Miles, William Thomas Stead (2010) *Ecology, behaviour and predator-prey interactions of Great Skuas and Leach's Storm-petrels at St Kilda.* PhD thesis.

Ecology, behaviour and predator-prey interactions of Great Skuas and Leach’s Storm-petrels at St Kilda

W. T. S. Miles

Submitted for the degree of Doctor of Philosophy
to the Faculty of Biomedical and Life Sciences, University of Glasgow

June 2010

For

Alison & Patrick

Margaret & Gurney, Edna & Dennis

…after sunset, a first shadowy bird would appear
circling over the ruins, seen intermittently
because of its wide circuit in the thickening light.
The fast jerky flight seemed feather-light,
to have a buoyant butterfly aimlessness.
Another appeared, and another.

Island Going (1949*): Leach's Petrel*

Declaration

I declare that the work described in this thesis is of my own composition and has been carried out entirely by myself unless otherwise cited or acknowledged.

Will Miles

Glasgow 2010

ABSTRACT

At the St Kilda archipelago, Outer Hebrides, declines have been recorded in the Leach's Storm-petrel breeding population, the largest in Britain and Ireland, and rapid increases in the population of Great Skuas. Leach's Storm-petrels have frequently been found in the diet of Great Skuas at St Kilda, where storm-petrels are active on land only at night and, unusually, skuas often hunt after dark. Apparent severe skua predation of Leach's Storm-petrels has raised conservation concerns regarding the sustainability of the St Kilda Leach's Storm-petrel population. However, it was recognised that this particular predator-prey relationship is a globally rare phenomenon, had not previously been studied for long at St Kilda (and never elsewhere), and warranted further research before conservation management interventions could be considered. Additionally, research on Leach's Storm-petrel ecology at St Kilda was desirable in its own right, because the species had rarely been studied in the UK, due to its highly pelagic lifestyle and very remote breeding locations. The aim of this study was to increase our understanding of the ecology, behaviour and predator-prey interactions of Great Skuas and Leach's Storm-petrels at St Kilda.

Results showed that Great Skua predation of Leach's Storm-petrels was considerable and sustained. Estimated numbers of Leach's Storm-petrels consumed annually by skuas were variable but averaged approximately 21,000 individuals per year. There was strong evidence from storm-petrel ringing and behavioural observations conducted at night that skuas fed predominantly on non-breeding Leach's Storm-petrels, which likely visit the archipelago in very large numbers each year, from huge colonies elsewhere, and probably play an important role in reducing predation impacts on the breeding population at St Kilda. It was found that Leach's Storm-petrels did not exhibit any specialised counter-predator adaptations to Great Skuas, and were very easily captured at night on the surface of the breeding colonies by skuas on foot. However, prey specialisation by skuas on nocturnally active seabirds (predominantly storm-petrels) did not create fitness advantages over prey specialisation on diurnally active seabirds or fish. Leach's Storm-petrel specialist skua pairs were very few and all pairs exhibited a tendency to feed on a diversity of prey and to switch prey-types between years. Adult and juvenile Leach's Storm-petrels were highly sensitive to light, and artificial light reduction measures in autumn helped prevent storm-petrel attractions and mortality in the village on Hirta. The St Kilda Great Skua population was found to be declining slightly, in contrast to the exponential growth recorded between 1990 and 2000, and Leach's Storm-petrel conservation issues now appear less severe than had been expected.

Contents

Acknowledgements

This research was funded by the Natural Environment Research Council and The National Trust for Scotland through a CASE studentship to the University of Glasgow.

First and foremost I would like to thank Bob Furness and Richard Luxmoore for the opportunity to carry out this project. I am extremely grateful to Bob, my main supervisor, for his brilliant support throughout, his light management style, superb advice, quick help, patience, tolerance of birding, and electric sense of humour. My thanks go to Richard for his additional and unstinting guidance and constructive criticism, his expertise in matters regarding St Kilda, conservation and NTS, and for his supremely positive and friendly encouragement at all times.

I have thoroughly enjoyed my time in Glasgow and on St Kilda doing this project and I could not have done the work without the help and company of the Glasgow University Ornithology Group, the St Kilda NTS staff, three excellent long-term field assistants, the JNCC boys, the staff of the St Kilda Radar Base facility, my storm-petrel dream team in 2008, *Petrels Night and Day* (The Sound Approach team), the crew of the *Orca*, and without several cakes from home. I am very grateful to Gillian Gilbert and Nancy Harrison, to Mark Bolton, Keith Hamer, Neil Metcalfe, Dan Haydon, Kate Arnold, Kate Griffiths, Hawthorne Bayer, Katherine Herborn, Liz Masden, Flavie Vial, Bernie Zonfrillo, Susan Bain, Jill Harden, Ricardo Palma, Bill Montevecchi, April Hedd, Richard Phillips, Liz Mackley, Matt Parsons, Ian Mitchell, Roddy Mavor, Cliff Black, Lachie MacLeod, Roddy MacLeod, Magnus Robb, Killian Mullarney, Angus Campbell, Seumas Morrison, Kiki from the *Orca*, Rebecca Green, Claire Smith, Uwe and Julie Stoneman, Mike Pennington and Dave Okill.

For great company, ornithological expertise within work and without, and an array of laughs and sparkling friendship on St Kilda and other Scottish islands, my special thanks to Sarah Money, Rory Tallack, Deryk and Hollie Shaw, Roger Riddington, Sam Dennis, Ian McNee, Sju Hammer, Morag MacDonald, Steve Votier, Tony Bicknell, Stuart Murray, Terry Fountain, Martin Culshaw and Dave Fairhurst.

Introduction

Islands, and the species which inhabit islands, are crucial themes in biology and conservation (Darwin 1859, MacArthur & Wilson 1967, Berry 2009). The study of island communities is important in understanding the ecology, variation and evolution of species, but also the functioning of more complex ecosystems (MacArthur & Wilson 1967, Tjorve 2010). Islands present unique opportunities for ecological study because trophic relationships are relatively confined and on many islands there are unusual species with novel interactions (Buzas 1972, Williamson 1996). Among island organisms, ecological adaptation has been diverse and often drastic, and many endemic species have evolved (Frank 2010, Fernando de Leon et al. 2010). Relative to total land area, islands hold a disproportionately high quota of the earth's biodiversity (Diamond 1989, Quammen 1996). Clearly, island ecosystems and biodiversity warrant study in their own right, but conservationists view this as particularly important, given that many island species have recently suffered extinctions or become threatened (Diamond 1989, Case 1996, Simberloff 2000, Terborgh et al. 2001). Island-nesting birds, in particular seabirds, have a higher proportion of threatened species than any other group (Steadman 1995, BirdLife International 2004). In many cases this status has been caused by heavy predation of remote populations by recently colonised mammalian and avian predators (Phillips et al. 1999a, Gaston 2004, De Leon et al. 2006, Rayner et al. 2007, Le Corre 2008).

Predation is a critical and normal process in ecosystem dynamics. Natural selection for prey-capture and predator-avoidance is evident in many aspects of the ecology and evolution of species, including foraging behaviour, breeding habits, morphology and population sizes (Krebs & Davies 1993, Edelaar & Wright 2006, Lind & Cresswell 2006). Many studies of island seabird populations have focused on the impact of non-native predatory mammals, such as rats and cats, which have colonised many islands worldwide in association with humans (Simberloff 1995, Clout & Russell 2008, Jeschke 2008, Rutherford et al. 2009, Traveset et al. 2009, Jones & Ryan 2010, Pontier et al. 2010). Cats, rats and mice have had very severe impacts on populations of island-nesting petrels *Procellariiformes*, including albatrosses *Diomedeidae*, shearwaters *Puffinus*, and storm-petrels *Hydrobatidae*, and many eradication programs have been implemented to rid islands of alien mammals (Brooke & Hilton 2002, Wanless 2007, Wanless et al. 2007, Bellingham et al. 2010, Ratcliffe et al. 2010). Under normal circumstances, petrel populations do experience some predation, but by animals which have not been artificially introduced, for example predatory birds such as skuas *Stercorariidae* (Fraser 1984, Watanuki 1986, Ryan 1991, Mougeot et al. 1998, Weidinger 1998, Brooke et al. 1999, Stenhouse & Montivecchi 2000, Stenhouse et al. 2000, Phillips et al. 2004, Oro et al. 2005).

Skuas are large generalist predators (adults >1.2kg), closely related to gulls *Laridae*, but with mostly dark plumage, claws, hard scutes on the legs and a prominent distal nail on the bill (rhamphotheca). The taxonomy of skuas is in debate, but the family comprises at least seven species; including three smaller species (wing span < 125cm: Pomarine Skua *Stercorarius pomarinus*, Arctic Skua *S. parasiticus* and Long-tailed Skua *S. longicaudus*) and at least four large-bodied species (wing span > 125cm: Great Skua *S. skua* and the *Catharacta* skuas, including Brown Skua *C. antarctica*, Chilean Skua *C. chilensis* and South Polar Skua, *C. maccormicki*). The *Catharacta* skuas are widespread in the southern hemisphere, occur on islands with large petrel populations, and feed heavily on seabirds (Furness 1987). The only large skua to occur in the northern hemisphere is the Great Skua, which breeds in Iceland, the Faroes, northern Scotland, Spitzbergen, Bear Island and northern Norway, and has an estimated global population of c.16, 000 breeding pairs, most in Scotland (c. 9600 pairs; Mitchell et al. 2004). Great skuas eat a diverse variety of prey including fish, shellfish and seabirds, foods being caught by direct predation, scavenging and kleptoparasitism (Furness 1987).

On islands in the southern hemisphere, many studies have been made of the foraging, behavioural and population ecology of *Catharacta* skuas and their petrel prey, which includes rare and endemic gadfly petrels *Pterodroma*, prions *Pachyptila* and storm-petrels (Ramos et al. 1997, Moncops et al. 1998, Mougeot et al. 1998, Weidinger 1998, Brooke et al. 1999, Berrow 2000, Mougeot et al. 2000a, Brooke 2004, Hahn & Peter 2003, Phillips et al. 2004, Varpe & Tveraa 2005, Janicke et al. 2007). Subantarctic populations of petrels have evolved ways to help avoid predation, for example by breeding colonially, nesting in burrows and crevices, being active on land only at night, and by recognising the calls of skuas (Ramos et al. 1997, Mougeot & Bretagnolle 2000a, Mougeot & Bretagnolle 2000b, Stenhouse et al. 2000, Brooke 2004). However, the hunting adaptations of skuas are diverse and innovative, and have included prey specialisation on one species, nocturnal foraging, and novel prey capture techniques such as digging petrels out from their underground nest chambers (Furness 1987).

In contrast to the southern hemisphere, predation of shearwaters and storm-petrels by skuas in the northern hemisphere has been rare, and there have been very few records from north of the equator of skuas consuming species of petrel that are active on land only at night. The relative scarcity of the phenomenon is probably because the species diversity of nocturnally active petrels is much lower in the northern hemisphere than in the southern hemisphere and the extent of range overlap with skua populations is relatively very limited (Furness 1987, Brooke 2004). However, during the 1990s, for the first time, very heavy predation of storm-petrels by a northern hemisphere skua was recorded: the predation of Leach's Storm-petrels *Oceanodroma leucorhoa* by Great Skuas at St Kilda (Phillips et al. 1997).

* * * * * * *

St Kilda archipelago, Outer Hebrides, NW Scotland (57°49´N 8°35´W), is a World Heritage Site, Special Protection Area (SPA) and Site of Special Scientific Interest (SSSI) with internationally important seabird populations (Mitchell et al. 2004). Great Skuas first bred at St Kilda in 1963 and numbers rose slowly until 1990 (66 pairs), after which a rapid expansion began (Phillips et al. 1999a). The skua population on the main island at St Kilda (Hirta) increased at a rate of 22.1% per annum between 1994 (128 pairs) and 1997 (233 pairs). During studies of this population growth, many skua pellets (regurgitated indigestible prey-remains) were found containing Leach's Storm-petrels (Phillips et al. 1997, Phillips et al. 1999b). Leach's Storm-petrel is a highly pelagic small seabird (adults <50g), that comes to land only to breed or search for breeding sites, visits the breeding colonies only at night, nests colonially in underground chambers on remote islands close to the continental shelf, and 'wanders' between potential breeding sites before reaching breeding age, at (on average) five years old (Snow & Perrins 1998, Brooke 2004, Mitchell et al. 2004). This behaviour makes populations of Leach's Storm-petrels extremely difficult to survey (Berrow 2000, Ambaigas 2004, De Leon et al. 2006, Gutierrez et al. 2006, Hounsome et al. 2006). The world population has been estimated to be between 9,000,000 and 10,600,000 pairs; not accounting for unpaired birds of pre-breeding age, which are likely to number several million extra individuals (Brooke 2004, Mitchell et al. 2004, Votier et al. 2005).

Complete Leach's Storm-petrel population surveys were first attempted at St Kilda in 1999 and 2000 and all islands were included: Hirta, Dùn, Soay and Boreray. In total, 45,433 apparently occupied sites of breeding Leach's Storm-petrels were found at the archipelago (95%LCI = 34,310, 95%UCI = 61,398), representing 94% of the estimated British and Irish total (48,357 apparently occupied sites) and the largest colony in the western Atlantic (Mitchell et al. 2004). A repeat survey was carried out in 2003 on the largest sub-population at St Kilda, on Dùn, and this suggested that a 50% decline in breeding numbers had occurred, from 28,000 apparently occupied sites found in 1999 down to 14,000 four years later (O'Brien et al. 2003, Newson et al. 2008). Recent changes in the skua population, evidence of storm-petrels in skua pellets, and storm-petrel consumption estimates from skua predation modelling, prompted strong suspicions that the decline in Leach's Storm-petrels on Dùn was due to skua predation (Mitchell et al. 2004, Phillips et al 1999a, Phillips et al. 1999b).

In 2004, a short pilot study was carried out to collect and assess evidence of petrel predation by skuas at St Kilda (Votier et al. 2005). Storm-petrels were found to form a high proportion of the diet of skuas, radio-tracked skuas were highly active at night and, using night-vision equipment, skuas were directly observed hunting storm-petrels on the breeding colonies. These findings, the decline recorded in the Dùn Leach's Storm-petrel sub-population, and the perceived threat posed by an apparently increasing skua population, raised concerns regarding the UK importance and conservation of the St Kilda Leach's Storm-petrel population. It was recognised, however, that predation of Leach's Storm-petrels by Great Skuas was a rare phenomenon away from St Kilda, had not been studied for long on Hirta in 2004 (and never elsewhere), and that the situation warranted further research before any conservation management interventions could be considered. Additionally, further research on the ecology of Leach's Storm-petrels at St Kilda was desirable in its own right, because the species had rarely ever been studied in the UK, due to its elusive habits and the remote locations of breeding colonies. The overall aim of this study is to increase our understanding of the ecology, behaviour and predator-prey interactions of Great Skuas and Leach's Storm-petrels at St Kilda. The overall purpose is to make possible an informed assessment of conservation issues.

* * * * * * *

The chapters of this thesis are each written as a discrete paper presenting data that does not feature in other chapters. However, in a few cases, data in different chapters were collected using the same techniques, for example analyses of skua pellets to assess diet, and this has necessitated a degree of repetition of methods, which I have tried to keep to a minimum. For the sake of possible future publication, each chapter is intended to stand alone as a paper, so each has its own acknowledgements section and tables and figures are presented at the end of the corresponding Results section, or section in which otherwise first mentioned, rather than being embedded within the text. All references are in a single combined list at the end of the thesis. I have followed the convention of not capitalising common names of mammals but all other common names are capitalised.

Chapter 1 aims to determine the extent to which skua pairs kill nocturnally active petrels (in particular storm-petrels), the degree of dietary specialisation on this prey, whether reproductive and physical fitness advantages are associated with nocturnal foraging on storm-petrels and shearwaters, and how rapidly the skua population is growing at St Kilda. I assess the incidence of storm-petrels and shearwaters in the diet of skuas using pellets, measure the occurrence of dietary specialisation in the skua population, and, using reproductive and adult body condition parameters, compare the fitness of skua pairs of different diet types. Additionally, I examine how the St Kilda skua population is changing in size, with reference to other colonies in Scotland.

The aims of **Chapter 2** are to quantify the occurrence of Leach's Storm-petrels in the diet of skua pairs breeding at St Kilda, define the numbers and distribution of Leach's Storm-petrel specialist pairs, investigate the influence of skua nest location on dietary specialism, and assess whether Leach’s Storm-petrels eaten by skuas are breeding or non-breeding individuals. Skua pellet analyses and colour-ringing are used to assess the diet of pairs and the extent to which individual pairs ate Leach’s Storm-petrels in 2007, 2008 and 2009. Using brood-patch and biometric measurements from Leach’s Storm-petrels ringed during the study, I investigate whether the breeding status and age of Leach’s Storm-petrels eaten by skuas can be determined from remains found in pellets, and evaluate results in relation to night-time observations of the behaviour of Leach’s Storm-petrels and Great Skuas at the storm-petrel breeding colonies at St Kilda.

In **Chapter 3**, I use bioenergetics models to estimate annual energy and prey consumption by Great Skuas at St Kilda and aim to determine how many Leach’s Storm-petrels are consumed by skuas each year, whether heavy predation occurs, and whether predation of petrels is at all sustained between years. I assess the impacts and implications of Leach’s storm-petrel predation by skuas, estimate annual consumption of other seabirds, fish and goose barnacles, and consider the importance at St Kilda of non-breeding Leach’s Storm-petrels that ‘wander’ between colonies prior to breeding.

Chapter 4 describes aspects of Leach’s Storm-petrel anti-predation behaviour. This chapter aims to assess how finely attuned the breeding ecology of Leach’s Storm-petrels is to light conditions at night and whether the species recognizes and responds to acoustic and visual signals from Great Skuas. Using night-vision equipment, light sensors and petrel mist-netting, I investigate counter-predator adaptations of Leach’s Storm-petrels correlatively in relation to changing natural light levels and experimentally in relation to the sight, sound and threat of skuas.

In **Chapter 5** I investigate the impacts of a potential cause of mortality to storm-petrels at St Kilda other than skuas: artificial lights. Petrels are attracted to lights at night, sometimes become grounded, and may be killed via collision with buildings or predation by birds and mammals on land. I assess effects of artificial lighting and moonlight on petrels at St Kilda and in this chapter aim to determine the numbers, ages and mortality of petrels attracted to the lights in the village on Hirta, the influence of the lunar cycle on attraction of storm-petrels and shearwaters to lights, and possible mitigation measures to reduce light-attraction and petrel mortality.

Variation in Leach’s Storm-petrel plumage was surprising and extreme among birds examined at St Kilda and in **Chapter 6** I report observations made from adults and juveniles. Plumage differences between Leach’s Storm-petrels of different ages had not previously been studied in detail and in this chapter I aim to elucidate plumage characters that may be encountered by other ringers and birdwatchers in the UK, with consideration of aberrant plumages which resemble features of other species of storm-petrel.

Chapter 7 reports one of the biggest surprises of the study, which was that in 2007 exceptional numbers of Snowy Owls *Bubo scandiacus* visited St Kilda and were found to depredate Great Skuas. In this chapter I aim to make an accurate record of the number of individual Snowy Owls present at St Kilda, their behaviour and use of habitat, the diet of the birds, and their interactions with skuas.

In the final section of the thesis, the **General Discussion**, I summarise the main findings of the study, discuss the likely occurrence and implications of non-breeding Leach’s Storm-petrels at St Kilda, and comment on conservation issues concerning the Great Skua and Leach’s Storm-petrel populations at the archipelago.

Chapter 1

Storm-petrel and shearwater predation and fitness consequences in Great Skuas *Stercorarius skua*

ABSTRACT

Specialisation on particular foraging methods and prey can lead to improved reproductive fitness for predators. Large numbers of storm-petrels have been found in the diet of Great Skuas at St Kilda, Outer Hebrides, where storm-petrels are active on land only at night and, unusually, skuas often forage after dark. This three-year study aimed to define the extent of storm-petrel and shearwater predation within the skua population, assess the occurrence of prey-specialisation, and determine whether fitness advantages were associated with specialising on different prey, in particular nocturnally active petrels. Additionally, I investigated recent skua population changes at St Kilda in relation to other populations in Scotland. Over 40% of breeding skua pairs ate storm-petrels and shearwaters in each year of this study but most also fed on other prey caught during the day rather than at night. Prey specialisation on nocturnally active seabirds (petrels) did not create fitness advantages over prey specialisation on diurnally active seabirds or fish. However, mean egg-laying date, one proxy for skua fitness quality, was consistently earlier for dietary specialist pairs than dietary generalists. The St Kilda skua population was observed to be declining slightly, as were the largest populations in Scotland. We conclude that current declines in the St Kilda population, and a lack of any fitness advantages from specialising on nocturnally active petrels over specialising on other prey, mean that the extent to which skuas predate storm-petrels at St Kilda, although unique within Scotland, is unlikely to rapidly increase or become dominant.

INTRODUCTION

Ecological adaptation by individuals of a species can lead to fitness advantages and improved survival by natural selection. Examples of this are multitudinous and diverse, but among seabirds have included many different behavioural adaptations to improve foraging opportunities, which in turn improved fitness (Furness 1987, Hatchwell 1991, Brooke 2004, Gaston 2004, Phillips et al. 2007, Troupe et al. 2009). Colonisation of new breeding grounds by seabirds can provide better access to unexploited food resources, the ability of individuals to try new ways of hunting can lead to easy capture of novel and abundant prey, and behavioural cognition and imitation can result in advantageous foraging techniques becoming widespread within seabird populations (Greig et al. 1983, Caldow & Furness 2000, Gill et al. 2002, Davis & Renner 2003, Hahn & Peter 2003, Votier et al. 2005). Many studies have shown that innovative and successful foraging is crucial to the fitness of seabirds, affecting adult survival, the maintenance of good body condition, the ability to attract a mate, the processes of nesting, and the successful fledging and survival of young (Hamer et al. 1991, Annett & Pierotti 1999, Oro & Furness 2002, Gaston 2004, Mitchell et al. 2004, Votier et al. 2004a, Davis et al. 2005, Mattern et al. 2009, Sorensen et al. 2010).

Gulls *Larus* and skuas *Stercorarius* are dietary generalists and feed on a great variety of birds, fish, shellfish and anthropogenic waste by direct predation, kleptoparasitism and scavenging. However, population changes and variation in reproductive performance have been described in these groups, caused by individuals adopting very particular foraging strategies and prey (Furness 1987, Pierotti & Annett 1991, Ryan & Moloney 1991, Watanuki 1992, Spear 1993, Phillips et al. 1999a, Votier et al. 2004b, 2004c & 2007). For example, reproductive success of Herring Gulls *Larus argentatus* and Lesser Black-backed Gulls *Larus fuscus* has greatly increased in cities, and urban populations have grown rapidly throughout the UK, owing to individual adaptation to food resources available at inland rubbish dumps and to nearby roofs and chimneys for nesting (Rock 2005). At Hermaness, Shetland, Great Skua *Stercorarius skua* pairs specialising on seabird prey by direct predation showed higher reproductive fitness than pairs specialising on fish; indicated by earlier egg-laying, larger clutch volumes and higher chick body condition in seabird specialists (Votier et al. 2004a). These observations were made at a time when fisheries discards and sandeels in Shetland were extremely scarce, and low fitness in skuas specialising on fish was likely driven by a period of reduced prey availability (Votier et al. 2004a, Votier et al. 2004c). During the start of this period, in the 1980s, many Great Skuas emigrated from the UK breeding strongholds in Shetland and colonised other islands in Scotland (Phillips et al. 1999a, Votier et al. 2007).

Immigration and rapid population growth were observed at St Kilda, Outer Hebrides, where skuas began to exploit the nationally important numbers of seabirds nesting at the archipelago (Phillips et al. 1999a & 1999b). St Kilda holds the largest breeding population of Leach's Storm-petrels *Oceanodroma leucorhoa* in Britain and Ireland, as well as populations of European Storm-petrels *Hydrobates pelagicus* and Manx Shearwaters *Puffinus puffinus,* and individual skuas began to depredate these petrels by foraging at night, the only time when the petrels are active on land (Phillips et al. 1999b, Brook 2004, Mitchell et al. 2004, Votier et al. 2005). In a UK context, St Kilda is unusual in having large breeding populations of three species of seabird that are active on land only at night (all other species at the archipelago are most active during the day). Sustained nocturnal foraging for petrels by Great Skuas had not previously been reported and the behaviour was unusual for the species (Votier 2005). However, in the southern hemisphere, on islands where breeding ranges of skuas such as South Polar *Catharacta maccormicki* and Brown Skuas *Catharacta skua lönnbergi* overlap with those of storm-petrels *Hydrobatidae*, shearwaters *Puffinus*, gadfly petrels *Pterodroma* and prions *Pachyptila*, very heavy predation exclusively of petrels has frequently been observed (Furness 1987, Moncorps et al. 1998, Weidinger 1998, Brooke et al. 1999, Mougeot & Bretagnolle 2000b, Phillips et al. 2004). Studies of skua foraging patterns and seabird predation at St Kilda, made between 1996 and 2004, suggested predation of nocturnal seabirds was common, many skua pairs had learnt to forage at night, and several thousand storm-petrels and shearwaters were annually killed by skuas (Phillips et al. 1999b, Votier et al. 2005). This, combined with a 48% decrease found between 1999 and 2003 in the largest Leach's Storm-petrel subcolony at St Kilda, on Dùn, raised concerns over the conservation of petrels on the islands (Newson et al. 2008). An increasing Great Skua population was quickly blamed for the apparent demise of Leach's Storm-petrels at St Kilda. Unknown, however, was the extent to which skua pairs killed nocturnal seabirds, the degree of dietary specialisation on this prey, whether fitness advantages were associated with nocturnal foraging on petrels, whether increasing numbers of skuas were adopting this behaviour, or how rapidly the skua population was growing. Here I present the results of a three-year study to address these unknowns. I assess the incidence of storm-petrels and shearwaters in the diet of skuas; measure the occurrence of dietary specialisation on nocturnal seabirds, diurnal seabirds and fish across the skua population; use reproductive and adult body condition parameters to compare the fitness of skua pairs of different diet types; and determine how the St Kilda skua population is changing, with reference to other colonies in Scotland.

METHODS

Study site and skua populations

The study was carried out at the St Kilda archipelago (57°49′N, 08°35′W), Outer Hebrides, during the breeding seasons of 2007, 2008 and 2009. St Kilda is a Site of Special Scientific Interest, a Special Protection Area and a UNESCO World Heritage Site for its cultural and natural value, in particular for breeding seabirds. Over 670,000 seabirds of fifteen different species nest on the islands (Mitchell et al. 2004). The site is of special importance for breeding numbers of Northern Gannet *Morus bassanus* (60,400 apparently occupied nest sites in 1994, making it the world’s largest colony; Mitchell et al. 2004), Leach’s Storm-petrel (estimated 45,400 apparently occupied breeding sites; Mitchell et al. 2004) and Great Skua (>1% world breeding population; Mitchell et al. 2004). More than 90% of adult Great Skuas breeding at St Kilda have nested on the largest island in the group, Hirta (Phillips et al. 1999a, Murray 2002). Complete surveys of the breeding population of Great Skuas on this island were carried out in every year of this study by searches for all nests in all areas of suitable habitat, repeated eight times (minimum) in each breeding season. Numbers of pairs breeding on the other islands (Dùn, Soay and Boreray) were surveyed on the few occasions that sea conditions permitted landing. This was never possible on Soay and the most recent estimated breeding numbers (22 apparently occupied nests sites found in 1999, Murray 2002) were used in the sum total breeding population estimates of Great Skuas at St Kilda for each year. To allow comparison of long-term Great Skua population changes at St Kilda with trends at other highly populated sites, data from this study are presented alongside Great Skua breeding population estimates from Handa (Sutherland), Fair Isle, Noss, Hermaness and Foula (Shetland) from 1900 to 2009 (Furness 1987, Phillips et al. 1999a, Pennington et al. 2004, Shetland Bird Reports 1980-2008, Fair Isle Bird Reports 1950-2008, Green et al. 2009, M. Pennington & D. Shaw pers. comm. 2010).

Diet assessment

Diet of breeding adult Great Skuas was assessed on Hirta by identification of prey remains in regurgitated pellets of indigestible material, collected from every known nesting territory on the island in each year. For each territory, a circular area of 15m radius from the nest was checked for pellets, by the observer walking in a tight spiral from the nest out to the circumference, at all times searching a $2m^2$ area immediately ahead. Pellet searches lasted 20 minutes per territory. Great Skua pairs defend their territories against conspecifics highly aggressively, thus pellets within a territory can be confidently assigned to one pair (Votier et al. 2004a). Territories were visited every 10 to 15 days from May (egg laying) to mid-August (fledging), all pellets were collected and removed to prevent recounting, and all prey remains identified to the lowest possible taxon using established identification criteria (Votier et al. 2001, 2003, 2004b). Skua pellets are typically of similar size, colours and texture, and I was confident that these variables did not bias pellet-finding towards particular prey types. Fish pellets are slightly looser and more prone to disintegrate over time (20+ days) than bird or Goose Barnacle pellets, but relatively frequent pellet collection aimed to negate any bias introduced by this potential difference. The diet of each pair, the annual relative composition of different prey-types, was determined by calculation of the relative proportions of total meals consumed of different prey-types (1 meal = quantity of food present in a bird's proventriculus on its return from feeding; Phillips et al. 1999b). Following Votier et al. (2004b), I did not assume that one meal resulted in the production of one pellet, and calculated numbers of meals by applying correction factors to pellet frequencies, determined from studies of captive Great Skuas fed different fish and bird prey (Votier et al. 2001, 2004a, 2004b). In contrast to other prey items, auk *Alcidae*, fish and goose barnacle *Lepas* sp. remains in pellets could not be identified to species level so these remains were classified into three generalised categories to include all species. Total numbers of meals were calculated from the total numbers of pellets collected in all territories for each of the following prey-types: Leach's Storm-petrel, European Storm-petrel, Manx Shearwater, Fulmar *Fulmarus glacialis*, Kittiwake *Rissa tridactyla*, auk (including Common Guillemot *Uria aalge*, Razorbill *Alca torda*, Black Guillemot *Cepphus grylle* and Atlantic Puffin *Fratercula arctica*), fish, and goose barnacles. Pellets that were not these prey-types, or contained more than one prey-type, or could not be identified were extremely few (<1%), and omitted from analyses. Number of goose barnacle pellets produced per meal was estimated by counting the number of goose barnacle half-shells found in pellets and comparing this with the number of half-shells estimated by Phillips et al. (1999b) to be consumed per meal of goose barnacles. I calculated that approximately 2 goose barnacle pellets were produced per meal and used this value as the correction factor to calculate numbers of meals from numbers of pellets of goose barnacle in all years. Skua pairs were treated as a single unit because both members are represented by one territory and it is impossible to assign collected pellets to the male and female separately (Votier et al. 2004a). Dietary specialist and generalist pairs were identified according to relative prey composition and assigned to one of the following four diet type categories: storm-petrel and shearwater specialist (>70% of diet these prey-types, which are active on land only at night - nocturnal seabird prey), auk, fulmar and kittiwake specialist (>70% of diet these prey-types, which are most active on land only during the day - diurnal seabird prey), fish specialist (>70% of diet fish), and generalist (<50% of diet any one prey-type). The 70% threshold for specialists was selected following Votier et al. (2004a) and allowed comparison to be made between St Kilda and specialist skua diet analyses from Shetland.

Reproductive fitness

Four parameters were used as proxies for the reproductive fitness of Great Skua pairs on Hirta: egg laying date, clutch volume, number of eggs hatched and chick condition (Phillips 1999a, Votier 2004a). Nests were located during the egg-laying period (May), their exact positions marked using a handheld GPS, and each visited every 10-15 days throughout the breeding season until mid-August, using the GPS for location guiding. Following Votier et al. (2004a), after clutch completion, eggs were weighed to 0.01g using an electronic balance, length and breadth of each egg were measured to

0.1mm using Vernier callipers, and internal egg volumes (cm^3) calculated as 0.00048 (egg shape constant), x length x breadth^2. Total clutch volumes were calculated for two-egg clutches only (normal clutch size). Egg laying-date was determined by direct observation or by subtraction of 29 days (normal incubation period; Furness 1987, Phillips et al. 1999a & 1999b) from the date of first egg hatching. Where neither laying or hatching date were observed directly, hatching date was calculated by measurement of chicks' maximum flattened wing chord to the nearest 1mm and estimation of chick age (days since hatching) by reference to the logistic growth curve of wing-length to age described by Furness (1983). For the few nests (<5%) where egg laying and hatching dates were not observed directly and no chicks were found, hatching date was estimated from egg density, calculated as egg weight (g) / (egg breadth^2 (cm^2) x egg length (cm) x 0.507), and by reference to the curve of diminishing egg density with egg age described by Furness & Furness (1981). Number of eggs hatched was determined during nest visits from the number of complete shells of hatched eggs, and number of chicks found per territory. This is prone to inaccuracy (see discussion) and for statistical analyses egg hatching success was defined for each pair simply as eggs hatched or not hatched (1/0). Chicks were fitted with a single, uniquely numbered, British Trust for Ornithology incoloy ring once foot size was adequate to prevent ring loss. All chicks found during the linear phase of growth (13-34 days old; Furness 1983) were weighed to the nearest 1g and the maximum flattened wing chord measured to the nearest 1mm. An index of chick condition was calculated as the deviation of observed chick weight from expected weight at a particular age, expressed as a proportion of the expected value. Only one value was calculated per chick. Chick age was determined from wing length (as above) and expected chick weights calculated using the regression described by Furness (1983) of age against weight of healthy chicks which fledge. To show how reproductive fitness may vary between skua pairs with different specialist and generalist diets, measures of reproductive fitness parameters are presented (mean ± S.E.) for all skua pairs in each of the four diet type categories defined above.

Adult condition

Two parameters were used to assess the physical condition of adults: pectoral muscle condition and body mass relative to body size. These respectively provide indication of protein and lipid reserves (Bolton et al. 1991, Kalmbach et al. 2004). During incubation, adult skuas on Hirta were trapped at the nest using a remote-controlled spring trap in 2007 and 2008. However, this was generally unsuccessful and, on average, fewer than 10 adult skuas were trapped each year as birds refused to sit under the trap. Previous exposure to the technique on St Kilda, prior to 2007, meant that most pairs were already very familiar with procedures, recognised the equipment even if camouflaged, and were adept at avoiding capture. In 2009, I trapped 40 skuas on Hirta using a new method: a remote-controlled camouflaged lasso placed next to nests, that when triggered by radio handset to recoil, fastened securely around an incubating bird’s leg. To correct for possible effects of heterogeneity in individual quality, skuas were sampled in 2009 from all areas of the colony on Hirta. Maximum flattened wing chord, total head and bill length, sternum length, minimum tarsus length and body mass were measured for all trapped birds. Using methods described by Bolton et al. (1991), a profile of the pectoral muscle was recorded for each bird and each individual was sexed using molecular techniques developed by Griffiths et al. (1998). Due to the extent of sexual dimorphism in Great Skuas and potential as a source of bias, calculation of indices of body mass (BMI) and pectoral muscle condition (PMC) must be carried out separately for males and females (Votier et al. 2004a). Incubation is carried out predominantly by the female (Furness 1987) and in 2009 only a small sample of males was trapped (14 individuals); these were omitted from analyses. PMC and BMI were calculated for females trapped in 2009 (26 individuals) using the methods described by Votier et al. (2004a). Female PMC and BMI values are presented against the proportion of nocturnal seabird (storm-petrels and shearwaters), diurnal seabird (auk, fulmars and kittiwakes) and fish prey in the diet of the respective pair (during the incubation period only), to investigate how adult fitness may vary with prevalence of these prey types in the diet. During the incubation period, the male feeds the female at the nest (Furness 1987), so it seemed reasonable to assume that the diet of the pair during this period, as assessed from pellets found in the pair territory, was representative of the diet of the respective individual, incubating female sampled.

Statistical analyses

To test whether the observed distributions of storm-petrel and shearwater prey in the diet of skua pairs were random in each year, and to help assess the occurrence of specialist pairs within the breeding population, observed frequencies were compared with a Poisson distribution using G-tests. Frequencies of pairs feeding on different specialist and generalist diet types in each year and frequencies of different storm-petrel and shearwater prey-types in the diet of pairs specialising on these nocturnal seabirds in each year were tested for homogeneity using chi-squared tests. Effects of year and diet type on reproductive fitness parameters were investigated using a general linear model in which laying-date, clutch volume and chick condition were response variables (each normally distributed and modelled separately) and diet and year included as fixed effects. A generalized linear model with binomial distribution and logit-link function was used to investigate effects of diet and year (fixed effects) on egg hatching success (response variable). The effects of diet on adult body condition (PCI and BMI) were assessed using a general linear model in which mass (body mass or pectoral muscle mass, each modelled separately) was the response variable, with body size included as a covariate and prey-type proportions as a fixed effect. The three different prey-types (nocturnal seabirds, diurnal seabirds and fish) were each modelled separately. Arcsine transformations were used for proportional data. Frequencies of pairs of Great Skuas nesting on different islands at St Kilda were tested for homogeneity using chi-squared tests. Analyses were performed using R version 2.10.1.

RESULTS

Dietary composition and specialisation

Total pellets collected in each year numbered 2876 in 2007, 2094 in 2008 and 2358 in 2009. Between 5 and 110 pellets were found in most (>95%) skua territories in each year. From pellets, 96 Great Skua pairs were identified as feeding on storm-petrels and shearwaters in 2007 (51% of breeding population on Hirta), 70 pairs in 2008 (50% of breeding population) and 73 pairs in 2009 (42% of breeding population).

The observed distribution of storm-petrel and shearwater prey consumed by skua pairs was significantly different from an expected Poisson distribution in all years (Figure 1.1; 2007, $G_{adj, 9} = 107.7$, $P<0.01$; 2008, $G_{adj, 9} = 70.2$, $P<0.01$; 2009, $G_{adj, 9} = 30.0$, $P<0.01$). The majority of pairs which fed on storm-petrels and shearwaters did not do so heavily; however, in all years, an unexpected slight peak was seen in the number of specialist pairs (proportion of diet > 0.7). This was in contrast to the pattern expected were the data to conform to a Poisson distribution, and highlighted the degree of specialisation among pairs within the breeding population on Hirta (Figure 1.1). Numbers of storm-petrel and shearwater specialist pairs were universally low compared with auk, fulmar and kittiwake specialist, fish specialist and generalist pairs; frequencies of skua pairs in these diet type categories differed significantly in all years (Table 1.1; 2007, $\chi^2_3 = 12.59$, $P<0.01$; 2008, $\chi^2_3 = 33.81$, $P<0.01$; 2009, $\chi^2_3 = 11.47$, $P<0.01$). Within the diet of skua pairs which specialised on storm-petrel and shearwater prey, frequencies of particular storm-petrel and shearwater prey-types differed significantly (2007, $\chi^2_3 = 17.05$, $P<0.01$; 2008, $\chi^2_3 = 135.98$, $P<0.01$; 2009, $\chi^2_3 = 17.28$, $P<0.01$), with storm-petrels, in particular Leach's Storm-petrels, being by far the most abundant nocturnal seabird prey-type consumed by specialists in all years (Figure 1.2). Few pairs fed solely on nocturnal seabird prey: 4 in 2007, 2 in 2008 and 3 in 2009 (Figure 1.1), representing 2.1%, 1.4% and 1.7% of the total breeding skua population on Hirta in each year respectively.

Fitness parameters

There were significant differences found between the laying-dates of dietary specialist and generalist skua pairs, with no differences found between years and no interactions (GLM: diet, $t = 2.01$, $P<0.05$; year, $t = -1.68$, N.S.). In all years, mean laying-date of dietary generalist skua pairs was later than mean laying-dates of nocturnal seabird, diurnal seabird and fish specialists, which were extremely close, always within 2 days of each other, and in 2008 were May 12 for all three specialist categories (Figure 1.3). No significant effects of diet type or year on clutch volume were detected and no interactions (Table 2; GLM: diet, $t = 0.04$, N.S.; year, $t = 0.33$, N.S.). Mean number of eggs hatched by generalist pairs was consistently high relative to most other diet type categories, but relatively low in all years for auk, fulmar and kittiwake specialist pairs (Table 1.2). Diet type and year were found to have a significant effect on egg hatching success (GLM: diet, z = 3.130, P<0.01; year, z = 1.551, N.S.). Post-hoc analyses in which each year was modelled separately were carried out to investigate these effects, and this revealed that diet type had a significant effect on egg hatching success only in 2008 (GLM: 2007, z = 1.908, N.S.; 2008, z = 2.129, P<0.05; 2009, z = 1.320, N.S.). In 2008, hatching success was relatively high for nocturnal seabird specialist and generalist pairs (proportion of all nests with hatched eggs = 80% and 83% respectively) but relatively low for diurnal seabird and fish specialist pairs (proportion of all nests with hatched eggs = 47% and 61% respectively). Chick condition did not vary significantly with diet but did with year, without interactions (GLM: diet, t = 0.351, N.S.; year, t = -3.96, P<0.01). Variability in chick condition was extremely high within all diet type categories in all years (Figure 1.4). Mean values were positive and relatively high for all diet type categories in 2007, closer to 0 in 2008 and mostly negative in 2009 (Figure 1.4). No significant effects were detected between the proportion of the diet comprised of nocturnal seabirds, of diurnal seabirds or of fish and the two body condition parameters measured (Pectoral Muscle Condition GLM: nocturnal seabirds, t = -1.474, N.S.; diurnal seabirds, t = 0.754, N.S.; fish, t = 1.235, N.S.; Body Mass GLM: nocturnal seabirds, t = -2.200, N.S.; diurnal seabirds, t = 0.226, N.S.; fish, t = 1.716, N.S.; Figure 1.5 and 1.6).

Population size at St Kilda

Breeding population sizes of Great Skua pairs (considered in this case to be equivalent to Apparently Occupied Territories (AOTs), since all territories observed appeared to be occupied by two adults) on Hirta in 2007, 2008 and 2009 are presented in Table 1.1. Owing to bad weather and sea conditions, also transport limitations, nest surveying visits were made to Dùn only in 2008 and 2009 and to Boreray in 2009. On both islands nests were very few compared with Hirta: 4 were found on Dùn in each year and 10 apparently occupied nest territories located on Boreray. These values were used with those for Hirta and Soay (see methods) to estimate the sum total population of Great Skuas breeding at St Kilda in 2007 (225 pairs), 2008 (175 pairs) and 2009 (210 pairs). Estimates from this study represent a decrease in the St Kilda population size since the peak count of 240 pairs recorded in 2000 (Figure 1.7a). Numbers of skua pairs on the four different islands at St Kilda significantly differed in all years (2007, $\chi^2_3 = 420.7$, $P<0.001$; 2008, $\chi^2_3 = 280.3$, $P<0.001$; 2009, $\chi^2_3 = 378.1$, $P<0.001$), with fewest on Dùn, low numbers on Soay and Boreray, and the vast majority on Hirta.

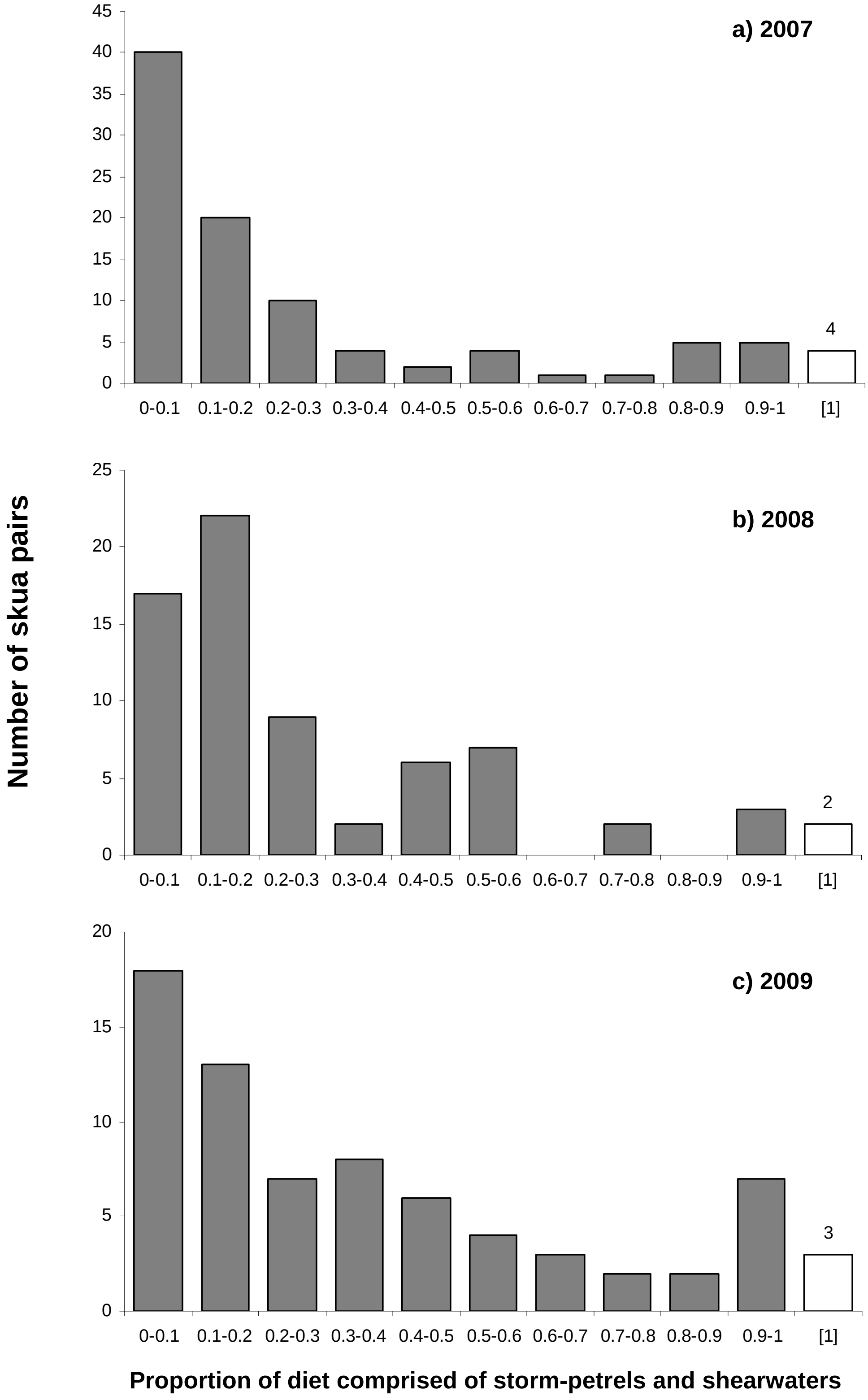
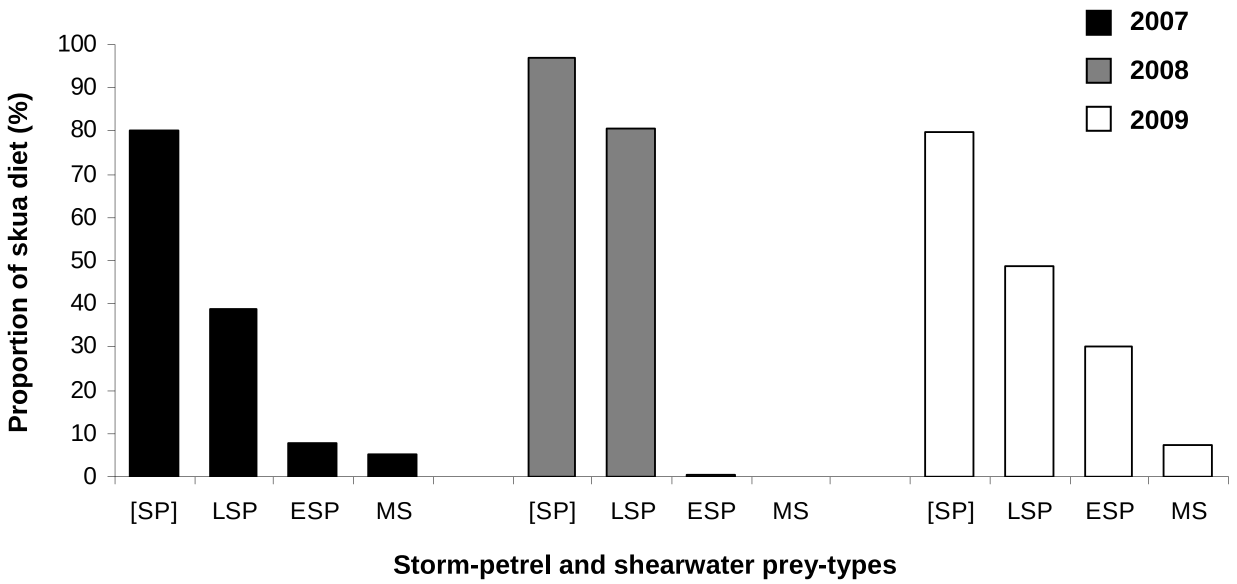


Figure 1.1. Proportional occurrence of storm-petrels and shearwaters (nocturnal seabird prey) in the diet of Great Skua pairs on Hirta, St Kilda, Outer Hebrides, as identified from pellet analyses. Pairs with more than 70% storm-petrels and shearwaters in diet were considered specialists. Total numbers of pairs which fed entirely on storm-petrels and shearwaters are included in 0.9-1 categories but for clarity also shown in isolation (proportion of diet = [1], white bars). Pairs that did not feed on storm-petrels and shearwaters (proportion of diet = 0) are not included in this figure but numbered 97 pairs in 2007, 71 pairs in 2008 and 104 pairs in 2009.

Table 1.1. Great Skua pairs with specialist and generalist diet types on Hirta, St Kilda, Outer Hebrides, as identified from pellet analysis (n = total population of Great Skua pairs breeding on Hirta).

Skua diet type		**2007** **(n = 189)**	**2008** **(n = 139)**	**2009** **(n = 174)**
Storm-petrel & shearwater specialists	Total pairs	11	5	11
(>70% nocturnal seabird prey)	Proportion of population	5.8%	3.6%	6.3%
Auk, fulmar & kittiwake specialists	Total pairs	25	19	31
(>70% diurnal seabird prey)	Proportion of population	13.2%	13.7%	17.8%
Fish specialists	Total pairs	22	18	32
(>70% fish prey)	Proportion of population	11.6%	12.9%	18.4%
Generalists	Total pairs	35	42	24
(<50% of any one prey-type)	Proportion of population	18.5%	30.2%	13.8%



[SP] = Total storm-petrels, including those unidentifiable to species level from pellets plus totals of both following species
LSP = Leach's Storm-petrels
ESP = European Storm-petrels
MS = Manx Shearwaters

Figure 1.2. Relative composition of different storm-petrel and shearwater prey-types in the diet of Great Skua pairs specialising on these nocturnal seabirds on Hirta, St Kilda, Outer Hebrides, in 2007, 2008 and 2009, as identified from pellet analyses.

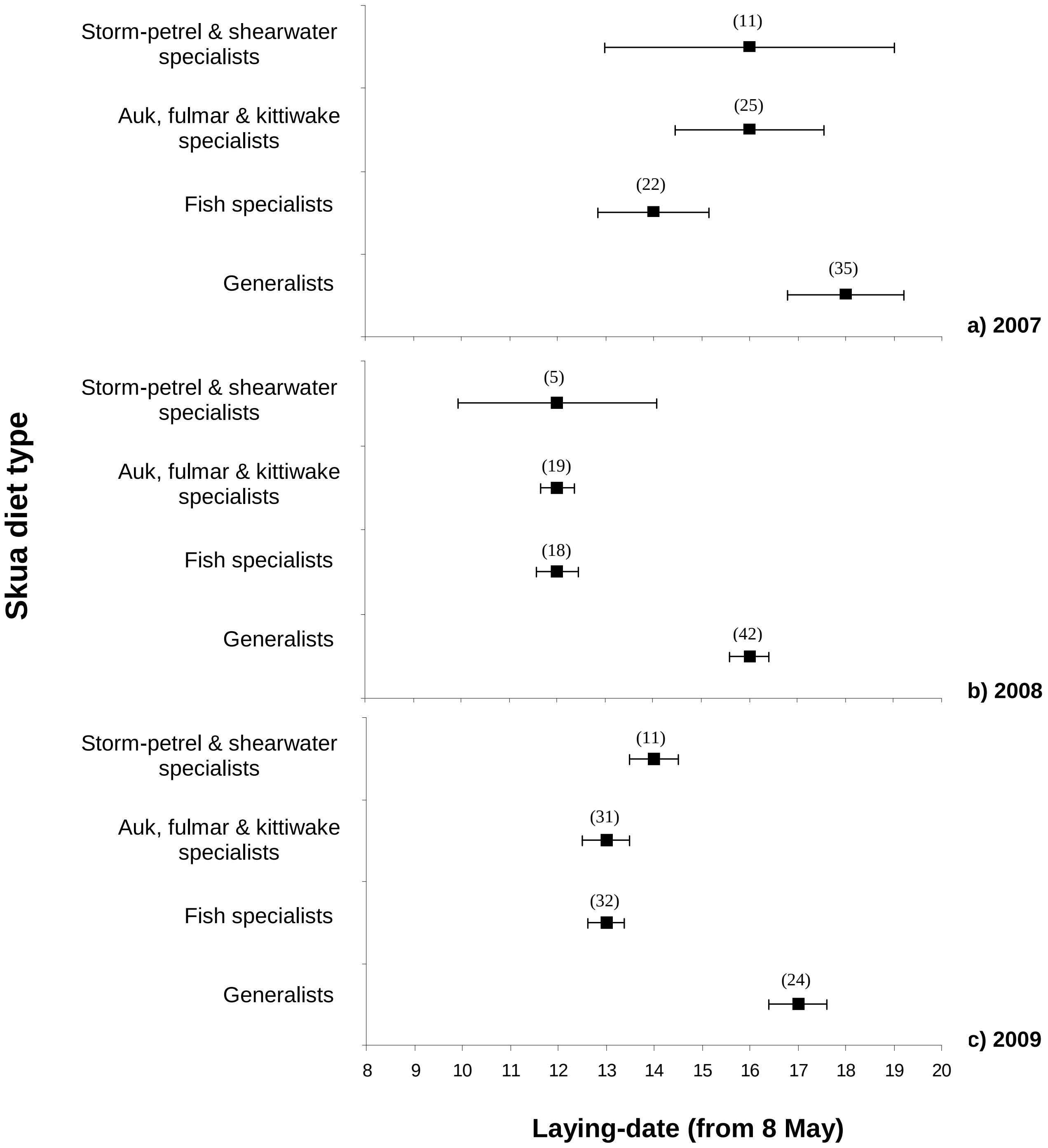


Figure 1.3. Mean egg laying dates ± S.E. of Great Skua pairs of different diet types on Hirta, St Kilda, Outer Hebrides, in 2007, 2008 and 2009. Numbers in parentheses = skua pair sample sizes.

Table 1.2. Mean clutch volumes and eggs hatched per pair ± S.E. for Great Skua pairs of different diet types on Hirta, St Kilda, Outer Hebrides in 2007, 2008 and 2009.

Skua diet type		**2007**	**2008**	**2009**
		Clutch volume (cm^3)		
Storm-petrel & shearwater specialists	Mean	164.17	169.20	163.82
	S. E.	± 3.82	± 3.91	± 4.26
Auk, fulmar & kittiwake specialists	Mean	162.79	163.56	166.44
	S. E.	± 3.24	± 3.10	± 2.29
Fish specialists	Mean	166.70	171.68	168.11
	S. E.	± 2.93	± 2.62	± 2.24
Generalists	Mean	165.52	166.60	161.22
	S. E.	± 2.27	± 2.43	± 3.39
		Eggs hatched per pair		
Storm-petrel & shearwater specialists	Mean	0.55	1.20	0.91
	S. E.	± 0.21	± 0.37	± 0.25
Auk, fulmar & kittiwake specialists	Mean	0.60	0.68	0.84
	S. E.	± 0.14	± 0.19	± 0.12
Fish specialists	Mean	1.18	0.78	0.88
	S. E.	± 0.17	± 0.19	± 0.13
Generalists	Mean	0.91	1.21	1.25
	S. E.	± 0.13	± 0.11	± 0.15

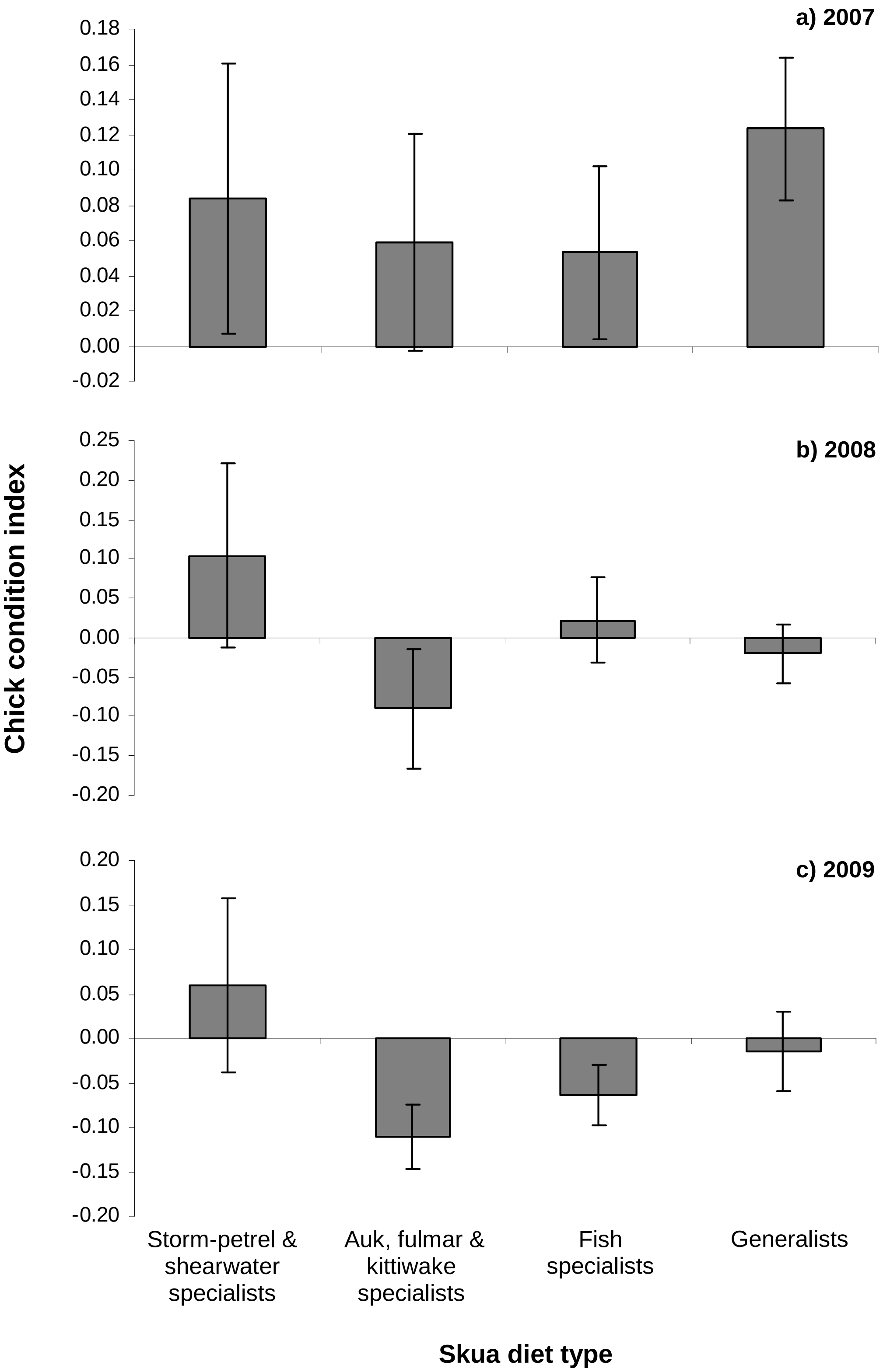


Figure 1.4. Mean chick condition index ± S.E. for Great Skua pairs of different diet types on Hirta, St Kilda, Outer Hebrides, in 2007, 2008 and 2009.

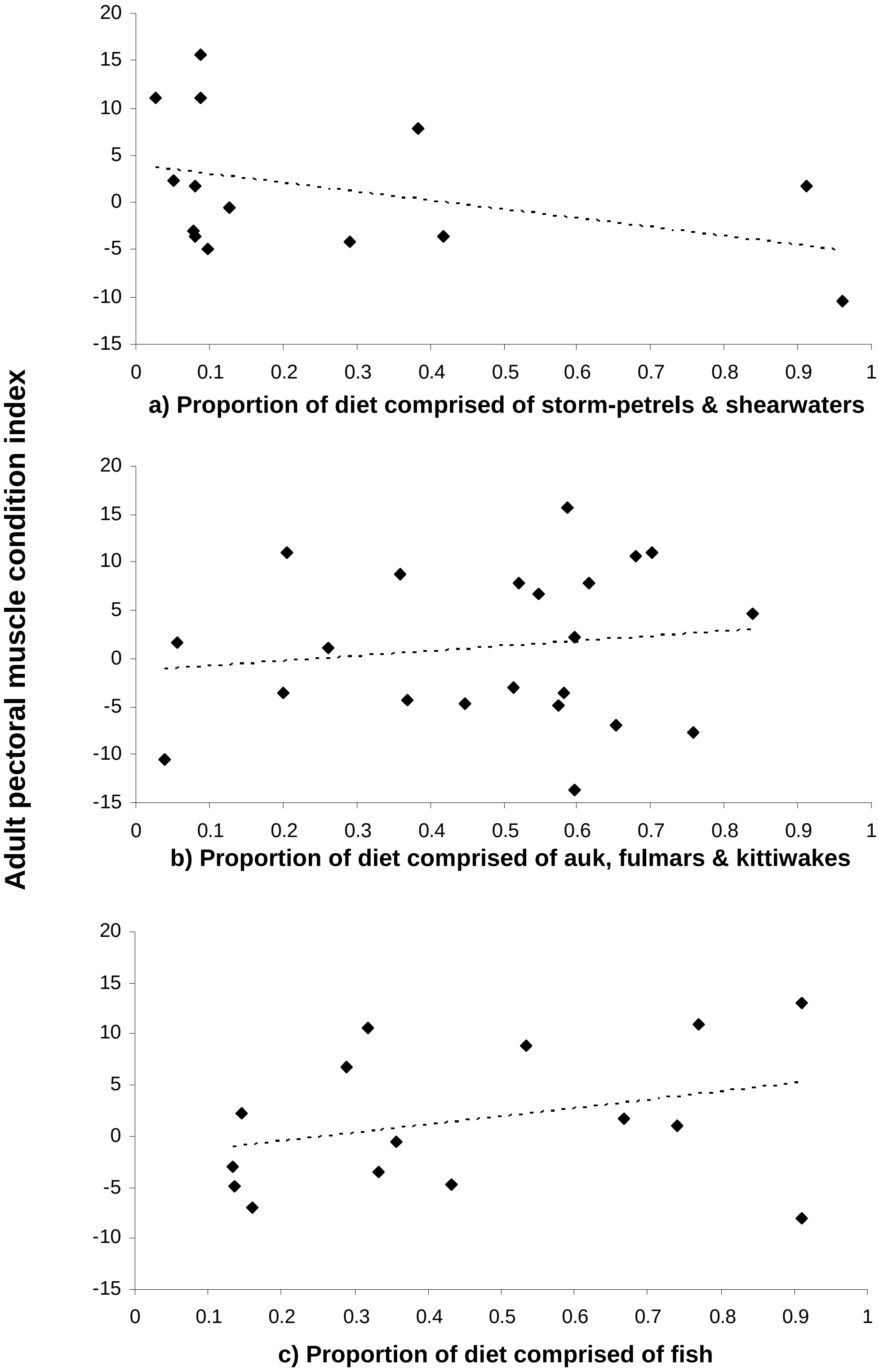


Figure 1.5. Adult pectoral muscle condition indices and proportions of different prey types in the diet (during the incubation period) of female Great Skuas trapped during incubation on Hirta, St Kilda, Outer Hebrides in 2009. Dashed lines show trends only (no significant relationships were detected).

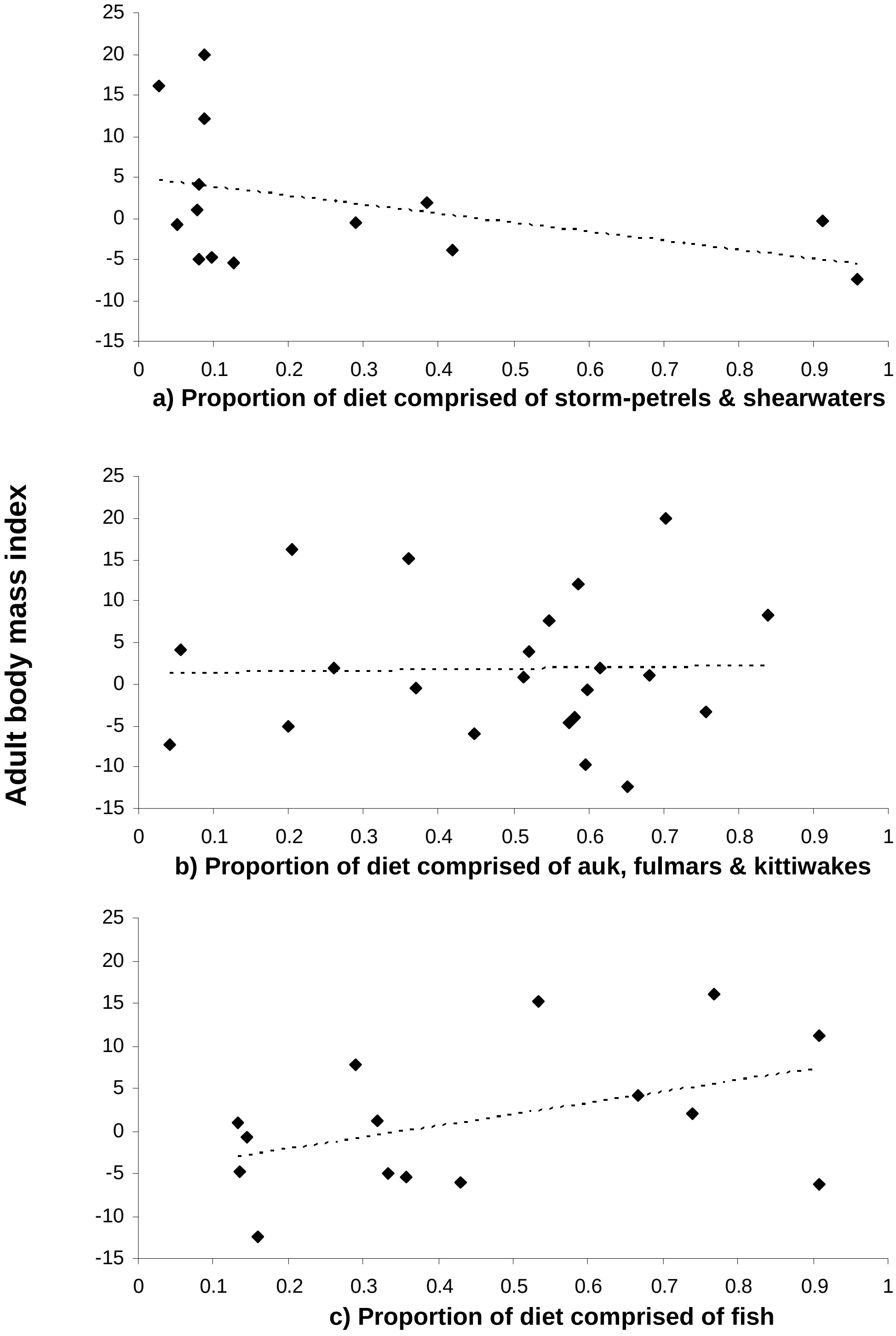


Figure 1.6. Adult body mass indices and proportions of different prey types in the diet (during the incubation period) of female Great Skuas trapped during incubation on Hirta, St Kilda, Outer Hebrides in 2009. Dashed lines show trends only (no significant relationships were detected).

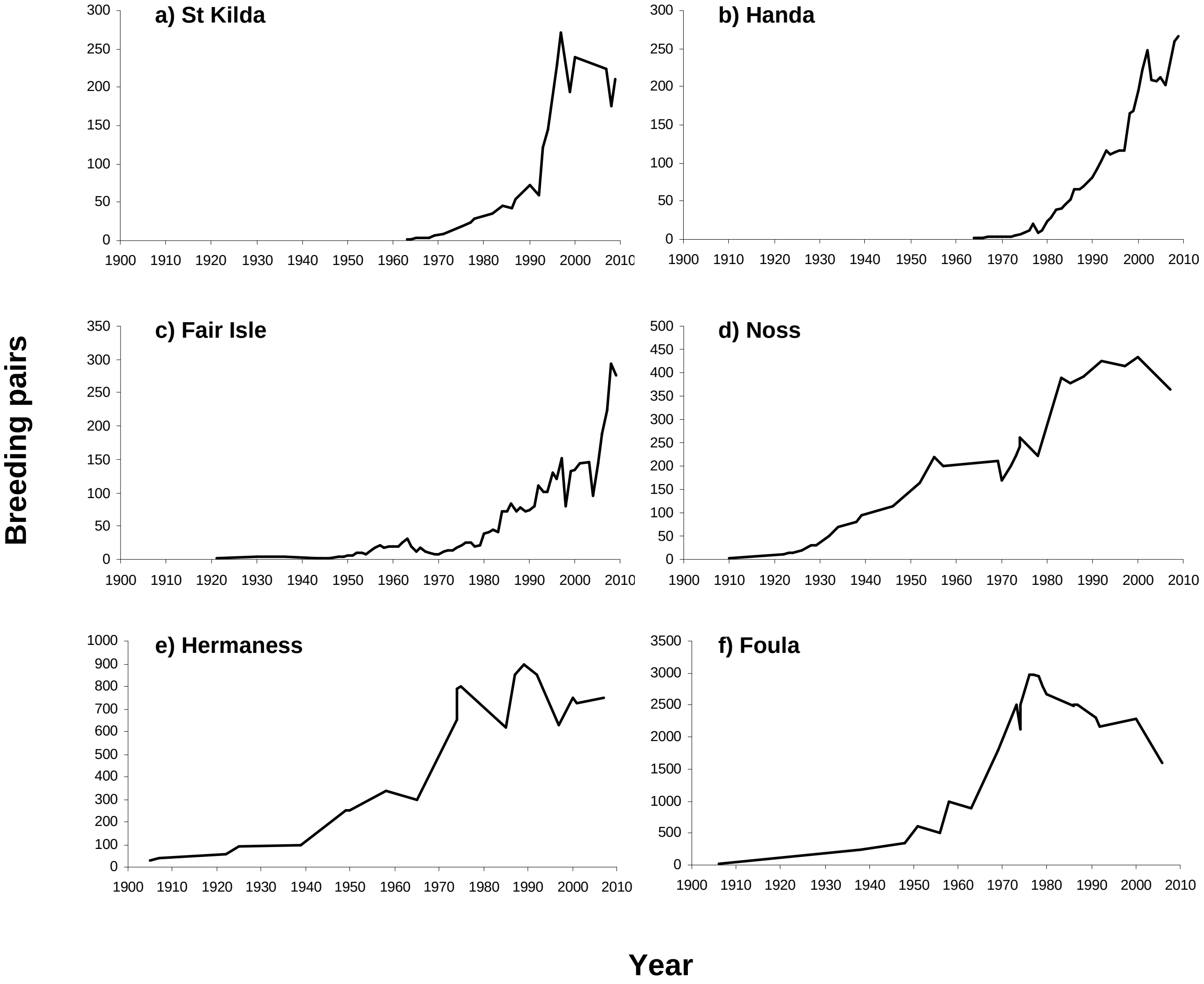


Figure 1.7. Population changes in total breeding pairs of Great Skuas at St Kilda (Outer Hebrides), Handa (Sutherland), Fair Isle, Noss, Hermaness and Foula (Shetland) from 1900 to 2009. (Furness 1987, Phillips et al. 1999b, Pennington et al. 2004, Shetland Bird Reports 1980-2008, Fair Isle Bird Reports 1950-2008, Green et al. 2009, M. Pennington & D. Shaw pers. comm. 2010).

DISCUSSION

Storm-petrel and shearwater predation

In all years, predation of storm-petrels and shearwaters was widespread on Hirta: between 40% and 50% of all skua pairs ate this prey in every year of the study. Few pairs (<7%) specialised, and very few (<3%) fed exclusively, on storm-petrels and shearwaters in any year. This was slightly unexpected, given that Leach's Storm-petrels, European Storm-petrels and Manx Shearwaters come in to land and are available to skuas only at night, whereas all other prey taken at St Kilda is most available and hunted by skuas only during the day (Furness 1987, Votier 2004b, pers. obs. 2007, 2008 & 2009). Therefore, skuas that fed on storm-petrels and shearwaters but not exclusively (the vast majority of pairs), presumably foraged at times during the day *and* night, rather than solely by nocturnal foraging, or diurnal foraging as on Shetland (Furness 1987, Votier 2004b, Votier 2007). These results are similar to the activity patterns observed by Votier et al. (2005) of four male great skuas which fed mostly on storm-petrels at St Kilda in 2004. Each bird was radio tracked during the breeding season, all were found to be active during the day and night, and no foraging patterns in particular synchrony with nocturnal prey activity on land were detected.

In this study, the behaviour, inferred from diet analyses, of most skua pairs which fed on storm-petrels and shearwaters at St Kilda conformed more to an opportunistic, generalist, foraging strategy than to strategies of foraging specialisation on one or few particular prey (Krebs & Davies 1993, Kruuk 1995). This suggests there may be disadvantages associated with specialisation on one kind of prey every year, and perhaps some degree of dietary flexibility within and between years is advantageous for survival and reproduction. Predation of storm-petrels and shearwaters may be limited at St Kilda by many variable factors, such as prey availability or intra-specific competition for foraging territories, all of which may necessitate foraging on alternative (diurnal) prey. Equally though, the reverse could be true, and perhaps limitations to availability of diurnal prey cause skuas also to hunt storm-petrels and shearwaters. It is difficult to assess whether the relative composition of different seabird prey in the diet of skua pairs reflects annual variation in seabird populations at St Kilda; complete surveys of all seabird populations are not made every year at the archipelago. Further study would be useful to determine the factors which drive many skua pairs to eat a relatively small proportion of nocturnal prey (<30%), with diurnal prey forming the bulk of the diet. The latest seabird population estimates for St Kilda show that diurnal seabirds are more abundant than nocturnal seabirds (c.448,000 auks, fulmars and kittiwakes to c.72,000 storm-petrels and shearwaters), so perhaps the relative occurrence of these two groups in the diet of skuas is broadly a reflection of relative availability (Mitchell et al. 2004, Newson et al. 2008).

The proportion of the breeding population of skuas on Hirta which ate storm-petrels, and the proportion of pairs which specialised on this prey, remained relatively stable throughout the study. Numbers of skuas feeding and specialising on storm-petrels and shearwaters did not increase with each year; which, from a conservation perspective, may be good news for storm-petrel and shearwater breeding populations. Access restrictions to Soay and Boreray meant diet analyses could not be made for the small number of skua pairs on these islands. On Dùn, diet analyses were incomplete compared with Hirta, owing to access and time limitations on Dùn, but showed that all four skua pairs on this island ate both nocturnal and diurnal seabirds: predominantly Leach’s Storm-petrels and Puffins. At all colonies other than St Kilda, Great Skuas have been observed hunting only during the day and to be generally inactive throughout the night (Furness 1987, Votier et al. 2005). The extent of nocturnal foraging found among pairs at St Kilda was unique within Scotland.

Skua fitness and diet

No evidence was found to suggest that feeding on storm-petrels and shearwaters resulted in outstanding reproductive fitness or body condition advantages for skuas. Leach’s Storm-petrels were the dominant prey-type in the diet of skua pairs specialising on nocturnal seabirds, and pairs with this diet exhibited no better measures of body condition or breeding performance in all years than pairs specialising on diurnal seabirds or on fish. As in gulls, early egg-laying is associated with higher phenotypic quality in Great Skuas (Spaans 1971, Coulson & Porter 1985, Ratcliffe et al. 1998, Votier et al. 2004a). Egg-laying date of dietary specialist pairs was consistently earlier than of dietary generalists, suggesting that specialisation confers fitness advantages. We do not know if dietary specialist pairs at St Kilda were the same individuals each year nor, if so, whether specialist pairs ate predominantly the same prey each year. Trapping adult skuas and use of colour ringing was not possible on the scale required to individually mark all dietary specialist pairs for identification between years. Given the very few pairs found to specialise exclusively on storm-petrels and shearwaters, we conclude that it is advantageous to the fitness of skuas to specialise on one or just a few prey-types, but probably disadvantageous to do so rigidly and not remain flexible to alternative foraging opportunities. It may be that dietary specialist pairs switch prey between years. This possibility is discussed in more detail in Chapter 2.

Future studies using the lasso trap to capture a large sample size of adults and measure body condition could be useful, particularly for males. During incubation the male feeds the female (Votier et al. 2004a), so our use of body condition parameters measured from females with diet composition measured from the respective pair was not biased by potential differences in diet between the sexes. In 2008, hatching success was higher for dietary generalist pairs and those specialising on storm-petrels and shearwaters than for pairs specialising on auks, fulmars and kittiwakes and on fish. It is difficult to know the reason for this, but one possibility is a scarcity of sandeels close to St Kilda early in the breeding season. Theoretically, this could reduce numbers of auks and kittiwakes (predominantly sandeel predators) at St Kilda during the skua incubation period, as well as reduce numbers of Mackerel *Scomber scombrus* and Herring *Clupea harengus* close to the islands (also sandeel predators), which would be available to Gannets, and available to skuas via kleptoparasitism. Overall, reduced sandeel availability could therefore influence skua fitness in the way indicated by hatching success in 2008, via reduced availability of diurnal seabird and fish prey during the skua incubation period, but not of nocturnal petrels, which feed on cephalopods, crustaceans and invertebrates rather than predominantly on sandeels (Brooke 2004). No evidence was found to suggest any degree of spatial autocorrelation in hatching success, using basic spatial analyses performed using ArcGIS version 9.2. However, it is worth considering that measuring the number of eggs hatched by a skua pair is perhaps prone to greater inaccuracy than any other fitness parameter. If, for example, eggs and chicks were removed by predators or were not found, then the total number of eggs hatched could be underestimated; and with only 3 intervals of measurement (0, 1 or 2), this could have a relatively strong bias on results.

On Shetland in 1998 and 1999, differences were found in the reproductive fitness of skua pairs specialising on fish and pairs specialising on seabirds, with the latter being fitter (Votier et al. 2004a & 2004c). It was rather surprising to find no such differences in this study; however, the results from Shetland reflect a dependency of skuas on sandeels and fisheries discards (mostly whitefish, in particular undersized Haddock *Melanogrammus aeglefinus* and Whiting *Merlangius merlangus*) built up between 1960 and 1980, but low availability of this prey during the 1990s in comparison with seabirds (Votier et al. 2004a, 2004b & 2004c). Sandeels and whitefish were not encountered frequently in the diet of Great Skuas during this study, and no evidence was found to suggest that skuas were dependent on this prey or that individual fitness was reduced by a lack of it at St Kilda. Fish remains found in skua pellets on Hirta in 2007, 2008 and 2009 (n = 963) were mostly from Mackerel and Herring, apparently stolen from the huge population of Gannets on Boreray (pers. obs. 2007, 2008 & 2009).

Population distribution and changes

The distribution of skua nests across the islands at St Kilda, with the great majority on Hirta (>79% in all years), largely reflects the tendency for colonial nesting by Great Skuas and initial colonisation of the archipelago at Gleann Mor on Hirta from 1963 (Furness 1987, Phillips et al. 1999a). Considering the extremely close proximity of Dùn to Hirta, the relatively vast numbers of storm-petrels and puffins which breed on Dùn, and the tendency of skuas in the southern hemisphere to nest directly on top of colonies of their burrow-nesting seabird prey, it is rather surprising that no more than four pairs of skuas nested on Dùn. This island holds the largest sub-colony of Leach's Storm-petrels at St Kilda; minimum estimates: c.12700 apparently occupied nest sites (pairs) on Dùn, c.5500 on Boreray, c.1600 on Hirta, and c.900 on Soay (Newson et al. 2008). It seems likely that the vegetation structure on Dùn provides particularly favourable nesting conditions for Leach's Storm-petrels, yet some difficulty for skuas to nest. Dùn is the only island at St Kilda without sheep, and a relatively thick layer of ungrazed vegetation has developed, particularly over the north-west half of the island. Leach's Storm-petrels nest within the very thick, soft, layer of grass stems on Dùn, at particularly high density in the north-west half of the island. Elsewhere on St Kilda there is no thick surface vegetation, due to grazing, and storm-petrels nest in deep, solid, burrows and natural cracks in the soil and rock, at much lower density (JNCC unpublished data 2000, Mitchell et al. 2004, Newson et al. 2008, S. Votier pers. comm. 2008, pers. obs. 2008 & 2009). The matted tangle of soft, deep grass stems on Dùn is apparently ideal for relatively very many Leach's Storm-petrels to form burrows and nest chambers. Conversely, the structure of the vegetation on Dùn is apparently far from ideal for skuas to nest because the grass layer is generally deep, spongy, and too soft for nest formation and to support eggs, while the relatively rigid and dense stands of taller plants, such as umbellifers *Apiacea*, appear to exclude nesting due to the difficulties they impose on skuas alighting and manoeuvring once on land. Skua nests found on Dùn were all in positions where vegetation was relatively sparse, such as on thinly-grassed rock platforms on the periphery of the island.

Figure 1.7a shows how the total breeding population of Great Skuas has changed at St Kilda. Total population estimates for years of this study included a population value for Soay from the latest survey (in 1999). This was due to access limitations to the island. However, approximate estimation of the Soay skua population was made in 2007, 2008 and 2009 by viewing the island from Hirta, numbers counted were universally low (c.40-50 individuals seen every year), and use of the 1999 breeding population estimate (22 pairs) did not seem inappropriate. A gradual increase in skua pairs at St Kilda was seen between 1963 and 1990, then exponential growth to a peak of 240 pairs in 2000, and a slight decline since 2000, recorded by this study. Initial colonisation followed by the period of exponential growth has been attributed to immigration of skuas from the large breeding populations on Shetland, in response to reduced availability of whitefish discards and sandeels at commercial fisheries around Shetland from 1980 onwards (Phillips et al. 1999a, Votier et al. 2004c). Influx of birds seems to have now ceased and the St Kilda population has plateaued and entered a period of slight decline.

Colonisation and population growth patterns at St Kilda and Handa are similar (Figure 1.7b), it is thought due to the same reasons, and perhaps a distinct plateau in the population on Handa will become evident (Votier et al. 2004c). In contrast to the relatively small skua colonies at St Kilda and Handa, the large Shetland colonies (Figure1.7d-f: Noss, Hermaness and Foula) have generally shown a pattern of rapid growth between 1950 and 1980, followed by levelling-off, slight fluctuation or decline of populations since 1980. Rapid growth of these colonies is attributed to a high abundance of the Shetland sandeel stock plus increased food availability from commercial fisheries discards between 1950 and 1980, and associated increases in skua productivity and survival; however, a reduction in sandeel stocks and whitefish discards followed, during the 1980s and 1990s. These latest changes are considered the driving factors for the large Shetland populations to plateau and decline, causing prospecting birds to leave for new islands with abundant alternative seabird prey, such as St Kilda and Handa, and the reproductive fitness and annual productivity of Shetland skuas feeding on fish to drop (Furness 1987, Votier et al. 2004a, 2004b & 2004c). Fair Isle does not conform to these linked patterns of population change at large and small colonies since 1950. Occasional human control has limited the skua population on Fair Isle; but not recently, and it has rapidly grown since 2000 (Figure 1.7c). It will be interesting to see whether future population changes on Fair Isle resemble those at small colonies such as St Kilda, or whether the population will continue to grow to resemble that of the island’s geographical counterpart in Shetland: Foula. At St Kilda, we conclude that current decline in the total skua population, as well as lack of fitness advantages from specialising on nocturnal seabirds above other prey, mean that predation of storm-petrels and shearwaters by skuas is unlikely to increase or this type of dietary specialisation to proliferate and become dominant.

ACKNOWLEDGEMENTS

WM was funded by NERC and NTS through a CASE studentship to Glasgow University. I am extremely grateful to Tony Bicknell, Sjurdur Hammer, Elizabeth Mackley, Roger Riddington and Steve Votier for help with fieldwork on St Kilda and to staff of the radar base facility on Hirta for their technical assistance. Special thanks are due to Rebecca Green, Mike Pennington, Deryk Shaw, Claire Smith, Uwe and Julie Stoneman, and Eliza Leat for useful discussion and guidance on breeding numbers of skuas on Handa and Shetland, to Angus Campbell and Cliff Black for transport to Dùn and Boreray, to Kate Griffiths for DNA-sexing of trapped skuas, and to Susan Bain and Sarah Money for logistical support on Hirta and Dùn.

Chapter 2

Prey specialisation on Leach's Storm-petrels *Oceanodroma leucorhoa* by Great Skuas *Stercorarius skua* at St Kilda

ABSTRACT

Many seabirds have been consumed by Great Skuas at St Kilda, including large numbers of Leach’s Storm-petrels. Nationally important populations of Great Skuas and Leach’s Storm-petrels breed at St Kilda and it has been suggested these may be mutually unsustainable without management intervention, involving removal of skua pairs specialising on Leach’s Storm-petrel prey. However, prior to this study, little was known of the extent to which each skua pair ate Leach’s Storm-petrels each year, the numbers and distribution of Leach’s Storm-petrel specialist pairs, and whether Leach’s Storm-petrels eaten by skuas were resident breeders or transitory non-breeding individuals. Skua nest mapping, analyses of pair diet and colour ringing of individuals at St Kilda in 2007, 2008 and 2009 revealed that although many skua pairs ate Leach’s Storm-petrels, specialist pairs were few, fed on a variety of other prey-types, and did not specialise on Leach’s Storm-petrels every year. Throughout the skua population, prey switching between years was found to be a common phenomenon and all pairs consumed a diversity of different prey-types. The proportion of Leach’s Storm-petrels in the diet of pairs was not associated with nest position and proximity to storm-petrel breeding colonies. Recoveries of Leach’s Storm-petrels ringed and measured during the study, as well as night-time observations of individuals at the breeding colonies, and of skuas hunting them, strongly suggested that Great Skuas fed more on transitory non-breeding Leach’s Storm-petrels than on resident breeders at St Kilda.

INTRODUCTION

During recent decades, the population of Great Skuas *Stercorarius skua* at St Kilda, Outer Hebrides, has increased exponentially (Phillips et al. 1999a). The St Kilda archipelago (57°49′N, 08°35′W) comprises 4 main islands: Hirta, Dùn, Boreray and Soay. The first pair of Great Skuas to nest at St Kilda did so alone on Hirta in 1963, but by 1997 total numbers had risen to 271 pairs, more than 1% of the world population (Phillips et al. 1999a, Mitchell et al. 2004). Rapid growth was in large part due to immigration of adults and young from the species' breeding strongholds in Shetland, driven by reduced availability of sandeel and fisheries discard prey in the North Sea around Shetland (Phillips et al. 1997, 1999a, 1999b, Votier et al. 2004c). An abundance of alternative seabird prey was available to skuas at St Kilda, which the rising population consumed in unusually large quantities compared with the diet of skuas in Shetland (Phillips et al. 1997, 1999b, Murray 2002, Votier et al. 2004a, 2004b). Phillips et al. (1997) found that between 1994 and 1996 the occurrence of seabirds in the diet of skuas at St Kilda was approximately five times that found on Foula, Shetland, and estimated that in 1996 Great Skuas at St Kilda consumed a total of 40,800 seabirds of 7 different species (Phillips et al. 1999b).

Leach's Storm-petrels *Oceanodroma leucorhoa* occur in very high numbers at St Kilda relative to other breeding sites in the UK; the archipelago holds an estimated total of 45,400 apparently occupied breeding sites, this 94% of the British and Irish breeding population (Mitchell et al. 2004). The total predicted number of seabirds consumed by skuas at St Kilda in 1996 (Phillips et al. 1999b) included an estimated 14, 850 Leach's Storm-petrels, approximately one sixth of the total estimated breeding population at the islands (Mitchell et al. 2004, Newson et al. 2008). Other predation studies at St Kilda have since confirmed an ongoing high level of storm-petrel predation by Great Skuas; this occurs only at night, unusually for the species, previously thought to hunt only during the day (Votier et al. 2005). Concerns over the conservation of Leach's Storm-petrels at St Kilda and the potential impacts of skuas were heightened when a decrease in the Leach's Storm-petrel breeding population on Dùn was recorded, from 27, 704 apparently occupied breeding sites (AOS) in 1999 to 14, 490 AOS in 2003 (O'Brien et al. 2003, Newson et al. 2008). St Kilda is a UNESCO World Heritage Site, SSSI and Special Protection Area, with both Great

Skua and Leach's Storm-petrel listed as qualifying species, but maintenance of large populations of both of these species appeared to be mutually exclusive (Votier et al. 2005, Mitchell et al. 2004, Newson et al. 2008). Possible management interventions have been considered, including an experimental removal of Great Skua pairs specialising on Leach's Storm-petrels. Studies on Shetland have shown that specialist skuas at certain colonies may inflict particularly high levels of predation on seabird species such as Kittiwakes *Rissa tridactyla* (Oro & Furness 2002, Votier et al. 2004a, 2004b). At Benidorm Island, western Mediterranean, a ten-year study beginning in 1993 found that heavy predation of European Storm-petrels *Hydrobates pelagicus* by Yellow-legged Gulls *Larus michahellis* was primarily carried out by a few storm-petrel specialist gulls (Oro et al. 2005).

Prior to any conservation action taking place at St Kilda, it was recognised that crucial information was lacking (Votier et al. 2005). In particular, little was known of the extent to which Leach's Storm-petrels occurred in the diet of individual skua pairs, the distribution and numbers of Leach's Storm-petrel specialist pairs, the possible influence of skua nest location on dietary specialism, and whether Leach's Storm-petrels eaten by skuas were breeding or non-breeding individuals. This paper presents the results of a three-year study in which skua pellet analyses and colour-ringing were used to assess the diet of individual skua pairs and degree of specialisation on Leach's Storm-petrels in each year. This study also examines the position of skua nests and the diet composition of pairs in relation to their proximity to Leach's Storm-petrel breeding colonies. Additionally, using brood-patch and biometric measurements from breeding, non-breeding and juvenile Leach's Storm-petrels which were ringed during the study, I investigate whether the breeding status and age of ringed and unringed Leach's Storm-petrels eaten by skuas can be determined from remains found in pellets, and evaluate results in relation to night-time observations of the behaviour of Leach's Storm-petrels at the breeding colonies and of Great Skuas hunting at St Kilda.

METHODS

Skua diet assessment

The study was carried out at the St Kilda archipelago on the islands of Hirta and Dùn during the breeding seasons of 2007, 2008 and 2009. Diet of breeding adult Great Skuas was assessed by identification of prey remains in regurgitated pellets of indigestible material, collected from every known nesting territory on the islands. For each territory, a circular area of 15m radius from the nest was checked for pellets, by the observer walking in a tight spiral from the nest out to the circumference, at all times searching a $2m^2$ area immediately ahead. Pellet searches lasted 20 minutes per territory. Complete surveys of the nesting population of Great Skuas on Hirta were carried out by searches for all nests in all areas of suitable habitat, repeated eight times (minimum) in each breeding season. Numbers of pairs nesting on Dùn, a smaller island separated from Hirta by a 300m wide tidal channel, were surveyed on occasions that sea conditions permitted landing by boat. Pellets found within a nesting territory can be confidently assigned to one pair because male and female Great Skuas defend their territory against conspecifics highly aggressively (Votier et al. 2004a). All territories on Hirta were visited every 10 to 15 days from May (egg laying) to mid-August (fledging). Pellets were collected from within each territory, removed to prevent recounting, and all prey remains identified to the lowest possible taxon using established identification criteria (Votier et al. 2001, 2003, 2004b). All pellets found containing Leach's Storm-petrel remains were dissected in case they contained uniquely numbered metal storm-petrel rings (see Adam & Booth 1999). Skua pellets are typically of similar size, colours and texture, and I was confident that these variables did not bias pellet-finding towards particular prey types. Fish pellets are slightly looser and more prone to disintegrate over time (20+ days) than bird or Goose Barnacle pellets, but relatively frequent pellet collection aimed to negate any bias introduced by this potential difference.

The diet of each skua pair, the annual relative composition of different prey eaten, was determined by calculation of the relative proportions of total meals consumed of different prey-types (1 meal = quantity of food present in a bird's proventriculus on its return from feeding; Phillips et al. 1999b). Following Votier et al. (2004b), I did not assume that one meal resulted in the production of one pellet. Numbers of meals were calculated by applying correction factors to pellet frequencies, determined from studies of captive Great Skuas fed different seabird and fish prey (Votier et al. 2001, 2004a, 2004b). In contrast to other prey items, auk *Alcidae*, fish and goose barnacle *Lepas* sp. remains in pellets could not be identified to species level so these remains were classified into three generalised categories to include all species. Total numbers of meals were calculated from the total numbers of pellets collected in all territories for each of the following prey-types: Leach's Storm-petrel, European Storm-petrel, Manx Shearwater, Northern Fulmar *Fulmarus glacialis*, Black-legged Kittiwake *Rissa tridactyla*, auk (including Common Guillemot *Uria aalge*, Razorbill *Alca torda*, Black Guillemot *Cepphus grylle* and Atlantic Puffin *Fratercula arctica*), fish, and goose barnacles. Pellets that were not these prey-types, that could not be identified or that contained more than one prey-type were extremely few (<1%) and were omitted from analyses. Number of goose barnacle pellets produced per meal was estimated by counting the number of goose barnacle half-shells found in pellets and comparing this with the number of half-shells estimated by Phillips et al. (1999b) to be consumed per meal of goose barnacles. I calculated that approximately 2 goose barnacle pellets were produced per meal and used this value as the correction factor to calculate numbers of meals from numbers of pellets of goose barnacle in all years. Skua pairs were treated as a single unit because both members are represented by one territory and it is impossible to assign collected pellets to the male and female separately (Votier et al. 2004a). Pairs were classified as Leach's Storm-petrel specialists when the relative proportion of their annual diet that was Leach's Storm-petrels exceeded 70%; an established threshold for dietary specialism selected following Votier et al. (2004a).

Skua nest positions and pair identity

The position of every skua nest was recorded as a 10-digit British National Grid reference and marked using a handheld GPS, also used for location guiding on return visits. Colour-ringing studies have shown that nest positions of individual Great Skua pairs vary little between years; most pairs make their nest on or within only a few meters of the exact position of the previous year's nest (Furness 1987, Hamer & Furness 1991, Phillips et al. 1999a). This behaviour was a useful guide to the identity of pairs on St Kilda in years of this study, in combination with individual colour rings. Under British Trust for Ornithology (BTO) licence, in 2007 and 2008 adults skuas feeding on Leach's Storm-petrels were trapped at the nest using a spring trap and individually marked using four darvic colour rings, two on each tarsus. Many skuas at St Kilda already bore individual colour rings from a previous study on range expansion (Phillips et al. 1999a), including birds which fed on Leach's Storm-petrels during our study, and in such cases there was no need for us to attempt trapping for ringing purposes. Plumage colouration and patterning of Great Skuas is extremely variable between individuals and birds often show unique features, particularly around the eyes, nape and crown, which remain constant throughout their lifetime and allow long-term individual identification (Furness 1987, Olsen & Larsson 1997). In the very few cases during this study where neither the male nor female in a pair feeding on Leach's Storm-petrels had colour rings or could be trapped, the pair was identified between years by nest location and from photographs taken of the bird's unique individual features.

Leach's Storm-petrel ringing and measurements

Adult Leach's Storm-petrels were mist-netted on Hirta at a breeding colony, Carn Mór, and at a location over 1km away from any known breeding colonies, the Feather Store, between mid-May and early August in 2007, 2008 and 2009 under BTO and Scottish Natural Heritage (SNH) Schedule 1 species licensing. Leach's Storm-petrel tape-lures were used at the Feather Store, but not at Carn Mór, with volume set at a constant level matching that of real calls. As part of a DNA study conducted by the University of Plymouth, under Home Office licence, a small number of breeding adult Leach's Storm-petrels were temporarily removed from burrows at Carn Mór and on Dùn in July 2008 for blood sampling. Juvenile Leach's Storm-petrels were found and collected around the village on Hirta in September 2008 and 2009, on occasions when they were attracted to the domestic lighting of the St Kilda radar base facility at night and became grounded (Miles et al. 2010). Every bird mist-netted, sampled from a burrow or found grounded by lights was fitted with a uniquely numbered metal BTO ring, measured, and released alive. Maximum flattened wing chord was measured to 1mm using a wing rule, weight was measured to 0.1g using an electronic balance and, on a sample of birds, tarsus length (minimum), culmen length (bill tip to feathering), bill depth (immediately in front of nose tube) and total head and bill length were measured to 0.1mm using Vernier callipers. With the exception of weight, these parameters were selected because representative of parts of the skeleton and plumage which are not digestible by skuas. If differences in these parameters were detected between Leach's Storm-petrels of different breeding status or age (e.g. breeding/non-breeding adults or adults/juveniles) then it could prove possible to determine the breeding status or age of birds eaten by skuas from measurement of skeletal remains and wings found in pellets. Throughout incubation and the early stages of chick rearing (mid-May to early August), the lower belly of male and female Leach's Storm-petrels that are breeding becomes bare of feathers and highly vascularised (the brood patch) to maximise heat transfer from adult to egg or chick (Huntingdon & Burtt 1972, Brooke 2004, Money et al. 2008). The brood patch region of every bird ringed was inspected and scored for feathering on a scale from 0 to 5 (0 = fully feathered, 5 = area entirely bare of feathers) and for vascularisation on a scale from 0 to 2 (0 = skin as normal with no evidence of capillaries close to the surface, 2 = brood patch heavily vascularised with obvious dense capillary network at skin's surface). Any adult bird mist-netted at Carn Mór or sampled from a burrow at Carn Mór or on Dùn between mid-May and early August that scored 5/2 for brood patch (5 for feathering and 2 for vascularisation) we considered to be a breeding adult, while any caught at the Feather Store scoring 0/0 during this period we considered to be a non-breeding adult (see Table 2.3). Variation in brood patch feathering during the peak incubation period for Leach's Storm-petrels at St Kilda (late May to mid-July; Money et al. 2008) was investigated using data from birds mist-netted and examined at Carn Mór and at the Feather Store in 2007. During the study, a small number of Leach's Storm-petrels were encountered that already had been ringed. These data are summarised in Table 4. All other data from Leach's Storm-petrels (Table 2.3 and Figure 2.4) are from the first capture only of birds that had not been previously ringed or measured.

Statistical and spatial analyses

Statistical analyses were performed using R version 2.10.1. To test whether the observed distributions of Leach's Storm-petrel prey in the diet of Great Skua pairs were random in each year, and to help assess the occurrence of specialist pairs within the breeding population, observed frequencies were compared with a Poisson distribution using G-tests. The diet composition of each skua pair nesting on Dùn and each pair specialising on Leach's Storm-petrels nesting on Hirta was tested for homogeneity between years using chi-squared tests. Arcsine transformations were used for proportional data. Skua nests were mapped, and distances between each nest and Leach's storm-petrel colonies were calculated, using ArcGIS version 9.2. Correlations between the distance that skua pairs nested from Leach's Storm-petrel colonies and the proportion of the annual diet of skua pairs comprised of Leach's Storm-petrels were assessed using Spearman's rank tests. Effects of age/breeding status on biometric parameters were investigated using a general linear model; in which age/breeding status was included as a fixed effect with three categories (breeding adult, non-breeding adult and juvenile), year was included as a fixed effect, and wing length, tarsus length, culmen length, bill depth and total head and bill length were response variables (each normally distributed and modelled separately). In cases where no year effect was detected, the data were pooled and the model rerun with year effect removed. Relative frequencies of Leach's Storm-petrels with different brood patch feathering (6 score categories, 0 to 5) that were mist-netted on a breeding colony (at Carn Mór) and off a breeding colony (at the Feather Store) were tested for homogeneity using a chi-squared test.

RESULTS

Skua predation of Leach's Storm-petrels

Total skua nests on Hirta numbered 189 in 2007, 139 in 2008 and 174 in 2009. Due to hazardous sea conditions and weather, visits could be made to Dùn only in 2008 and 2009. In each year a total of four nests were found; however, in 2008, time on the island was critically limited by sea conditions and diet analyses were carried out on only two nest territories. Total pellets collected in each year on Hirta numbered 2876 in 2007, 2094 in 2008 and 2358 in 2009, and on Dùn, 148 in 2008 and 232 in 2009. Between 5 and 110 pellets were found in most (>95%) skua territories in each year. From pellets, 26 Great Skua pairs on Hirta were identified as feeding on Leach's Storm-petrels in 2007 (14% of Hirta breeding population), 33 pairs in 2008 (24% of breeding population) and 36 pairs in 2009 (21% of breeding population). The observed distribution of Leach's Storm-petrel prey consumed by skua pairs was significantly different from an expected Poisson distribution in all years (Figure 2.1; 2007, $G_{adj,\,9} = 20.25$, $P<0.05$; 2008, $G_{adj,\,9} = 31.39$, $P<0.05$; 2009, $G_{adj,\,9} = 17.21$, $P<0.05$). The majority of pairs which fed on Leach's Storm-petrels did not do so heavily, with this prey forming less than 30% of the diet for more than 55% of pairs which took Leach's Storm-petrels in all years (Figure 2.1). However, an unexpected slight peak was seen in the number of specialist pairs (proportion of diet > 0.7), which was in contrast to the pattern expected were the data to conform to a Poisson distribution and highlighted the degree of specialisation among pairs within the breeding population on Hirta (Figure 2.1). All pairs on Dùn were identified as feeding on Leach's Storm-petrels in every year that data were collected.

Total numbers of skua pairs found specialising on Leach's Storm-petrels in each year were very few: on Hirta, 2 in 2007, 2 in 2008 and 4 in 2009, and on Dùn, 1 in 2008 and 2 in 2009 (Figure 2.1). Only 1 pair on Hirta (H4, Table 2.1) and 1 pair on Dùn (D2, Table 2.2) specialised on Leach's Storm-petrels in two years of the study. All other pairs identified as specialising on Leach's Storm-petrels did so in one year only. The annual diet of pairs differed significantly from the previous year in which it was measured for every Leach's Storm-petrel specialist pair on Hirta, throughout all years of the study (Table 2.1; H1, 2009 $\chi^2_4 = 143.45$, $P<0.01$; H2, 2009 $\chi^2_4 = 172.48$, $P<0.01$; H3, 2008 $\chi^2_3 = 739.12$, $P<0.01$, 2009 $\chi^2_4 = 74.47$, $P<0.01$; H4, 2009 $\chi^2_2 = 80.81$, $P<0.01$; H5, 2009 $\chi^2_6 = 93.02$, $P<0.01$; H6, 2008 $\chi^2_4 = 102.20$, $P<0.01$, 2009 $\chi^2_2 = 52.11$, $P<0.01$; H7, 2008 $\chi^2_6 = 44.86$, $P<0.01$, 2009 $\chi^2_6 = 93.24$, $P<0.01$). Among pairs nesting on Dùn this was not so; in the few cases that it was measured in more than one year, the annual diet of pairs did not differ significantly between years (Table 2.2; D1, 2009 $\chi^2_2 = 14.32$, N.S.; D2, 2009 $\chi^2_3 = 14.46$, N.S.). Total number of different prey-types consumed during the three years of study (prey-type diversity) ranged from 3 to 7 (mean = 5.4) for pairs on Hirta found to specialise on Leach's Storm-petrels (Table 2.1). All pairs which specialised on Leach's Storm-petrels on Hirta were identified between years using individual colour rings; however, for three nests it was only possible to individually identify one member of the pair in this way throughout the study. There were four nests where the male and the female were both individually identified throughout the study and the pair comprised the same two birds in every year (Table 2.1).

Great Skua and Leach's Storm-petrel breeding distributions

Figure 2.2 shows the latest known breeding distributions on Hirta and Dùn of Great Skuas (this study) and Leach's Storm-petrels (JNCC unpublished data 2000, Pers. obs. 2007-09). Only on Dùn did the species' breeding areas overlap. Leach's Storm-petrel breeding colonies on Hirta were limited to the west coast and the majority (85.7%) of skua pairs found on Hirta with more than 50% Leach's Storm-petrels in their annual diet nested on the west side of the island (Figure 2.2). However, Figure 2.3 shows that no further evidence was found of an inverse relationship between the distance that skua pairs nested from Leach's Storm-petrel colonies and the proportion of the annual diet of skua pairs that was Leach's Storm-petrels (Figure 2.3); no strong relationships were observed nor any significant correlations detected between these two parameters in any year (Figure 2.3; 2007, Spearman's rank correlation coefficient = -0.364, N.S.; 2008, Spearman's rank correlation coefficient = -0.303, N.S.; 2009, Spearman's rank correlation coefficient = 0.132, N.S.). Notable was that skua pairs nesting on Dùn did not all specialise on Leach's Storm-petrels, even though every skua nesting territory was located directly on top of the Leach's Storm-petrel breeding colony (Figure 2.3b & 2.3c), the largest in Britain and Ireland (Mitchell et al. 2004).

Leach's Storm-petrel biometrics, brood-patches and recaptures

Table 2.3 summarises Leach's Storm-petrel biometric parameters (mean ± S.E.) measured from breeding adults, non-breeding adults and juveniles and gives total numbers measured during the study. Biometric measurements did not vary significantly with age/breeding status or year, with the exception of head and bill length (GLM: wing, t = 0.328, N.S.; tarsus, t = 0.569, N.S.; bill depth, t = -1.858, N.S.; culmen, t = -1.956, N.S.; head & bill, t = -6.042, $P<0.01$, year, t = -2.294, $P<0.05$). Results suggested that head and bill length (also culmen length) tended to be shorter in birds we classified as non-breeding adults than in breeding adults (see Table 2.3). Post-hoc analyses of head and bill lengths and culmen lengths measured from birds classified on brood patch score as non-breeding adults (n=17) and breeding adults (n=21) were performed using general linear models in which each year was modelled separately. Adult bird type was included as a fixed effect with two categories (breeding and non-breeding) and head and bill length and culmen length were response variables (each normally distributed and modelled separately). This revealed that head and bill length and culmen length varied significantly with adult bird type in 2008 (GLM: culmen, $t = -0.0098$, $P<0.01$; head & bill, $t = 0.0069$, $P<0.01$) and both tended to be shorter in non-breeding adults than in breeders, but with overlap in range (Culmen length: range of non-breeding adult = 15.0mm to 16.8mm, range of breeding adult = 15.7mm to 17.1mm; Total head & bill length: range of non-breeding adult = 37.2mm to 41.6mm, range of breeding adult = 38.4mm to 42.8mm).

The distributions of frequencies of Leach's Storm-petrels with different brood patch feathering significantly differed between Carn Mór and the Feather Store ($\chi^2_9 = 45.24$, $P<0.01$; see Figure 2.4). On the breeding colony, at Carn Mór, birds with a brood patch feathering score of 5 were mist-netted far more frequently than birds with lower scoring brood patches (Figure 2.4). Away from the breeding colonies, at the Feather Store, numbers of birds mist-netted with each different brood patch feathering score were relatively even (Figure 2.4). During the study, we captured or found a total of 21 Leach's Storm-petrels on Hirta that were already bearing a ring (Table 2.4). The vast majority of these (95%) were both ringed and recaptured at Carn Mór, where a total of 148 birds were mist-netted, whereas a total of 352 were mist-netted at the Feather Store. Only one Leach's Storm-petrel mist-netted and ringed at the Feather Store was recaptured: its semi-digested remains were found as a pellet in the nesting territory of skua pair H2 (see Table 2.4 and Figure 2.2), the only skua pellet of the study found to contain a storm-petrel ring.

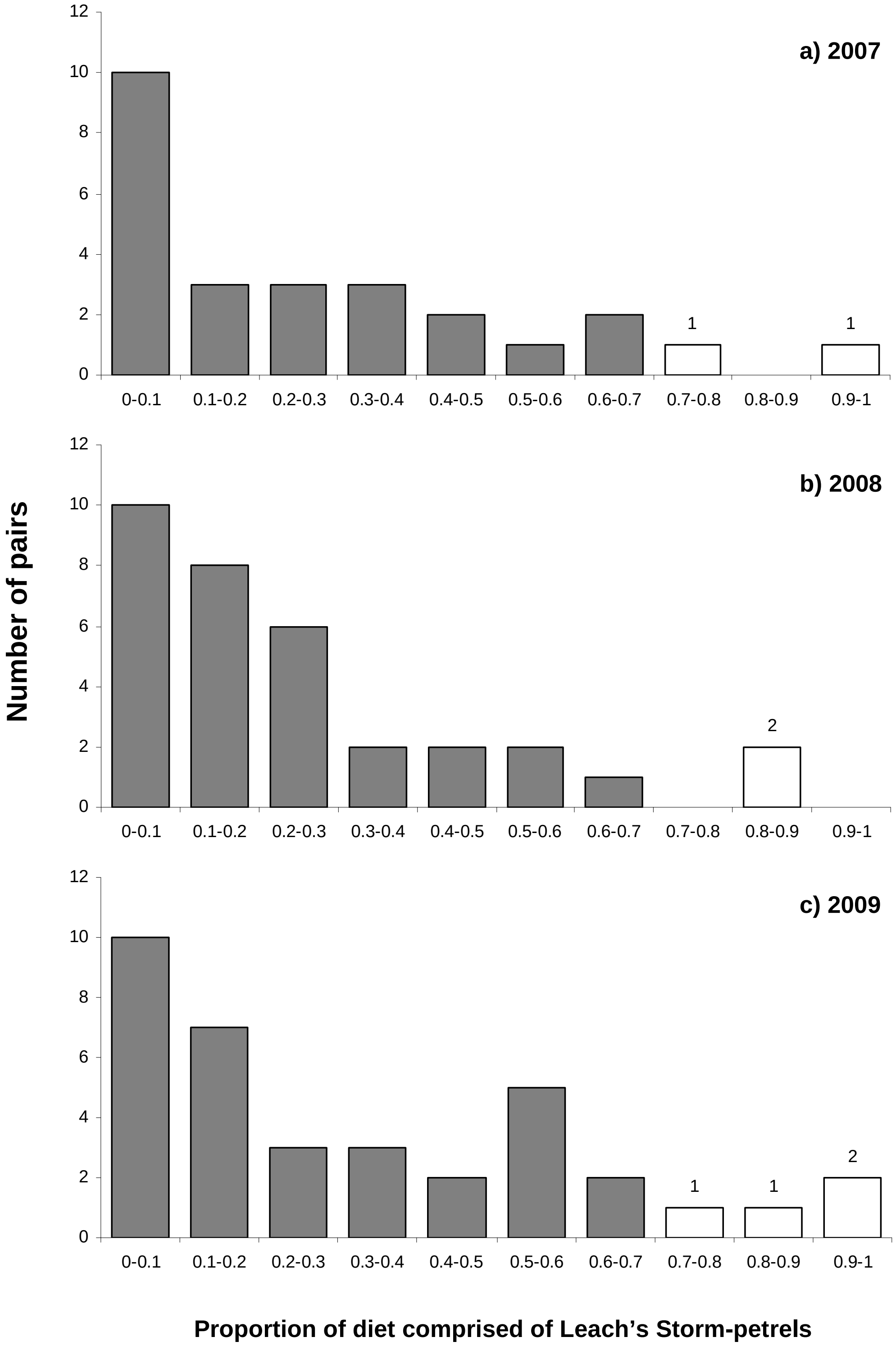


Figure 2.1. Proportional occurrence of Leach's Storm-petrels in the diet of Great Skua pairs on Hirta, St Kilda, Outer Hebrides, as identified from pellet analyses. Pairs with more than 70% Leach's Storm-petrels in diet were considered specialists (white bars). Pairs that did not feed on Leach's Storm-petrels (proportion of diet = 0) are not included in this figure but numbered 163 pairs in 2007, 106 pairs in 2008 and 138 pairs in 2009.

Table 2.1. Different prey-type proportions in the annual diet of Great skua pairs that specialised on Leach's Storm-petrels (>70% diet) in one or more years of this study, as identified from pellet analysis, and nested on Hirta, St Kilda, Outer Hebrides. (n = annual sample size of pellets collected; if < 10 then data were excluded from analyses.)

Nest	Year	Pellets (n)	Prey-type proportions									Total prey-types	
			Leach's Storm-petrel	European Storm-petrel	Manx Shearwater	Fulmar	Kittiwake	Auk	Fish	Goose Barnacles		Annual	3-year
H1	2007	44	**0.83**	0	0	**0.08**	0	0	**0.09**	0		3	5
	2008	(no nest)	-	-	-	-	-	-	-	-		-	
	2009	13	0	0	0	0	0	**0.32**	**0.59**	**0.09**	**	3	
H2	2007	10	**1**	0	0	0	0	0	0	0		1	4
	2008	(no nest)	-	-	-	-	-	-	-	-		-	
	2009	42	**0.56**	**0.11**	0	0	0	**0.09**	**0.24**	0	**	4	
H3[†]	2007	14	**0.03**	0	0	**0.05**	0	**0.15**	**0.77**	0		4	6
	2008	92	**1**	0	0	0	0	0	0	0	**	1	
	2009	19	**0.02**	**0.04**	0	0	**0.05**	**0.07**	**0.82**	0	**	5	
H4[†]	2007	(2)	-	-	-	-	-	-	-	-		-	3
	2008	43	**0.94**	0	0	0	0	**0.06**	0	0		2	
	2009	48	**0.76**	0	**0.21**	0	0	**0.03**	0	0	**	3	
H5[†]	2007	22	0	0	0	**0.04**	**0.06**	**0.62**	**0.24**	**0.04**		5	7
	2008	(1)	-	-	-	-	-	-	-	-		-	
	2009	58	**0.94**	**0.02**	0	**0.02**	0	**0.02**	0	0	**	4	
H6	2007	19	0	0	**0.29**	**0.41**	0	**0.19**	0	**0.11**		4	6
	2008	16	**0.55**	0	0	0	0	**0.45**	0	0	**	2	
	2009	32	**0.88**	**0.06**	0	**0.06**	0	0	0	0	**	3	
H7[†]	2007	110	**0.42**	0	**0.07**	**0.09**	0	**0.19**	**0.21**	**0.02**		6	7
	2008	37	**0.31**	**0.01**	0	**0.21**	0	**0.04**	**0.43**	0	**	5	
	2009	11	**1**	0	0	0	0	0	0	0	**	1	

[†] Nests where the male and the female were both individually identified and the pair comprised the exact same two birds in every year.
** Diet composition differed significantly from the previous year in which measured (P<0.01, Chi-squared tests for homogeneity with arcsine transformations).

Table 2.2. Different prey-type proportions in the annual diet of Great skua pairs that nested on Dùn, St Kilda, Outer Hebrides, as identified from pellet analysis (n = annual sample size of pellets collected).

Nest	Year	Pellets (n)	Prey-type proportions									Total prey-types	
			Leach's Storm-petrel	European Storm-petrel	Manx Shearwater	Fulmar	Kittiwake	Auk	Fish	Goose Barnacles		Annual	All years
D1	2008	69	**0.74**	0	**0.05**	0	0	**0.21**	0	0		3	3
	2009	81	**0.70**	0	0	0	0	**0.30**	0	0	(N.S.)	2	
D2	2008	79	**0.63**	0	**0.05**	**0.08**	0	**0.24**	0	0		4	4
	2009	73	**0.59**	0	0	**0.07**	0	**0.34**	0	0	(N.S.)	3	
D3	2009	18	**0.37**	0	0	0	0	**0.63**	0	0		2	2
D4	2009	60	**0.79**	0	0	**0.05**	0	**0.16**	0	0		3	3

(N.S.) = Diet composition did not significantly differ from the previous year (Chi-squared tests for homogeneity with arcsine transformations).

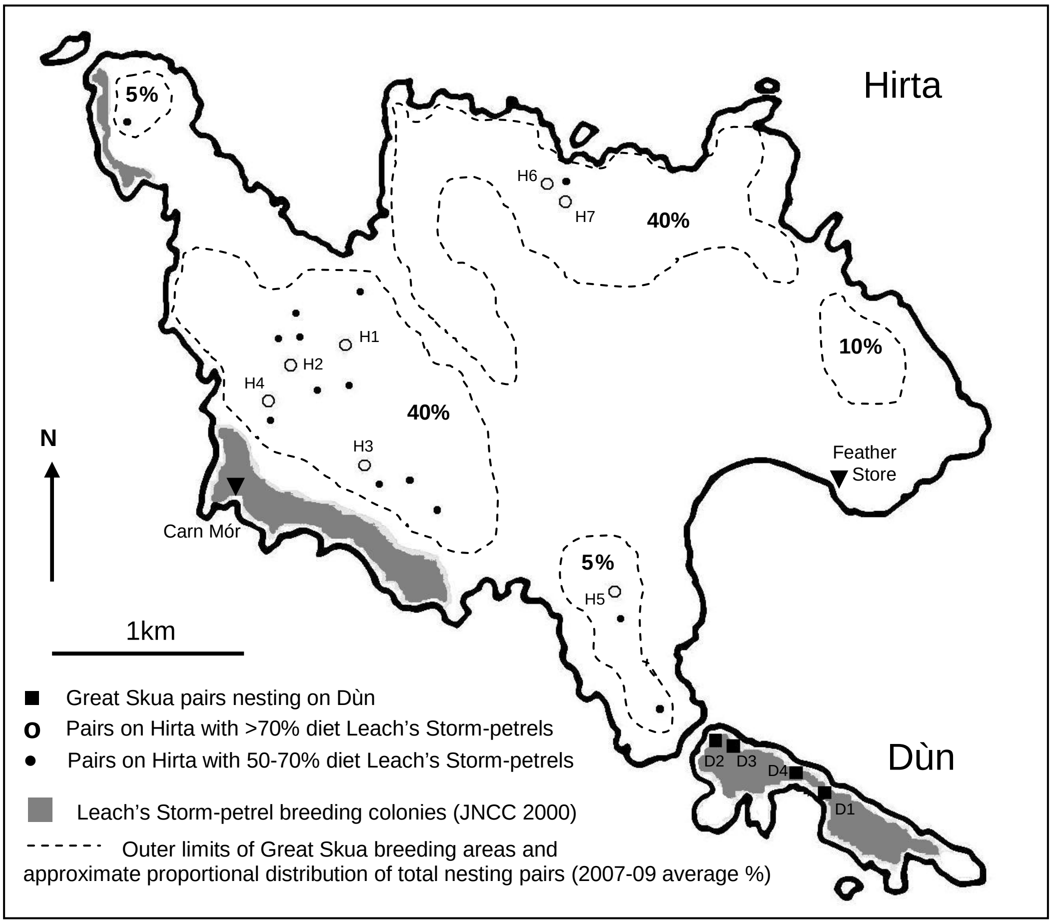


Figure 2.2. Islands of Hirta and Dùn, St Kilda, Outer Hebrides, showing locations of Leach's Storm-petrel and Great Skua breeding areas, including nests of all Great Skua pairs nesting on Dùn and nests of Great Skua pairs on Hirta with 50-70% and >70% of annual diet comprising of Leach's Storm-petrels in 2007, 2008 and/or 2009. Nest identification labels H1 to H7 and D1 to D4 refer to corresponding nests in Table 1 and 2. Leach's Storm-petrels were mist-netted for ringing and measurement at Carn Mór and at the Feather Store.

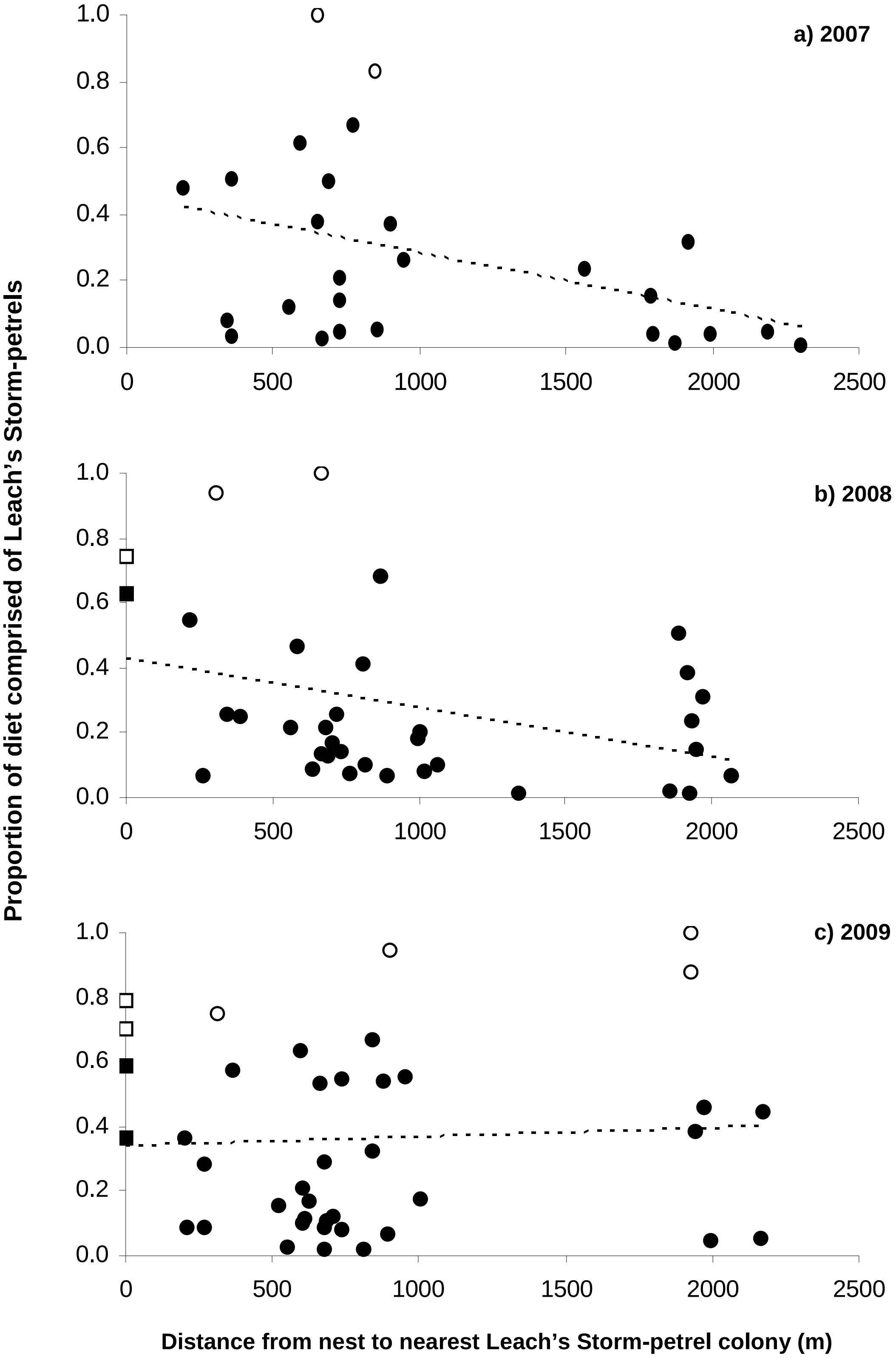


Figure 2.3. Proportion of annual diet that was Leach's Storm-petrels and distance from nest to nearest Leach's Storm-petrel colony for Great Skua pairs nesting on Hirta (circles) and Dùn (squares), St Kilda, Outer Hebrides. Unfilled points indicate skuas pairs specialising on Leach's Storm-petrels (>70% diet). Dashed lines show trends only (no significant relationships were detected).

Table 2.3. Wing, tarsus and head biometric measurements (mean ± S.E.) of breeding adult, non-breeding adult and juvenile Leach's Storm-petrels at St Kilda, Outer Hebrides.

Biometric measurement	Breeding adult				Non-breeding adult				Juvenile			
	(n)	mean	±	S.E.	(n)	mean	±	S.E.	(n)	mean	±	S.E.
Wing length (mm)	65	160.66	±	0.45	77	160.91	±	0.36	34	160.85	±	0.68
Tarsus length (mm)	21	24.67	±	0.14	17	24.80	±	0.17	34	24.79	±	0.14
Bill depth in front of tube (mm)	21	4.97	±	0.05	17	5.05	±	0.05	34	4.44	±	0.04
Culmen length (mm)	21	16.30	±	0.09	17	15.89	±	0.12	34	15.97	±	0.11
Head and bill length (mm)	21	41.30	±	0.25	17	40.20	±	0.30	34	37.39	±	0.21

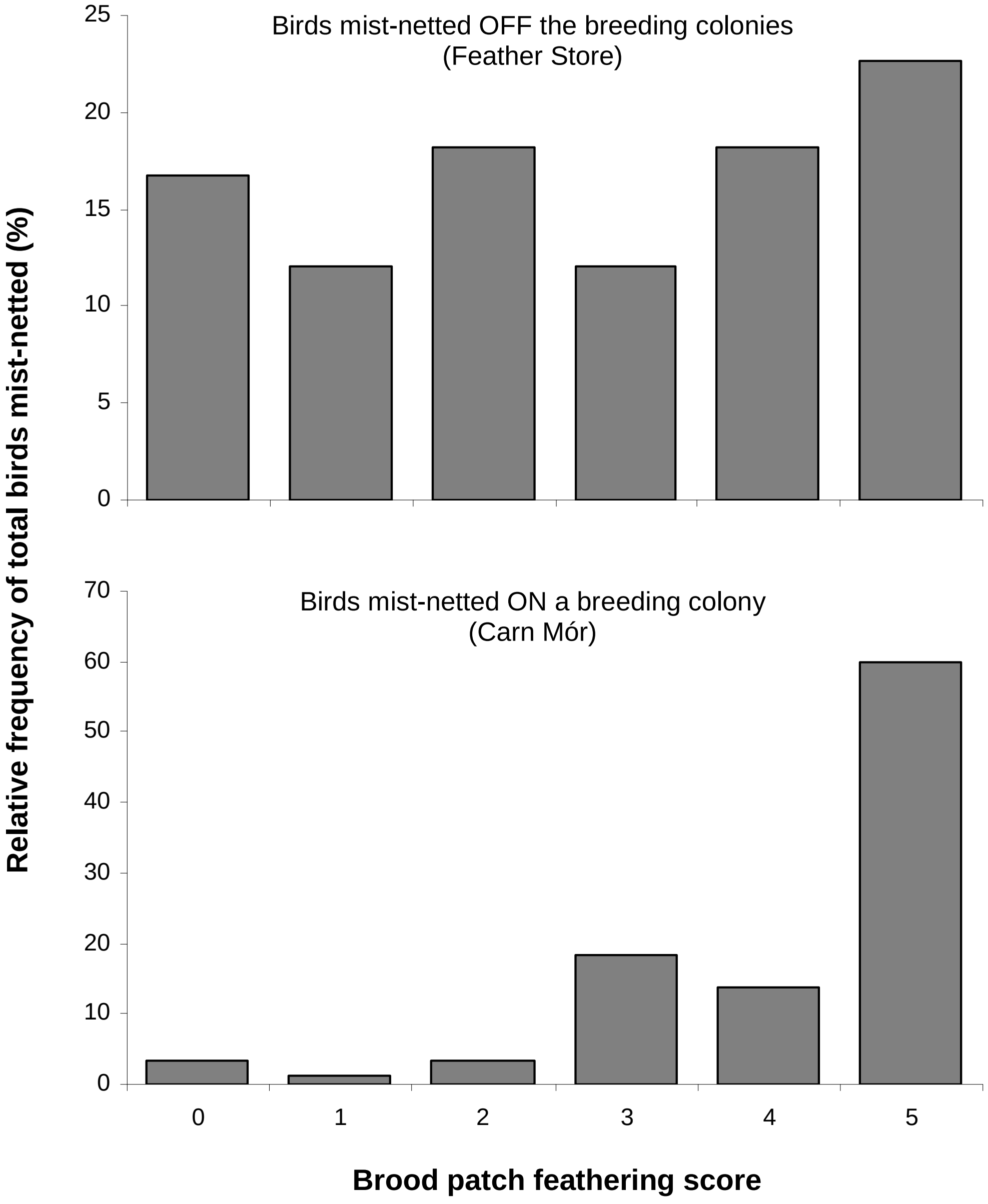


Figure 2.4. Relative proportions of Leach's Storm-petrels with different brood patch feathering, scored 0 (fully-feathered) to 5 (brood patch area entirely bare of feathers), that were mist-netted on a breeding colony at Carn Mór (n = 87) and away from the breeding colonies at the Feather Store (n = 66) on Hirta, St Kilda, Outer Hebrides, during the incubation period (late May to mid-July) in 2007.

Table 2.4. Leach's Storm-petrels captured or found already bearing a BTO metal ring in 2007, 2008 and 2009 on Hirta, St Kilda, Outer Hebrides, with circumstances of first capture, when ringing occurred.

Leach's Storm-petrels captured or found during this study already bearing a BTO metal ring				Ring no.	First capture (when ringed)		
#	Year	Location	Circumstances		Year	Location	Circumstances
1.	2007	Carn Mór	Alive, mist-netted	NT04350	2004	Carn Mór	Alive, mist-netted
2.	2007	Carn Mór	Alive, mist-netted	BX99623	2004	Carn Mór	Alive, mist-netted
3.	2007	Carn Mór	Alive, mist-netted	NT49941	2005	Carn Mór	Alive, mist-netted
4.	2007	Carn Mór	Alive, mist-netted	NT49930	2005	Carn Mór	Alive, mist-netted
5.	2007	Carn Mór	Alive, mist-netted	NT49856	2005	Carn Mór	Alive, mist-netted
6.	2007	Carn Mór	Alive, mist-netted	NT49855	2005	Carn Mór	Alive, mist-netted
7.	2007	Carn Mór	Alive, mist-netted	NT49845	2005	Carn Mór	Alive, mist-netted
8.	2007	Carn Mór	Alive, mist-netted	NT49830	2005	Carn Mór	Alive, mist-netted
9.	2007	Carn Mór	Alive, mist-netted	NS58341	2007	Carn Mór	Alive, mist-netted
10.	2007	Carn Mór	Alive, mist-netted	NS58339	2007	Carn Mór	Alive, mist-netted
11.	2007	Carn Mór	Alive, mist-netted	NS58334	2007	Carn Mór	Alive, mist-netted
12.	2007	Carn Mór	Alive, mist-netted	NS58332	2007	Carn Mór	Alive, mist-netted
13.	2007	Carn Mór	Alive, mist-netted	NS58322	2007	Carn Mór	Alive, mist-netted
14.	2007	Carn Mór	Alive, mist-netted	NS58317	2007	Carn Mór	Alive, mist-netted
15.	2008	Carn Mór	Alive, mist-netted	NT04283	2004	Carn Mór	Alive, mist-netted
16.	2008	Carn Mór	Alive, mist-netted	NT49976	2005	Carn Mór	Alive, mist-netted
17.	2008	Carn Mór	Alive, mist-netted	NS58412	2007	Carn Mór	Alive, mist-netted
18.	2008	Carn Mór	Alive, mist-netted	NS58377	2007	Carn Mór	Alive, mist-netted
19.	2008	Carn Mór	Alive, mist-netted	NS58374	2007	Carn Mór	Alive, mist-netted
20.	2008	Carn Mór	Alive, mist-netted	NS58318	2007	Carn Mór	Alive, mist-netted
21.	2009	Skua nest H2	Dead, in skua pellet	NS58567	2008	Feather Store	Alive, mist-netted

DISCUSSION

Prey-specialisation on Leach’s Storm-petrels by Great Skuas

Great Skua pairs found specialising on Leach’s Storm-petrels on Hirta and Dùn were few in total, numbering six pairs or fewer in all years of the study. Specialist pairs did not all nest on or very close to Leach’s Storm-petrel breeding colonies; the only pairs to do so were on Dùn. This may have been due to differences in terrain where storm-petrels breed on the two islands. On Hirta, the Leach’s Storm-petrels colonies are on steep slopes, strewn with boulders and much scree. This terrain is largely unsuitable for Great Skuas to nest and has not been colonised at St Kilda to date. The terrain where storm-petrels breed on Dùn is much flatter, with areas of open grassland and fewer boulders, and is apparently slightly more suitable for nesting skuas.

On islands in the southern hemisphere, such as Nelson Island, South Shetland, Bird Island, South Georgia, and Mayes Island, Kerguelen, many Brown Skuas *Catharacta skua lönnbergi* and South Polar Skuas *Catharacta maccormicki* specialise on burrow-nesting petrels and very often nest within breeding colonies of their prey (Mougeot et al. 1998, Weidinger 1998, Mougeot & Bretagnolle 2000b, Phillips et al. 2004). It was initially surprising to find how few skua pairs were nesting on Dùn and specialising on Leach’s Storm-petrels in comparison with Hirta, especially considering the flat, grassy, terrain on Dùn and relative abundance of breeding Leach’s Storm-petrels (Newson et al. 2008). However, it is possible that certain aspects of the island’s vegetation are less hospitable to nesting skuas than might at first appear. Dùn is the only island at St Kilda without sheep and, unlike on Hirta, Soay and Boreray, there are swathes of ungrazed emergent vegetation, such as umbellifers *Apiacea*, which stand relatively tall and rigid. Also, the grass sward on Dùn is comparatively very deep, loose, and extremely spongy. These specific features possibly make alighting on Dùn and the formation of a secure nest extremely difficult for skuas, and the island perhaps is unsuitable for rapid colonisation by many breeding pairs.

There was a tendency for skua pairs specialising on Leach’s Storm-petrels on Hirta to be found nesting in the west half of the island, towards the location of the

Leach's Storm-petrel breeding colonies (Figure 2.2). This was also true of pairs identified with 50-70% Leach's Storm-petrels in their diet (Figure 2.2). Given this distribution, the three pairs with more than 50% Leach's Storm-petrels in their diet that nested in relative isolation in the north east quarter of Hirta seemed rather anomalous (pairs H6, H7 and one other, see Figure 2.2). It is tempting to speculate that there may be an unknown Leach's Storm-petrel colony close to the nest location of these three pairs; perhaps on the nearby cliff to the north (Conachair), which is the highest in Britain and has areas of apparently suitable storm-petrel breeding habitat which are inaccessible to surveyors (JNCC unpublished data 2000). Access to several areas of St Kilda, including Boreray and Soay, is very problematic for survey work and research, due to the steepness of the terrain, frequent bad weather conditions and dangerous sea states. Compared with Hirta, there are few skua nests on Boreray and Soay (an estimated 10 and 22 pairs respectively, see Chapter 1; Murray 2002). Visits to these to assess diet would have been extremely useful, but unfortunately proved to be impossible during the study, and we were extremely fortunate to be able to land on Dùn.

During this study we identified Great Skua pairs specialising on Leach's Storm-petrels. From these data it is possible to estimate numbers of *individuals* specialising on Leach's Storm-petrels, assuming that Great Skuas mate either: 1) assortatively with respect to diet (i.e. Leach's Storm-petrel specialists always mate with Leach's Storm-petrel specialists), or 2) randomly with respect to diet (i.e. mate selection is entirely independent of diet).

Let p = proportion of population (individuals) specialising on Leach's Storm-petrels:

1) If Great Skuas mate completely assortatively with respect to diet:

The observed proportion of specialist pairs = the proportion of specialist individuals = p

2) If Great Skuas mate completely randomly with respect to diet:

The observed proportion of specialist pairs = $p \times p$
Therefore: $p = (\text{proportion of population (pairs) specialising on Leach's Storm-petrels})^{0.5}$

Following the above, if Great Skuas mate completely assortatively with respect to diet then, on Hirta for example, 0.011 of the Great Skua breeding population (individuals) specialised on Leach’s Storm-petrels in 2007, 0.014 in 2008 and 0.023 in 2009. If Great Skuas mate completely randomly with respect to diet then, on Hirta, 0.103 of the Great Skua breeding population (individuals) specialised on Leach’s Storm-petrels in 2007, 0.120 in 2008 and 0.152 in 2009. Equating these proportions into numbers of individuals, we can therefore say that between 4 and 39 individual Great Skuas on Hirta specialised on Leach’s Storm-petrels in 2007, between 4 and 33 in 2008 and between 8 and 53 in 2009, depending on the degree to which diet is related to mate selection (on a scale from completely assortative to completely random). Despite the small number of Great Skua pairs identified as specialising on Leach’s Storm-petrels during this study, we can only assume that there were a correspondingly small number of specialist individuals if we are confident that Great Skuas on St Kilda mate completely assortatively with respect to diet. If we accept the possibility of random mating then the number of specialist pairs could be substantially higher. Using data from this study, there is a degree of uncertainty over the precise figures, but certainly it is possible that there were more Leach’s Storm-petrel specialist individuals in the population each year than the number of specialist pairs might imply. This has implications for the effectiveness of any future management of Great Skua pairs on St Kilda according to prey-type(s). A future study to develop methods to identify the diet of individuals within pairs could be useful. DNA methods could possibly be used to identify which individual skua produced which pellets in a breeding territory, since it is sometimes possible to trap both adults at the nest for tissue sampling and DNA from cells of the gut lining should be present in regurgitated pellets.

Great Skua prey diversity and switching

Skua pairs on Hirta identified as specialising on Leach’s Storm-petrels did not feed solely on that prey-type and a diversity of other prey-types were found in the diets of these pairs. Three or more different prey-types were found in the diet of all Leach’s Storm-petrel specialist pairs on Hirta during the study and none were found to specialise on Leach’s Storm-petrels in all years. In years when pairs did not specialise on Leach’s Storm-petrels, most fed on a broad variety of seabird and fish prey, without any specialisation (Table 2.1). However, one pair (H3) specialised on fish in

2007 (>77% of diet), on Leach's Storm-petrels in 2008 (100% of diet), and then on fish again in 2009 (82% of diet), with consumption of an additional 5 other different prey-types during the three year period. Both the male and female of this particular pair were colour ringed individuals and the pair comprised the same individuals in all years of the study. It was entirely unexpected to witness such prey switching behaviour and to find that the diets of 'specialists' were varied and differed greatly between years. In some cases, where I could identify only one individual in a pair throughout the study, prey switching may have been driven by the identified individual taking a new (and unidentified) partner during the study, with different dietary 'tastes' to their predecessor (also unidentified). Yet prey switching and high prey-type diversity was also observed in pairs where both birds were identified every year and the two individuals known for certain not to change during the entire study.

A simple review of the diet of all skua pairs nesting on Hirta in 2007, 2008 and 2009 was carried out to try to assess the occurrence of pairs feeding on only one prey type (Leach's Storm-petrels, European Storm-petrels, Manx Shearwaters, Northern Fulmars, Black-legged Kittiwakes, auks, fish or goose barnacles). This is summarised in Table 2.5 (see below). Less than 15% of pairs fed solely on one prey type in any one year of the study, indicating there was at least some prey diversity (two or more prey-types) in the annual diet of the majority of pairs each year (>85%). Very few pairs (5 or fewer) fed on only one prey type for two years, and none did so for three years, thus all pairs which fed on one prey-type in one year of the study at some point switched to or from feeding on a greater diversity of prey (two or more prey-types). Feeding exclusively on one prey-type without any diversity or switching between years did not occur. High prey diversity and prey switching are traits of opportunistic generalist predators such as gulls, skuas and many species of raptor. It is likely that a degree of dietary flexibility can be an advantage for survival, particularly if prey populations are prone to fluctuation. However, reproductive advantages associated with prey specialisation have been widely reported in gulls and skuas, so the extent of prey diversity and switching found at St Kilda was surprising (Pierotti & Annett 1991, Watanuki 1992, Votier et al. 2004a). Understandably, it has often been assumed that dietary specialist pairs in skua populations are the same individuals each year. At St Kilda, skua pairs specialising on Leach's Storm-petrels were certainly not always the same individuals each year. This has negative implications for the effectiveness of any experimental removal of specialists. Dietary data from skua nests on Dùn were relatively few, but it was notable that the diet composition of pairs on this island did not change between years, in contrast to the general pattern on Hirta. Skua pairs on Dùn nest at far lower density and in closer proximity to very large seabird populations than do pairs on Hirta. It is possible that competition for access to seabird prey is more intense among pairs on Hirta, because they do not face a relative excess of prey within a very short range of their nests, so may have to compete for, adapt to, and switch to different prey-types more than pairs on Dùn. Feeding conditions on Dùn would seem very favourable to skuas and the relative lack of colonisation of the island perhaps is further evidence that nesting is inhibited by the ungrazed rank vegetation structure.

Breeding and non-breeding Leach's Storm-petrels

Clear differences were not found between the biometric measurements of Leach's Storm-petrels identified as breeding adults, non-breeding adults and juveniles (Table 2.3). Therefore I was unable to assign the remains of Leach's Storm-petrels found in skua pellets to these different bird types. In 2008, evidence was found that non-breeding Leach's Storm-petrels had shorter bills (culmen) than breeding birds, but given the small sample size of data, I treat this finding with caution. It would be useful to make further comparisons of the biometrics of birds trapped at breeding colonies that have brood patches bare of feathers and are heavily vascularised, with the biometrics of birds trapped at sites away from breeding colonies that have fully feathered brood patches. Potential use of bill length to identify the breeding status of Leach's Storm-petrels found in pellets may be limited by the occurrence of complete skull and bill arrangements in pellets. During this study, very few pellets (<40) were found containing these particular structures and, of those found, in most cases the bill was broken or lacking the sheath and could not be accurately measured.

One pellet which did contain a fully intact skull and bill, as well as most of the rest of the skeleton, was that containing ring NS58567. The culmen of this bird measured 15.5mm, which was indicative that the bird was a non-breeder, as within the (2008) range found for non-breeders (15.0-16.8mm) but outside that of breeders (15.7-17.1mm). When ringed at the Feather Store on 26 July 2008, the brood patch area of this individual scored 3 for feathering and 1 for vascularisation which, given the date, was not perfect for identification of the bird as a non-breeder. However, this brood patch score was not in any way typical of a breeding bird (i.e. score was not 5/2) and, together with the bill length and location of first capture (see below), it seems extremely likely that the bird was not breeding. All other Leach's Storm-petrels found during the study already bearing a ring (20 in total) were ringed and recaptured alive during mist-netting at Carn Mór, scored 5/2 for brood patch, in most cases were re-trapped at least one year after having been ringed and, overall, it seems very likely that these individuals were all breeding adults. In total, 14% of all the birds that were captured by mist-net at the Carn Mór breeding colony were found to be already ringed (these probably all breeding adults; 14% = (20/148) x 100), but by contrast only 0.2% of Leach's Storm-petrels captured by skuas and found in pellets were found to be ringed (only one ring found; 0.2% = (1 / (total number of Leach's Storm-petrel pellets found and examined / average number of pellets produced by Great Skuas per storm-petrel eaten)) x 100 = (1 / (1289/2.5)) x 100). If the one ring found among the 1289 skua pellets examined was from a breeding adult, the proportion of the total number of Leach's Storm-petrels consumed by skuas that are breeding adults (P) is given as follows:

a = Number of rings from breeding adults found in pellets = 1
b = Number of Leach's Storm-petrels found in skua pellets = (1289/2.5) = 516
c = Proportion of breeding adults that are ringed = (20/148) = 0.14

$$\begin{aligned} a &= b \times c \times P \\ P &= a / (b \times c) \\ &= 1 / (516 \times 0.14) \\ &= 0.01 \end{aligned}$$

This result is subject to considerable uncertainty, but is still extremely suggestive that breeding adults likely form a very small proportion of the total number of Leach's Storm-petrels consumed by skuas at St Kilda. The value of 0.01 should be viewed as a theoretical maximum, given that there is evidence to suggest that the ringed bird that was found in a pellet was actually a non-breeder. Using an estimate of 21,000 individuals for the total number of Leach's Storm-petrels consumed by skuas per year (see Chapter 3), the total number of breeding adult Leach's Storm-petrels consumed annually can be calculated = 21,000 x 0.01 = 210 individuals (maximum estimate). Overall, it seems reasonable to conclude from ring-recoveries that Great Skuas predominantly catch non-breeding birds and kill relatively very few breeders.

This conclusion is in general agreement with observations of the behaviour of hunting Great Skuas and Leach's Storm-petrels on the breeding colonies on Dùn and at Carn Mór, made using a Leica BIM 35 night scope (image intensifier) at St Kilda in 2007, 2008 and 2009 (see Chapter 4). Leach's Storm-petrels showed two discrete types of behaviour at colonies: some birds flew directly in to the colony and quickly disappeared down a burrow, but others meandered in, landed, and spent prolonged periods shuffling about, flapping and calling on the surface of the colony. The former were likely breeding birds returning to active nests, while the latter appeared to be non-breeders prospecting for nest sites and mates, and much more vulnerable to skua attack (see Chapter 4; Furness 1987, Brooke 1990). Skuas hunting Leach's Storm-petrels were observed to patrol the surfaces of the colonies, on foot, looking for storm-petrels exposed on the ground, and not to chase many in flight or to dig nesting individuals out from burrows. Non-breeding Leach's Storm-petrels on the surface of the breeding colonies were entirely oblivious to skuas, did not recognise the sight and sounds of skuas as a threat, and were very easily captured and eaten (see Chapter 4).

Most Leach's Storm-petrels mist-netted at the Feather Store during the peak incubation period in 2007 scored between 0 and 4 for brood patch feathering, while those mist-netted at Carn Mór mostly scored 5 (Figure 2.4). This suggests that most birds caught during this period at the Feather Store were not breeding, since partial feathering of the brood patch during peak incubation is not typical of breeding birds (Snow & Perrins 1998, Redfern & Clark 2001, Brooke 2004). There is evidence that non-breeding European Storm-petrels respond to tape-lures more than breeders, and our results suggest this is also likely true of Leach's Storm-petrels (Fowler et al. 1982, Okill & Bolton 2005). Ringing recoveries have shown that tape-lured European Storm-petrels are mostly pre-breeding young birds that are highly transitory and travel long distances prospecting potential breeding colonies (Furness & Baillie 1981, Fowler et al. 1982, Fowler & Okill 1988, Okill & Bolton 2005). We did not recover at St Kilda any Leach’s Storm-petrels that were ringed at the Feather Store, other than one in a skua pellet, and it seems likely that birds caught at the Feather Store were mostly transitory non-breeding individuals attracted by the tape, that soon departed to visit colonies elsewhere. Further evidence of this was that a bird ringed at the Feather Store on 5 July 2007, 5 days later was mist-netted 282km away from St Kilda at Sule Skerry, Orkney. In conclusion, although many skua pairs eat Leach’s Storm-petrels at St Kilda, pairs identified as Leach’s Storm-petrel specialists were few, fed on a variety of prey-types, and did not specialise on Leach’s Storm-petrels every year. It was not possible to determine for sure the breeding status of Leach’s Storm-petrels eaten by skuas using storm-petrel biometric measurements; however, from ring recoveries it seems very likely that skuas feed more on transitory non-breeding Leach’s Storm-petrels than on resident breeders.

Table 2.5. Summary of the occurrence of Great Skua pairs feeding on only one prey-type (Leach's Storm-petrels, European Storm-petrels, Manx Shearwaters, Fulmars, Kittiwakes, Auks, Fish or Goose Barnacles) on Hirta, St Kilda, Outer Hebrides in 2007, 2008 and 2009.

Great skua pair feeding behaviour, as identified from pellet analyses	Total pairs
Fed on only 1 prey-type in 2007	16 (8%)
Fed on only 1 prey-type in 2008	19 (14%)
Fed on only 1 prey-type in 2009	22 (13%)
Fed on only 1 prey-type in 1 or more years of the study (known different pairs)	51
Fed on only 1 prey-type in any 2 years	5
Fed on only 1 prey-type in any 2 consecutive years	4
Fed on the same 1 prey-type in any 2 consecutive years	3
Fed on only 1 prey-type in all 3 years of study	0

ACKNOWLEDGEMENTS

WM was funded by NERC and NTS through a CASE studentship to Glasgow University. Special thanks to Tony Bicknell, Sjurdur Hammer, Elizabeth Mackley, Roger Riddington, Deryk Shaw, Rory Tallack and Steve Votier for help with fieldwork on St Kilda. I am very grateful to the staff of the radar base facility on Hirta for their technical assistance, also to Angus Campbell and Cliff Black for transport to Dùn, and to Susan Bain and Sarah Money for logistical support on Hirta and Dùn.

Chapter 3

Quantities of Leach’s Storm-petrels *Oceanodroma leucorhoa* and other prey eaten by Great Skuas *Stercorarius skua* at St Kilda

ABSTRACT

At St Kilda, Outer Hebrides, between 1999 and 2003 a 50% decline was recorded in the largest Leach’s Storm-petrel breeding colony in Britain and Ireland. It was suspected that this could be attributed to predation by Great Skuas on the islands. Here I use bioenergetics and prey-consumption models to estimate annual predation rates of Leach’s Storm-petrels and other prey eaten by Great Skuas in 2007, 2008 and 2009. Incorporating the results of population surveys and analyses of the diet of adult breeders, young and non-breeding skuas, estimates were made of the energy and amounts of seabirds, fish and shellfish consumed in each year. Estimates accounted for all breeding and non-breeding activities each year, for all individuals, for the entire period that skuas were present at St Kilda. Over 37, 000 seabirds were estimated to be killed by Great Skuas each year, mostly auks and storm-petrels. However, in two out of three years, the prey-type consumed in greatest quantity by mass was fish. Results are discussed in relation to prey availability. Annual predation of Leach’s Storm-petrels was sustained and considerable: mean annual consumption was estimated to be approximately 21,000 individuals. However, a resurvey of the St Kilda Leach’s Storm-petrel colony in 2006 found there had been no significant decline since 2003 and that the breeding population appeared relatively stable (Newson et al. 2008). I conclude that Great Skuas at St Kilda eat extremely large numbers of non-breeding Leach’s Storm-petrels, rather than breeders, and that thousands of non-breeders likely visit the archipelago every year from colonies elsewhere, such as those found in Iceland and Newfoundland.

INTRODUCTION

Prey availability can affect the size and foraging behaviour of predator populations in different ways. Population sizes of specialist predators are often limited by prey availability, whereas population sizes of generalist predators are less closely related, because generalists are not always dependent on the population density of one prey-type (Nielsen 1999, Garrott et al. 2009, Ford et al. 2010). If one prey-type is unavailable, generalists can adapt their foraging behaviour to consume a wide range of alternatives (Phillips et al. 2004, Quigley et al. 2008, Friedlaender et al. 2009). This can impose very high predation pressure on several different prey-types, resulting in limitation of prey population densities (De Leon et al. 2006, Fargallo et al. 2009, Montevecchi et al. 2009, Innes et al. 2010). In marine ecosystems, gulls *Larus* and skuas *Stercorarius* are generalist predators which feed on many species of fish, birds and molluscs by direct predation, kleptoparasitism and scavenging of adults, young and eggs (Furness 1987, Malling-Olsen & Larson 2003). Human refuse is also exploited, for example large numbers of gulls feed on domestic waste at coastal (and inland) rubbish tips and both gulls and skuas feed on waste from commercial fisheries, discarded at sea and at coastal processing plants (Votier et al. 2004c, 2007, Neves et al. 2006, Skorka & Wojcik 2008, Navarro et al. 2009).

In the North Sea, an increase in direct predation of seabirds by Great Skuas *Stercorarius skua* was found to occur with decreases in the availability of fisheries discards and of small shoaling pelagic fish such as sandeels *Ammodytes marinus* (Votier et al. 2004a). Likewise, in the Northwest Atlantic, increases in predation of Leach's Storm-petrels *Oceanodroma leucorhoa* by gulls occurred following decreases in availability of inshore spawning Capelin *Mallotus villosus* (Stenhouse & Montevecchi 1999). Predation of seabirds by gulls and skuas can be considerable, for example at Mayes Island, Kerguelen, an estimated 55,000 petrels of at least eight species were eaten by Brown Skuas *Catharacta antarctica lönnbergi* in the skua breeding season of 1992 (Mougeot et al. 1998). Estimation of numbers of seabirds killed by skuas and gulls is crucial in assessment of the potential impacts that predation may have on seabird populations, particularly in the case of prey species of conservation concern (Weidinger 1998, Oro et al. 2005). Heavy predation can result in dramatic declines in prey populations. For example Black-legged Kittiwakes *Rissa* *tridactyla* have rapidly declined in most of Shetland, it is thought largely as a result of predation by Great Skuas (Heubeck et al. 1997, Oro & Furness 2002), and at St Kilda, Outer Hebrides, predation by Great Skuas is thought the most likely cause of a severe decline in the breeding population of Leach's Storm-petrels on the island of Dùn, by approximately 13,000 pairs between 1999 and 2003 (Phillips et al. 1999b, Newson et al. 2008).

Changes in size of the storm-petrel population on Dùn have been a particular concern for UK conservation of Leach's Storm-petrels because St Kilda holds more than 94% of the total breeding pairs in Britain and Ireland (Mitchell et al. 2004, Votier et al. 2005, Newson et al. 2008). In the latest complete census, an estimated total of 45,433 apparently occupied breeding sites (AOS) of Leach's Storm-petrels were found at St Kilda, compared with 1,425 AOS on the Flannan Isles, the second largest UK colony (Mitchell et al. 2004). Phillips et al. (1999b) estimated that Great Skuas consumed approximately 14,800 Leach's Storm-petrels at St Kilda in 1996, a level of predation thought likely to be unsustainable. Given the sharp decline discovered in breeding numbers on Dùn between 1999 and 2003, predation pressure from skuas seemed likely, albeit at a slightly lower level than estimated in 1996, and an assessment of numbers of Leach's Storm-petrels consumed by skuas in more recent years was considered imperative (Votier et al. 2005, Newson et al. 2008).

Prior to this study, it was not known how many Leach's Storm-petrels were consumed by Great Skuas at St Kilda, whether heavy predation occurred, or whether predation was at all sustained, in any years other than 1996. In this study I estimate numbers of Leach's Storm-petrels consumed by Great Skuas in 2007, 2008 and 2009, assess the impacts and implications of storm-petrel predation by skuas, and consider storm-petrel consumption estimates for 1996 along with recent Leach's Storm-petrel population changes at St Kilda. Additionally, I estimate consumption of other seabirds, fish and goose barnacles and compare this with estimates for 1996, as well as with estimates of storm-petrel consumption in these years. Prey consumption estimates were made for each year using predictive bioenergetics and prey consumption models described by Phillips et al. (1999b), incorporating recent advances in understanding of pellet production by skuas and of the field metabolic rates of dietary-specialist skuas (Votier et al. 2001, 2004b). These models and techniques were selected because they allowed comparison of prey consumption estimates for 2007, 2008 and 2009 (this study) to be made with those for 1996 (Phillips et al. 1999b). Additionally, this particular model-based approach was preferred because it is relatively holistic, since it accounts for the energy requirements and prey consumption of adult breeders, young and non-breeders, for all breeding and non-breeding activities, during the entire period that skuas are present at St Kilda each year, and across four years in total. Estimates of total numbers of storm-petrels predated by avian predators, for example gulls, have been made using absolute counts of hard storm-petrel body-parts, particularly the tibia, found in pellets (e.g. Oro et al. 2005). However, this method was not used here because it relies on complete collection of all pellets produced during a study period and is most appropriate at sites where all areas/islands are entirely accessible, unlike at St Kilda. Furthermore, the method does not account for numbers of storm-petrels predated by non-breeders and by breeding birds at times outside of the breeding season, and this information I wished to include.

METHODS

Study site

The study was carried out on Hirta, the largest island in the St Kilda archipelago (57°49′N, 08°35′W), Outer Hebrides, during the breeding seasons of 2007, 2008 and 2009. More than 90% of adult Great Skuas breeding at St Kilda nest on Hirta (Phillips et al. 1999a, Murray 2002). Access to the islands other than Hirta (Dùn, Boreray & Soay) is extremely difficult owing to their relatively very steep shores, few landing sites and usually dangerous sea conditions, and was very rarely achieved. St Kilda is a Site of Special Scientific Interest, a Special Protection Area, and a UNESCO World Heritage Site for its cultural and natural value. Over 670,000 seabirds breed on the islands, including (approximate latest minimum estimates): 90,000 Leach's Storm-petrels *Oceanodroma leucorhoa*, 2,000 European Storm-petrels *Hydrobates pelagicus*, 10,000 Manx Shearwaters *Puffinus puffinus*, 137,000 Northern Fulmars *Fulmar glacialis*, 121,000 Northern Gannets *Morus bassanus*, 23,000 Common Guillemots *Uria aalge*, 2,500 Razorbills *Alca torda* and 285,000

Atlantic puffins *Fratercula arctica* (Murray 2002, Mitchell et al 2004, Newson et al. 2008).

Bioenergetics model

Energy requirements of Great Skua breeding adults, non-breeding adults and chicks on Hirta for the entire duration that they were present each year were estimated using life-history parameters (Table 3.1). Numbers of breeding pairs of Great Skuas were determined by a complete census of nests each year. Numbers of non-breeders attending the only club site at St Kilda, on Hirta, were determined by direct counts of individuals at 6 to 10 day intervals throughout the breeding period and a mean calculated for each year. Food assimilation efficiency of 0.76 was used throughout, calculated by Hilton et al. (2000) from controlled feeding trials of captive Great Skuas fed sandeels and Whiting *Merlangius merlangus*. Mean clutch size and brood size at 20 days were recorded from frequent systematic visits to all nests throughout each breeding season. Published values of basal metabolic rate (BMR, Bryant & Furness 1995) and estimates of field metabolic rate (FMR, Caldow 1988, Votier et al. 2004b) were used in the model, the latter calculated from multiples of BMR according to the cost of performing specific activities. Estimates determined by Votier et al. (2004b) of FMR:BMR ratios for skua pairs specialising on seabird prey and on fish prey were used, with an average value incorporated for generalist pairs feeding on both these prey types without specialisation. I classified pairs as bird specialist (seabirds >70% of diet), fish specialists (fish >70% diet) or generalists (non-specialist diet, seabirds and fish each <70%), according to diet composition of each pair determined from pellets. Following Votier et al. (2004b), a value of 1.5 x BMR was used for Great Skua metabolic rate during incubation ($\mathrm{FMB}_{\mathrm{INCUBATION}}$:BMR ratio), for one adult in each pair for the incubation period. Clutch production, incubation and maintenance costs were excluded from energy calculations for non-breeders and it was assumed that the energetic benefits to non-breeders of not rearing chicks were offset by poor foraging efficiency compared with breeders (following Cairns et al. 1990, Phillips et al. 1999b, Votier et al. 2004b). Total energy required by adults for clutch formation and by chicks (hatching to departure from the colony) was calculated using the same method described by Phillips et al. (1999b) and Votier et al. (2004b). A sensitivity analysis was performed on the model for each year by increasing parameter values by 1% and testing a range of likely extremes for all parameters.

Diet composition

Diet of breeding adult skuas and chicks on Hirta was estimated from analyses of regurgitated pellets collected from every known nesting territory on the island in each year. For each territory, a circular area of 15m radius from the nest was checked for pellets, by the observer walking in a tight spiral from the nest out to the circumference, at all times searching a $2m^2$ area immediately ahead. Pellet searches lasted 20 minutes per territory. Territories were visited every 10 to 15 days from May (egg laying) to mid-August (fledging). Skua pellets are typically of similar size, colours and texture, and I was confident that these variables did not bias pellet-finding towards particular prey types. Fish pellets are slightly looser and more prone to disintegrate over time (20+ days) than bird or Goose Barnacle pellets, but relatively frequent pellet collection aimed to negate any bias introduced by this potential difference. *Contra* Phillips et al. (1999b) and Votier et al. (2004b), I did not carry out separate analyses of diet for pre-breeding adults and chicks by assessment of undigested prey-remains, regurgitated when birds were trapped and handled for biometric measurement and ringing. In 2007, extremely few adults and young that were handled regurgitated, so my sample size of regurgitates from the first year was tiny. Regurgitation by skuas during handling may occur more when the birds are stressed, but this I wished to minimise. Diet of non-breeders was assessed by searches of the club site for pellets during the same period and at the same frequency as searches of nest territories. Pellets were identified to the lowest possible taxon using published prey identification criteria (Votier et al. 2001, 2003, 2004b), and removed to prevent recounting. Relative composition of different prey types in the diet of the colony was determined by calculation of the relative proportions of total meals consumed of different prey-types (1 meal = quantity of food present in a bird's proventriculus on its return from feeding, Phillips et al. 1999b). Following Votier et al. (2004b), I did not assume that one meal resulted in the production of one pellet, and calculated numbers of meals by applying correction factors to pellet frequencies, determined from studies of captive Great Skuas fed different fish and bird prey (Votier et al. 2001, 2004a, 2004b). Unlike other prey items, Auk, fish and goose barnacle *Lepas* sp. remains in pellets could not be readily identified to species level so remains were classified into three generalised categories to include all species. Total numbers of meals were calculated from the total numbers of pellets collected for each of the following prey-type categories: Leach's Storm-petrel, European Storm-petrel, Manx Shearwater, Fulmar, Kittiwake, auk (including Common Guillemot, Razorbill, Black Guillemot *Cepphus grylle* and Atlantic Puffin), fish, and goose barnacles. Very few pellets (<1%) were found that were not these prey-types or that could not be identified and these were omitted from analyses. Number of goose barnacle pellets produced per meal was estimated by counting the number of goose barnacle half-shells found in pellets and comparing this with the number of half-shells estimated by Phillips et al. (1999b) to be consumed per meal of goose barnacles. I calculated that approximately 2 goose barnacle pellets were produced per meal and used this value as the correction factor to calculate numbers of meals from numbers of pellets of goose barnacle in all years.

Prey energy content and meal mass

Most pellets of fish prey included large bones and spinal sections from Mackerel *Scomber scombrus* and Herring *Clupea harengus* and the vast majority of these remains were of sufficient size to indicate they had come from fish of at least 100g. Few pellets were found containing very small fish bones or scales but in such cases also contained several otoliths, representative of more than one fish. Following Votier et al. (2004b) and Phillips et al. (1999b), I used the average fish wet meal mass of 100g proposed by Furness and Hislop (1981) and a mean energy content value of $5.2kJg^{-1}$ for fish meals (Hislop et al. 1991). For goose barnacle meal energy content we used a value of $1.9kJg^{-1}$ and an average wet meal mass of 40g, as determined by Phillips et al. (1999b). Wet meal mass of bird meat was assumed to be 100g for species too large to be swallowed whole (Furness & Hislop 1981) and bird meat energy content to be $10.9kJg^{-1}$, following Phillips et al. (1999b) and Votier et al. (2004b). It was assumed that only 65% of fresh body mass from carcasses of larger seabirds (Manx Shearwaters, Fulmars, Kittiwakes and auks) was consumed, due to the high proportion of indigestible material in these species, and that they are not swallowed whole (Phillips et al. 1999b). Compared with other seabirds, mean energy content of meals of Leach's and European Storm-petrels was adjusted downwards by

65% (= 7.1kJg^{-1}), because storm-petrels are swallowed whole and a greater proportion of material ingested will be indigestible or of low calorific value compared with larger seabird prey, which is normally purer meat selectively taken from a carcass (Phillips et al. 1999b). Because swallowed whole, Leach's and European Storm-petrel wet meal mass was assumed to be equal to the average mass of individuals, approximately 45g and 25g respectively (Brooke 2004).

Prey consumption model

Using the above values of energy content and mass of meals with our estimates of the relative proportions of meals of different prey-types in the colony diet, the percentage energy contribution of each different prey-type was calculated. These percentages were then used with values from the bioenergetics model of total energy consumption by skuas on Hirta, to estimate the total amount of energy supplied by each prey-type. Separate analyses were carried out for adult breeders plus young, and non-breeders. The total weight of each prey-type consumed was then back-calculated using prey calorific densities. Numbers of seabirds consumed by Great Skuas on Hirta were calculated from total weight consumed, using known mean body weights of the birds eaten (Snow & Perrins 1998). An intermediate body weight between Atlantic Puffin and Common Guillemot was used for auks, as individual species could not be consistently identified from remains in pellets. Following Phillips et al. (1999b) and Votier et al. (2004b), performance of the model was tested by increasing input values by 1% and by introducing a range of likely extremes. Extreme limits of prey calorific densities (± 25%), mean meal mass of birds and fish (± 30%) and mean meal mass of goose barnacles (± 50%) were tested in accordance with published values (following Phillips et al. 1999b). Due to possible error inherent in using pellets to assess Great Skua diet (see discussion), extreme limits for the proportion of different prey-types in the diet were set at ± 50%. Total numbers of different seabird prey-types consumed by Great Skuas at St Kilda were estimated for 1996 by input into our models of the population size and diet parameters determined by Phillips at St Kilda in 1996 (Phillips et al. 1999b). Total numbers of prey consumed at St Kilda in 2007, 2008 and 2009 were determined by input into the models of our population size and diet composition parameters for Hirta for each year, plus the most recent Great Skua population size estimates for Dùn (visited in 2008 and 2009; 4 nests found in each year), Soay (not visited, 22 apparently occupied nest territories recorded in 1999, Murray 2002) and Boreray (visited only in 2009; 10 apparently occupied nest territories found).

RESULTS

Bioenergetics model

Table 3.2 shows the energy requirements of the Great Skua population on Hirta in each year, in total: 1137.4 x10^5 kJ in 2007, 872.5 x10^5 kJ in 2008 and 1039.2 x10^5 kJ in 2009. The largest component of each season's total was for the maintenance and activity of breeding adults (70-80%). Chicks and non-breeding adults had much lower energy demands (≈10% and 10-20% of annual totals, respectively). Changes in parameter estimates following the sensitivity analysis resulted in very similar patterns of change in model outputs between years (Table 3.3). Causes of greatest change were size of the breeding population, adult BMR and food assimilation efficiency. The need for accuracy in these parameters is crucial because for each a 1% change altered the model output by almost 1%, unlike other parameters for which relative response magnitude was much lower. Greatest absolute change in model outputs following input of parameter extremes was caused by estimated maximum numbers of non-breeders and duration of the post-fledging period; both were set relatively very high (see discussion).

Prey consumption model

Estimates of prey energy content, meal mass and the contribution of each prey-type in the diet were used to calculate the relative energy contributions of each prey-type for adult breeders and chicks, and non-breeders on Hirta (see Table 3.4 for all values). Relative energy contribution and prey caloric values (Table 3.4) were used with absolute estimates of the total energy required by skuas per season (Table 3.2), to calculate the total mass consumed of each prey-type (Table 3.5). In all years, fish and auks were consumed in greater weight than any other prey-type. More fish meat was consumed in 2007 and 2009 (6103.87kg and 6226.25kg, respectively) than auks, but in 2008 the reverse was true (3997.03kg auks compared with 2951.37kg fish). In all years, breeding adults and chicks consumed over 75% of the total mass of prey taken. Annual weight proportions of goose barnacles consumed by skuas on Hirta were consistently small compared with proportions of fish and seabirds: 5.7% goose barnacles in 2007, 2.5% in 2008 and 2.7% in 2009.

Estimates of numbers of seabirds consumed by Great Skuas on Hirta are shown in Table 3.6, in total: 29,761 in 2007, 35,948 in 2008 and 53,752 in 2009. In all years, storm-petrels (European and Leach’s combined) were the seabird prey-type consumed in highest numbers. In 2008 and 2009, numbers of Leach’s Storm-petrels consumed were alone higher than any other. In 2007, only the number of auks taken was slightly higher than that of Leach’s Storm-petrels. Compared with numbers of auks and Leach’s Storm-petrels consumed (>8000 in all years), all other prey-types were taken in relatively moderate numbers (<4000 in all years); with the one exception of European Storm-petrels in 2009, when approximately 14000 were eaten (an increase of +293% from 2008 and +416% from 2007). Between-year changes in numbers of Leach’s Storm-petrels consumed on Hirta were positive and large (numbers up by +94% in 2008 and +41% in 2009). Numbers of auks taken diminished in each year, down by -16% in 2008 and by -19% in 2009; in contrast to total numbers of storm-petrels taken, which for both species increased annually. Estimated total numbers of auks and storm-petrels consumed at St Kilda (all islands, Table 3.7) followed the same trends as for Hirta from 2007 to 2009 (Table 3.6): numbers of auks taken decreased but numbers of storm-petrels increased in each year. Greater numbers of Manx Shearwaters, Fulmars, Kittiwakes and auks were consumed in 2007, 2008 and 2009, than in 1996. In 2008 and 2009 this was also true for Leach’s Storm-petrels, and in 2009, for European Storm-petrels. Numbers of Manx Shearwaters, Fulmars and Kittiwakes consumed at St Kilda in 2008 were lower than in 2007 (down by -5.8%, -19.6% and -43.0%, respectively), but higher in 2009 than in 2008 (up by +3.3%, +7.8% and +193.8%, respectively). In 2008 and 2009, combined annual totals of numbers of Manx Shearwaters, Fulmars, Kittiwakes and auks were less (by 11,204 individuals in 2008 and 32,631 in 2009) than the total numbers of storm-petrels consumed in these two years, mostly Leach’s. Overall, numbers of Leach’s Storm-petrels consumed were far greater than for any other seabird prey-type (Table 3.6 and 3.7), and in 2009 the estimated total of Leach’s Storm-petrels consumed at St Kilda outnumbered the sum total of all other seabirds taken (Table 3.7).

The results of the prey consumption model sensitivity analysis are shown in appendix 3.1. Results are consistent between years. Changes to values of bird caloric density, large bird meal mass and the proportion of fish in the diet had greatest effects on estimated amounts of prey consumed compared with changes made to all other parameters. Altering the proportion of each different bird prey-type in the diet of skuas caused relatively large change in the output value for numbers of that prey-type consumed but, in most cases, also smaller changes in the opposite direction to numbers consumed for all other prey-types. Compared with the effects of changes made to fish and bird prey proportions, effects of altering proportions of goose barnacles in the diet were minimal. Changes to the proportion of any prey-type in the diet of breeders and young had a greater effect than changes to prey-type proportions for non-breeders, for which only very minor changes to model outputs resulted.

Table 3.1. Parameters used in the bioenergetics model

	2007	2008	2009	Source
Breeding pairs on Hirta	189	139	174	This study
Non-breeding birds on Hirta	48	69	53	This study
Pre-breeding period	≈ 30 days	≈ 30 days	≈ 30 days	Phillips et al. 1999
Incubation period	29 days	29 days	29 days	Furness 1978
Chick-rearing period (St Kilda)	≈ 47 days	≈ 47 days	≈ 47 days	Phillips et al. 1999
Post-fledging period (St Kilda)	≈ 18 days	≈ 18 days	≈ 18 days	Phillips et al. 1999
Adult BMR	538 KJ day^{-1}	538 KJ day^{-1}	538 KJ day^{-1}	Bryant & Furness 1995
Adult FMR:BMR ratio				
Bird specialists (>70% bird)	2.15	2.15	2.15	Votier et al. 2004
Fish specialists (> 70% fish)	3.5	3.5	3.5	Votier et al. 2004
Generalist	2.83	2.83	2.83	(Mean of specialist values) Votier et al. 2004
Adult FMR$_{\text{INCUBATION}}$:BMR	1.5	1.5	1.5	Votier et al. 2004
Mean clutch size	1.78	1.79	1.78	This study
Mean brood size at 20 days	1.33	1.19	1.2	This study
Mean brood size at fledging (St Kilda)	0.84	0.84	0.84	Phillips, Thompson & Hamer 1997
Mean fresh egg mass	96 g	96 g	96 g	Furness 1978
Mean egg energy density	6.45 KJ g^{-1}	6.45 KJ g^{-1}	6.45 KJ g^{-1}	Meathrel & Ryder 1987; Meathrel et al. 1987
Egg synthesis efficiency	0.75	0.75	0.75	Rickleffs 1974, 1983
Food assimilation efficiency	0.76	0.76	0.76	Hilton et al. 2000
Mean chick fledging mass (St Kilda)	1170 g	1170 g	1170 g	Phillips, Thompson & Hamer 1997

Table 3.2. a) Energy requirements of Great Skuas in 2007 on Hirta, St Kilda, Outer Hebrides.

2007	Individual / pair				Entire colony			
	Daily		Whole season		Daily		Whole season	
Breeding adults								
Maintenance and activity								
Bird specialists	1522.0	kJ bird $^{-1}$	182.1	x 10^3 kJ pair^{-1}	203.9	x 10^3 kJ	243.9	x 10^5 kJ
Fish specialists	2477.6	kJ bird $^{-1}$	286.7	x 10^3 kJ pair^{-1}	237.9	x 10^3 kJ	275.2	x 10^5 kJ
Generalists	2003.3	kJ bird $^{-1}$	234.8	x 10^3 kJ pair^{-1}	296.5	x 10^3 kJ	347.4	x 10^5 kJ
Egg production costs								
Bird specialists	-		1933.6	kJ pair $^{-1}$	-		259.1	x 10^3 kJ
Fish specialists	-		1933.6	kJ pair $^{-1}$	-		185.6	x 10^3 kJ
Generalists	-		1933.6	kJ pair $^{-1}$	-		286.2	x 10^3 kJ
Incubation costs	1061.8	kJ bird $^{-1}$	30793.4	kJ pair $^{-1}$	200.7	x 10^3 kJ		
Non-breeding adults								
Maintenance and activity	2003.3	kJ bird $^{-1}$	248.4	x 10^3 kJ bird^{-1}	96.2	x 10^3 kJ	119.2	x 10^5 kJ
Chicks								
Hatching to fledging								
Bird specialists	-		45722.9	kJ chick $^{-1}$	-		40.7	x 10^5 kJ
Fish specialists	-		45722.9	kJ chick $^{-1}$	-		29.2	x 10^5 kJ
Generalists	-		45722.9	kJ chick $^{-1}$	-		45.0	x 10^5 kJ
Fledging to departure								
Bird specialists	1025	kJ fledgling $^{-1}$	18450	kJ fledgling $^{-1}$	57687	kJ	10.4	x 10^5 kJ
Fish specialists	1025	kJ fledgling $^{-1}$	18450	kJ fledgling $^{-1}$	41328	kJ	7.4	x 10^5 kJ
Generalists	1025	kJ fledgling $^{-1}$	18450	kJ fledgling $^{-1}$	63714	kJ	11.5	x 10^5 kJ
Total colony energy requirement							**1137.4**	**x 10^5 kJ**

Table 3.2. b) Energy requirements of Great Skuas in 2008 on Hirta, St Kilda, Outer Hebrides.

2008	Individual / pair				Entire colony			
	Daily		Whole season		Daily		Whole season	
Breeding adults								
Maintenance and activity								
Bird specialists	1522.0	kJ bird $^{-1}$	182.1	x 10^3 kJ pair $^{-1}$	225.3	x 10^3 kJ	269.4	x 10^5 kJ
Fish specialists	2477.6	kJ bird $^{-1}$	286.7	x 10^3 kJ pair $^{-1}$	113.9	x 10^3 kJ	131.9	x 10^5 kJ
Generalists	2003.3	kJ bird $^{-1}$	234.8	x 10^3 kJ pair $^{-1}$	168.3	x 10^3 kJ	197.2	x 10^5 kJ
Egg production costs								
Bird specialists	-		1944.5	kJ pair $^{-1}$	-		287.8	x 10^3 kJ
Fish specialists	-		1944.5	kJ pair $^{-1}$	-		89.4	x 10^3 kJ
Generalists	-		1944.5	kJ pair $^{-1}$	-		163.3	x 10^3 kJ
Incubation costs	1061.8	kJ bird $^{-1}$	30793.4	kJ pair $^{-1}$	147.6	x 10^3 kJ		
Non-breeding adults								
Maintenance and activity	2003.3	kJ bird $^{-1}$	248.4	x 10^3 kJ bird $^{-1}$	138.2	x 10^3 kJ	171.4	x 10^5 kJ
Chicks								
Hatching to fledging								
Bird specialists	-		45722.9	kJ chick $^{-1}$	-		40.3	x 10^5 kJ
Fish specialists	-		45722.9	kJ chick $^{-1}$	-		12.5	x 10^5 kJ
Generalists	-		45722.9	kJ chick $^{-1}$	-		22.9	x 10^5 kJ
Fledging to departure								
Bird specialists	1025	kJ fledgling $^{-1}$	18450	kJ fledgling $^{-1}$	63714	kJ	11.5	x 10^5 kJ
Fish specialists	1025	kJ fledgling $^{-1}$	18450	kJ fledgling $^{-1}$	19803	kJ	3.6	x 10^5 kJ
Generalists	1025	kJ fledgling $^{-1}$	18450	kJ fledgling $^{-1}$	36162	kJ	6.5	x 10^5 kJ
Total colony energy requirement							**872.5**	**x 10^5 kJ**

Table 3.2. c) Energy requirements of Great Skuas in 2009 on Hirta, St Kilda, Outer Hebrides.

2009	Individual / pair				Entire colony			
	Daily		Whole season		Daily		Whole season	
Breeding adults								
Maintenance and activity								
Bird specialists	1522.0	kJ bird^{-1}	182.1	x 10^{3} kJ pair^{-1}	237.4	x 10^{3} kJ	284	x 10^{5} kJ
Fish specialists	2477.6	kJ bird^{-1}	286.7	x 10^{3} kJ pair^{-1}	208.1	x 10^{3} kJ	240.8	x 10^{5} kJ
Generalists	2003.3	kJ bird^{-1}	234.8	x 10^{3} kJ pair^{-1}	216.4	x 10^{3} kJ	253.5	x 10^{5} kJ
Egg production costs								
Bird specialists	-		1933.6	kJ pair^{-1}	-		301.6	x 10^{3} kJ
Fish specialists	-		1933.6	kJ pair^{-1}	-		162.4	x 10^{3} kJ
Generalists	-		1933.6	kJ pair^{-1}	-		208.8	x 10^{3} kJ
Incubation costs	1061.8	kJ bird^{-1}	30793.4	kJ pair^{-1}	184.8	x 10^{3} kJ		
Non-breeding adults								
Maintenance and activity	2003.3	kJ bird^{-1}	248.4	x 10^{3} kJ bird^{-1}	106.2	x 10^{3} kJ	131.7	x 10^{5} kJ
Chicks								
Hatching to fledging								
Bird specialists	-		45722.9	kJ chick^{-1}	-		42.8	x 10^{5} kJ
Fish specialists	-		45722.9	kJ chick^{-1}	-		23.0	x 10^{5} kJ
Generalists	-		45722.9	kJ chick^{-1}	-		29.6	x 10^{5} kJ
Fledging to departure								
Bird specialists	1025	kJ fledgling^{-1}	18450	kJ fledgling^{-1}	67158	kJ	12.1	x 10^{5} kJ
Fish specialists	1025	kJ fledgling^{-1}	18450	kJ fledgling^{-1}	36162	kJ	6.5	x 10^{5} kJ
Generalists	1025	kJ fledgling^{-1}	18450	kJ fledgling^{-1}	46494	kJ	8.4	x 10^{5} kJ
Total colony energy requirement							**1039.2**	**x 10^{5} kJ**

Table 3.3. Sensitivity analysis for the bioenergetics model

	% change in output following 1% increase			Range of parameter extremes (%)	% change following parameter extremes					
	2007	2008	2009		2007		2008		2009	
Breeding pairs	0.89	0.80	0.87	± 10	± 8.95		± 8.03		± 8.73	
Non-breeding birds	0.17	0.20	0.13	+ 200, - 10	+ 20.97	-1.05	+ 39.29	-1.96	+ 25.34	-1.27
Pre-breeding period	0.22	0.30	0.27	± 50	± 11.00		± 11.10		± 11.09	
Incubation period	0.08	0.10	0.08	± 10	± 0.75		± 0.95		± 0.81	
Chick-rearing period	0.34	0.35	0.35	± 10	± 3.45		± 3.48		± 3.47	
Post-fledging period	0.16	0.16	0.16	+ 300, - 50	+ 47.34	-7.89	+ 47.37	-7.90	+ 47.69	-7.95
Adult BMR	0.87	0.88	0.88	± 10	± 8.67		± 8.82		± 8.76	
Adult FMR:BMR ratio										
Bird specialists	0.20	0.28	0.25	± 20	± 3.93		± 5.65		± 5.00	
Fish specialists	0.23	0.14	0.22	± 20	± 4.58		± 2.86		± 4.38	
Generalist	0.39	0.41	0.35	± 20	± 7.81		± 8.15		± 7.09	
Adult $FMR_{INCUBATION}$:BMR	0.05	0.05	0.05	± 20	± 1.02		± 0.98		± 1.03	
Mean clutch size	< 0.01	< 0.01	< 0.01	± 10	± 0.06		± 0.06		± 0.06	
Mean brood size at 20 days	0.10	0.09	0.09	± 10	± 1.01		± 0.87		± 0.92	
Mean brood size at fledging	0.03	0.02	0.03	± 10	± 0.26		± 0.25		± 0.26	
Mean fresh egg mass	< 0.01	< 0.01	< 0.01	± 10	± 0.06		± 0.06		± 0.06	
Mean egg energy density	< 0.01	< 0.01	< 0.01	± 10	± 0.06		± 0.06		± 0.06	
Egg synthesis efficiency	< 0.01	< 0.01	< 0.01	± 10	+ 0.07	-0.06	+ 0.07	-0.06	+ 0.07	-0.06
Food assimilation efficiency	-0.86	-0.88	-0.87	± 8	+ 7.59	-6.47	+ 7.73	-6.54	+ 7.67	-6.53
Mean chick fledging mass	0.10	0.09	0.09	± 10	± 1.03		± 0.88		± 0.93	
Energy requirement of fledglings	0.03	0.02	0.03	± 20	± 0.52		± 0.49		± 0.51	

Table 3.4. Different prey-types consumed and their energy content and wet meal mass, frequency in the diet and relative contribution to the energy requirements of adult breeders and young, and non-breeding Great Skuas on Hirta, St Kilda, Outer Hebrides.

				2007				**2008**				**2009**			
				Adult breeders and young		Non-breeders		Adult breeders and young		Non-breeders		Adult breeders and young		Non-breeders	
	Caloric content (kJ g^{-1})	Wet meal mass (g)	Meal energy content (kJ)	% all meals	% energy	% all meals	% energy	% all meals	% energy	% all meals	% energy	% all meals	% energy	% all meals	% energy
Leach's Storm-petrel	7.1	45	318.8	5.5	2.5	6.6	3.2	17.9	7.8	3.2	1.4	15.1	7.7	16	8.1
European Storm-petrel	7.1	25	177.1	1.8	0.5	0.5	0.1	2.8	0.7	3.8	0.9	8.9	2.5	5.3	1.5
Manx Shearwater	10.9	100	1090	2.1	3.3	2.2	3.7	1.1	1.6	11.1	16.3	2.1	3.7	0.8	1.4
Fulmar	10.9	100	1090	10.2	15.9	4.9	8.2	9.1	13.6	14	20.6	8.5	14.8	4.6	7.9
Kittiwake	10.9	100	1090	2.2	3.4	4.5	7.5	1.6	2.4	2.4	3.5	3.7	6.4	5.5	9.5
Auk	10.9	100	1090	28.4	44.3	32.4	54.4	36.6	54.6	21.1	31.0	18.8	32.8	24.2	41.8
Fish	5.2	100	520	38.7	28.8	25	20.0	26.6	15.7	36.3	25.4	37.9	31.5	34.9	28.8
Goose Barnacle	1.9	40	76	11.1	1.2	23.9	2.8	4.3	0.4	8.3	0.9	5	0.6	8.8	1.1

Table 3.5. Total mass (kg) of different prey-types consumed by adult breeders and young, and non-breeding Great Skuas on Hirta, St Kilda, Outer Hebrides.

	2007			**2008**			**2009**		
	Adult breeders and young	Non-breeders	**Total**	Adult breeders and young	Non-breeders	**Total**	Adult breeders and young	Non-breeders	**Total**
Leach's Storm-petrel	361.02	54.51	**415.53**	772.36	33.28	**805.64**	985.76	150.19	**1135.96**
European Storm-petrel	65.64	2.29	**67.93**	67.12	21.95	**89.07**	322.79	27.64	**350.42**
Manx Shearwater	306.32	40.38	**346.70**	105.47	256.51	**361.98**	304.65	16.69	**321.34**
Fulmar	1487.84	89.93	**1577.77**	872.56	323.52	**1196.08**	1233.11	95.96	**1329.07**
Kittiwake	320.91	82.59	**403.50**	153.42	55.46	**208.88**	536.77	114.73	**651.50**
Auk	4142.61	594.64	**4737.25**	3509.43	487.59	**3997.03**	2727.35	504.81	**3232.17**
Fish	5645.04	458.83	**6103.87**	2112.53	838.84	**2951.37**	5498.23	728.01	**6226.25**
Goose Barnacle	647.65	175.46	**823.10**	164.92	76.72	**241.64**	290.14	73.43	**363.57**
Total			**14475.65**			**9851.69**			**13610.27**

Table 3.6. Numbers of seabirds consumed by adult breeders and young, and non-breeding Great Skuas on Hirta, St Kilda, Outer Hebrides in 2007, 2008 and 2009.

		2007			**2008**			**2009**		
	Prey Mass (g)	Adult breeders and young	Non-breeders	**Total**	Adult breeders and young	Non-breeders	**Total**	Adult breeders and young	Non-breeders	**Total**
Leach's Storm-petrels	45	8023	1211	**9234**	17164	739	**17903**	21906	3338	**25243**
European Storm-petrels	25	2626	92	**2717**	2685	878	**3563**	12911	1106	**14017**
Manx Shearwaters	420	1122	148	**1270**	386	940	**1326**	1116	61	**1177**
Fulmars	800	2861	173	**3034**	1678	622	**2300**	2371	185	**2556**
Kittiwakes	375	1317	339	**1655**	629	228	**857**	2202	471	**2673**
Auks	615	10363	1488	**11851**	8779	1220	**9999**	6823	1263	**8085**
Total seabirds				**29761**			**35948**			**53752**
Total seabirds excluding storm-petrels				**17810**			**14482**			**14491**

Table 3.7. Estimated total numbers of seabirds consumed by Great Skuas at St Kilda (all islands), Outer Hebrides, in 1996 (using population size and diet parameters of Phillips et al. 1999) and in 2007, 2008 and 2009. n = estimated total numbers of Great Skua pairs nesting at St Kilda.

	1996	**2007**	**2008**	**2009**	**4-year mean**	**Change from 2007 to 2008**		**Change from 2008 to 2009**	
	n = 229	**n = 225**	**n = 175**	**n = 210**		(numbers)	(%)	(numbers)	(%)
Leach's Storm-petrel	13775	11699	26550	32965	21247	+14852	+127.0	+6415	+24.2
European Storm-petrel	6960	3524	4916	18568	8492	+1392	+39.5	+13652	+277.7
Manx Shearwater	223	1615	1521	1570	1232	-94	-5.8	+49	+3.3
Fulmar	737	3913	3146	3392	2797	-768	-19.6	+246	+7.8
Kittiwake	1078	2060	1174	3449	1940	-886	-43.0	+2275	+193.8
Auks	6370	15034	14422	10490	11579	-612	-4.1	-3932	-27.259

DISCUSSION

Model performance

Before discussing prey consumption and implications for seabird populations, it is important to consider the accuracy of models and potential sources of bias. Sensitivity analyses revealed the parameters for which potential inaccuracy had most effect on model outputs. Greatest effect on outputs resulted from potential inaccuracy in adult BMR values and associated adult BMR:FMR ratios, generally recognised as a source of uncertainty in these models (Adams et al. 1991, Phillips et al. 1999a, Votier et al. 2004b). Published values of adult BMR:FMR for most seabirds are multiples of between 3 and 4, so the value of 3.5 used for fish specialists was not unusual (Bryant & Furness 1995, Ellis & Gabrielsen 2002, Gabrielsen et al. 1991). Use of slightly lower values for bird specialists and generalists seemed entirely appropriate, as these were determined from the results of studies of Great Skuas to specifically define these two parameters (Votier et al. 2004b). Potential inaccuracy in food assimilation efficiency and in breeding population size estimates was also found to cause large effects on outputs. The value of 0.76 used for food assimilation efficiency was determined from controlled feeding trials of Great Skuas, so it was reasonable to assume this was accurate (Phillips et al. 1999b, Hilton et al. 2000, Votier et al. 2004b). Estimates of breeding population size were made during up to twenty nest surveys per season of all areas of suitable skua nesting habitat on Hirta, and for this island values are considered to be correct. Ideally, the study would have included simialar surveys of Great Skua breeding population sizes on Dùn, Soay and Boreray in each year. This was impossible, due to severe practical and weather constraints affecting landing on these islands. The most recent estimates of total numbers of breeding skua pairs on Dùn, Soay and Boreray had to be used, but potential effects of inaccuracy were likely to be limited because total numbers of breeders on these islands were small compared with Hirta.

Parameter extremes for numbers of non-breeders and the duration of the post-fledging period were set high for sensitivity analyses, since it is very difficult to assess the turn-over of different non-breeding individuals visiting St Kilda through the season or to define the exact date that skuas leave the islands after breeding. In agreement with counts made in 1996 by Phillips (1999b), numbers of non-breeders counted at the club site on Hirta did not greatly vary through the breeding seasons so, despite the possibility that entirely different individuals were seen at each count, use of a mean value is unlikely to be misrepresentative or a great source of error in model outputs. Post-fledging, skuas were seen on St Kilda until early October; however, numbers on the islands rapidly diminished after August and counts made in September and October suggested fewer than twenty birds were then normally present. The value of 18 days post-fledging period (Phillips et al. 1999b) seemed entirely reasonable to use in the model and representative of the behaviour of most of the population during this study.

Assessment of skua diet using pellets is sometimes prone to error, for example via misidentification of prey remains. Identification of prey-types was carried out with caution, strictly following the methods determined by Votier et al. (2001, 2003, 2004b, 2004c, 2005). Prey remains that could not be identified easily in the field were identified later by reference to lab specimens. It seems reasonable to assume methods of calculation of numbers of meals from numbers of pellets of different prey-types were realistic, as based on data collected from feeding trials using captive Great Skuas and subsequent validity testing (Votier et al. 2001, 2004a, 2004b, 2007). Nonetheless, there were still some reservations about using this data because the sample sizes for the feeding trials were mostly very small (Votier et al. 2001); however, the information was the best available and use of it was considered a worthwhile improvement on the predation modelling previously carried out for St Kilda (Phillips et al. 1999b). Overall, sources of greatest potential inaccuracy and bias, considered above, are very similar to those encountered in previous studies (Phillips et al. 1999b, Votier et al. 2004b). I did not find any additional or unexpected sources of error to contradict the conclusions of previous studies regarding performance of the models: that estimates of energy requirement and prey consumption from the models are reasonably accurate and valid (Phillips et al. 1999b, Votier et al. 2004b).

General consumption of fish, seabirds and goose barnacles

This study shows that, by mass, fish and auks are the most important prey for Great Skuas on Hirta, followed in decreasing order by fulmars, storm-petrels and shearwaters, goose barnacles, and kittiwakes. Relatively high incidence of Mackerel and Herring remains in pellets suggested fish prey was obtained mostly by kleptoparasitism, as these two species of fish are rarely captured directly by Great Skuas, whereas they are frequently caught by Gannets (Furness 1987, Mitchell et al. 2004). This inference is supported by observations at Boreray, the largest Northern Gannet colony in the UK, where in excess of one hundred skuas were frequently seen in all years robbing gannets returning to their nests with fish (Mitchell et al. 2004, Pers. Obs. 2007, 2008 & 2009). Although relatively minor, the quantity of goose barnacles consumed in each year was slightly unexpected, as on no occasion were skuas directly observed capturing and eating this prey-type, presumably mostly found on flotsam away from land.

Estimated numbers of seabirds consumed by Great Skuas at St Kilda in each year were substantial (Table 3.7). However, the scale of predation was not unprecedented, and was broadly similar to levels of predation found in other studies, for example at St Kilda, Shetland, Kerguelen, Hokkaido and Newfoundland (Watanuki 1986, Mougeot et al. 1998, Phillips et al. 1999b, Stenhouse et al. 2000, Votier et al. 2004c). Annual numbers of Leach’s Storm-petrels consumed were variable and surprisingly high (discussed below) but numbers of European Storm-petrels particularly so, relative to breeding population estimates of this species at St Kilda. Approximately 1,100 apparently occupied breeding sites of European Storm-petrel were found during the last complete survey (Mitchell 2004), but at least triple this number of individuals was estimated to have been eaten by skuas in every year of this study, and in 1996. The most recent estimate of total number of Manx Shearwaters breeding at St Kilda in 1999 / 2000 was approximately 10,000 individuals (Mitchell et al. 2004). Compared with this figure, and with numbers of storm-petrels eaten, numbers of Manx Shearwaters consumed were relatively low (4-year mean < 1300); although, cumulatively, total consumption would surpass 10,000 individuals in nine years.

It is difficult to assess the impacts of skua predation on seabird populations at St Kilda, since complete surveys of the breeding populations of seabirds are not possible every year, due to the large scale of the archipelago, its remoteness and difficult terrain, and the expense, manpower and good weather required. However, sample-plot surveys of breeding Guillemot and Kittiwake populations were carried out in 2009 and 2008 respectively, and indicated a 51% decline in Guillemot numbers between 2003 and 2009 and a 37% decline in Kittiwake numbers between 2006 and 2008 (Money 2008, NTS and JNCC unpublished data 2009). Such declines could possibly be due to predation of breeding adults by Great Skuas. However, in the case of Guillemots, it is very difficult to be certain of this because, with the exception of skulls and feet (found rarely), Guillemot remains found in pellets cannot be confidently differentiated from those of other auks. Although Great Skuas consumed extremely large numbers of auks in each year of this study, we do not know exactly how many were killed of each of the four species that breed on St Kilda. Relative to storm-petrels, Manx Shearwaters and Kittiwakes, total numbers of auks consumed each year were low (4-year mean ≈ 11500) in comparison with estimated total breeding population sizes (≈ 312,000 total individuals in 1999/2000, Mitchell et al. 2004). Numbers of non-breeding auks at the islands are unknown, but could quite easily number at least 100,000 individuals, additional to breeders and potentially available to skuas (Harris 1984, Cairns et al. 1990, Phillips et al. 2004). If auks were generally declining between 2003 and 2009 at St Kilda, then it is conceivable that increases in numbers of storm-petrels consumed by skuas in 2007, 2008 and 2009 could be a response to reduction in the availability of auks; this is also suggested perhaps by the diminishing numbers of auks consumed in each of these years. Future complete surveys of breeding Atlantic Puffins, Razorbills, Common Guillemots, Black Guillemots *Cepphus grylle* and Kittiwakes at St Kilda, with counts of apparently non-breeding individuals, would help to assess the likelihood of this possibility and how prey density dependent factors might have influenced the between-year variation in the numbers of different seabirds eaten estimated in this study.

Without results from such surveys, nor any complete surveys of storm-petrels at St Kilda other than just one for 'Seabird 2000' (when different islands where surveyed in different years: Dùn in 1999, Boreray and Soay in 2000, and Hirta in

1999-2000; Mitchell et al. 2004), it is extremely difficult to comment on the large variation in estimated numbers of seabirds eaten by skuas in years of this study, further than to say that this was due to variation in the relative proportions of different seabirds in the diet each year. Given the considerations above regarding model performance and accuracy we consider it extremely unlikely that measurement and calculation of the relative proportions of different seabirds in the diet of skuas each year was prone to error. However, taking Leach's Storm-petrel as an example, if the proportion of this prey-type had been determined inaccurately by up to 1% in each year, then estimates of total Leach's Storm-petrels consumed each year on Hirta would have been inaccurate to the following limits: 2007, consumption = 9234 ± 74 individuals (0.80% potential error); 2008, consumption = 17903 ± 183 individuals (1.02% potential error); 2009, consumption = 25243 ± 215 individuals (0.85% potential error). Potential error in the model output values is small in each year with such hypothetical inaccuracy in the input parameter. Overall, it seems extremely unlikely that year to year variation in estimates of numbers of Leach's Storm-petrel consumed is due to errors in estimation. Execution of a complete baseline survey of total numbers of Leach's Storm-petrels breeding at St Kilda in any one year was outside the scope of this study, but is extremely necessary, and would greatly help with assessment of how the breeding (and non-breeding) Leach's Storm-petrel population may fluctuate (see below).

In 2008, a total of 957 apparently occupied Kittiwake nest sites were recorded during a complete survey at St Kilda, yet an estimated 1174 Kittiwakes were consumed by skuas in that year. Given such a relatively small (and apparently declining) breeding population and yet relatively high predation pressure, Kittiwakes are surely under extreme threat as a breeding species at St Kilda and it is slightly surprising that a breeding population still exists (see also Phillips et al. 1999b). However, for this species as well as auks, we do not know the exact predation rate of breeders, the extent to which non-breeders and breeders from elsewhere may occur at St Kilda, the extent to which these individuals may be consumed by skuas, or the occurrence of Kittiwakes and auks at St Kilda outside their breeding seasons (April to July). Perhaps one possibility is that non-breeding Kittiwakes may occur at St Kilda more than is realised, have been heavily predated by skuas, and that this has lessened impacts of predation on the breeding population, which still survives at a much reduced and limited size (see discussion of this scenario in more detail below for Leach's Storm-petrels). The likelihood of this possibility can only be evaluated by regular surveys of the Kittiwake breeding population, surveys of apparently non-breeding individuals, and estimates of skua predation of Kittiwakes in future. Although greatest numbers occur between April and September, Northern Fulmars nest above ground and are present at St Kilda year round, so it is likely that this species is more available to skuas than other species with shorter breeding seasons (e.g. guillemots and Razorbills) or that nest in burrows (e.g. puffins and storm-petrels). However, relatively few fulmars were consumed by skuas compared with storm-petrels and auks (Table 3.7), and in comparison with estimated total numbers of fulmars at St Kilda: c.68,000 breeding pairs, plus additional non-breeders that likely number more than 102,000 individuals (Dunnet 1991, Phillips et al. 1999a, Mitchell et al. 2004). Fulmars however are larger, heavier and stronger than most other seabirds at St Kilda and can defend themselves by vomiting stomach oil, so perhaps it is less effort for skuas to kill auks and storm-petrels.

Predation of Leach's Storm-petrels

Leach's Storm-petrel consumption was considerable; comparable estimates are presented in Table 3.7 for the years of this study and 1996. Estimated numbers of Leach's Storm-petrels consumed in 2008 and 2009 were greater than in 1996, by factors of 1.9 and 2.4 respectively. Given the magnitude of these values, I first checked the methods and the validity of parameter estimates (see discussion above). Prey consumption estimates made for 1996 using the methods in this study were lower than estimates made by Phillips for 1996 and, overall, our methods seemed relatively conservative. Comparisons of our results with those of prey-consumption studies made elsewhere in the UK and abroad were made. Where breeding ranges of generalist predators such as gulls and skuas overlap with those of petrels, auks and kittiwakes, it is not unusual for predation rates to be impressively high (Nelson 1989, Mougeot et al. 1998, Brooke et al. 1999, Stenhouse & Montevecchi 1999, Weidinger 1998, Finey et al. 2001, Massaro et al. 2001, Davoren et al. 2002, Le Corré 2008). Results were relatively unexpected in the context of St Kilda, but similar annual predation of tens of thousands of Leach's Storm-petrels by gulls has been found on islands elsewhere, for example at Great Island, Newfoundland, and at Daikoku Island in north Japan (Stenhouse et al. 2000, Watanuki 1986).

Breeding Leach's Storm-petrels were surveyed on Dùn in 2006 and the population size was found to have not changed significantly since 2003 (Newson et al. 2008). In 2006 the population was estimated at 12,770 apparently occupied nest sites and appeared to be relatively stable (Newson et al. 2008). Given the very large numbers of Leach's Storm-petrels estimated during this study and in 1996 to have been consumed annually, this suggests annual predation by skuas is not solely of breeders on Dùn. Assuming population changes on Dùn between 1999 and 2003 and 2003 and 2006 are representative of changes in the breeding Leach's Storm-petrel population at St Kilda as a whole, and that the total population numbered 45,433 pairs in 1999, I calculated the theoretical mean annual losses of breeding individuals at St Kilda between 1999, 2003 and 2006 (Table 3.8; see below). Estimated mean values of annual losses of breeders (Table 3.8) are all lower than any value of estimated annual consumption of Leach's Storm-petrels found in years of this study and 1996 (Table 3.7, Phillips et al 1999a), and generally differences are considerable; for example, the differences between the estimated annual loss of breeders from 1999 to 2003 and the estimated numbers of Leach's Storm-petrels consumed in 2008 (difference = 15,646 individuals), 2009 (difference = 22,061 individuals), and the 4-year mean including 1996 (difference = 3,948 individuals). Such differences, as well the results from the two most recent population surveys, strongly imply that many 'additional' Leach's Storm-petrels may be present and predated at St Kilda each year that are not part of the breeding population. Leach's Storm-petrels typically have a protracted pre-breeding period, often amounting to five or more years, during which they visit potential breeding colonies and gradually begin courtship (Brooke 2004). At the largest colonies, non-breeding birds engaged in these behaviours can amount to tens of thousands of individuals during any one breeding season (Brooke 2004, Votier et al. 2005).

It seems reasonable to infer that breeding storm-petrels at St Kilda are not consistently predated and that very large numbers of non-breeders are also available and consumed. The question could even be posed: do Great Skuas kill *only* non-breeding Leach's Storm-petrels at St Kilda and therefore might changes in the breeding population be due to factors other than predation by skuas? Annual predation of tens of thousands of non-breeding petrels by skuas on sub-Antarctic islands such as Gough and Mayes Islands, and by gulls on islands in Newfoundland, has occurred apparently without greatly influencing petrel breeding population sizes (Furness 1987, Mougeot & Bretagnolle 2000, Robertson et al. 2006). Predation of many non-breeders but not breeders may be explained by discrepancies in their behaviour. Unlike breeders, non-breeding petrels often spend much time above ground on the surface of colonies, looking for nest sites and displaying to potential mates, which increases their predation-risk (Furness 1987). If tens of thousands of non-breeding Leach's Storm-petrels are consumed by skuas at St Kilda, then this raises questions as to the availability and source of these birds.

Availability of non-breeding Leach's Storm-petrels

Using estimates of Leach's Storm-petrel total population size (Stroud et al. 2001, Mitchell et al. 2004), age of first breeding (Brooke et al. 2004), productivity (Money et al. 2008 & Money unpublished data 2008), and survival (Brooke et al. 2004, Votier et al. 2005), it is possible to construct simple life tables to estimate numbers of non-breeders, of pre-breeding age, potentially available in different breeding locations and areas (Table 3.9, see below). At St Kilda, this illustrates that approximately 35,000 non-breeding individuals are potentially available in any one year, given a breeding population size of 45,433 pairs (Mitchell et al. 2004). This assumes that Leach's Storm-petrels at St Kilda are an entirely isolated population. However, it seems likely that the St Kilda Leach's Storm-petrel population is not isolated from others and is subject to immigration of young and non-breeding birds from other colonies. Currently, no morphological, vocal, behavioural or genetic evidence has been found to suggest that the St Kilda population is isolated from any other colony in the Atlantic. During the course of this study, under licence, 103 feather lice were sampled from 58 adult and juvenile Leach's Storm-petrels at St Kilda, in case evidence of host population isolation could be detected from parasites by a simple pilot study (Paterson et al. 1995, Proctor & Owens 2000, Proctor 2003). Upon identification, all samples were found to be the same species, *Halipeurus pelagicus*: an extremely common louse, widespread, previously found on at least fourteen different species of storm-petrel of 4 genera worldwide, including Leach’s Storm-petrels at Pacific Islands and at North Rona, Scotland (R. Palma pers. comm. 2010).

It is entirely conceivable that large numbers of wandering non-breeding Leach’s and European Storm-petrels visit St Kilda every year from other colonies, given ringing recoveries from these species which prove both can travel prodigious distances between countries, and even continents, relatively rapidly (Huntingdon et al. 1996, Wernham et al. 2002, Okill & Bolton 2005, Robb & Mullarney 2008). Wandering behaviour, predation, and occurrence at St Kilda, and elsewhere, of non-breeding storm-petrels ringed on Hirta during years of this study are discussed in Chapters 2 and 4. For a highly pelagic and aerial species such as Leach’s Storm-petrel, the sea is of course no barrier, and perhaps young individuals originating from the large breeding colonies in Iceland and Newfoundland prospect St Kilda for breeding opportunities very frequently (Brooke 2004, Mitchell et al. 2004). If non-breeding Leach’s Storm-petrels fledged at colonies in the North Atlantic, or even elsewhere in the world, annually travel far across oceans and prospect different islands for breeding opportunities, total numbers visiting St Kilda in any year could be huge and exceed total breeding numbers (see Table 3.9). A complete baseline survey of total numbers of Leach’s Storm-petrels breeding at St Kilda is crucial, and further studies using DNA markers (microsatellites and SNPs) would be extremely useful to try to determine the provenance of breeding and non-breeding Leach’s Storm-petrels at St Kilda and the extent of immigration from other colonies in the North Atlantic. In conclusion, Great Skuas annually consume very large numbers of Leach’s Storm-petrels at St Kilda; however, the latest survey of breeding Leach’s Storm-petrels showed the population to be stable and not significantly changing. It seems likely that thousands of non-breeding Leach’s Storm-petrels visit the archipelago, are available to skuas, and may originate from colonies far from the UK.

Table 3.8. Estimates of total Leach's Storm-petrel population sizes at St Kilda (all islands) in 1999, 2003 and 2006, rates of population decline, and estimates of annual losses of breeding individuals.

Total St Kilda breeding population estimate for 1999 [a] =	45433	apparently occupied burrows
Percentage decline from 1999 to 2003 [b] =	48	%
Estimated total breeding population in 2003 =	23625	apparently occupied burrows
Percentage decline from 2003 to 2006 [b] =	12	%
Estimated total breeding population in 2006 =	20790	apparently occupied burrows
Estimated annual loss in breeding population 1999 to 2003 (mean) =	10904	individuals per year
2003 to 2006 (mean) =	1890	individuals per year
1999 to 2006 (mean) =	7041	individuals per year

a Combined total for all islands of St Kilda, surveyed for 'Seabird 2000' in 1999/2000 (Mitchell et al. 2004)

b Percentage declines recorded in the (largest) population on Dùn (Newson et al. 2008)

Table 3.9. Minimum estimates of numbers of non-breeding Leach's Storm-petrels derived from estimated minimum numbers of pairs breeding at St Kilda (1999/2000), at colonies around the Atlantic, and at all colonies worldwide.

	St Kilda	**N. Atlantic**	**Atlantic**	**World**
Breeding pairs [a]	45433	4900000	4920000	9000000
Mean breeding success (eggs to fledged young) [b]	0.62	0.62	0.62	0.62
First-year survival rate [c]	0.37	0.37	0.37	0.37
Adult survival rate [d]	0.8	0.8	0.8	0.8
Mean age at first breeding [d]	6	6	6	6
Number of chicks	28168	3038000	3050400	5580000
Immatures in year 1	10422	1124060	1128648	2064600
Immatures in year 2	8338	899248	902918	1651680
Immatures in year 3	6670	719398	722335	1321344
Immatures in year 4	5336	575519	577868	1057075
Immatures in year 5	4269	460415	462294	845660
Total non-breeders, of pre-breeding age, in year 5	**35036**	**3778640**	**3794063**	**6940359**

a Stroud et al. 2001, Mitchell et al. 2004

b Money et al. 2008 & Money 2008 unpublished data (St Kilda)

c Votier et al. 2005

d Brooke 2004

ACKNOWLEDGEMENTS

WM was funded by NERC and NTS through a CASE studentship to Glasgow University. Special thanks to Ricardo Palma for identification of all feather lice and a wealth of useful information, to Tony Bicknell, Sjurdur Hammer, Elizabeth Mackley, Elizabeth Masden, Roger Riddington, Deryk Shaw and Steve Votier for help with fieldwork on St Kilda, and to staff of the radar base facility on Hirta for their technical assistance. I am extremely grateful to Uve and Julie Stoneman for supplying the results of the most recent JNCC and NTS auk and fulmar surveys at St Kilda, and to Susan Bain and Sarah Money for logistical support on Hirta and Dùn.

APPENDIX I

Appendix 3.1. Sensitivity analysis for the prey consumption model, showing percentage changes in output estimates for fish (kg), goose barnacles (kg), total birds consumed (numbers), and total different seabird types consumed (numbers of Leach’s Storm-petrels (LSP), European Storm-petrels (ESP), Manx Shearwaters, Fulmars, Kittiwakes and Auks) resulting from a 1% change in input parameters and probable extremes in input parameters.

2007	% change in input parameter	% change in fish mass	% change in goose barnacle mass	% change in bird numbers	LSP	ESP	Manx Shearwater	Fulmar	Kittiwake	Auk sp.
Fish caloric density	+ 1	-0.28	-0.27	-0.28	-0.28	-0.28	-0.28	-0.28	-0.27	-0.28
	+ 25	-6.58	-6.31	-6.50	-6.47	-6.66	-6.49	-6.61	-6.32	-6.48
	- 25	7.58	7.23	7.48	7.44	7.68	7.48	7.62	7.26	7.45
Goose barnacle caloric density	+ 1	-0.01	-0.02	-0.01	-0.01	-0.01	-0.01	-0.01	-0.02	-0.01
	+ 25	-0.33	-0.38	-0.35	-0.35	-0.31	-0.35	-0.32	-0.38	-0.35
	- 25	0.33	0.39	0.35	0.36	0.32	0.35	0.33	0.39	0.35
Bird caloric density	+ 1	-0.70	-0.71	-0.70	-0.70	-0.70	-0.70	-0.70	-0.71	-0.70
	+ 25	-14.98	-15.16	-15.04	-15.06	-14.93	-15.04	-14.96	-15.15	-15.05
	- 25	21.40	21.78	21.51	21.55	21.29	21.51	21.35	21.75	21.54
Fish meal mass	+ 1	0.72	-0.27	-0.28	-0.28	-0.28	-0.28	-0.28	-0.27	-0.28
	+ 30	19.88	-7.47	-7.69	-7.66	-7.88	-7.69	-7.83	-7.49	-7.67
	- 30	-23.53	8.81	9.11	9.06	9.36	9.11	9.29	8.84	9.08
Goose barnacle meal mass	+ 1	-0.01	0.98	-0.01	-0.01	-0.01	-0.01	-0.01	-0.02	-0.01
	+ 50	-0.66	48.85	-0.69	-0.70	-0.63	-0.69	-0.65	-0.76	-0.70
	- 25	0.33	-24.71	0.35	0.36	0.32	0.35	0.33	0.39	0.35
Large bird meal mass	+ 1	-0.67	-0.68	-0.08	-0.67	-0.67	0.32	0.32	0.31	0.32
	+ 30	-16.84	-17.03	-1.98	-16.92	-16.78	8.03	8.14	7.87	8.02
	- 30	25.40	25.85	2.99	25.58	25.26	-12.12	-12.26	-11.92	-12.10
Leach's Storm-petrel mass	+ 1	-0.03	-0.03	0.28	0.97	-0.03	-0.03	-0.03	-0.03	-0.03
	+ 10	-0.26	-0.27	2.84	9.71	-0.25	-0.26	-0.25	-0.27	-0.26
	- 10	0.26	0.27	-2.85	-9.76	0.25	0.26	0.26	0.27	0.26
European Storm-petrel mass	+ 1	0.00	0.00	0.09	0.00	1.00	0.00	0.00	0.00	0.00
	+ 10	-0.04	-0.04	0.87	-0.04	9.95	-0.04	-0.04	-0.04	-0.04
	- 10	0.04	0.04	-0.87	0.04	-9.96	0.04	0.04	0.04	0.04
Percentage carcass utilization	+ 1	-0.03	-0.03	-0.62	-0.03	-0.03	-1.02	-1.02	-1.02	-1.02
	+ 25	-0.74	-0.76	-12.63	-0.75	-0.74	-20.60	-20.59	-20.61	-20.60
	- 25	0.76	0.77	20.86	0.76	0.75	34.35	34.34	34.36	34.35
Proportion Leach’s Storm-petrel										
Breeding adults and young	+1	0.01	-0.03	0.21	0.90	-0.39	-0.30	-0.04	-0.26	0.00
	+ 50	0.58	-1.52	10.83	45.60	-19.83	-15.34	-2.13	-13.12	0.22
	- 50	-0.56	1.48	-10.48	-44.14	19.20	14.84	2.06	12.70	-0.21
Non-breeders	+1	0.00	0.00	0.03	0.14	-0.06	-0.05	-0.01	-0.03	0.00
	+ 50	0.02	0.03	1.67	6.98	-3.18	-2.30	-0.44	-1.75	0.08
	- 50	-0.02	-0.03	-1.60	-6.69	3.05	2.20	0.42	1.68	-0.08
Proportion European Storm-petrel										
Breeding adults and young	+1	0.01	-0.01	0.07	-0.03	0.98	-0.10	-0.01	-0.08	0.01
	+ 50	0.38	-0.33	3.70	-1.40	49.40	-4.79	-0.49	-4.09	0.26
	- 50	-0.38	0.32	-3.64	1.38	-48.67	4.72	0.48	4.03	-0.25
Non-breeders	+1	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00
	+ 50	0.01	0.02	0.13	-0.04	1.70	-0.16	-0.03	-0.12	0.01
	- 50	-0.01	-0.02	-0.13	0.04	-1.69	0.16	0.03	0.12	-0.01

Proportion Manx Shearwater										
Breeding adults and young	+1	-0.02	-0.03	-0.02	-0.06	-0.17	0.87	-0.04	-0.12	-0.02
	+ 50	-1.00	-1.60	-0.83	-2.96	-8.67	43.25	-2.03	-5.94	-1.07
	- 50	1.02	1.63	0.84	3.00	8.79	-43.86	2.06	6.02	1.08
Non-breeders	+1	0.00	-0.01	0.00	-0.01	-0.02	0.11	0.00	-0.02	0.00
	+ 50	-0.11	-0.31	-0.12	-0.41	-1.08	5.69	-0.23	-0.87	-0.16
	- 50	0.11	0.31	0.12	0.42	1.10	-5.78	0.23	0.88	0.16
Proportion Fulmar										
Breeding adults and young	+1	-0.10	-0.16	-0.18	-0.29	-0.85	-0.67	0.88	-0.58	-0.10
	+ 50	-4.73	-7.59	-8.72	-14.00	-41.01	-32.56	42.48	-28.09	-5.05
	- 50	5.07	8.13	9.34	14.98	43.90	34.86	-45.48	30.08	5.41
Non-breeders	+1	0.00	-0.01	-0.01	-0.02	-0.05	-0.04	0.05	-0.04	-0.01
	+ 50	-0.23	-0.68	-0.56	-0.91	-2.38	-2.02	2.70	-1.92	-0.35
	- 50	0.24	0.70	0.58	0.94	2.47	2.09	-2.80	1.99	0.36
Proportion Kittiwake										
Breeding adults and young	+1	-0.02	-0.03	-0.01	-0.06	-0.18	-0.15	-0.04	0.78	-0.02
	+ 50	-1.05	-1.68	-0.60	-3.10	-9.08	-7.21	-2.13	38.89	-1.12
	- 50	1.06	1.71	0.61	3.14	9.21	7.32	2.16	-39.47	1.14
Non-breeders	+1	0.00	-0.01	0.00	-0.02	-0.04	-0.04	-0.01	0.20	-0.01
	+ 50	-0.21	-0.62	-0.17	-0.84	-2.19	-1.86	-0.46	9.75	-0.32
	- 50	0.22	0.64	0.18	0.86	2.26	1.92	0.47	-10.07	0.33
Proportion auk sp.										
Breeding adults and young	+1	-0.27	-0.44	-0.41	-0.80	-2.36	-1.87	-0.55	-1.61	0.71
	+ 50	-12.49	-19.99	-17.74	-36.83	-96.62	-85.61	-25.34	-73.87	32.28
	- 50	15.06	24.15	22.66	44.53	130.46	103.58	30.62	89.38	-39.14
Non-breeders	+1	-0.03	-0.09	-0.06	-0.12	-0.32	-0.27	-0.07	-0.26	0.10
	+ 50	-1.44	-4.18	-1.80	-5.53	-3.38	-11.65	-3.02	-11.62	4.21
	- 50	1.78	5.14	3.49	6.93	18.13	15.40	3.80	14.61	-5.45
Proportion fish										
Breeding adults and young	+1	1.02	-0.31	-0.78	-0.79	-2.87	-2.24	-0.42	-1.92	-0.08
	+ 50	50.46	-17.80	-34.98	-42.35	-96.62	-88.35	-23.46	-79.53	-6.11
	- 50	-48.49	14.81	37.19	37.31	136.46	106.34	19.72	91.20	3.84
Non-breeders	+1	0.08	-0.02	-0.06	-0.06	-0.24	-0.18	-0.04	-0.15	0.00
	+ 50	4.13	-0.94	-2.46	-3.23	-3.38	-9.38	-1.96	-7.71	-0.30
	- 50	-3.89	0.81	3.03	2.98	11.53	8.73	1.81	7.14	0.24
Proportion goose barnacle										
Breeding adults and young	+1	0.06	0.87	-0.15	-0.16	-0.75	-0.57	-0.04	-0.49	0.05
	+ 50	3.38	46.21	-8.09	-8.20	-39.41	-30.16	-2.27	-25.70	2.51
	- 50	-3.03	-41.39	7.25	7.34	35.30	27.01	2.03	23.02	-2.25
Non-breeders	+1	0.01	0.27	-0.04	-0.03	-0.22	-0.15	-0.03	-0.10	0.02
	+ 50	0.48	15.18	-1.38	-2.02	-3.38	-8.67	-1.46	-5.97	1.02
	- 50	-0.39	-11.86	1.70	1.53	9.85	6.70	1.12	4.58	-0.83

2008 **(Appendix 3.1 continued)**	% change in input parameter	% change in fish mass	% change in goose barnacle mass	% change in bird numbers	LSP	ESP	Manx Shearwater	Fulmar	Kittiwake	Auk sp.
Fish caloric density	+ 1	-0.07	-0.21	-0.20	-0.19	-0.20	-0.23	-0.21	-0.21	-0.20
	+ 25	-1.70	-4.98	-4.70	-4.58	-4.88	-5.55	-4.91	-4.90	-4.69
	- 25	1.93	5.55	5.20	5.04	5.42	6.26	5.46	5.45	5.19
Goose barnacle caloric density	+ 1	0.09	0.22	0.19	0.17	0.20	0.27	0.21	0.21	0.19
	+ 25	-0.06	-0.14	-0.12	-0.12	-0.14	-0.18	-0.14	-0.14	-0.12
	- 25	0.18	0.43	0.38	0.35	0.41	0.55	0.42	0.42	0.37
Bird caloric density	+ 1	-0.36	-1.30	-1.32	-1.32	-1.31	-1.27	-1.31	-1.31	-1.32
	+ 25	-4.42	-16.39	-16.62	-16.73	-16.48	-15.91	-16.45	-16.45	-16.63
	- 25	6.42	24.40	24.91	25.14	24.59	23.36	24.53	24.54	24.92
Fish meal mass	+ 1	0.93	-0.21	-0.20	-0.19	-0.20	-0.23	-0.21	-0.21	-0.20
	+ 30	27.38	-5.92	-5.59	-5.44	-5.79	-6.59	-5.84	-5.83	-5.58
	- 30	-28.36	6.73	6.31	6.11	6.57	7.61	6.62	6.61	6.29
Goose barnacle meal mass	+ 1	0.00	0.99	0.00	0.00	-0.01	-0.01	-0.01	-0.01	0.00
	+ 50	-0.12	49.57	-0.25	-0.23	-0.27	-0.37	-0.28	-0.28	-0.25
	- 25	0.06	-24.89	0.12	0.12	0.14	0.18	0.14	0.14	0.12

Large bird meal mass	+ 1	-0.20	-0.71	-0.32	-0.72	-0.71	0.28	0.28	0.28	0.28
	+ 30	-5.02	-17.75	-7.84	-17.79	-17.76	7.01	6.92	6.92	6.89
	- 30	7.75	27.51	12.16	27.61	27.54	-10.84	-10.73	-10.73	-10.69
Leach's Storm-petrel mass	+ 1	0.00	-0.06	0.43	0.92	-0.06	-0.03	-0.06	-0.06	-0.07
	+ 10	-0.04	-0.57	4.25	9.18	-0.62	-0.32	-0.60	-0.61	-0.70
	- 10	0.04	0.58	-4.31	-9.32	0.63	0.33	0.61	0.61	0.71
European Storm-petrel mass	+ 1	0.00	-0.01	0.09	-0.01	0.99	-0.01	-0.01	-0.01	-0.01
	+ 10	-0.03	-0.08	0.92	-0.07	9.92	-0.08	-0.07	-0.07	-0.07
	- 10	0.03	0.08	-0.92	0.07	-9.93	0.08	0.07	0.07	0.07
Percentage carcass utilization	+ 1	-0.01	-0.07	-0.48	-0.08	-0.07	-1.03	-1.06	-1.06	-1.07
	+ 25	-0.16	-1.60	-9.80	-2.01	-1.70	-20.81	-21.33	-21.34	-21.51
	- 25	0.16	1.66	15.64	2.10	1.77	34.72	35.65	35.66	35.96
Proportion Leach’s Storm-petrel										
Breeding adults and young	+1	-0.07	-0.34	0.41	1.06	-0.61	-0.65	-0.13	-1.10	0.03
	+ 50	-3.44	-17.87	21.71	55.20	-32.34	-29.14	-7.08	-57.95	1.21
	- 50	3.44	16.02	-19.72	-50.25	29.11	30.83	6.23	52.31	-1.32
Non-breeders	+1	0.00	-0.01	0.02	0.04	-0.03	-0.02	0.00	-0.05	0.00
	+ 50	0.08	-0.60	0.82	2.12	-1.27	-0.83	-0.20	-2.31	-0.02
	- 50	-0.07	0.59	-0.81	-2.08	1.25	0.82	0.20	2.27	0.02
Proportion European Storm-petrel										
Breeding adults and young	+1	-0.01	-0.05	0.07	0.00	0.77	-0.10	-0.02	-0.17	0.01
	+ 50	-0.54	-2.45	3.55	-0.01	38.94	-5.03	-0.81	-8.46	0.49
	- 50	0.54	2.39	-3.47	0.01	-38.09	4.92	0.79	8.28	-0.48
Non-breeders	+1	0.00	-0.01	0.02	-0.01	0.25	-0.01	0.00	-0.05	0.00
	+ 50	0.21	-0.58	1.04	-0.29	12.88	-0.70	-0.13	-2.65	0.02
	- 50	-0.20	0.56	-1.01	0.29	-12.50	0.68	0.12	2.57	-0.02
Proportion Manx Shearwater										
Breeding adults and young	+1	0.00	-0.03	-0.01	-0.02	-0.05	0.29	-0.02	-0.08	-0.01
	+ 50	-0.21	-1.48	-0.37	-0.75	-2.37	14.42	-0.88	-3.85	-0.50
	- 50	0.21	1.49	0.37	0.76	2.39	-14.52	0.89	3.88	0.50
Non-breeders	+1	-0.03	-0.08	-0.01	-0.02	-0.12	0.66	-0.05	-0.19	-0.02
	+ 50	-1.56	-4.00	-0.58	-1.13	-5.80	31.84	-2.39	-9.37	-0.85
	- 50	1.67	4.29	0.62	1.21	6.22	-34.15	2.57	10.05	0.92
Proportion Fulmar										
Breeding adults and young	+1	-0.03	-0.25	-0.11	-0.13	-0.39	-0.36	0.69	-0.64	-0.08
	+ 50	-1.75	-11.95	-5.29	-6.09	-19.13	-17.55	33.39	-31.07	-3.99
	- 50	1.75	12.67	5.61	6.45	20.27	18.61	-35.38	32.93	4.23
Non-breeders	+1	-0.04	-0.10	-0.03	-0.03	-0.15	-0.19	0.25	-0.24	-0.02
	+ 50	-1.95	-5.00	-1.58	-1.41	-7.25	-9.10	11.81	-11.72	-1.07
	- 50	2.13	5.46	1.72	1.54	7.92	9.94	-12.90	12.80	1.17
Proportion Kittiwake										
Breeding adults and young	+1	-0.01	-0.04	-0.01	-0.02	-0.07	-0.06	-0.03	0.73	-0.01
	+ 50	-0.31	-2.15	-0.42	-1.10	-3.44	-3.16	-1.28	36.16	-0.72
	- 50	0.31	2.17	0.43	1.11	3.48	3.19	1.30	-36.54	0.73
Non-breeders	+1	-0.01	-0.02	0.00	-0.01	-0.03	-0.03	-0.01	0.26	0.00
	+ 50	-0.35	-0.89	-0.09	-0.25	-1.29	-1.62	-0.53	12.98	-0.19
	- 50	0.35	0.90	0.09	0.25	1.31	1.64	0.54	-13.17	0.19
Proportion auk sp.										
Breeding adults and young	+1	-0.14	-0.99	-0.37	-0.50	-1.58	-1.45	-0.59	-2.57	0.67
	+ 50	-7.03	-45.08	-16.78	-24.96	-71.02	-29.14	-27.92	-73.45	26.27
	- 50	7.03	56.01	21.14	28.54	89.63	82.27	33.38	145.61	-38.09
Non-breeders	+1	-0.06	-0.16	-0.04	-0.04	-0.23	-0.29	-0.09	-0.37	0.11
	+ 50	-2.88	-7.38	-1.91	-2.08	-10.70	-13.43	-4.41	-17.29	4.96
	- 50	3.29	8.43	2.18	2.38	12.22	15.35	5.04	19.75	-5.67
Proportion fish										
Breeding adults and young	+1	0.72	-0.56	-0.27	-0.14	-0.97	-0.99	-0.26	-1.70	-0.03
	+ 50	35.79	-29.31	-13.95	-8.28	-50.60	-29.14	-13.95	-87.52	-2.72
	- 50	-35.79	26.96	12.95	6.73	47.02	47.75	12.37	82.00	1.56
Non-breeders	+1	0.31	-0.17	-0.10	-0.06	-0.31	-0.27	-0.08	-0.55	-0.02
	+ 50	16.23	-8.89	-5.01	-3.31	-16.45	-13.98	-3.97	-28.79	-0.99
	- 50	-14.83	8.12	4.58	3.02	15.03	12.78	3.62	26.30	0.91

Proportion goose barnacle										
Breeding adults and young	+1	-0.02	0.71	-0.02	0.01	-0.13	-0.15	-0.02	-0.25	0.02
	+ 50	-0.83	36.25	-0.88	0.31	-6.87	-7.70	-1.00	-12.87	1.07
	- 50	0.83	-34.81	0.85	-0.30	6.60	7.39	0.96	12.35	-1.03
Non-breeders	+1	0.01	0.34	-0.01	-0.01	-0.06	-0.02	0.00	-0.11	0.00
	+ 50	0.66	17.79	-0.76	-0.63	-3.01	-1.08	-0.10	-5.75	0.13
	- 50	-0.61	-16.47	0.70	0.58	2.78	1.00	0.09	5.32	-0.12

2009 (**Appendix 3.1 continued**)	% change in input parameter	% change in fish mass	% change in goose barnacle mass	% change in bird numbers	LSP	ESP	Manx Shearwater	Fulmar	Kittiwake	Auk sp.
Fish caloric density	+ 1	-0.31	-0.31	-0.31	-0.31	-0.31	-0.31	-0.31	-0.31	-0.31
	+ 25	-7.23	-7.18	-7.23	-7.22	-7.25	-7.27	-7.26	-7.20	-7.21
	- 25	8.46	8.39	8.45	8.44	8.49	8.51	8.49	8.41	8.42
Goose barnacle caloric density	+ 1	-0.01	-0.01	-0.01	-0.01	-0.01	-0.01	-0.01	-0.01	-0.01
	+ 25	-0.16	-0.17	-0.17	-0.17	-0.16	-0.16	-0.16	-0.17	-0.17
	- 25	0.17	0.18	0.17	0.17	0.16	0.16	0.16	0.17	0.17
Bird caloric density	+ 1	-1.10	-1.10	-1.10	-1.10	-1.10	-1.10	-1.10	-1.10	-1.10
	+ 25	-14.56	-14.59	-14.56	-14.56	-14.54	-14.53	-14.54	-14.58	-14.57
	- 25	20.54	20.61	20.54	20.55	20.51	20.49	20.50	20.59	20.57
Fish meal mass	+ 1	0.69	-0.31	-0.31	-0.31	-0.31	-0.31	-0.31	-0.31	-0.31
	+ 30	18.88	-8.49	-8.55	-8.54	-8.58	-8.60	-8.58	-8.51	-8.53
	- 30	-22.78	10.24	10.32	10.31	10.36	10.39	10.37	10.26	10.28
Goose barnacle meal mass	+ 1	-0.01	0.99	-0.01	-0.01	-0.01	-0.01	-0.01	-0.01	-0.01
	+ 50	-0.33	49.48	-0.33	-0.33	-0.32	-0.31	-0.32	-0.34	-0.34
	- 25	0.17	-24.87	0.17	0.17	0.16	0.16	0.16	0.17	0.17
Large bird meal mass	+ 1	-0.58	-0.58	-0.31	-0.58	-0.58	0.42	0.42	0.42	0.42
	+ 30	-14.82	-14.88	-7.94	-14.83	-14.80	10.78	10.77	10.68	10.70
	- 30	21.07	21.19	11.28	21.09	21.02	-15.31	-15.29	-15.19	-15.21
Leach's Storm-petrel mass	+ 1	-0.08	-0.08	0.39	0.92	-0.08	-0.08	-0.08	-0.08	-0.08
	+ 10	-0.77	-0.77	3.89	9.15	-0.77	-0.77	-0.77	-0.77	-0.77
	- 10	0.78	0.78	-3.95	-9.30	0.78	0.78	0.78	0.78	0.78
European Storm-petrel mass	+ 1	-0.02	-0.02	0.24	-0.02	0.98	-0.02	-0.02	-0.02	-0.02
	+ 10	-0.24	-0.23	2.36	-0.24	9.73	-0.25	-0.24	-0.23	-0.24
	- 10	0.24	0.23	-2.37	0.24	-9.78	0.25	0.25	0.23	0.24
Percentage carcass utilization	+ 1	-0.10	-0.10	-0.37	-0.10	-0.10	-1.09	-1.09	-1.09	-1.09
	+ 25	-2.47	-2.46	-7.73	-2.47	-2.48	-21.99	-21.98	-21.97	-21.97
	- 25	2.60	2.59	11.82	2.60	2.61	36.82	36.81	36.79	36.79
Proportion Leach's Storm-petrel										
Breeding adults and young	+1	0.04	-0.26	0.37	0.96	-0.13	-0.88	-0.14	-0.40	-0.01
	+ 50	2.00	-13.92	19.29	50.24	-6.90	-46.27	-7.51	-20.94	-0.65
	- 50	-1.81	12.59	-17.45	-45.46	6.24	41.86	6.79	18.95	0.59
Non-breeders	+1	0.00	-0.03	0.06	0.15	-0.03	-0.14	-0.03	-0.05	0.00
	+ 50	0.17	-1.76	2.86	7.58	-1.40	-5.19	-1.53	-2.98	-0.01
	- 50	-0.22	1.48	-2.61	-6.94	1.22	6.79	1.34	2.60	-0.08
Proportion European Storm-petrel										
Breeding adults and young	+1	0.04	-0.14	0.24	0.00	1.00	-0.50	-0.06	-0.22	0.01
	+ 50	2.23	-7.17	12.32	-0.10	51.96	-25.87	-3.27	-11.24	0.63
	- 50	-2.06	6.60	-11.35	0.09	-47.87	23.84	3.01	10.35	-0.58
Non-breeders	+1	0.00	-0.01	0.02	0.00	0.08	-0.05	-0.01	-0.02	0.00
	+ 50	0.16	-0.39	1.02	0.01	4.24	-2.39	-0.43	-0.81	0.14
	- 50	-0.15	0.37	-0.97	-0.01	-4.04	2.28	0.41	0.77	-0.13
Proportion Manx Shearwater										
Breeding adults and young	+1	-0.02	-0.06	-0.02	-0.03	-0.05	0.93	-0.05	-0.08	-0.03
	+ 50	-1.03	-3.00	-0.80	-1.53	-2.26	46.30	-2.35	-3.95	-1.32
	- 50	1.05	3.04	0.81	1.55	2.29	-47.03	2.38	4.02	1.35
Non-breeders	+1	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00
	+ 50	-0.05	-0.19	-0.04	-0.09	-0.11	2.57	-0.11	-0.23	-0.08
	- 50	0.05	0.19	0.04	0.09	0.11	-2.59	0.11	0.24	0.08

Proportion Fulmar										
Breeding adults and young	+1	-0.08	-0.24	-0.11	-0.12	-0.18	-0.61	0.87	-0.32	-0.11
	+ 50	-4.09	-11.85	-5.38	-6.05	-8.92	-29.48	42.11	-15.64	-5.24
	- 50	4.35	12.62	5.73	6.45	9.51	31.41	-44.87	16.66	5.58
Non-breeders	+1	-0.01	-0.02	-0.01	-0.01	-0.01	-0.04	0.07	-0.03	-0.01
	+ 50	-0.30	-1.08	-0.41	-0.49	-0.61	-2.18	3.43	-1.33	-0.47
	- 50	0.31	1.12	0.42	0.51	0.63	2.26	-3.55	1.38	0.49
Proportion Kittiwake										
Breeding adults and young	+1	-0.04	-0.11	-0.02	-0.05	-0.08	-0.26	-0.08	0.80	-0.05
	+ 50	-1.81	-5.25	-1.15	-2.68	-3.95	-13.06	-4.11	39.51	-2.32
	- 50	1.86	5.39	1.19	2.75	4.06	13.43	4.22	-40.62	2.38
Non-breeders	+1	-0.01	-0.03	0.00	-0.01	-0.01	-0.05	-0.02	0.17	-0.01
	+ 50	-0.36	-1.29	-0.23	-0.58	-0.73	-2.60	-0.75	8.28	-0.56
	- 50	0.38	1.34	0.24	0.61	0.76	2.71	0.78	-8.62	0.58
Proportion auk sp.										
Breeding adults and young	+1	-0.19	-0.54	-0.21	-0.28	-0.41	-1.34	-0.42	-0.71	0.72
	+ 50	-8.71	-25.26	-9.90	-12.90	-19.03	-62.87	-19.78	-33.34	33.89
	- 50	10.03	29.07	11.39	14.85	21.90	72.35	22.76	38.37	-39.01
Non-breeders	+1	-0.03	-0.12	-0.04	-0.05	-0.07	-0.23	-0.07	-0.14	0.13
	+ 50	-1.64	-5.52	-1.76	-2.55	-3.08	-5.19	-3.14	-6.69	5.57
	- 50	1.79	6.34	2.07	2.87	3.60	12.83	3.69	7.81	-7.04
Proportion fish										
Breeding adults and young	+1	0.98	-0.78	-0.37	-0.21	-0.46	-2.34	-0.49	-1.11	-0.15
	+ 50	50.44	-41.47	-19.83	-12.18	-24.97	-94.81	-26.55	-59.23	-8.72
	- 50	-46.49	36.69	17.61	10.14	21.66	110.73	23.07	52.73	7.04
Non-breeders	+1	0.13	-0.09	-0.05	-0.03	-0.07	-0.32	-0.07	-0.14	-0.02
	+ 50	6.24	-5.40	-2.67	-1.81	-3.62	-5.19	-3.84	-7.77	-1.30
	- 50	-6.13	4.46	2.38	1.32	3.15	15.14	3.37	6.74	0.77
Proportion goose barnacle										
Breeding adults and young	+1	0.03	0.84	-0.01	0.01	-0.02	-0.27	-0.03	-0.11	0.01
	+ 50	1.66	43.31	-0.69	0.36	-1.18	-13.89	-1.37	-5.84	0.75
	- 50	-1.57	-40.98	0.65	-0.34	1.12	13.14	1.30	5.52	-0.71
Non-breeders	+1	0.01	0.22	0.00	0.00	-0.01	-0.08	-0.01	-0.02	0.01
	+ 50	0.37	11.63	-0.22	0.12	-0.58	-4.02	-0.67	-1.22	0.37
	- 50	-0.34	-10.56	0.20	-0.11	0.53	3.65	0.61	1.11	-0.33

Chapter 4

Behavioural adaptation in storm-petrels under high predation risk: avoidance of light but not predators

Submitted as:

Miles, W. T. S., Parsons, M., Luxmoore, R. & Furness, R. W. 2010. Behavioural adaptation in storm-petrels under high predation risk: avoidance of light but not predators. *Ibis*

ABSTRACT

Many species of bird recognise acoustic and visual cues given by their predators and have complex defence adaptations to reduce predation risk. Recognition of the threat posed by particular predatory species and specialised counter-predator behaviours are common. In this study we investigated anti-predation and predator recognition behaviours in a highly pelagic seabird, the Leach's Storm-petrel *Oceanodroma leucorhoa*, at a site where predation risk from Great Skuas *Stercorarius skua* is exceptionally high. Leach's Storm-petrels breed in burrows and come to land only at night. Counter-predator adaptations were investigated correlatively in relation to changing natural light levels at night, and experimentally in relation to nocturnal visual and acoustic signals from Great Skuas. We found that sexual vocal activity and colony attendance by Leach's Storm-petrels were finely attuned to between- and within-night changes in light conditions, were highest when nights were darkest, and that this behaviour likely reduced individuals' predation risk on land from Great Skuas via predator swamping. However, specific recognition of Great Skuas and specialised defence and avoidance behaviours were found entirely lacking. Skuas were frequently observed capturing Leach's Storm-petrels on the ground, in the air, at the darkest times of night and on nights with very little moonlight. Leach's Storm-petrels showed no specific counter-predator adaptations, were apparently entirely naïve to the threat posed by Great Skuas, and were captured extremely easily. Lack of specialised behavioural adaptations in Leach's Storm-petrels against Great Skuas may be because spatial overlap of breeding distributions of these two species appears to be a very rare and recent phenomenon.

INTRODUCTION

Natural attack and defence adaptations are abundant and diverse between predators and prey. Prey defences depend on detection and recognition of direct signals from predators, such as visual, auditory or olfactory stimuli, or indirect receipt of warnings from other individuals, for example hearing predator-specific alarm calls or seeing rapid aggregation of individuals under threat (Duckworth 1991, Lima 2009, Møller 2009, Nocera & Ratcliffe 2009). Among seabirds, reproductive behaviour is strongly influenced by predators (Nelson 1989, Mougeot & Bretagnolle 2000b, Votier et al. 2004b, Matias et al. 2009). The evolutionary origin of colonial nesting is ultimately unknown, but there is little doubt that this behaviour provides protection to most species of seabird via predator swamping (Walker & Elliott 2005, Fauchald 2009, Kirkman 2009). Ground-nesting seabirds are at risk of nest predation by land animals and therefore have frequently nested in areas inaccessible to most predators, such as on cliffs and remote islands (Camphuysen & de Vreeze 2005, Barrett 2008, Jovani 2008). When predation risk is high, skuas *Stercorariidae* and terns *Sternidae* use aggressive mobbing behaviour to deter terrestrial predators from their nesting territories, and some large petrels, for example the Northern Fulmar *Fulmarus glacialis*, can spit substantial quantities of foul-smelling stomach oil at predators to deter attack or egg robbery (Furness 1987, Olsen & Larsson 1995, Brook 2004).

The petrels (families *Procellariidae*, *Pelecanoididae* and *Hydrobatidae*) are all colonial and most species breed in the southern hemisphere on sub-Antarctic islands, where many are preyed on by skuas (Ryan & Moloney 1991, Moncorps et al. 1998, Weidinger 1998, Brooke 2004, Varpe & Tveraa 2005). Burrow-nesting and nocturnality on land are common to the breeding ecology of many Prions *Pachyptila*, Shearwaters *Puffinus* and Storm-petrels Hydrobatidae, and these adaptations are thought to have evolved in response to terrestrial predation pressure during daylight (Watanuki 1986, Brooke & Prince 1991, Mougeot & Bretagnolle 2000b, Brooke 2004). However, skuas in the southern hemisphere are adept at locating petrels at night, even those in burrows (Furness 1987, Brooke et al. 1999, Phillips et al. 2004). Field-based experiments have shown that Brown Skuas *Catharacta antarctica lönnbergi* breeding on Mayes and Verte Islands in the Kerguelen archipelago, for example recognize sexual vocalizations of breeding petrels and use these for precise location and selection of prey (Mougeot & Bretagnolle 2000a). Conversely, it has been shown that as a defence against skuas, petrels of those species most heavily depredated at Mayes and Verte Islands recognize the vocalizations made by skuas, and then become silent to avoid detection (Mougeot & Bretagnolle 2000a).

Predation of nocturnally active petrels by skuas is thought to be a very rare phenomenon in the northern Hemisphere, and extensive occurrence has only been observed on the islands of Hirta and Dùn, in the St Kilda archipelago. Here, Great Skuas *Stercorarius skua* have been found to be killing very large numbers of Leach's Storm-petrels *Oceanodroma leucorhoa,* a highly pelagic seabird active on land only at night (Phillips et al. 1999a, Brooke 2004, Votier et al. 2004). Using energy and prey consumption models with dietary analysis from skua pellets, it was estimated that in 1996 Great Skuas consumed c.14, 800 Leach's Storm-petrels at St Kilda (Phillips et al. 1999). Evidence of sustained high annual storm-petrel predation since 1996 was found during a pilot study made in 2004 of skua-petrel interactions at St Kilda (Votier et al. 2005). The situation at St Kilda presented a unique opportunity to study counter-predator adaptations used against skuas by their storm-petrel prey in the northern hemisphere. Furthermore, two aspects of the skua-petrel interactions at St Kilda led us to investigate this relationship in more detail: 1) Great Skua numbers have increased rapidly on the archipelago since the first pair nested there in 1963 (Phillips 1999b); 2) there is evidence that the numbers of Leach's Storm-petrels now being killed by skuas is unsustainable (Miles et al. 2010 in prep). Loss of breeding Leach's Storm-petrels using nest burrows on St Kilda was estimated to have been 49,000 individuals in the period from 1999 to 2006 (Newson et al. 2008). This situation contrasts with that on many sub-Antarctic islands, where skuas apparently have no major reductive effects on breeding numbers of petrels, despite taking breeding species as their main prey (Furness 1987, Mougeot et al. 1998).

In this paper we assess how finely attuned colony attendance and sexual vocal activity behaviours of Leach's Storm-petrels are to changing natural light conditions at night, and experimentally investigate how the species responds to signals from its main predator on St Kilda, the Great Skua. Given the high predation pressure from skuas at St Kilda, we predicted that Leach's Storm-petrels would exhibit behavioral defence adaptations against predation; including visiting land and vocalizing most at times of lowest light intensity, and specific predator recognition and avoidance behaviors against Great Skuas.

METHODS

Study areas

The study was conducted in the summers of 2007, 2008 and 2009 on Hirta, the largest island in the St Kilda archipelago (57°49′N, 08°35′W), Outer Hebrides. Most data came from Hirta, with the exception of observations of Great Skuas foraging at night on the smaller island of Dùn, made by viewing Dùn from Hirta across a 300m wide channel separating the islands. Unlike Hirta, access onto Dùn is severely limited by its very steep shoreline and frequently high sea swells, making landing impossible on most days. Great Skuas nest on the islands' flatter grassland, 5 pairs on Dùn (2009) and 174 pairs on Hirta (2009). Dùn holds the largest Leach's Storm-petrel breeding colony in Britain and Ireland, in total c. 12,700 apparently occupied nesting burrows (Newson *et al.* 2008). Habitat on the islands is primarily vegetated sea cliffs and maritime heath and grassland, grazed by Soay Sheep *Ovis aries*.

Vocal activity, colony attendance and light conditions

Leach's Storm-petrel vocal activity was assessed at the Carn Mór breeding colony on Hirta in 2007, between 10 June and 20 July when weather permitted safe access to the cliff for the night. To determine how the frequency of sexual vocalisations (chatter calls) of Leach's Storm-petrels and light levels changed through the night, number of chatter calls heard in one minute was counted in every half-hour period between 2330 and 0400hrs BST. Two counts were made for each period, at intervals of 15 minutes, and the average recorded. Simultaneously to counts, light level (luminance) was measured to 0.001 lux using a Megatron DL3 digital light meter (www.megatron.co.uk). All data were collected from one safe position on the cliff, from which we did not move during the hours of darkness. To see and determine the normal behaviour of Leach's Storm-petrels at their breeding colony at night and how they are captured by Great Skuas on Hirta, between measurements of chatter call rate, observations of petrel and skua behaviour were made using a Leica BIM 35 night scope image intensifier (uk.leica-camera.com). In the same way, observations were also made looking from the southern tip of Hirta across to Dùn in June and July in each year of the study on a total of twenty-one nights. On one night that observations were made of Dùn (24 June 2007), moonlight was bright (66% of face illuminated at midnight) and the sky was entirely clear except for very occasional large clouds moving rapidly eastwards. These conditions were unlike any others experienced during the study period, though not unprecedented at St Kilda (St Kilda Rangers' Reports 2005-2009). Occasional short-term reductions in light levels occurred throughout this night, when the islands were temporarily in the shadow of clouds. In response to these rapidly changing conditions, clearly visible even at dusk, with the aim to see if short-term changes in Leach's Storm-petrel vocal activity occurred with short-term changes in light conditions, at 0030hrs we began to measure light level and count Leach's Storm-petrel chatter calls per minute. This was repeated continuously at intervals of 15 minutes until 0300hrs. To assess how Leach's Storm-petrel colony attendance changed through the night, we used data collected prior to this study at Carn Mòr by a bird ringing team for the Joint Nature Conservation Committee. Leach's Storm-petrels were trapped using mist nets by a team of bird ringers working under British Trust for Ornithology (BTO) and Scottish Natural Heritage (SNH) Schedule 1 Species licences, on five nights in July 2004. Data recorded were the number of birds trapped within each half-hour period from 2330 to 0400hrs for all nights of trapping, and half-hourly mean numbers of birds ± S.E. for all nights are presented (JNCC 2004).

Experiments with acoustic predator signals

To investigate if Leach's Storm-petrels used auditory cues for predator detection, in 2008 we conducted playback experiments at night using recorded vocalisations of three test species: Great Skua (predator), Great Black-backed Gull *Larus marinus* (a predator at Canadian colonies of Leach's Storm-petrel and a very occasional predator of this species on St Kilda) and Northern Fulmar (control, resident breeder at St Kilda and not a predator of storm-petrels on St Kilda). For each test species, playback tracks only included calls known to be emitted at night by each species, from observations made at storm-petrel breeding colonies under natural conditions (Pers.

obs. pre-2008). Recorded tracks from at least five different individuals of each test species were used during the experiments. Playback experiments were carried out at the Carn Mòr Leach's Storm-petrel breeding colony between 6 and 18 July on nights we could safely access the cliff (seven in total). For any one test, Leach's Storm-petrel chatter calls were counted during one minute without any test vocalisation played (silent control), during one minute with a test vocalisation played (skua, gull or fulmar test playback), and again during one minute without any test vocalisation played (silent post-playback control). Each test lasted three minutes and was separated from any other by at least two minutes of silence. Following Mougeot and Bretagnolle (2000), if Leach's Storm-petrels recognised any of the test vocalisations, the expected response would be that sexual communication would temporarily cease and thus chatter call counts would be lower during playback and the silent post-playback period. The vocalisation used for playback in each test was selected in random sequence. For playback, we used an 8GB iPod Nano for track creation, storage and selection, coupled to a JBL *On Tour* 120-W speaker that was hidden in the cliff and could not be detected visually. Sound loudness was set so that to the human ear it matched that of natural calls and was kept constant. All tests were done by the same observer between 0130 and 0230hrs, the peak period for Leach's Storm-petrel vocalisations determined in 2007 (see results). All data were collected from one position on the cliff within the Leach's Storm-petrel colony.

Experiments with visual predator signals

To investigate if Leach's Storm-petrels recognised predators by sight and reacted to them, in 2008 and 2009 we conducted experiments using Great Skua and Northern Fulmar models (stationary dead specimens stuffed and posed). In 2008, experiments were carried out at Carn Mór between 1 and 30 July, on ten nights when the cliff was safely accessible. On all nights, one skua and one fulmar (control) model were each placed in a separate randomly selected position within the Leach's Storm-petrel colony area and observed using a Leica BIM 35 night scope. Frequency of different reactions to each model by Leach's Storm-petrels within one minute was then recorded for each model in turn (one directly after the other - observation order selected randomly), and this was repeated at 15-minute intervals from 0000 to 0330hrs on all nights. In accordance with apparent inter- and intra-specific Leach's

Storm-petrel behaviours seen in 2007 (see results) different reactions were categorically defined as: evasive flights, alarm call flights, non-contact mobbing dives, and aggressive contact attacks. During each night, observations of the models were also made outside of the standard one-minute count times (almost continuously), and behaviours of the storm-petrels and all interactions with the models then recorded on an ad hoc basis. Due to risks associated with the terrain, and to minimise effects of observer presence on the experiment, all data were collected by observation from one safe position on the cliff. This was selected to give good vantage of the Leach's Storm-petrel colony, but was also secluded and well hidden, outside of the storm-petrel breeding colony area, and always greater than 20m away from the test models.

In 2009, working under BTO and SNH licences, playback of recorded Leach's Storm-petrel chatter calls was used to simulate a new breeding colony on Hirta in an area where the species does not breed - Village Bay, more than 1km from any known Leach's Storm-petrel breeding sites. Such playback is a standard technique used by bird ringers to catch storm-petrels, and is thought mainly or exclusively to attract non-breeders (Redfern & Clarke 2001). For playback we used a camouflaged Sony *Personal Audio System 25-YN7L* stereo with a custom made looped track of calling Leach's Storm-petrels that included males and females. The 'playback colony' was switched on between 0000 and 0330hrs in the same place and at the same constant volume (matching that of natural calls) on ten nights, all within a period of exceptionally stable and calm weather between 21 June and 11 July. On each night, one 8m extra-fine meshed mist net was put up directly above the stereo in the same open position between 0000 and 0330hrs. All birds caught were fitted with a uniquely numbered metal BTO ring, to allow identification of any individuals caught more than once. The birds were measured, and then quickly released. Due to deliberate positioning of the stereo between a building and two steep hillsides, storm-petrels could only approach the playback colony from one direction, from the sea. On five randomly selected nights of the study, a pair of Great Skua models was positioned 2m apart and 5m away from the stereo in the direction of the sea. Any Leach's Storm-petrels approaching the playback colony on these nights, thus encountered the skuas before reaching the "colony" location (and mist net). This design aimed to test if Leach's Storm-petrels recognised the skuas and took evasive action in response to encountering them, and if therefore fewer were caught on nights when skuas were present. Weather was monitored using site-specific Met Office data for Village Bay, kindly made available by the MoD St Kilda Radar Base facility on Hirta. Throughout the entire study period conditions remained extremely stable, with low wind speeds (0 to 2 knots), wind direction at 140 degrees, temperature at approximately 12 ^{o}C on every night, complete cloud cover, and only very occasional rainfall (light drizzle on two nights, all others completely dry). Additional to aiding the investigation of skua effects, these conditions meant a relatively ‘controlled’ assessment could be made of effects on Leach’s storm-petrel colony attendance of cloud-base height and moon phase. Both of these variables changed frequently during the study period, unlike others, and are of particular interest due to their potential to affect light levels at night, given the sensitivity to this of Leach’s Storm-petrels (e.g. Harris 1974, Watanuki 1986, Brooke 2004). Nightly percentage of the moon’s face illuminated (moon phase) was obtained for Hirta from the U.S. Naval Meteorology and Oceanography Command (www.usno.navy.mil [Accessed January 2010]).

Statistical analyses

Analyses were performed using R version 2.10.1. Frequency distributions of Leach’s Storm-petrel vocal activity and colony attendance during nights in 2007 were analysed using Chi-squared tests for homogeneity. Spearman’s rank tests were used to investigate correlation between vocalisation frequencies and light level. Effects of playback of predator and control vocalisations on Leach’s Storm-petrel chatter call counts in 2008 were examined using a generalised linear model with a Poisson error distribution and log link function. Call count was treated as the dependent variable, with playback treatment (categories: silent control, test playback, silent post-playback control), date, time and individual track included as fixed effects. Playback test species were each modelled separately. A generalised linear mixed model with a Poisson error distribution and log link function was used to examine mist-netted Leach’s Storm-petrel nightly count data from 2009, in relation to skua presence, cloud-base height, moon phase (fixed effects), wind speed and rainfall (random effects).

RESULTS

Colony activity, light levels and cloud conditions

Leach's Storm-petrel chatter call activity was found to vary significantly through nights in 2007 ($\chi^2_6 = 36.76$, $P<0.01$); with greatest calling activity recorded between 0130 and 0300 and peaking between 0130 and 0200 (Figure 4.1). There was a significant negative correlation between chatter call activity and light level (Spearman's rank correlation coefficient = -0.787, $P<0.05$), with peak vocal activity occurring during the darkest period of the night (Figure 4.1). Numbers of Leach's Storm-petrels mist netted in 2004 also varied significantly through the night ($\chi^2_6 = 13.41$, $P<0.05$); with most caught between 0130 and 0300 and the catch rate peak between 0200 and 0230 (Figure 4.2). Light levels were not recorded by the ringing team in 2004, but the temporal pattern of colony attendance was similar to that of vocal activity seen in 2007. Overall, peak calling activity and colony attendance occurred between 0130 and 0230 during the darkest periods of nights (Figure 4.1 & 4.2). On the 24th June 2007, when occasional rapid short-term changes in cloud cover occurred during an otherwise clear night, highest Leach's Storm-petrel chatter call activity was recorded at 0215hrs. At this particular time, light level was exceptionally low due to temporary cloud cover, not present at any other time that data were recorded on that night (Figure 4.3).

Night-time observations of Leach's Storm-petrel activity at the breeding colonies at Carn Mór and on Dùn resulted in very frequent observations of two land-based behaviours. The normal appearance of the colonies at night was of very many storm-petrels, at peak times on Dùn several thousand, flying within the airspace close to the ground. However, birds were often seen to land and then either 1) quickly disappear underground, or 2) shuffle extensively across the colony surface, making frequent stops, wing flaps, and physical contact with other grounded individuals. Defensive and presumably sexual aggressive intra-specific behaviours were seen and heard, including: aggressive chasing on land and in the air by one individual directed at another, evasive flights away from an aggressor, alarm calling in response to an aggressor (invariably on land first, then in flight), aggressive attacks making physical contact on land or in the air, and repeated non-contact dives by one or more storm-petrels (apparent mobbing of an aggressor by up to ten individuals). On one night on

Dùn, the last behaviour was seen apparently directed at a hunting Great Skua by at least eight Leach's Storm-petrels (0035-0055, 23 July 2007). This, however, was the only example witnessed of behavioural interaction between Leach's Storm-petrels and any other species.

The number of Leach's Storm-petrels trapped per night during experiments to test visual predator signals in 2009 was influenced significantly by the percentage of the moon's face illuminated at night (with fewer birds when more of the moon was illuminated, GLMM: $z = -2.061$, $P<0.05$), and highly significantly by cloud-base height at night (with fewer birds when cloud base higher, GLMM: $z = -2.582$, $P<0.01$), with no interactions. Figure 4.4a shows the inverse relationship detected between cloud-base height and number of Leach's Storm-petrels caught during our study. More Leach's Storm-petrels were trapped on nights close to the new moon than were on nights when the moon was close to full illumination (Figure 4.4b).

Response to predator signals

Throughout experiments using skua and fulmar models in 2008, no evidence was found that Leach's Storm-petrels recognised or responded to visual predator signals. During 300 systematic observation periods, on no occasion was any reaction by a Leach's Storm-petrel observed to either the Great Skua or Northern Fulmar model, nor was any response seen during ad hoc observations at the Carn Mór breeding colony, during a total of thirty hours observation outside the systematic experimental periods on twelve nights. Normal behaviour of Leach's Storm-petrels was observed continuing as usual during the experiments, with apparent complete disregard for both models, and often at very close range to the skua (e.g. Figure 4.6).

No differences were found in 2008 between Leach's Storm-petrel chatter call counts made before, during and after playback of predator and control test species vocalisations, for any species tested and for any vocalisations of different individuals of the species tested (Figure 4.5); playback was consistently found not to influence call rate (GLM: Great Skua playback, $z = 0.792$, N.S., Great Black-backed Gull playback, $z = -0.555$, N.S., Northern Fulmar playback, $z = 0.577$, N.S.).

In 2009, numbers of Leach’s storm-petrels caught at the artificial “colony” site did not significantly differ between nights when skua models were present and absent (Figure 4.7); the presence of a pair of skuas located at an artificial Leach’s Storm-petrel “breeding colony”, on the only access route, was found to have no influence on the number of Leach’s Storm-petrels trapped per night visiting the colony (GLMM: $z = 0.281$, N.S.).

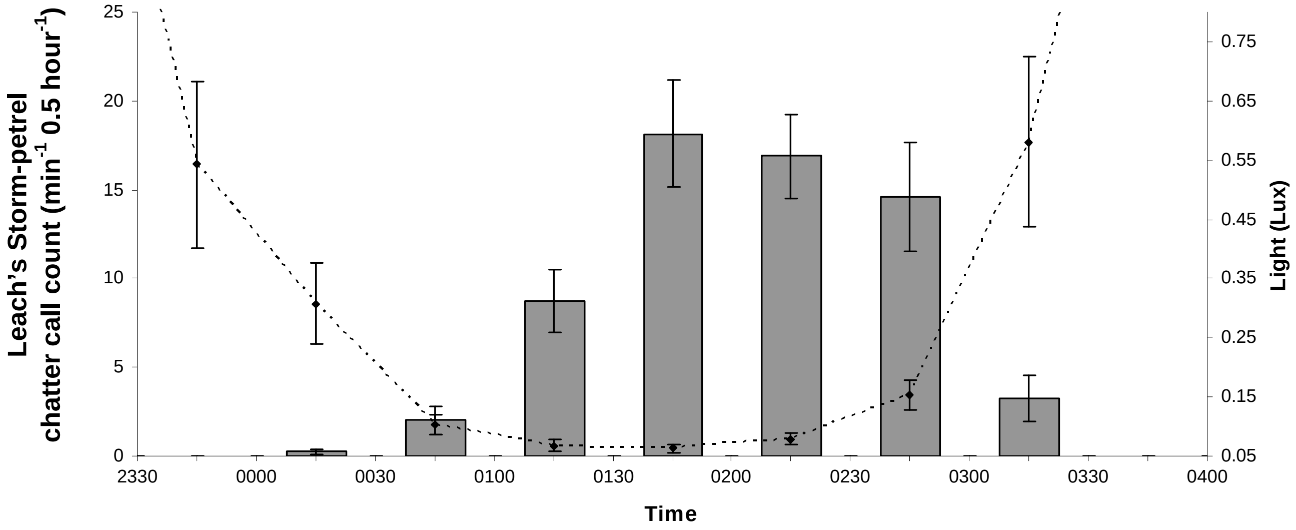


Figure 4.1. Frequency distribution of Leach's Storm-petrel chatter calls heard in 1 minute (bars, mean ± S.E.) and light level recorded simultaneously to counts (line, mean ± S.E.), within every half hour period from 2330 to 0400 on four nights in June and July 2007. Data were collected on the Leach's Storm-petrel breeding colony at Carn Mór on Hirta, St Kilda, Outer Hebrides.

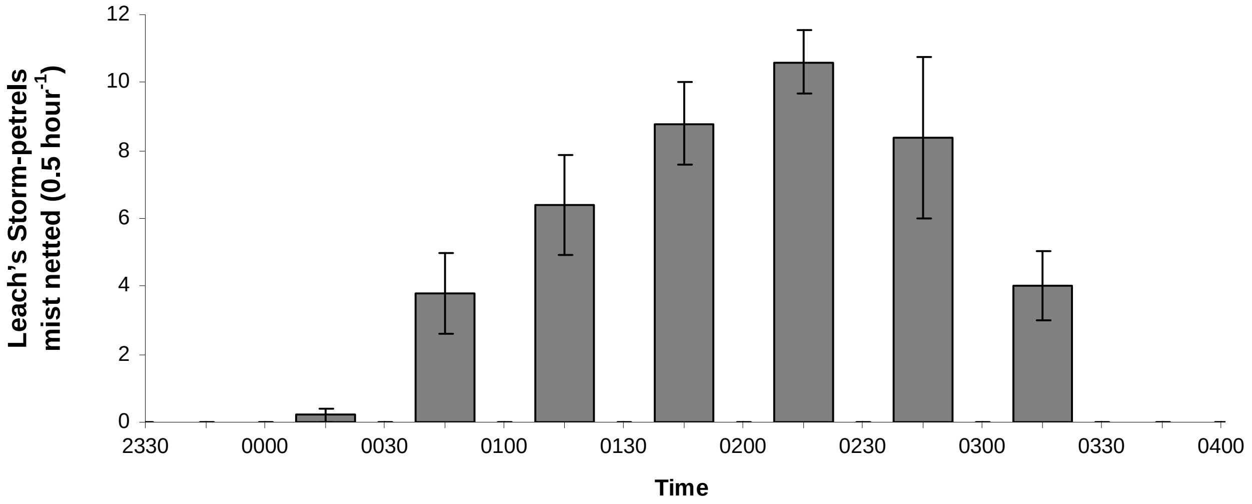


Figure 4.2. Frequency distribution of Leach's Storm-petrels mist netted (mean ± S.E.) in every half hour period between 2330 and 0400 on 5 nights in July 2004. Data were collected on the Leach's Storm-petrel breeding colony at Carn Mór on Hirta, St Kilda, Outer Hebrides (JNCC 2004).

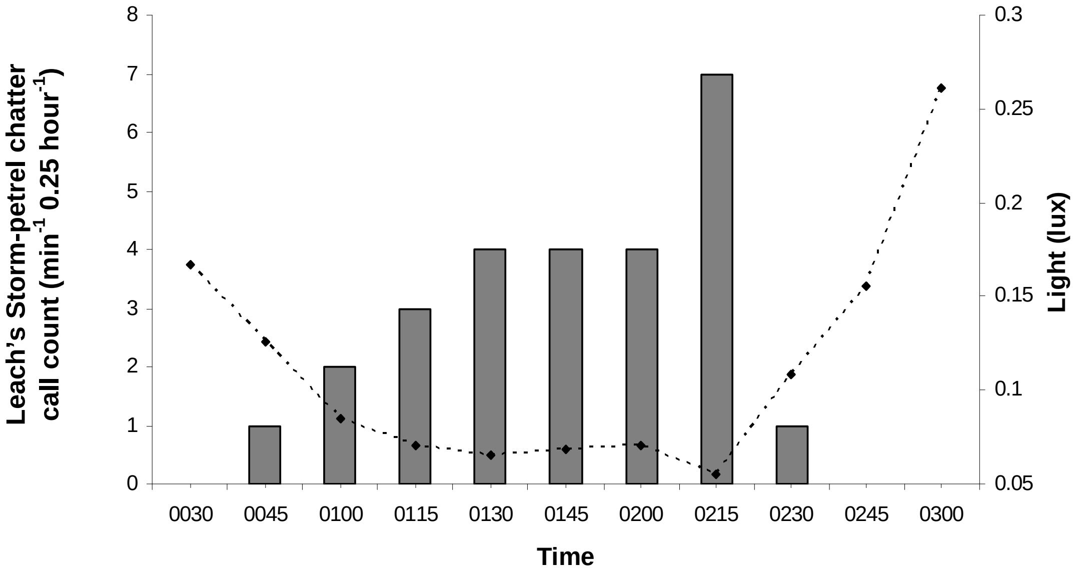
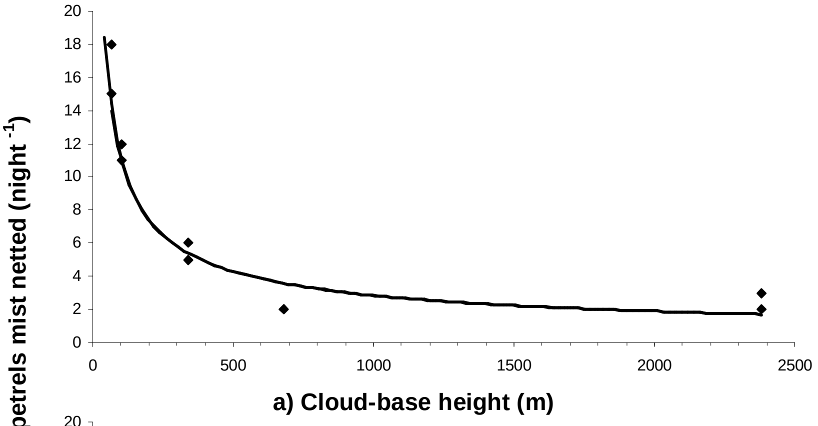
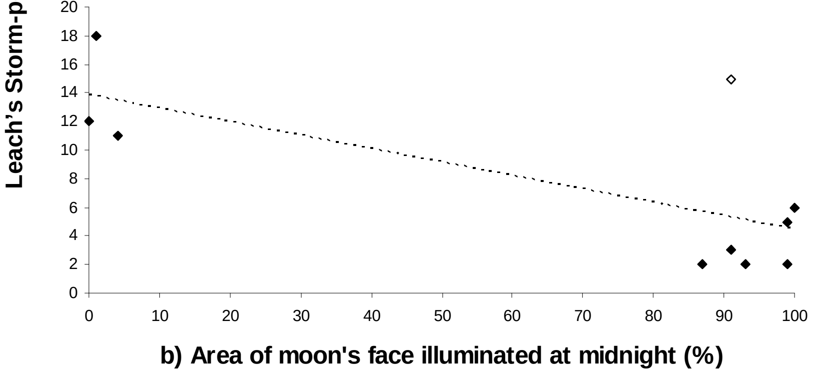


Figure 4.3. Frequency distribution of Leach's Storm-petrel chatter calls heard in 1 minute (bars) and light level, recorded at 15-minute intervals from 0030 to 0300 on 24 June 2007, during conditions of entirely clear sky except for occasional fast-moving very large clouds. The relatively very low light level recorded at 0215 was due to the islands temporarily being in the shadow of a cloud, unlike at all other times data were collected that night.



a) Cloud-base height (m)



b) Area of moon's face illuminated at midnight (%)

Figure 4.4. Numbers of Leach's Storm-petrels caught in a mist net per night during variable conditions of cloud-base height and moonlight (daily lunar phase) on ten nights between 21 June and 11 July 2009 in Village Bay on Hirta, St Kilda, Outer Hebrides. The obvious anomalous point (open diamond) represents a night when a high percentage of the moon's face was illuminated (91%) but on which cloud-base height was relatively very low (68m). This may represent an occasion when reductive effects of high moonlight level on numbers of Leach's Storm-petrels attending the colony were cancelled by a particularly thick cloud layer blocking light from the moon.

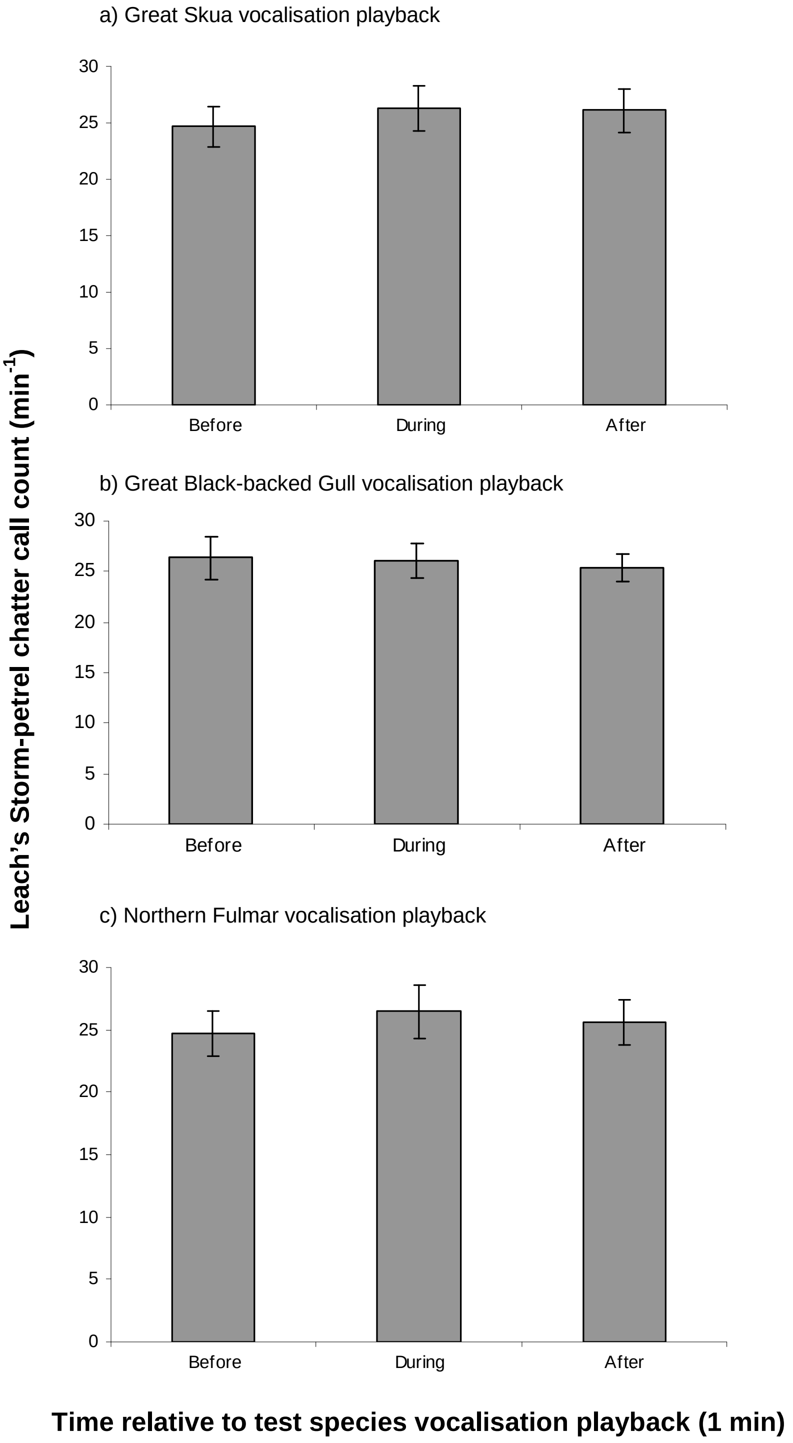


Figure 4.5. Leach's Storm-petrel chatter call counts (mean ± S.E.) in one minute before, during, and after one-minute playback of vocalisations of Great Skua (storm-petrel predator), Great Black-backed Gull (storm-petrel predator), and Northern Fulmar (control, not a storm-petrel predator on St Kilda). Data were collected between 0130 and 0230 on ten nights between 6 and 18 July 2008 at the Leach's Storm-petrel breeding colony at Carn Mór on Hirta, St Kilda, Outer Hebrides.

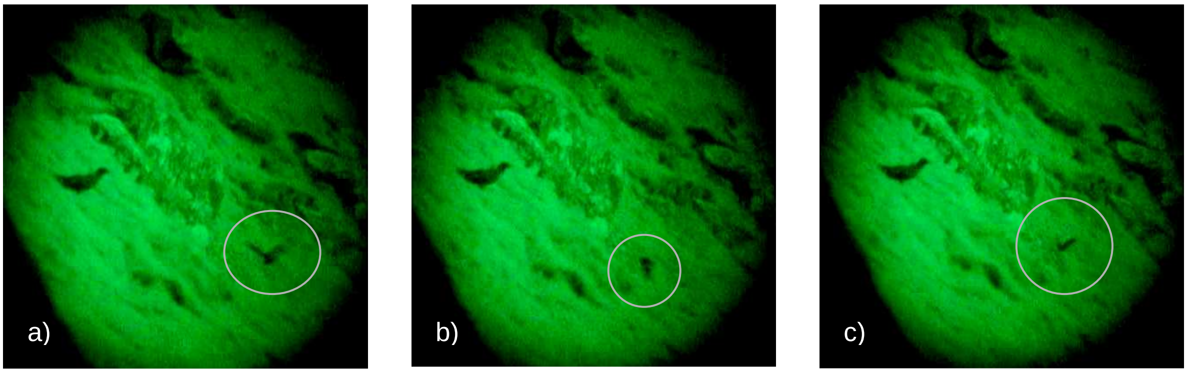


Figure 4.6. Stills from video footage filmed through a Leica BIM 35 night scope using a Samsung NV3 digital camera. This series shows a Leach's Storm-petrel (circled) flying towards a Great Skua test model (photograph a), landing directly in front of the skua at less than 3m range from it (photograph b), and moving towards the skua on foot while investigating the breeding colony's surface topography, with occasional wing flaps while on land (photograph c). Such behaviour by Leach's Storm-petrels was seen very regularly, was apparently quite normal and, in this case and all others witnessed, did not appear to be influenced in any way by the presence of a skua. On no occasion were Leach's Storm-petrels seen to react to the skua model; it was apparently ignored entirely. This was quite unlike the reactions of Great Skuas to the skua model, which included: calling at it, attacking it, and on one occasion trying to copulate with it. The control model (Northern Fulmar) was also recognised and attacked by Great Skuas. The above sequence was recorded on 18 July 2008, at the Leach's Storm-petrel breeding colony on the cliffs at Carn Mór on Hirta, St Kilda, Outer Hebrides.

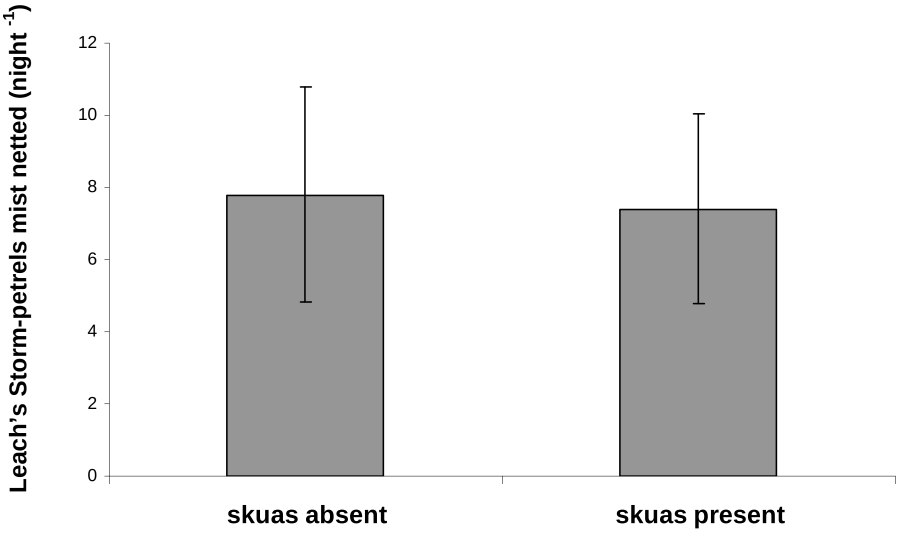


Figure 4.7. Numbers of Leach's Storm-petrels caught in a mist net per night (mean ± S.E.) at a simulated breeding colony when a pair of Great Skuas (models) absent and when present. The experiment was conducted on ten nights between 21 June and 11 July 2009 in Village Bay on Hirta, an area with no known breeding Leach's Storm-petrels and more than 1km away from any known breeding colonies, St Kilda, Outer Hebrides.

DISCUSSION

Light avoidance and behaviour of storm-petrels at the colony

Leach's Storm-petrel vocal activity and colony attendance were finely attuned to light levels at night, being higher at times when light conditions within-nights were darker. Also, between-night colony attendance was higher on darker nights; more birds were mist netted on nights with low moonlight. Similarly, when cloud base height was low and conditions very heavily overcast so that moonlight, late evening and early morning sunlight levels were much reduced, greater numbers of Leach's Storm-petrels were caught. This general pattern was also true during the one night when cloud conditions were observed shifting rapidly throughout the period from dusk until dawn; a short-term increase in Leach's Storm-petrel vocal activity occurred during a short-term drop in light levels when the islands were temporarily in the shadow of cloud. Overall, there was much evidence that Leach's Storm-petrel colony attendance and vocal behaviour on land are highly attuned to the degree of darkness at night, very closely track within-night changes and between-night differences in light levels, and that extreme light avoidance on land is characteristic of the species at St Kilda.

Results suggested that low cloud base height positively affects Leach's Storm-petrel colony attendance and that this may override negative effects caused by high moonlight levels (see Figure 4.4 legend and anomalous data point). This would make perfect sense if light effects on Leach's Storm-petrel colony attendance, from the moon in this case, are reduced in proportion to the presence of cloud. It was slightly surprising to find that colony attendance was significantly influenced by moonlight during the study in 2009, given that cloud cover was complete throughout all nights. However, moonlight effects on juvenile Leach's Storm-petrels attracted to artificial lights at St Kilda in the autumn of 2005 to 2009 occurred independently of within- and between-year weather effects, including cloud cover and cloud base height (Miles et al. 2010, St Kilda Warden's Reports 2005-2009). Further study of interactions between different cloud conditions (base height, density and layer depth), dusk to dawn light levels (considering both moon and sun), and petrel colony attendance, with larger sample sizes, would be very useful.

Data from tape luring may be representative mostly of non-breeding birds. There is evidence that a very high proportion of European Storm-petrels *Hydrobates pelagicus* attracted to tape lures are failed breeders and pre-breeding birds, and this may also be true for Leach's Storm-petrels (Furness & Baillie 1980, Fowler et al. 1982, Fowler & Okill 1988, Okill & Bolton 2005). Examination of brood-patches suggested most Leach's Storm-petrels that we caught using tape lures were probably non-breeders, as most had feathering across the brood patch area, rather than the region being bare of feathers and highly vascularised as is more typical of breeding birds (Furness & Baillie 1980). Data of within-night vocal activity and colony attendance of Leach's Storm-petrels may also be more representative of non-breeders than breeders, since calling frequency and time duration spent above ground at the breeding colonies have been found to be higher for non-breeding petrels than breeders (Watanuki 1986, McNeil et al. 1993, Mougeot & Bretagnolle 2000b, Brooke 2004). Unlike many small petrel species, for example Blue Petrel *Halobaena caerulea* and Thin-billed Prions *Pachyptila belcheri* (Mougeout & Bretagnolle 2000b), in June and July it is extremely difficult to determine non-breeding from breeding Leach's Storm-petrels using biometric measurements or plumage characters (Baker 1993, Miles 2010). Comparison of our observations using a night scope with studies made of the breeding behaviour of petrel species for which breeding status can be determined, suggests it is very likely that Leach's Storm-petrels seen to land and disappear quickly underground were breeders returning to their nest burrow, but birds seen remaining for relatively prolonged periods on the colony's surface were non-breeders investigating potential nest sites and calling and displaying to potential mates (Bretagnolle 2000b, Brooke 2004). Leach's Storm-petrels engaged in nuptial behaviours above and on the surface of the colony (almost certainly non-breeding birds) are apparently at far greater predation risk from skuas than those that disappear quickly underground (most likely breeding birds); an observation corroborated by other behavioural studies of breeding and non-breeding petrels (Storey 1984, Watanuki 1986, Bretagnolle 1990, McNeil et al. 1993, Brooke 2004). It is possible that petrels that disappear into burrows quickly are birds that have learned to recognise the threat posed by predators on the surface of the colonies and to avoid them by quickly going underground. This situation may exist at St Kilda, although the possibility that quick disappearance into a burrow is driven not by predator avoidance but by the need for breeding adults to get to their chick and to feed it as soon as possible is perhaps more likely, as this would be typical behaviour of breeding birds returning with food from a foraging trip to their young at the nest.

Great Skuas seen hunting on the Dùn and Carn Mòr storm-petrel colonies were most frequently observed foraging by running across the colonies' surfaces to capture petrels on land, which were clumsy and slow-moving and very easily intercepted (>100 sightings, Pers. obs. 2007, 2008 & 2009). Skua hunting activity was seen at all times of night, including the darkest periods between 0130 and 0230, and on nights close to the new moon (Pers. obs. 2007, 2008 & 2009). Capture of Leach's Storm-petrels in flight by skuas was seen less regularly (c.20 sightings, Pers. obs. 2007, 2008 & 2009). The occurrence of this capture technique was surprising, given that light levels sometimes were extremely low, aerial pursuit and prey capture is dependent on visual cues, and it has been suggested from studies made in the sub-Antarctic that these are of little use for skuas foraging for petrels at night (Schmidt-Nielsen 1997, Mougeot & Bretagnolle 2000a).

The sensitivity to darkness shown by Leach's Storm-petrels at St Kilda, in particular fewer birds on land when moonlight was brighter, was in total agreement with the behaviour of the species at Daikoku Island, Hokkaido (Watanuki 1986) and, for example, that of Blue Petrels and Thin-billed Prions at Kerguelen archipelago (Mougeot & Bretagnolle 2000b). At Kerguelen, highest petrel predation by Brown Skuas was recorded during nights with brightest moonlight (Mougeot & Bretagnolle 2000b). It is considered that predation risk for petrels visiting land has been higher when light levels are relatively high, and that sun- and moon-light avoidance on land are counter-predator adaptations which reduce individuals' conspicuousness on land and thus predation risk (Watanuki 1986, Mougeot & Bretagnolle 2000b, Brooke 2004). The precision of synchrony of Leach's Storm-petrel vocal activity and colony attendance with light levels within-nights at St Kilda was impressive, and I agree that this behaviour is likely an adaptation against predators. However, at St Kilda, given that skuas were observed successfully hunting in the darkest conditions at night, it seems likely that the behaviours I observed in Leach's Storm-petrels involving sensitivity to light probably reduce predation risk more via the effect of predator swamping (greater safety in numbers, highest at the darkest times of night) than by reduced conspicuousness to skuas.

Lack of predator recognition and avoidance

Results indicated that Leach’s Storm-petrels did not recognise acoustic or visual cues from Great Skuas at St Kilda, nor react in any way to the presence of skuas on the storm-petrel breeding colonies. Counter-predator adaptations by Leach’s Storm-petrels specific to Great Skuas, such as vigilance, early detection, alarm calling, silence or physical avoidance, were not observed; the prey apparently totally ignored its predator. Results were consistent even with use of vocalisations from different individuals of each predator and control species. Habituation of Leach’s Storm-petrels to the models seems extremely unlikely given that storm-petrel ringing at St Kilda has shown there is a very high turnover of different individuals at the archipelago each night, so models (and test vocalisations) were likely encountered by entirely new individuals during every experiment (Furness 1984, Furness & Baillie 1980, JNCC unpublished data 2004-2009). On many occasions Leach’s Storm-petrels were seen landing close to or directly in front of model and real Great Skuas. In cases of the latter, petrels were often attacked immediately and then eaten whole. Leach’s Storm-petrels appeared to be entirely vulnerable to predation by skuas on land; in particular grounded birds on the surface of the colonies. Given these results, it is understandable why very high numbers of Leach’s Storm-petrels have been eaten by Great Skuas at St Kilda, even though the mean mass of a typical meal eaten by Great Skuas (100g of fish or bird meat, Furness & Hislop 1981, Phillips et al. 1999a, Votier et al. 2004) is more than twice the total mass of an adult Leach’s Storm-petrel (≈ 45g, Snow & Perrins 1998), and this mostly bone and feather. Perhaps the ease of capture of Leach’s Storm-petrels compensates for their relatively low weight and nutritional value compared to typical meals of fish or bird meat from alcids, gulls, shearwaters or larger petrels (Phillips et al. 1999a, Votier et al. 2004).

Given the observed modes of foraging by skuas, behaviours observed of Leach’s Strom-petrels on land, and reported behaviour elsewhere of non-breeding petrels compared to breeders, it seems likely that most Leach’s Storm-petrels eaten at St Kilda are non-breeders (Storey 1984, Watanuki 1986, Bretagnolle 1990, McNeil et al. 1993, Brooke 2004). Skuas hunting on the petrel colonies probably pose a particularly high predation risk to non-breeding Leach’s Storm-petrels, when the latter are attracted to the colony by sexual vocalisations, remain on land for long periods, and investigate potential mates calling from burrows or from above ground. Lack of recognition and response by Leach's Storm-petrels to the Great Skua and Northern Fulmar models used in 2008 and 2009 could, theoretically, be due to poor model quality or that petrels simply did not see the models. However, this seems extremely unlikely as models were sufficiently realistic to elicit very close attentions from skuas (see Fig. 4.6 legend). Also, Leach's Storm-petrels were often observed through a night scope flying towards models and circumnavigating around them (to avoid collision and not in alarm), implying that models could be seen by petrels at least at close range. In 2009, the experimental design ensured Leach's Storm-petrels approaching the playback colony passed the skua models at extremely close range, and it seems unlikely that the models were not seen. Use of a pair of skuas for these experiments was realistic to observations of skua pairs hunting together on Dùn.

Leach's Storm-petrel is the only species of nocturnal petrel known to have been heavily predated by skuas in the northern hemisphere (Phillips et al. 1999a, Votier et al. 2005). In comparison with studies of petrel species most abundant and most frequently predated by skuas on islands in the southern hemisphere, the lack of predator recognition and counter-predator adaptations to skuas by Leach's Storm-petrels at St Kilda was surprising (Weidinger 1998, Mougeout & Bretagnolle 2000a, Brooke 2004, Varpe & Tveraa 2005). At Mayes and Verte Islands for example, of twelve breeding species of petrel, Blue Petrels, Thin-billed Prions and Common Diving Petrels *Pelecanoides urinatrix* are most abundant and most heavily predated, but these species were found to recognise vocalisations of their main predator, the Brown Skua, and to respond by reducing their vocal activity (Mougeot & Bretagnolle 2000a). However, adaptation to recognise and avoid predators takes generations to evolve, petrels are extremely long-lived and, unlike at Mayes and Verte Islands, skuas are relatively recent colonists to St Kilda (Phillips et al. 1999b, Brooke 2004). Skuas first colonised St Kilda in 1963 and this may be too recent for evolution of any defence adaptations by Leach's Storm-petrels to have occurred.

Leach's Storm-petrels are not predated heavily by any species other than Great Skuas on St Kilda, although they are eaten occasionally by Great Black-backed Gulls and Herring Gulls *Larus argentatus* (Mitchell et al. 2004, S. Murray pers. com., Pers. obs. 2007, 2008), extremely rarely by vagrant Short-eared Owls *Asio flammeus*

(Money 2005), and Leach's Storm-petrel eggs are probably predated by St Kilda Field Mice *Apodemus sylvaticus hirtensis* (Bicknell et al. 2009). Man is the only predator of storm-petrels discovered in the archaeological record at St Kilda, an UNESCO World Heritage Site intensively studied for its cultural and archaeological heritage, and such records are extremely rare, including direct consumption and egg collection (Steel 1994, Harman 1997). Until the arrival of Great Skuas, it seems likely that Leach's Storm-petrels at St Kilda experienced few or no predation pressures. Only time will tell whether Leach's Storm-petrels at St Kilda will evolve specialised defence behaviours against Great Skuas. In conclusion, our results suggest that sexual vocal activity and colony attendance by Leach's Storm-petrels are highest when nights are darkest, that adaptations to avoid light and reduce conspicuousness are finely attuned to between- and within-night changes in conditions, and this behaviour likely reduces individuals' predation risk on land from Great Skuas via predator swamping. However, predation risk remains high for Leach's Storm-petrels at St Kilda because specific predator recognition and counter-predator adaptations are lacking against Great Skuas, recent colonists which are able to capture storm-petrels on the ground and in the air, even at the darkest times of night and on nights with very little moonlight. Further research would be useful to determine whether nightly hunting success of Great Skuas on St Kilda varies with light conditions.

ACKNOWLEDGEMENTS

This work was supported by the Natural Environment Research Council and The National Trust for Scotland through a CASE studentship to Glasgow University. Special thanks are due to staff of the radar base facility on St Kilda for their technical assistance and weather data, to Elizabeth Mackley, Tony Bicknell and Sjurdur Hammer for help with fieldwork on St Kilda, and to Susan Bain and Sarah Money for logistical support on Hirta. We are extremely grateful to Terry Fountain for preparation of the skua and fulmar models and to Magnus Robb and The British Museum of Natural History for supply of digital audio tracks of seabird vocalisations.

Chapter 5

Effects of artificial lights and moonlight on Leach's Storm-petrels *Oceanodroma leucorhoa*, European Storm-petrels *Hydrobates pelagicus* and Manx Shearwaters *Puffinus puffinus* at St Kilda

Published as:

Miles, W., Money, S., Luxmoore, R. & Furness, R. W. 2010. Effects of artificial lights and moonlight on petrels at St Kilda. *Bird Study* 57: 244-251.

Capsule When moonlight levels are low, shearwaters and storm-petrels are attracted to artificial lighting at night at St Kilda and may be killed, but impacts are lessened by deliberate light reduction measures.

Aims To determine the scale and impacts of attraction of petrels to artificial lights at St Kilda, investigate influences of the lunar cycle, and assess effects of reducing artificial light emissions.

Methods Nightly numbers of Manx Shearwaters *Puffinus puffinus*, Leach's Storm-petrels *Oceanodroma leucorhoa* and European Storm-petrels *Hydrobates pelagicus* attracted by artificial lights were recorded in September and October 2005 to 2008. Effects of experimental reductions to light emissions in 2007 and 2008 were assessed, together with variation in annual moonlight, mortality rates, and age of birds found.

Results Reductions to light emissions caused a decrease in numbers of Leach's Storm-petrels attracted, but had less effect on attraction of Manx Shearwaters. Only juveniles were found, the majority after nights with little or no moonlight, and mortality was extremely infrequent. Only one European Storm-petrel was found, and Leach's Storm-petrel and Manx Shearwater totals were small compared to estimated breeding totals at St Kilda.

Conclusions Numbers of petrels attracted to artificial lights on St Kilda were low. However, reductions to light emissions were still beneficial in reducing numbers of young that became disorientated, grounded, or died during fledging periods. Therefore, reductions to light emissions should be encouraged. A review of this phenomenon across the UK found it to be rare in breeding areas away from St Kilda.

INTRODUCTION

Attraction to artificial lights has been observed in many different species of birds (Saunders 1930, Herbert 1970, Avery *et al.* 1976, Dick & Donaldson 1978, Harris *et al.* 1998). Among seabirds, burrow nesting and nocturnal species such as petrels (Procellariiformes) are particularly vulnerable (Klomp & Furness 1992, Jones & Francis 2003, Montevecchi 2006). Widespread mortality of petrels has been reported in many situations where these birds are attracted to artificial lights, especially on islands with large breeding populations of shearwaters, storm-petrels, and gadfly petrels (Reed *et al.* 1985, Muirhead & Furness 1988, Brooke 1990, Warham 1996, Brooke 2004, Imber *et al.* 2005, Montevecchi 2006, Salamolard *et al.* 2007, Rodríguez & Rodríguez 2009). Tens of thousands of light-disorientated and grounded petrels have been recorded, and many birds found dead, including threatened, endangered, and endemic species (Reed *et al.* 1985, Stewart *et al.* 1996, Jones 2001 Le Corre *et al.* 2002, Le Corre *et al.* 2003, Montevecchi 2006). On several islands, conservation measures have been implemented to reduce the impacts on petrels of artificial light from buildings and to decrease further threats to grounded petrels from mammalian predators (Le Corre *et al.* 2002, Montevecchi 2006). For example, on the island of Kauai, Hawaii, large numbers of Newell's Shearwaters *Puffinus newelli*, Madeiran Storm-petrels *Oceanodroma castro* and Dark-rumped Petrels *Pterodroma sandwichensis* have been attracted to bright lights of coastal resorts, but by shielding lights to prevent upwards radiation in the largest resorts, the number of birds attracted decreased by 40% (Reed *et al.* 1985). On Tenerife, Canary Islands, public awareness and civil cooperation with care and release schemes for petrels found around the heavily-lit resorts has resulted in the successful release to sea of 95% of nearly 10,000 petrels found between 1998 and 2006, including Cory's Shearwaters *Calonectris diomedea borealis*, Bulwer's Petrels *Bulweria bulwerii* and White-faced Storm-petrels *Pelagodroma marina* (Rodríguez & Rodríguez 2009).

In the UK at St Kilda, Outer Hebrides, Manx Shearwaters *Puffinus puffinus* and Leach's Storm-petrels *Oceanodroma leucorhoa* have been found grounded within the inhabited area of the only village, on the island of Hirta, annually since 1969 (St Kilda Rangers' Reports 1969-2004, St Kilda Rangers *pers. com.*). Although records have not been systematically documented every year, it is certain that in excess of ten thousand shearwaters, storm-petrels, and Atlantic Puffins *Fratercula arctica* have been found, and that these species are strongly attracted in autumn to the lights of buildings at night in the village, and formerly to streetlamps that were on at night along the shorefront (St Kilda Rangers' Reports 1969-2008, Harris 1984, Harris *et al.* 1998, St Kilda Rangers *pers. com.*, Miles & Money *pers. obs.*). In a successful attempt by the MOD and The National Trust for Scotland to reduce numbers of puffins found grounded on Hirta, these streetlamps were turned off by the St Kilda MOD base staff through the late 1990s, and have remained turned off to date. The village on Hirta faces the island of Dùn, across Village Bay, and it is assumed that young Manx Shearwaters and Leach's Storm-petrels attracted to the village lights are mostly fledglings from the large breeding colonies on Dùn, since these species do not breed on Hirta within sight of the village. Unlike puffins (Harris *et al.* 1998), storm-petrels and shearwaters attracted to artificial lights in the village on Hirta have not been studied and, until now, mortality rates, ages of all birds, and influences of the moon on the attraction of petrels to lights at St Kilda were unknown. Dùn holds the largest breeding colony of Leach's Storm-petrels in Britain and Ireland (Mitchell *et al.* 2004). Recent declines in this colony have been reported, from an estimated 27 704 apparently occupied sites (AOS) in 1999 to 14 490 AOS in 2003 and 12 770 AOS in 2006 (Newson *et al.* 2008). Predation of Leach's Storm-petrels by Great Skuas *Stercorarius skua* has been proposed as the most likely cause of a decline, but other possible mortality factors for petrels should not be ignored. This study aims to assess the numbers, ages and mortality of petrels attracted to the lights in the village on Hirta between 2005 and 2008; to determine the possible mitigating effects of reduced artificial lighting in the village at night; and to investigate the influence of the lunar cycle on storm-petrels and shearwaters found on Hirta.

METHODS

Study site, species, and collection of grounded petrels

St Kilda (57°47'N, 08°33'W) is located in the Outer Hebrides 66km west of Harris. This study was carried out on the largest island in the archipelago, Hirta, in the inhabited area (0.25km^2) of Village Bay. Petrels found grounded were Leach's Storm-petrels, European Storm-petrels and Manx Shearwaters. No other species of petrel has ever been found grounded on St Kilda due to light attraction, and these three are the only breeding petrels on the islands, other than Northern Fulmar *Fulmarus glacialis* (Murray 2002, Mitchell *et al.* 2004), which differs in not being an exclusively nocturnal visitor to land. In all years from 2005 to 2008, the entire perimeter of every inhabited building was systematically checked for grounded petrels, within the hour after dawn, every morning between 1 September and 16 October. These dates were chosen because the vast majority of grounded petrels found prior to this study had been recorded within this period (St Kilda Rangers' Reports 1969-2004). Searches also included thorough examination of all potential hiding places for grounded petrels, including pipe systems, nearby vehicles, and extraction vents. All birds examined were fledglings with newly grown fresh feathers and sometimes tufts of chick down still present. When estimating the ages of Leach's Storm-petrels reference was made to photographs of known adults examined during ringing and known juveniles from burrows, examined pre-fledging at St Kilda under licence. Birds examined were temporarily sheltered in the dark and on the same day released to sea at dusk. Sheltering the birds prevented any chance of otherwise exposed individuals being found by skuas, which commonly hunted within the village area during daylight (Miles & Money *pers. obs.*). The timing of release aimed to minimise this threat, but also to reduce the likelihood of the birds flying back towards artificial lights in the village, which were much less glaring at dusk than later in the night.

Artificial lighting and reduction measures

In 2005 to 2008, total artificial lighting at night in the village on Hirta included: thirty-two fixed outside lights, indoor lighting permanently on in two utility buildings (for access safety), and indoor lights left on at night with windows uncovered in up to fifteen rooms used for accommodation. Eleven buildings in the village were used or inhabited with lighting on during nights of this study, all but two being MOD buildings of the radar base facility. The small power station for the island was the most densely-lit building, with 24-hour indoor lighting and eight outside lights. In 2005 and 2006, many indoor lights in the village were left on at night, many left uncovered, outdoor lights left on, and no reductions to light emissions made. In 2007, at our request, measures to reduce light emissions to the absolute minimum in the village were kindly implemented by staff of the radar base and NTS. These changes included all outside lights being turned off and the windows of the majority of rooms being shielded at night by curtains, blinds, or custom-made boarding. However, effects of these measures on petrels were somewhat unclear from one year's trial (see results). In 2008, light-reduction methods were repeated as in 2007, but with an experimental period of 20 nights of no light reduction in the village, starting from the night of 22 September. The exact start date was determined by the day most convenient to the radar base staff for changing all light reduction measures on their buildings, and because of this could not be chosen entirely at random (see discussion). The timing and short duration of the 20-day control period were considered preferable to lights being left on and uncovered for the entire late summer and autumn in 2008, because attraction of fledgling puffins would be minimised in the late summer, and numbers of petrels attracted in different light conditions would potentially be comparable within-year as well as between years.

Influence of moon phase and position

We investigated possible effects of moonlight on numbers of petrels found attracted to lights in the village using two explanatory variables: the phase of the moon and the length of time that the moon was above the horizon at night. Data of percentage of the moon's face illuminated (moon phase) and percentage total duration that the moon was above the horizon at sea level between sunset and sunrise were calculated for the years of this study using annual and daily data for St Kilda from the U.S. Naval Meteorology and Oceanography Command (www.usno.navy.mil [Accessed April 2009]). Effects of the moon on daily numbers of Leach's Storm-petrels and Manx Shearwaters found in the village were investigated using a generalised linear model with a Poisson error distribution and log link function. All analyses were performed using R version 2.8.1.

RESULTS

Numbers, ages, and mortality of grounded petrels

Over the four years we collected 59 Manx Shearwaters, 45 Leach's Storm-petrels and 1 European Storm-petrel (Table 5.1). Fewer than 3% of birds were found dead in this study, all in 2006 (Table 5.1). They included one Leach's Storm-petrel which had become trapped in an open drain-hole and drowned, another which had landed in an open and partially-full diesel sump and become entirely saturated in fuel, and, exceptionally, one Manx Shearwater found hanging next to an outside light with its head lodged in a ventilation grill and its neck broken. Subsequently the drain-hole was covered and the diesel sump kept drained and dry at all times. All other birds (>97%) were found alive, and successfully released to sea on the same day.

Between and within year differences in petrel numbers and artificial light

Numbers of Leach's Storm-petrels found in the village (Table 5.1) differed significantly between years (test for homogeneity: $\chi^2_3 = 38.65$, $P<0.01$). The only year that none were found was 2007, when village lighting was reduced for the entire autumn period. In 2008, numbers of Leach's Storm-petrels differed significantly between periods with and without light reduction measures in place (test for homogeneity: $\chi^2_1 = 4.16$, $P<0.05$); however, the total number of individuals found was very small (Table 5.1). Birds were found only during the period when light reduction measures were not in use, and the first individuals were discovered on the morning of 23 September, immediately following the first night that outdoor lights were on and lighting left uncovered in the village (Figure 5.1). Leach's Storm-petrels were never found during any time in this study when measures to minimise artificial light emissions were in place. Numbers of Manx Shearwaters found in the village (Table 5.1) also differed significantly between years (test for homogeneity: $\chi^2_3 = 18.48$, $P<0.01$). Unlike Leach's Storm-petrels, Manx Shearwaters were found in all years, including 2007 (Table 5.1 & Figure 5.1). In 2008, numbers of Manx Shearwaters differed between periods with and without light reduction measures implemented at night (test for homogeneity: $\chi^2_1 = 15.06$, $P<0.01$). Shearwaters were found only within the 20-night period that no light reduction measures were in place and the first on the morning of 23 September, immediately following lights first going on (Figure 5.1). Also during this period, on 4 October, the only European Storm-petrel of the study was found.

Effects of the moon on petrels and shearwater responses to artificial light

The number of Leach's Storm-petrels and Manx Shearwaters found in the village attracted to lights was influenced significantly by the percentage of the moon's face illuminated at night (GLM: $z = -3.768$, $P<0.001$) and by the percentage of the night that the moon was above the horizon (GLM: $z = -2.243$, $P<0.05$), with no significant interactions. Species was tested in the model as an additional explanatory variable and effects found to be non-significant. Figure 5.1 shows that, overall, the vast majority of Leach's Storm-petrels and Manx Shearwaters were found at times of very low moonlight, for example after nights when less than 20% of the moon's face was illuminated and after nights when the moon was above the horizon at sea level for less than 20% of time between sunset and sunrise.

Table 5.1. Numbers of Leach's Storm-petrels *Oceanodroma leucorhoa*, European Storm-petrels *Hydrobates pelagicus* and Manx Shearwaters *Puffinus puffinus* found between 1 September and 16 October around buildings in the village on Hirta, St Kilda, in different conditions of artificial lighting, in 2005 to 2008. Counts given in brackets are numbers of birds found dead.

Year	**2005**	**2006**	**2007**	**2008**		**Total**
Village night lighting	ON	ON	REDUCED	REDUCED (1 JUL - 21 SEP) (12 OCT- 16 OCT)	ON (22 SEP - 11 OCT)	
Number of birds found						
Leach's Petrel	11	28 (2)	0	0	6	45
Storm Petrel	0	0	0	0	1	1
Manx Shearwater	5	10 (1)	27	0	17	59
Total	16	38	27	0	24	105

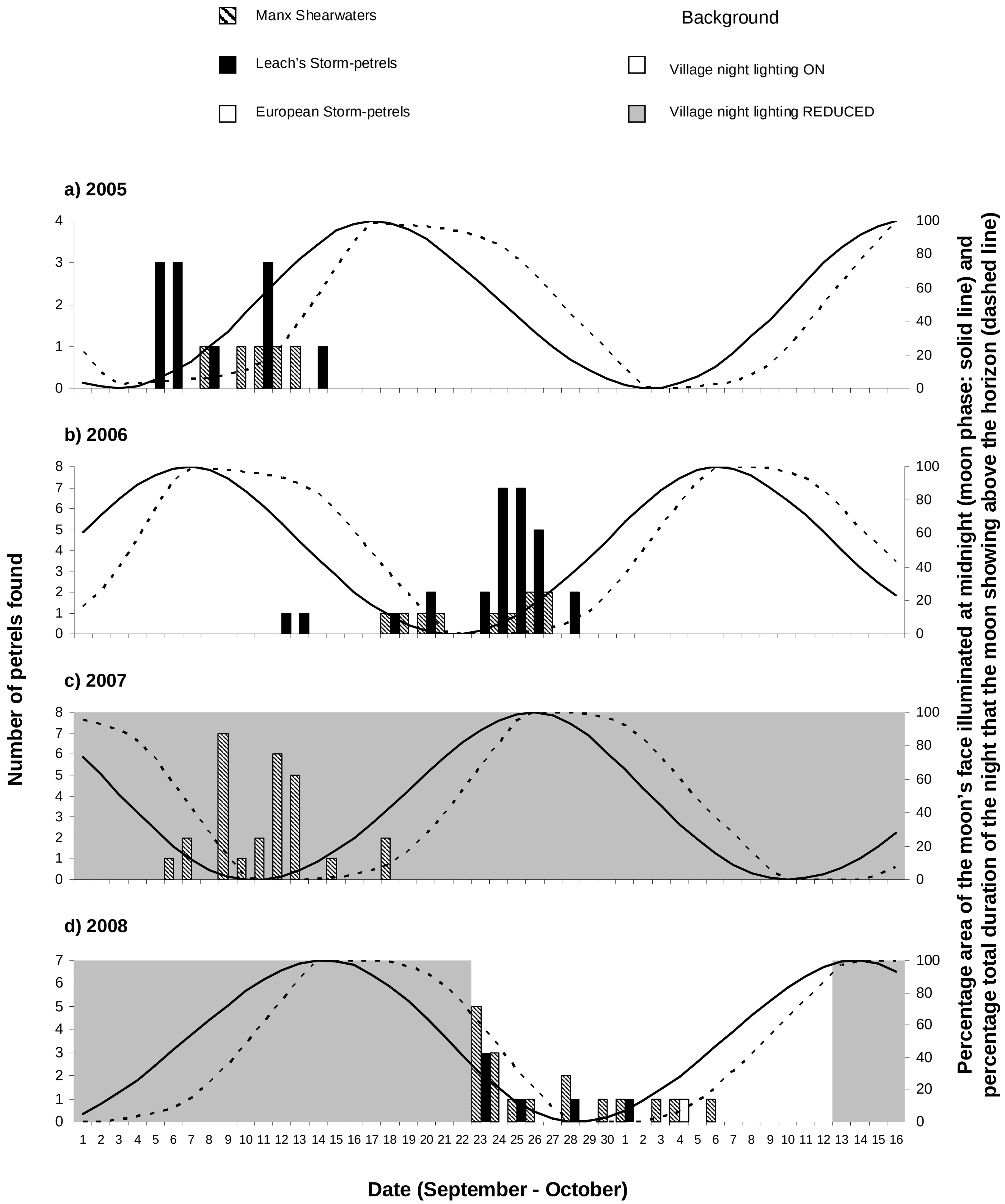


Figure 5.1. Distribution of numbers of Manx Shearwaters *Puffinus puffinus*, Leach's Storm-petrels *Oceanodroma leucorhoa* and European Storm-petrels *Hydrobates pelagicus* found around buildings in the village on Hirta, St Kilda, between 1st September and 16th October, with different conditions of artificial lighting (background), moon phase (solid line), and total duration that the moon above the horizon at night (dashed line) in 2005 to 2008.

DISCUSSION

Assessment of numbers and ages of petrels attracted to artificial lights

Total numbers of Leach’s Storm-petrels, European Storm-petrels and Manx Shearwaters found during this study (Table 5.1) were very low compared to the estimated combined total of over 60 000 individuals of these species which have annually bred at St Kilda (Mitchell *et al.* 2004, Newson *et al.* 2008). Adult breeding activity of these species may continue at the colonies until November (Brooke 2004) but only juvenile petrels were found during the study period. This strongly suggests that, in September and October, adults are not normally influenced by artificial lighting at night on Hirta. Outside of this period, it is likely that effects of the lighting on adults are also minimal. Only Manx Shearwaters have ever been found attracted to lights on St Kilda outside of the species’ normal fledging times. Less than ten have been reported in total, and all were thought to be early or late fledglings, based on the time of year (all broadly within the autumn period) and presence of chick down in their plumage (S. Murray pers. comm. 2009, St Kilda Rangers’ Reports 1969-2008, Snow & Perrins 1998, Brooke 2004).

Juveniles were the only age group attracted by artificial lights on Hirta in this study, but it is difficult to state the scale of effects precisely. Measures of Leach’s Strom-petrel, European Storm-petrel and Manx Shearwater productivity do not exist for all years of the study, so estimates of the proportions of the total number of fledged juveniles that were attracted to lights each year cannot be determined for all species. However, it is very likely that such estimates would be extremely small, as very low numbers of petrels were found in comparison to the most recent estimates of breeding population sizes at St Kilda (Mitchell *et al.* 2004, Newson *et al.* 2008).

Effects of artificial light reduction and moonlight

Between-year differences in numbers of Leach’s Storm-petrels found in the village were probably due to deliberate reductions in light emissions rather than other unknown year effects. There was a significant within-year difference in numbers of Leach’s Storm-petrels found in 2008, between times when light reduction methods were in place and the deliberate control period when light emissions were not reduced. Also, numbers of Leach’s Storm-petrels found in the village differed significantly between 2007, when lights were off, and the period in 2008 when lights were on (test for homogeneity: $\chi^2_1 = 4.16$, $P < 0.05$). These differences are very suggestive that differences in numbers of birds found in different years occurred in response to deliberate changes in artificial light conditions. Considering the two most obvious possible other influences (annual productivity and annual weather effects), there is little to suggest that differences in numbers were not due to the deliberate changes in light reduction measures. Productivity estimates for the species in 2007 and 2008 were not significantly different (Money *et al.* 2008, Money 2008 unpublished data) and, although particularly high numbers of seabirds are found during foggy weather (Harrow 1976, Verheijen 1981, Warham 1990, Jones 2001), low-visibility and extreme weather conditions in the village on Hirta were recorded very infrequently in 2007 and 2008 (St Kilda Ranger’s Reports, 2007 & 2008). It was unfortunate that, due to practical limitations, the start of the period with lighting on in 2008 could not be chosen entirely randomly, so experimental control was not perfect in this respect. However, the results showed no indication of being an artefact of experimental design, and, considering this potential bias alongside the other three years’ data, overall, the data seemed strongly indicative and convincing that deliberate reductions to light emissions during this study reduced attraction of Leach’s Storm-petrels.

Unlike Leach’s Storm-petrels, a high number of Manx Shearwaters was found in 2007, and effects of reducing light emissions on the numbers of birds attracted to the village were apparently not the same for Manx Shearwaters as for Leach’s Storm-petrels that year. Given the measures in place to reduce lighting to the absolute minimum throughout 2007, it seems possible that Manx Shearwaters may still be attracted by very weak lighting, even the extremely low-level emissions on St Kilda in 2007 which did not affect the smaller species of petrel breeding at the site. Greater sensitivity to artificial lights in larger species of petrels has been suggested in other studies, for example differences between shearwaters and storm-petrels in Hawaii and in the Canary Islands (Telfer *et al.* 1987, Rodríguez & Rodríguez 2009). Additional evidence for this theory at St Kilda is that European Storm-petrels are the smallest species to breed on Hirta and nest in walls next to the MOD base (unlike Leach’s

Storm-petrels and Manx Shearwaters), yet have hardly ever been found grounded around buildings at any time of year, and are apparently the least sensitive to light (St Kilda Rangers' Reports 1969-2008, Murray 2002, Miles & Money pers. obs.). One other possibility, however, is that Manx Shearwaters may be more attracted by sounds at night than storm-petrels and that certain noises continue to attract shearwaters at times when artificial lighting is minimal or even non-existent. On Hirta, Manx Shearwaters have most frequently been found close to extractors and generators that were continuously emitting low frequency sounds, including in all years of this study. It seems likely that attraction to these sound emissions could be one explanation as to why shearwaters were found in 2007 during reduced light conditions.

Effects of the lunar cycle and position of the moon above the horizon on numbers of grounded petrels were similar in this study to those found in other studies: most petrels were found at times of least moonlight (Verheijen 1980, Telfer *et al.* 1987, Le Corre *et al.* 2002, Rodríguez & Rodríguez 2009). In 2008, a separate study was carried out on the phenology of Leach's Storm-petrels at St Kilda, in which fledging dates were recorded (Money 2008, unpublished data). Thirteen birds, out of twenty-eight studied, fledged between the first and last quarter of the lunar cycle (7 to 22 September), including three on nights around the full moon (14 to 16 September). In other studies on light attraction of petrels, the possibility has been suggested that fewer juveniles have been found at times of greatest moonlight (e.g. full moon) because fledging was inhibited on these nights (Imber 1975, Rodríguez & Rodríguez 2009). However, for Leach's Storm-petrels at St Kilda in 2008, the phenology study suggested this was not so. The lack of grounded Leach's Storm-petrels at times of greatest moonlight was perhaps more probably due to the relative glare and attraction of artificial lights diminishing on nights when ambient light from the moon was particularly bright and long-lasting.

Occurrences of light-induced mortality of petrels at St Kilda and in the UK

Mortality of petrels found attracted to lights was very low at St Kilda (< 3%). This has also been found in similar studies on much larger and more populated islands (more petrels and more people), for example Réunion Island (<10%) and Tenerife (<6%) (Le Corre *et al* 2002, Rodríguez & Rodríguez 2009). Considering the decline in

Leach's Storm-petrels reported from Dùn (Newson *et al* 2008), in relation to our results, the possibility that high mortality of breeding and non-breeding storm-petrels may have occurred in the UK away from St Kilda was reviewed, by searching all regional bird reports and county avifaunas for records of light induced effects and mortality of Leach's and European Storm-petrels, for all areas of the UK with storm-petrel breeding colonies (Mitchell *et al.* 2004), in all years from 1990 to 2006 (Table 5.2, see below). Most frequent were records of attraction to lighthouses and harbour lighting, but unusual records included: individuals coming to flashes from a garden fireworks display (e.g. Egilsay, Orkney, 5 November 2005); attraction to oil terminal flares (e.g. Sullom Voe, Shetland, 3 November 2000); and several individuals attracted to moth traps (e.g. Skaw, Shetland, 30 July 2004). Given the time period and area covered (Shetland, Orkney, all regions of the UK north and west coasts, Scillies, and the Channel Islands), records were surprisingly few in total (<120 individuals). However, the proportion of all records of storm-petrels found dead (21%) was high in comparison with our study at St Kilda (<2%). Perhaps because records from regions of the UK other than St Kilda were not all made systematically, they were possibly biased by a greater likelihood of dead birds being found during casual observations than live and potentially transitory individuals. Even with this consideration, the results of this search strongly suggest that in areas of the UK with storm-petrel breeding colonies away from St Kilda, mortality of Leach's Storm-petrels and European Storm-petrels due to light attraction has also been very low in comparison to estimated UK breeding population sizes (Mitchell *et al.* 2004). It was notable that the highest proportions of all Leach's Storm-petrel and European Storm-petrel records (70% and 86.6% respectively) came from Bardsey lighthouse. This may partly be explained by relatively high observer coverage at this light source, but even taking this into account, this site has a high attraction power to birds in comparison to other intensively watched sites with lighthouses, such as North Ronaldsay and Fair Isle (Bardsey, Fair Isle, North Ronaldsay, and Orkney Bird Reports 1990-2006). Possible reasons suggested for this have included differences in lighthouse beam characteristics (e.g. light frequency and rotation rate), as well as site location differences relative to species' migration routes and breeding areas, migration bottlenecks, seabird foraging ranges, and seasonal and local weather patterns (Saunders 1930, Herbert 1970, Verheijen 1981, Bardsey Bird Reports 1990-2006, Brooke 1990, Jones 2001, Jones & Francis 2003, D. Shaw pers. comm. 2009).

Overall, in areas of the UK with breeding storm-petrels, it seems that very low numbers of individuals are affected by artificial lighting relative to estimates of total breeding population sizes, and light attraction is not a cause of high mortality.

The status of St Kilda as a SSSI, SPA, and World Heritage site means that increases in the number of brightly-lit buildings on the archipelago are unlikely. The inhabited village is the only area of Hirta with lighting on at night, with the exception of one MOD building on the hilltop which has outside lighting occasionally left on. Petrels have been discovered near this building during the daytime by staff of the radar base, but very few birds have been found, less than annually, and the vast majority of these were alive. There are no other sources of artificial light on land at St Kilda and it is rare for brightly-lit ships to anchor for long near the islands. In conclusion, numbers of petrels attracted to artificial lights on St Kilda are low, very few are killed by the phenomenon, but reductions to artificial light emissions should be encouraged since they are beneficial in reducing numbers of fledglings that are grounded.

Table 5.2. Total annual numbers and mortality of Leach's Storm-petrels *Oceanodroma leucorhoa* and European Storm-petrels *Hydrobates pelagicus* recorded at artificial light sources in regional bird reports and avifaunas, for all regions of the UK with storm-petrel breeding colonies other than St Kilda, for all years from 1990 to 2006.

Year	Leach's Petrels found	European Storm Petrels found
1990	2	8
1991	0	2
1992	1	2
1993	0	2
1994	3	8
1995	2	3
1996	0	2
1997	4	0
1998	2	2
1999	1	6
2000	3	3
2001	0	0
2002	8	16
2003	0	1
2004	3	16
2005	1	9
2006	0	2
Total	30	82
Total found dead	8 (26.7%)	15 (18.3%)

ACKNOWLEDGEMENTS

WM was funded by NERC and NTS through a CASE studentship to Glasgow University. SM was employed by NTS in 2005 to 2008 as the St Kilda Seabird and Marine Ranger. Special thanks are due to staff of the radar base facility on St Kilda for their technical assistance, patient cooperation, and help during this study, in particular to Cliff Black and Lachie MacLeod. We are also very grateful to the St Kilda NTS staff and Rangers for past records and personal communication of their experiences, Stuart Murray for supply and discussion of St Kilda bird records, Deryk Shaw for advice on lighthouse-attraction of petrels at Bird Observatories, Rory Tallack for excellent help with fieldwork in 2008, and Susan Bain for logistical support on Hirta. Jenny Gill, Dan Haydon, Elizabeth Masden and an anonymous referee provided useful comments on an earlier draft.

Chapter 6

Variation in plumages of adult and juvenile Leach’s Storm-petrels *Oceanodroma leucorhoa* at St Kilda

Published as:

Miles, W. T. S. 2010. Variation in the appearance of adult and juvenile Leach’s Storm-petrels *Oceanodroma leucorhoa* on St Kilda. *British Birds* 103: 721-727.

Appendix 6.1 accepted as a short book chapter:

Miles, W. T. S. 2010. Leach’s Petrel *Oceanodroma leucorhoa*. In: Baker, K. (& Coiffait et al. (eds.)), *Identification Guide to European Non-passerines (revised edition)*. British Trust for Ornithology, Thetford (in prep).

INTRODUCTION

St Kilda, Outer Hebrides, is the stronghold for Leach's Storm-petrels in Britain and Ireland, having 94% of the breeding population: an estimated total of 45,400 occupied nesting sites (Mitchell et al 2004, Forester et al 2007). In 2007 and 2008, considerable variation was observed within and between adult and juvenile plumages of Leach's Storm-petrels on St Kilda, during research being carried out by the University of Glasgow and National Trust for Scotland, studying Great Skua *Stercorarius skua* and Leach's Storm-petrel population dynamics and predator-prey interactions. During fieldwork between mid-May and late October, Leach's Storm-petrels were observed in-hand when mist-netted for ringing, when sampled (temporarily and under licence) at burrows, and when juveniles were found on land post-fledging, apparently disorientated by artificial lights in the village. Individuals were also observed in field conditions in natural light at sea, when adults mist-netted and ringed around dawn, and fledged juveniles found on land, where viewed through optics after release out to sea (the latter during daylight to prevent possible further disorientation towards artificial lighting at night). Additionally, observations of Leach's Storm-petrels in field conditions at sea, and over land, were made extensively using a Leica BIM 35 night scope. This enabled very clear sight of a sample of the tens of thousands of breeding and non-breeding Leach's Storm-petrels that come to St Kilda during darkness. In these circumstances, good views were obtained of the plumage structure, tone, pattern and variation of many individuals at sea in a variety of weather conditions. Excellent views were also obtained of the swarms of Leach's Storm-petrels present at their cliff-slope breeding colonies at night, where many individuals in flight could be studied at very close proximity (often at less than 1m range). Geographical variation in Leach's Storm-petrel plumage is well documented between distant populations across the Pacific and Atlantic, and in relation to unexpected occurrences of dark-rumped storm-petrels (e.g. Ainley 1980, Bourne & Jehr 1982, Ainley 1983, Power & Ainley 1986, Vaughan 1990, Bretagnolle et al 1991, Cubbitt et al 1992, Morrison 1998, Brooke 2004, Howell & Patteson 2008). However, plumage variation is not well documented within the British breeding sites. From a birding and ringing perspective, this article summarizes observations of plumage colour, pattern, structure and variation within and between adult and juvenile Leach's Storm-petrels observed at St Kilda in 2007 and 2008, with consideration of potential similarities to other species of storm-petrel. Variation from typical adult and juvenile plumages is summarized for all features in which it could be seen clearly through standard optics or the naked eye and where biometric measurements were unnecessary.

ADULTS

Adult plumage is defined here as any non-juvenile plumage. Observations were made between mid-May and August 2007 and mid-May and late October 2008, with the greatest proportion during the most intensive ringing periods in July. Throughout these months, adults were seen in-hand during mist-netting sessions at and away from the breeding colonies (total = 570 birds), and seen in-field at the breeding colonies at night and at sea during night and day (total = 4000+ sightings). These observations included both breeding and non-breeding adults.

Typical plumage

Plumage features of the vast majority of adult birds observed at St Kilda closely matched standard descriptions of the species found in monographs and field guides. However, throughout the observation period (May to October inclusive), the dark plumage colouration and tones of almost every adult encountered were brown in all areas, rather than the black and grey tones often quoted. The only exceptions to this were a very few moulting or freshly moulted individuals, and juveniles (see below). Even the pale carpal bars of all adults, including those recently moulted, were tinted brown, very heavily in some cases, and were often very poorly defined within the other brown tones of the wing. This was particularly striking in comparison to the distinctive pure pale-grey carpal bars of juveniles (see Fig. 6.1). In agreement with (e.g.) Flood and Thomas (2007) and Onley and Scofield (2007), browner colouration was synonymous with older plumage, probably resulted from bleaching and wear, and typified the increasingly worn plumage of adults throughout the late spring, summer and early autumn. Noticeable at St Kilda, was the brown colouration of adult primaries in comparison to those of very fresh juveniles, which were bluish-black (e.g. Fig. 6.2). Also, the differences between tip shape of the primaries of adults, which are broader and more rounded, and juveniles, which are thinner and more pointed (Fig. 6.2).

Figure 6.1. Close-up of inner wings of Leach's Storm-petrels *Oceanodroma leucorhoa*, St Kilda, Outer Hebrides, September 2008. Adult (left) and newly-fledged juvenile (right) plumages, showing typical colours, tones, and differences in the definition of the pale carpal bar. Unusual and unexpected abrasion of the juvenile greater coverts can also be seen.

Figure 6.2. Outer wings of Leach's Storm-petrels *Oceanodroma leucorhoa*, St Kilda, Outer Hebrides, September 2008. Typical adult (a) and typical newly-fledged juvenile (b), showing differences between colour tones and between shape of the primary tips, and an example of a newly-fledged juvenile found (untouched) with an unexpected, damaged, and heavily worn wing condition (c).

Plumage variation

<u>Rump patch:</u> A spectrum of shape and patterning of the rump patches of adult Leach's Storm-petrels was encountered in-hand on St Kilda (see Fig. 6.3). The vast majority of adults seen in-hand and in-field had a classic 'text-book' rump, very like Figure 6.3c: large, white, V-shaped, extending slightly onto the rump sides, with a central dark dividing line, very narrow dark shaft streaking to the white feathers, and occasional, indistinct, small dark spots at the upper and lower ends of the rump. Less common, on about 1 in every 10 birds, was a rump patch that appeared more square-

shaped than V-shaped. An example of this is Figure 6.3b, also an example of a rump virtually lacking a clear central dark dividing line. One of the biggest surprises was how frequently birds were observed (estimated 30% of all sightings), both in-hand and in-field, with little or no central dark divide to the rump, or with a square or band-shaped rump, or with white extending far down the rump sides, or with all three. In rare cases of the latter, in-field, the species identification of the individual was at first particularly confusing (see below). At extreme ends of the spectrum are the rump patches shown in Figures 6.3a and 6.3d. White rump patches with no dark shaft streaking, no dark spotting, and very little suggestion of a dark central divide, thus entirely pure white (e.g. Fig. 6.3a), were very rare. As were very dark rump patches: figure 3d the darkest encountered, judged to score 8 on the Ainley scale (1 = entirely white to 11 = entirely dark, Ainley 1980). Colour, shape and pattern of this rump was produced partly by an unusually large amount of dark pigmentation to the upper, lower and central (otherwise white) feathering, but more, by extensive wear and abrasion of many of the white feathers, revealing underlying darker plumage. This, and very similar rump patterns, were also witnessed in field conditions, but none darker.

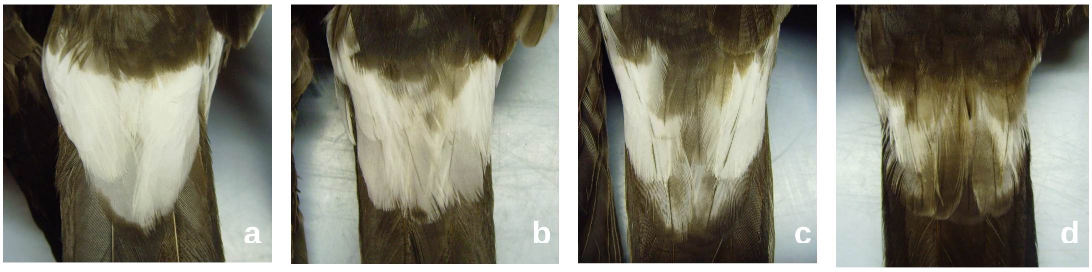


Figure 6.3. Rump patches of different adult Leach's Storm-petrels *Oceanodroma leucorhoa*, St Kilda, Outer Hebrides, July 2008. Variation spanned between the purest white (a) and darkest (d), including squarer shaped patches (e.g. b) and typical pattern (e.g. c).

<u>Primary shaft bases:</u> Tone of the feather shafts at the bases of the outer primaries was examined in-hand, specifically: the region extending out immediately beyond the tips of the primary coverts for white colouration, as seen in Swinhoe's Storm-petrels *Oceanodroma monorhis*. Most Leach's had blackish-brown or dark brown colouration to the region examined (see Fig. 6.4a). However, light brown to pale yellow shaft bases (e.g. Fig. 6.4b) were also seen, although slightly less often, on about one in every four individuals. Only one individual (of 570) had clear white

bases to the outer primary shafts (Fig. 6.4c). Pale brown, yellow or white colouration to the primary shafts beyond the tips of the primary coverts never extended out more than 2cm, reduced towards the inner primaries, was never observed on more than the outer 6 primaries, and could not be seen on birds at sea during day or night observations but could on several birds seen at very close (<10m) range in-field at the breeding colonies. There were no signs that paleness of the outer primary shaft bases is positively correlated with darkness of the rump in Leach's Storm-petrels. It should be noted, however, that relatively few Leach's Petrels were encountered at St Kilda with extremes of either of these features.

Figure 6.4. Primary bases and coverts of different adult Leach's Storm-petrels *Oceanodroma leucorhoa*, St Kilda, Outer Hebrides, July 2008. Variation in colour of the outer primary shaft bases immediately beyond the primary coverts is shown: examples of brownish-black (a) and yellow (b) seen frequently, alongside white found in only one individual (c).

Tail shape: Leach's Storm-petrels observed in-hand and in-field at St Kilda mostly exhibited the classic, deeply-forked, tail. However, a surprising number were seen with square-shaped, shallowly forked, or asymmetrical tails. Approximately 100 sightings (from 4000+) were noted of Leach's Storm-petrels in field conditions exhibiting abnormal tail shapes. In most of these cases, the tail appeared rather short and square-shaped. In-hand, unusual tail shapes were also encountered, typically one in every twenty birds handled. Most of these were asymmetrical, a few shallowly forked, but none fully square-shaped. It is likely that tail abnormalities other than short and fully square shapes are difficult to see, and were under-recorded, during sightings in-field compared to in-hand. Figure 6.5 shows an example of an aberrant asymmetric tail, where the right side appears short and square, and the left normal. This shape was caused by total loss of the outermost feather and loss of the tips of the second, third and fourth outermost tail feathers on the right side, making all feathers on that side roughly equal in length to the shortest (inner) feathers. Feather losses and damage did not always result in an unusually shaped tail. Aberrant loss of entire single tail feathers, apparently unrelated to annual moult, was encountered quite frequently, on approximately 10% of birds seen in-hand. Loss of primary, secondary and tail feather tips was rarer, only observed in adults on approximately 5% of all individuals. This likely occurred due to feather tips snapping off when weakened by extreme weathering or bleaching, particularly of the areas exposed in the closed wing and tail positions. Figure 6.5 (left photograph) shows how the tip portion of the second outermost tail feather on the left side has bleached lighter brown, and is likely to be structurally weak, due to exposure to sunlight, weather and the sea even when the tail is fully closed.

Normal ageing, moult and re-growth of the tail can greatly reduce the forked appearance, and in rare cases temporarily produce a square or only very slightly forked shape (e.g. Flood & Thomas 2007, Robb et al 2008). Therefore, unusual tail-shapes of the birds observed in-field between June and September around St Kilda may have been due to normal feather loss and renewal, rather than aberrant total or partial losses and damage. However, this seems unlikely, as during the entire fieldwork period, of the total birds examined in hand, only four (0.7%) were found with extensive tail moult, with two of these exhibiting unexpected moult sequences compared to other studies (e.g. Ainley et al 1976). Also, the basic tail shape of all four birds, including those moulting the outer tail feathers (e.g. Fig. 6.5), was very deep-forked and symmetrical in comparison to the abnormal tail shapes caused by aberrant feather losses and damage, seen more frequently.

Figure 6.5. Unexpected tail conditions of different adult Leach's Storm-petrels *Oceanodroma leucorhoa*, St Kilda, Outer Hebrides, July 2008. Examples of aberrant asymmetry (left) and tail moult (right) with the deep-forked tail shape remaining even whilst the outer feathers are renewed.

Timing of moult: The majority of adults examined in-hand showed no sign of active wing, tail, head or body moult, and never could any signs of moult be seen in the many individuals observed in-field. Variation was limited to 4 birds showing extensive tail moult (see above) and approximately 20 individuals (3.5%) with signs of body moult, all mist-netted in July. None were seen at St Kilda with signs of moult in the primaries, secondaries or tertials in any months of observation (May to October). This was not particularly surprising, as moult of the wings usually starts after birds leave the breeding grounds (Baker 1993). All individuals with tail moult were also undergoing body moult, for example shown in Figure 6.6 (right photograph). This bird also shows a rather square shaped rump patch with little trace of a dark central divide. In all cases, moulting individuals were mist-netted away from the breeding colonies by attraction to tape-lure (under licence), and are more likely to have been non-breeders than breeders. Signs of moult were therefore not totally unexpected, as non-breeders begin moult at least one month before breeders, starting with the body as early as April or May and flight feathers in August or September (Baker 1993, BWPi 2006). Slightly more unexpected was one individual caught in July 2007 (Fig. 6.6, left photograph), which in all plumage areas had extraordinarily fresh-looking feathers, relative to every other adult examined. Small, black, unworn tips to the white rump feathers; all feathers very glossy and unworn; slight brown tones restricted to the carpal bars and feather shafts of the wings; and all other areas unbleached and uniform dark grayish-black, strongly suggested the plumage was very fresh and this adult had completed full wing, tail, head and body moult very recently. This timing, and the bird's relatively tiny white rump patch, was unique.

Figure 6.6. Adult Leach's Storm-petrels *Oceanodroma leucorhoa*, St Kilda, Outer Hebrides, July 2007 and 2008. A freshly moulted individual with entirely new plumage (left), and close-up of the body and tail of a different individual during moult (right), showing contrast between the old plumage (brown) and new (glossy greyish-black).

Similarities with other species

Within the plumage variation of Leach's Storm-petrels observed in-hand and in-field were features very closely resembling those of other storm-petrels of the genus *Oceanodroma*, including 'band-rumped' species (e.g. Madeiran *O. castro*, Monteiro's *O. monteiroi*, and Cape Verde *O. jabejabe* Storm-petrels) and 'dark-rumped' species (e.g. Swinhoe's *O.monorhis*, Markham's *O. markhami*, and Black *O. melania* Storm-petrels). The plumage variation encountered at St Kilda frequently created initial difficulties for species identification, but only during in-field observations, and never to the point of precluding final positive species identification as Leach's for any individual encountered. For example, differences between a typical adult Leach's Storm-petrel and two adults with extremes of variation seen in field conditions at sea at St Kilda are summarized in Figure 6.7.

Plumage features of band-rumped *Oceanodroma* storm petrels encountered within the plumage variation of Leach's Storm-petrels at St Kilda included: 1) band-shaped rump patches with no central dark divide and with white extending far down the rump sides; 2) short and square-shaped tails; 3) long wings relative to other Leach's Storm-petrels. The latter was only noted in-field, on birds with short and square-shaped tails, and was probably an illusion created by decreased tail (and overall body-) length changing perceived proportions of wing length (see Figure 6.7, middle left petrel). Abnormal, very long, wing lengths were not recorded from 400 birds measured in-hand on St Kilda. Variant Leach’s Storm-petrels showing all three of the above features were only seen on two separate occasions. Both were observed in-field, at extremely close (<3m) range, very clearly through a night scope, for at least 15 minutes, and, in face of initial excitement that here was a different species, both were heard to emit classic Leach’s Storm-petrel chatter calls! An image of one of these individuals can be seen in figure 8, showing the ‘band-rumped’ features and, also, the impression of round-tipped wings, apparent as the bird flexed, soared and hovered at two meters range around the peak of a crag.

Figure 6.7. Adult and newly fledged juvenile Leach’s Storm-petrels *Oceanodroma leucorhoa*. Typical plumages and examples of plumage variations seen in field conditions at St Kilda, Outer Hebrides, 2007 and 2008. Adults (summer and autumn): typical plumage (top); and individuals encountered with plumage variations suggestive at first of ‘band-rumped’ (middle left) and ‘dark-rumped’ (bottom left) species of *Oceanodroma* storm-petrels. Newly-fledged juveniles (autumn): typical very fresh plumage (middle right); and another very freshly plumaged individual but with unexpected abrasion and damage to primaries and tail (bottom right). In flat light, during typical overcast days at St Kilda, the differences in colour and tone of the adult and very fresh juvenile plumages could be clearly seen and differentiated at sea at close range (up to 200m distance). However, caution may be necessary for separating these ages in many other field situations, as the plumages of both could also appear similarly brown-greyish black, particularly at long-range or when the sky and sea were brighter. Additionally, the plumage features of very fresh juveniles are likely to quickly change, becoming darker, slightly browner, less distinctive, and more adult-like, with wear and bleaching throughout the autumn, winter and spring before moult: beginning as early as April in the second year (Baker 1993, Ginn & Melville 2000, Blomdahl et al 2003).

Figure 6.8. Field drawing of an adult Leach's Storm-petrel *Oceanodroma leucorhoa*, seen through a night scope at extremely close (< 2m) range on the species' breeding colony at Carn Mòr, St Kilda, Outer Hebrides, 20th July 2008. This individual was at first thought possibly to be a different species of *Oceanodroma* storm petrel, such as Madeiran *O. castro*, due to its band-rumped, square-tailed and long-winged appearance. However, other characters, including bill structure, carpal bar pattern, and flight style, were more typical of Leach's, and it was soon heard repeatedly emitting a classic, and very loud, Leach's chatter call.

Plumage features of dark-rumped *Oceanodroma* storm petrels' encountered within the plumage variation of Leach's Storm-petrels at St Kilda included: 1) white bases to the outer primary shafts; 2) partially dark rump patches, appearing wholly dark only when seen at long range at sea. These features were never both seen together on one bird and, unlike the variation suggestive of 'band-rumped' species, never appeared well-defined or unchanging in field conditions, or seriously suggestive of any species other than Leach's. Wear and abrasion of the white rump feathers shown on Figure 6.3d (photographed 26th July 2008) would be prone to continue until the rump was moulted and feathers renewed. Moult of the rump feathers could occur normally as late as February or March of the following year (Ginn & Melville 2000, Flood & Thomas 2007), during which time it is totally conceivable that the white feathering may entirely wear away, and the rump patch become all-dark in appearance.

JUVENILES

Observations were made in September and October 2008, from individuals encountered on land after apparent disorientation post-fledging and when sampled (temporarily and under licence) from burrows for parasite collection. All individuals were examined in-hand, had extremely fresh plumage, and had likely experienced very little or no exposure to light, weather and the sea, because those found on land had apparently only just fledged, and those from burrows were within a few days of fledging (determined by endoscope during separate phenology studies - S. Money pers. comm.). Juveniles sampled numbered 19 in total: 6 found landed and 13 in burrows. Only those found disorientated on land were seen well in field conditions at sea: through optics, upon release during daylight.

Typical plumage

Despite the small sample size, plumage features were seen which were universal to all juveniles examined and which were surprisingly different from the adult plumage. Most striking were a lack of any distinct brown tones in the juvenile plumage and strong contrast of the head, lesser coverts, median coverts, scapulars and mantle which were grey, with the tail (see Fig. 6.9) and wings (e.g. Fig. 6.2) which were jet black with blue sheen. Also, the carpal bars were bright, purely pale-grey, and very well defined between the darker grey and black tones of the rest of the inner wing (see Fig. 6.1). These features were always visible in-hand and in-field at close range in flat light (see Fig. 6.7). Contrast between colour and tone of the outer wing and between the shape of the primary tips of an adult and juvenile in September (described above) is shown in Figure 6.2. Differences in shape of the separate primary tips were only visible on birds seen in-hand. However, in-field, the wings of newly-fledged, unworn, juveniles looked much more sharply pointed than wings of adults and this effect was likely caused by differences in tip shape of the outer primaries. All juveniles also exhibited very clear, and in most cases broad, white outer edges to the tertials (e.g. Fig. 6.9) which, in field conditions, were only visible at very close range (see Fig. 6.7). The rump patches of the majority of birds (e.g. Fig. 6.9) were large, white, unworn, V-shaped, extended slightly onto the rump sides, had only slight suggestion of a central dark dividing line, and had extremely thin dark shaft streaking and neat, narrow, black edges to the tips of all the white feathers. All plumage, including wings and tail, was very fresh, unworn and glossy for the majority of individuals.

Figure 6.9. Tertials, rump and tail of newly-fledged juvenile Leach's Storm-petrels *Oceanodroma leucorhoa*, St Kilda, Outer Hebrides, September 2008. White outer edges to the tertials, unworn juvenile rump pattern, and contrast between the grey mantle tone and black tail are shown on a typical individual (left). Less typical and totally unexpected (right) are heavy abrasion, matting and twisting of the tail feathers, abrasion to the tertials, and no trace of a central dark divide to the rump.

Plumage variation

Little variation was found between individuals, with exception of the two features below. Variation was not seen within shaft bases of the outer primaries beyond the primary coverts (dark bluish-black), unworn tail shape (symmetrical and deeply forked) or timing of moult (no signs of moult). Features akin to other species of storm petrel were not found.

Rump patch: Variation was very slight, limited to 5 individuals lacking any trace of a central dark divide (e.g. see Fig. 6.9). Band-shaped or partially dark rumps were totally absent from all juveniles examined.

Wing and tail damage: Unexpected, severe abrasion and damage was found to the wings and tail of 2 juveniles found on land and 4 from within burrows. Given the birds' lack of any prolonged exposure outside of burrows, lack of any human handling when the damage was encountered, as well as the very short duration and extreme care taken when birds were handled, it was rather extraordinary to discover 32% of otherwise very freshly-plumaged juveniles with particular areas of extensive feather damage, including: primary tips missing (see Fig. 6.2c); heavy abrasion to coverts (e.g. Fig. 6.1); and webs of primaries, secondaries, tertials and tails misshapen, matted and frayed (e.g. Fig. 6.2c and Fig. 6.9). It begged questions of how the damage occurred, if it is a normal phenomenon, and if these juveniles moult and replace the damaged feathers soon after fledging. Sticky and very abrasive grit and mud inside burrows, infestations of feather parasites, or frequent acidic leaching of rainwater through burrows and over petrels, may be possible agents of the damage, visible at close range at sea (e.g. Fig. 6.7). There was no evidence of high parasite burdens on these birds, but 2008 was exceptionally wet in late summer, and so flooding of burrows may have been unusually prevalent that season. Storm-blown juveniles with such abraded and damaged extremities seen at sea or wrecked inland in September and October could easily be mistaken for adults with heavily worn plumage.

ACKNOWLEDGEMENTS

WM was funded by NERC and NTS through a CASE studentship to Glasgow University. Thanks to Tony Bicknell, Terry Fountain (Photo: fig. 6), Elizabeth Mackley, Elizabeth Masden, Roger Riddington, Deryk Shaw, Rory Tallack (Photos: figs. 1, 2 and 9) and Steve Votier for great company, advice, and help with fieldwork on Hirta and Dùn; to Sarah Money (NTS), Susan Bain (NTS), and staff on the QinetiQ base for excellent guidance and logistical support on St Kilda; and to Matt Parsons and Ian Mitchell (JNCC) for their encouragement, enthusiasm, and loan of the night-scope. Special thanks to Bob Furness and Richard Luxmoore for project supervision, and critical feedback on the draft.

APPENDIX I

Appendix 6.1. *Accepted as:* Miles, W. T. S. 2010. Leach’s Petrel *Oceanodroma leucorhoa*. In: Baker, K. (& Coiffait et al. (eds.)), *Identification Guide to European Non-passerines (revised edition).* British Trust for Ornithology, Thetford (in prep).

LEACH'S PETREL *Oceanodroma leucorhoa*

Identification From Storm Petrel and Wilson’s Petrel *Oceanites oceanicus* by larger size, prominent long pale carpal bars, forked tail (17-23mm, shortest to longest tail feathers, tl-t6), and white rump patch usually V-shaped (nominate *leucorhoa*). Madeiran Petrel *Oceanodroma castro* has completely white band-shaped rump and less deeply forked tail (<13mm, usually 5-8mm). Swinhoe’s Petrel *Oceanodroma monorhis* has all-dark rump (no trace of white) and extensive white base regions to shafts of outer primaries (p10-p5).

Autumn/Winter

lw (3/5) Most have remains of chick down on body when leaving nest burrow; otherwise, head, body, lesser- and median-coverts of newly fledged birds grey-black with slightly paler grey fringes (without brown tones). Primaries, secondaries, and tail jet black with blue sheen (in contrast to head and body). Tertials grey-black with paler grey fringes and white tips. Outer primaries comparatively pointed at tip (Fig). Greater-coverts pale, milky-grey with white fringes. Rump feathers white with thin black shafts and narrow black fringes to tips (forming small anchor shapes towards tail). Outer web of t6 sometimes narrowly edged pure white but usually paler than rest of tail, especially towards rump.

NOTE: Greater-covert and tertial edges become worn in late autumn and winter (reducing amount of white), dark plumage tones fade quickly (becoming slightly brown), and individual variation occurs; making distinction from adults sometimes difficult (especially from non-breeders that have completed body, tail and wing moult relatively early).

Adult (4/6) Outer primaries rounded at tip (Fig). Greater-coverts appear uniform and distinctly brown tinted (even when fresh), lacking white fringes. No distinct contrast between tone of head and body against tone of primaries and secondaries (all typically brownish black).

Spring/Summer

1s (5) Greater-coverts and tertials may show traces of white edges, though often indistinct or absent due to wear. Primary tip shape helpful if unworn and sharply pointed; however, intermediate primary shapes occur and such birds should not be aged without reference to other features. Birds in active wing moult in spring will likely be of this age (but beware adults with suspended moult).

NOTE: 1st-summer birds assumed not to visit breeding colonies, most 1s birds probably stay far off-shore, possibly in equatorial wintering areas.

Adult (4/6) As Autumn/Winter. Dark plumage tones becoming browner and slightly paler with age. Occasional birds in late June and July with entirely new and unworn plumage (comparatively black and glossy); likely to be non-breeders that completed moult exceptionally early.

Moult

5 Complete post-juvenile moult starting in April of 2nd calendar year with flight feathers, completed by October-December.

Adult Complete post-breeding moult starting with body during breeding cycle (June onwards). Tail replacement begins in August. Remiges moulted after leaving breeding grounds in September/October. Inner primary moult may suspend until winter quarters are reached; resumed November onwards, completed by February (March). Non-breeders moult earlier, beginning with body in May or June and flight feathers from August or September (very rarely in June/July).

Individual variation Extensive in rump patch; white V-shape with black central divide typical, but pure white and band-shaped (resembling Madeiran Petrel), mostly dark (resembling Swinhoe’s Petrel), and diverse intermediate patterns occur. White surface feathers of rump also become worn relatively quickly, often to reveal underlying darker plumage (V-shape of white feathers and 1w black shafts and tip fringes transient, changing rapidly due to wear and abrasion, and fading of shafts). Aberrant loss or renewal of one, two, occasionally three, tail feathers common. Tips of t4-t6 prone to heavy abrasion and shaft breakages causing asymmetrical, shallowly forked, and square tail shapes (latter two uncommon, but can resemble Madeiran Petrel). Pale yellow/white shaft bases to outer primaries (similar to Swinhoe’s Petrel) occur frequently, although rarely extensive or pure white (<0.5% birds examined at St Kilda, *n*=700).

NOTE: Appearance of black, grey and brown plumage tones very variable according to light (e.g. under artificial light at night).

Geographical variation Within nominate *leucorhoa* negligible, except birds from southern region of East Pacific range (slightly smaller, more frequently dark rumped). Three other subspecies recognized (N. America).

Biometrics Full-grown. Nominate *leucorhoa* (BWP).

Wing	♂158	(3.76;47)	148-165	♀158	(3.56:54)	152-166
Bill	15.7	(0.46;50)	14.2-16.6	15.7	(0.50;56)	14.7-16.9
Tarsus	24.0	(0.58:50)	22.9-25.5	24.1	(0.70;55)	22.3-25.5

References Ainley, Lewis & Morrell (1976), Baker (1984), Power & Ainley (1986), Brooke (2004), Hedd & Monetevecchi 2006, Flood & Thomas (2007), Rob, Mullarney & The Sound Approach (2008), Miles (2010).

Reference list

Ainley, D.G., Lewis, T.J. & Morrell, S. (1976) Moult in Leach’s and Ashy Storm-petrels. Wilson Bulletin, 88: 76-95.

Baker (1984), A guide to ageing and sexing non-passerines (part 9). Ringers’ Bulletin, 6: 70-74.

Brooke, M. (2004) Leach’s Storm Petrel. In: *Albatrosses and Petrels across the World* pp407-410. Oxford University Press Inc., New York.

Flood, R.L. & Thomas, B. (2007) Identification of ‘black-and-white’ storm-petrels of the North Atlantic. British Birds, 100: 407-442.

Hedd, A. & Montevecchi, W.A. (2006) Diet and trophic position of Leach’s Storm-petrel *Oceanodroma leucorhoa* during breeding and moult, inferred from stable isotope analysis of feathers. Marine Ecology Progress Series 322: 291-301.

Miles, W. (2010) Variation in the appearance of adult and juvenile Leach’s Storm-petrels *Oceanodroma leucorhoa* on St Kilda. British Birds 103: 721-727.

Power, D.M. & Ainley, D.G. (1986) Seabird geographic variation: similarity among populations of Leach’s Storm-petrel. The Auk, 103: 575-585.

Robb, M. & Mullarney, K. & The Sound Approach (2008) *Petrels night and day: A Sound Approach Guide*. The Sound Approach Poole, Dorset. 300pp.

Chapter 7

Behaviour and diet of non-breeding Snowy Owls *Bubo scandiacus* at St Kilda

Published as:

Miles, W. T. S. & Money, S. 2008. Behaviour and diet of non breeding Snowy Owls on St Kilda. *Scottish Birds* 28: 11-18.

ABSTRACT

We report numbers of individual Snowy Owls, their behaviour, and diet on Hirta, St Kilda, between late May and early August 2007. Five different individuals were identified and movement of different individuals to and from Hirta was regular. Compared with previous records, sightings in 2007 were very frequent and the number of different birds recorded was high. Favoured roost sites were perches sheltered by natural or ancient artificial stone structures, with good vantage. Territorial, courtship or nesting behaviour was not observed on any occasion. Prey species recorded in the diet were few. Most commonly found were remains of the endemic subspecies of St Kilda Field Mouse and adult Atlantic Puffins, including a 27 year old ringed bird. A Great Skua chick was the only other prey species found in pellets.

INTRODUCTION

Snowy Owls *Bubo scandiacus* are scarce vagrants to Scotland (Forrester et al 2007). Records are almost annual and are most frequent from the Northern and Western Isles (Scottish Bird Reports 1970-2001, Thom 1986). Individuals have arrived in all months of the year, but there is a clear peak in April and May (Forrester et al 2007). Long staying Snowy Owls are not infrequent, but the only records of nesting in the UK are a pair which bred annually on Fetlar, Shetland, between 1967 and 1975 (Tulloch 1968, Sharrock 1976, Pennington et al 2004). Diet of these birds was studied by pellet analysis and consisted primarily of Rabbits *Oryctolagus cuniculus* and wader chicks (Robinson & Becker 1986). Worldwide, Snowy Owls prey mostly on small mammals, although feeding on birds is not at all uncommon (eg del Hoyo et al 1999, Hakala et al 2006). There have been very few studies of the diet of non breeding Snowy Owls in Scotland. Systematic collection of pellets is difficult in this situation, as migrant owls may not stay for long, can range over very large areas, and numbers of individuals present are not always easy to assess (Scottish Bird Reports 1970-2001). Ageing and sexing single owls in the field is not always straightforward, except in the case of adult males (Forrester et al 2007). On St Kilda, 12 Snowy Owls have been recorded in 9 of the 45 years from 1962 to 2006 (Harris & Murray 1978, Murray 2002, Murray pers comm 2007). In 2007, there were exceptional numbers of Snowy Owls on St Kilda, involving several different individuals. This study was carried out on Hirta, St Kilda, between late May and early August 2007, and aimed to make an accurate record of the number of individuals present, to observe their behaviour and use of habitat, and to record their diet.

METHODS

The study was conducted on Hirta, the largest island in the St Kilda archipelago (57°49′N, 08°35′W), an area of 628.5h with elevation to 426m. Habitat is primarily vegetated sea cliffs and maritime heath and grassland, dotted by ruins of many hundreds of cleits – stone shelters historically used by St Kildans for drying and storing seabirds. Data were collected between 20 May and 6 August 2007. The number of individual Snowy Owls on Hirta was assessed by direct observations, detailed field notes of plumage, and digital photographs of all birds encountered, also used to help judge birds' sex and age. Particular attention was paid to the exact positions and extent of black spots and barring in the plumage.

Positions of roosting birds were noted daily, as an indication of where best to search for indigestible prey remains (regurgitated as pellets) and of habitat use by roosting Snowy Owls. Observations of other Snowy Owl behaviour, such as interactions with each other and with other species, were made incidentally and recorded by detailed field notes and, where possible, digital photography.

Diet was assessed from pellets, collected from the areas on Hirta where owls were seen to roost. Roosts were systematically checked for pellets every 6-8 days, even in periods when no owls were known to be present on Hirta. Pellets ranged in condition from warm, wet and slimy (very fresh) to dry, bleached and cracked (at least a few days old). Distinction of Snowy Owl pellets from those of Great Skua *Stercorarius skua* and Great Black-backed Gull *Larus marinus* was very easy, based on pellet size, Snowy Owl pellets were more than twice the size of pellets dropped by skuas and gulls, cylindrical compared to the oval shape of those of skuas and gulls and the texture of feather and fur remains tended to be more finely ground and compacted in Snowy Owl pellets. Skulls were absent from many pellets, and so regurgitated remains were mostly identified from a combination of tarso-metatarsi, pelvises, jaws, vertebrae, claws, feathers, fur and skin remains. Age classes of bird prey were determined, where possible, by comparison of the size, shape and skin colour of relatively undigested and complex remains, such as complete leg and foot arrangements from differently aged Atlantic Puffins *Fratercula arctica*. Presence in a pellet of one or more identifiable remains of an individual animal was considered representative of one occurrence as prey, identical remains of 2 individuals of the same species representative of 2 occurrences, etc, even if other major skeletal elements were missing. The proportion of total prey, expressed as percentage mass of all individuals recorded from pellets for each prey species, was calculated using mean adult and unfledged juvenile weights published by Boyd (1956) and Cramp et al (1985).

RESULTS

By comparison of field observations, notes and photographs, a total of 5 different Snowy Owls were identified on Hirta between 24 May and 5 August 2007 (Table 7.1). The study lasted 77 days and owls were seen on 63 days. Two birds were present together from 4 to 19 June (an adult male and adult female) and 10 July to 1 August (2 sub adult males), but on other dates only single birds were seen. Display or nesting behaviours (eg Murie 1929, Sutton & Parmelee 1956, Watson 1956, Tulloch 1968) were not observed on any occasion. Birds' age and sex were judged by reference to information on plumage characters from previous studies and photographic identification resources (eg Josephson 1980, Cramp et al 1985, British Birds Interactive 2007). In most cases we were confident in determining males from females. Age was more difficult to assess from plumage. Two birds did not show adult plumages but younger plumages not easily assignable to an exact age class (eg first year, second year, etc.), so were categorised 'sub adult'. Age and sex is parenthesised for Individual 1 (Table 7.1) because it showed plumage characters almost entirely typical of a first year male yet not absolutely distinct from characters shown by some females.

Snowy Owls were most frequently seen roosting on, or within, stone structures: either natural crevices among crags and boulders (e.g. Figure 7.1) or perched within the ruins of cleits. Only occasionally were Snowy Owls seen roosting away from these very sheltered habitats, when perched out on relatively open grassland in shallow dips or hollows in the ground. Roost sites were relatively few, some were heavily used, and they were localised, mostly away from the coast (Figure 7.2). By far the majority were high up on the slopes of hills, in good vantage positions. Only once was a bird seen roosting at the base of a hillside, within one of the cleits in Village Bay. On the occasions when 2 Snowy Owls were seen on Hirta simultaneously, roost sites were sometimes relatively close together, down to a minimum estimate of 10 metres. No aggressive or territorial behaviour was observed between individuals and they seemed highly tolerant of each other. Interactions between Snowy Owls and other bird species were seen infrequently and rarely involved owls that were roosting. Snowy Owls were occasionally seen in flight during daylight and were then often mobbed by Great Skuas, Ravens *Corvus corax* and Hooded Crows *Corvus cornix*. Great Skuas far outnumbered corvids on Hirta, and Snowy Owls were mobbed relatively heavily by skuas, sometimes involving over 20 individuals (never more than 10 Crows or 2 Ravens) chasing any one owl. Surprisingly, actual contact between birds during mobbing was very rare. Mobbing of a roosting Snowy Owl was seen on only one occasion and involved a Great Skua pair mobbing a male owl (Individual 4) perched in a relatively exposed position in open grassland, presumably within the skuas' nesting territory.

A total of 24 pellets were found and all contained remains of at least one identifiable prey species (Table 7.2). Remains from more than one prey species were found in 4 pellets, 3 containing a mixture of adult Atlantic Puffin and St Kilda Field Mouse *Apodemus sylvaticus hirtensis* remains and one a mixture of adult Atlantic Puffin and juvenile Great Skua remains. Prey species found most frequently in pellets were St Kilda Field Mouse (32 individuals from 14 pellets) and adult Atlantic Puffin (12 individuals from 12 pellets). Least frequent were remains from one juvenile Atlantic Puffin and from one juvenile Great Skua. Although mice predominated in the diet in terms of numbers, the much larger size of puffins means that the Snowy Owls obtained a far greater proportion of prey, in terms of total mass of individuals consumed, from puffins than from mice (Table 7.2).

Table 7.1. Summary of different individual Snowy Owls seen on Hirta, St Kilda, between 24 May and 6 August 2007

Individual	**Duration seen on Hirta**	**Sex & age**	**Summary of plumage features used to distinguish individual**
1	24 May - 31 May	(M 1st year)	Black spotting on forehead & crown. Nape, neck & neck sides clean white. Large white bib. Dense, narrow black barring on under parts. Heavy black barring across scapulars, mantle, back and wing feathers.
2	4 June – 19 June	F adult	Black spotting on forehead, crown, nape & neck sides. Black barring on under parts. Small white bib. Very large black sub terminal crescents on tips of almost all feathers across mantle, back, scapulars and wings.
3	4 June – 29 June	M adult	All plumage clean white except for occasional very small black spots on outer primaries and very occasional black spots on scapulars. Extremely faint and sparse narrow brown barring on lower belly.
4	8 July – 1 August	M sub adult	All plumage clean white except for very infrequent small black spots and bars on scapulars, mantle, back and wing feathers. Heavy black barring on tertials.
5	10 July – 5 August	M sub adult	Faint brown spotting on forehead. Crown, nape, neck & neck sides clean white. Very large white bib. Dense, very faint, narrow brown barring on under parts. Black barring across scapulars, mantle, back and wing feathers.

Table 7.2. Summary of diet of non breeding Snowy Owls on Hirta, St Kilda, from 24 May to 6 August 2007

Prey species	**Number of pellets (n=24) in which prey species occurred**	**Number of individuals**	**Proportion of total prey**	
			(% no. individuals)	**(% mass individuals)**
St Kilda Field Mouse *Apodemus sylvaticus hirtensis*	14	32	69.6	16.8
Atlantic Puffin (adult) *Fratercula arctica*	12	12	26	63.5
Atlantic Puffin (juvenile) *Fratercula arctica*	1	1	2.2	3.6
Great Skua (juvenile) *Stercorarius skua*	1	1	2.2	16.1

Figure 7.1. Adult male Snowy Owl (Individual 3, Table 1) at a typical roost site on Hirta: sheltered by boulders and high on the ridge of a hill. Feet and talons were occasionally seen used in defence against Great Skuas.

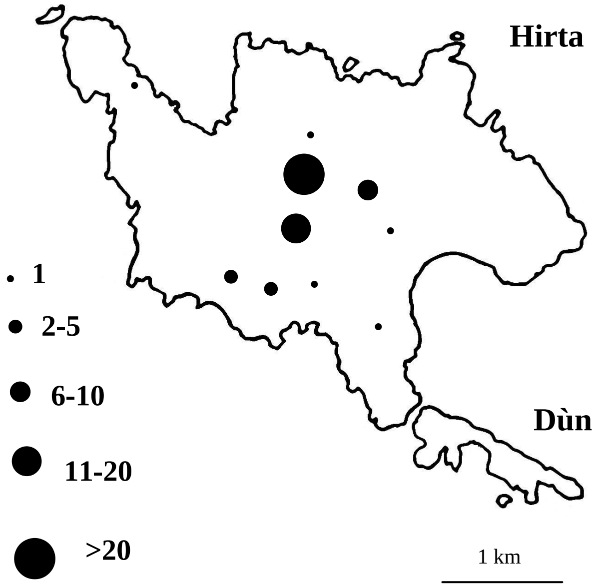


Figure 7.2. Distribution of Snowy Owl roost sites observed on the islands of Hirta and Dùn, St Kilda, between 24 May and 6 August 2007. Size of circles indicates the number of times roost sites were seen in use.

DISCUSSION

The number of individual Snowy Owls recorded during the study was surprisingly high, relative to previous records on Hirta since 1962. These, and the duration of sightings on Hirta, were indicative of a relatively high turn over and movement of Snowy Owls to and from St Kilda between late May and early August in 2007. Outside of the period of this study, there were records of Snowy Owls on St Kilda in 2007 in April, early May, late August and September. However, those records were not detailed or systematic in recording the identification of individuals, duration of stay, behaviour, or diet, so are extremely difficult to relate to this study. They do, however, emphasise the exceptionally frequent occurrence and movement of Snowy Owls on St Kilda in 2007. Identification of individual owls was only possible in this study from daily observations, detailed field notes, and digital photographs of all birds encountered. Without these, it is possible that numbers may have occasionally been underestimated in the past. When identifying individuals, careful consideration was given to effects of plumage bleaching, wear and moult, especially as the study progressed into July and August, when these processes have greatest effect (Josephson 1980, Cramp et al 1985). Even so, plumage details of Snowy Owls encountered in this study, particularly the exact position, shape and size of dark spots and bars, appeared highly specific to individuals. This supports observations of individual variation from other studies and Scottish records of Snowy Owls (Tulloch 1968, Josephson 1980, Forrester et al 2007). It is possible that comparison of detailed photographs of Snowy Owls' plumage could be used with caution to identify individuals and their movements within the UK. This would be particularly useful in areas with relatively frequent records of Snowy Owls, for example to identify inter island movements and numbers of Snowy Owls within the Western Isles. Despite identification of individual Snowy Owls in this study from plumage, we still found it difficult to age and, to a lesser extent, sex birds on plumage criteria. Sexual dimorphism was especially difficult to judge in the field. However, size differences between the sexes and plumage differences between age classes are not always discrete (Earhart & Johnson 1970, Josephson 1980).

Roost sites sheltered by natural and artificial stone structures were apparently favoured above roost sites on more open ground. This may have been due to more sheltered sites affording protection from very bad weather conditions which are frequent on St Kilda and from skuas and corvids which mob the owls. Large areas of the open grassland and maritime heath on Hirta are occupied by breeding Great Skuas (>180 pairs) and owls may have been deterred from using these areas by the highly aggressive behaviour of skuas defending their nesting territories. Snowy Owls seen being mobbed in flight and, on one occasion, on the ground by skuas, did not seem very reactive to the treatment, and mostly avoided dive bombing from skuas simply by briefly ducking down out of the way. However, no owl was ever seen in a position very close to skua eggs or chicks. Defensive behaviour by adult skuas is usually most intense when the clutch and chicks are under greatest threat (Furness 1987). Perhaps owls are more reactive to this degree of mobbing intensity, and are then deterred effectively. Only very rarely was actual contact observed between a Snowy Owl and skuas mobbing it, and only when owls were in flight. On these occasions the owls' reaction was spectacular. After the moment of contact, and typically when the next mobbing dive was made, the owl would flip over, momentarily fly upside down and bare or swipe its talons up at the attacker. This usually caused mobbing to cease immediately. The only other major response seen to be made by Snowy Owls in response to mobbing behaviour was loud wing clapping in flight. This, however, was apparently very rare and only seen on 3 occasions. Owls were occasionally flushed accidentally by humans from particularly secluded roost positions. In this case, they usually moved to a new roost position close by, did not fly far and never to a different island in the archipelago. The owls were silent in flight and never heard making any vocalisations. Roosting Snowy Owls were generally very visible, despite their sheltered locations, but it is conceivable that owls occasionally roosted undetected on Hirta and therefore the duration that individuals were present may be underestimated. The likelihood of such inaccuracy is probably low, however, given that after the first day that any individual owl was not seen on Hirta, it was never sighted again during the study period. Snowy Owls were never seen on Soay, Dun or Boreray, but observer coverage was incidental and limited by access restrictions and suitable vantage points from Hirta.

Other than sheep and humans, the St Kilda Field Mouse is the only terrestrial mammal present on Hirta, and it was not surprising that the species formed a high proportion (69.6%) of the total individuals found in Snowy Owl pellets. The mouse is an endemic subspecies to the archipelago but its population size is not well known. Snowy Owls have been shown to favour mammalian prey if available (eg Murie 1929, Gross 1944, Robinson & Becker 1986) so the fact that adult puffins formed the majority of prey by mass may indicate that density of mice on Hirta was inadequate to allow owls to feed entirely on a mammalian diet. It should be noted, however, that the sample size of pellets was small although representative of several owls. The small number of pellets found at roost sites also suggests that prey remains may have been regurgitated away from these areas, possibly on the hunting grounds where they were likely to lie undiscovered. Frequency of body parts of prey found in pellets was variable between prey species. Skeletal remains of mice were representative of the entire body (including skulls and jaws), while skeletal remains of puffins were much less representative, typically comprising complete leg and foot arrangements, ribs, spine and occasional other body parts, but never remains of the head. This supports other studies that suggested prey handling by Snowy Owls differs according to prey species (eg Wiggins 1953, Williams & Frank 1979). In this case, mice were apparently swallowed whole but puffins were swallowed in pieces less than, or equal to, body size minus the head. One of the greatest surprises of the study was a metal BTO ring found on a puffin tarsus in a Snowy Owl pellet. This puffin had been ringed as a newly fledged juvenile on Hirta in 1980. Surprisingly, Snowy Owl pellets did not contain remains from any of the other 17 species of seabird that breed on Hirta, apart from a single Great Skua chick. Prey selection by Snowy Owls of burrow nesting and nocturnal seabirds, such as alcids and storm-petrels, has been recorded in North America (Williams & Frank 1979). Puffin colonies on St Kilda are in close proximity to very large colonies of Leach's Petrels *Oceanodroma leucorhoa*, European Storm-petrels *Hydrobates pelagicus* and Manx Shearwaters *Puffinus puffinus*, so perhaps remains from other species would have been found in Snowy Owl pellets, had the sample size been larger in this study. Foraging behaviour of Snowy Owls was never directly observed. Owls were seen roosting at all times of the day and it seems likely that prey was caught mostly at night. Predation of puffins, however, may have occurred more towards dusk and dawn, when puffins are more active at their colonies than they are during the night, when most are underground or out at sea (Harris 1984). We found no evidence of Snowy Owls attempting to catch nocturnal seabirds, such as storm petrels and shearwaters. Predation of nocturnal seabirds by Great Skuas is generally a very unusual occurrence, but is relatively common on St Kilda where skuas feed extensively on Leach’s petrels (Votier et al. 2005). The owl pellet containing skua remains was found before most juvenile skuas on Hirta had fledged. Finding remains from a juvenile Great Skua in a Snowy Owl pellet was therefore surprising, as when young skuas are under threat from predators the parents are generally adept at defence. It begs the question of whether this juvenile skua was eaten because it had been left undefended at night by parents away hunting storm petrels. Species of prey found in Snowy Owl pellets in this study are only seasonally abundant on Hirta, as in winter the majority of seabirds are absent and mouse numbers are much reduced (Quine 2000, Mitchell et al 2004). Previous records of Snowy Owls on St Kilda include one from 14-28 November 1962 (Harris & Murray 1978, Murray 2002), which presumably would have had to survive mainly on mice, as few seabirds would be present on the archipelago in November. From pellet analysis in future, it would be interesting to know what exactly is eaten by Snowy Owls present on the islands in winter.

ACKNOWLEDGEMENTS

WM was funded by NERC and NTS through a CASE studentship to Glasgow University. SM was employed by NTS in 2007 as the St Kilda Seabird and Marine Ranger. Thanks to Martin Culshaw, Johanne Ferguson, Christina McAvoy and Roddy McCleod for access to their digital photographs and references, as well as to Terry Fountain - for many images, including Figure 1. Thanks to Stuart Murray for his helpful suggestions and St Kilda Snowy Owl records from 2000 to 2006. Helpful comments on the draft were given by Bob Furness, Richard Luxmoore and Roger Riddington.

General Discussion

Summary of main findings

Great Skuas at St Kilda exert a sustained and considerable predation pressure on Leach's Storm-petrels. Estimated annual numbers of Leach's Storm-petrels eaten by skuas were variable but averaged approximately 21,000 individuals per year, and never less than 11,600. With this level of predation it is surprising that the two most recent population surveys of Leach's Storm-petrels breeding at St Kilda (made on Dùn in 2003 and 2006) did not show any significant decline (Newson et al. 2008). It is extremely likely that 'wandering' non-breeding Leach's Storm-petrels from other colonies play an important role in reducing predation impacts on the resident breeding birds (see below).

The St Kilda Great Skua population was found to be declining slightly, in contrast to the exponential growth recorded between 1990 and 2000. Nocturnal foraging on storm-petrels and shearwaters was widespread and common throughout the population; a unique situation within Scotland. Prey specialisation by skua pairs on nocturnally active seabirds, diurnally active seabirds or fish was relatively rare and inconsistent, although limited fitness advantages were associated with dietary specialisation over a non-specialist, generalist diet. Most pairs, including dietary specialists, fed on a diversity of prey, including a variety of species of seabird, fish and shellfish, and prey switching between years was extremely common. Dietary flexibility is likely an advantage for skuas at St Kilda, where intra-specific competition is apparently intense and prey populations seem prone to fluctuate (Mitchell et al. 2004, Money 2007 & 2008, Newson et al. 2008, JNCC unpublished data 2009). Very few skua pairs (<7) were found to specialise on Leach's Storm-petrels in any one year of the study, and none were observed to do so consistently in every year.

Night time observations of the behaviour of Leach's Storm-petrels and Great Skuas, as well as evidence from recaptured Leach's Storm-petrels which had been ringed and measured at St Kilda, suggested that individuals eaten by skuas were mostly non-breeders. Skuas were observed successfully hunting Leach's Storm-petrels in a range of light conditions, including extreme darkness, primarily by pursuit on foot of grounded storm-petrels but also, occasionally, by chasing individuals in flight. Vocal activity and colony attendance by Leach's Storm-petrels were finely attuned to changes in natural light conditions (both highest when nights were darkest), and this likely reduces predation risk on land via predator swamping. However, specific recognition of Great Skuas and specialised counter-predator adaptations were found to be totally lacking. Leach's Storm-petrels were apparently entirely naïve to the threat posed by Great Skuas, and individuals on the surface of the breeding colonies were captured easily by skuas, apparently with very little effort.

Mortality of Leach's Storm-petrels due to attraction to artificial lights was found to be very uncommon at St Kilda and elsewhere in the UK, although in most years a small number of juvenile petrels are found (alive) grounded on land in the autumn close to lights. Deliberate light reduction measures mitigated the attraction of storm-petrels to artificial lights at St Kilda. However, such measures did not always reduce numbers of young Manx Shearwaters found grounded. More so than storm-petrels, shearwaters seem to be attracted by artificial low-frequency sounds, as well as lights. Examination of Leach's Storm-petrels that were found grounded near lights, that were mist-netted, and that were temporarily sampled from burrows during the study period, showed that distinctive differences exist between the plumage of adults and juveniles; also, that the plumage of adults is highly variable and certain features can resemble those of other species of storm-petrel. One of the biggest surprises of the study was to find a predator on St Kilda that killed skuas. Unusually high numbers of Snowy Owls were encountered at the archipelago in all years, but particularly in 2007, and were found to predate Puffins, the endemic St Kilda Field Mouse, and Great Skuas.

The potential importance of non-breeding Leach's Storm-petrels at St Kilda

Estimates of annual numbers of Leach's Storm-petrels eaten by Great Skuas at St Kilda were consistently high, and would have a sustained, severe impact on the breeding population if additional, non-breeding birds were not available. No significant change in the breeding population was shown from the most recent two population surveys (on Dùn in 2003 and 2006); the population appeared relatively stable and it seems extremely likely that during the breeding season there is a substantial 'input' of non-breeding birds to the archipelago, some of which are eaten by skuas.

Non-breeding Leach's Storm-petrels wander between colonies during the breeding season (Wernham et al. 2002, Brooke 2004). Given the species' almost entirely pelagic lifestyle, as well as storm-petrel ringing recoveries showing trans-ocean movements, it is extremely likely that during the breeding season non-breeding Leach's Storm-petrels originating from colonies away from the UK temporarily visit St Kilda. Theoretically, such 'visitors' could number over a million different birds per year if, for example, non-breeders originating from the huge Leach's Storm-petrel colonies on Newfoundland and Iceland wander far around the North Atlantic prior to breeding. This does not seem an unlikely scenario, given that Leach's Storm-petrel is a highly aerial species to which the sea is no barrier, has a protracted pre-breeding period (average five years), and we know that individuals can travel huge distances across oceans in relatively little time. For example, Leach's Storm-petrels ringed in Newfoundland have been found in the Bay of Biscay (Huntingdon et al. 1996). Additionally, in the 1960's, as part of a homing experiment, seven individuals were taken from burrows on Kent Island, New Brunswick, flown by plane to England and released from Selsey Bill, Sussex (Billings 1968). The fastest two birds got back to their burrows 13.7 days later, having flown 4800km across the Atlantic Ocean at an average speed of 350km per day!

I propose that tens of thousands of non-breeding Leach's Storm-petrels temporarily visit St Kilda every year but do not originate from the archipelago. It is probably these birds that are eaten in greatest quantity by skuas and not the resident breeders, since breeding petrels apparently fly directly to their burrow, whereas prospecting immatures spend much time flying and vocalising over and on the surface of the colony. Non-breeding Leach's Storm-petrels fledged from colonies far from St Kilda, but which may visit the archipelago, are therefore potentially very important to the sustained existence of the St Kilda breeding population. 'Vagrant' non-breeders may in effect protect the resident breeders from predation. Non-breeders fledged from colonies other than St Kilda may also help sustain the St Kilda breeding colony by selecting to nest at the site and themselves adding to the breeding population.

To date, no evidence has been found to suggest that the St Kilda Leach's Storm-petrel colony is isolated from other colonies in the Atlantic (nor from most others in the Pacific) or that mixing of non-breeding individuals between colonies does not occur. Absolute differences in the genetics, morphology, vocalisations, parasites or life history of individuals have so far not been found between birds sampled at different colonies in the Atlantic (Paterson & Snyder 1999, Brooke 2004, Robb et al. 2008, R. Palma pers. com. 2009). Conversely, evidence from ringing recoveries has shown that individuals often visit more than one breeding colony during the breeding season and are entirely capable of travelling long distances across the sea between colonies. The human tendency to conceptualise islands as insular ecosystems isolated by the sea does not seem so appropriate with regard to the ecology of a highly pelagic and far-flying seabird such as Leach's Storm-petrel.

Currently, the University of Plymouth is carrying out a research project to determine the genetic identity of breeding and non-breeding Leach's Storm-petrels at colonies in Iceland, Newfoundland and the UK, including St Kilda, and the degree of mixing of individuals between colonies. It is hoped that this will shed much light on the extent to which non-breeding individuals born at colonies away from the UK may annually occur at St Kilda, and whether many settle to breed at the archipelago.

* * * * * * *

The behaviour of non-breeding Leach's Storm-petrels at breeding colonies is not well known, other than that individuals visit different colonies before breeding and apparently spend much time on the surface of colonies at night, inspecting burrows and emitting sexual vocalisations. However, it is likely that non-breeders 'try out' courtship, pairing, burrow occupancy, nest building and egg-laying in one or more years prior to successful breeding. Evidence for this, for example comes from studies of the breeding ecology of storm-petrels at St Kilda, Shetland and the Azores, where natural burrows and artificial nest boxes have often been found containing nesting material or an adult storm-petrel, but then no egg was laid or sometimes an egg was laid but soon abandoned (Bolton 1996, Bolton et al. 2004, Money 2007 &

2008, Money et al. 2008, JNCC unpublished data 2007). It is not known precisely how often non-breeding Leach's Storm-petrels occupy burrows during the daytime or lay and abandon eggs at active breeding colonies each year. However, studies of the phenology of Leach's Storm-petrels at St Kilda, made during the daytime in 2007 and 2008 using an endoscope, revealed that no egg was laid in 26% (2007) and 14% (2008) of burrows in which birds were seen during the breeding season (Money 2007 & 2008, Money et al. 2008). Furthermore, in up to 34% of occupied burrows, either no egg was laid or an egg was laid but very soon abandoned (Money 2007 & 2008, Money et al. 2008). It is possible that desertion of burrows and eggs may have occurred due to observer disturbance; however, this seems unlikely given that burrows were only ever accessed using an endoscope, which was particularly thin and delicate, was never pushed actually into an occupied nest chamber (adults, eggs and chicks were typically viewed from a point well away from the chamber, within the access tunnel), and which did not seem to elicit any signs of stress in the birds that were viewed. During these studies, all active burrows were initially identified by a Leach's Storm-petrel responding vocally from within the burrow to tape playback of the species' chatter call (Money et al. 2008). The results suggest that non-breeding Leach's Storm-petrels occupy burrows during daytime (but do not lay eggs), respond to tape playback, and typically form a relatively high proportion of the total 'apparently occupied' burrows at a breeding colony (e.g. up to 26%). Active burrows where no eggs were laid were occupied by individuals for only a few days in total (1 to 4), typically during the early part of the breeding season in June (Money 2007 & 2008, Money et al. 2008). It is tempting to speculate that birds which occupied burrows in this fashion perhaps went on to do the same at other colonies later in the season, possibly very far away from St Kilda.

Burrow occupancy and response to tape play-back in June by non-breeding Leach's Storm-petrels has potentially important consequences on the interpretation of Leach's Storm-petrel population survey results. Population surveys of Leach's Storm-petrels in the UK, since 1999 have been carried out in June by tape playback methods (Mitchell et al. 2004, Murray et al. 2008, Newson et al. 2008). Playback surveys involve counting the number of active burrows in a given area (those from which Leach's Storm-petrels vocally respond to playback of chatter calls), and application of a calibration factor equal to the proportion of birds, from the total number present, that respond to tape playback on any one day (see Ratcliffe et al. 1998 and Mitchell et al. 2004). The timing of surveys in June is to coincide with the peak incubation period of Leach's Storm-petrels, and thus peak burrow occupancy by breeding birds, and results are generally interpreted as being representative of population sizes of breeders. However, given the results from the phenology studies at St Kilda in 2007 and 2008, it has to be considered that Leach's Storm-petrel population size estimates derived from tape playback methods likely include a relatively large, yet variable, proportion of non-breeding birds.

Potentially, the accuracy and interpretation of tape playback population surveys is very severely affected by non-breeding Leach's Storm-petrels, owing to the high and variable annual numbers of these individuals that apparently occupy nest sites, their variable responsiveness to tape playback, the typically short duration of their burrow occupancy, and the fact that when not in a burrow at the colony being surveyed, these individuals could be 'testing' burrows at colonies elsewhere (possibly on other islands being surveyed for Leach's Storm-petrels in the same year!). Further research into different ways to monitor and survey breeding Leach's Storm-petrels and to improve the accuracy of tape playback survey methods would be extremely worthwhile. Currently, it seems storm-petrel tape playback surveys may be prone to considerable inaccuracy due to non-breeders, but that this method is relatively quick, non-invasive, practical, and the best we have got.

Conservation issues

In the chapters of this study I have tried to avoid commenting on conservation issues and possible management interventions to any great extent because, ultimately, these are decided by environmental policy leaders and land owners. There is considerable evidence that Great Skuas at St Kilda eat tens of thousands of Leach's Storm-petrels every year, and have likely been doing so since at least 1996. The majority of Leach's Storm-petrels consumed by skuas are apparently not breeding birds, but are non-breeders that visit St Kilda every breeding season, it seems likely in very large numbers from colonies elsewhere, such as those in Iceland and Newfoundland. Therefore, St Kilda could be considered a sink site for thousands of wandering non-breeding Leach’s Storm-petrels from the UK colonies, probably from other colonies in the North Atlantic, and possibly from some colonies even further afield.

It is extremely difficult to know what impacts skua predation may have on the Leach’s Storm-petrel breeding colony at St Kilda. The latest two Leach’s Storm-petrel population surveys, carried out on Dùn in 2003 and 2006, did not show a significant change in the population. However, it is not easy to interpret the results of population surveys at the archipelago, given that all have been carried out using tape playback methods and there is great potential (see above) for results from this technique to be inaccurate. Additionally, there has never been a complete annual survey of the Leach’s Storm-petrel colony at St Kilda that included all islands, and most data regarding ‘the population at St Kilda’ are from tape playback surveys carried out on one island only: Dùn. A complete tape playback survey was attempted at the archipelago as part of the JNCC ‘Seabird 2000’ monitoring project, but some islands were surveyed in 1999 and others in 2000 (Mitchell et al. 2004). Leach’s Storm-petrel surveys at St Kilda were outside of the scope of this study; they require considerable manpower and are financially very costly, so it is understandable that few have been made and that these have tended not to include all islands. However, for interpretation of the impacts that skuas may or may not have on the St Kilda Leach’s Storm-petrel breeding population, admission of the potential inaccuracies of tape playback surveys, further research to improve the accuracy of breeding storm-petrel monitoring methods, and at least two complete annual surveys of the St Kilda Leach’s Storm-petrel colony, including all islands, are very necessary. In terms of defining the conservation status of Leach’s Storm-petrel as a breeding species at St Kilda, the first step surely must be to measure the size of the breeding colony as accurately as possible, including all islands in the same year, and to determine a future monitoring program.

Given the most recent information we have regarding Leach’s Storm-petrel population trends at St Kilda, showing that the colony on Dùn is apparently no longer rapidly declining, removal of skuas feeding on storm-petrels at the archipelago does not seem appropriate on conservation grounds, as a necessity to ensure the survival of Leach’s Storm-petrels. From a global perspective, such conservation management of the skua population at St Kilda for the benefit of Leach’s Storm-petrels has always been extremely questionable, given that the total world population of Great Skuas is estimated to be over five hundred times *smaller* than that of Leach's Storm-petrels (c 16,000 pairs and c. 9,000,000 pairs (minimum), respectively; Mitchell et al. 2004). Also, in practical terms, this study has shown than for the purposes of an experimental skua cull it would be extremely difficult to identify the pairs that fed most on Leach's Storm-petrels, because all pairs exhibited a tendency to switch prey between years.

Conservation interventions to selectively cull breeding Great Skuas at St Kilda do not seem particularly appropriate or feasible but, if required, interventions to increase the breeding numbers of Leach's Storm-petrels could perhaps be achieved relatively easily by habitat management. At St Kilda, the density of active Leach's Storm-petrel burrows is highest on Dùn, where the vegetation is not grazed and the birds form nesting chambers deep within the soft, dense layer of matted grass stems. The vegetation structure on Dùn is quite unlike anywhere else at the archipelago, where there is no thick grass sward because the islands are heavily grazed by sheep. Here, Leach's Storm-petrel nesting chambers occur only in natural rock crevices and deep within solid earth, at relatively low density. An experimental exclusion of sheep from sectors of the land that is currently grazed would potentially create areas with a grass sward more suitable for Leach's Storm-petrels to nest in at higher density, and could increase total breeding numbers.

Conclusions

Predation of Leach's Storm-petrels by Great Skuas at St Kilda is a very common phenomenon but as a UK conservation issue is perhaps less severe than previously thought. Currently, the population of Great Skuas at St Kilda is not increasing and, according to the latest information, the Leach's Storm-petrel colony on Dùn is no longer rapidly decreasing. Future monitoring of these populations is highly desirable. There is a particular need for the size of the Leach's Storm-petrel breeding colony at St Kilda to be measured entirely in one year, and as accurately as possible, as there are shortfalls in the completeness and accuracy of previous surveys. Adult and juvenile Leach's Storm-petrels are highly sensitive to light and further use of artificial light reduction measures in the village on Hirta in the autumn would help prevent storm-petrel attractions and groundings. At present, Leach's Storm-petrels at St Kilda apparently have no specialised counter-predator adaptations to Great Skuas. Only time will tell how critical this may be, and whether or not Leach's Storm-petrels will develop defence adaptations specific to skuas. Deliberate, selective removal of skuas does not seem an appropriate strategy for Leach's Storm-petrel conservation. An increase in breeding numbers of Leach's Storm-petrels at St Kilda could perhaps be achieved by excluding sheep from sections of the islands currently grazed; allowing thick grass swards to develop in which Leach's Storm-petrels apparently nest at relatively high density.

APPENDIX I

Personality in captivity reflects personality in the wild

Published as:

Herborn, K. A., Macleod, R., Miles, W. T. S., Schofield, A. N. B., Alexander, L. & Arnold, K. 2010. Personality in captivity reflects personality in the wild. *Animal Behaviour* 79: 835-843.

Personality in captivity reflects personality in the wild

Katherine A. Herborn[a,] *, Ross Macleod[a], Will T. S. Miles[a], Anneka N. B. Schofield[a], Lucille Alexander[b] and Kathryn E. Arnold[a]

[a]Division of Ecology and Evolutionary Biology, Faculty of Biomedical and Life Sciences, University of Glasgow

[b]WALTHAM® Centre for Pet Nutrition

* Research project leader and correspondence: K. Herborn

K. Herborn
Division of Ecology and Evolutionary Biology, Graham Kerr Building, University of Glasgow, Glasgow, U.K.
Tel. +44 141 3306626
Fax. +44 141 3305971
k.herborn.1@research.gla.ac.uk

Key Words: animal personalities, behavioural syndrome, blue tit, *Cyanistes caeruleus*, exploration, neophobia, risk-responsiveness

ABSTRACT

To investigate the ecological significance of personality, researchers generally measure behavioural traits in captivity. Whether behaviour in captivity is analogous to behaviour in the wild however, is seldom tested. We compared individual behaviour between captivity and the wild in blue tits (*Cyanistes caeruleus*). Over two winters, blue tits (N = 125) were briefly brought into captivity to measure exploratory tendency and neophobia using variants of standard personality assays. Each was then released, fitted with a Passive Integrated Transponder tag. Using an electronic monitoring system, individuals' use of feeders was then recorded as they foraged in the wild. We used variation in the discovery of new feeders to score 91 birds for exploratory tendency in the wild. At eight permanent feeding stations, 78 birds were assayed for neophobia in the wild. Behavioural variation in the captive personality trials was independent of permanent (e.g. sex) and non-permanent (e.g. condition or weather) sources of between-individual variation at capture. Individual exploratory tendency and neophobia were consistent and repeatable in captivity, and analogous traits repeatable in the wild, thus all constituted personality traits in the blue tit. Exploratory tendency and neophobia were not correlated with each other, either in the captive or wild context. Therefore they are independent traits in blue tits, in contrast to many species. Finally, exploratory tendency and neophobia measured in captivity positively predicted the analogous traits measured in the wild. Reflecting differences in the use of feeding opportunities, personality in captivity therefore revealed relevant differences in foraging behaviour between individuals.

INTRODUCTION

Confronted with the same environmental or behavioural stimuli, even within a homogenous captive environment, individuals of the same species often differ markedly in their behaviour (Verbeek et al. 1996; Gosling 2001). Notable axes of variation are aggression (aggressive-passive; Huntingford 1976), activity (active-inactive; Sih et al 1992), sociality (sociable-antisocial; Cote & Clobert 2007), exploratory tendency (fast-slow explorer; Verbeek et al. 1994) and risk-responsiveness (risk-prone-risk-averse, neophobic-neophilic or bold-shy; Clark & Ehlinger 1987; Wilson et al. 1993; Van Oers et al. 2004).Where differences in behaviour between individuals are stable across a range of situations or contexts, we refer to this variation as "personality" (Gosling 2001). Heritability in personality traits (Dingemanse et al. 2002; Drent et al. 2003; Van Oers et al. 2004) and differences in fitness or survival between personality types (Fraser et al. 2001; Dingemanse et al. 2004; Bell 2005) suggest that personality may reflect ecologically significant variation between individuals.

Few studies measure personality in the wild (but see Coleman & Wilson 1998; Réale et al. 2000; Réale & Festa-Bianchet 2003; Briffa et al. 2008; Hollander et al. 2008). To investigate the ecological significance of personality, researchers generally measure behaviour in captivity and compare the distribution or fitness of individuals in the wild thereafter (Dingemanse et al. 2004; Bell 2005). Studying behaviour in captivity has numerous advantages, notably allowing researchers to control the conditions under which all individuals are tested (Campbell et al. 2009). However, classifying personality in captivity may be misleading for two reasons. First, behaviour changes as wild individuals adapt to the captive environment (Butler et al. 2006). Where there are systematic differences in the rate of acclimation between personality types therefore, testing in captivity may exaggerate or even generate behavioural differences between personality types. For example, risk-averse or "shy" individuals take longer to recover from handling or capture stress and also to eat in a novel environment than risk-prone or "bold" individuals (Wilson et al. 1993; Van Oers et al. 2004, 2005). As food is usually withdrawn prior to personality trials and often returned within trials to stimulate behaviour, residual stress, hunger or condition may then motivate shy but not bold individuals to a greater extent in captivity than in the wild. Therefore, it is important to test that behavioural differences between personality types extend beyond the captive environment.

Second, classifying behaviour in captivity may be misleading because behaviour is often highly context specific. Isolation from the appropriate context may suppress or subvert personality traits in captivity. For example, studies carried out in captivity, in artificially constructed dominance interactions, find no linear relationship between rank and exploratory tendency in great tits (*Parus major*), and an overall a negative correlation between these traits (Verbeek et al. 1999). However in the wild, this relationship is only negative between non-territorial juvenile males, and in contests between territorial males on neutral ground, fast-explorers dominate slow explorers (Dingemanse & de Goede 2004). Indeed, within their own territory, males were dominant regardless of personality, so the absence of a territorial context in captivity may limit our ability to predict the ecological significance of captive personality traits. Another important contextual difference may be social isolation in captivity, as numerous studies suggest individuals modify their risk-taking behaviour in relation to the presence and identity of conspecifics (Van Oers et al. 2005; Boogert et al. 2006; Stöwe et al. 2006; Apfelbeck & Raess 2008; Pike et al. 2008). The relationship between different behavioural traits may also be context dependent. Bell and Sih (2007), for example find that aggression and risk-taking in a predator-naïve population of sticklebacks correlate only after exposure to a predator, suggesting that the absence of the predator-prey context affects captive personality trait estimates. Without comparing behaviour in captivity to behaviour in the wild therefore, it is impossible to assess whether or indeed which personality traits directly contribute to fitness differences observed between personality types.

We investigated individual variation in exploratory tendency and neophobia (risk-responsiveness toward novel objects) in a population of blue tits (*Cyanistes caeruleus*). To measure this variation, we used variants of two classic behavioural assays in captivity and developed versions of these for use in the wild: Verbeek et al.'s (1994) exploration test and Greenberg's (1983) novel object test. Verbeek et al.'s (1994) exploration test assigns exploratory tendency by movement in a novel captive environment. Whilst it is difficult to quantify movement *per se* in the wild, we may compare the movement of individuals by their presence at certain targets. Dingemanse et al. (2003), for example, have used the distance between the origin and endpoint of post-natal dispersal as a measure of differences in dispersal behaviour in the great tit. Here, we used presence or absence at new feeding sites, introduced within a network of established feeding stations, as a measure of exploratory tendency during foraging. Greenberg's (1983) novel object test assigns "neophobia", the aversion to the unfamiliar, by the latency to return to a known resource, for example a food bowl or nest site, in the presence of a novel object (see also Van Oers et al., 2004, 2005). The novel object appears to generate a motivational conflict between desires to obtain the resource and to avoid any unknown risks associated with the novel object (Daisley et al. 2005). This test is often used in the wild, where novel objects are introduced to familiar feeding sites, but usually for unmarked individuals (Webster & Lefebvre 2000, 2001; Echeverría et al. 2006). Using variants of these established tests, exploratory tendency and neophobia in species from a variety of taxa are often, but not universally, correlated (Clark & Ehlinger 1987; Wilson et al. 1993; but see Mettke-Hofmann et al. 2002; Coleman & Wilson 1998). Our aims were threefold: first, to determine whether variation between individuals in these trials was repeatable, and hence whether exploratory tendency and neophobia constitute personality traits in the blue tit. Second, as trait correlations may differ between contexts, to assess whether neophobia and exploratory tendency are themselves correlated in either captivity or the wild. And third, to compare exploratory tendency and neophobia measured in captivity with the analogous traits measured in the wild for the same, marked individuals.

METHODS

Studies were conducted between 2007 and 2009 in oak dominated woodland on the east bank of Loch Lomond, UK (56°08'N 4°37'W). In October 2007, we first established eight feeding stations at approximately 500m intervals. These feeding stations were removed at the end of Feburary 2008 and reinstalled in the same positions between October 2008 and February 2009. Each feeding station consisted of two tubular Defender™ feeders (35cm height, 7cm diameter) hung above one another from a bracket on an oak trunk, at approximately 2m and 3m above ground level respectively. The feeders were stocked with peanut granules, and covered with a tube of grey laminated paper to disguise cues about the amount of food available. There was one small feeding hole, so only one bird could feed at a time. We attached a wooden rectangular perch (8cm x 5cm) under this hole, onto which we laid flat a rectangular metal hoop antenna (8cm x 5cm; TROVAN®, United Kingdom). Between November and February, we captured birds as they approached the feeding stations, using mist-nets. We mist-netted three times at each feeding station in the 2007-8 season, and twice in the 2008-9 season, generally between dawn and noon, to ensure equal disturbance at each site. One hundred and twenty-five blue tits were trapped over this time (4-17 per site in 2007-8, 2-10 per site in 2008-9), and taken into captivity for personality trait testing. On first capture, each bird was fitted with a unique Passively Integrated Transponder ("PIT" tag; 11.5 mm x 2.1 mm, <0.1g, Trovan Unique™) attached to a plastic leg ring with Araldite™ glue (as Macleod et al. 2005). The PIT tag weighs less than 1% of the body mass of a blue tit hence is unlikely to affect individual behaviour. On entering the electromagnetic field generated within the antenna loop, the PIT tag produces an amplitude modulated code signal. Using an electronic monitoring system (Trovan™ LID665) we were able to identify individual birds as they used the feeders, from which we derived our wild measures of personality traits. In 2007-8, wild exploration trials were carried out between 1st February 2008 and 28th February 2008 and wild neophobia trials between 19th December 2007 and 28th February 2008. In 2008-9, both trials ran between the 11th January 2009 and 28th February. A total of 91 birds were detected at feeders in the wild: 61 in 2007-8 and 30 in 2008-9.

Personality Trials in Captivity

Birds arrived in captivity generally between 10:00 and 12:00, within 15 minutes journey time from their capture site. They were housed indoors, at a temperature of 17°C±1°C and, to conduct all tests within the captive period whilst standardising captive conditions across birds, a longer than natural 12:12 hour light:dark regime. Each bird was housed individually in a 150cm x 50cm x 50cm cage. Peanut granules, Haiths' Prosecto™ insectivorous mix and water were provided ad libitum, along with around ten *Tenebrio molitor* and two *Galleria mellonella* larvae per day. All birds were observed eating within 10 minutes of arrival in captivity. They were then left undisturbed for a minimum of 2 hours. An exploration trial was run after this period, followed by a further hour without disturbance. Neophobia trials ran between 13:00 and 17:00 on day 1 and were repeated between 08:00 and 11:00 on day 2. Following trials on day 2 in 2007-8, birds were blood sampled and then released at the site of capture at least one hour before sunset. In 2008-9, after blood sampling they were kept undisturbed in captivity for a further night, and released after a second exploration trial on the morning of day 3.

Exploratory tendency in captivity

The exploration trial was conducted within what would become the home cage of the focal bird. Each cage contained six perches, three in each half, that were covered with plastic plant vines to increase habitat complexity. The cage bottom was lined with white paper. On arrival into captivity, the bird was introduced to one side of the cage only, selected at random, the other blocked off by an opaque metal divider. We anticipated that the two hours in the cage prior to testing would create a "familiar" and, behind the divider, a "novel" environment. To assay exploratory tendency and not neophobia, the arrangement of plastic plants and perches was the same in each cage half, so that the novel environment was novel only in that it was unexplored. Prior to the trial, the food bowl and any spilt food were removed from the cage to motivate birds toward foraging activity. After thirty minutes, the water bowl was also removed. After a further thirty minutes, the observer removed the cage divider, stepped behind a screen, and observed the focal bird through a small hole for 10 minutes. Unlike other exploration trials (e.g. Verbeek et al. 1994), individuals had the option of remaining within the familiar environment. We allowed this option to help distinguish activity due to exploration from activity due to escape behaviours in the novel environment, as the birds had only been in captivity for a short period prior to testing (Mettke-Hofmann et al. 2009). A movement was defined as a hop or flight between two perches and/or the floor, the cage wall or the front and rear of the cage. The number of movements in each side of the cage was recorded, with the endpoint of each movement defining the side of the cage: novel or familiar. After the test, food and water were returned and the bird was allowed free access to the entire cage.

In 2008-9, birds underwent a second exploration trial, on day 3. On arrival into captivity, birds were randomly allotted to a cage lined either with white paper (as in

2007-8) or brown paper. The arrangement and size of perches and artificial plant material were similar between these cage types, but different leaf shapes were used in the brown versus white-lined cages. Our aim was to create two similar but distinct environments and, controlling for cage order and bird identity, there was no difference in activity (LME $t_{43} = -0.14$, $p = 0.89$) or exploration ($t_{43} = 0.49$, $p = 0.63$) between brown versus white-lined cage types. Trials were conducted as 2007-8 for days 1 and 2. After collecting a blood sample on day 2 (when birds in 2007-8 were released), we then moved each bird to one half of a new home cage, of the other cage type. They were left undisturbed until the following morning, when exploration trials began one hour after the lights were switched on.

We accounted for differences in overall activity level between birds by deducting the number of movements in the familiar environment from the number in the novel environment. This residual activity in the novel environment from the first exploration trial was our measure of exploratory tendency. We used the number of movements in the trial rather than latency to first enter the novel environment (as used in Verbeek et al. 1994) because here 56 birds entered then exited immediately as the divider was removed, and this appeared to reflect an escape or startle response toward the removal of the divider rather than exploration (K.H. pers. obs.). To investigate whether activity in general or activity specifically in the novel environment then correlated with captive neophobia or with exploration in the wild, we conducted separate analyses using the total number of movements in the first exploration trial as a measure of activity during the captive exploration trial. Four birds were excluded from the first exploration trial due to accidental disturbance immediately prior to testing, and three (including one of the above) from the second exploration trial. Exploratory tendency (Shapiro–Wilks test: $W_{120} = 0.94$, $p < 0.0001$) and activity during the exploration trial ($W_{120} = 0.95$, $p < 0.0001$) were leptokurtic and it was not possible to normalise their distributions.

Neophobia in captivity

The neophobia trial had two phases: a novel object phase and a disturbance control phase. Each bird took part in one trial on day 1 and another (with a different novel object) on day 2. Food and water were removed for thirty minutes prior to each phase.

In the novel object phase, the observer then returned the food bowl with one of two novel objects placed inside. The objects were a luminous pink plastic frog and a half of a purple rubber ball, of similar size (approximately 4cm diameter and 4cm height). The latency to approach the familiar food bowl was recorded. The object was then removed and the water returned.

Independent of differences in response toward a novel object, individuals may also differ in their motivation to feed, or their response to disturbance by the observer returning the food bowl to the cage (Van Oers et al. 2005). To control for this, we also measured latency to feed by the same procedure but without a novel object, returning the familiar food bowl only. This disturbance control phase was performed either one hour before or one hour after each novel object phase. The order of novel object and disturbance control phases was randomized on each day. One bird was excluded from one trial in the disturbance control phase due to a disruption during the trial. Of 79 birds, one bird did not approach within 10 minutes in either phase, and was excluded from analyses. A further 3 birds did not approach during the novel object phase, 1 bird during the disturbance control phase, 9 birds in only one trial of the novel object phase and 3 in only one trial of the disturbance control phase. Birds which participated in both replicates performed consistently between day 1 and day 2 in disturbance control (LME with order of trials as a random effect: $F_{1, 117} = 3.27$, $p = < 0.0001$) and novel object phases ($F_{1, 106} = 2.3$, $p = < 0.0001$) so a mean was calculated per phase per individual. Birds that approached the food bowl in only one trial of a phase were given the latency of that trial rather than a mean.

Neophobia was defined as the latency to feed in the presence of a novel object. In the wild neophobia trials (see below), birds were not disturbed as the novel object was introduced – i.e. pure neophobia was measured. Therefore, to discount the affect of disturbance from neophobia in captivity, we deducted mean latency in the control disturbance phase from mean latency in the novel object phase. As such, the 4 birds that did not approach in either trial of one phase were also excluded from the analyses. Mean risk responsiveness was leptokurtic (Shapiro–Wilks test: $W_{78} = 0.89$, $p = <0.0001$) and it was not possible to normalise this distribution.

Between-individual sources of variation

To accurately measure repeatability of behaviour in captivity, and hence define personality traits, we must first eliminate or control for covariance between behaviour and permanent (e.g. sex) or non-permanent (e.g. condition) differences between individuals that may also generate consistent individual differences in behaviour.

Permanent variables (that would not change within a field season) were wing length, age and sex. Wing length was used as a measure of overall body size; wing length was not measured in one bird. Age (juvenile/adult) was determined from plumage traits (Jenni & Winkler 1994); there were 67 juveniles and 58 adults. Sex was determined using a molecular technique from a blood sample taken at the end of day 2 in captivity (Arnold et al. 2007); there were 32 females and 86 males, and 7 birds were not sexed. Whilst dominance in Parids is highly context specific (Dingemanse & de Goede 2004), in general smaller, juvenile and female Parids are subordinate at feeders. As such, they may be more likely to take risks during foraging, and hence be faster to explore or less neophobic than larger birds, adults or males respectively.

Non-permanent variables were a combination of morphometric and environmental variables collated at capture. Morphometric measures reflecting an individual’s current state were body mass and condition. Condition was calculated as the residual of body mass at capture regressed on tarsus length (Griffiths et al. 1999); a condition measure was not obtained in one bird. Environmental variables that would affect opportunity for foraging immediately prior to entering captivity and hence starvation risk were day length, rainfall (mm) and minimum and maximum temperature for the day of, and day prior to, capture. Weather data were collated from Met office records for Glasgow Bishopton. Together, these variables should reflect or affect an individual’s perceived starvation risk on entry at capture, and hence may have short term affects on individual behaviour in captivity.

Personality Trials in the Wild

Exploratory tendency in the wild

In the wild exploration trial, birds were scored for whether or not they discovered new feeders installed within the study site. In each of nine consecutive replicates in 2007-8, and 16 consecutive replicates in 2008-9, a new feeder was installed an average of 160 meters (range: 110m-260m) from one of the eight established feeding stations. To avoid influencing concurrent neophobia trials, it was located such that the two closest feeding stations were out-with experimental manipulations. The feeder was positioned 1.5m from the nearest mature oak on a 1.5m high pole. The location was otherwise selected at random, but in 2008-9 chosen such that each permanent feeding station was closest to the new feeder on two occasions during the season, about a month apart; an arrangement used in the calculation of repeatability of wild exploratory tendency (see statistical methods). It was installed before sunrise, left undisturbed for three days, and then removed after sunset. We used PIT tag records from established feeding stations to deduce which individuals were identifiable (i.e. had not lost their PIT tags) in the wild during a replicate. As birds were added to the study as the season progressed, replication was uneven between individuals. For each replicate in which a bird participated, it was scored 0 or 1 for discovering the new feeder, using PIT tag records. Ninety-one birds were detected in the wild and included in on average 10 replicates of this trial (range 2-16). Exploratory tendency was then defined by the number of new feeders an individual did discover relative to the number it could have discovered (i.e. the number of replicates in which it participated).

Difference in site coverage by individuals may have affected the probability that they discovered new feeders, so at the end of the field season, we used PIT tag records to deduce which permanent feeders each bird had used. On average, birds used 1.8 of the eight permanent feeding stations (range 1-4). To account for differences in the distance birds would have to travel to discover each new feeder, we then calculated the distance between the nearest of these permanent feeders and the position of the new feeder in each replicate for each bird. These variables were included in the analyses of wild exploratory tendency (see statistical methods).

Neophobia in the wild

In the wild neophobia trial, birds were scored for the latency to return to an established feeding station following introduction of a “novel object”: a colourful feeder cover, substituted for the familiar grey cover. Installed at least three months prior to the study the eight “familiar” feeding stations, each with two tubular feeders with grey covers, were analogous to the familiar food bowl in the captive trials. In 2007-8, for three days prior to an experimental manipulation, we used PIT tag records to establish which individuals used and hence were familiar with the grey feeders at a given site. On the fourth day, between 12:00 and 16:30 (but on one occasion at 18:30), one of the grey covers was substituted for a coloured cover (blue, green, red or yellow). This cover was left on for 3 or 4 days then the grey cover was returned. In 2008-9, the coloured cover was left on for 1 day, starting between 12:00 and 15:00, so in both years PIT tag data was censored at 24 hours after presentation of the coloured feeder cover. In each year, this process was repeated four times at each site a minimum of 10 days apart, twice modifying the upper feeder and twice the lower feeder. The four colours were presented in a different order and combination of positions (upper or lower) at each site. Using a subset of data from 2007-8, we compared the number of PIT tag records in the first hour after introduction of the novel cover to the mean of the same hour in the three previous control days, and found a significant reduction in use of the novel feeder relative to the control (Mann-Whitney U test: $U_{24} = -2.34$, $p = 0.03$). Therefore, at the population level, the novel feeder cover elicited a neophobic response.

After introduction of a novel cover, for each bird, we used PIT tag records to count the number of visits to the control feeder before the first visit to the novel feeder. The PIT tag readers recorded the time a bird was first detected on the feeder and then whether it was still present at 2 seconds intervals until not detected. As such, a visit was defined as a record separated from previous or subsequent records by more than 3 seconds. Birds that used the novel coloured feeder first, i.e. immediately on returning to the feeding station, were given a count of zero. Birds which encountered the same colour at more than one site were included only in their first experience of that colour.

A limitation of our method is that we do not know whether a long latency to use the novel feeder reflected aversion to the feeder or simply absence from a site. Therefore we calculated the average foraging bout length using PIT tag records from experimental periods in 2007-8 as follows: the median interval between an individual's feeding station visits was two minutes, with an upper inter-quartile limit of 14 minutes. A feeding bout was then defined as a period of feeding station use bounded by periods of 14 or more minutes with no records of that bird. Using this definition, across birds the median feeding bout length at a feeding station was 42 minutes. Birds that took longer than our average feeding bout of 42 minutes to use a novel feeder after first returning to a feeding station were assumed to have left the site and were excluded from that replicate. Compared to birds taking under 42 minutes, these excluded birds were not particularly neophobic (or neophilic) in captivity (Mann-Whitney U test: $U_{97} = 330$, $p = 0.22$). Under this criterion, we obtained wild neophobia scores from seventy-eight birds, 53 from 2007-8 and 25 from 2008-9, with an average of 2 replicates per bird (range: 1 – 4). Seventy-five of these 78 birds had a captive neophobia score.

Ethical Note

All work was carried out in accordance with ASAB/ABS's guidelines for the treatment of animals in research. Work was under license of the UK Home Office and subject to ethical review by WALTHAM® Centre for Pet Nutrition and the University of Glasgow. Captive studies were completed and feeders removed 2 months before the first record of nest building in the area. Whilst we routinely weighed the birds prior to release to ensure they had not lost more than 10% body mass in captivity, there was on average a body mass gain (2.97% ± 7.3%). Following release at the site of capture, 108 out of the 125 birds were later recorded using the feeders or re-trapped in the area. Permission for holding birds in captivity and for using PIT Tags was obtained from Scottish Natural Heritage and the British Trust for Ornithology respectively.

Statistical Methods

Analyses were carried out using R 2.9.1 (R development core team, 2009). There were no differences in behavioural data between years so data was pooled across years.

Defining personality traits in captivity

We first determined whether permanent (sex, age and wing length) or non-permanent (body mass or condition, and weather and day length) between-individual variation at capture explained a significant proportion of variation in behaviour in each captive personality trial replicate. Captive personality traits were not normally distributed so we used nonparametric Mann-Whitney U-tests or Kendall rank sum correlations. We applied a Bonferonni correction for multiple comparisons, with a p-value of less than 0.004 for significance.

Consistency across days was analysed using a mixed model, with trial order as a random effect. We then calculated repeatability of captive personality measures using the mean squares from an analysis of variance, with the repeated measures of neophobia or exploratory tendency as the dependent variable and individual identity as the independent variable, following Lessells & Boag (1987). Repeatability is the proportion of variation in a trait that is explained by differences between individuals, thus larger values reflect greater within individual consistency.

Defining personality traits in the wild

Personality traits were measured repeatedly in the wild (up to 16 replicates of the exploration trial and up to 4 replicates of the neophobia trial per individual). In all analyses using wild data therefore, we accounted for repeated measures by using Generalized Linear Mixed Models (GLMMs), with a wild personality trait as the dependent variable and individual identity as a random factor. Wild exploratory tendency was binary (discovered versus not discovered) and wild neophobia a count (visits to the control feeder), thus GLMMs used either a binomial or Poisson error structure respectively. In this and all subsequent analyses of wild personality traits, we also included two variables with each wild personality trait to control for experimental variation between replicates. First, in the exploration trial, feeder discovery may depend on the distance between an individual's nearest permanent feeding station and a given new feeder. Similarly, feeder discovery may be affected by the number of permanent feeding stations an individual used (i.e. their coverage of the study site). Therefore, distance and the number of sites used were included as covariates in all analyses of wild exploratory tendency. Second, in the neophobia trial, the latency to approach a novel feeder may depend on colour or height biases. Therefore feeder colour and feeder position (upper or lower) were included as fixed main effects and an interaction (colour x position) in all analyses of wild neophobia.

Analyses of repeatability used only birds that participated in more than one replicate of a trial. Repeatability of wild personality traits was calculated using the variance component estimates for individual identity from these GLMMs, following Lessels & Boag (1987; see also Quinn & Cresswell 2005). The significance of repeatability estimates was determined using a likelihood ratio (LRT) chi-square test between the GLMM including and a GLMM excluding individual identity.

In the exploration trial, variation in feeder discovery was low, with only 47 of 91 birds discovering any new feeders. As such, high repeatability would be misleading, resulting from all individuals scoring mostly "0"s rather than consistent individual variation (i.e. between birds with mostly "1"s and birds with mostly "0"s). Feeder discovery (and hence behavioural variation) was highest amongst individuals using the closest permanent feeding station to the new feeder within a given replicate. In 2008-9, we conducted two replicates of the exploration trial within the vicinity of each permanent feeding station, around a month apart (see methods: exploratory tendency in the wild). To analyse repeatability therefore, we limited the data for each 2008-9 replicate to only birds that were using the nearest permanent feeding station and that took part in both replicates at that permanent feeding station (i.e. were PIT-tagged and not currently in captivity). Permanent feeding station identity was then included in the GLMM as a fixed effect and repeatability calculated using the variance component from individual identity nested within permanent feeding station as a random factor.

Correlations between traits

For analyses on captive traits, we performed a Kendall rank sum correlation. For analysis of wild traits, we constructed a GLMM with wild neophobia as the dependent variable. To generate a single measure of wild exploratory tendency per bird for the independent variable, which accounted for unequal replication between individuals, we created a two-vector variable with the number of feeders an individual discovered over the number of replicates in which it took part as the binomial denominator. To generate a single measure of distance between new and permanent feeding stations per individual, we took the mean distance across replicates. Along with feeder colour and position, the number of sites an individual used and this mean distance were included in the GLMM, as covariates. To test the significance of wild exploratory tendency as an explanation for variation in wild neophobia, we performing an LRT chi-square test between the GLMM including and a GLMM excluding wild exploratory tendency.

Correlations between captive- and wild personality traits

GLMMs were similar to those used when calculating repeatability of wild traits (see above). We tested whether captive personality measures explained a significant proportion of variation in wild behaviour by adding the analogous captive personality measure to these GLMMs as an independent variable, and performing a LRT chi-square test between the GLMM including and a GLMM excluding that independent variable.

RESULTS

Definition of the Captive Exploration Trait

We observed considerable behavioural variation among birds during the 10 minute trials. The number of movements ranged from zero to 605 (novel side: median = 132, IQR = 123; familiar side: median = 113, IQR = 118). In the second trial, birds were significantly more active (paired Mann-Whitney *U* test: U_{43} 151, $p < 0.0001$).

However, exploratory tendency (activity in the novel environment minus activity in the familiar environment) did not differ between trials (paired Mann-Whitney *U* test: U_{43} 501, p = 0.95).

Exploration scores did not differ between sexes or ages, (all p > 0.42), therefore data were pooled to analyse other sources of between-individual variation. With the Bonferroni correction threshold p-value of 0.004, all other morphometric and environmental variables were non-significant. Therefore consistency and repeatability of these traits were calculated on actual scores. Controlling for trial order, exploratory tendency (LME: $F_{1,43}$ 1.7, p = 0.04) and activity in the exploration trial ($F_{1,43}$ = 3.39, p = 0.0001) were consistent across replicates. Exploratory tendency across day 1 and day 3 ($F_{1,43}$ 1.71, p = 0.04, r = 0.27) and activity during the exploration trials were significantly repeatable ($F_{1,43}$ 2.56, p = 0.001, r = 0.42).

Definition of the Captive Neophobia Trait

We observed considerable individual variation during the 10 minute trials. Latencies to return to the food bowl in the novel object phase (median = 23s, IQR = 95.8s) or disturbance phase (median = 9s, IQR = 32s) varied between 1 and 590 seconds. Mean latency in the novel object phase was significantly greater than in disturbance phase, indicating that the presence of the novel object modified behaviour (paired Mann-Whitney *U* test: U_{119} = 5023, p = 0.0006).

Neophobia scores did not differ between sexes or ages (all p > 0.11), therefore data were pooled to analyse other sources of between-individual variation. As with the exploration score, all other morphometric or environmental variables were non-significant (all p > 0.1). Therefore consistency and repeatability of this trait was calculated on actual scores. Controlling for trial order, the neophobia score (novel object phase latency minus disturbance phase latency) calculated for each day was consistent across days (LME: $F_{1,103}$ = 1.77, p = 0.002). Neophobia across day 1 and day 2 was significantly repeatable (ANOVA: $F_{1,103}$ 1.77, p = 0.002, r = 0.28).

Definition of wild personality traits

In the wild exploration trial, individual discovery of feeders across two replicates within the vicinity of a given permanent feeding station was near significantly repeatable (i.e. individuals generally found both or neither feeder; GLMM: LRT χ^2 5.29, $p = 0.07$, $N = 23$ birds, $r = 0.16$). In the wild neophobia trial, individual latency to approach the novel feeder was significantly repeatable (GLMM: LRT $\chi^2 = 126.83$, $p < 0.0001$, $N = 43$ birds, $r = 0.55$).

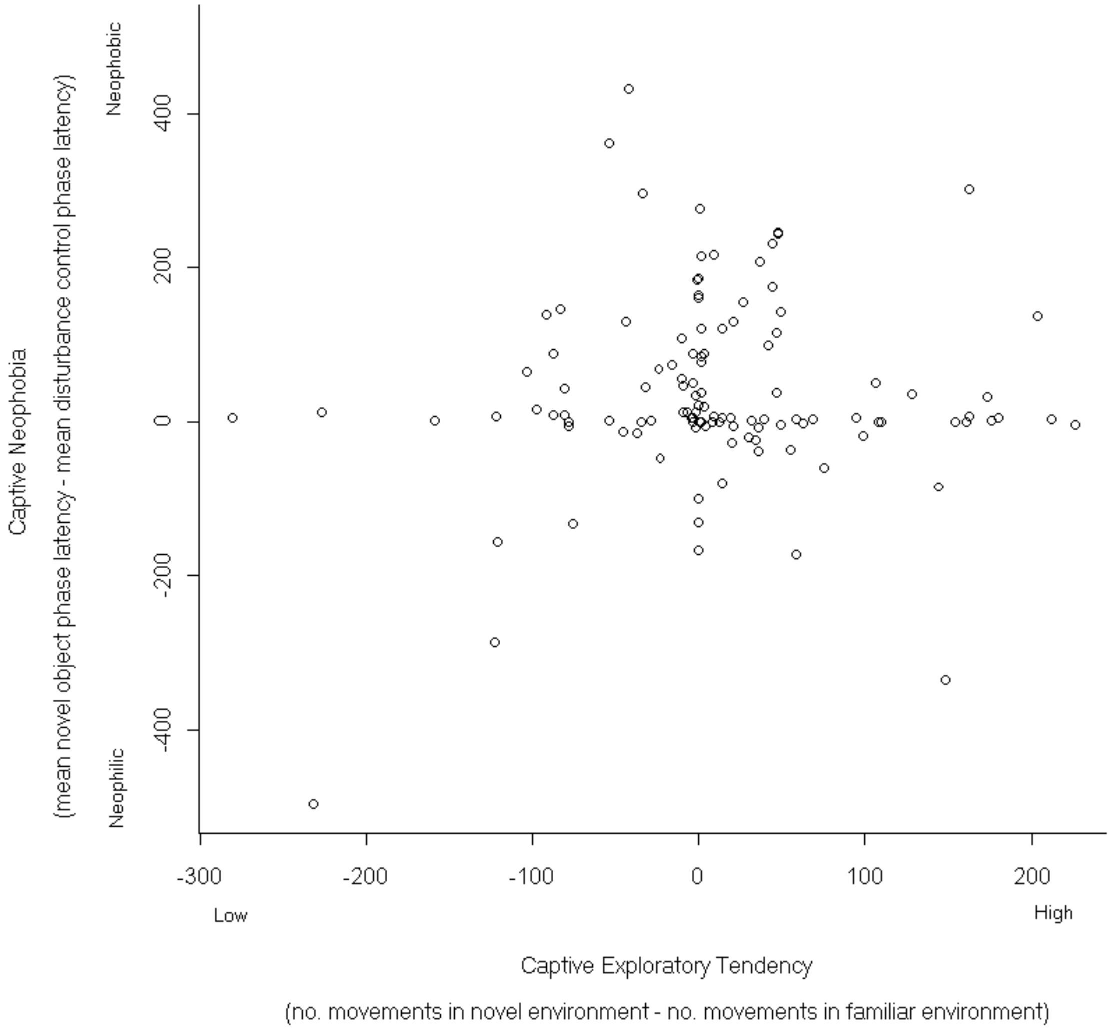
Correlations between Traits within Contexts

In captivity, neophobia did not correlate with exploratory tendency (Kendall rank correlation: tau = -0.62, $N = 115$, $p = 0.54$; see Fig. 1a) or activity in the captive exploration trial (Kendall rank correlation: tau = -0.74, $N = 115$, $p = 0.46$). Similarly, in the wild, the proportion of feeders discovered in the exploration trial did not predict an individual's neophobia (GLMM: LRT $\chi^2 = 0.66$, $N = 78$ birds, $p = 0.72$; see Fig. 1b).

Correlations between Captive and Wild Measures

Wild exploratory tendency had a significant positive relationship with captive exploratory tendency (GLMM: LRT $\chi^2 = 3.889$, $N = 91$ birds, $p = 0.04$; see Fig. 2a). There was no relationship between activity during the captive exploration trial and wild exploratory tendency (GLMM: LRT $\chi^2 = 0.002$, $N = 91$ birds, $p = 0.97$; see Fig. 2b) thus the relationship between captive and wild traits relates specifically to activity in the novel environment, i.e. exploratory tendency. Wild neophobia had a significant positive relationship with captive neophobia (GLMM: LRT $\chi^2 = 48.28$, $N = 75$, $p < 0.0001$; see Fig. 2c).

1a



(See following page for Figure legend)

1b

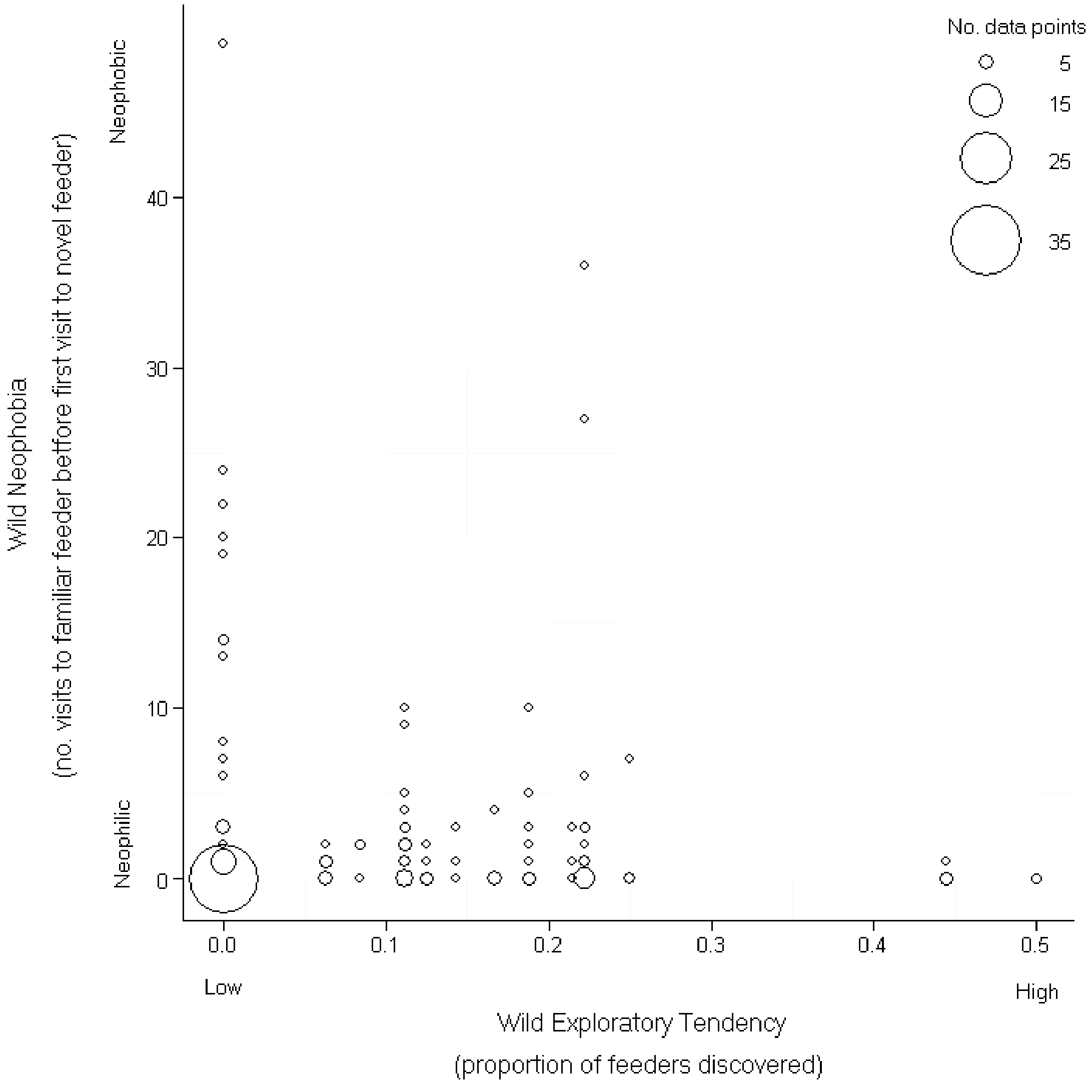
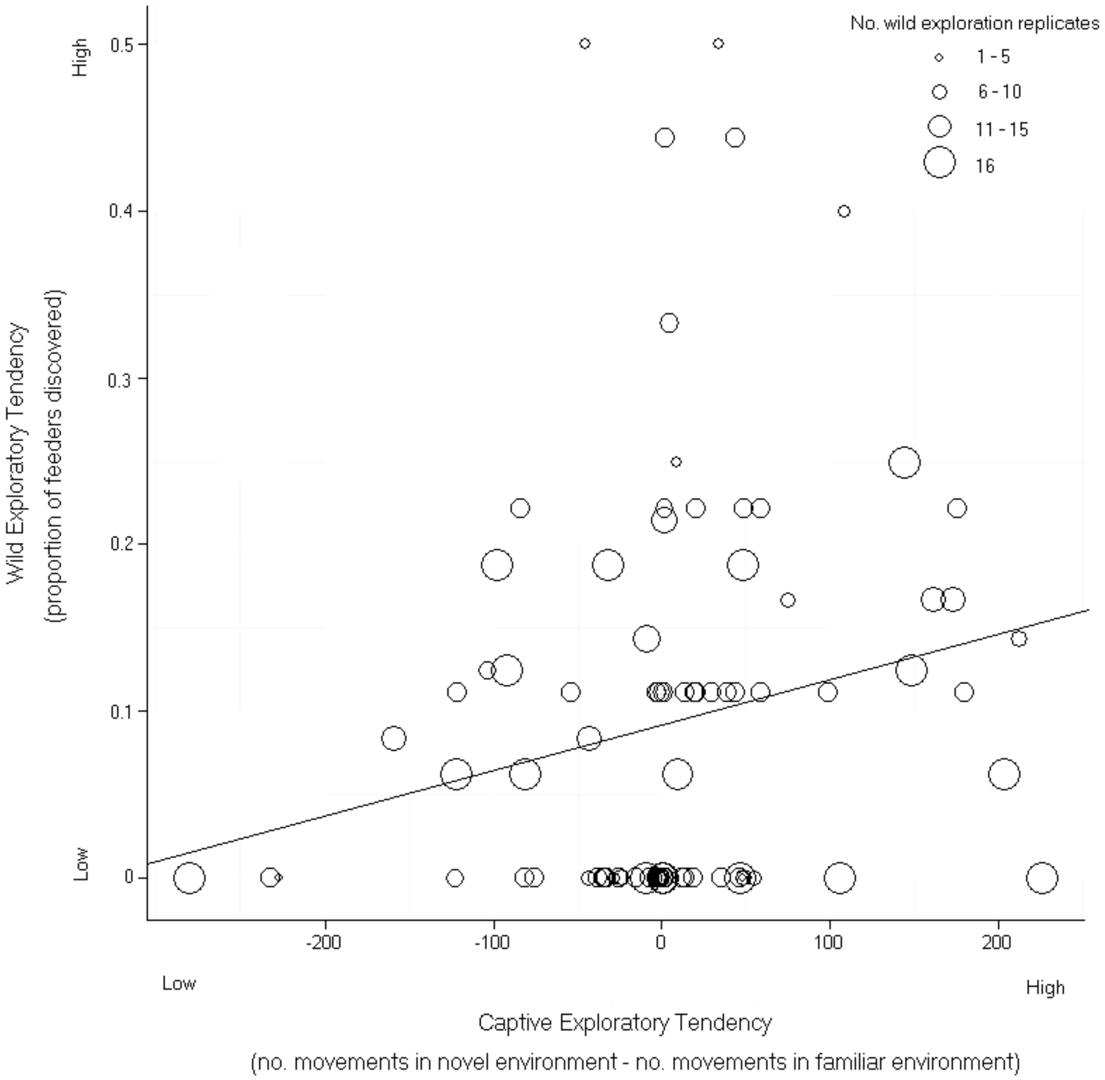


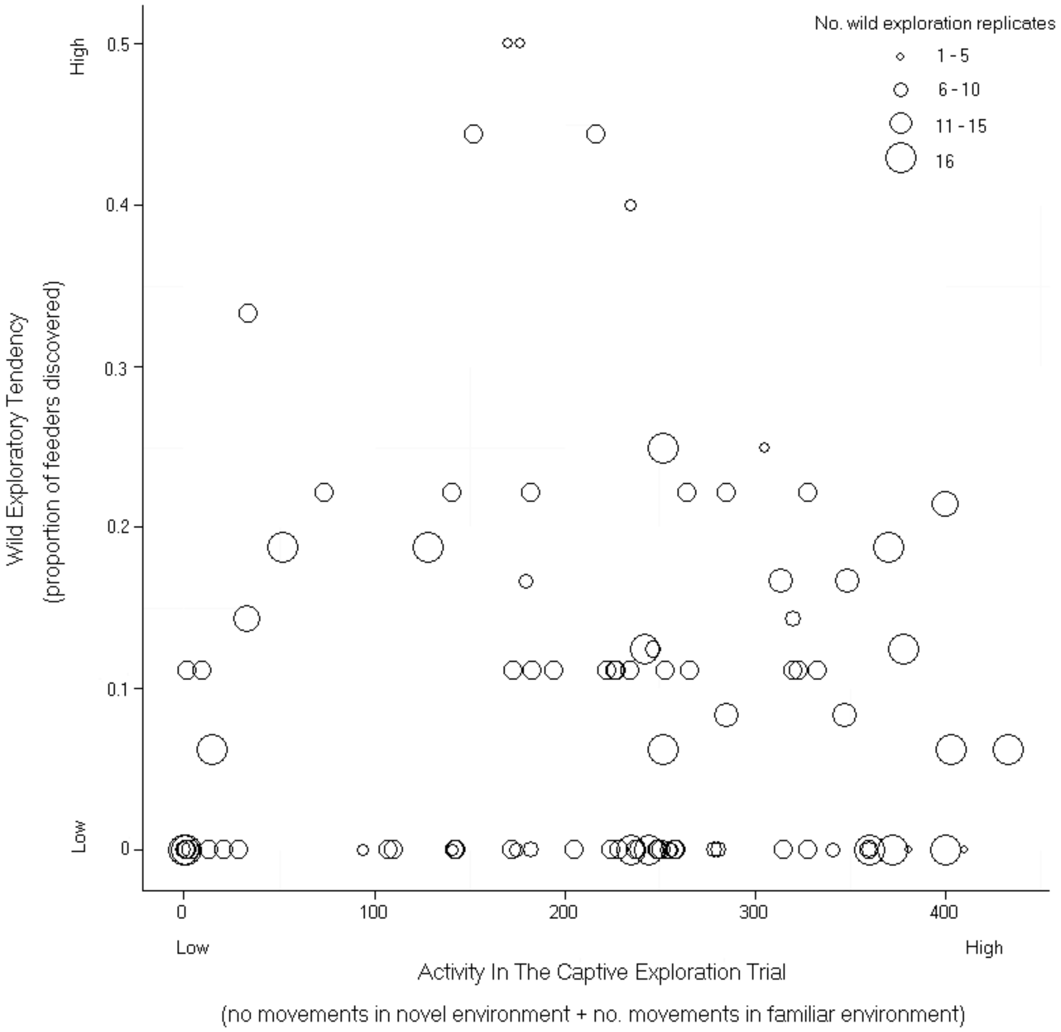
Figure 1a & 1b The absence of relationships between exploratory tendency and neophobia. a) Absence of relationship between captive exploratory tendency and captive neophobia (N = 115 birds). b) Absence of relationship between wild exploratory tendency and wild neophobia; individuals represented between 1 and 4 times; where multiple data points occur on the same point this is indicated by the point size (N = 78 birds).

2a



(See following page but one for Figure legend)

2b



(See following page for Figure legend)

2c

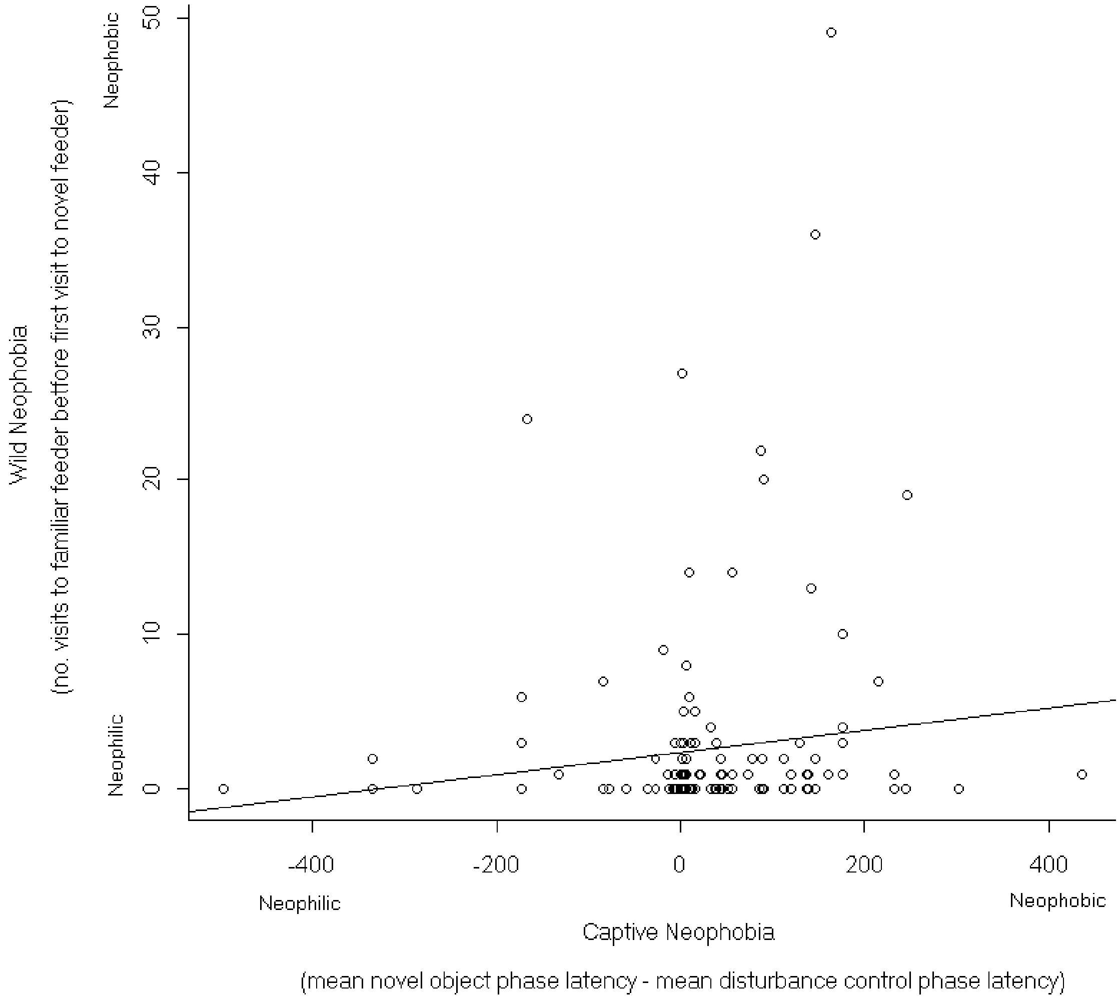


Figure 2a, 2b & 2c Relationships between traits measured in captivity and the wild. a) Positive relationship between captive exploratory tendency and wild exploratory tendency; replicates of wild exploration trial per bird indicated by point size (N = 91 birds). b) Absence of relationship between activity in the captive exploration trial and wild exploratory tendency; replicates of wild exploration trial per bird indicated by point size (N = 91 birds). c) Positive relationship between captive neophobia and wild neophobia; individuals represented between 1 and 4 times (N = 75 birds).

DISCUSSION

In this study, we showed that personality traits measured in captivity were a reflection of behavioural differences between individuals foraging in the wild. First, variation between blue tits in exploratory tendency and neophobia were repeatable in captivity, and analogous traits repeatable in the wild. Second, captive measures of exploratory tendency and neophobia were not correlated within individuals, and this was also true of the analogous wild traits. Finally, captive measures of exploratory tendency and neophobia then predicted the analogous wild measures of these traits. Birds that were relatively exploratory in captivity were also more likely to find new feeders in the wild and vice versa. Similarly, an individual’s neophobia measured in captivity correlated positively with its latency to approach novel colour feeders in the wild. As our wild measures of personality relate to differences in the use of feeding opportunities, the traits we have measured in captivity appear to represent ecologically relevant differences between individuals.

Whilst many studies use behaviour in captivity to explain differences in fitness observed between individuals in the wild, few directly compare behaviour between captivity and the wild, as we have done. Referring to captive studies on great tits for example, Dingemanse et al. (2004) suggest lower survival of slow than fast exploring females in food poor winters relate to differences in propensity to capitalise upon patchily distributed food. In captive studies, fast exploring great tits are quicker to form foraging routines, more aggressive, and more likely to use social cues than slow explorers: all attributes that support monopolisation of clumped resources (Verbeek et al. 1994, 1996; Marchetti & Drent 2000). From captive studies, it appears likely that exploratory tendency also reflects differences between individuals in information-gathering: when returned to formally novel environments, search behaviour is often then directed toward locations or cues that were associated with food during the preceding novel environment trials (Mettke-Hofmann & Gwinner 2004). Our findings complement these captive observations as here, exploratory tendency in captivity appeared connected to the ability or propensity to seek out new feeding sites in the wild. In particular, the absence of correlation between activity during the exploration trial and feeder discovery in the wild suggests that it was attention to the novel environment specifically, where new information may be gathered, rather than activity *per se* that affected feeder discovery.

We also demonstrated that neophobia measured in captivity reflected differences in neophobia in the wild. Neophobia in free-living birds is associated with reactions to other novel foraging situations, for example dietary conservatism toward new food types or propensity to innovate to obtain food in a novel foraging task (Webster & Lefebvre 2001; Thomas et al. 2003). As such, the ecological significance of our trait may be as a measure of propensity to approach and hence learn about new feeding opportunities. However, if exposure to the novel object elicits a physiological stress response, i.e. a release of the stress hormone corticosterone, it may also be a measure of response to stressors in general. Whether novel objects elicit a physiological stress response however is so far tested only in Japanese quail (*Coturnix japonica*), which do show an elevation in corticosterone (Daisley 2004), and starlings (*Sturnus vulgaris*), which do not (compared to a disturbance control; Apfelbeck & Raess 2008). That great tits (Groothuis & Carere 2005) and the blue tits in our study exhibit a behavioural aversion toward novel objects suggests the object may cause a stress response. Indeed, in great tits, individual corticosterone responses derived from a handling trial predict behavioural responses in novel object trials, suggesting similar physiological mechanisms may underlie the response to handling and novel objects (Groothuis & Carere 2005). However, stereotypical stress behaviours are not necessarily evidence of physiological stress, for example blue tits disturbed at the nest prior to trapping exhibit aggressive behaviour and alarm call, yet show no greater corticosterone response than birds trapped unawares (Muller et al. 2006). Therefore, we should be cautious of assuming neophobia is a measure of response to stressors in general. To assess the ecological significance of our neophobia trait, future work should be addressed at investigating both whether the novel object trial elicits a physiological stress response, and also comparing neophobia with measures of risk-responsiveness toward different potential stressors.

That we did not find a correlation between exploratory tendency and neophobia in our population of blue tits, either in captivity or in the wild, was surprising. Exploratory tendency and neophobia or risk-taking are positively correlated in species from a variety of taxa, and in the closely related great tit this appears to be under genetic control (Van Oers et al. 2005). In these species, neophobia and exploratory tendency may be two measures of a single approach-avoidance trait, with risk-prone, fast exploring or “proactive” individuals at one extreme and risk-averse, slow exploring “reactive” individuals at the other. In other words, Verbeek et al.’s (1994) novel environment trial and Greenberg’s (1983) novel object trial may be regarded as approach-avoidance in a novel and a familiar environment respectively (Clark & Ehlinger 1987; Wilson et al. 1993; Johnson & Sih 2007). Though our captive methods differ slightly from those employed by Verbeek et al. (1994), the lack of proactive-reactive personality trait is unlikely to be an artefact of methodology, as we have tested a small sample of great tits using our protocol and found the correlation anticipated (K.A. Herborn & K.E. Arnold, unpublished data). Whilst the contrast to great tits is surprising, divergences in trait correlations between closely related species (e.g. Mettke-Hofmann et al. 2002; Mettke-Hofmann & Gwinner 2004) and even populations of the same species (Bell & Sih 2007; Dingemanse et al. 2007) can be explained by different selection pressures. Consequently, we suggest the traits we have assayed in the blue tit are distinct, and hence the ecological significance of each trait should be considered independently.

Differences between individuals, such as body condition or weather at capture, did not explain a significant proportion of the variation in captive behaviour. This contradicted out prediction that variables increasing starvation risk, such as short day length and poor weather (and hence reduced recent foraging opportunity) would lessen neophobia or increase propensity to explore in the short term. In the wild, Parids modify behaviour rapidly in response to environmental conditions, for example attuning foraging behaviour and hence body fat to changes in starvation and predation risk (Macleod et al. 1995). That behaviour in the captive personality trials was consistent between the first and subsequent days in captivity suggests the birds may equally adjust their perception of starvation risk rapidly to the conditions and availability of food in the captive environment. The absence of state effects is consistent with previous work on wild great tits (Hollander et al. 2008), and encouraging for studies seeking to compare personality between individuals drawn from different times or environments.

In conclusion, personality measures drawn in captivity revealed differences between individuals in their natural foraging behaviour. In directly comparing individuals between captivity and the wild, this study on blue tits joins few similar *in situ* versus *ex situ* studies of personality (birds: Hollander et al. 2008; fish: Wilson & McLaughlin 2007; Coleman & Wilson 1998; Brown et al. 2005; molluscs: Briffa et al. 2008). As such, it is an important validation of research based purely on captive measures of personality. Moreover, it lends weight to the growing evidence that wild animals have personality traits that are expressed consistently across contexts.

ACKNOWLEDGMENTS

We thank E.H.K. Leat, M. Gastañaga, B. Zonfrillo, R. Brennan, S. Wilson, D. Fettes for help in the field, and N. Mirzai and T. Wallis for help with the electronic monitoring system. Genetic sexing was carried out by A. Adam and K. Stift. KH was funded by a BBSRC Industrial Case studentship with WALTHAM®, and KA by a Royal Society University Research Fellowship. All work was carried out under licence from the UK Home Office. The manuscript was improved by comments from A. Pilastro, B. Heidinger, A.L. le Vin, S.D. Larcombe, L.J. Henderson and two anonymous reviewers.

Reference list

Adam, R. G. & Booth, C. J. 1999. Storm-petrel Hydrobates pelagicus rings in Great Black-backed Gull *Larus marinus* pellets. *Ringing & Migration* 19: 298.

Adams, N. J., Abrams, R. W., Siegfried, W. R., Nagy, K. A. & Kaplan, I. R. 1991. Energy expenditure and food consumption by breeding Cape Gannets *Morus capensis*. *Marine Ecology Progress Series* 70: 1-9.

Ainley, D. G. 1980. Geographic variation in Leach's storm-petrel. *Auk* 97: 837-853.

Ainley, D. G. 1983. Further Notes on Variation in Leach's Storm-Petrel. *Auk* 100: 230-233.

Ainley, D. G., Lewis, T. J., & Morrell, S. 1976. Moult in Leach's and Ashy storm-petrels. *The Wilson Bulletin* 88: 76-95.

Ambagis, J. 2004. A comparison of census and monitoring techniques for Leach's storm petrel. *Waterbirds* 27: 211-215.

Annett, C. A. & Pierotti, R. 1999. Long-term reproductive output in Western Gulls: consequences of alternate tactics in diet choice. *Ecology* 80: 288-297.

Apfelbeck, B. & Raess, M. 2008. Behavioural and hormonal effects of social isolation and neophobia in a gregarious bird species, the European starling (*Sturnus vulgaris*). *Hormones and Behaviour* 54: 435-441.

Arnold, K. E., Ramsay, S. L., Donaldson, C. & Adam, A. 2007. Parental prey selection affects risk-taking behaviour and spatial learning in avian offspring. *Proceedings of the Royal Society B: Biological Sciences* 274: 2563–2569.

Atkinson, R. 1949. Island Going. Birlinn Limited, Edinburgh.

Avery, M., Springer, P. F. & Cassel, F. 1976. The effects of a tall tower on nocturnal bird migration – a portable ceilometer study. *Auk* 93: 281-291.

Baker, K. 1993*. Identification Guide to European Non-Passerines: BTO Guide 24*. British Trust for Ornithology, Thetford.

Barrett, R. T. 2008. Recent establishments and extinctions of Northern Gannet *Morus bassanus* colonies in North Norway. *Ornis Norvegica* 31: 172-182.

Bell, A. M. 2005. Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *Journal of Evolutionary Biology* 18: 464-473.

Bell, A. M. & Sih, A. 2007. Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters* 10: 828-834.

Bellingham, P. J., Towns, D. R., Cameron, E. K., Davis, J. J., Wardle, D. A., Wilmshurst, J. M. & Mulder, C. P. H. 2010. New Zealand island restoration: seabirds, predators, and the importance of history. *New Zealand Journal of Ecology* 34: 115-136.

Berrow, S. D. 2000. The use of acoustics to monitor burrow-nesting white-chinned petrels *Procellaria aequinoctialis* at Bird Island, South Georgia. *Polar Biology* 23: 575-579.

Berry, R. J. 2009. *Islands*. HarperCollins Publishers, London.

Bicknell, T. W. J., Reid, J. B. & Votier, S. C. 2009. Probable predation of Leach’s Storm-petrel *Oceanodroma leucorhoa* eggs by St Kilda Field Mice *Apodemus sylvaticus hirtensis*. *Bird Study* 56: 419-422.

Billings, S. M. 1968. Homing in Leach’s Storm-petrel. *Auk* 85: 36-43.

BirdLife International. 2004. *Threatened Birds of the World 2004* (CD-ROM). BirdLife International, Cambridge, UK.

Blomdahl, A., Briefe, B., & Holmström. N. 2003. *Flight identification of European Seabirds.* Christopher Helm, London.

Bolton, M. 1996. Energy expenditure, body-weight and foraging performance of Storm Petrels *Hydrobates pelagicus* breeding in artificial nesting chambers. *Ibis* 138: 405-409.

Bolton, M., Medeiros, R., Hothersall, B. & Campos, A. 2004. The use of artificial breeding chambers as a conservation measure for cavity-nesting procellariiform seabirds: a case study of the Madeiran storm petrel (*Oceanodroma castro*). *Biological Conservation*: 116: 73-80.

Bolton, M., Monaghan, P. & Houston, D. C. 1991. An improved technique for estimating pectoral muscle protein condition from body measurements of live gulls. *Ibis* 133: 264-270.

Boogert, N. J., Reader, S. M. & Laland, K. N. 2006. The relation between social rank, neophobia and individual learning in starlings. *Animal Behaviour* 72: 1229-1239.

Bourne, W. R. P. & Jehl, J. R. 1982. Variation and nomenclature of Leach's storm-petrels. *Auk* 99: 793-797.

Boyd, J. M. 1956. The St Kilda Field Mouse (*Apodemus sylvaticus hirtensis*), population in the village area, Hirta, May 1955. *Oikos* 7: 110-116.

Bretagnolle, V. 1990. Behavioural affinities of the Blue Petrel *Halobaena caerulea*. *Ibis* 132: 102-105.

Bretagnolle, V., Carruthers, M., Cubitt, M., Bioret, F., & Cuillandre, J-P. 1991. Six captures of a dark-rumped, fork-tailed storm-petrel in the northeastern Atlantic. *Ibis* 133: 351-356.

Briffa, M., Rundle, S. D. & Fryer, A. 2008. Comparing the strength of behavioural plasticity and consistency across situations: animal personalities in the hermit crab *Pagurus bernhardus*. *Proceedings of the Royal Society B: Biological Sciences* 275: 1305-1311.

Brooke, M. 1990. *The Manx Shearwater*. Academic Press Ltd, London.

Brooke, M. 2004. *Albatrosses and Petrels across the World*. Oxford University Press, Oxford.

Brooke, M. & Hilton, G. M. 2002. Prioritising the world's islands for vertebrate eradication programs. *Aliens* 16: 12-13.

Brooke, M., Keith, D. & Røv, N. 1999. Exploitation of inland-breeding Antarctic petrels by south polar skuas. *Oecologia* 121: 25-31.

Brooke, M. & Prince, P. A. 1991. *Nocturnality in seabirds*. In: Acta XX Congressus Internationalis Ornithologici (Ed. by the International Ornithological Congress), pp. 1113-1121. Wellington: New Zealand Ornithological Trust Board.

Brown, C., Jones, F., & Braithwaite, V. 2005. In situ examination of boldness-shyness traits in the tropical poeciliid, *Brachyraphis episcopi*. *Animal Behaviour* 70: 1003-1009.

Bryant, D. M. & Furness, R. W. 1995. Basal metabolic rates of North Atlantic seabirds. *Ibis* 137: 219-226.

Butler, S. J., Whittingham, M. J., Quinn, J. L. & Cresswell, W. 2006. Time in captivity, individual differences and foraging behaviour in wild-caught chaffinches. *Behaviour* 143: 535-548.

Buzas, M. A. 1972. Patterns of species diversity and their explanation. *Taxon* 21: 275-286.

BWPi, 2006. *Birds of the Western Palearctic, interactive DVD.* BirdGuides & Oxford University Press, Oxford.

Cairns, D. K., Montevecchi, W., A., Birt-Friesen, V., L. & Macko, S., A. 1990. Energy expenditures, activity budgets and prey harvest of breeding common murres. *Studies in Avian Biology* 14: 84-92.

Caldow, R. W. G. 1988. *Studies on the morphology, feeding behaviour and breeding biology of skuas with reference to kleptoparasitism.* PhD Thesis, University of Glasgow, Glasgow.

Caldow, R. W. G. & Furness, R. W. 2000. The effect of food availability on the foraging behaviour of breeding Great Skuas and Arctic Skuas. *Journal of Avian Biology* 31: 367-375.

Campbell, D. L. M., Weiner, S. A., Starks, P. T. & Hauber, M. E. 2009. Context and control: behavioural ecology experiments in the laboratory. *Annales Zoologici Fennici* 46: 112-123.

Camphuysen, K. C. J. & de Vreeze, F. 2005. Black-legged Kittiwakes *Rissa tridactyla* nesting on an offshore platform in the Netherlands. *Limosa* 78: 65-74.

Case, T. J. 1996. Global patterns in the establishment and distribution of exotic birds. *Biological Conservation* 78: 69.

Clark, A. B. & Ehlinger, T. J. 1987. Pattern and adaptation in individual behavioral differences. In: *Perspectives in Ethology* (Ed. by Bateson, P.P.G & Klopfer, P.H.), pp. 1-47. 4th edn. New York: Plenum.

Clout, M. N. & Russell, J. C. 2008. The invasion ecology of mammals: a global perspective. *Wildlife Research* 35: 180-184.

Coleman, K., & Wilson, D. S. 1998. Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Animal Behaviour* 56: 927-936.

Cote, J. & Clobert, J. 2007. Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society Series B – Biological Sciences* 274: 383-390.

Coulson, J. C. & Porter, J. M. 1985. Reproductive success of Kittiwakes *Rissa tridactyla*: the roles of clutch size, chick growth rates and parental quality. *Ibis* 127: 450-466.

Cramp, S., Brooks, D. J., Dunn, E., Gillmor, R., Hollom, P. A. D., Hudson, R., Nicholson, E. M., Ogilvie, M. A., Olney, P. J. S., Roselaar, C. S., Simmons, K. E. L., Voous, K. H., Wallace, D. I. M., Wattel, J., Wilson, M. G. 1985. *The Birds of the Western Palaearctic*. *Vol. IV*. Oxford University Press, Oxford.

Cubbitt, M., Carruthers, M., & Zino, F. 1992. Unravelling the mystery of the Tyne petrels. *Birding World* 5: 438-442.

Daisley, J. N. Bromundt, V. Möstl, E. & Kotrschal, K. 2005. Enhanced yolk testosterone influences behavioral phenotype independent of sex in Japanese quail chicks *Coturnix japonica. Hormones and Behavior* 47: 185-194.

Darwin, C. R. 1859. *The Origin of Species*. Oxford University Press, Oxford.

Davis, L. S. & Renner, M. 2003. *Penguins*. Yale University Press, London.

Davis, S. E., Nager, R. G. & Furness, R. W. 2005. Food availability affects adult survival as well as breeding success of Parasitic Jaegers. *Ecology* 86: 1047-1056.

Davoren, G. K., Montevecchi, W. A. & Anderson, J. T. 2002. Scale-dependent associations of predators and prey: constraints imposed by flightlessness of common murres. *Marine Ecology Progress Series* 245: 259-272.

De Leon, A., Minguez, E., Harvey, P., Meek, E., Crane, J. E. & Furness, R. W. 2006. Factors affecting breeding distribution of Storm-petrels *Hydrobates pelagicus* in Orkney and Shetland. *Bird Study* 53: 64-72.

Del Hoyo, J., Elliot, A. & Sargatal, J. (eds). 1999. *Handbook of the Birds of the World. Vol.5. Barn-owls to Hummingbirds*. Lynx Edicions, Barcelona.

Dennis, R. H., Hogg, R. H., Brown, A., Forrester, R. W., Bates, D. J., Wood, A. D., Murray, R. (eds). 1970-2001. *Scottish Bird Report*. Issues from 1970 to 2001. The Scottish Ornithologists Club, Aberlady.

Diamond, J. 1989. The present, past and future of human-caused extinctions. *Philosophical Transactions of the Royal Society (London) B* 235: 469-476.

Dick, M. H. & Donaldson, W. 1978. Fishing vessel endangered by Crested Auklet landings. *Condor* 80: 235-236.

Dingemanse, N. J. & De Goede, P. 2004. The relation between dominance and exploratory behaviour is context-dependent in wild great tits. *Behavioural Ecology* 15: 1023-1030.

Dingemanse, N. J., Both, C., Drent, P. J. & Tinbergen, J. M. 2004. Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society Series B – Biological Sciences* 271: 847-852.

Dingemanse, N. J., Both, C., Drent, P. J., van Oers, K. & van Noordwijk, A. J. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour* 64: 929-937.

Dingemanse, N. J., Both, C., van Noordwijk, A. J., Rutten, A. L. & Drent, P. J. 2003. Natal dispersal and personalities in great tits (*Parus major*). *Proceedings of the Royal Society Series B – Biological Sciences* 270: 741-747.

Dingemanse, N. J., Wright, J., Kazem, A. J. N., Thomas, D. K., Hickling, R. & Dawnay, N. 2007. Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology* 76: 1128-1138.

Drent, P. J., van Oers, K. and van Noordwijk, A. J. 2003. Realised heritability of personalities in the great tit (*Parus major*). *Proceedings of the Royal Society Series B – Biological Sciences* 270: 45-51

Duckworth, J. W. 1991. Responses of breeding Reed Warblers *Acrocephalus scirpaceus* to mounts of Sparrowhawk *Accipiter nisus*, Cuckoo *Cuculus canorus* and Jay *Garrulus glandarius*. *Ibis* 133: 68-74.

Dunnet, G. M. 1991. Population studies of the fulmar on Eynhallow, Orkney Islands. *Ibis* 133: 24-27.

Earhart, C. M. & Johnson, N. K. 1970. Size dimorphism and food habits of North American owls. *Condor* 72: 251-264.

Echeverría, A. I., Vassallo, A. I. & Isacch, J. P. 2006. Experimental analysis of novelty responses in a bird assemblage inhabiting a suburban marsh. *Canadian Journal of Zoology* 84: 974-980.

Edelaar, P. & Wright, J. 2006. Potential prey make excellent ornithologists: adaptive, flexibile responses to avian predation threat by Arabian babblers *Turdoides squamiceps* living at a migratory hot-spot. *Ibis* 148: 664-671.

Ellis, H. I. & Gabrielsen, G. W. 2002. *Energetics of free-ranging seabirds*. Pp. 359-407. In: Schreiber, E. A. & Burger, J. (eds.). 2002. Biology of Marine Birds. CRC Press, London.

Fargallo, J. A., Martinez-Padilla, J., Vinuela, J., Blanco, G., Torre, I., Vergara, P., & De Neve, L. 2009. Kestrel-prey dynamic in a Mediterranean region: the effect of generalist predation and climatic factors. PloS ONE: 4(2), Article No.: e4311.

Fernando de Leon, L., Bermingham, E., Podos, J. & Hendry, A. P. 2010. Divergence with gene flow as facilitated by ecological differences: within-island variation in Darwin's finches. *Philosophical Transactions of the Royal Society of London B Biological Sciences* 365: 1041-1052.

Fair Isle Bird Reports (various authors). 1950-2008. Fair Isle Bird Observatory bird reports archive, Fair Isle, Shetland.

Fauchald, P. 2009. Spatial interaction between seabirds and prey: review and synthesis. *Marine Ecology Progress Series* 391: 139-151.

Finney, S. K., Wanless, S., Harris, M. P. & Monaghan, P. 2001. The impact of gulls on puffin reproductive performance: an experimental test of two management strategies. *Biological Conservation* 98: 159-165.

Flood, R. & Thomas, B. 2007. Identification of 'black-and-white' storm-petrels of the North Atlantic. *British Birds* 100: 407-442.

Ford, J. K. B., Ellis, G. M., Olesiuk, P.F. & Balcolm, K. C. 2010. Linking killer whale survival and prey abundance: food limitation in the oceans' apex predator? *Biology Letters* 6: 139-142.

Forrester, R. W., Andrews, I. J., McInerny C. J., Murray, R. D., McGowan, R. Y., Zonfrillo, B., Betts, M. W., Jardine, D.C., & Grundy, D. S. (eds). 2007. *The Birds of Scotland*. The Scottish Ornithologists' Club, Aberlady.

Fowler, J. A. & Okill, J. D. 1988. Recaptures of storm-petrels tape-lured in Shetland. *Ringing and Migration* 9: 49-50.

Fowler, J. A., Okill, J. D. & Marshall, B. 1982. A retrap analysis of Storm-petrels tape-lured in Shetland. *Ringing and Migration* 4: 1-7.

Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N. & Skalski, G. T. 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *American Naturalist* 158: 124-135.

Freidlaender, A. S., Hazen, E. L., Nowacek, D. P., Halpin, P. N., Ware, C., Weinrich, M. T., Hurst, T. & Wiley, D. 2009. Diel changes in humpback whale *Megaptera novaeangliae* feeding behaviour in response to sand lance Ammodytes spp. behaviour and distribution. *Marine Ecology Progress Series* 395: 91-100.

Furness, R. W. 1983. Variations in size and growth of Great Skuas *Catharacta skua* chicks in relation to adult age, hatching date, egg volume, brood size and hatching sequence. *Journal of Zoology* 199: 101-116.

Furness, R. W. 1984. Leach's petrel populations on St Kilda. *British Ecological Society Bulletin* 15: 84-87.

Furness, R. W. 1987. *The Skuas*. T & AD Poyser, Calton.

Furness, R. W. & Baillie, S. R. 1981. Factors affecting capture rate and biometrics of storm petrels at St Kilda. *Ringing & Migration* 3: 137-148.

Furness, R. W. & Furness, B. L. 1981. A technique for estimating the hatching dates of eggs of unknown laying date. *Ibis* 123: 98-102.

Furness, R. W. & Hislop, J. R. G. 1981. Diets and feeding ecology of Great Skuas *Catharacta skua* during the breeding season. *Journal of Zoology, London* 195: 1-23.

Frank, S. J. 2010. Genetics, evolution and conservation of island plants. *Journal of Plant Biology* 53: 1-9.

Fraser, M. W. 1984. Foods of subantarctic skuas on Inaccessible Island. *Ostrich* 55: 192-195.

Gabrielsen, G. W., Taylor, J. R. E., Konarzewski, M. & Mehlum, F. 1991. Field and laboratory metabolism and thermoregulation in dovekies (*Alle alle*). *Auk* 108: 71-78.

Garrott, R., A., White, P. J. & Rotella, J. J. 2009. *The Madison headwaters elk herd: transitioning from bottom-up regulation to top-down limitation*. Pp. 489-517. In: Garrott, R., A., White, P. J. & Watson, F. G. R. (eds.). 2009. The ecology of large mammals in central Yellowstone: sixteen years of integrated field studies. Elsevier, Amsterdam, Boston.

Gaston, A. J. 2004. *Seabirds: A Natural History*. Christopher Helm, London.

Ginn, H. B., & Melville, D. S. 2000. *MOULT in Birds*. The British Trust for Ornithology, Thetford.

Gill, V. A., Hatch, S. A. & Lanctot, R. B. 2002. Sensitivity of breeding parameters to food supply in Black-legged Kittiwakes *Rissa tridactyla*. *Ibis* 144: 268-283.

Gosling, S. D. 2001. From mice to men: what can we learn about personality from animal research? *Psychological Bulletin* 127: 45-86.

Green, R., Smith, C. & Jones, T. 2009. Breeding ecology and diet of Great and Arctic Skuas on Handa Island in 2009. *Handa Island skua project annual report 2009*, Scottish Wildlife Trust report archives, Edinburgh. http://www.handaskuas.org

Greenberg, R. 1983. The role of neophobia in determining the degree of foraging specialization in some migrant warblers. *The American Naturalist* 122: 444-453.

Greig, S. A., Coulson, J. C. & Monaghan, P. 1983. Age-related differences in foraging success in the Herring Gull *Larus argentatus*. *Animal Behaviour* 31: 1237-1243.

Griffiths, R., Double, M. C., Orr, K. & Dawson, R. G. 1998. A DNA test to sex most birds. *Molecular Ecology* 7: 1071-1075.

Groothuis, T. G. G. & Carare, C. 2005. Avian personalities: characterization and epigenesis. *Neuroscience and Biobehavioural Reviews* 29: 137-150.

Gross, A. O. 1944. Food of the Snowy Owl. *Auk* 61: 1-18.

Gutierrez, R., Lopez, F., Ramal, A. & Guinart, E. 2006. Coastal Mediterranean storm-petrel *Hydrobates pelagicus* populations: isolated small breeding sites or outlying subcolonies of larger breeding colonies? *Atlantic Seabirds* 8: 31-40.

Hahn, S. & Peter, H-U. 2003. Feeding territoriality and the reproductive consequences in Brown Skuas Catharacta Antarctica lönnbergi. *Polar Biology* 26: 552-559.

Hakala, A., Huhtala, K., Kaikusalo, A., Pulliainen, E., Sulkava, S. 2006. Diet of Finnish Snowy Owls *Nyctea scandiaca*. *Ornis Fennica* 83:59-65.

Hamer, K. C. & Furness, R. W. 1991. Age-specific breeding performance and reproductive effort in Great Skuas *Catharacta skua*. *Journal of Animal Ecology* 60: 693-704.

Hamer, K. C., Furness, R. W. & Caldow, R. W. 1991. The effect of changes in food availability on the breeding ecology of Great Skuas *Catharacta skua*. *Journal of Zoology* 223: 175-188.

Hatchwell, B. J. 1991. The feeding ecology of young Guillemots *Uria aalge* on Skomer Island, Wales. *Ibis* 133: 153-161.

Harman, M. 1997. *An Isle Called Hirta: A history and culture of St Kilda to 1930*. Maclean Press, Isle of Skye.

Harris, S. W. 1974. Status, chronology and ecology of nesting storm-petrels in northern California. *Condor* 76: 249-261.

Harris, M. P. 1984. *The Puffin*. T. & A. D. Poyser, Calton, Staffordshire.

Harris, M. P. & Murray, S. 1978. *Birds of St Kilda*. Institute of Terrestrial Ecology, Cambridge.

Harris, M. P., Murray, S. & Wanless, S. 1998. Long-term changes in breeding performance of Puffins *Fratercula arctica* on St Kilda. *Bird Study* 45: 371-374.

Harrow, G. 1976. Some observations of Hutton's Shearwater. *Notornis* 23: 269-288.

Heubeck, M., Mellor, R., M. & Harvey, P., V. 1997. Changes in the breeding distribution and numbers of Kittiwakes *Rissa tridactyla* around Unst, Shetland, and the presumed role of predation by Great Skuas *Catharacta skua*. *Seabird* 19: 12-21.

Herbert, A. D. 1970. Spatial disorientation in birds. *Wilson Bull.* 82: 400-419.

Hilton, G. M., Furness, R. W. & Houston, D. C. 2000. A comparative study of digestion in North Atlantic seabirds. *Journal of Avian Biology* 31: 36-46.

Hislop, J. R. G., Harris, M. P. & Smith, J. G. M. 1991. Variation in the calorific value and total energy content of the lesser sandeel *Ammodytes marinus* and other fish preyed on by seabirds. *Journal of Zoology, London* 224: 501-517.

Hollander, F. A., Overveld, T. V., Tokka, I. & Matthysen, E. 2008. Personality and nest defence in the great tit (*Parus major*). *Ethology* 114: 405-412.

Howell, S. N. G., & Patteson J. B. 2008. A Swinhoe's Petrel off North Carolina, USA and a review of dark storm-petrel identification. *Birding World* 21: 255-262.

Hughes, N. K. & Banks, P. B. 2010. Interacting effects of predation risk and signal patchiness on activity and communication in house mice. *Journal of Animal Ecology* 79: 88-97.

Hounsome, M. V., Insley, H., Elliott, S., Graham, K. L. & Mayhew, P. 2006. Monitoring European storm-petrels *Hydrobates pelagicus*: a comparison of the results provided by mark/recapture and tape response methods. *Atlantic Seabirds* 8: 5-20.

Huntingdon, C. E. and Burtt, E. H. 1972. *Breeding age and longevity in Leach's Storm-petrel (Oceanodroma leucorhoa).* p.653, Proc. 15th Int. Orn. Congr. (K. H. Voous, eds.).

Huntingdon, C. E., Butler, R. G., Mauck, R. A. 1996. *Leach's Storm-petrel Oceanodroma leucorhoa*. In: Poole, A. & Gill, F. (eds.), The birds of North America 233. Philadelphia/Washington DC.

Huntingford, F. A. 1976. The relationship between anti-predator behaviour and aggression among conspecifics in three-spined stickleback, *Gasterosteus aculeatus*. *Animal Behaviour* 24: 245-260.

Imber, M. J. 1975. Behaviour of petrels in relation to the moon and artificial lights. *Notornis* 22: 302-306.

Imber, M. J., Taylor, G. A., Tennyson, A. J. D., Aikman, H. A., Scofield, R. P., Ballantyne, J. & Crockett, D. E. 2005. Non-breeding behaviour of Magenta Petrel *Pterodroma magentae* at Chatham Island, New Zealand. *Ibis* 147: 758-763.

Innes, J., Kelly, D., Overton, J. M. & Gillies, C. 2010. Predation and other factors currently limiting New Zealand forest birds. *New Zealand Journal of Ecology* 34: 86-114.

Janicke, T., Ritz, M. S., Hahn, S. & Peter, H-U. 2007. Sex recognition in Brown Skuas: do acoustic signals matter? *Journal of Ornithology* 148: 565-569.

Jenni, L. & Winkler, R. 1994. *Moult and ageing of European passerines*. London: Academic Press.

Jeschke, J. M. 2008. Across islands and continents, mammals are more successful invaders than birds. *Diversity and Distributions* 14: 913-916.

Johnson, J. C. & Sih, A. 2007. Fear, food, sex and parental care: a syndrome of boldness in the fishing spider, *Dolomedes triton*. *Animal Behaviour* 74: 1131-1138.

Joint Nature Conservancy Commission ‘Seabird 2000’ survey sheets (various authors). 2000. *Seabird 2000 survey sheets, St Kilda storm-petrels*. Joint Nature Conservancy Commission seabird records archive, Inverdee House, Aberdeen.

Jones, P. H. 2001. *Night-time attractions of Manx Shearwaters to the lighthouse at Bardsey, Gwynedd, U.K.* In Zonfrillo, B., Camara, D. B., Bolton, M. & Perrins, C. M. (eds) Proceedings of the First Manx Shearwater Conference, Funchal, Madeira, 2000.

Jones, J. & Francis, C. M. 2003. The effects of light characteristics on avian mortality at lighthouses. *J. Avian Biol.* 34: 328-333.

Jones, M. G. W. & Ryan, P. G. 2010. Evidence of mouse attacks on albatross chicks on sub-Antarctic Marion Island. *Antarctic Science* 22: 39-42.

Josephson, B. 1980. Aging and Sexing Snowy Owls. *Journal of Field Ornithology* 51: 150-159.

Jovani, R., Mavor, R. & Oro, D. 2008. Hidden patterns of colony size variations in seabirds: a logarithmic point of view. *Oikos* 117: 1774-1781.

Kalmbach, E., Griffiths, R., Crane, J. E. & Furness, R. W. 2004. Effects of experimentally increased egg production on female body condition and laying dates in the great skua *Stercorarius skua*. *Journal of Avian Biology* 35: 501-514.

Kirkman, S. P. Evaluating seal-seabird interactions in southern Africa: a critical review. *African Journal of Marine Science* 31: 1-18.

Klomp, N. I. & Furness, R. W. 1992. Patterns of chick feeding in Cory’s Shearwaters and the associations with ambient light. *Colon. Waterbird.* 15: 95-102.

Krebs, J. R. & Davies, N. B. 1993. *An Introduction to Behavioural Ecology*. Blackwell Publishing, Oxford.

Kruuk, H. 1995. *Wild Otters: Predation and Populations*. Oxford University Press, Oxford.

Le Corre, M. 2008. Cats, rats and seabirds. *Nature* 451: 134-135.

Le Corre, M., Ghestemme, T., Salamolard, M. & Couzi, F. X. 2003. Rescue of the Mascarene Petrel, a critically endangered seabird of Réunion Island, Indian Ocean. *Condor* 105: 387-391.

Le Corre, M., Ollivier, A., Ribes, S. & Jouventin, P. 2002. Light-induced mortality of petrels: a four-year study from Réunion Island (Indian Ocean). *Biol. Conserv.* 105: 93-102.

Lessells, C. M. & Boag, P. T. 1987. Unrepeatable repeatabilities: a common mistake. *Auk* 104: 116–121.

Lima, S. L. 2009. Predators and the breeding bird: behavioural and reproductive flexibility under the risk of predation. *Biological Reviews* 84: 485-513.

Lind, J. & Cresswell, W. 2006. Anti-predation behaviour during bird migration; the benefit of studying multiple behavioural dimensions. *Journal of Ornithology* 147: 310-316.

MacArthur, R. H. & Wilson, E. O. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, NJ.

Macleod, R., Gosler, A. G. & Cresswell, W. 2005. Diurnal mass gain strategies and perceived predation risk in the great tit *Parus major*. *Journal of Animal Ecology* 74: 956-964.

Malling-Olsen, K. & Larson, H. 2003. *Gulls of Europe, Asia and North America*. Christopher Helm, London.

Marchetti, C. & Drent, P. J. 2000. Individual differences in the use of social information in foraging by captive great tits. *Animal Behaviour* 60: 131-140.

Massaro, M., Chardine, J. W. & Jones, I. L. 2001. Relationships between Black-legged Kittiwake nest site characteristics and susceptibility to predation by large gulls. *Condor* 103: 793-801.

Matias, R., Rebelo, R., Granadeiro, J. P. & Catry, P. 2009. Predation by Madeiran Wall Lizards *Teira dugesii* on Cory's Shearwater *Colonectris diomedea* hatchlings at Selvagem Grande, North Atlantic. *Waterbirds* 32: 600-603.

Mattern, T., Houston, D. M., Lalas, C., Setiawan, A. N. & Davis, L. S. 2009. Diet composition, continuity in prey availability and marine habitat – keystones to population stability in the Snares Penguin *Eudyptes robustus*. *Emu* 109: 204-213.

McNeil, R., Drapeau, P. & Pierrotti, R. 1993. *Nocturnality in colonial waterbirds: occurrence, special adaptations and suspected benefits*. In: Current Ornithology, Vol. 10 (Ed. by D. M. Power), pp. 187-246. Plenum, New York.

Mettke-Hofmann, C. & Gwinner, E. 2004. Differential assessment of environmental information in a migratory and a non-migratory passerine. *Animal Behaviour* 68: 1079-1086.

Mettke-Hofmann, C., Lorentzen, S., Schlicht, E., Schneider, J. & Werner, F. 2009. Spatial neophilia and spatial neophobia in resident and migratory warblers (*Sylvia*). *Ethology* 115: 482-492.

Mettke-Hofmann, C., Winkler, H. & Leisler, B. 2002. The significance of ecological factors for exploration and neophobia in parrots. *Ethology* 108: 249-272.

Miles, W. T. S. 2010. Variation in the appearance of adult and juvenile Leach's Storm-petrels *Oceanodroma leucorhoa* on St Kilda. *British Birds* 103: 721-727.

Miles, W., Money, S., Luxmoore, R. & Furness, R. W. 2010. Effects of artificial lights and moonlight on petrels at St Kilda. *Bird Study* 57: 244-251.

Mitchell, P. I., Newton, S. F., Ratcliffe, N. & Dunn, T. E. 2004. *Seabird Populations of Britain and Ireland*. Christopher Helm, A & C Black Publishers Ltd., London.

Møller, A. P. 2009. Basal metabolic rate and risk-taking behaviour in birds. *Journal of Evolutionary Biology* 22: 2420-2429.

Moncorps, S., Chapuis, J. L., Haubreux, D. & Bretagnolle, V. 1998. Diet of the Brown Skua *Catharacta skua lönnbergi* on the Kerguelen achipelago: comparisons between techniques and between islands. *Polar Biology* 19: 9-16.

Money, S. L. 2005 - 2008. *St Kilda Seabird Ranger's Report*. Scottish Natural Heritage and The National Trust for Scotland St Kilda reports archive, The National Trust for Scotland, Wemyss House, Edinburgh.

Money, S., Söhle, I. & Parsons, M. 2008. A pilot study of the phenology and breeding success of Leach's Storm-petrel *Oceanodroma leucorhoa* on St Kilda, Western Isles. *Seabird* 21: 98-101.

Montevecchi, W. A. 2006. *Influences of artificial light on marine birds*. In: Rich, C. & Longcore, T. (eds) Ecological Consequences of Artificial Night Lighting: 94-113. Island Press: Washington, D. C

Montevecchi, W. A., Benvenuti, S., Garthe, S., Davoren, G. K. & Fifield, D. 2009. Flexible foraging tactics by a large opportunistic seabird preying on forage- and large pelagic fishes. *Marine Ecology Progress Series* 385: 295-306.

Mougeot, F. & Bretagnolle, V. 2000a. Predation risk and moonlight avoidance in nocturnal seabirds. *Journal of Avian Biology* 31:376-386.

Mougeot, F. & Bretagnolle, V. 2000b. Predation as a cost of sexual communication in nocturnal seabirds: an experimental approach using acoustic signals. *Animal Behaviour* 60: 647-656.

Mougeot, F., Genevois, F. & Bretagnolle, V. 1998. Predation on burrowing petrels by the brown skua *Catharacta skua lönnbergi* at Mayes Island, Kerguelen. *Journal of Zoology* 244: 429-438.

Morrison, S. 1998. All-dark petrels of the North Atlantic. *British Birds* 91: 541-560.

Müller, C., Jenni-Eiermann, S., Blondel, J., Perret, P., Caro, S. P., Lambrechts, M. & Jenni, L. 2006. Effect of human presence and handling on circulating corticosterone levels in breeding blue tits (*Parus caeruleus*). *General and Comparative Endocrinology* 148**:** 163–171.

Muirhead, S. J. & Furness R. W. 1988. Heavy metal concentrations in the tissues of seabirds from Gough Island, South Atlantic Ocean. *Mar. Pollut. Bull.* 19: 278-283.

Murie, O. J. 1929. Nesting of the Snowy Owl. *Condor* 31: 3-12.

Murray, S. 2002. *Birds of St Kilda*. Scottish Ornithologists Club, Musselburgh.

Murray, S., Money, S. L., Griffin, A. & Mitchell, P. I. 2008. A survey of Leach's *Oceanodroma leucorhoa* and European Storm-petrel *Hydrobates pelagicus* populations on North Rona and Sula Sgeir, Western Isles, Scotland. *Seabird* 21: 32-43.

Navarro, J., Louzao, M., Igual, J. M., Oro, D., Delgado, A., Arcos, J. M., Genovart, M., Hobson, K., A. & Forero, M., G. 2009. Seasonal changes in the diet of a critically endangered seabird and the importance of trawling discards. *Marine Biology* 156: 2571-2578.

Nelson, D. A. 1989. Gull predation of Cassin's Auklet varies with the Lunar cycle. *Auk* 106: 495-497.

Neves, V. C., Murdoch, N. & Furness, R. W. 2006. Population status and diet of the Yellow-legged Gull in the Azores. *Arquipelago* 23: 59-73.

Newson, S. E., Mitchell, P. I., Parsons, M., O'Brien, S. H., Austin, G. E., Benn, S., Black, J., Blackburn, J., Brodie, B., Humpheys, E., Leech, D., Prior, M. & Webster, M. 2008. Population decline of Leach's Storm-petrel *Oceanodroma leucorhoa* within the largest colony in Britain and Ireland. *Seabird* 21: 77-84

Nielsen, O. K. 1999. Gyrfalcon predation on Ptarmigan: numerical and functional responses. *Journal of Animal Ecology* 68: 1034-1050.

Nocera, J. J. & Ratcliffe, L. M. 2009. Migrant and resident birds adjust antipredator behaviour in response to social information accuracy. *Behavioural Ecology* 21: 121-128.

O'Brien, S., Mitchell, P. I. & Parsons, M. 2003. *Seabird monitoring on St Kilda 2003*. JNCC internal report, Aberdeen.

Okill, J. D. & Bolton, M. 2005. Ages of Storm Petrels *Hydrobates pelagicus* prospecting potential breeding colonies. *Ringing and Migration* 22: 205-208.

Olsen, K. M. & Larsson, H. 1997. *Skuas and Jaegers*. Yale University Press.

Olsen, K. M. & Larsson, H. 2005. *Terns of Europe and North America*. Christopher Helm, London.

Onley, D., & Scofield, P. 2007. *Albatrosses, Petrels and Shearwaters of the World*. Christopher Helm, London.

Oro, D., de Leon, A., Minguez, E. & Furness, R. W. 2005. Estimating predation on breeding European Storm-petrels *Hydrobates pelagicus* by Yellow-legged Gulls *Larus michahellis*. *Journal of Zoology* 265: 421-429.

Oro, D. & Furness, R. W. 2002. Influences of food availability and predation on survival of Kittiwakes. *Ecology* 83: 2516-2528.

Paterson, A. M., Gray, R. D. & Wallis, G. P. 1995. Of lice and men: the return of the 'comparative parasitology' debate. *Parasitology Today* 11: 158-160.

Paterson, I. G. & Snyder, M. 1999. Molecular genetic (RAPD) analysis of Leach's Storm-petrels. *Auk* 116: 338-344.

Pennington, M., Osborne, K., Harvey, P., Riddington, R., Okill, D., Ellis, P. & Heubeck, M. 2004. *The Birds of Shetland*. Christopher Helm, London.

Phillips, R. A., Bearhop, S., Hamer, K. C. & Thompson, D. R. 1999a. Rapid population growth of great skuas *Catharacta skua* at St Kilda: implications for management and conservation. *Bird Study* 46: 174-183

Phillips, R. A., Catry, P., Thompson, D. R., Hamer, K. C. & Furness, R. W. 1997. Inter-colony variation in diet and reproductive performance of great skuas *Catharacta skua*. *Marine Ecology-Progress Series* 152: 285-293.

Phillips, R. A., Croxall, J. P., Silk, J. R. D. & Briggs, D. R. 2007. Foraging ecology of albatrosses and petrels from South Georgia: two decades of insights from tracking technologies. *Aquatic Conservation – Marine and Freshwater Ecosystems* 17: 6-21.

Phillips, R. A., Phlan, B. & Forster, I. P. 2004. Diet and long-term changes in population size and productivity of Brown Skuas *Catharacta antarctica lönnbergi* at Bird Island, South Georgia. *Polar Biology* 27: 555-561.

Phillips, R. A., Thompson, D. R. & Hamer, K. C. 1999b. The impact of great skua predation on seabird populations at St Kilda: a bioenergetics model. *Journal of Applied Ecology* 36: 218-232.

Pierotti, R. & Annett, C. 1991. Diet and reproductive output in seabirds. *Bioscience* 40: 568-575.

Pike, T. W., Samanta, M., Lindström, J. & Royle, N. J. 2008. Behavioural phenotype affects social interactions in an animal network. *Proceedings of the Royal Society Series B – Biological Sciences* 275: 2515-2520.

Pontier, D., Fouchet, D. & Bried, J. 2010. Can cat predation help competitors coexist in seabird communities? *Journal of Theoretical Biology* 262: 90-96.

Power, D. M., & Ainley, D. G. 1986. Seabird geographic variation: similarity among populations of Leach's Storm-petrel. *Auk* 103: 575-585.

Proctor, H. C. 2003. Feather mites (Acari: Astigmata): ecology, behaviour and evolution. *Annual Review of Entomology* 48: 185-209.

Proctor, H. & Owens, I. 2000. Mites and birds: diversity, parasitism and coevolution. *Trends in Ecology and Evolution* 15: 358-364.

Quammen, D. 1996. *The song of the Dodo: island biogeography in an age of extinctions*. Scribner, New York.

Quigley, C., Armstrong, R, Nevin, O. T. & Ramsey, A. D. 2008. A study of the winter diet of reintroduced Red Kites *Milvus milvus* from North East England. *Avian Biology Research* 1: 48.

Quine, D. 2000. *St Kilda*. Colin Baxter Photography Ltd, Grantown-on-Spey.

Quinn, J. L. & Cresswell, W. 2005. Personality, anti-predation behaviour and behavioural plasticity in the chaffinch *Fringilla coelebs*. *Behaviour* 142: 1377-1402.

R Development Core Team. 2009. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ramos, J. A., Monteiro, L. R., Sola, E. & Monitz, Z. 1997. Characteristics and competition for nest cavities in burrowing Procellariiformes. *The Condor* 99: 634-641.

Ratcliffe, N., Bell, M., Pelembe, T., Boyle, D., Benajamin, R., White, R., Godley, B., Stevenson, J. & Sanders, S. 2010. The eradication of feral cats from Ascension Island and its subsequent recolonization by seabirds. *Oryx* 44: 20-29.

Ratcliffe, N., Furness, R. W. & Hamer, K. 1998. The interactive effect of age and food supply on the breeding ecology of Great Skuas. *Journal of Animal Ecology* 67: 853-862.

Ratcliffe, N., Vaughn, D., Whyte, C. & Shepherd, M. 1998. Development of playback census methods for Storm Petrels. *Bird Study* 45: 302-312.

Rayner, M. J., Hauber, M. E., Imber, M. J., Stamp, R. K. & Clout, M. N. 2007. Spatial heterogeneity of mesopredator release within an oceanic island system. *Proceedings of the National Academy of Sciences* 104: 20862-20865.

Réale, D. & Festa-Bianchet, M. 2003. Predator-induced natural selection on temperament in bighorn ewes. *Animal Behaviour* 65: 463-470.

Réale, D., Gallant, B. Y., Leblanc, M. & Festa-Bianchet, M. 2000. Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Animal Behaviour* 60: 589-597.

Redfern, C. P. F. & Clarke, J. A. 2001. *Ringer's Manual*. BTO, Thetford.

Reed, J. R., Sincock, J. L. & Hailman, J. P. 1985. Light attraction in endangered Procellaiiform birds: reduction by shielding upwards radiation. *Auk* 102: 377-383.

Regional and Observatory UK Bird Reports: Shetland, Orkney, all regions of the UK north and west coasts, Scillies, and the Channel Islands (various authors) 1990 – 2006. British Trust for Ornithology, Royal Society for the Protection of Birds, Scottish Ornithologists Club and Fair Isle Bird Observatory bird report archives. BTO, The Nunnery, Thetford. RSPB, The Lodge, Sandy, Bedfordshire. SOC, Waterston House, Aberlady. Fair Isle Bird Observatory, Shetland.

Riddington, R. (current ed.) 2007. *British Birds Interactive*. CD Archive 1907 to 2007: Snowy Owl photographic references. Birdguides, www.birdguides.com

Robb, M. & Mullarney, K. 2008. *Petrels night and day*. The Sound Approach, Dorset.

Robinson, M. & Becker, C. D. 1986. Snowy Owls on Fetlar. *British Birds* 79: 228-242.

Rock, P. 2005. Urban gulls: problems and solutions. *British Birds* 98: 338-355.

Rodríguez, A. & Rodríguez, B. 2009. Attraction of petrels to artificial lights in the Canary Islands: effects of moon phase and age class. *Ibis* 151: 299-310.

Rutherford, M., Harper, G. A. & Moller, H. 2009. Denning behaviour of ship rats *Rattus rattus* on Taukihepa, a seabird breeding island. *New Zealand Journal of Zoology* 36: 343-353.

Ryan, P. G. & Moloney, C. L. 1991. Prey selection and temporal variation in the diet of sub-antarctic skuas at Inaccessible Island, Tristan-da-Cunha. *Ostrich* 62: 52-58.

Salamolard, M., Ghestemme, T. & Couzi, F. X. 2007. Impact of city lights on Barau’s Petrels, *Pterodroma baraui* on La Reunion Island and measures for reducing their impact. *Ostrich* 78: 449-452.

Saunders, W. E. 1930. The destruction of birds at Long Poing light-house, Ontario, on four nights in 1929. *Auk* 47: 507-511

Schmidt-Nielsen, K. 1997. *Animal Physiology: Adaptation and Environment, 5th Edition*. Cambridge University Press, Cambridge.

Sih, A., Kats, L. B. & Moore, R. D. 1992. Effects of predatory sunfish on the density, drift and refuge use of stream salamander larvae. *Ecology* 73: 1418–1430.

Sharrock, J. T. R. 1976. *The Atlas of Breeding Birds in Britain and Ireland*. British Trust for Ornithology, Thetford.

Shetland Bird Reports (various authors). 1980-2008. Fair Isle Bird Observatory bird reports archive, Fair Isle, Shetland.

Simberloff, D. 1995. Why do introduced species appear to devastate islands more than mainland areas? *Pacific Science* 49: 87-97.

Simberloff, D. 2000. Extinction-proneness of island species – causes and management implications. *Raffles Bulletin of Zoology* 48: 1-9.

Skorka, P. & Wojcik, J. D. 2008. Habitat utilisation, feeding tactics and age related feeding efficiency in the Caspian Gull *Larus cachinnan*s. *Journal of Ornithology* 149: 31-39.

Snow, D. W. & Perrins, C. M. (Eds.). 1998. *The Birds of the Western Palaearctic concise edition. Vol. 1*. Oxford University Press, Oxford.

Sorensen, M. C., Hipfner, J. M., Kyser, T. K. & Norris, D. R. 2010. Pre-breeding diet influences ornament size in the Rhinoceros Auklet *Cerorhinca monocerata*. *Ibis* 152: 29-37.

Spaans, A. L. 1971. On the feeding ecology of the Herring Gull *Larus argentatus* Pont. in the northern part of the Netherlands. *Ardea* 59: 75-240.

Spear, L. B. 1993. Dynamics and effect of Western Gulls feeding in a colony of guillemots and Brandt's Cormorants. *Journal of Animal Ecology* 62: 399-414.

St Kilda Ranger's Reports (various authors) 2005 - 2008. Scottish Natural Heritage and The National Trust for Scotland St Kilda reports archive. The National Trust for Scotland, Wemyss House, Edinburgh.

Steadman, D. W. 1995. Prehistoric extinctions of Pacific island birds: biodiversity meets zooarchaeology. *Science* 267: 1123-1131.

Steel, T. 1994. *The Life and Death of St Kilda*. HarperCollinsPublishers, Hammersmith, London.

Stenhouse, I. J. & Montevecchi, W. A. 1999. Indirect effects of the availability of caplin and fishery discards: gull predation on breeding storm-petrels. *Marine Ecology Progress Series* 184: 303-307.

Stenhouse, I. J. & Montevecchi, W. A. 2000. Habitat utilization and breeding success in Leach's storm-petrel: the importance of sociality. *Can. J. Zool.* 78: 1267-1274.

Stenhouse, I. J., Robertson, G. J. & Montevecchi, W. A. 2000. Herring Gull *Larus argentatus* predation on Leach's Storm-petrels *Oceanodrom leucorhoa* breeding on Great Island, Newfoundland. *Atlantic Seabirds* 2: 35-44.

Stewart, F. M., Furness, R. W. & Monteiro, L. R. 1996. Relationships between heavy metal and metallotheionein concentrations in Lesser Black-backed Gulls, *Larus fuscus*, and Cory's Shearwater, *Calonectris diomedea*. *Arch. Environ. Con. Tox.* 30: 299-305.

Storey, E. A. 1984. Function of Manx Shearwater calls in mate attraction. *Behaviour* 89: 73-89.

Stöwe, M., Bugnyar, T., Loretto, M. C., Schloegl, C., Range, F. & Kotrschal, K. 2006. Novel object exploration in ravens (*Corvus corax*): effects of social relationships. *Behavioural Processes* 73: 68-75.

Strauss, S. Y., Lau, J. A. & Carroll, S. P. 2006. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecology Letters* 9: 357-374.

Stroud, D. A., Chambers, D., Cook, S., Buxton, N., Fraser, B., Clement, P., Lewis, P., McLean, I., Baker, H. & Whitehead, S. 2001. *The UK SPA Network: Its Scope and Content*. Joint Nature Conservation Committee, Peterborough.

Sutton, G. M. & Parmelee, D. F. 1956. Breeding of the Snowy Owl in Southeastern Baffin Island. *Condor* 58: 273-282.

Taoka, M., Won, P. O. & Okumura, H. 1989. Vocal behaviour of Swinhoe's Storm-petrel (*Oceanodroma monorhis*). *Auk* 106: 471-475.

Telfer, T. C., Sincock, J. L., Byrd, G. V. & Reed, J. R. 1987. Attraction of Hawaiian seabirds to lights: conservation efforts and effects of moon phase. *Wildlife Soc. Bull.*15: 406-413.

Terborgh, J., Lopez, L., Nunez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G. H., Lambert, T. D. & Balbas, L. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294: 1923-1926.

Thom, V. M. 1986. *Birds in Scotland*. T & A D Poyser, Calton.

Thomas, R. J., Marples, N. M., Cuthill, I. C., Takahashi, M. & Gibson, E. A. 2003. Prey selection by birds can facilitate the initial evolution of novel colour morphs in prey populations. *Oikos* 101: 458-466.

Tjorve, E. 2010. How to resolve the SLOSS debate: lessons from species diversity models. *Journal of Theoretical Biology* 264: 604-612.

Traveset, A., Nogales, M., Alcover, J. A., Delgado, J. D., Lopez-Darias, M., Godoy, D., Igual, J. M. & Bover, P. 2009. A review on the effects of alien rodents in the Balearic (Western Mediterranean Sea) and Canary Islands (Eastern Atlantic Ocean). *Biological Invasions* 11: 1653-1670.

Troup, C., Sixtus, C. R. & Paterson, A. M. 2009. The long commute: Southern Royal Albatross *Diomedea epomophora* foraging trips during incubation. *New Zealand Natural Sciences* 34: 19-28.

Tulloch, R. J. 1968. Snowy Owls breeding in Shetland in 1967. *British Birds* 61: 119-132.

Van Oers, K.**,** Klunder, M. & Drent, P. J. 2005. Context dependence of personalities: risk-taking behaviour in a social and a non-social situation. *Behavioural Ecology* 16: 716-723.

Van Oers, K., Drent, P. J. de Goede, P. and van Noordwijk, A. J. 2004. Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. *Proceedings of the Royal Society Series B – Biological Sciences* 271: 65-73.

Varpe, Ø. & Tveraa, T. 2005. Chick survival in relation to nest site: is the Antarctic petrel hiding from its predator? *Polar Biology* 28: 388-394.

Vaughan, T. 1990. Variation in Leach’s Petrel. *Birding World* 3: 318.

Verbeek, M. E. M, Boon, A. & Drent, P. J. 1996. Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour* 133: 945-963.

Verbeek, M. E. M., Drent, P. J. & Wiepkema, P. R. 1994. Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour* 48: 1113–1121.

Verbeek, M. E. M., Goede, P., Drent, P. J. & Wiepkema, P. R. 1999. Individual behavioural characteristics and dominance in aviary groups of great tits. *Behaviour* 136: 23-48.

Verheijen, F. J. 1980. The moon: a neglected factor in studies on collisions of nocturnal migrant birds with tall lighted structures and with aircraft. *Vogelwarte* 30: 305-320.

Verheijen, F. J. 1981. Bird kills at tall lighted structures in the USA in the period 1935-1973 and kills at a Dutch lighthouse in the period 1924-1928 show similar lunar periodicity. *Ardea* 69: 199-203.

Votier, S. C., Bearhop, S., Crane, J. E., Arcos, J. M. & Furness, R. W. 2007. Seabird predation by Great Skuas *Stercorarius skua* – intra-specific competition for food? *Journal of Avian Biology* 38: 234-246.

Votier, S. C., Bearhop, S., MacCormick, A., Ratcliffe, N. & Furness, R. W. 2003. Assessing the diet of great skuas *Catharacta skua* using five different techniques. *Polar Biology* 26: 20-26.

Votier, S. C., Bearhop, S., Ratcliffe, N. & Furness, R. W. 2001. Pellets as indicators of diet in great skuas *Catharacta skua*. *Bird Study* 48: 373-376.

Votier, S. C., Bearhop, S., Ratcliffe, N. & Furness, R. W. 2004a. Reproductive consequences for Great Skuas specializing as seabird predators. *The Condor* 106: 275-287.

Votier, S. C., Bearhop, S., Ratcliffe, N., Phillips, P. A. & Furness, R. W. 2004b. Predation by Great Skuas at a large Shetland colony. *Journal of Applied Ecology* 41: 1117-1128.

Votier, S. C., Crane, J. E., Bearhop, S., de Leon, A., McSorley, C. A., Minguez, E., Mitchell, I. P., Parsons, M., Phillips, R. A. & Furness, R. W. 2005. Nocturnal foraging by great skuas *Stercorarius skua*: implications for conservation of storm-petrel populations. *Journal of Ornithology* 147: 405-413.

Votier, S. C., Furness, R. W., Bearhop, S., Crane, J., Caldow, R. W. G., Catry, P., Ensor, K., Hamer, K., Hudson, A. V., Kalmbach, E., Klomp, N. I., Pfeiffer, S., Phillips, R. A., Prieto, I. & Thompson, D. R. 2004c. Changes in fisheries discard rates and seabird communities. *Nature* 427: 727-730.

Walker, K. & Elliott, G. 2005. Population changes and biology of the Antipodean wandering albatross (*Diomedea antipodensis*). *Notornis* 52: 206-214.

Wanless, R. M. 2007. *The impact of the introduced house mouse on the seabirds of Gough Island*. PhD Thesis, University of Cape Town.

Wanless, R. M., Angel, A., Cuthbert, R. J., Hilton, G. M. & Ryan, P. G. 2007. Can predation by invasive mice drive seabird extinctions? *Biology Letters* 3: 241-244.

Warham, J. 1990. *The Petrels: Their Ecology and Breeding Systems*. Academic Press Ltd, London.

Warham, J. 1996. *Behaviour, Population Biology and Physiology of Petrels*. Academic Press Ltd, London.

Watanuki, Y. 1986. Moonlight avoidance behaviour in Leach’s petrel as a defence against Slaty-backed gulls. *The Auk* 103: 14-22.

Watanuki, Y. 1992. Individual diet differences, parental care and reproductive success in Slaty-backed Gulls. *Condor* 94: 159-171.

Watson, A. 1957. The behaviour, breeding, and food-ecology of the Snowy Owl *Nyctea scandiaca*. *Ibis* 99: 419-462.

Webster, S. & Lefebvre, L. 2000. Neophobia by the lesser-antillean bullfinch, a foraging specialist, and the bananaquit, a nectar specialist. *Wilson Bulletin* 112: 424–427.

Webster, S. & Lefebvre, L. 2001. Problem solving and neophobia in a columbiform–passeriform assemblage in Barbados. *Animal Behaviour* 62: 23-32.

Weidinger, K. 1998. Effect of predation by skuas on breeding success of the Cape petrel *Daption capense* at Nelson Island, Antarctica. *Polar Biology* 20: 170-177.

Wernham, C. V., Toms, M. P., Marchant, J. H., Clark, J. A., Siriwardena, G. M. & Baillie, S. R. (eds). 2002. *The Migration Atlas: movements of the birds of Britain & Ireland*. T. & A. D. Poyser, London.

Wiggins, I. L. 1953. Foraging activities of the Snowy Owl (*Nyctea scandiacus*) during a period of low Lemming population. *Auk* 70: 366-367.

Williams, P. L. & Frank, L. G. 1979. Diet of the Snowy Owl in the absence of small mammals. *Condor* 81: 213-21.

Williamson, M. 1996. *Biological invasions*. Chapman & Hall, London.

Wilson, D. S. & McLaughlin, R. L. 2007. Behavioural syndromes in brook charr, *Salvelinus fontinalis*: prey-search in the field corresponds with space use in novel laboratory situations. *Animal Behaviour* 74: 689-698.

Wilson, D. S., Coleman, K., Clark, A. B. & Biederman, L. 1993. Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. *Journal of Comparative Psychology* 107: 250-260.