Winter distribution and foraging activity of Great Skuas *Stercorarius skua*

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School of Engineering and Natural Sciences
Life and Environmental Sciences
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90 ECTS thesis submitted in partial fulfilment of a
Magister Scientiarum degree in Biology

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Útdráttur

Sjófuglar eru flestir langlífir, með háar lífslíkur á milli ára, verða seint kynþroska og eignast fá afkvæmi á ári. Flestar rannsóknir á sjófuglum hafa verið gerðar á varptíma en ástæða þessa er aðallega sú að sjófuglar halda sig í byggðum (kóloníum) og flestir þeirra dvelja langdvölum á hafi úti utan varptíma. Þekking okkar á vistfræði sjófugla að vetrarlagi er þess vegna afar takmörkuð.

Sumarið 2008 voru dægurritar settir á 40 fullorðna skúma (*Stercorarius skua*) á Breiðamerkursandi, Íslandi, 16 á eyjunni Foula, Skotlandi og 24 á Bjarnareyju, Noregi. Þegar dægurritarnir voru endurheimtir á sömu stöðum næstu 3 ár, var unnt að finna út staðsetningar fuglanna yfir vetratímann (staðsetningar teknar tvisvar á dag) út frá birtustigi með tilliti til tíma. Dægurritarnir skrá einnig upplýsingar um seltustig en út frá þeim upplýsingum má meta hve miklum tíma fuglarnir eru að eyða í fæðuöflun (á flugi) á móti tíma varið í hvíld (sitjandi á sjó). Alls endurheimtust 23 dægurritar með gögnum á árunum 2009-2011.

Rannsóknarspurningar verkefnisins voru:

1) Hvar eru vetrarstöðvar skúma frá Íslandi, Noregi og Skotlandi?

2) Hversu mikinn tíma eru skúmarnir að nota í fæðuleit á vetrarsvæðum sínum og er það mismunandi á milli vetrasvæða?

Vetrarsvæðunum var skipt í fimm svæði; (1) NV-Afríka, (2) Íberíuskagi, (3) Biscay flói, (4) austurströnd N-Ameríku og (5) hafsvæðið vestur af Írlandi. Íslenskir skúmar dreifðu sér á svæði 1, 2, 3 og 4. Skoskir fuglar héldu sig eingöngu austanmegin Atlantshafsins, á svæði 1, 2 og 3 og fuglar frá Bjarnareyju voru á öllum vetrarsvæðunum. Einnig tóku fimm einstaklingar sig til og ferðuðust á milli vetrarsvæða veturinn 2008-2009.

Þar sem 17 af 22 skúmum héldu sig á einu ákveðnu vetrarsvæði veturinn 2008-2009 var hægt að finna út hvort munur væri á tíma í fæðuleit (á flugi) á milli vetrarsvæða. Fuglar á öllum svæðum virtust eyða svipuðum tíma á flugi fyrir utan svæði 1, NV-Afríku, þar sem töluvert minni tími fór í flug en á hinum svæðunum. Fimm einstaklingar ferðuðust á milli vetrasvæða en virtust hagnast lítið á því að skipta um svæði. Undantekning á þessu var fugl 5749 sem fór frá svæði þar sem miklum tíma var varið á flugi, yfir á svæði 1, þar sem minni tími fór í flug og minnkaði þar með töluvert tíma varið í fæðuleit. Þetta bendir til þess að svæði 1, NV-Afríka, bjóði upp á hagstæðari fæðustöðvar fyrir fuglana heldur en hin svæðin og skúmarnir geti því lágmarkað orkukostnað sinn á því svæði yfir veturinn.

Abstract

Most seabirds have long life expectancy, high annual survival rate, delayed maturity and low annual productivity. However, a vast majority of studies on seabirds have focused on their breeding or life-history parameters during the breeding season. This is partly a consequence of the fact that most seabirds are colonial breeders and many of them hardly spend any time on land outside the breeding season. General knowledge on the winter ecology of seabirds therefore is limited.

In 2008, geolocators were deployed on adult breeding Great Skuas (*Stercorarius skua*) at three locations; 40 at Breiðamerkursandur, Iceland, 16 in Foula, Scotland and 24 in Bjørnøya, Norway. When recaptured over the next years, (1) the global position during previous year could be calculated from light level readings (twice per day) with reference to time; and (2) saltwater immersion data could be used to study foraging time activity (time in flight) compared to time resting (sitting on the water). Twenty-three geolocators were recaptured over the years 2009-2011.

The research questions of the project were:

1) What are the wintering distributions of Great Skuas from Iceland, Scotland and Norway?

2) How much time are they spending in foraging activity over the winter and does it differ between the respective winter areas?

Great Skuas from different breeding areas spread differently between winter quarters. The winter quarters were divided into five main areas (1) NW-Africa, (2) coast of Iberia, (3) Bay of Biscay, (4) eastern coast of N-America and (5) West of Ireland. Icelandic Great Skuas were at areas 1, 2, 3 and 4. Birds from Foula were only observed in areas at east Atlantic in areas 1, 2 and 3. Birds from Bjørnøya were observed at all winter areas. Furthermore, five individuals travelled between winter areas over the winter 2008-2009.

With the geolocators, the time birds spent in foraging activity (in flight) could be estimated and since the winter areas for individual birds were known, foraging activity could be compared between winter areas. Great Skuas at all winter areas seem to spend similar time in foraging except for birds at Area 1, where they spent much less time in flight than in any other area. The five individuals that travelled between areas seemed to gain little by moving, except for bird 5749 that went to Area 1 from a more active area and therefore decreased it's time spent foraging. These findings indicate that Area 1, NW-Africa, provides particularly good feeding opportunities that allow the birds to spend more time resting and therefore limit their energy expenditure over the winter.

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Synopsis

Introduction

Most seabirds have long life expectancy due to high annual survival rate, delayed maturity and production of relatively few offspring per breeding season (Ratcliffe *et al*. 2002, Schreiber & Burger 2002). Furthermore, seabirds are likely to skip breeding or manipulate brood size when conditions are unfavourable and await future breeding opportunities (Erikstad *et al*. 1998, Cubaynes *et al.* 2010). In favourable years with great amounts of food availability may result in increased numbers of birds breeding and fewer non-breeders in the population (Furness 1987, Ratcliffe *et al.* 2002). Consequently, the population size changes relatively slowly from year to year (Furness *et al.* 2006).

Seabirds are almost all colonial or semi-colonial breeders, so they can be studied in large numbers at a colony, and many of them hardly spend any time on land outside the breeding season (Schreiber & Burger 2002). Therefore, a vast majority of studies on seabirds have focused on their breeding or life-history parameters during the breeding season and fewer studies have focused on winter ecology of seabirds. Individual recognition is necessary in many ecological studies such as when connecting factors working on individuals on different sites at different times. Conventional methods of tracking birds on land (e.g. with colour-rings), are not plausible for birds that spend most of their time out on the ocean and thus, the birds cannot be seen or accounted for during large part of the year.

During the last few decades, studies on seabirds at the individual level outside the breeding season have expanded dramatically. New and constantly developing tracking techniques like satellite transmitters, GPS transmitters and geolocational data loggers (or geolocators) have opened a new era for migration studies of seabirds. The accuracy of geolocators is lower (generally 180-200 km) than for GPS transmitters. Nevertheless geolocators remain a cheaper alternative and thus ideal for locating main wintering areas for birds that are expected to travel long distances (Phillips *et al.* 2004), in particular for species with previously unknown winter areas or migration routes. The data loggers are in some cases also programmed to record other environmental parameters such as temperature, salinity and underwater depth. Such data can give important information on the behaviour of the bird e.g. time spent flying or diving.

The Great Skua *Stercorarius skua* is a northern hemisphere seabird breeding from Iceland and Faeroes to Scotland, Norway and Spitsbergen (Harrison 1983). The world population is about 16,000 breeding pairs with the largest numbers, about 9000 pairs, breeding in Orkney and Shetland in Scotland (Mitchell *et al*. 2004). There are about 5400 breeding pairs in Iceland, with 80% of the Icelandic breeding population and the greatest density at Skeiðarásandur, Öræfi and Breiðamerkursandur (Lund-Hansen & Lange 1991). Iceland is considered to be the second most important breeding area for Great Skuas, after Shetland (Lund-Hansen & Lange 1991). At Svalbard the Great Skua is considered to be quite recent immigrant as the first record of breeding was 1970 at Bjørnøya and 1976 at Spitsbergen (Strøm 2006). It occurs at high densities at Spitsbergen and Bjørnøya (Strøm 2006) but at Bjørnøya there are at least 350 pairs (Strøm 2007) which is considered to be the largest Great Skua colony in the Barents Sea (Strøm 2006).

The Great Skua is a typical seabird that normally breeds for the first time when 4 to 9 years old, almost always lays 2 eggs (Furness 1987), has a high annual survival, around 90% survival rate between years (Furness 1987, Ratcliffe *et al.* 2002) and can live up to old age, the oldest recorded individual being 34 years old (Robinson & Clark 2011). Great Skuas tend to recruit to breed at a nest site close to their birthplace (Klomp & Furness 1992) and like most seabirds they show mate and site fidelity from year to year (Furness 1987).

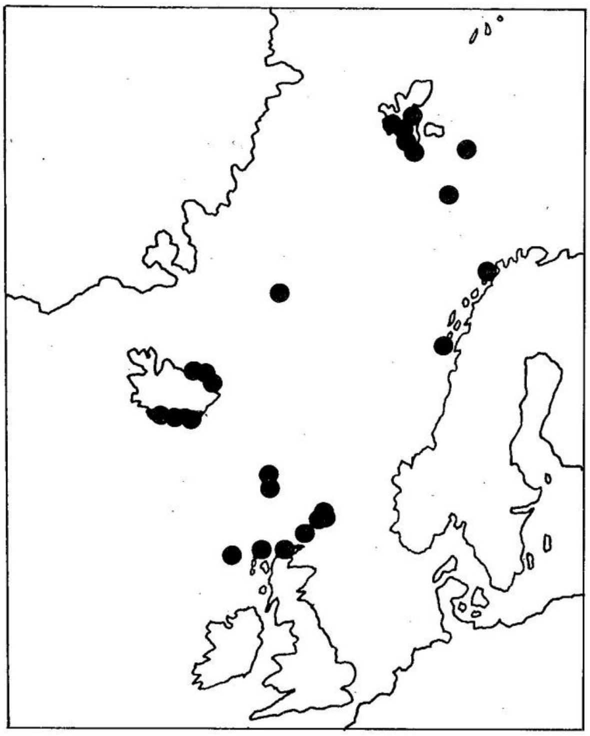

Figure 1-1. Breeding range of Great Skuas *Stercorarius skua* (Furness 1987).

The Great Skuas have been protected during the breeding period in Iceland since 1994 (Petersen 1998) and are protected in Scotland by UK law. In addition, about 80% of the breeding Great Skuas in Scotland are located within Special Protection Areas (SPAs) and are therefore also strongly protected by European law. Great Skuas are also protected by laws in Norway and Svalbard. The Faroe Islands differ from other Great Skua breeding sites as the birds have not been protected, apart from the period 1897 until 1954 due to dramatic decline in late 19 century (Furness 1987). Currently, Great Skuas are not effectively protected by law in the Faeroes and are culled in some numbers from time to time (R.W. Furness pers. comm.).

The Great Skua has been extensively studied on the breeding grounds, mainly on Foula, an island west of mainland Shetland, Scotland (Furness *et al.* 2006). However, very limited information is available on the migration and wintering grounds for all species of the family Stercorariidae (Phillips *et al.* 2007, Kopp *et al.* 2011). Approximately 70 thousand Great Skua chicks have been metal ringed in the UK and all recoveries of adult birds have been from the eastern part of the Atlantic, mostly from the coasts of Iberia (Wernham *et al*. 2002). Results from a recent study were satellite PTT and data loggers were put on breeding birds from Foula, indicate that half of the Scottish population will winter off the coast of Iberia and the other half off the coast of NW-Africa (Furness *et al*. 2006). According to this same study, the birds mainly travel along the continental shelf not far from the coastline rather than being oceanic.

Nearly 19 thousand Great Skua chicks were metal ringed in Iceland from 1921 to 1995 (Petersen & Gudmundsson 1998) and the recoveries are distributed from both sides of the Atlantic (Furness 1987). A total of 212 recoveries have been reported of Icelandic birds from abroad and 2/3 of them, or 134, have been throughout Europe and five in N-Africa. The remaining 1/3 of recoveries, or 68, were from west of the Atlantic: 50 in Greenland, 13 in N-America and five in S-America (Icelandic Institute of Natural History, unpublished data).

Furthermore, a study on six Icelandic breeders tagged with satellite transmitters in 2002 and 2003 suggested that the Icelandic Great Skuas dispersed more than birds from the

UK (T. Alerstam, T. & G.A. Gudmundsson, unpublished). One of the Icelandic birds migrated in a southwest direction and passed Newfoundland on its way along the coast of New York. The same individual was tracked to 20°N on a southward migration in the middle of the Atlantic Ocean the following autumn (G.A. Gudmundsson, pers. comm.).

Thus, both ringing recoveries and limited satellite data indicate that Icelandic Great Skuas have a more dispersed migration and wintering distribution than Great Skuas from the UK. This is of interest as these populations are not located far from each other and there are connections between them. Birds ringed in Scotland and in the Faeroes have been reported in Iceland (Petersen 1998). Also the rapid growth of the population and recoveries from northern Norway and Svalbard of birds ringed as chicks in Scotland suggest that many of the birds originated from that area (Strøm 2006).

Great Skuas are top predators with a wide food niche. They scavenge, prey on birds, fish and sometimes even mammals. Like other Stercorariidae, they also pirate other birds for their food, this is called kleptoparasitism, but they do not practice that as much as for example Arctic Skuas (*Stercorarius parasiticus*) which are more specialised kleptoparasites (Furness 1987). Great Skuas are also known to scavenge discards from fishing boats and trawlers during the breeding season (Bearhop *et al.* 2001) and it is likely that they show that same behaviour to some extent during winter. Food and feeding methods are fairly well known during the breeding season, particularly from Shetland, but less is known about feeding during the non-breeding season (Furness 1987).

The winter ecology of Great Skuas is poorly studied since the winter areas had not been described, for the Icelandic and Norwegian birds until now. The geolocators also made it possible to study the foraging activity of the Great Skuas (i.e. time spent flying) by measuring time dry over the day during the whole winter. For birds that do not go onto land during the winter such as Great Skuas, the behaviour of birds can be deduced from a salt-water sensor in the logger. When a bird is sitting on the sea, the sensor is immersed in salt water so a current flows. When the bird is flying the sensor is dry and no current flows. Recording time wet or dry provides data on the swimming and flying activity of the bird. These data can be used as a proxy for foraging effort, where time spent foraging can be an indicator for varying feeding conditions (Caldow & Furness 2000, Phillips *et al.* 2007, Garthe *et al.* in press).

Due to poor knowledge on migration, wintering grounds and winter ecology of Great Skuas, all studies on this aspect are of great value. From an ecological perspective, the links between wintering and breeding grounds are of high importance for our understanding of factors affecting the annual life cycles of birds.

The research questions of the project were:

1) What are the migration patterns and the wintering distribution of Great Skuas from Iceland, Scotland and Norway?

2) How much time are they spending in foraging activity (in flight) during winter and does the level of activity differ between the respective winter areas?

Methods

Study area

This study was conducted at three study sites over the years 2008-2011. The first study site was at Bjørnøya (74°29’N, 18°46’E), which is located in the Barents Sea about 450 km north of Norway (Magnusdottir *et al.* 2012). The second study site was in Iceland where the colony was located in Öræfi, southeast Iceland, with the main study area at Breiðamerkursandur (63°52’N, 16°29’W) which has the largest concentration of Great Skuas breeding in Iceland, with up to 50 pairs/km^2 (Lund-Hansen & Lange 1991). The third study site was Foula (60°08’N, 2°05’W) a small peat-covered island west of mainland Shetland. Foula holds the largest Great Skua colony in Scotland (Magnusdottir *et al.* 2012).

Capture techniques

The birds were caught on nests during incubation with electronic noose traps. Eggs were temporarily placed in an insulated box padded with cotton wool, and replaced by dummy eggs. When the bird returned to the nest, a radio control activated the trap, pulling a noose tight around the bird’s legs. No attempt was made to catch equal numbers of both sexes, especially since usually only one bird was attending the territory at the time of the capture and females tend to do most of the incubation (Furness 1987). A handheld GPS unit was used to record the position of each nest where a bird was trapped to mark the territories so they could be revisited next year to recover the geolocators.

Geolocators

Geolocators from British Antarctic Survey particularly suited for leg-mounting on large and medium sized seabirds were attached to colour rings. Two types of geolocators were used, Mk5 and Mk7 which both weigh 3.6 grams. Geolocators were deployed on breeding birds in June 2008 in all study colonies. In Iceland 40 geolocators were put on adult birds, 16 on Foula, Shetland and 24 in Bjørnøya. The same types of geolocators had successfully been deployed on Great Skuas in Shetland using the same technique (Furness *et al.* 2006).

In summer 2009 the same territories were revisited and returned birds located. Unfortunately, a vast majority of the Great Skuas had lost their geolocators, mostly because the colour ring had broken where the logger was attached. Despite this, 11 geolocators were retrieved in Iceland, 4 on Shetland and 5 on Bjørnøya. In 2010, two more geolocators were retrieved on Bjørnøya, which had two years’ data on them. Lastly in 2011, one geolocator was recovered at Bjørnøya with three years’ data.

Light data

Using geolocators it is possible to calculate the position of the birds (twice per day) from light level readings with reference to time. This has been a highly effective technique for the tracking of long distance migratory species (Phillips *et al.* 2004). The loggers measured light level every minute, and recorded the maximum light level at the end of every 10 minute period (Magnusdottir *et al.* 2012).

The data was decompressed after downloading using purpose-built software from BASTrak. The downloaded data were then run through the software TransEdit, a program used to analyse the decompressed data files (.lig format) produced by BASTrak in order to identify sunrise and sunset times, which are used to calculate position: latitude from day (or night) length, and longitude from the time of local midday (or midnight) relative to GMT. The data needed to be checked manually and unrealistic points very far inland were removed from the dataset as well as points that can occur because of light-level interference, for example from artificial light during the night or shadows over the daytime.

The edited .lig data were then taken from TransEdit and put into the program BirdTracker which converts the sunrise and sunset data into location data that are shown on an inbuilt world map. To isolate the winter areas of the birds the period's 01.11.2008-01.02.2009 and 01.11.2009-01.02.2010 were used for the birds equipped with geolocators in 2008 and recovered 2009 and 2010 respectively. Data from the bird caught at Bjørnøya 2011 have not been analysed in detail, although the winter areas of that bird were identified.

Kernel density was used to define the main winter area; four Kernels were used, 25%, 50%, 75% and 95%. The Kernel density tells us at what density the data points are by daily records, 25% Kernel being the densest, and 95% the least dense place. To find the Kernel density of the birds a program called Home-Ranger was used. The Home-Ranger calculates the Kernel density of the birds from each colony, so the global locations made by that were then put in ArcGIS for mapping.

Activity data

As the geolocators measured saltwater immersion every 3 seconds (Mk5 loggers) or every second (Mk7 loggers) the activity of the birds were recorded and classified, into two categories 1) sitting on sea surface resting; or 2) flying (not touching the sea surface). Great Skuas are not seen on land during the non-breeding season and therefore it can be assumed that they spend all their time at sea. Their foraging effort (i.e. time spent in flight) can therefore be measured during the winter. For the activity data, only the time period 01.11.2008-01.02.2009 was used.

The activity data were analysed with respect to time of day and proportion of time spent in flight during daylight compared with proportion of time airborn during darkness. The daylight period was determined from the light measurements recorded by the logger, and corresponded approximately to the time from the start of civil twilight at dawn to the end of civil twilight at dusk, i.e. when the sun is 6° below the horizon.

Birds that were faithful to one area throughout the winter were used to compare foraging effort between wintering areas. Thus, activity data between winter areas and months, analysis was restricted to the 17 birds that used only one winter area (hereafter site faithful) in 2008-2009. Birds that moved between wintering areas within the winter 2008-2009 (hereafter travellers) were examined to see if they maintained similar, more or less foraging effort after switching wintering areas. Furthermore, activity within each area used by the five travellers was compared to activity data obtained for the same areas from the analysis of the 17 site faithful birds.

Result and discussion

Winter Areas of Great Skuas

Geolocators retrieved from 23 Great Skuas over the years 2009-2011 provided data showing that that the birds spent the majority of the winter in five main winter areas. These areas are: Area 1 off the coast of northwest Africa, Area 2 off the coast of Iberia, Area 3 in the Bay of Biscay, Area 4 off the eastern coast of North America and Area 5 west of Ireland (Figure 1-2). Winter areas for Great Skuas from Shetland have been known for some time, both by ringing recoveries and satellite transmitters (PTT) and geolocation data loggers, indicating that adult birds winter exclusively on the continental shelf of southern Europe and northwest Africa (Magnusdottir *et al.* 2012). However winter areas for Great Skuas from Bjørnøya were almost unknown and ringing recoveries of Great Skuas from Iceland have been reported from both sides of the Atlantic, indicating that adult Icelandic birds disperse more than Great Skuas from Shetland.

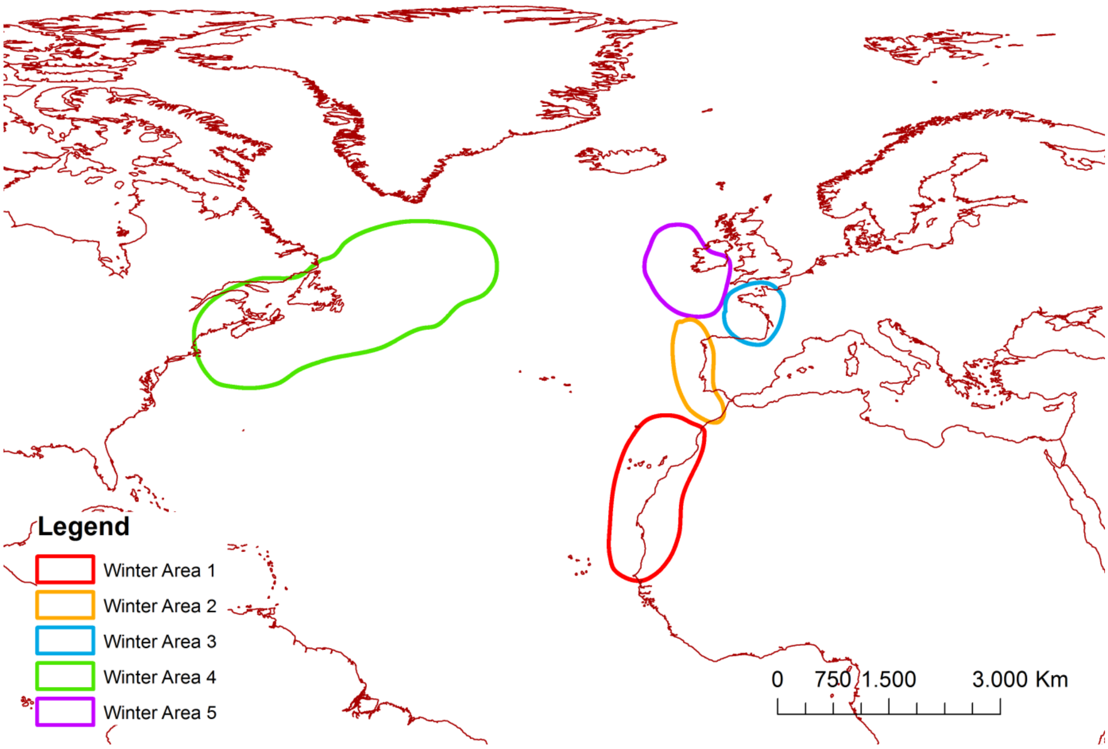

Figure 1-2. The winter areas of Great Skuas *Stercorarius skua*, as determined by 22 individuals equipped with geolocators in winter 2008-2009.

With the geolocators it was clear that the Shetland birds were only using two main winter areas, both on the eastern coast of the Atlantic, NW-Africa (Area 1) and Iberia (Area 2). The Icelandic birds show more distribution going to both sides of the Atlantic, to NW-Africa (Area 1), Iberia (Area 2), Bay of Biscay (Area 3) and N-America (Area 4). The Bjørnøya birds were most widely distributed using all winter areas, and thereby showing more similar distribution to the Icelandic birds, rather than the Shetland birds. However, the Bjørnøya birds tended to stay in greater proportion on the eastern Atlantic than Icelandic birds.

The two Great Skuas captured at Bjørnøya in 2010 and the one in 2011 showed site fidelity to their wintering grounds over all the winters. It therefore seems that Great Skuas tend to use the same wintering grounds from year to year. These birds did not travel between winter areas, but it would be interesting to see if birds that do travel between wintering areas repeat the same travelling pattern the next winter, or stay at the current area instead of travelling. However, there is only one winter of data for the five travellers, so it remains unknown whether travelling is an individual strategy, repeated between seasons, or behaviour specific to a given winter for a given individual.

Migration information of the Great Skuas is limited since equinoxes occur when the birds are migrating (March and September). Equinoxes render latitudinal positioning of geolocators impossible due to equal length of day and night and therefore their locations are lost over few days during that time. Still some migration movements were tracked which indicate that not all the birds travel the shortest route to their wintering areas. One Great Skua, bird 4561, that bred in Iceland flew by the British Isles before heading to wintering grounds close to Newfoundland and stayed there the whole winter. Another Icelandic Great Skua, bird 5765, wintered close to Newfoundland the whole winter, but spent some time west of Ireland before heading back to the breeding grounds.

Foraging Activity of Great Skuas

With the salt-water sensor on the geolocators, estimations of the foraging activity, measured as proportion of time spent flying, could be made for the birds during winter. This could then be used to compare the activity between different winter areas. There seemed to be no difference in activity between winter areas, with the exception of NW-Africa (Area 1) where there was much less activity. This seems to indicate that most areas provide similar feeding opportunities with the exception of NW-Africa that seems to have particularly good feeding grounds, allowing the birds to minimise their foraging effort. Similarly, only one of five travelling Great Skuas (bird 5749) that reduced its foraging effort by changing wintering grounds, when it travelled from Iberia (Area 2) to NW-Africa (Area 1). The other 4 travellers showed no changes in their foraging effort after they relocated to a new winter area. Since there is no evidence linking the activity pattern to breeding success of the birds, it is difficult to assume that winter areas with less foraging effort are really better for the birds. However, where the birds minimise their foraging effort they don’t risk their life expectancy as much as for areas where they have to work harder for their meals. Ratcliffe *et al.* 2002 suggested from a few recovered dead colour ringed Great Skuas, that highest mortality rates happens during migration or at the wintering areas. These findings indicate that environmental factors during winter affect survival of Great Skuas.

Compared to time spent flying during the day (18-44%), Great Skuas spent most of their time resting on the water at nights or 89-94% of the total time in darkness. This is in agreement with studies on albatrosses and petrels (Catry *et al.* 2004, Phillips *et al.* 2008, Mackley *et al.* 2011) and even one study of five Great Skuas from Shetland, where the birds spent more time flying during the day than the night (Meraz Hernando 2011).

Since the birds were caught at nest during the breeding season, more females were caught than males, but males tend to do little of the incubation (Furness 1987). However, there seem to be no sexual segregation between winter areas or in foraging activity. Males tended to occupy same winter areas as females and looking at their foraging activity, no obvious difference was between the foraging efforts of males versus females.

Conclusions

It is now clear that Great Skuas from different breeding grounds tend to use different wintering areas. The reason for this is unknown but it might be due to genetic differences between these populations or learned or imprinted behaviour. Even though breeding birds are to some extent linked together between colonies, for example some birds that hatched in Shetland now breed in Bjørnøya; there seem to be a tendency for each population to spend the winter in particular areas.

Activity of Great Skuas over the wintering season had not been known and therefore the results were really interesting. Only NW-Africa had statistically lower foraging activity than all the other winter areas, which can be concluded that this area provides good feeding opportunities and is therefore relatively important. This area should therefore be studied in more details since it might be a key area for wintering seabirds.

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Wintering areas of Great Skuas *Stercorarius skua* from Bjørnøya, Iceland and Shetland

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Abstract

Our understanding of seabird migrations and winter habitat use has improved rapidly in recent years with the deployment of satellite transmitters and of geolocation data-loggers. Understanding the at-sea distribution and migrations of seabirds is becoming increasingly important as pressures on marine environments increases, especially considering seabird movements and use of areas where they are at risk from a range of marine threats is critical to ensuring their conservation. The aims were to assess the winter distribution of adult Great Skuas *Stercorarius skua* breeding in three different countries. Geolocation data-loggers were deployed on breeding adults at colonies in Shetland (Scotland), southeast Iceland, and Bjørnøya (Norway) in 2008. Loggers were recovered when birds returned to breed next years and downloaded data were processed to map the location of each individual throughout the winter period. Adult Great Skuas from Scotland wintered off northwest Africa and southern Europe. Adults from Iceland mostly wintered off Canada, with small numbers visiting northwest Africa and Europe. Although adults from Bjørnøya migrated to similar areas as did birds from Iceland, a slightly greater proportion wintered off Europe, and most used areas further north than birds from Scotland. Although three birds studied over consecutive winters used the same small area in all years, four individuals moved between different areas within the same winter. Great Skuas show clear variation in migrations among breeding regions, and some evidence of individual consistency.

Introduction

Our understanding of seabird migrations and winter habitat use has improved rapidly in recent years with the deployment of satellite transmitters on large species (Phillips *et al*. 2007, Bugoni *et al*. 2009) and of geolocation data-loggers on a wide range of seabirds (Phillips *et al*. 2004, 2005, Burger & Shaffer 2008). Many species undertake long-distance migrations from breeding colonies to wintering areas (Wernham *et al.* 2002, Burger & Shaffer 2008). They may often show consistent use of clearly defined and relatively small winter home ranges (Phillips *et al.* 2005, Kubetzki *et al.* 2009), and in some cases clear evidence of regular migration staging sites (Stenhouse *et al.* 2011). Understanding the at-sea distribution and migrations of seabirds is becoming increasingly important as pressures on marine environments increase. Such pressures include not only hazards of oil pollution for seabirds and impacts of changes in fisheries practices and fish stocks (Mitchell *et al.* 2004), but now also risk of collision with, or disturbance by, renewable energy devices (Masden *et al.* 2010). The cumulative impacts of these devices on seabird populations will depend on the extent to which seabirds utilize specific areas where they are constructed. Understanding seabird movements and use of areas where they are at risk from a range of marine threats is critical to ensuring their conservation. Ship-based surveys are expensive, and hence the most effective means of obtaining detailed data on habitat use is to deploy tracking devices on birds of known origin and breeding status.

Great Skuas *Stercorarius skua* are endemic to the northeast Atlantic, breeding in colonies from western Scotland (56° N), to Svalbard, Norway (80° N). The species is one of the world's rarer birds, with a total population of only some 16 000 breeding pairs (Mitchell *et al.* 2004). Great Skuas are closely associated with marine fisheries, where they scavenge behind fishing vessels (Votier *et al.* 2008), and they also fly at heights that make them potentially vulnerable to collision with wind turbines (Garthe & Hüppop 2004). The largest numbers breed off northern Scotland in Orkney and Shetland (about 9000 pairs, Mitchell *et al.* 2004), in southeast Iceland (about 5000 pairs, Lund-Hansen & Lange 1991, Mitchell *et al.* 2004) and on Bjørnøya (Bear Island), Norway (at least 350 pairs, Strøm 2007). Within Scotland, 80% of the breeding Great Skuas are located within Special Protection Areas (SPAs), so are strongly protected by European law. Numerical trends of the two major populations, in Scotland and Iceland, have been different over the last 150 years. Numbers have approximately doubled every 12 years from 1900 to 1990 in Scotland but they have remained approximately stable in Iceland (Mitchell *et al.* 2004). Very few birds ringed as chicks in one of these countries have been recovered as adults in the other (Wernham *et al.* 2002). In contrast, the Bjørnøya colony was only founded in 1970 (Vader 1980) and numbers have increased very rapidly and, therefore, must have received many immigrants. Empirical evidence for this comes from sightings of birds breeding at Bjørnøya and other Barents Sea colonies that were originally ringed as chicks in Scotland and Iceland (Strøm 2006).

Ring recovery data (Klomp & Furness 1992, Wernham *et al.* 2002) indicate that adult Great Skuas from Scotland winter exclusively on the continental shelf of southern Europe and northwest Africa. This conclusion was supported by deployment of satellite transmitters (PTTs) and geolocation data-loggers on breeding adults in Foula, Shetland, in 2002 and 2003 (Crane 2005). Seven of those birds wintered off northwest Africa, five off Iberia and two in the Bay of Biscay (Crane 2005). Wintering areas of Icelandic birds are less certain, but ring recovery data suggest that some of these birds may visit the western North Atlantic rather than Europe (Furness 1987). Wintering areas of birds from Bjørnøya are almost unknown, although there are a few recoveries of ringed birds from the North Sea (Bakken *et al.* 2003; H. Strøm unpubl. data). Here we present data from geolocation dataloggers which were deployed in 2008 on breeding adult Great Skuas at colonies in Shetland (Scotland), Iceland and

Bjørnøya to determine the winter distributions of individuals from these three distinct breeding areas. We specifically test the hypothesis, derived from previous ringing, that Great Skuas breeding in Iceland show different migration routes and wintering areas from Great Skuas breeding in Scotland.

Methods

Study areas

This study was conducted at three study sites over the years 2008–10. The study site in Scotland, was Foula (60°08′N, 2°05′W) a small peat-covered island west of mainland Shetland. It holds the largest Great Skua colony in Scotland. The study site in Iceland was in Öræfi, southeast Iceland, with the main study area at Breiðamerkursandur (63°52′N, 16°29′W). This area has the largest concentration of Great Skuas breeding in Iceland (Lund-Hansen & Lange 1991). The study site in Norway was at Bjørnøya, Svalbard (74°26′N, 19°02′E), which is located in the Barents Sea about 450 km north of mainland Norway.

Catching techniques

The birds were caught on the nest during incubation with electronic noose traps. Eggs were temporarily placed in an insulated box padded with cotton wool, and replaced by dummy eggs. When the bird came back to incubate, a radio control activated the trap, pulling a noose tight around the bird's legs. Birds were sexed from red blood cells or feather pulp (taken under appropriate national licences in each country) after DNA extraction and PCR amplification of CHD genes using primers 2550F (Fridolfsson & Ellegren 1999) and 2757R (R. Griffiths pers. comm.).

Tracking devices

Using geolocators, it was possible to calculate the position of each bird (twice per day) from light level readings with reference to calendar date. This has been a highly effective technique for the tracking of long-distance migratory species (Phillips *et al.* 2004). The loggers measure light level every minute, and record the maximum light level at the end of every 10 minute period. In June 2008, geolocators (British Antarctic Survey, Cambridge, UK) were deployed attached by cable ties to colour rings on breeding birds in Iceland (n=40), Shetland (n=16), and Bjørnøya (n=24). We deployed fewest loggers in Shetland because migrations of these birds were already known from ring recoveries and from tracking in 2002 and 2003, and most in Iceland because we suspected that some birds (but possibly a small proportion) from Iceland might winter in the western North Atlantic. In summer 2009 the areas around the same territories were revisited and returned birds located. Unfortunately, many of the skuas had removed their geolocators, mostly by breaking the colour ring where the logger was attached or stretching the cable tie allowing the logger to fall off. In spite of this, 11 geolocators were retrieved in Iceland, 4 in Shetland, and 5 in Bjørnøya. In 2010, another two geolocators were retrieved in Bjørnøya, providing two years of data. Logger recovery rates were, therefore, similar at all three sites (around 28%). In 2011 another logger was retrieved in Bjørnøya, providing data for three consecutive winters. Data from that logger have not yet been analyzed in detail and are only mentioned briefly in the present paper in the context of consistent use of winter areas.

The data were decompressed after downloading using BASTRAK software. The downloaded data were then run through the software TRANSEDIT to identify sunrise and sunset times, which were used to calculate position: latitude from day (or night) length, and longitude from the time of local midday (or midnight) relative to GMT, with BIRDTRACKER software. To map the winter areas of the birds, we selected data from 1 November 2008 to 1 February 2009, and for the two birds recaptured in 2010, also the winter from 1 November 2009 to 1 February 2010. Data were filtered to remove the few data points that were affected by light-level interference. Mapping was performed in ARCGIS, with kernel density analysis used to map 25%, 50%, 75% and 95% winter home ranges of birds from each breeding area. In order to exclude any effect of year when comparing distribution of birds from different colonies, kernel analyses were restricted to data from the 2008/09 winter.

Results

All geolocators that were retrieved provided data throughout our defined winter period. All 7 birds from Bjørnøya were females, as were 8 of 11 birds from Iceland, and 3 of the 4 from Shetland. However, there was no obvious sexual segregation: the male from Shetland wintered off northwest Africa, as did two Shetland females, and two males from Iceland wintered off Newfoundland, which was an area also used by females from that colony.

The tracked birds spent the majority of the winter in five main areas: Area 1 was off the coast of northwest Africa; Area 2 was off the coast of Iberia; Area 3 was the Bay of Biscay; Area 4 was off the eastern coast of North America; and Area 5 was west of Ireland (Fig. 2-1). The Great Skuas from Shetland showed the smallest overall winter distribution (Fig. 2-2) using only two main regions in the east Atlantic; close to the coastline of Iberia (Area 2) and off northwest Africa (Area 1). Two birds spent the winter off northwest Africa, mainly by the coast of Morocco and Western Sahara. One bird stayed by the coast of Iberia, and another began its winter off Iberia but then moved in mid-December to northwest Africa, where it remained for the rest of the winter.

Icelandic Great Skuas used four of the areas (Table 2-1, Fig. 2-3): five birds wintered close to Newfoundland and south of Greenland; two wintered in the Bay of Biscay; two wintered off northwest Africa, mainly by the coast of Mauritania and Western Sahara; two used both the east and west Atlantic Ocean. Of these last two, one bird was close to Newfoundland until mid-December, it then travelled across the Atlantic Ocean to waters off the Iberian Peninsula where it remained for the rest of the winter. The other bird spent the early winter in the east Atlantic Ocean, close to the Bay of Biscay, but then travelled across to the west Atlantic in mid-November, staying close to Newfoundland until 7 January before then migrating back to the east Atlantic for several weeks prior to its return to the breeding colony in Iceland.

The five Great Skuas recaptured in 2009 on Bjørnøya spent the winter in two main areas, on either side of the Atlantic Ocean (Fig. 2-4). One migrated to Newfoundland (Area 4), as did the majority of Icelandic Great Skuas. One travelled to Newfoundland, where it remained until mid-December before crossing the Atlantic to spend the rest of the winter close to the Bay of Biscay (Area 3). Two Great Skuas from Bjørnøya spent the whole winter west of Ireland (Area 5), and one started west of Ireland then moved to the Bay of Biscay and afterwards to the Iberian Peninsula (Area 2). Both birds from Bjørnøya for which there were two years of data returned to the same wintering grounds in consecutive years. One of these was close to Newfoundland (Area 4), while the other was off northwest Africa, mainly by the coast of Morocco, Western Sahara and Mauritania (Fig. 2-5). The bird for which we obtained three years’ worth of data also returned consistently to one wintering area (west of Ireland; Area 5) each year.

Discussion

Trapping Great Skuas on their nests tends to catch females because males do little of the incubation (Furness 1987). The strong bias in our sample towards females makes it impossible to be sure that both sexes show the same winter distributions, but the few males we sampled seemed to show much the same distribution as females from the same colony. Data on carbon stable isotope ratios in winter-grown feathers from Great Skuas breeding in Shetland showed no evidence of sexual segregation during winter (R.W. Furness unpubl. data). Similarly, there is no evidence from either tracking or stable isotope analysis of feathers that male and female Brown Skuas *Stercorarius lonnbergi* exhibit sexual segregation during the non-breeding period (Phillips *et al.* 2007).

Adult Great Skuas from Shetland wintered off northwest Africa, Iberia or, to a smaller extent, in the Bay of Biscay. Adults from Iceland predominantly wintered off Newfoundland, but even on the east of the Atlantic frequented a wider range of areas, and tended to winter further north than birds from Shetland (compare Figs. 2-2 & 2-3). Adults from Bjørnøya showed a distribution more similar to that of birds from Iceland rather than Shetland, but with a slightly greater representation on the eastern side of the Atlantic than seen in birds from Iceland (Figs. 2-3 & 2-4). The more northerly winter distribution of Great Skua adults from Bjørnøya and more southerly winter distribution of adults from Shetland correlated with the differences in latitudes of the three breeding populations. On average, birds from Bjørnøya travelled the furthest, and those from Shetland the least, from breeding colony to wintering areas (Figs. 2-2, 2-3 and 2-4). The present data do not suggest a pattern of chain migration or of leap-frog migration (Newton 2007), but show consistent differences among populations in preferred wintering areas as well as considerable, but apparently consistent, individual variation. It is unclear whether the differences in migration routes of Icelandic and Shetland Great Skuas to distinct wintering areas on opposite sides of the Atlantic reflect genetic differences in migratory direction, or represent learned behaviours. Whatever the explanation, the differences have the potential to reduce competition for food in winter between birds from these two major populations. Given that at least some of the Great Skuas breeding in Bjørnøya were hatched in Shetland, it is perhaps surprising that their winter distribution matches much more closely that of Icelandic birds. However, some immigrants to the expanding colony at Bjørnøya are known to have originated from Iceland (Strøm 2006).

The ecology of Great Skuas during winter is not well known. Observations suggest that they often associate with trawlers discarding waste from demersal fish catches (Veen *et al.* 2003, Camphuysen & van der Meer 2005). All of the five main wintering areas in the present study (Fig. 2-1) support large fisheries for demersal fish, but also hold large stocks of pelagic fish (Caddy & Garibaldi 2000, Food and Agriculture Organization [FAO] 2008). Amounts of fish being discarded by trawlers catching demersal fish have changed very considerably in many areas over recent decades; for example, with the collapse of Cod *Gadus morhua* stocks on the Grand Banks, reductions in fishing effort in the North Sea (Votier *et al*. 2004), and increases in trawl fisheries on the northwest African continental shelf (Kelleher 2005). It seems unlikely that the relative advantages of foraging in each of these areas have remained constant over time. However, there is as yet no evidence to suggest that individuals wintering in a particular area gain fitness benefits over birds using a different area (cf. Bogdanova *et al.* 2011).

The high proportion of Shetland adults shown to winter off northwest Africa in the present study was unexpected, since ring recovery data had suggested that very few adults from any Scottish colony winter that far south (Klomp & Furness 1992) and recent ring recovery data do not show any marked change in recovery locations (Meraz Hernando 2011).

The logger data suggest that there has been a recent change in wintering areas, with Scottish Great Skuas moving further south, perhaps to exploit the increased amounts of discards from fishing boats on the northwest African continental shelf (ter Hofstede & Dickey-Collas 2006) and increasing pelagic fish stocks there (FAO 2008). Unfortunately there were too few ring recoveries from the same time period as our tracking study to test whether the distribution of recoveries has changed. However, the lack of ring recoveries of adult Great Skuas from West Africa is not simply because dead birds from that region are not reported. There have been numerous recoveries of juvenile and immature Great Skuas from West Africa, indicating that younger birds have been visiting that region during the decades when adults were not recovered there (Klomp & Furness 1992, Wernham *et al.* 2002). This supports the inference that many Scottish adult Great Skuas have recently changed their winter distribution from southern Europe to West Africa.

Although we have detailed data over two successive winters for only two individuals, both these birds returned to the same general area in 2009/10 as they had used in 2008/09; each had quite distinct migration strategies, preferring either the East or the West Atlantic Ocean (Fig. 2-5). A third bird providing data for three successive winters also showed consistent use of the same small area (in the Celtic Sea, west of Ireland; Area 5 in Fig. 2-1) each winter. Consistent use by individual birds of the same wintering range each year may allow them to develop an intimate knowledge of the local foraging opportunities and so may enhance their survival and body condition, and has also been seen in some other seabirds (Phillips *et al.* 2005, Hatch *et al.* 2010, Bogdanova *et al.* 2011, Dias *et al.* 2011).

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Tables and figures.

Table 2-1. Wintering distributions of Great Skuas *Stercorarius skua*, equipped with geolocators, from Bjørnøya, Iceland and Shetland by areas defined in Figure 2-1. Birds that moved between areas are allocated as 0.5 to each of the two areas used, or in one case 0.3 to each of the three areas used.

	NW Africa (Area 1)	**Iberia (Area 2)**	**Bay of Biscay (Area 3)**	**North America (Area 4)**	**West of Ireland (Area 5)**	**Total**
Bjørnøya 2008/09	1	0.3	0.8	2.5	2.3	7
Iceland 2008/09	2	0.5	2.5	6	0	11
Shetland 2008/09	3	0.5	0.5	0	0	4

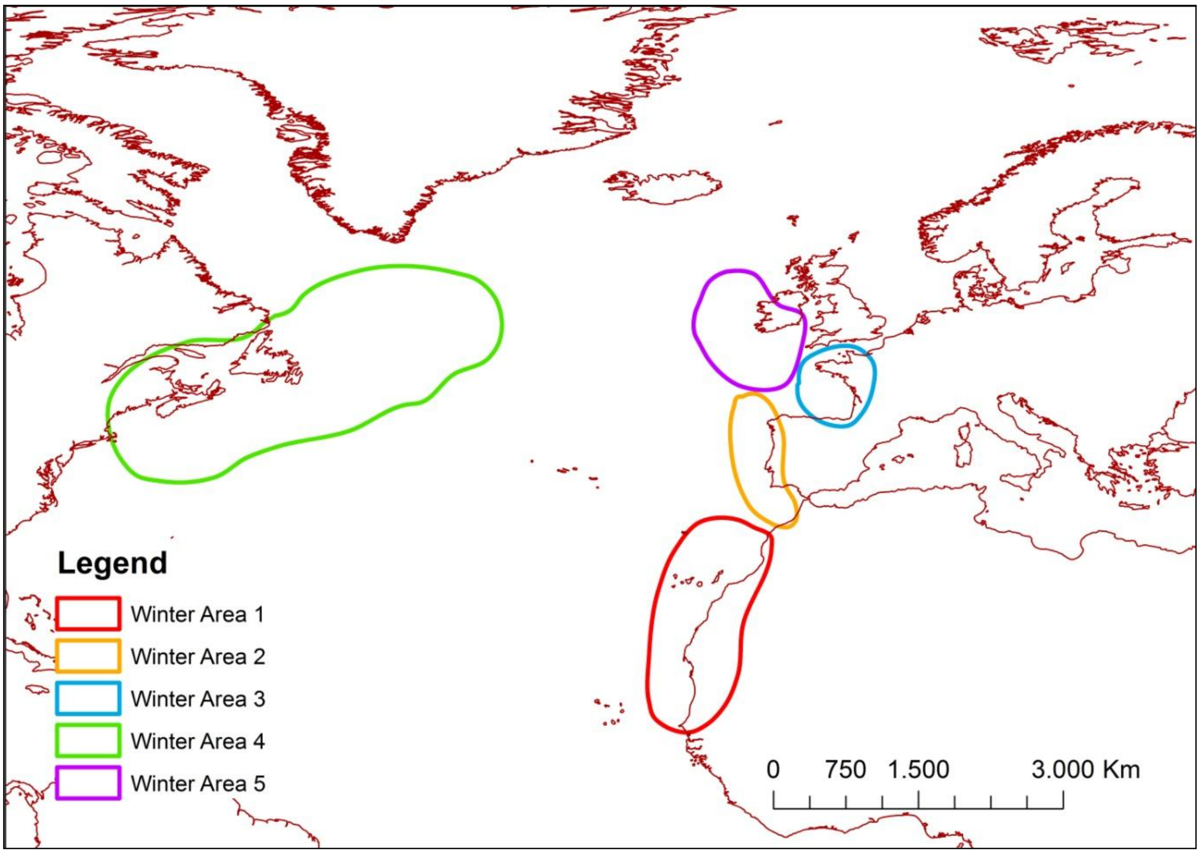

Figure 2-1. Wintering areas used by Great Skuas *Stercorarius skua* tracked from Shetland, Iceland and Bjørnøya the winter 2008-2009. Area 1 "northwest Africa", area 2 "Iberia", area 3 "Bay of Biscay", area 4 "North America", and area 5 "West of Ireland".

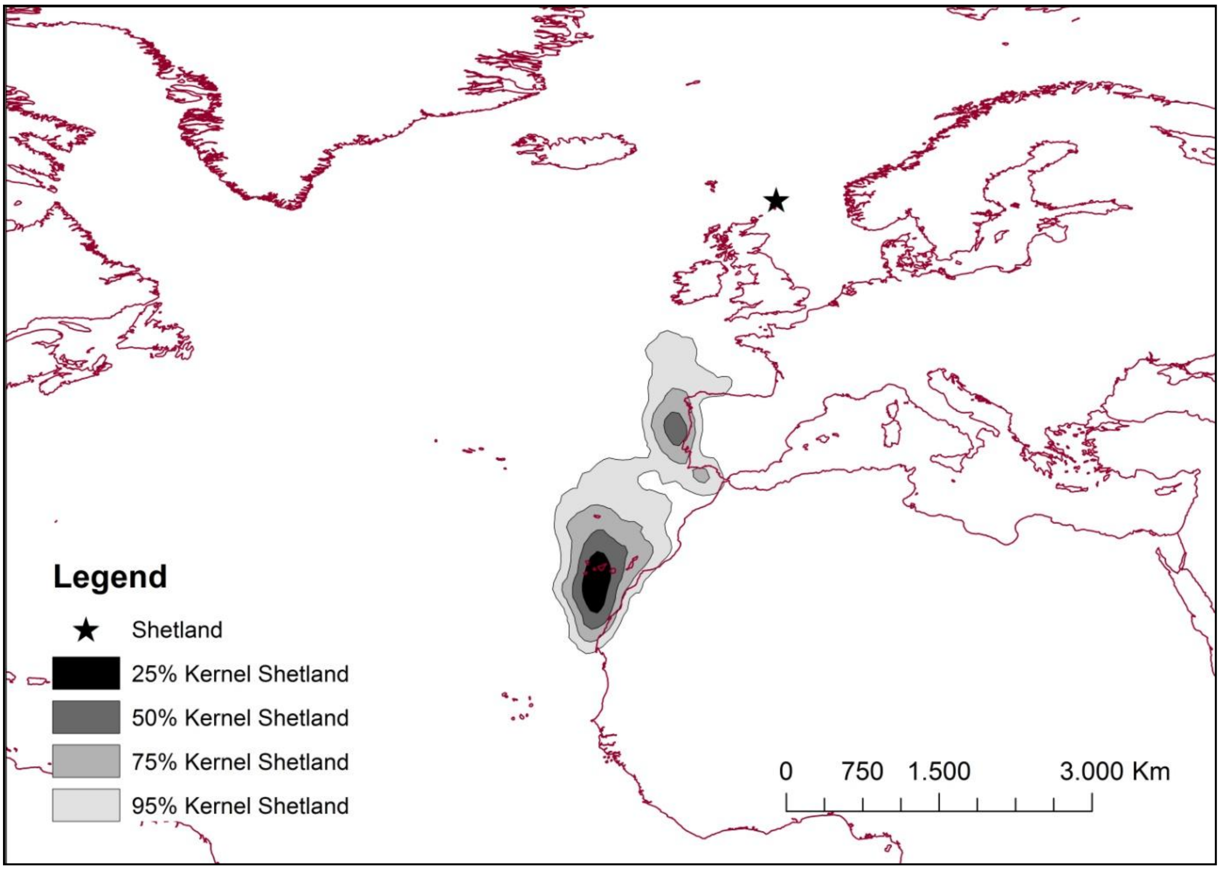

Figure 2-2. Kernel density distribution of Shetland Great Skuas *Stercorarius skua* tracked in winter 2008/09.

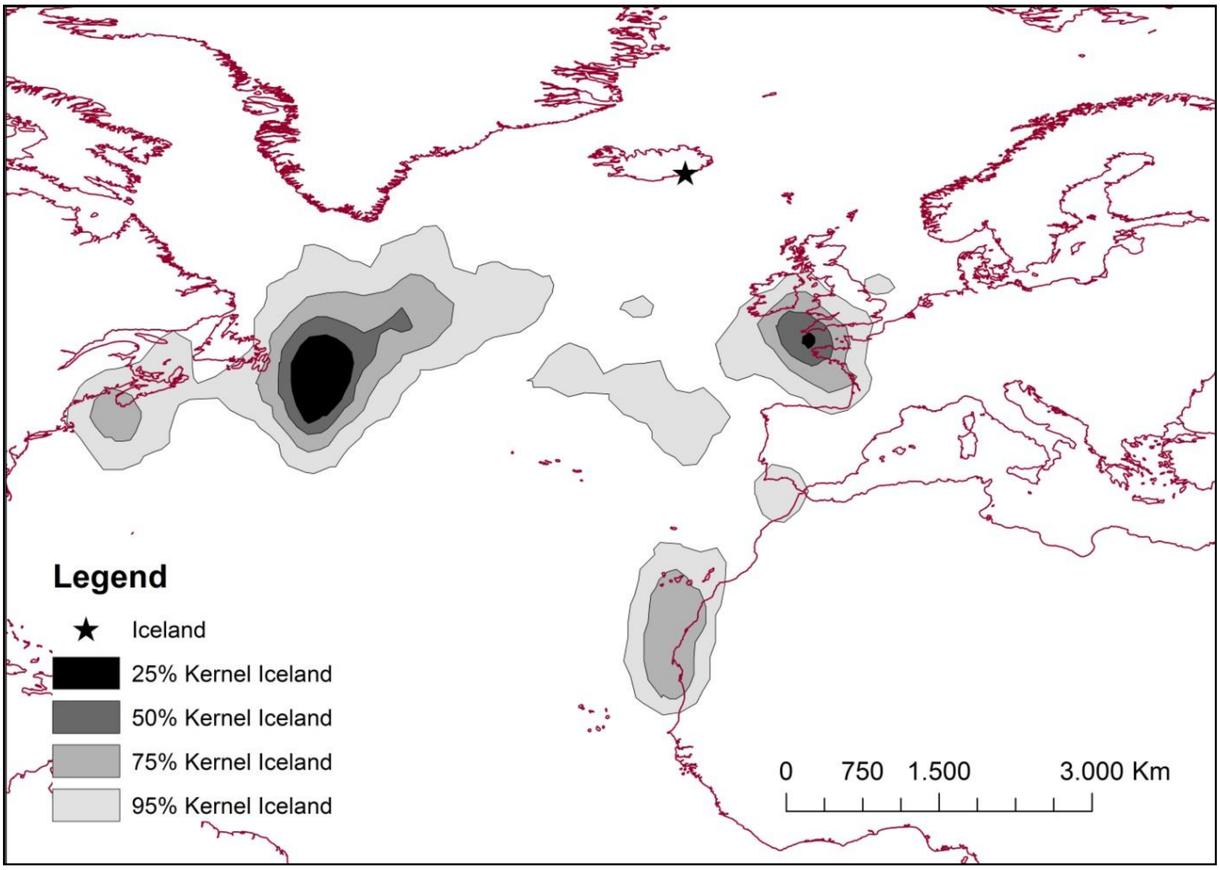

Figure 2-3. Kernel density distribution of Icelandic Great Skuas *Stercorarius skua* tracked in winter 2008/09.

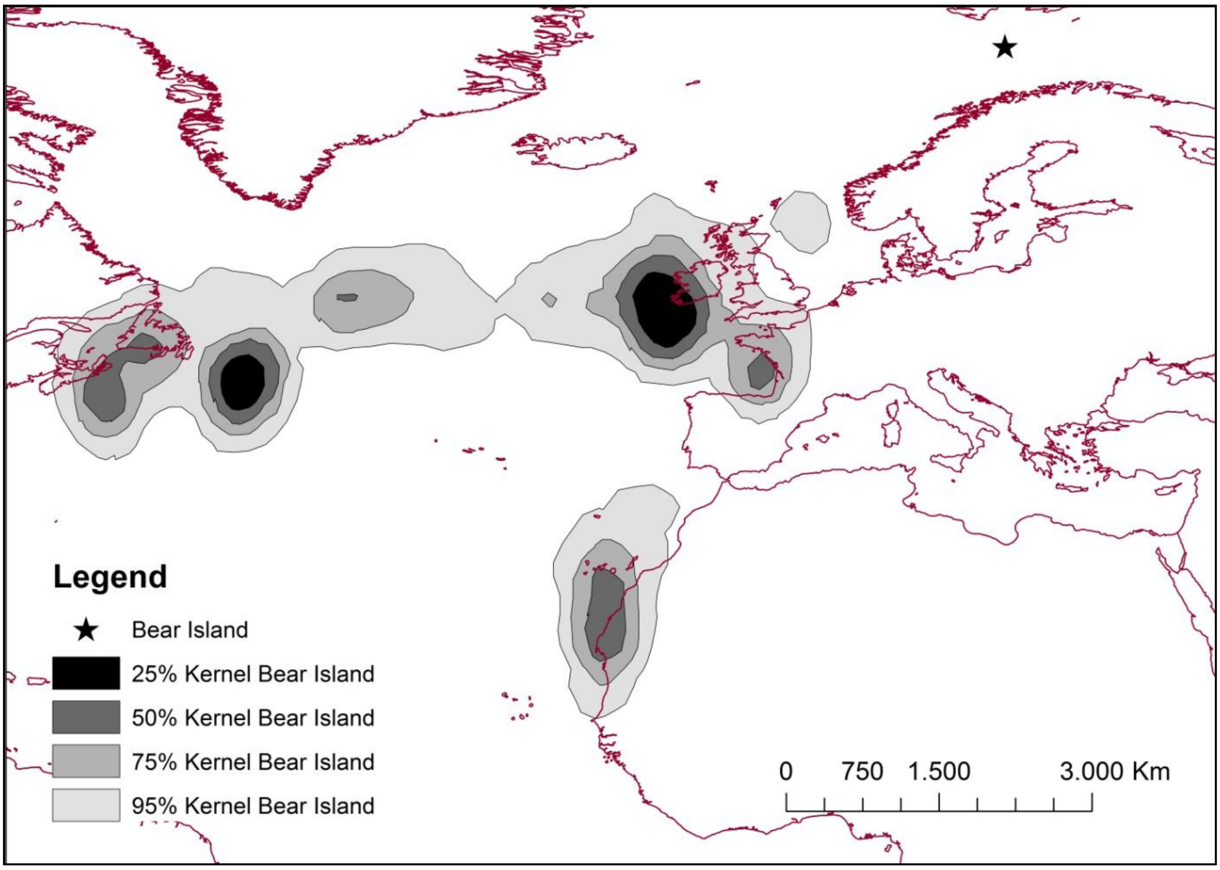

Figure 2-4. Kernel density distribution of Bjørnøya Great Skuas *Stercorarius skua* tracked in winter 2008/09.

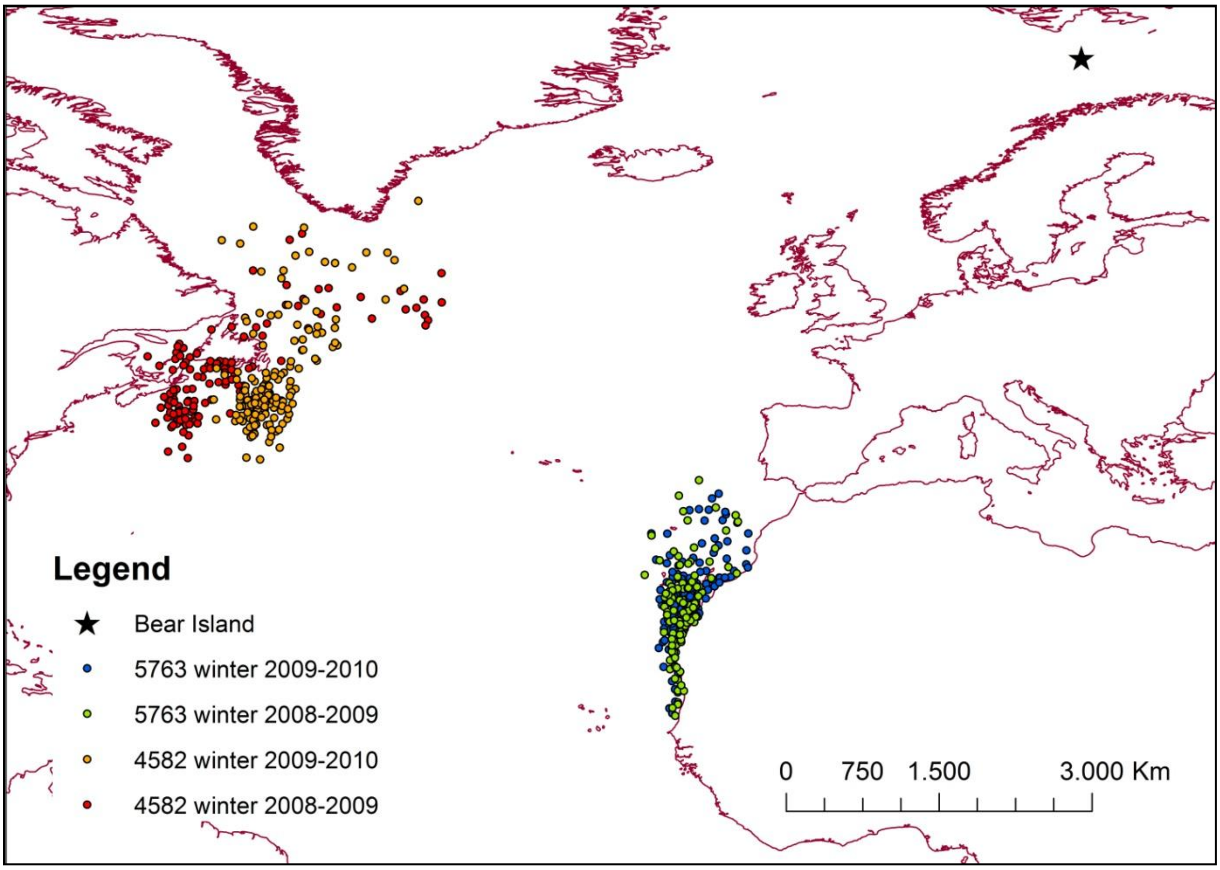

Figure 2-5. Distribution of Great Skuas *Stercorarius skua* from Bjørnøya tracked in two consecutive winters, 2008/09 and 2009/10.

Foraging activity of Great Skuas *Stercorarius skua* in the winter 2008-2009

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Abstract
Very limited information exists on winter ecology of many seabirds because of the difficulty of studying them away from the breeding grounds. Rapid development in technology over the last few decades has made studies of seabirds during the winter possible. In 2008 geolocators equipped with a saltwater sensor were put on adult Great Skuas *Stercorarius skua* at three different colonies. With the geolocators it is possible to measure the foraging activity of the birds over the whole winter. Feeding opportunities were compared between the five different winter areas. We assume that birds with low flight activity are spending less energy in foraging compared to birds that spend more time in flight. There seemed to be no difference in foraging activity between the five areas when looking at 17 birds that were site-faithful to their winter areas, except for NW-Africa (Area 1) which had much lower foraging activity compared to all the other areas. This was again confirmed by looking at the five birds that travelled between winter areas, where the only bird that altered its foraging activity by changing areas was bird 5749 that went from Iberia (Area 2) to NW-Africa (Area 1). This indicates that NW-Africa provides particularly good feeding opportunities that allow the birds to spend more time resting and therefore limit their energy expenditure over the winter.

Introduction

Birds using different wintering grounds will face different survival challenges. Few studies have dealt with the question how much environmental conditions on wintering grounds influence the breeding performance of birds in the following breeding season (Catry *et al.* 2011, Bogdanova *et al.* 2011, Öst *et al.* 2011). For some bird groups, quality of wintering grounds has been linked with performance on breeding grounds (Norris *et al.* 2004, Gunnarsson *et al.* 2005, Trinder *et al.* 2009). Bogdanova *et al.* (2011) showed that winter distribution of Black-legged Kittiwake *Rissa tridactyla* varies greatly in relation to prior breeding outcomes, where unsuccessful breeders dispersed over relatively larger areas when compared with successful ones.

Great Skuas *Stercorarius skua* have been extensively studied on the breeding grounds, mainly on Foula, Shetland (Furness *et al.* 2006). But due to technical difficulties of studying these birds away from the breeding grounds, very limited information is available on the non-breeding period of all Stercorariidae (Phillips *et al.* 2007, Kopp *et al.* 2011). Fast developments in logger technology have opened for opportunities in studying winter ecology of seabirds. For example, geolocators can now be devised to obtain light level readings, temperature measurements, saltwater immersion measurements and diving depth. This new technology has opened for possibilities to study seabirds during the non-breeding season and more learned about their winter ecology (Phillips *et al*. 2007, Mackley *et al.* 2010, Garthe *et al.* in press).

Great Skuas are not seen on land during the non-breeding season and therefore it has been assumed that they spend all their time at sea. The geolocators have made it possible to study the foraging activity (foraging effort) of the Great Skuas (i.e. time spent flying) on daily basis during the whole winter. For birds that do not spend time on land during the winter, such as many seabirds, the foraging effort of birds can be deduced from a salt-water sensor in the geolocator. When a bird sits on the sea (resting) the sensor becomes immersed in salt water so a current flows, whereas during flight the sensor is dry. Recording time wet equals resting and time dry equals flying and their proportion provides a proxy for foraging effort, where time spent flying (=foraging) an indicator for varying feeding conditions (Caldow & Furness 2000, Phillips *et al.* 2007, Garthe *et al*. in press). We assume that a low proportion of time spent in foraging effort indicates a favourable wintering ground with good food supplies, enabling the birds to minimize time searching and thereby the associated energy expenditure.

Wintering areas of Great Skuas from three breeding colonies in North Atlantic have been mapped using data from 23 geolocators, obtained over the winters 2008-2009, 2009-2010 and 2010-2011 (Magnusdottir *et al.* 2012). Winter areas of Great Skuas from Foula, Shetland had been studied earlier (Furness *et al.* 2006) but this study identified main winter areas for Great Skuas from Iceland and Bjørnøya as well as from Shetland. These main winter areas are: Area 1 is off the coast of northwest Africa, Area 2 is off the coast of Iberia, Area 3 is in the Bay of Biscay, Area 4 is off the eastern coast of North America and Area 5 is west of Ireland (Magnusdottir *et al*. 2012).

As has been suggested that albatrosses and petrels (Catry *et al.* 2004 & 2009, Phalan *et al.* 2007, Phillips *et al.* 2008, Mackley *et al.* 2011) spend more time foraging during the day than night. Therefore, the same can be expected for Great Skuas. Catry *et al.* (2009) showed that Wedge-tailed Shearwaters *Puffinus pacificus* spent up to 86% of their time on water while dark during the non-breeding season, whereas during daylight they spent about 50% of their time in flight. A similar pattern was shown for Grey-headed Albatrosses *Thalassarche* *chrysostoma* which spent up to 90% of the night resting while during the day they spent most of their time in flight (Catry *et al.* 2004). Furthermore, Great Skuas breeding in Shetland spent more time during the day foraging than during nights (Meraz Hernando 2010).

Harsh winters or changes by human activities such as fisheries and pollution may have a major effect on the Great Skua population. Improved knowledge of the winter ecology of this species is needed, to ensure protection of key marine areas (Louzao *et al.* 2009). The aim of the study was to learn how much time Great Skuas spend in foraging activity during the winter and if it varies between the five winter areas identified by Magnusdottir *et al.* (2012; Figure 3-1).

Methods

1. Study areas

In June 2008, 80 geolocators were put on Great Skuas in three different study areas located in Iceland, Norway and Scotland (Magnusdottir *et al.* 2012). In Iceland the study colony was located in Öræfi, southeast Iceland, with the main study area at Breiðamerkursandur (63°52'N, 16°29'W). In Norway the study area was located at Bjørnøya (74°29'N, 18°47'E) and in Scotland the study area was located on Foula (60°08'N, 2°05'W) a small island west of mainland Shetland.

2. Catching techniques

The birds were captured on nests during incubation with electronic noose traps. The noose was put around the nest and a remotely controlled electronic device pinned down with nails nearby. Dummy eggs were used to prevent the bird from breaking the eggs. When the birds came back to their nests a radio control was used to activate the trap and the noose tightened around the bird's legs. No attempt was made to capture equal number of males and females, especially because usually only one bird from each pair was attending the territory at the time of the capture. The birds were then recaptured at same territories in June 2009.

3. Instruments

Geolocators from British Antarctic Survey that were particularly suited for leg-mounting on large and medium sized seabirds were attached with cable ties to colour rings that were put on the birds tarsus (Figure 3-2). With the saltwater sensor on the geolocators the foraging activity of the Great Skuas was measured over the whole winter. The frequency of logging data from the salt water switch was once every 3 seconds (Mk5) or every second (Mk7), throughout the year.

4. Analyses

The activity data were comprised of two parts, proportion of time spent flying during daylight hours and during darkness. The daylight period was determined from the light measurements recorded by the logger, and corresponded approximately to the time from the onset of civil twilight at dawn to the end of civil twilight dusk, i.e. when the sun's centre is 6° below the horizon.

When comparing foraging effort between winter areas, time of day or night was included as an explanatory variable. Due to small sample size of males, sex was not considered as an explanatory variable in analyses. However, individual's variation was included as a random effect (Mackley *et al*. 2010). Here, individuals are labelled by sex in the presentation of findings.

Firstly, birds that were faithful to one area throughout the winter were used to compare foraging effort between wintering areas. Thus, foraging effort between winter areas and months, analysis was restricted to the 17 birds that used only one winter area (hereafter site-faithful) in 2008-2009. Secondly, birds that moved between wintering areas within the winter 2008-2009 (hereafter travellers) were examined to see if they maintained similar, more or less foraging effort after switching wintering areas. Furthermore, foraging effort for each area used by the five travellers was compared to foraging effort obtained for the same areas from the analysis of the 17 faithful birds.

For the birds that travelled between winter areas, the activity for each area and month was defined. The five birds travelled as follows (Magnusdottir *et al.* 2011): (1) bird 4565 went from west of Ireland (Area 5) in mid December to Bay of Biscay (Area 3) and then moved again in beginning of January to the coast of Iberia (Area 2); (2) bird 5758 went from N-America (Area 4) to Bay of Biscay (Area 3) in mid December; (3) bird 5749 went from the coast of Iberia (Area 2) to NW-Africa (Area 1) in mid December; (4) bird 4595 went from N-America (Area 4) to the coast of Iberia (Area 2) in mid December; and (5) bird 5769 went from Bay of Biscay (Area 3) to N-America (Area 4) in mid November and then again from N-America to west of Ireland (Area 5) in beginning of January.

Analyses of the foraging effort of site-faithful birds were carried out using a mixed linear model (PROC MIXED) in the SAS System (SAS Institute 1999), where time period (day vs. night), winter area (Area 1 NW-Africa, Area 2 Iberia, Area 3 Bay of Biscay, Area 4 N-America and Area 5 west of Ireland) and month (Nov, Dec, Jan) and all interactions were explanatory fixed effects, and individual site-faithful birds nested within the wintering area*time of day interaction, were explanatory random effects. The percentage of seconds spent in flight, the index of foraging effort, was the dependent variable. Foraging effort of the five travellers was compared to average LSMEANS values per area and month obtained for the faithful birds. Here, the comparison was intended to examine if travellers were able to change their inferred foraging effort by switching wintering areas.

Results

The mixed model indicated that foraging effort of site-faithful birds differed between winter areas but that the difference was dependent on time of day, indicated by a significant winter area*time of day interaction (Table 2-1).

LSMEANS comparisons reported that flying activity was higher during day than during night for all five winter areas (Table 3-2). In all winter areas the Great Skuas spent 5-10% of the time in flight during the night, while over the day the time spent in flight was 15-45% of the overall time (Tables 3-3A and 3-3B).

During the day, foraging activity was similar between winter areas 2, 3, 4, and 5 whereas foraging activity was lower in Area 1 compared to all the other wintering areas. During the night, foraging activity was similar and extremely low between all five winter areas (Table 3-3B).

The solution for individual birds (random effects) indicated that there was no variation between birds within winter areas, with the exception of winter area 4 during the day, (t=2.36, DF=64, P=0.0216). Otherwise, t-values were lower than 1.33 and corresponding P-values higher than 0.18. Bird 4561 at Area 4 seems to have a small difference from other birds within same area during both day and night

There was little or no variation between individuals and even 4 of 5 birds that travelled between winter areas did not change their activity following relocation (Figure 3-3). An exception was bird 5749 which was the only bird that travelled from a more active area (Area 2) to a less active area (Area 1). Area 1 happened to be the only area that was statistically different from the other areas during the day for site-faithful birds. The activity for that bird decreased after it arrived at Area 1 (Figure 3-4).

No difference in activity was observed in foraging effort of males and females because of the majority of our birds were females (Figure 3-5).

Discussion

A difference was observed in foraging effort between Area 1 (NW-Africa) and the other winter areas. Birds staying in Area 1 spent less time in flight, and therefore used less time foraging and more time resting on the ocean. Garthe *et al.* (in press) reported this same pattern for Northern Gannets *Morus bassanus*, wintering off West Africa, which spent less time in flight during the day, compared to birds wintering in Bay of Biscay and in the North Sea. Since both of these studies show that birds spend less time in flight in West Africa as compared to other areas, NW-Africa may provide particularly good feeding opportunities that allow the birds to spend more time resting on the ocean. However, birds travelling to NW-Africa are spending more energy in migration than birds travelling shorter distances, such as birds wintering in Bay of Biscay or Iberia. Wintering of West Africa may represent a trade-off because going there incurs the longest migration distance for Great Skuas. Birds spending time in more northerly, colder waters use more energy for thermoregulation than birds spending time in more southerly (Garthe *et al.* in press). Therefore, the costs of thermoregulation alone in the northern areas may cancel out energy saved by avoiding the longer migration (Garthe *et al.* in press). However, food availability and weather conditions are more likely to determine suitability of different areas.

There was no observed individual variation in activity patterns of the tracked Great Skuas within each winter area, except possibly for Area 4, where also there was the biggest sample size of birds. It can be concluded that individuals within the same winter areas behave similarly, as shown for Grey-headed Albatrosses which also showed relatively little variation within and between individuals (Catry *et al.* 2004). However, Mackley *et al.* (2010) showed by using loggers on greater number of individuals than Catry *et al.* (2004), that there is greater variation between individual albatrosses of four species than previously reported. Therefore, the question arises whether sample size can affect the result as well as if the study applies for one year or more, by having too few samples we cannot see any difference between individuals.

There were no differences in foraging effort between the months, November, December and January during winter, neither for day or night. Therefore, winter conditions at each area seem stable over the whole winter period. This study was limited to one winter but harsh winter conditions may occur every now and then and may affect the survival of the Great Skuas. However, there is little evidence connecting environmental conditions to adult survival. Long lived species should be able to survive difficult winter situations more readily than short lived species since they are more likely to move to a more favourable environment if necessary (Schreiber & Burger 2002). However, if environmental conditions were fluctuating a difference in foraging effort would be noticeable in the birds between months, where reduction of food availability should lead to increased activity behaviour.

As expected, there was a huge difference between activities of Great Skuas during the days compared to nights. This might be a consequence of difficulty of seeing prey during darkness as has been suggested for albatrosses and petrels (Catry *et al.* 2004, Phillips *et al.* 2008, Mackley *et al.* 2011). This has been shown for four albatross species that with increasing night length the species spent significantly more time on the water (Phalan *et al.* 2007). A reason for this might also be that Great Skuas at breeding colonies usually stop feeding some time before darkness falls and rather return to the territory at night to sleep (Furness 1987). Meraz Hernando (2011) proved that to be the case, at least for 5 Great Skuas from Foula that carried GPS data loggers. The birds were spending more time flying between 08:00-24:00 and less during nights over the migration and winter periods. Here, it is confirmed that Great Skuas seem to spend majority of the night resting on the sea during the non-breeding period.

Despite small sample size, no difference in activity could be seen between the sexes within winter areas 1 and 4. This has also been shown for Black-browed Albatrosses *Thalassarche melanophris* and Wandering Albatrosses *Diomedea exulans*, that there are no significant differences in the proportions of time spent on the water by males compared with females during the non-breeding period (Mackley *et al.* 2010) and for the Wedge-tailed Shearwater *Puffinus pacificus* there were no evidence of sex-related differences in activities (Catry *et al.* 2009). Even for species that show some sexual dimorphism like Cory's Shearwater (where males are larger than females), Ramos *et al.* (2009) found that the sexes do not differ in foraging trip duration and feeding ecology during the incubation period.

The reason for birds to travel between winter areas must be to find places with better feeding opportunities to reduce their foraging costs. Most of the travellers did not gain anything from changing winter areas in terms of an apparent reduction in foraging effort, except for bird 5749 that was the only bird that went from a more active area to Area 1 with less activity. For the others it can be said that they even put more energy cost by their attempt to try to find a better winter area by wasting energy by flying long distances. These data show birds over one winter, and it would therefore be interesting to see activity data for travelling birds over more than one winter, to see if they learn from their former experience and thus rather stay in one area rather than to spend energy into travelling. Travelling between wintering areas seem though to take relatively short time, since a trip over the Atlantic Ocean took about seven days for bird 5769. The birds seem to spend some time travelling between areas, but this might also be because they are feeding along the way and not going directly to a new winter area.

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Tables and figures

Table 3-1. Explanatory variables and their interactions from a mixed model on foraging effort of 17 Great Skuas *Stercorarius skua* that were tracked within five winter areas in winter 2008-2009. F-tests were deemed significant at ά<0.05.

Explanatory variable	Num df	Den df	F Value	P
Winter area	4	64	2.43	0.0569
Month	2	64	0.07	0.9331
Time of day	1	64	122.56	0.0001
Winter area*time of day	4	64	3.75	0.0084
Winter area*Month	8	64	0.48	0.8637
Month*time of day	2	64	0.52	0.5997
Winter*Month*timeofd	8	64	1.29	0.2661

Num df = numerator degrees of freedom for F-test
Den df = denominator degrees of freedom for F-test

Table 3-2. Comparison of LSMEAN time spent flying, compared between day and night of Great Skuas *Stercorarius skua* tracked in 2008-2009 within each of five winter areas. Tests were deemed significant at ά<0.05.

	LSMEAN time spent flying		Difference	SE	t	P
Winter Area	Day	Night				
1	17.8	7.8	10.0	3.9	2.5	0.0129
2	38.8	7.1	31.7	8.1	3.9	0.0002
3	33.6	4.9	28.7	4.5	6.4	0.0001
4	29.7	4.7	25.0	2.2	11.3	0.0001
5	33.2	6.6	26.6	3.8	7.0	0.0001

Table 3-3A. Comparison of LSMEAN time spent flying of Great Skuas *Stercorarius skua* tracked in 2008-2009, compared between winter areas during daylight hours (see Table A for the LSMEANS for each area). Tests were deemed significant at ά<0.05.

Winter areas		Difference	SE	t	P
1	2	-21.1	6.4	-3.30	0.0014
1	3	-15.8	4.2	-3.73	0.0003
1	4	-11.9	3.2	-3.74	0.0003
1	5	-15.4	3.9	-3.98	0.0001
2	3	5.3	6.6	0.80	0.4248
2	4	9.1	6.0	1.53	0.1299
2	5	5.7	6.3	0.89	0.3758
3	4	3.8	3.6	1.08	0.2824
3	5	0.4	4.2	0.09	0.9277
4	5	-3.5	3.1	-1.11	0.2690

Difference = LSMEAN time spent flying per area subtracted from one another.

Table 3-3B. Comparison of LSMEAN time spent flying of Great Skuas *Stercorarius skua,* tracked in 2008-2009, compared between winter areas during night (see Table A for the LSMEANS for each area). Tests were deemed significant at ά<0.05.

Winter areas		Difference	SE	t	P
1	2	0.7	6.4	0.11	0.9108
1	3	2.9	4.2	0.69	0.4909
1	4	3.1	3.2	0.96	0.3381
1	5	1.2	3.9	0.30	0.7655
2	3	2.2	6.6	0.34	0.7376
2	4	2.4	6.0	0.40	0.6929
2	5	0.4	6.3	0.07	0.9449
3	4	0.2	3.6	0.04	0.9660
3	5	-1.8	4.2	-0.42	0.6723
4	5	-1.9	3.1	-0.62	0.5387

Difference = LSMEAN time spent flying per area subtracted from one another.

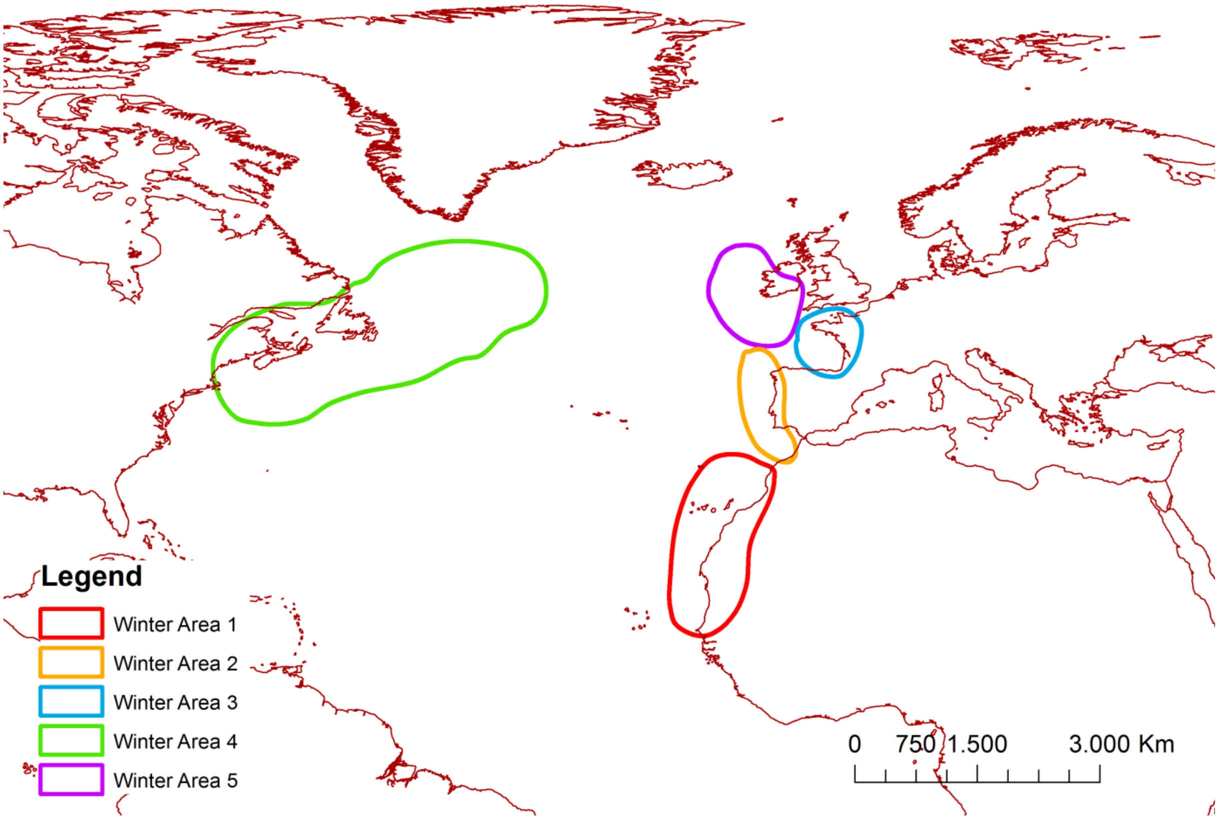

Figure 3-1. The winter areas of Great Skuas *Stercorarius skua* 2008-2009 as shown by Magnusdottir *et al.* 2012. Area 1 "NW-Africa", Area 2 "Iberia", Area 3 "Bay of Biscay", Area 4 "N-America", Area 5 "west of Ireland".

Figure 3-2. The attachment of the geolocators to a colour ring on Great Skua *Stercorarius skua*.

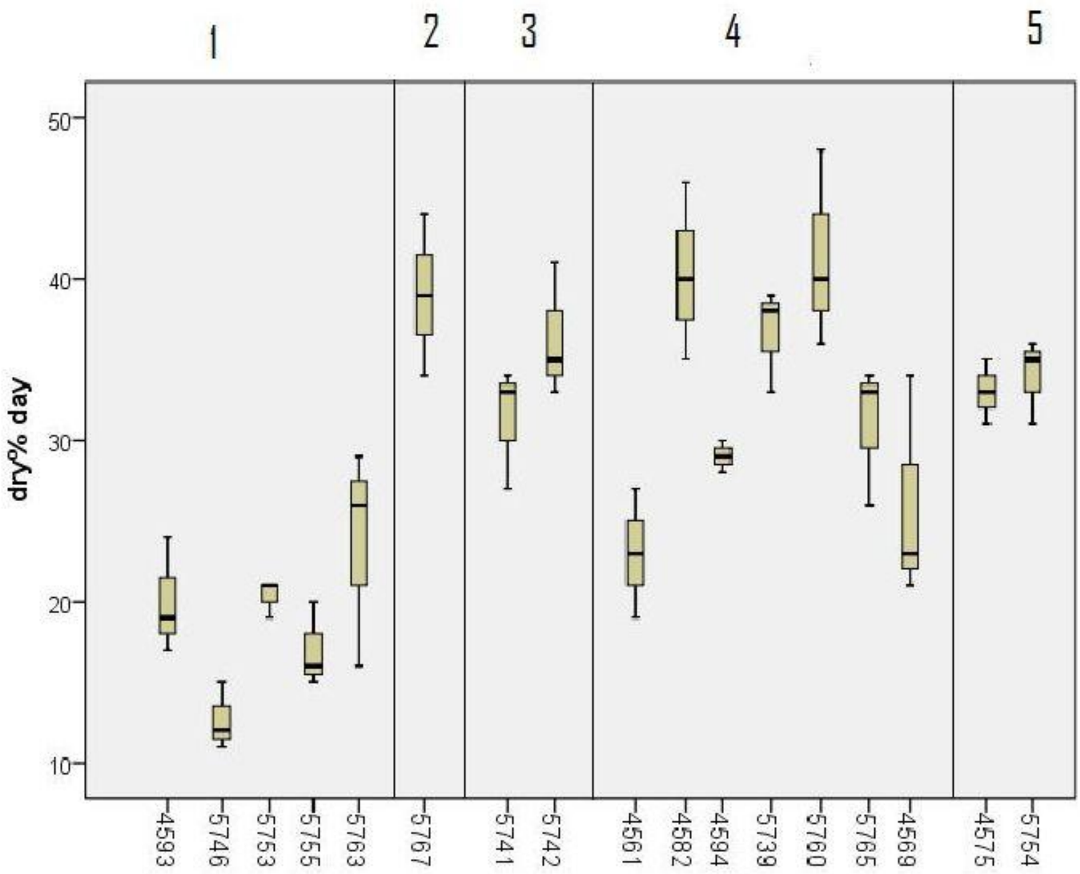

Figure 3-3. The foraging effort of the 17 site-faithful Great Skuas *Stercorarius skua* tracked in five winter areas. Mean foraging effort for each day over the dates 1 November 2008 – 31 January 2009 was used to find the foraging effort of each bird.

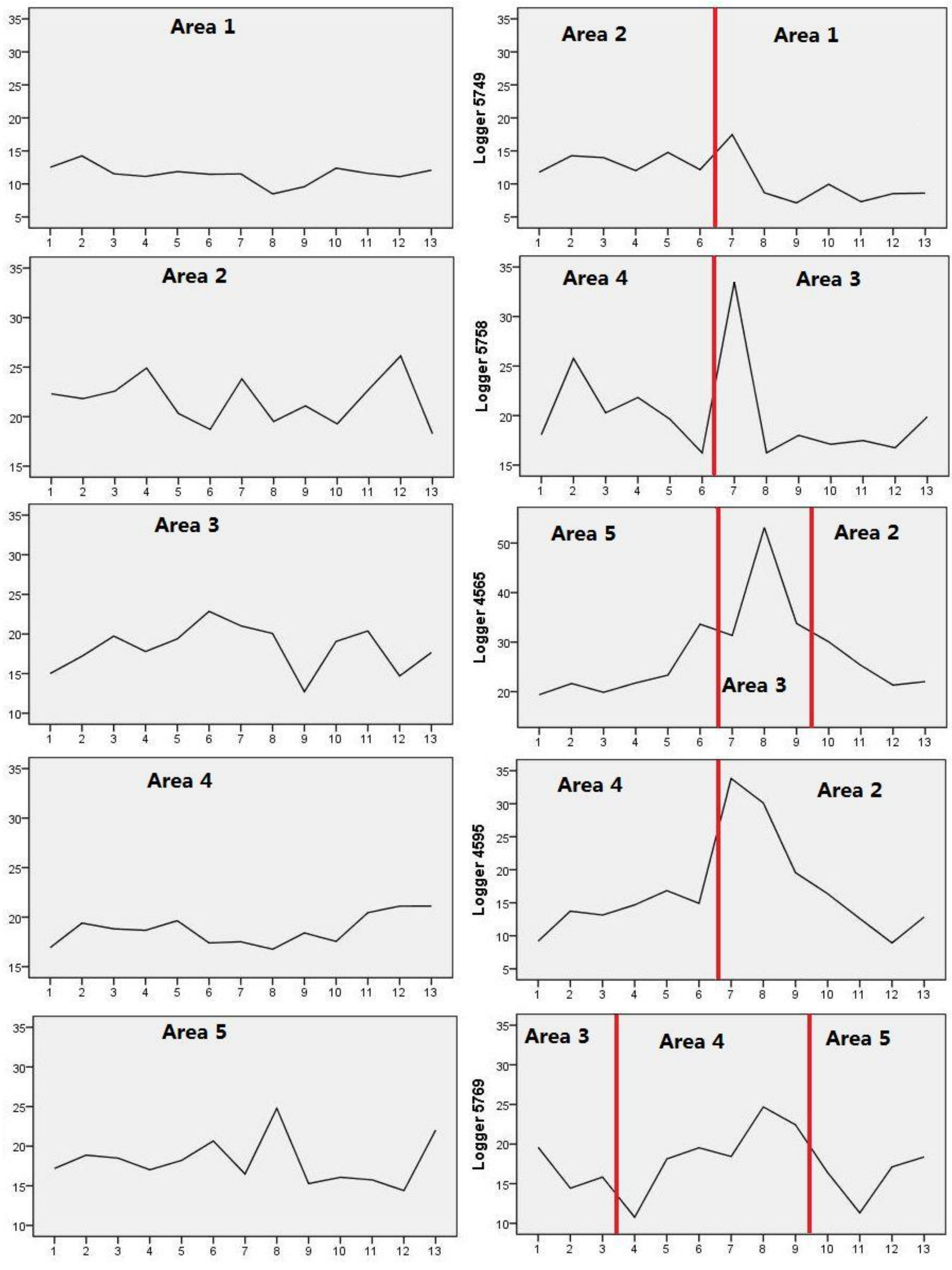

Figure 3-4. To the left the average foraging effort of the faithful Great Skua *Stercorarius skua* tracked in winter 2008-2009 between weeks for each area. To the left is the foraging effort of travellers between weeks, from 1 Nov-31 Jan. Note that for bird 4565 the Y-axis spans 55% foraging effort instead of 35%.

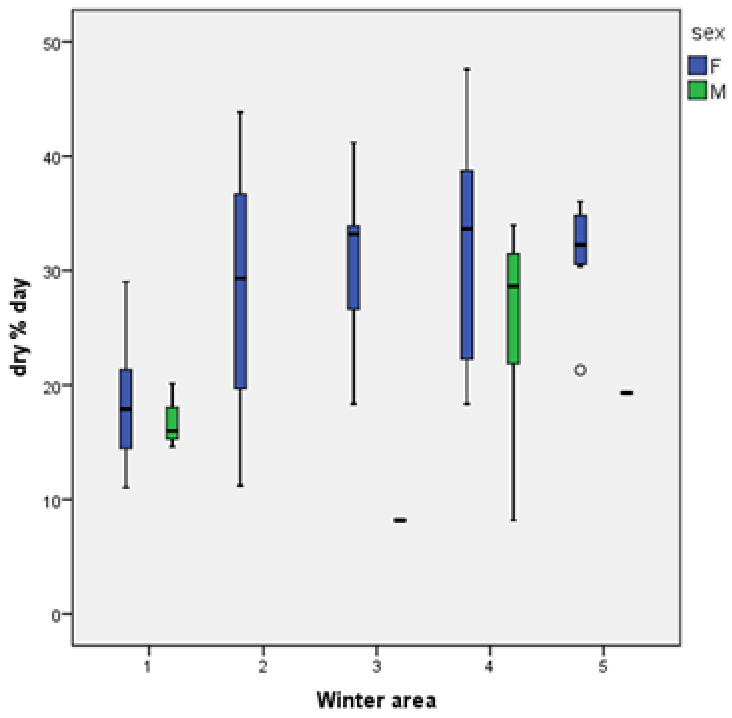

Figure 3-5. Average foraging effort during daylight hours, measured as precent time spent in flight, of female Great Skuas *Stercorarius skua* and of males the winter 2008-2009.