean mass peaking at the start of the breeding season (September), decreasing through to the end of breeding and steadily increasing again (Figure 3). Body condition shows two peaks and troughs. The December-February decrease in mean body weight is probably accounted for by the simultaneously decreasing body condition as well as increasing numbers of smaller individuals in the population. A Tukey post-hoc comparison showed that the apparently low mean weight in July was not significantly different from the two preceding or the two following months. The significant increase in mean body weight at the end of winter contrasts with the significant decrease in body condition, and supports the finding that smaller mice are selectively removed from the population between July and September, while also showing that even surviving mice were not maintaining condition.

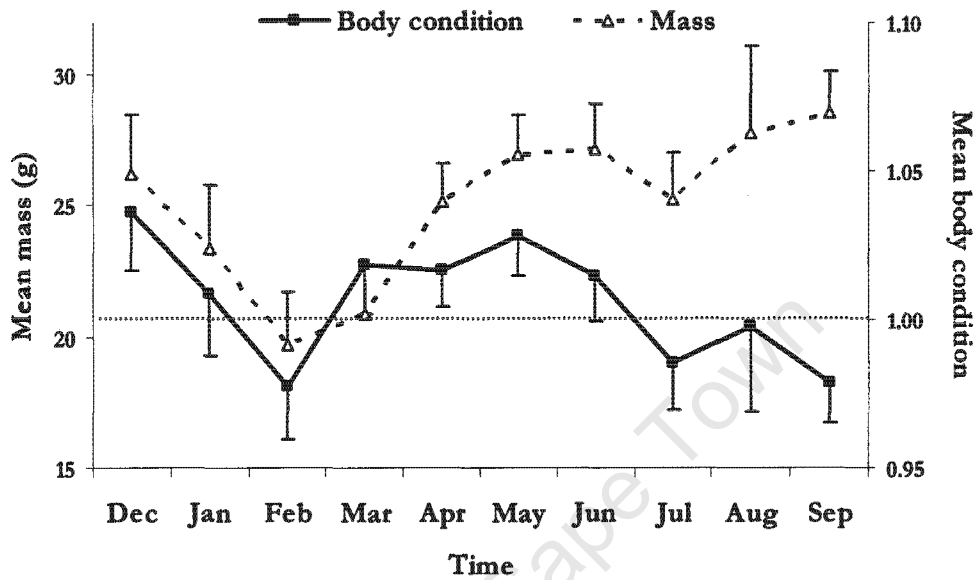

Figure 3. Monthly changes in mean body mass (g) and mean body condition of mice trapped in the lowlands of Gough Island, 2003-2004. Vertical bars denote CI but only half-bars are shown for readability; the dotted horizontal line denotes the population mean in body condition (=1.0). The December and March-June peaks in body condition differed significantly from the February and July-September troughs. The February-March trough in body mass differed significantly from all months except January, which differed significantly only from September (see text for details).

Mice from the highlands showed a bimodal seasonal pattern in body condition changes similar to that of the lowlands, although the timing of the changes differed. Very small sample sizes may have limited my ability to detect significant differences between periods, and only the August-September trough differed significantly from the June-July peak. Mean body mass, unlike in the lowlands, showed a relatively minor decrease from summer to late-winter (Figure 4), but the differences were not significant (ANOVA, $F_{4, 136}$=1.63, p=0.17).

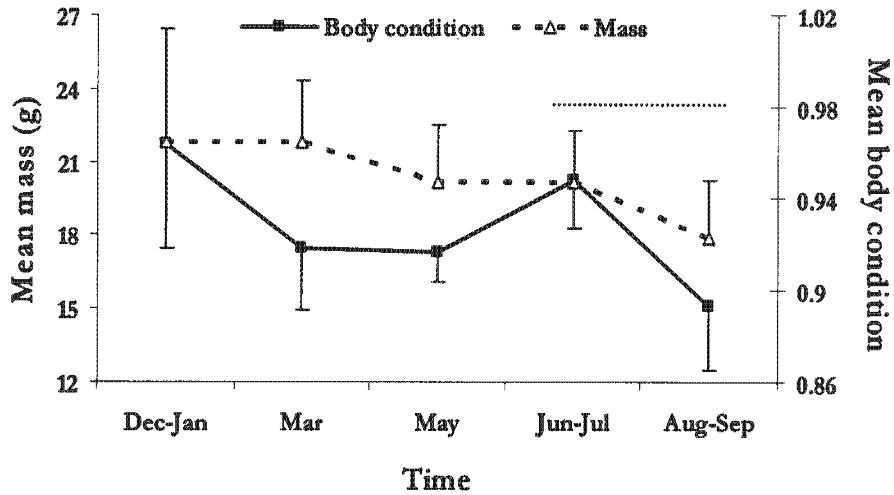

Figure 4. Monthly/bi-monthly changes in mean body mass (g) and mean body condition of mice from the highlands of Gough Island. Vertical bars indicate CI but only half-bars are shown for readability; the dotted horizontal bar denotes significant between-month differences in body condition.

Table 3. Monthly differences in mean body mass and body condition from lowland mice trapped on Gough Island in 2004. Levels of significance are: *≤0.05, **≤0.01, ***≤0.001.

Body mass						
Nov-Dec	Feb***	Mar*				
Jan	Sep*					
Feb	Apr***	May***	Jun***	Jul**	Aug**	Sep***
Mar	Apr*	May***	Jun***	Jul*	Aug*	Sep***
Body condition						
Nov-Dec	Feb***	Jul**	Sep***			
Feb	Mar*	Apr*	May***	Jun*		
May	Jul**					
Sep	Mar*	Apr**	May***	Jun*		

In the lowlands, body condition went from a high in mid-summer to a significantly lower value in February, at the end of the breeding season. It climbed again through autumn, peaking once more in May before it dropped in middle and late winter. There was significant temporal variation in the body condition of lowland mice (ANOVA:

$F_{9, 438}$=6.56, p<0.001) and the Tukey post-hoc comparison identified significant differences between all the peaks and troughs (Table 3). The equivalent non-parametric test (small sample sizes in some months prohibited a parametric test) for the highland mouse population also showed significant differences (Kruskal-Wallis ANOVA: $H_{4, 140}$=12.29, p=0.015), but the post-hoc comparison of Z values revealed significant differences only between June-July and August-September (p=0.012) (Figure 4). Mice in the highlands had significantly lower body condition than mice from the lowlands (F_1=78, p<0.001). Small and unequal samples sizes (and months with no data) of mice in the highlands meant that I could not control for season in the altitudinal comparison, however, the strength of the significance lends some confidence to this result.

Density estimate

The seasonal changes in lowland mouse densities (Figure 5) were in keeping with expectations, based on the timing of reproduction of the mice in 2004. Densities increased through the summer, peaking at the end of the breeding season, and then decreased at the end of winter; by September (the start of the next breeding season) densities were essentially the same as they were the previous October. There are three noticeable altitudinal differences in the seasonal pattern of population density. First, differences in densities were greatest in the middle of the breeding season (November-January), when estimated lowland densities were more than three times higher than in the highlands. Second, in the highlands there was a lag in the summer density increase relative to the lowlands. Third, the highlands showed a more than three-fold density increase between the low point in December and the high peak in March, compared to a two-fold increase between October and February in the lowlands.

Discussion

From a conservation perspective, eradicating the invasive alien mice would be a significant step in restoring the ecology of Gough Island (Jones et al. 2003a,b; Cuthbert & Hilton 2004; Angel & Cooper 2006). Eradicating rodents from islands greater than *ca* 100 ha requires complex operations, including the use of helicopters and highly trained personnel. Such operations are very expensive, ranging from hundreds of thousands to millions of US dollars (McClelland & Tyree 2002; Martins et al. 2006; Donlan & Wilcox 2007). The paucity of mouse eradication attempts relative to those of rats (Figure 6) probably derives from the poorly studied/described impacts of mice on charismatic insular fauna such as seabirds (Wanless et al. 2007). Thus while factors determining the success of rat eradications are fairly well understood, and some have argued against an upper island-size-limit for successful rat eradications (Lavoie et al. 2007), the techniques to eradicate mice successfully are still being developed and factors influencing operational outcomes are poorly understood. Given the above, a mouse eradication attempt on Gough is likely to cost in excess of US$3 million (J. Parkes pers. comm.), and a clear understanding of mouse biology, demography and the window of time when laying bait will be most effective is essential before making a conservation outlay of that nature.

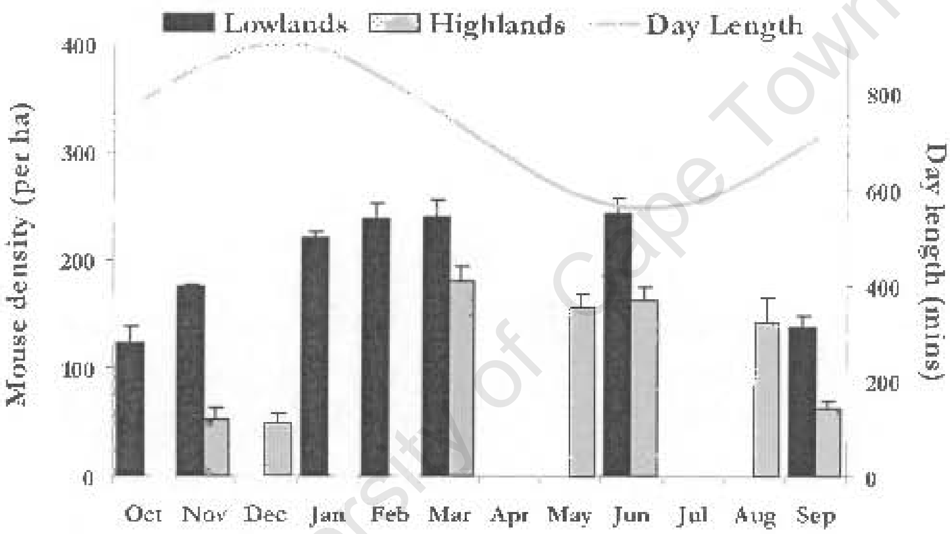

Figure 5. Seasonal changes in estimated mouse densities in the highlands and lowlands of Gough Island in 2005-2006. Vertical bars denote CI. Seasons indicated by day length (total minutes between sunrise and sunset).

Mouse populations on Gough and on other Southern Ocean islands are not known to undergo the extreme inter-annual density fluctuations or reach plague-like densities that mainland populations do (Singleton et al. 2001; Ferreira et al. 2006). Furthermore, mouse populations in temperate and high-latitude environments are characterised by pronounced seasons with high winter mortality rates (e.g. Ferreira et al. 2006). These exert a moderating influence on inter-annual population cycles but facilitate an annual cycle (Berry 1968; Efford et al. 1988; Avenant & Smith 2004; Ferreira et al. 2006). The patterns of seasonal reproduction and changes in densities in the mice on Gough, while drawn from a limited data set, conform to this general pattern. Similarly, the range of mouse densities on Gough is similar to those reported from Marion Island, although the timing of peaks and troughs is slightly different (Ferreira et al. 2006).

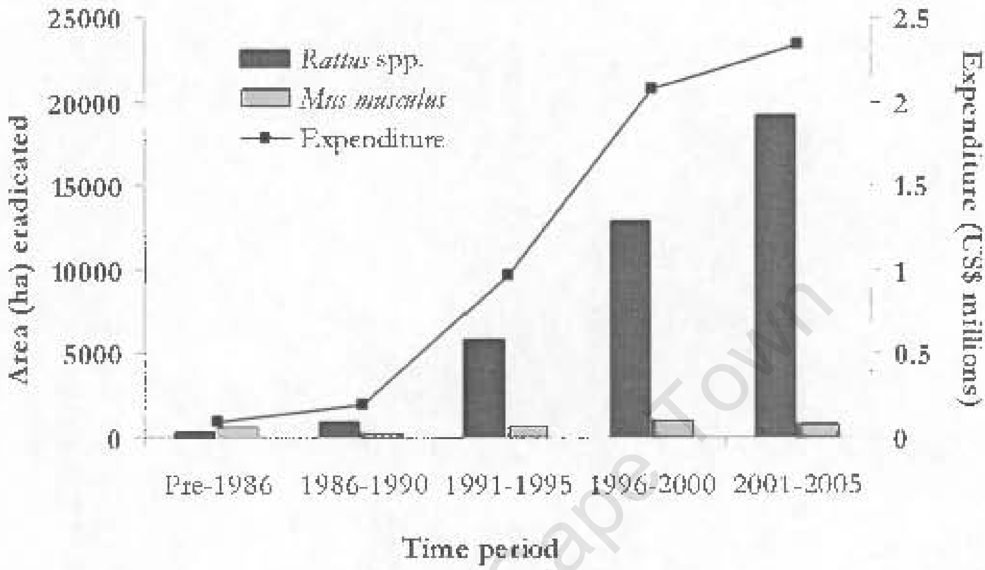

Figure 6. Island area cleared of rats (*Rattus* spp.) and mice (*Mus musculus*). All known efforts prior to 1986 are summed. Modified from Wanless et al. (2007)

The timing of reproduction in house mice varies greatly among populations. In general, they can breed year-round when given access to enough food (Laurie 1946; Rowe et al. 1964; Bronson 1979; Tait 1981; Bronson 1998), although mice on Marion Island did not survive better or enter a reproductive state during a food supplementation experiment (van Aarde & Jackson 2006). The seasonality of reproduction of mice on Gough Island is therefore in line with predictions, given the seasonal nature of the island's environment. However, the duration of reproduction varied substantially between 1999/2000 and 2003/04 on Gough. Breeding ended two months earlier in 2004 than in 2000 (zero reproductively active females in March 2004 versus May 2000). The proportion of scrotal males showed a similar pattern, with the notable addition that after May 2004 there were no scrotal males in the population, whereas scrotal males were recorded in all months in 2000. The inter-annual patterns were similar to New Zealand mice during mast seedfall years (high food abundance, referred to hereafter as a 'good' year) versus non-mast years (hereafter referred to as a 'poor' year) (King 1982; Ruscoe et al. 2005). In good years, reproduction started early, peaked early and ended early relative to poor years. A second, well-understood factor affecting reproductive effort in rodents, and especially in house mice, is population density (Rowe et al. 1964; King 1982; Nelson et al. 1991; Adler & Levins 1994; Leirs et al. 1997; Singleton et al. 2001; Ruscoe et al. 2005; Singleton et al. 2005; Ferreira et al. 2006). Thus, somewhat counter-intuitively, in good years, reproductive effort is down-regulated as the season progress due to high densities (arising from high recruitment rates early in the breeding season). Singleton et al. (2001) describe the same pattern in mainland Australia.

Other house mouse populations on Subantarctic islands appear to have much more prolonged breeding seasons than on Gough (Table 4). Although the austral breeding seasons all appear to start in September, they continue well into winter at other locations, despite these being at higher latitudes and therefore subject to more extreme weather conditions and more pronounced photoperiod shifts (Efford et al. 1988; Pye 1993; Matthewson et al. 1994; Avenant & Smith 2004). The Gough mice should, in theory, be able to breed into May or June, at least as late as more southerly islands, because of its more temperate climate (warmer temperatures, more daylight hours, e.g. Pye 1993). That they do not is most likely the result of density-dependent effects on their reproduction and, proximally, limited food supply (Case 1978; King 1982; Adler & Beatty 1997; Choquenot & Ruscoe 2000; Singleton et al. 2001; Michaux et al. 2002; Singleton et al. 2005; Ferreira et al. 2006). The extreme hunger of mice during winter was anecdotally evidenced when despite placing more than one snap-trap per m^2 (75 traps in a 64 m^2 grid) in two trapping sessions in June and July 2004 in the lowlands, every trap was visited, triggered and no bait was left on any trap. All bait was even eaten out from under trapped mice. By comparison, in August, 22 mice were trapped out of 75 traps, and 42 traps still had bait on them in the morning. Throughout winter, mice scavenged a large percentage of carcasses before they were collected and in one June trapping session only 14 out of 58 mice still in the traps had not been so thoroughly scavenged that some information could be obtained. Scavenging rendered fewer than 5% of mice unusable from November-February and August. Trap rates actually increased three-fold between summer (when the population is at its highest but trap rates were lowest) and mid-winter, when densities were almost twice as low as summer. These results suggest that hunger (also shown in patterns of body condition) and probably home-range size differ widely between summer and winter. Lastly, the complete absence of male mice showing scrotal testes in any month has not been reported from other Subantarctic populations, and suggests that mice were severely stressed in the Gough winter of 2004 (Pye 1993; Avenant & Smith 2004).

Table 4. Breeding season and mean litter sizes of house mouse populations.

	Latitude	Breeding season	Litter size	Reference
Gough Island	40° S	Sep - Feb/Apr	7.67	This study
Macquarie Island	54° S	Sep - Jun	6.6	Pye (1979)
Marion Island	46° S	Sep - May	7.2	Matthewson (1993)
Mana Island	41° S	Sep - Jun	7.1	Efford et al. (1988)
Rangitoto Island	36° S	?Sep - Jun	6.7	Miller & Miller (1995)
England	53° N	Year-round	6.38	Berry (1964)
England	53° N	Year-round	4.83	Rowe et al. (1964)
SE Australia	35° S	Variable	6.67*	Singleton (2001)

* Approximate

On Gough there was a tendency for monthly litter size to decrease as the breeding season progressed. Elsewhere, litter size decreases and reproductive season shortens in response to increasing density (Rowe et al. 1964; King 1982; Singleton et al. 2001; Singleton et al. 2005). Inter-annual differences in litter size and timing of reproduction therefore depend either on differences in food availability (but see Ylönen et al. (2003) for lack of effect in an experimentally food-supplemented wild population), different mouse densities at the start of the breeding seasons, or some combination of the two. On Gough, variation in weather conditions between winters easily could affect energetic demands and produce variations in annual survival, especially in the critical period from June-August. The 57% difference in estimated September densities in 1991 vs 2006 support this concept. The higher proportion of breeding mice and the longer season in 1999/2000 compared to 2003/04 could have arisen from low food availability and/or lower densities at the start of the breeding season in 1999 relative to 2003.

The observed inter-annual variability in breeding season suggests that reproduction ends when carrying capacity is reached. This would result in upper mouse densities being constrained and they are not expected to be much higher in other years compared to what has been observed. This implies that the absolute number of mice at the end of the breeding season (whenever that may be) is determined extrinsically (ultimately as a function of primary productivity). The time of year at which breeding stops would then be determined by densities at the start of breeding and annual variations in phenology and productivity of food-plants and invertebrates (Singleton et al. 2001; Singleton et al. 2005). For example, a harsh winter (below-average temperatures, above-average cloud-cover or precipitation) could result in lower survival. Low densities at the start of the breeding season would (initially) cause relatively low population increase and ultimately a longer breeding season (Berry 1968; Singleton et al. 2001; Singleton et al. 2005). However, the magnitude of these inter-annual variations is likely to be small relative to the cycles that mainland rodent populations undergo, due to the climatic stability of oceanic islands (Rowe-Rowe et al. 1989; Pye 1993).

Traditional theories of sex ratio skews in mammals ascribe the proximal mechanism to maternal adaptive manipulation of offspring sex (see Rosenfeld & Roberts (2004) for review). However, with only two (discontinuous) years of sex ratio data and no data on sex ratios of offspring, the significant reversal of a skew sex ratio between 1999/2000 and 2003/04 is difficult to interpret and I only present a tentative hypothesis. Differences in sex ratios between years have also been reported from Marion Island, without definitive explanations (Avenant & Smith 2004). First, a study of wild-caught female house mice demonstrated that neither maternal condition nor litter size has an effect on offspring sex ratios (Krackow 1997), although nutritional stress at a critical period in pregnancy causes females to produce fewer male offspring (Meikle & Thornton 1995). Second, adult male survival is reduced in mouse populations at high densities (Southwick 1958; Rowe et al. 1964). At first glance these facts and data from Gough are in agreement. Putative lower densities in 1999/2000 coincided with a higher proportion of males than in 2003/04. If density-mediated, male-biased mortality occurs only in the breeding season (possibly the result of lethal aggressive interactions over mates or territories) then whatever bias occurred at the end of the breeding season would persist through the following winter. These factors could explain the pattern of fewer males in 2003/04 and the persistence of the ratios from the breeding season through the winter. However, they do not explain a male bias from the start of breeding and continuing through winter in 1999/2000. This somewhat enigmatic result merits further investigation.

There is evidence of slight sexual dimorphism in the Gough mice; I could find no other examples in the literature reviewed. The altitudinal differences in body size were considerably bigger than the sexual differences. There were also highly significant altitudinal differences in body condition, with highland mice in worse condition than lowland mice, despite existing in a colder, wetter environment and therefore requiring greater energetic reserves. These factors are postulated to promote increased body size (Case 1978; Lomolino 1985; Michaux et al. 2002; Lomolino 2005). Mid-summer (November and December) densities in the highlands were three times lower than in the lowlands. All these results show that the highlands represent a marginal environment for mice, relative to the lowlands. The seasonal pattern of density changes in the highlands is slightly odd, because despite ostensible breeding from September there was no discernable increase in density by December. The increase in densities in the highlands in winter might reflect immigration of mice, either forced out of the better, low-lying areas as resources become scarcer, or to take advantage of avian food resources in the highlands. This requires further research.

Why are the mice on Gough the largest-bodied of all known free-living house mouse populations (Rowe-Rowe & Crafford 1992; Angel & Cooper 2006)? A lack of inter-specific competition and/or predation is considered important in driving the degree of expression of various Island Syndrome characters (Adler & Levins 1994; Yom-Tov et al. 1999), and especially gigantism (Case 1978; Dayan & Simberloff 1998; Michaux et al. 2002; Millien 2004). If this is valid, then two facts are pertinent. First, Gough is one of relatively few islands where house mice are the only introduced mammal (Chapter 1). Second, systematic predation by Subantarctic Skuas *Catharacta antarctica* or Gough Moorhens *Gallinula comeri* (the only potential predators on Gough) is unlikely. Another important driver of large body size in small mammals is periods of food shortage associated with cold, seasonal environments (Lindstedt & Boyce 1985). Figure 2 shows that either larger-bodied mice on Gough have a significantly better survival through the critical end-of-winter population decrease, or that there is a sudden increase in the growth rate of the mice in this period. Given that average body condition drops to its lowest in this period, the latter option is improbable. The absence of significant predators or competitors and a selective advantage of larger body size appear to have facilitated character release and promoted the evolution of the most extreme example of insular gigantism for this species. The importance of these influences could be tested through the study of "natural" experiments on other islands where competitors and predators of mice have been eradicated, but where mice remain, for example on Marion or St. Paul islands (van Aarde et al. 1996; Bester et al. 2000; Micol & Jouventin 2002). I predict that mice in such populations may evolve to be bigger or express other features of the Island Syndrome, such as higher densities.

Cold temperatures and food shortages cannot be the only drivers of large body-size, for two reasons. First, the highland mice on Gough presumably suffer greater temperature extremes and (as their significantly lower body condition shows) undergo greater food-stress in winter than do mice in the lowlands, yet highland mice are smaller. Second, two other Subantarctic islands, Antipodes and Marion, have had mice as the only introduced mammal for the bulk of the *ca* 150 years since their introduction (Berry et al. 1978; McIntosh 2001), yet mice have not evolved greater size on either Marion (mean=21.0 g) or Antipodes (mean=19.8 g). These islands are at higher latitudes (46°S and 49°S, respectively) than Gough (40°S) and therefore have similar, if not harsher, colder environments. Phylogentic constraint is being investigated as a reason for this apparent anomaly at Marion Island (P.G. Ryan pers. comm.). I posit an alternative: that energetic constraints limit the growth rate of mice. The densities of nesting seabirds on Gough Island are much greater in the lowlands than the highlands (Angel & Cooper 2006). The energetic hypothesis is that lowland mice have access to better energetic resources (either by preying on seabirds or because more seabirds promotes greater plant and invertebrate productivity) and can thus grow bigger than highland mice. This could be tested directly on Gough, and by comparison analyses with Marion and Antipodes islands.

My discussion of body condition and density changes is focussed largely on the results from the lowlands, as the data are more finely resolved. Nevertheless, indications are that the patterns observed in the highlands were similar. The decrease from a mid-summer high in body condition ended in February, also the month in which the last breeding females were trapped. That average body condition decreases as the breeding season progresses is no surprise. First, there are increasing numbers of mice, all competing for the same resources. Second, breeding mice might be sacrificing body condition in order to produce offspring. The February trough in body condition was followed by a rapid and significant increase in condition until June, suggesting that the late summer decrease reflects, to some extent, the effort invested (and consequently the costs incurred) during the reproductive months. The high March-June condition indices are difficult to interpret, but possibly indicate adaptive weight gain ahead of the expected lean mid- to late-winter months. However, this raises the question why, if mice (re)gained condition so rapidly, did they cease breeding so early? The marked inter-annual differences in the cessation of breeding rule out photoperiod cues and make temperature cues highly unlikely. Social control, e.g. the suppression of oestrus above a threshold density, is a possibility, but there is no evidence for this, and the eruptive 'plagues' of house mice reported from Australia and New Zealand suggest this is unlikely (King 1982; Singleton et al. 2001; Singleton et al. 2005). Alternatively, survival through late-winter appears biased towards large individuals. Thus selection on Gough may have favoured mice which cease breeding relatively early in the season (and thereby enhance their own survival and chances of breeding in a second season), because later-born mice will be small in late winter, probably suffer lower survival as a result and therefore represent wasted reproductive effort. The failure to induce breeding in Marion mice during winter, despite provisioning of supplemental food (Ferreira et al. 2006) strongly suggests that food availability is not the only factor determining breeding periodicity in Subantarctic island mice. These competing possibilities merit further research.

The monthly changes in mouse density on Gough mice differed from Marion Island. The latter population showed a consistent density decrease through winter (Ferreira et al. 2006), whereas on Gough (especially noticeable in the lowland data) the strongest period of decrease was the end of winter, which coincided (as expected) with the period of decreasing body condition. The range of monthly density estimates for the lowlands (123-244 mice/ha) encompasses the density estimates of 224 mice/ha from 1991 (Rowe-Rowe & Crafford 1992), although the latter was for September, and is substantially higher than the estimated 138 mice/ha for September 2006. This result supports the concept that densities at the start of each breeding season can vary quite widely, leading to inter-annual differences in reproductive patterns such as has been observed on Gough.

Implications for eradication

A fundamental principle of eradication is that all target individuals are exposed to risk (GISP 2005). A single pregnant female or one survivor of each sex can result in failure. Breeding rodents complicate matters for two reasons. First, pregnant/nursing females are believed to be more neophobic than at other times and may thus avoid baits (J. Parkes pers. comm.). Similarly, pups close to being weaned can survive their mother's death and could potentially begin foraging for themselves after the bait has decayed. Thus a once-off bait application programme should only be attempted after breeding has ended. Mice on Gough apparently do not breed in winter, between May and August. The conservative approach may be to confine an attempt to between June and August as this is when mice on other Subantarctic islands stop breeding. This opens a significant window of opportunity for a baiting operation. Eradication of rodents from large islands is predicated on a number of things, but arguably the most important is the knowledge that the population undergoes a predictable decrease as a result of food limitation, at which time the presentation of highly palatable bait is likely to be eaten by every single individual. Estimates of population density in 2006 (Figure 5) show the expected winter decrease in late winter in both highlands and lowlands. Figure 2 shows that lowland body condition started a downward trend in June, although July was the first month to be significantly lower than the post-breeding peak in condition. Between July and August-September the proportion of large-bodied mice in the population increased significantly. In other words, mortality of smaller mice must have been at its most acute then. I assume that at this time mice are unable to maintain condition, rather than undergoing adaptive weight loss. The most likely factor driving patterns of density and body condition decreases is limited food resources (Adler & Beatty 1997). In a seasonal environment such as on Gough, this makes intuitive biological sense. First, there has been no seed production for several months. Second, it is extremely unlikely that any significant invertebrate reproduction occurs during winter, and thus stocks are probably at their lowest in late winter. Congruent results of extreme hunger, low body condition and decreasing density point to June-August as being a critical time for mouse survival and thus also for a toxic baiting operation. The differences between density, body size and body condition in mice from the highlands and lowlands all suggest that the highland areas are suboptimal for mice. Following from this, highland mice are expected to be more motivated to accept bait than mice in the lowlands. The feasibility of such an eradication is currently being assessed, which *inter alia* aims to assess the likelihood of 100% of the mice being exposed to and taking poison bait (Angel & Cooper 2006). These findings are encouraging because they suggest that if bait can be spread at sufficient density in all mouse home-ranges, and is applied in June-August, there is a high chance of meeting the requirement that all mice take lethal doses of bait, and thus the eradication of mice from Gough Island is possible. Further research into bait palatability, toxicity, optimal baiting densities and percentages of bait acceptance during this time window would lend greater confidence to an assessment of the feasibility of eradication.

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CHAPTER 7

Synthesis of key results and directions for future research

Background

The research that I have presented was initiated in response to the alarming discovery that Tristan Albatross *Diomedea dabbenena* and Atlantic Petrel *Pterodroma incerta* breeding success was extremely low in 2001 (Cuthbert 2004; Cuthbert & Hilton 2004; Cuthbert et al. 2004). Despite the fact that predatory house mice *Mus musculus* were the prime suspects for the pattern in both species, there were significant uncertainties about the 2001 findings. These included the possibility that predation occurred in 2001 but that it was an exceptional year, or that disease, starvation or some other cause was a major driver of the low breeding success and that predation by mice was marginal (i.e. causing insignificant deaths) or incidental (i.e. attacking sick or weak individuals that were already doomed). Thus a major objective for the field work was to determine if mice were in fact responsible for the majority of chick failures.

Introduction

In this final chapter, I draw together the key results from the thesis and discuss some of the unanswered questions. Rather than leave open-ended questions, I erect hypotheses that might account for the unexplained patterns, based on our understanding of the ecology of the mice, seabirds and terrestrial ecosystem on Gough Island.

This research is based for the most part on a single field season. Each chapter comprises a study entire unto itself, drawn together by the common thread of predation by mice on Gough Island's seabirds. The thesis covers a broad sweep of topics at an island where the ecology has received only patchy research. It is thus not too surprising that there are aspects of the research from each chapter for which more focussed study is recommended. Some of the results defy rigorous explanation using the data I collected. Considerations in this chapter go explicitly beyond the bounds of my data. They are often speculative, but present ideas for future research to either refute or confirm. In a departure from traditional synthesis chapters, they are presented as a narrative in a more discursive style, partly to distinguish them from the more robust analyses of data in the rest of this thesis. Dry, dispassionate descriptions of what (for me personally) were astonishing and horrific discoveries are to be found in the rest of the thesis.

Key result 1: mice are responsible for chick mortality

Atlantic Petrel eggs hatch mostly in August, which is unfortunate given the timing of the annual visits to Gough and resulted in truncated seasons of study. When I arrived in October 2003, Atlantic Petrel chicks were already 6-12 weeks old. Concerns about the frequency of widespread predation such as apparently occurred in 2001, were exacerbated through the first Atlantic Petrel study, from October 2003-January 2004. Very few predation events were recorded, a positive result for the petrels but a negative result in the context of a field study on mouse impacts. However, observations were restricted to the second part of the chick-rearing stage. The following year (covering the incubation and early chick-rearing periods) proved to be an extremely poor year for chick survival, which provided unequivocal evidence that mice were responsible for a truly alarming rate of failure. In September 2006 I returned to Gough and was able to set up another Atlantic Petrel study, with kind assistance from Brian Bowie who checked on burrows after I had left. Although the period of study did not overlap much with the 2004 study, failure rates were again far higher than 2003. Thus it appears that 2003 was unusual, with so few attacks compared to all other years of study and including three years covering the same nest period (2000, 2001 and 2006). However, the failure rate before the study commenced in 2003 is unknown. The evidence from 2004 strongly suggests that small chicks in August and September are most vulnerable. While it is impossible to separate definitively the effect of time-of-year from chick age, August and early September may well be periods of the most intense predation because mice are in significantly lowered body condition at that time (Chapter 6). Thus there may have been significant predation before the study commenced in 2003. Alternatively, spatio-temporal variation in attack rates is likely, although the magnitude of this effect in the lowlands (where the Atlantic Petrels breed) is completely unknown.

The first evidence of significant predation by mice was obtained on 20 April 2004, when I checked study nests in Green Hill to find widespread wounds and fresh carcasses of Tristan Albatross chicks. These could only have been caused by mice. Video evidence, more wounded chicks and widespread albatross chick failures subsequently confirmed that mice were the source of the wounds and the ultimate cause of deaths. Thus by 30 April, a major objective of the research had been more-or-less achieved.

Key result 2: predation by mice is sufficient to drive population decreases

The population-level impacts of the observed failure rates are sufficient to drive decreases in both Atlantic Petrels and Tristan Albatrosses. This is all-the-more troubling because Gough is effectively the last breeding site for both species. The Atlantic Petrel population is *ca* 1.8 million pairs (Cuthbert 2004), and despite high predation rates they are in no immediate danger of extinction. In contrast, the situation for the Tristan Albatross is particularly acute, because adult mortality (most probably from mortality associated with fishery interactions) is apparently severe and a population model predicted a negative trend regardless of other parameters. The poor observed breeding success is alone also sufficient to drive decreases, but in concert with low post-fledging survival it compounds the decrease. The total adult population is *ca* 5400 birds, but the model predicts that with observed parameters it could decrease to *ca* 1000 birds (equivalent to about 500 nesting attempts annually) within 30 years.

It seems likely that mice have been preying on seabird chicks since the 1800s. Back-of-the-envelope calculations of possible pre-predation population numbers illustrate the possible population size to which the impacted species could recover (all else being equal). For the Tristan Albatross, from 1612 pairs in 2005 (Chapter 4) and an annual decrease of 1%, there may have been as many as 7500 pairs nesting before mice attacks began (guestimated to be 1850). For the Atlantic Petrel population, Cuthbert (2004) estimated that on Gough it was decreasing at 1.7-3.5% per year, based on a fairly crude population model. Using the lower rate of decrease (1.7%) and hindcasting from 1.8 million pairs at present yields an estimate of 22.5 million pairs in 1850. Density-dependent effects may have prevented either population from achieving those sizes.

Key result 3: lowland mice rely heavily on seabirds but highland mice don't

Stable isotope analyses, while confounded to a degree by an enigmatic nitrogen isotope signature for mice, nevertheless indicate some key results. First, mice in the lowlands do appear to rely to a significant degree on consumption of Atlantic Petrel chicks in August and

September. Standard ecological theory predicts that reduction in the supply of an important prey resource will, all else being equal, result in a concomitant reduction in predator numbers (Begon et al. 2003). For the Atlantic Petrels, reduced densities should cause reduced numbers of chicks being preyed upon and the petrel population should ultimately equilibrate to a lower density at but one which can sustain low levels of mouse predation on chicks. In contrast, the highland mice, while devastating the albatross nests in many areas, appear to gain relatively little nutritional reward from the attacks. In the context of a cold Subantarctic winter, if mice are hungry and attack chicks to sate that hunger, the number of chicks available should be irrelevant (until they become a limiting factor), and the total number of failures should be relatively consistent over time. The findings of Chapter 3 (that the number of chicks available determines the number of failures) implies that albatross chicks are not necessarily an important part of the diets of highland mice. This is in agreement with the isotopic analysis. Thus the importance of predation in the Tristan Albatross population dynamics is likely to diminish as the population decreases. As noted in Chapter 5, however, diminished fertility from reduced nitrogen input as seabird numbers decrease (e.g. Croll et al. 2005; Fukami et al. 2006) might have an ameliorating or an aggravating effect on predation rates in the highlands.

Enigmatic results

Tristan albatross predation

Spatio-temporal variation in Tristan Albatross failures between 2001-2006 are very difficult to predict, with the exception that Gonydale appears to be affected least by predation and thus experiences consistently high breeding success. Why are the patterns between sites not consistent within a year, with predation going up in one year in all areas and down in another year, relating to island-wide phenomena such as weather conditions or primary productivity? Further, there were consistently large differences in annual failure rates between Green Hill and Gonydale. However, stable isotope analysis showed that the total marine input to the two systems was similar, meaning that the densities of all nesting seabirds (which are responsible for marine nitrogen in the highlands) in the two areas must be very similar, and plant productivity from the fertilising effects of seabirds is likely to be the same. The relative abundances of major plant groups were essentially identical, too, as one would expect from adjacent sites at the same altitude, on slopes with similar aspect and orientation. Density estimates from mouse mark-recapture data from the two sites were closely matched. Why the difference in mouse predation? I suspect that part of the answer to this otherwise enigmatic result comes from the analysis of stable isotopes. In Chapter 5 I conclude that the contribution that seabird consumption makes to highland mouse diets is negligible in both Green Hill and Gonydale. This may seem surprising, however it is probable that highland mice gain less energetically (in absolute terms) from attacking an albatross chick than lowland mice do from attacking an Atlantic Petrel chick. This is because albatross chicks are on the surface, and weakened birds are almost inevitably killed by Subantarctic Skuas *Catharacta antarctica* and Giant-Petrels *Macronectes* spp., which will then consume the vast bulk of the chick's flesh. By contrast, Atlantic Petrel chicks mostly die underground, and unless a Gough Moorhen *Gallinula comeri* scavenges the carcass (e.g. Wanless & Wilson in press), mice will consume it entirely. Also, there are three orders of magnitude more nesting Atlantic Petrels than Tristan Albatrosses (although the difference in biomass is less). Thus, if albatross consumption does indeed constitute a relatively trivial part of the diet, the incremental survival value in preying on them must also be small. Undoubtedly those mice that do eat from wounded chicks before the scavenging birds arrive will benefit from doing so, but the evidence suggests that there is a weak pressure for mice to attack albatrosses. A weak selective pressure could explain why the behaviour, once evolved, does not spread rapidly through the population and is not maintained at consistently high levels, either spatially or temporally.

Possible explanation for the highland patterns

How is this ostensibly variable behaviour maintained or spread through the mouse population in the highlands? Several lines of evidence suggest that attacking albatrosses is a learned behaviour for mice. I speculate that cultural transmission is responsible for the observed patterns (Wanless et al. 2005). House mice are not long-lived (on Gough it is very unlikely that any survive a second winter), are not known to engage in post-weaning parental care and do not normally forage collectively (Bronson 1979; van Aarde & Jackson 2006). Also, each year attacks on albatross chicks can only commence in March, when chicks hatch. Attacks continue until late September, but appear to cease some time in October (when chicks are almost fully grown, fully feathered and increasingly mobile). Therefore, during summer as the mouse population increases, no young mice have the opportunity to attack albatrosses, and unless it is instinctive, they cannot possess knowledge of how to attack an albatross successfully. That knowledge, however, may persist between years in mice that survive into a second winter.

Several observations about the extent and nature of attacks give insight into the mechanism of attacks. First, chick and adult albatrosses have an entirely inadequate response to mouse attacks, suggesting that there is little or no danger to mice that attack chicks. Second, several chicks had healed wounds, showing that not all attacks cause fatalities. I also found a chick with down missing from several patches and multiple (>10) small bite marks, suggesting that a mouse (or mice) had attacked it repeatedly, but hadn't relocated the previous bite marks and eventually desisted the attack. Third, video evidence of attacks suggests that not all mice are equally keyed-in to the resource. For example, some mice were clearly attracted by the ongoing attack and spent time thoroughly investigating the albatross without actually biting it or getting any nutritional benefit. Collectively these observations suggest that the evolution of this behaviour is complex, possibly involving several levels of ability/learned behaviour in mice. It certainly is not as simple as learning to de-husk the seed of an introduced plant, or learning to dig into peat to find moth pupae. Mice may have to learn a novel suite of behaviours before attacking an albatross chick is sufficiently rewarding to them for the behaviour to persist. However, not all mice need learn the full suite of behaviours. It could be that some few mice act as catalysts by attacking albatrosses and opening up wounds, whereas others simply learn to take advantage of the opportunities this created. Novel behaviours potentially include:

1. to make the direct association of a large, warm, living, moving animal with food
2. to burrow through or remove the thick down or feathers from an area before attacking
3. to bite through the skin and concentrate the attacks to make a hole (to "access the food")
4. to repeatedly bite this large, mobile animal, and that persistence pays
5. to understand that the bird moves when under attack, but that it is not likely to be dangerous for them.

Variable rates of transmission/learning could produce the observed inconsistent inter-annual predation levels. Also, the more albatrosses there are, the more opportunities there are to learn and the faster the behaviour is likely to spread, which would explain the significant positive relationship between total nesting attempts and total failures, an otherwise puzzling result. This hypothesis is compatible with some of the major findings of the thesis. First, the more chicks are available, the more they get attacked. Second, the 'local area effect', where nests that failed in a given month were significantly closer to the nearest nest that failed the previous month than predicted by chance. Third, it would also accommodate the differences between Green Hill (lots of mice know, transmission rates are high, and attack rates are also high) and Gonydale (few mice know, so transmission rates are low and attack rates are low), as well as the 'random walk' of annual breeding success in the long-term study colony in Tafelkop (Chapter 3). The ostensible delay in the onset of attacks in the Albatross Plain study nests was probably a coincidence. In the round-island survey of chicks done on 28-30 April, a wounded chick was found in Albatross Plain, but at the opposite (northern) end to the study nests. Another three wounded chicks were found nearby, in an area that is technically the Spire Crag sub-colony, but to all other intents and purposes those nests form part of the Albatross Plain area. Thus attacks were happening in Albatross Plain from April, but were only detected in the southern section, where the study nests were located, in May. This finding is compatible with the cultural transmission of a learned behaviour, but is difficult to reconcile with the alternative, that resource-limitation drove mice to attack chicks at different times within a sub-colony.

Another explanation (which does not necessarily preclude cultural transmission) provides a slightly more optimistic view for the albatrosses. It arises from the observation that some chicks do not get attacked, despite being very close (<20 m) to three or four attacked nests. Also, some chicks are attacked, but survive. Perhaps these individuals behave in a way that discourages mice from attacking, possibly by being more active or responding more vigorously to being climbed on or bitten, making it difficult for mice to create an open wound and lowering the energetic returns of attacking. This raises the possibility that natural selection can act on the albatrosses, with those that are behaviourally equipped to better respond to attacks surviving better. If attacks have been occurring since the 1800s, as Comer's observations imply (Verrill 1895), then there may have been sufficient time for natural selection to act. It is possible that chicks with increasingly precocial development of mouse-deterring behaviours are being selected for, and thus the time-window for possible attacks is shortening. However, the delayed onset of attacks in Gonydale, which increased from August, is somewhat in opposition to this theory. Perhaps attacks in Gonydale have already pared the population down to include mostly breeders with genes for deterring attacks, and mice regularly attempt to attack Gonydale chicks, but are mostly unsuccessful.

If the cultural transmission hypothesis is true, then the pattern of albatross chick failures gives some hope for the diminution of attacks concomitant with decreased Tristan Albatross nesting densities. Chapter 3 shows that the total number of failures in a year is largely a function of the number of nesting attempts, which suggests that if the predatory behaviour is spread amongst mice, it is retarded at low nest densities. Thus as the Tristan Albatross population density decreases, attacks should decrease in frequency and breeding success should increase.

Predation on petrels

Several results from the Atlantic Petrel study are surprising. As for the Tristan Albatrosses, some chicks did not get attacked. Oddly, mice even attempted to eat spilled food from the down of one, but the chick was otherwise unmolested by mice. Further, why does virtually every single Atlantic Petrel burrow get visited, if not used as a home, by mice, but only some chicks are attacked? Why did attacks on one of the two wounded chicks in 2003 cease before significant damage was inflicted, allowing the chick to survive and fledge? The stable isotope data (Chapter 5) suggest that almost all mice in the lowlands prey on seabird chicks to some extent in late winter. Although skua numbers increase in July, their densities and the corresponding provision of seabird carcasses is too low to explain the sudden increase in seabird consumption, and the result is interpreted as being almost entirely due to mice attacking Atlantic Petrel chicks. If most mice are reticent to attack large chicks, then perhaps some chicks survive because there is a temporary glut of small/young Atlantic Petrel chicks in August and September. The pattern of attacks on Atlantic Petrel chicks in 2004 was non-random: mice targeted the smallest preferentially (until chicks were older than about 10 days). This supports the small-chick-glut hypothesis. It also suggests that mice learn that smaller chicks are easier to kill, or are more rewarding to attack for some other reason. Exactly how mice determine the size/suitability of a chick for attack in the absolute darkness of a burrow at night is unknown. It may be that chicks' scent changes with age (in nature or in strength), which mice have learned to cue into, or that they probe a chick by nibbling and gauge likely effort required to subdue the chick based on the strength of its reaction.

At the end of the first Atlantic Petrel study season in the lowlands I removed the burrow cameras. Rather than leave them lying idle until the next Atlantic Petrel season in June, I deployed them in three Great Shearwater *Puffinus gravis* burrows. On 9 April 2004, mice were filmed attacking and killing one of the three chicks. This was somewhat unexpected, because in 2001, 67 Great Shearwater nests were monitored, and fledging success (percentage of eggs hatched that produced a fledged chick) was 93%, with no evidence of mouse predation at all (Cuthbert 2005). Analysis of the percentage volume of mouse stomachs made up by seabirds showed a strong peak in March (but almost nothing in April). Mouse stable isotopes showed a strong peak in $\delta^{15}N$ values in April, which could have been due to seabird consumption, but the corresponding $\delta^{13}C$ value was no different from other months, militating against large-scale seabird consumption. These equivocal results nonetheless suggest that in some years, some mice may prey on seabird chicks in March and/or April, and this merits further research.

Wider relevance

Devastating impacts of predation by rats *Rattus* spp. on seabirds are legion, and include fatal attacks on adult Laysan Albatrosses *Phoebastria immutabilis* on Kure Atoll (Kepler 1967; Atkinson 1978; Bell 1978; Moors & Atkinson 1984; Atkinson 1985; Brooke 1995). In Chapter 1 I review evidence of mice preying on seabirds, which amounts to reports from just five islands. Do these differences mean that rats are naturally predatory, but mice are not? Probably not, because on all the islands with (probable or confirmed) mouse attacks on seabirds, mice are the only introduced mammal. This suggests instead that where mice co-occur with rats, they are suppressed through predation (e.g. Russell & Clout 2004; Witmer et al. 2007) and the breadth of their niche is constrained by competition. The very broad range of habitats that house mice have invaded, from deserts to tropics and extreme-latitude islands, which includes surviving and breeding in permanent, total darkness inside -10° C freezers, makes them unexcelled opportunists (Laurie 1946; Bronson 1979). In retrospect it is not that surprising that, when freed from constraints of predation and competition, their niche broadens to encompass behaviours typically associated with rats, such as predation of seabird chicks (Courchamp et al. 1999). This, however, does not necessarily vitiate the hypothesis that it is difficult for mice to learn to attack an albatross chick.

I have argued that ecologically, mice are really just small rats. Mouse predation on procellariiform seabirds has arisen *de novo* on at least five islands (assuming the reported impacts were genuine predation vs scavenging). On Marion Island, wounded Wandering Albatross *Diomedea exulans* chicks have been found recently (pers. obs.), strongly suggesting mouse attacks are occurring on albatross chicks for the first time, but within 20 years of the eradication of cats (Bester et al. 2000). This points to a relatively rapid (re?)evolution of predatory behaviour there. It is thus quite reasonable to assume that attacks on Gough Island, especially on smaller, burrow-nesting species, began shortly after colonisation by mice. I predict an increase in the incidence of Wandering Albatross chick mortality on Marion Island, and also significant chick mortality on winter-breeding burrowing petrels there. Antipodes [Wandering] Albatrosses *Diomedea [exulans] antipodensis* on Antipodes Island do not appear to be vulnerable to attacks, although this has not been explicitly investigated, the island has not been studied in winter in recent years and predation may have been overlooked (K. Walker in litt.). It serves as a closely analogous system to Gough, and a comparative study on mouse biology and impacts would undoubtedly yield deeper insights into the causal mechanisms that promote predatory behaviour. Similarly, eradication has rendered mice the only introduced mammal on St Paul Island (South Indian Ocean) and Australie Island (Kerguelen Archipelago, South Indian Ocean), and research on mouse impacts or lack thereof would be illuminating (Micol & Jouventin 2002).

There has been an explosion of rat eradication effort in the past 10-15 years (Towns & Broome 2003). However, for reasons that remain unclear, simultaneous eradication of rats and mice has not yet been achieved (discussed briefly in Chapter 1). There may have been doubt about the significance of mouse impacts prior to this study, but the verdict is in: mice cannot be ignored as a conservation threat to seabirds on islands, at least where they are, or become through introduction or eradication of other species, the only introduced mammal (contra Witmer et al. 2007).

In Chapter 1 I discussed the lack of conservation attention that has been given to house mice on islands, and speculated that part of the reason for this was a lack of dramatic, visible impacts. Descriptions of the impacts of mice preying on island-endemic invertebrates and causing extinctions, e.g. on Antipodes Island (Marris 2000) and Marion Island (Chown et al. 2002) or precipitating potentially irreversible changes to ecosystem functioning, e.g. Marion Island (Smith et al. 2002), have, to the best of my knowledge, failed to generate wide scientific, popular or conservation interest. By contrast, descriptions of conclusive proof that mice were preying on Gough Island's endemic seabirds (Angel et al. 2005; Wanless et al. 2005) led to substantial media interest (e.g. Marris 2005; Dangerfield 2006; Pearce 2006; Millius 2007), an unsolicited offer of support for eradication from the New Zealand Department of Conservation (G.M. Hilton pers. comm.) and the establishment of a committee to raise funds and oversee a process aimed at eradicating mice (Angel & Cooper 2006). The subsequent publication describing those impacts in a peer-reviewed, international journal (Wanless et al. 2007) led to renewed media interest. The relative importance of conserving endemic invertebrates or plants is, in theory, the same as conserving charismatic fauna such as albatrosses. However, the evidence suggests that in reality, less visible fauna and flora tend not to generate sympathetic responses or to drive island conservation actions. It is my belief that negative biodiversity impacts of mice (or other invasive species) on any endemic island biota, either direct or indirect (such as through changing nutrient cycles, synergy with other invasive species or changes to other major ecosystem processes) is sufficient grounds to merit immediate remedial action. Demonstrating negative impacts on charismatic species such as seabirds should not be a prerequisite for planning island conservation and restoration projects or securing funding for such projects.

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APPENDIX 1

Stable isotope data from plants, invertebrates and seabirds (probable dietary sources of house mice *Mus musculus*) on Gough Island. Stable isotope data are presented in conventional δ notation, denoting parts per thousand (‰).

Plant samples

Table 1. Stable isotope values of plants collected from Gough Island in September 2006. Low altitude samples were collected from the SE coastal plain on mouse trapping grids. Green Hill and Gonydale are highland sites. Analyses are presented in Chapter 5.

Genus	Altitude	Grid/Transect	$\delta^{15}N$	$\delta^{13}C$	%N	%C
Acaena	Low	B2	12.11	-30.34	3.06	44.21
Acaena	Low	B2	10.65	-30.72	2.96	44.10
Acaena	Low	B2	10.73	-30.77	2.85	43.27
Acaena	Low	B2	12.36	-29.90	3.66	44.39
Acaena	Low	B2	12.29	-30.36	4.04	41.78
Histiopteris	Low	B2	15.31	-25.69	7.28	49.38
Histiopteris	Low	B2	11.83	-26.28	6.64	49.23
Histiopteris	Low	B2	14.07	-27.09	7.47	49.59
Histiopteris	Low	B2	18.25	-28.25	6.42	49.71
Histiopteris	Low	B2	12.27	-26.89	6.20	48.45
Scirpus	Low	A1	10.01	-24.95	1.22	43.56
Scirpus	Low	A1	8.06	-26.48	1.37	42.09
Scirpus	Low	A1	12.36	-29.02	1.56	44.33
Scirpus	Low	A1	11.00	-25.65	1.24	42.58
Scirpus	Low	A1	7.85	-28.76	1.09	44.44
Scirpus	Low	A2	12.39	-26.85	1.14	41.46
Scirpus	Low	A2	14.57	-26.69	1.31	40.84
Scirpus	Low	A2	12.96	-28.25	1.03	41.58
Scirpus	Low	A2	12.07	-27.30	1.36	42.63
Scirpus	Low	A2	13.24	-28.56	1.17	41.46
Scirpus	Low	A3	11.90	-25.47	0.91	43.37
Scirpus	Low	A3	8.74	-24.15	1.08	44.54
Scirpus	Low	A3	12.65	-26.55	1.45	42.93
Scirpus	Low	A3	7.62	-26.88	1.39	43.73
Scirpus	Low	A3	8.49	-24.23	1.20	44.68
Scirpus	Low	B1	12.58	-25.25	1.47	40.90
Scirpus	Low	B1	15.92	-32.38	1.02	42.07
Scirpus	Low	B1	16.90	-26.32	1.95	40.11
Scirpus	Low	B1	13.89	-27.28	0.98	41.85
Scirpus	Low	B1	11.40	-28.24	1.03	40.69

Genus	Altitude	Plot/Transect	$\delta^{15}N$	$\delta^{13}C$	%N	%C
Scirpus	Low	B2	11.34	-26.05	1.10	44.32
Scirpus	Low	B2	13.22	-32.08	1.69	42.81
Scirpus	Low	B2	10.70	-27.26	1.29	43.04
Scirpus	Low	B2	14.19	-26.81	1.12	44.60
Scirpus	Low	B2	14.81	-27.71	1.57	43.68
Scirpus	Low	B3	12.14	-26.85	0.88	40.99
Scirpus	Low	B3	11.90	-26.66	1.91	40.62
Scirpus	Low	C1	8.33	-27.70	0.94	43.82
Scirpus	Low	C1	8.67	-27.96	1.52	45.60
Scirpus	Low	C2	9.22	-26.01	1.21	43.43
Scirpus	Low	C2	9.39	-27.48	1.11	43.49
Scirpus	Low	C2	6.31	-26.11	1.67	44.58
Scirpus	Low	C2	8.25	-26.10	1.00	42.68
Scirpus	Low	C3	12.41	-26.41	1.39	42.76
Scirpus	Low	C3	9.24	-26.77	1.05	44.68
Scirpus	Low	C3	8.87	-26.71	0.79	45.23
Scirpus	Low	C3	16.60	-26.64	1.14	44.51
Scirpus	Low	C3	13.26	-28.36	1.26	43.69
Acaena	Green Hill	A	-0.03	-27.81	2.45	44.04
Acaena	Green Hill	A	7.47	-29.29	2.45	43.81
Acaena	Green Hill	A	2.17	-28.40	2.12	44.03
Acaena	Green Hill	A	-0.28	-27.95	1.81	44.32
Acaena	Green Hill	A	4.71	-28.31	2.10	43.26
Acaena	Green Hill	A	6.55	-28.56	2.50	44.29
Apium	Green Hill	A	0.39	-27.97	3.55	43.06
Apium	Green Hill	A	6.72	-27.86	4.85	47.47
Apium	Green Hill	A	1.74	-26.25	3.73	41.66
Apium	Green Hill	A	2.03	-27.12	4.03	43.79
Apium	Green Hill	A	2.20	-27.27	3.13	39.04
Apium	Green Hill	A	2.65	-28.04	3.63	41.28
Empetrum (flower)	Green Hill	A	6.13	-25.37	1.67	50.96
Empetrum (leaf)	Green Hill	A	4.92	-26.66	1.36	52.04
Scirpus	Green Hill	A	7.40	-25.69	1.83	41.94
Scirpus	Green Hill	A	9.67	-25.57	0.79	40.85
Scirpus	Green Hill	A	5.87	-25.61	1.70	43.33
Scirpus	Green Hill	A	4.75	-27.26	1.04	44.97
Scirpus	Green Hill	A	7.22	-28.23	1.80	42.96
Scirpus	Green Hill	A	4.21	-26.73	1.39	43.34
Scirpus	Green Hill	A	6.15	-26.33	1.62	44.30
Scirpus	Green Hill	A	4.05	-24.87	0.62	42.74
Acaena	Green Hill	B	4.12	-28.34	2.11	43.01
Acaena	Green Hill	B	1.32	-28.65	1.87	43.54

Genus	Altitude	Plot/Transect	$\delta^{15}N$	$\delta^{13}C$	%N	%C
Acaena	Green Hill	B	8.88	-27.25	2.86	43.78
Acaena	Green Hill	B	8.40	-27.44	2.88	44.30
Acaena	Green Hill	B	4.04	-27.32	2.37	43.63
Acaena	Green Hill	B	2.20	-28.32	1.79	42.90
Apium	Green Hill	B	4.30	-25.74	2.18	40.22
Apium	Green Hill	B	-3.63	-27.04	2.15	35.20
Apium	Green Hill	B	1.45	-28.36	3.05	44.48
Apium	Green Hill	B	7.86	-26.49	3.90	38.33
Apium	Green Hill	B	3.01	-28.53	3.37	42.32
Apium	Green Hill	B	5.75	-28.22	3.46	40.61
Empetrum (leaf)	Green Hill	B	2.42	-26.45	1.41	49.73
Empetrum (leaf)	Green Hill	B	-1.81	-27.65	0.94	52.04
Empetrum (leaf)	Green Hill	B	3.41	-26.49	1.21	53.39
Scirpus	Green Hill	B	11.37	-26.54	1.93	42.89
Scirpus	Green Hill	B	6.48	-24.33	1.12	43.37
Scirpus	Green Hill	B	7.71	-30.43	1.64	43.92
Scirpus	Green Hill	B	4.72	-26.17	0.98	44.87
Scirpus	Green Hill	B	9.99	-27.36	2.52	43.63
Scirpus	Green Hill	B	7.77	-24.26	1.35	43.00
Scirpus	Green Hill	B	6.29	-27.50	1.72	44.84
Scirpus	Green Hill	B	7.57	-26.82	1.27	42.22
Acaena	Green Hill	C	4.38	-28.02	1.68	44.03
Acaena	Green Hill	C	3.60	-28.34	2.32	43.09
Acaena	Green Hill	C	1.28	-28.12	1.97	43.83
Acaena	Green Hill	C	2.39	-28.17	2.94	45.54
Acaena	Green Hill	C	0.14	-28.28	2.32	44.80
Acaena	Green Hill	C	1.28	-27.30	2.03	43.92
Apium	Green Hill	C	0.17	-27.83	3.82	42.78
Apium	Green Hill	C	5.33	-27.59	3.75	39.22
Apium	Green Hill	C	1.62	-27.59	3.73	40.86
Apium	Green Hill	C	2.71	-27.19	3.92	40.14
Apium	Green Hill	C	-1.39	-28.66	2.96	42.42
Empetrum (leaf)	Green Hill	C	4.69	-27.75	1.45	51.56
Empetrum (leaf)	Green Hill	C	0.98	-27.82	1.20	53.63
Scirpus	Green Hill	C	12.35	-26.85	1.53	43.52
Scirpus	Green Hill	C	5.01	-26.14	1.55	44.34
Scirpus	Green Hill	C	4.76	-27.34	0.66	42.12
Scirpus	Green Hill	C	8.81	-26.75	0.79	41.74
Scirpus	Green Hill	C	3.51	-26.91	1.70	44.99
Scirpus	Green Hill	C	6.98	-27.19	1.18	42.52
Scirpus	Green Hill	C	2.26	-26.77	1.86	44.64
Scirpus	Green Hill	C	3.41	-27.25	1.75	44.64
Acaena	Green Hill	D	-1.00	-28.58	2.05	43.05

Genus	Altitude	Plot/Transect	$\delta^{15}N$	$\delta^{13}C$	%N	%C
Acaena	Green Hill	D	1.96	-28.26	1.99	42.55
Empetrum (flower)	Green Hill	D	0.52	-26.89	1.65	51.43
Empetrum (flower)	Green Hill	D	-1.84	-27.22	1.49	51.52
Empetrum (flower)	Green Hill	D	-2.57	-26.34	1.31	50.99
Empetrum (leaf)	Green Hill	D	-1.00	-27.92	1.09	53.10
Empetrum (leaf)	Green Hill	D	-3.77	-28.81	0.75	55.41
Empetrum (leaf)	Green Hill	D	-0.46	-28.08	0.97	53.32
Empetrum (leaf)	Green Hill	D	-1.09	-26.99	0.96	54.12
Scirpus	Green Hill	D	6.02	-26.58	2.37	45.49
Scirpus	Green Hill	D	2.39	-27.11	2.16	45.22
Scirpus	Green Hill	D	3.44	-27.24	2.06	45.52
Scirpus	Green Hill	D	5.48	-27.13	1.24	43.05
Scirpus	Green Hill	D	6.61	-27.50	2.00	45.52
Scirpus	Green Hill	D	6.03	-24.82	2.55	44.57
Acaena	Green Hill	Mouse grid	4.19	-29.45	2.71	43.87
Apium	Green Hill	Mouse grid	4.76	-28.26	4.50	44.50
Apium	Green Hill	Mouse grid	-2.93	-25.95	2.80	40.33
Apium	Green Hill	Mouse grid	-1.62	-28.22	3.76	43.96
Empetrum (flower)	Green Hill	Mouse grid	-2.61	-27.12	1.35	53.45
Empetrum (flower)	Green Hill	Mouse grid	1.35	-27.91	1.46	53.07
Empetrum (flower)	Green Hill	Mouse grid	-0.45	-26.44	1.42	51.17
Nertera	Green Hill	Mouse grid	0.38	-26.97	1.27	45.51
Nertera	Green Hill	Mouse grid	-3.86	-28.75	1.53	42.30
Nertera	Green Hill	Mouse grid	-1.26	-29.17	1.41	45.36
Nertera	Green Hill	Mouse grid	-1.75	-27.93	1.52	45.67
Scirpus	Green Hill	Mouse grid	5.28	-26.51	1.63	45.92
Scirpus	Green Hill	Mouse grid	-0.79	-26.17	1.40	44.67
Scirpus	Green Hill	Mouse grid	3.60	-27.08	2.33	44.74
Acaena	Gonydale	A	3.45	-27.25	2.26	42.82
Acaena	Gonydale	A	1.83	-30.44	1.96	43.09
Apium	Gonydale	A	3.06	-27.57	4.59	44.54
Apium	Gonydale	A	1.22	-27.14	4.34	41.13
Apium	Gonydale	A	-0.15	-27.37	4.25	44.52
Apium	Gonydale	A	-2.97	-27.25	3.01	43.70
Empetrum (flower)	Gonydale	A	5.73	-26.81	1.39	49.40
Empetrum (flower)	Gonydale	A	2.66	-26.59	1.22	51.44
Empetrum (leaf)	Gonydale	A	4.81	-27.50	1.44	50.83
Empetrum (leaf)	Gonydale	A	3.66	-27.40	1.07	51.84
Scirpus	Gonydale	A	4.17	-26.40	1.42	42.46
Scirpus	Gonydale	A	2.33	-26.63	1.02	43.69
Scirpus	Gonydale	A	4.37	-27.51	1.81	42.40
Scirpus	Gonydale	A	3.06	-27.04	0.73	44.01
Scirpus	Gonydale	A	3.61	-25.04	1.07	43.68

Genus	Altitude	Plot/Transect	$\delta^{15}N$	$\delta^{13}C$	%N	%C
Acaena	Gonydale	B	2.59	-28.11	1.95	43.02
Acaena	Gonydale	B	1.31	-29.04	2.28	42.74
Acaena	Gonydale	B	1.82	-27.98	2.54	42.87
Apium	Gonydale	B	-1.90	-27.19	2.25	41.55
Apium	Gonydale	B	-0.46	-28.03	3.86	44.70
Apium	Gonydale	B	-1.14	-28.17	2.79	41.08
Empetrum (flower)	Gonydale	B	3.98	-26.50	1.26	51.06
Empetrum (flower)	Gonydale	B	1.31	-25.84	1.59	50.31
Empetrum (leaf)	Gonydale	B	5.09	-27.86	1.09	52.64
Empetrum (leaf)	Gonydale	B	-0.56	-27.26	0.97	52.88
Empetrum (leaf)	Gonydale	B	2.74	-28.42	1.44	52.78
Nertera	Gonydale	B	-1.11	-27.17	1.59	44.92
Nertera	Gonydale	B	-2.25	-29.03	2.72	43.04
Nertera	Gonydale	B	-1.61	-28.32	1.04	39.50
Nertera	Gonydale	B	-2.48	-29.92	2.21	41.32
Scirpus	Gonydale	B	4.66	-28.75	1.26	44.03
Scirpus	Gonydale	B	3.31	-26.99	1.20	43.98
Scirpus	Gonydale	B	6.24	-27.53	2.36	43.55
Scirpus	Gonydale	B	2.15	-27.28	1.57	43.58
Scirpus	Gonydale	B	2.90	-27.59	1.69	45.06
Acaena	Gonydale	C	5.37	-29.75	2.22	42.47
Acaena	Gonydale	C	0.86	-28.52	2.04	42.69
Acaena	Gonydale	C	-0.68	-30.34	1.33	45.18
Acaena	Gonydale	C	1.22	-27.17	2.54	43.07
Empetrum (flower)	Gonydale	C	0.18	-26.91	1.60	50.24
Empetrum (leaf)	Gonydale	C	-2.31	-27.88	1.03	53.46
Empetrum (leaf)	Gonydale	C	-0.05	-28.27	1.34	51.94
Nertera	Gonydale	C	-2.95	-29.13	1.31	39.70
Scirpus	Gonydale	C	4.19	-26.25	1.22	43.06
Scirpus	Gonydale	C	2.66	-25.37	0.91	43.43
Scirpus	Gonydale	C	3.04	-26.76	1.41	42.19
Scirpus	Gonydale	C	3.26	-28.03	1.61	41.92
Scirpus	Gonydale	C	3.46	-25.80	1.99	44.01
Acaena	Gonydale	D	2.54	-29.33	1.63	42.67
Acaena	Gonydale	D	2.62	-27.81	2.12	43.44
Acaena	Gonydale	D	4.29	-27.84	2.38	40.93
Acaena	Gonydale	D	3.11	-28.17	1.90	42.29
Empetrum (flower)	Gonydale	D	6.30	-26.24	1.39	51.12
Empetrum (flower)	Gonydale	D	3.48	-26.13	1.44	50.20
Empetrum (leaf)	Gonydale	D	5.97	-26.79	1.45	52.70
Empetrum (leaf)	Gonydale	D	4.86	-27.16	1.10	51.34
Nertera	Gonydale	D	-0.75	-28.00	1.04	41.49
Scirpus	Gonydale	D	3.01	-27.82	1.79	42.96

Genus	Altitude	Plot/Transect	$\delta^{15}N$	$\delta^{13}C$	%N	%C
Scirpus	Gonydale	D	5.49	-27.06	1.90	43.25
Scirpus	Gonydale	D	4.33	-25.26	1.34	44.89
Scirpus	Gonydale	D	5.21	-26.59	1.59	43.90
Scirpus	Gonydale	D	7.35	-27.54	1.42	44.10
Acaena	Gonydale	E	2.44	-29.96	1.68	44.93
Acaena	Gonydale	E	2.41	-27.56	1.74	43.38
Apium	Gonydale	E	0.99	-26.13	1.91	38.25
Empetrum (flower)	Gonydale	E	1.33	-27.70	1.06	51.90
Empetrum (leaf)	Gonydale	E	1.23	-28.24	1.26	52.59
Nertera	Gonydale	E	-5.67	-32.44	1.23	40.46
Nertera	Gonydale	E	-0.30	-31.03	1.50	40.23
Nertera	Gonydale	E	2.57	-28.25	2.15	41.58
Scirpus	Gonydale	E	2.17	-24.89	1.35	42.15
Scirpus	Gonydale	E	3.11	-25.28	1.99	44.50
Scirpus	Gonydale	E	3.86	-27.25	1.39	44.20
Scirpus	Gonydale	E	4.43	-27.65	0.64	44.07
Scirpus	Gonydale	E	6.04	-26.30	1.45	42.98
Scirpus	100 m contour		11.79	-27.51	0.81	44.86
Scirpus	150 m contour		13.76	-26.34	1.08	42.39
Scirpus	200 m contour		16.05	-25.53	0.89	42.67
Scirpus	250 m contour		10.77	-29.46	1.72	44.50
Scirpus	300 m contour		None	-27.62	2.38	44.36
Scirpus	350 m contour		8.67	-25.39	1.28	42.97
Scirpus	400 m contour		4.05	-27.18	1.90	43.90
Scirpus	450 m contour		5.45	-27.15	2.19	44.13

Invertebrate samples

Table 2. Stable isotope values of invertebrates collected from Gough Island November 2003-September 2006. Low altitude samples were collected from the SE coastal plain on grids where mice were trapped. High altitude samples were collected in Green Hill and Gonydale. Analyses are presented in Chapter 5.

Taxon	Altitude	$\delta^{15}N$	$\delta^{13}C$	%N	%C
Coleoptera	High	7.16	-23.92	8.96	43.39
Coleoptera	High	9.09	-24.53	9.12	44.71
Coleoptera	High	8.40	-24.69	11.48	46.68
Coleoptera	High	5.73	-24.24	12.16	46.87
Earthworm	High	3.71	-24.08	11.37	43.54
Moth adult	High	3.06	-27.04	12.63	46.18
Moth adult	High	2.82	-25.72	11.05	50.16
Moth adult	High	4.92	-28.34	9.72	54.68
Moth adult	High	6.20	-25.70	13.19	47.91
Moth larva	High	2.06	-26.37	11.17	45.22
Moth larva	High	3.88	-25.56	10.09	51.30
Predatory insect	High	18.16	-16.52	12.52	48.80
Predatory insect	High	18.98	-16.45	12.88	48.95
Spider	High	8.81	-22.66	19.68	63.86
Coleoptera	Low	10.52	-25.59	6.85	48.75
Coleoptera	Low	12.95	-25.58	7.47	49.53
Coleoptera	Low	11.58	-25.77	10.61	50.07
Coleoptera	Low	11.32	-24.84	10.12	51.82
Coleoptera	Low	12.90	-25.57	8.86	54.61
Coleoptera	Low	11.71	-25.27	10.05	52.78
Earthworm	Low	13.51	-25.83	9.98	47.95
Earthworm	Low	13.82	-24.92	10.52	46.57
Earthworm	Low	12.76	-23.03	13.08	44.55
Earthworm	Low	11.65	-23.94	13.01	43.87
Earthworm	Low	12.02	-23.90	13.82	45.63
Earthworm	Low	12.30	-24.22	11.79	45.52
Earthworm	Low	13.33	-22.72	12.99	43.88
Earthworm	Low	13.41	-24.95	11.34	43.79
Earthworm	Low	13.32	-24.93	8.59	44.82
Earthworm	Low	13.34	-24.19	12.10	44.42
Isopod	Low	15.17	-23.21	7.45	31.18
Isopod	Low	12.74	-22.60	5.49	26.37
Isopod	Low	14.03	-20.57	5.85	26.79
Isopod	Low	14.28	-22.90	5.14	26.24
Isopod	Low	12.68	-24.38	7.29	32.86
Isopod	Low	11.48	-24.77	4.30	33.82

Taxon	Altitude	$\delta^{15}N$	$\delta^{13}C$	%N	%C
Millipede	Low	12.33	-23.70	4.85	27.18
Millipede	Low	13.58	-26.07	9.44	43.44
Moth adult	Low	12.89	-24.29	6.79	52.35
Moth larva	Low	10.51	-27.46	7.88	40.46
Snail	Low	13.05	-21.35	5.95	40.33
Snail	Low	13.13	-24.09	4.19	26.57
Spider	Low	14.74	-24.24	5.52	54.30
Spider	Low	12.89	-25.25	10.07	41.40

Seabird samples

Table 3. Stable isotope values of seabird tissues collected from Gough Island in 2004. Analyses are presented in Chapter 5.

Species	Chick/Adult	Tissue	$\delta^{15}N$	$\delta^{13}C$	%N	%C
Atlantic Petrel	Adult	Feather	13.16	-17.63	14.15	46.82
Atlantic Petrel	Adult	Feather	12.77	-18.74	13.46	48.74
Atlantic Petrel	Adult	Feather	12.93	-21.50	12.26	54.44
Atlantic Petrel	Adult	Feather	13.64	-16.87	14.32	47.63
Atlantic Petrel	Adult	Feather	14.52	-17.19	14.53	47.39
Atlantic Petrel	Adult	Feather	13.57	-19.13	12.26	49.82
Atlantic Petrel	Adult	Feather	14.60	-16.20	14.23	46.10
Atlantic Petrel	Adult	Feather	12.90	-18.04	14.46	46.58
Atlantic Petrel	Adult	Muscle	14.57	-19.92	12.06	52.89
Atlantic Petrel	Adult	Muscle	13.03	-20.10	13.48	49.91
Atlantic Petrel	Adult	Muscle	11.37	-18.83	14.44	48.15
Atlantic Petrel	Adult	Muscle	13.01	-21.80	12.37	51.28
Atlantic Petrel	Adult	Muscle	12.92	-19.16	14.99	48.59
Atlantic Petrel	Adult	Muscle	12.80	-18.64	14.29	47.68
Atlantic Petrel	Adult	Muscle	10.83	-19.07	15.01	50.60
Atlantic Petrel	Adult	Muscle	14.18	-18.71	14.60	49.43
Atlantic Petrel	Chick	Feather	13.29	-19.49	13.80	48.70
Atlantic Petrel	Chick	Feather	13.86	-19.37	13.76	48.46
Atlantic Petrel	Chick	Feather	13.88	-18.99	14.39	47.52
Atlantic Petrel	Chick	Feather	14.58	-19.23	14.14	46.78
Atlantic Petrel	Chick	Feather	14.00	-19.46	13.79	48.47
Atlantic Petrel	Chick	Feather	13.69	-18.89	14.42	48.82
Atlantic Petrel	Chick	Muscle	14.18	-18.81	15.25	46.57
Atlantic Petrel	Chick	Muscle	13.41	-18.53	9.34	28.36
Atlantic Petrel	Chick	Muscle	13.48	-19.17	15.05	47.10
Atlantic Petrel	Chick	Muscle	13.08	-19.39	14.99	47.02
Atlantic Petrel	Chick	Muscle	13.42	-19.21	14.96	47.20
Atlantic Petrel	Chick	Muscle	13.02	-19.79	12.64	45.32
Broad-billed Prion	Adult	Feather	12.85	-15.89	14.29	46.31
Broad-billed Prion	Adult	Feather	9.81	-17.84	14.15	46.19
Broad-billed Prion	Adult	Muscle	10.92	-19.17	14.45	47.82
Broad-billed Prion	Adult	Muscle	9.56	-18.76	14.00	45.99
Kerguelen Petrel	Adult	Feather	11.82	-21.46	14.28	48.02
Kerguelen Petrel	Adult	Feather	13.14	-17.22	13.36	47.07
Kerguelen Petrel	Adult	Feather	9.22	-24.51	14.26	46.51
Kerguelen Petrel	Adult	Feather	13.64	-22.16	10.12	56.51
Kerguelen Petrel	Adult	Muscle	11.76	-20.54	14.96	46.34
Kerguelen Petrel	Adult	Muscle	10.45	-19.57	13.93	50.99

Species	Chick/Adult	Tissue	$\delta^{15}N$	$\delta^{13}C$	%N	%C
Kerguelen Petrel	Adult	Muscle	10.82	-23.76	13.09	51.34
Kerguelen Petrel	Adult	Muscle	13.07	-21.31	12.10	54.10
Soft-plumaged Petrel	Adult	Feather	10.80	-19.19	14.31	47.31
Soft-plumaged Petrel	Adult	Feather	9.04	-22.43	14.40	47.04
Soft-plumaged Petrel	Adult	Feather	14.13	-16.27	14.45	46.53
Soft-plumaged Petrel	Adult	Muscle	11.50	-19.38	14.35	48.49
Soft-plumaged Petrel	Adult	Muscle	13.77	-21.64	11.76	46.10
Soft-plumaged Petrel	Adult	Muscle	12.80	-17.95	14.86	49.26
Tristan Albatross	Adult	Feather	12.95	-15.77	12.04	42.59
Tristan Albatross	Adult	Feather	13.46	-16.40	11.72	42.20
Tristan Albatross	Adult	Feather	13.49	-16.38	11.84	42.20
Tristan Albatross	Adult	Feather	12.92	-16.41	11.80	42.01

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Can predation by invasive mice drive seabird extinctions?

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The house mouse, *Mus musculus*, is one of the most widespread and well-studied invasive mammals on islands. It was thought to pose little risk to seabirds, but video evidence from Gough Island, South Atlantic Ocean shows house mice killing chicks of two IUCN-listed seabird species. Mouse-induced mortality in 2004 was a significant cause of extremely poor breeding success for Tristan albatrosses, *Diomedea dabbenena* (0.27 fledglings/pair), and Atlantic petrels, *Pterodroma incerta* (0.33). Population models show that these levels of predation are sufficient to cause population decreases. Unlike many other islands, mice are the only introduced mammals on Gough Island. However, restoration programmes to eradicate rats and other introduced mammals from islands are increasing the number of islands where mice are the sole alien mammals. If these mouse populations are released from the ecological effects of predators and competitors, they too may become predatory on seabird chicks.

Keywords: invasive alien species; *Mus musculus*; island conservation; threatened seabirds

1. INTRODUCTION

Oceanic islands represent a small fraction of the Earth's land area, but hold a disproportionate percentage of global avian biodiversity (BirdLife International 2004). Many of these bird species are susceptible to extinction; more than 90% of avian extinctions since 1600 have been of island species, mainly due to predation by invasive mammals (Atkinson 1985; Steadman 1995). Rats, *Rattus* spp., are the most widely introduced mammals on islands and have devastating impacts on many bird populations (Atkinson 1985; BirdLife International 2004). Techniques are being developed to eradicate rats from ever larger islands, and conservation expenditure is increasingly devoted to this endeavour (figure 1). In contrast, mice are deemed to pose no serious threats to seabirds (Atkinson 1985). Consequently, eradication effort for rats in 2001–2005 was 25 times greater than mice and grew 50-fold from pre-1986 levels, while eradication efforts for mice remained virtually unchanged.

Gough Island (40° S, 9° W), South Atlantic Ocean is a World Heritage Site and a globally important seabird breeding colony (BirdLife International 2004). It has two endemic landbirds—the Gough moorhen *Gallinula comeri* (vulnerable) and Gough bunting *Rowettia goughensis* (vulnerable)—and the last viable breeding populations of two seabird species—the Tristan albatross *Diomedea dabbenena* (endangered) and the Atlantic petrel *Pterodroma incerta* (vulnerable) (BirdLife International 2004). House mice were introduced there before 1888 and are the only alien mammals present (Angel & Cooper 2006). In 2000/2001, unexpectedly high breeding failure of Tristan albatrosses and Atlantic petrels was reported on Gough (Cuthbert & Hilton 2004), and predation by mice was mooted. Here, we confirm that mice do attack and kill chicks up to 300 times their mass, and report a second season of low breeding success among affected seabirds. We argue that similar mouse predation may have been overlooked elsewhere, and may be most likely where mice are the sole alien mammal.

Electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2007.0120 or via http://www.journals.royalsoc.ac.uk.

2. MATERIAL AND METHODS

Research was conducted between January and September 2004. The breeding success (fledglings/pair) of Tristan albatross was estimated by counting all incubating adults (January) and all large chicks (September). From approximately 300 monitored nests (16% of the island total) in four sub-colonies, 256 chicks were examined one to three times per month for wounds. We used a χ^2-test to examine whether there was significant inter-colony variation in breeding success. Two wounded Tristan albatross chicks were filmed at night using an infrared video recorder. Evidence of attacks at other times was inferred from fresh wounds and stripped carcasses.

Three great shearwater *Puffinus gravis* and 60 Atlantic petrel chicks were monitored (January–April and July–September, respectively). Infrared cameras were deployed in nine Atlantic petrel and three great shearwater burrows and activities were recorded 24 hours per day on time-lapse recorders. Nests were filmed from hatching until the chick had fledged, died or we had left the island. Atlantic petrel nests were checked every 2–5 days and chicks were weighed and measured weekly; a healthy chick is defined as one that did not differ significantly from the expected weight for a given skeletal size measure.

3. RESULTS

Mice were filmed attacking and killing live healthy chicks of all the three study species. Both albatross chicks filmed being attacked died subsequently. Video evidence shows up to 10 mice attacking a chick, eating from three open wounds (figure 2*a*). Mice visited every filmed burrow, and attacked and killed one of the three great shearwater chicks and six out of nine Atlantic petrel chicks. No chicks displayed appropriate behavioural responses to attacks, even though mice had eaten through the body wall of one filmed albatross chick and were consuming the contents of the chick's abdominal cavity (figure 2*b*).

Most breeding failures in the albatross and petrels occurred when healthy chicks either disappeared or were reduced to stripped carcasses between nest checks. The first wounded albatross chicks (some of which were still being brooded) were found in March and attacks continued into September in all sub-colonies. Out of 256 monitored chicks, 19 were found wounded (of which 17 died) and 100 (39%)

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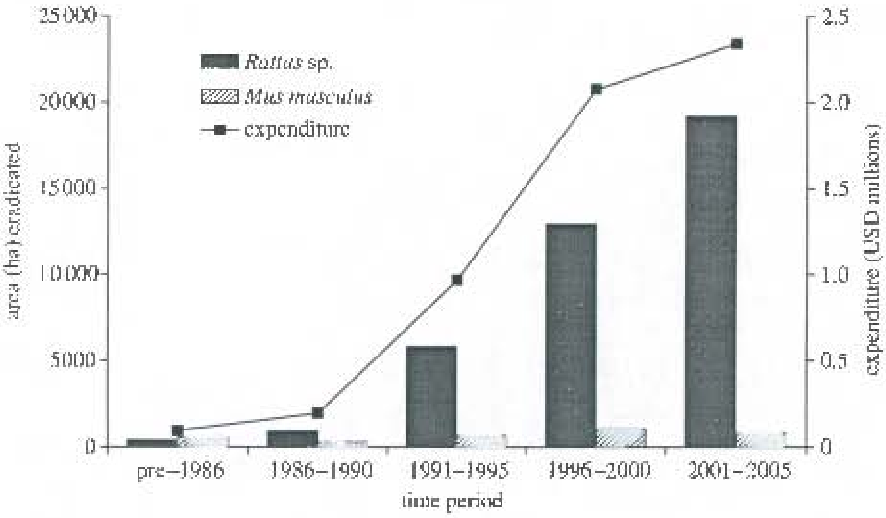

Figure 1. Island area cleared of rats (*Rattus* sp.) and mice (*Mus musculus*). All known efforts prior to 1986 are summed. The expenditure (*Rattus* only) is estimated for individual islands (Martins *et al.* 2006) and then summed. Data were accessed from an online database (Howald *et al.* 2005).

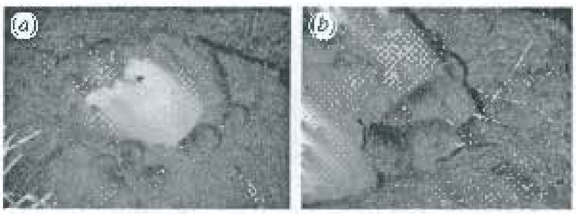

Figure 2. Images captured from video showing (*a*) 10 house mice attacking a Tristan albatross chick and (*b*) mice feeding at a hole eaten through the rump of the chick. The chick was dead the following morning.

had died by late September. However, estimated breeding success differed significantly in sub-colonies ($\chi^2_3=177$, $p<0.001$, range 0.12–0.89). Island-wide breeding success in 2004 was 0.27, identical to 2001. Attacks on Atlantic petrel chicks commenced at hatching in July, and by September, 20 out of 60 monitored chicks (33.3%) survived.

Chicks were all apparently healthy (as defined previously) when attacked, whereas we found three dead/moribund chicks without wounds. Mice do not appear to target weak or sick individuals. We conclude that the unusually high chick mortality in both species can be ascribed to mouse attacks with confidence.

4. DISCUSSION

An annual breeding success as low as 27% is unprecedented among *Diomedea* albatrosses (typically 60–75%; e.g. Croxall *et al.* 1990; Weimerskirch 1992; Elliott & Walker 2005). Cuthbert *et al.* (2004) reported a 28% decrease in the Tristan albatross population over 46 years and their population model identified low chick survival as a significant driver. Similarly, a population model for the Atlantic petrel predicts a decrease, given the observed low chick production (Cuthbert 2004). Mice appear to be largely responsible for high rates of chick mortality in both the species on Gough, and negative population trends are probable unless predation is reduced.

This is the first unequivocal proof that house mice are significant predators of healthy seabird chicks. Three published records of possible house mouse predation (Fugler *et al.* 1987; Ainley *et al.* 1990; Campos & Granadeiro 1999) were all on small chicks (less than 50 g) and could have been the result of mice scavenging/killing moribund chicks or taking abandoned eggs. Gough mice are relatively large compared with natural populations elsewhere (Berry *et al.* 1979). Nevertheless, they are much smaller than rats and it is astonishing that they can successfully attack Tristan albatross chicks that are more than 300 times heavier. Tristan albatross chicks thwart avian predators such as sub-Antarctic skuas, *Catharacta antarctica*, and southern giant petrels *Macronectes giganteus*. Why then are healthy, well-developed albatross chicks, weighing more than 8 kg, incapable of defending themselves against such diminutive predators? Island birds are particularly vulnerable to attacks from novel predators because they lack appropriate behavioural responses (Kepler 1967; Atkinson 1985). Also, not all attacks were fatal. Albatross chicks typically took several days to die, during which time the mice fed repeatedly on them, often opening multiple wounds. In some ways, this is closer to parasitism than to predation, analogous to finches in Galapagos pecking at tail feathers of seabird chicks and drinking their blood (Grant 1986), although, in that case, the chick seldom dies.

This is the first record of widespread and devastating predation by house mice on seabird chicks, despite mice having been introduced to many seabird islands. Has it been overlooked? Or is there something peculiar about Gough Island? The climate and native biota are not unusual, and it seems unlikely that some other condition, as yet undefined, could have given rise to predatory behaviour. Perhaps of more importance is that among 385 islands with bird species known to be sensitive to invasive species, only six, including Gough, have house mice as the only invasive mammal (Brooke & Hilton 2002). We suspect that where house mice are part of a complex of invasive mammals, the effects of dominance, competition and predation by larger species render mice less of a threat to native vertebrates (Courchamp *et al.* 1999). Recent events on Marion Island (46° S, 37° E) support this hypothesis. House mice became the sole introduced mammal following the eradication of cats, *Felis catus*, in the 1990s (Bester *et al.* 2000). Since 2004, several wandering albatross *Diomedea exulans* chicks have succumbed to wounds consistent with mouse attacks. This is the first time in over 20 years of intensive study that wounds of this nature have been recorded (Peter G. Ryan, unpublished data).

These findings are significant for both Gough and Marion islands and, more generally, for island conservation and the emerging discipline of invasion biology. On Gough, unmitigated predation by mice could contribute to the local extinction of Tristan albatrosses and Atlantic petrels. The winter timing of attacks makes grey petrels, *Procellaria cinerea*, and great-winged petrels, *Pterodroma macroptera*, both winter-breeding, burrowing species, likely to experience mouse predation. The Gough bunting population is likely to have decreased as a result of nest predation by mice (Cuthbert & Hilton 2004). If attacks on albatrosses are confirmed on Marion Island, several other species (e.g. winter-breeding, burrowing petrels) are likely to be subject to mouse predation there.

In a broader context, the conservation status of seabirds breeding on islands where mice are the sole introduced mammals needs to be studied. We predict that this phenomenon is more widespread than has been documented. In addition, costly mammal eradications are premised on projected conservation benefits (Krajick 2005). Our findings support the mesopredator release and competitor release hypotheses (Courchamp *et al.* 1999; Caut *et al.* in press) that the value of eradicating competitors and predators of mice (e.g. rats and cats) would be greatly enhanced also by eradicating mice. Conversely, some long-term benefits could be compromised if they are not. In light of these results, the prioritization given to mouse eradications in island restoration projects should be reviewed.

Invasion biologists seek to predict the risks and consequences of alien species introductions. Islands are often studied to understand the general principles of invasive patterns and processes. It is surprising that major discoveries can still be made about the behaviour of a well-studied species with a history of invasion stretching back several centuries. Our findings reveal how the characteristics of invasive species can be context specific and thus difficult to predict. In a more positive vein, they also generate testable predictions and suggest avenues for research into ecological interactions, which will benefit invasion biology theory and conservation practice.

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