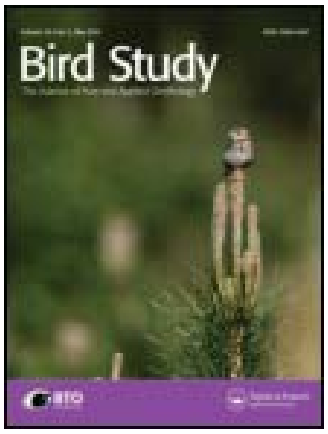

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Activity patterns of wintering Great Skuas *Stercorarius skua*

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Capsule Great Skuas *Stercorarius skua* wintering in different areas spent different amounts of time in flight (foraging or searching for food) and so may be experiencing different feeding conditions.

Aims To compare the daily percentage of time spent in flight (foraging or searching for food) between different wintering areas.

Methods In 2008, loggers equipped with a saltwater sensor were deployed on adult Great Skuas at three colonies in the northeast Atlantic, and the data used to compare foraging activity between the five main wintering areas.

Results The five areas used by 22 Great Skuas in winter were widely separated, from the northwest Atlantic to northwest Africa, and differ substantially in oceanography. The main difference in foraging effort among areas for individuals that were site-faithful was that the percentage of time per day spent in flight off northwest Africa was much lower than elsewhere. Among five birds that travelled between wintering areas, one reduced the percentage of time in flight after switching from Iberia to northwest Africa.

Conclusion The data suggest that feeding conditions were better off northwest Africa than elsewhere, at least during winter 2008/09. This allowed Great Skuas wintering in that region to spend more time resting, so probably reducing their overall energy expenditure.

Life cycles are complex, and conditions experienced in one season can constrain the events in another season, leading to long-term consequences for fitness (Norris *et al.* 2004, Sorensen *et al.* 2009). Birds using different wintering grounds can face different survival challenges; however, because of the difficulty of following birds outside their breeding grounds, few studies have investigated the extent to which environmental conditions on wintering grounds influence the breeding performance of birds in the following breeding season (Norris *et al.* 2004, Gunnarsson *et al.* 2005, Trinder *et al.* 2009, Catry *et al.* 2011, Öst *et al.* 2011). Similarly, the outcome of a breeding episode can influence timing of migration and the choice of wintering quarters; unsuccessful Black-legged Kittiwakes *Rissa tridactyla* disperse further than successful breeders (Bodganova *et al.* 2011), and failed Cory's Shearwaters *Calonectris diomedea* start most phases of migration sooner than successful birds and return earlier to the colony in the following season (Catry *et al.* 2011).

Outside the breeding season, many seabird species spend all their time at sea. Loggers that record saltwater immersion allow the study of foraging activity, or searching for food, by birds on a daily basis (Phalan *et al.* 2007, Phillips *et al.* 2007). Developments in logger technology have opened new opportunities for studying wintering ecology of seabirds by recording light levels (for geolocation), saltwater immersion and diving depth at high resolution (Phillips *et al.* 2007, Mackley *et al.*

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2010, Garthe *et al.* 2012). When a bird is resting on the sea, the two electrodes are immersed in salt water and allow current to flow, whereas during flight, the sensors remain dry and no current is recorded. While the sensors are dry the birds are flying and we assume they are foraging or searching for food. The proportion of time that the logger is dry provides a proxy for foraging effort, because a greater time spent flying is thought to be indicative of poor local feeding conditions and more time spent searching for food (Caldow & Furness 2000, Phillips *et al.* 2007, Garthe *et al.* 2012).

Great Skuas *Stercorarius skua* have been studied extensively on the breeding grounds, mainly on Foula, Shetland and St Kilda, Western Isles (Phillips *et al.* 1999, Furness *et al.* 2006). However, due to technical difficulties of studying these birds away from the breeding grounds, there have been fewer studies of the non-breeding period of all Stercorariidae (but see Phillips *et al.* 2007, Kopp *et al.* 2011, Sittler *et al.* 2011, Magnusdottir *et al.* 2012, Gilg *et al.* 2013).

Harsh winters or other changes in the marine environment (e.g. in fishery activities or levels of pollution) may have major effects on the Great Skua population, because this is one of the world's rarer bird species, with a world population of some 16 000 breeding pairs occupying a small range in the North Atlantic (Mitchell *et al.* 2004). Improved knowledge of the winter ecology of this species is therefore needed to ensure protection of key marine areas. The main aim of the study was to provide detailed information on the foraging activity of Great Skuas during winter to determine if there are differences in bird behaviour in response to prevailing environmental conditions in the five wintering areas (Area 1 northwest Africa, Area 2 Iberia, Area 3 Bay of Biscay, Area 4 North America and Area 5 west of Ireland) previously identified by Magnusdottir *et al.* (2012). We assumed that a low proportion of time spent in flight can indicate a favourable wintering ground with consistently good food supplies, enabling the birds to minimize time searching and thereby the associated energy expenditure. Our study may also therefore provide information on how the wintering ecology of seabirds might result in carry-over effects in the following breeding season.

Environmental conditions and differences in photoperiod can affect foraging effort, as can factors such as sex or individual feeding proficiency or preference. If environmental conditions fluctuate, then a difference in foraging effort may be noticeable between months, and in particular a reduction in food availability might be expected to lead to increased time spent in flight. With the exception mainly of some petrels, seabirds tend to feed mostly during the day (Mougeot & Bretagnolle 2000, Catry *et al.* 2004, 2009, Phalan *et al.* 2007, Phillips *et al.* 2008, Mackley *et al.* 2011). Similarly, we expected to find clear diurnal patterns in foraging activity of Great Skuas, particularly as radio-tracking indicated that individuals breeding in Scotland spend a much greater proportion of time away from their territory during the day than the night (Votier *et al.* 2006). Other studies have also identified sex-specific differences in foraging behaviour of seabirds (Catry *et al.* 2009, Mackley *et al.* 2010), therefore we also examined differences in time spent foraging between males and females tracked in our study.

METHODS

In June 2008, 80 combined geolocator-immersion loggers (British Antarctic Survey, UK) were deployed on Great Skuas in three different study areas; Iceland, Svalbard 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 Svalbard (Norway), the study area was located on 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.

The birds were captured on the nest during incubation with electronic noose traps. The noose was put around the nest and attached to a remotely controlled electronic device pinned down nearby. Dummy eggs were used to prevent egg breakage. When the birds returned to their nests, the trap was activated by remote control and the noose tightened around the bird's legs. No attempt was made to capture equal number of males and females, because usually only one bird from each pair was attending the territory at the time of the capture. The birds were then recaptured at the same territories in summers 2009 and 2010.

Loggers were attached with cable ties to colour rings that were put on the tarsus. These recorded timing of saltwater immersion, providing detailed information on at-sea activity patterns of the tracked Great Skuas throughout winter 2008/09. The very high proportion of time spent on the water during darkness (84–93%) recorded in a previous study using similar loggers on two closely related skua sub-species (Phillips *et al.* 2007), infers that unlike some other seabirds,

including puffins *Fratercula arctica* (Harris *et al.* 2010), skuas sitting on the sea surface do not spend substantial periods with the leg extended out of the water or retracted into the feathers. It can therefore be assumed that immersion data from skuas recorded by a logger on the tarsus provides an accurate indication of time spent in the water and in flight. Analyses were restricted to the period 1 November until 31 January to ensure that the birds were at the wintering areas and not travelling from, or toward, their breeding colony. The loggers test for saltwater immersion every 3 seconds, and these data are either binned into 10 minutes intervals (Mk5 loggers) or recorded as every change of state (from wet to dry, or vice versa) that lasts at least 6 seconds (Mk7 loggers).

The activity data were used to determine the proportion of time spent flying during daylight hours and during darkness from 1 November 2008 until 31 January 2009. The data were grouped into daylight and darkness periods based on the light measurements recorded directly by the logger, and corresponded approximately to the time from the onset of civil twilight at dawn, to the end of civil twilight at dusk, i.e. when the sun's centre is 6° below the horizon. We tested both to see if there were differences in activity during daylight, and during darkness, as birds in different areas might vary in the reliance on bioluminescent prey, use of moonlight, or in the proportion of time spent behind fishing vessels operating at night. When comparing foraging effort between wintering areas, period of the day (i.e. day versus night) was included as an explanatory factor.

Due to the small sample of males (4 out of 22 were male), sex was not included as an explanatory variable in analyses. However, individual identity was included as a random effect (Mackley *et al.* 2010).

The comparison of percentage of time spent flying (i.e. foraging effort), among wintering areas and months was restricted to the 17 birds that used only one wintering area (hereafter called site-faithful) in 2008/09. Wintering areas were determined from the light data recorded by the loggers using geolocation (for details see Magnusdottir *et al.* 2012). In addition, the activity patterns of five birds that moved between areas within winter 2008/09 (hereafter called travellers) were examined to see if they subsequently maintained, reduced or increased their foraging effort. In addition, foraging effort in each wintering area used by the 5 travellers was compared with that of the 17 site-faithful birds.

The movements of the five travellers were as follows (Magnusdottir *et al.* 2012): (1) bird 4565 went from west of Ireland (Area 5) on 20 December to Bay of Biscay (Area 3) and then moved again to the coast of Iberia in early January (Area 2); (2) bird 5758 went from North America (Area 4) on 12 December to Bay of Biscay (Area 3); (3) bird 5749 went from the coast of Iberia (Area 2) on 17 December to northwest Africa (Area 1); (4) bird 4595 went from North America (Area 4) on 16 December to the coast of Iberia (Area 2); (5) bird 5769 went from Bay of Biscay (Area 3) to North America (Area 4) in mid-November and then again from North America to west of Ireland (Area 5) on 7 January.

Analyses of the foraging activity 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 versus night), five wintering areas and month (November, December and January) and all interactions were included as fixed effects, and individual identity nested within the wintering area*time of day interaction, as a random effect. We chose to nest individual within both wintering area and time of day because the effect of individual could differ according to the level of both variables. The percentage of time spent in flight (the index of foraging effort), was the dependent variable. Percentage of time spent in flight of the five travellers was compared to average least-square mean values per area and month obtained for the site-faithful birds. Here, the comparison was to examine whether travellers changed their inferred foraging effort as a consequence of switching wintering areas.

RESULTS

Percentage of time spent in flight of site-faithful birds differed between wintering areas during daylight but was similar during darkness, as indicated by the significant wintering area*time of day interaction (Table 1).

Based on the least-square means comparisons, the percentage of time spent in flight was higher during daylight than darkness for all five wintering areas (Table 2). In all areas, the tracked Great Skuas spent 5–10% of their time in flight during the night, and 15–45% of their time in flight during daylight (Table 2).

During the night, the percentage of time spent in flight was uniformly low in all five wintering areas.

Table 1. Explanatory variables and their interactions from a mixed model of proportion of time spent in flight by 17 Great Skuas *S. skua* that were tracked within 5 wintering areas (northwest Africa (Area 1), Iberia (Area 2), Bay of Biscay (Area 3), the eastern coast of North America (Area 4) and west of Ireland (Area 5), in 2008–2009. *F*-tests were deemed significant at $\alpha < 0.05$.

Explanatory Variable	Num df	Den df	*F* Value	*P*
Winter area	4	64	2.4	0.06
Month	2	64	0.1	0.9
Time of day	1	64	122.6	0.01
Winter area*time of day	4	64	3.7	0.01
Winter area*Month	8	64	0.5	0.86
Month*time of day	2	64	0.5	0.60
Winter*Month*time of day	8	64	1.3	0.27

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

Table 2. Comparison of least-square mean percentage of time spent flying between day and night of Great Skuas *S. skua* tracked in 2008/09 within each of five wintering areas (northwest Africa (Area 1), Iberia (Area 2), Bay of Biscay (Area 3), the eastern coast of North America (Area 4) and west of Ireland (Area 5). Tests were deemed significant at $\alpha < 0.05$.

	Least-square mean time spent flying					
Winter Area	Day	Night	Difference	se	*t*	*P*
1	17.8	7.8	10.0	3.9	2.5	0.01
2	38.8	7.1	31.7	8.1	3.9	0.01
3	33.6	4.9	28.7	4.5	6.4	0.01
4	29.7	4.7	25.0	2.2	11.3	0.01
5	33.2	6.6	26.6	3.8	7.0	0.01

Since Great Skuas spend more time foraging during the day, comparisons between areas were of daytime activity levels. During daylight, the percentage of time spent in flight was significantly lower in northwest Africa (Area 1) than in the other four wintering areas, among which there were no significant differences (Area 2 Iberia, Area 3 Bay of Biscay, Area 4 North America and Area 5 west of Ireland): Table 3, Fig. 1.

There was no significant variation in percentage of time spent in flight between individual birds within wintering areas, as indicated by *t*-values < 1.3 and corresponding *P*-values > 0.18. A single exception was Bird 4561 within wintering Area 4 during the day, which spent a slightly lower percentage of time in flight compared with other birds ($t = 2.4$, df = 64, $P = 0.02$). Four of the five birds that travelled between wintering areas did not change their percent of time spent flying following relocation (Fig. 2). An exception was Bird 5749, a female, which was the only individual that travelled from an area where birds were more active (Area 2) to an area where birds were less active (Area 1); the percent of time spent in flight by that bird decreased after its arrival

Table 3. Comparison of least-square mean time spent flying of Great Skuas *S. skua* tracked in 2008/09 among wintering areas (northwest Africa (Area 1), Iberia (Area 2), Bay of Biscay (Area 3), the eastern coast of North America (Area 4) and west of Ireland (Area 5) during daylight and darkness. Tests were deemed significant at $\alpha < 0.05$.

Winter areas		Day *t*	Day *P*	Night *t*	Night *P*
1	2	−3.3	0.01	0.1	0.91
1	3	−3.7	0.01	0.7	0.49
1	4	−3.7	0.01	1.0	0.34
1	5	−4.0	0.01	0.3	0.77
2	3	0.8	0.42	0.3	0.74
2	4	1.5	0.13	0.4	0.69
2	5	0.9	0.38	0.1	0.94
3	4	1.1	0.28	0.0	0.97
3	5	0.1	0.93	−0.4	0.67
4	5	−1.1	0.27	−0.6	0.54

Difference = least-square mean time spent flying per area subtracted from one another.

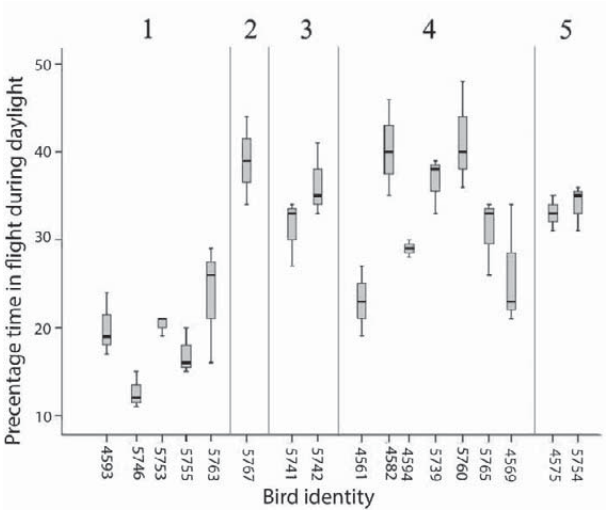

Figure 1. A boxplot that shows percentage of time spent in flight by 17 site-faithful Great Skuas *S. skua* tracked in 5 wintering areas (northwest Africa (Area 1), Iberia (Area 2), Bay of Biscay (Area 3), the eastern coast of North America (Area 4) and west of Ireland (Area 5) in 1 November 2008–31 January 2009. The boxplot includes 50% of the datapoints for time spent in flight and horizontal bar within the box shows the median for each bird.

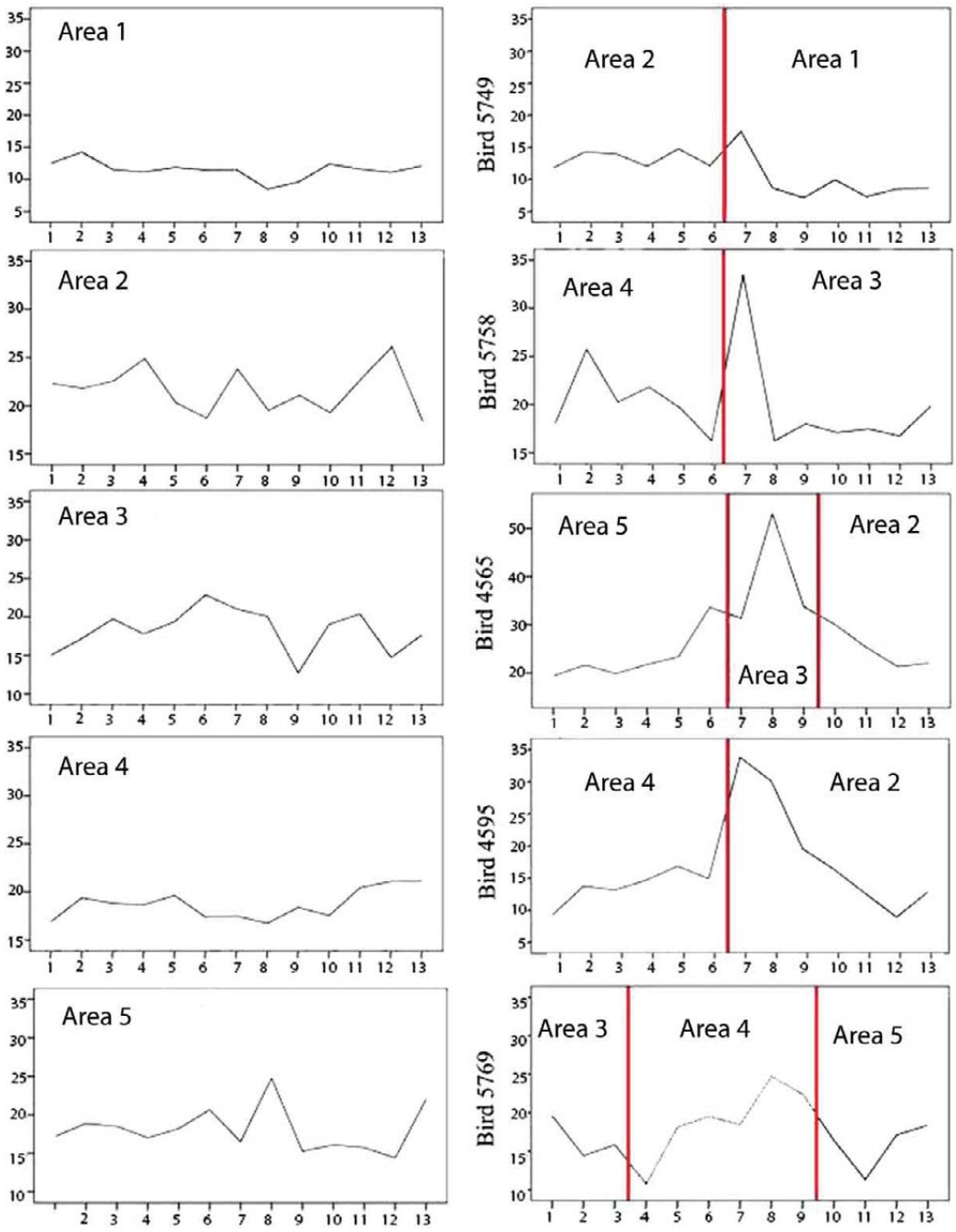

Figure 2. The average weekly proportion of time spent in flight by Great Skuas *S. skua* tracked in winter 2008/09 (1 November–31 January) to different wintering areas (northwest Africa (Area 1), Iberia (Area 2), Bay of Biscay (Area 3), the eastern coast of North America (Area 4) and west of Ireland (Area 5). The left-hand series of graphs show the data for site-faithful birds (which did not change area), and the right-hand series show the data for birds that switched areas in the same winter. Note the different scale on the *y*-axis for Bird 4565.

in Area 1 (Fig. 2). No difference in percent of time flying was observed between males and females, but there were only 4 males in the sample of 22 Great Skuas (Fig. 3).

DISCUSSION

The detailed analysis of activity patterns of wintering Great Skuas highlighted significant differences in the

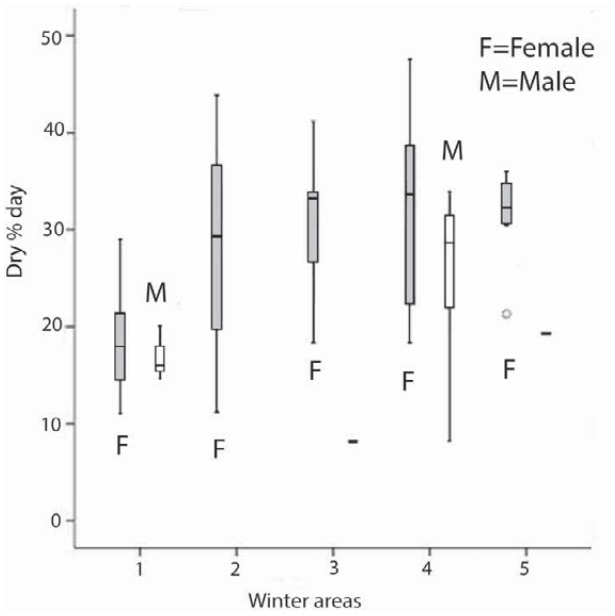

Figure 3. Percentage time spent in flight during daylight hours in winter 2008/09 by female and male Great Skuas *S. skua* that wintered in different regions (northwest Africa (Area 1), Iberia (Area 2), Bay of Biscay (Area 3), the eastern coast of North America (Area 4) and west of Ireland (Area 5).

percentage of time spent flying during daylight, but not darkness, between northwest Africa and the other non-breeding areas. Great Skuas wintering in northwest Africa spent less time flying and more time resting on the ocean, and therefore we conclude that they expend less energy in foraging. Garthe *et al.* (2012) reported the same pattern for Northern Gannets *Morus bassanus* wintering off west Africa, which spent less time flying during the day than those in the Bay of Biscay and North Sea. The similarity in these results between seasons suggests that feeding opportunities were particularly good off northwest Africa during the winters when these studies were carried out. However, for both species, northwest Africa is the most southerly wintering destination and so represents the longest migration distance from the colony. Presumably, therefore, birds expend more energy in transit to this region. Therefore, wintering off the west coast of Africa may represent a trade-off between the higher costs of migration and the benefits of better foraging conditions. Moreover, costs associated with thermoregulation should also be taken into account since they will be lower for birds occupying southerly locations compared to birds that winter in more northerly, colder waters (Garthe *et al.* 2012). However the assumption that foraging is better in an area where birds spend a small proportion of time in flight may not always be true: prey may be easy to locate but of poor quality; in such circumstances the bird may spend little time searching for prey patches but then allocate a lot of time or effort to capturing enough items to meet its nutritional needs.

Within each wintering area, there was no significant variation among individuals in percentage of time spent in flight, except possibly in waters off North America (Area 4) where the sample size was greatest. Although these results may reflect the relatively small samples, they are in accordance with studies of several other species, which showed that individuals within the same wintering areas behaved similarly (Catry *et al.* 2011, Mackley *et al.* 2011). However, this is not universal; albatrosses of four different species showed significant variation among individuals in activity patterns during the non-breeding period (Mackley *et al.* 2010).

Our data did not suggest any significant seasonal changes from November to January in percentage of time spent in flight during either daylight or darkness. Therefore, environmental conditions in each wintering area seem to be broadly stable from early November until end of January. This study was limited to one winter when conditions may have been relatively benign; however, harsh conditions probably occur in some years and can affect the survival of seabirds (Frederiksen *et al.* 2004, Smith & Gaston 2012).

As expected, the foraging activity of Great Skuas was significantly higher during daylight than darkness. Five Great Skuas tracked from Foula using GPS devices spent a greater proportion of time flying in the day than the night during their southerly migration and subsequent winter (Meraz-Hernando 2011). During the non-breeding period, the Great Skuas tracked in our study spent the majority of the night resting on the sea. Similarly, Brown Skuas *Stercorarius antarctica lonnbergi* and Falkland Skuas *Stercorarius antarctica* tend to spend much more time on the water during darkness than daylight over the winter period (Phillips *et al.* 2007). Most other seabirds are also diurnal, presumably because they have difficulty spotting prey during darkness (Catry *et al.* 2004, Mougeot & Bretagnolle 2000, Phalan *et al.* 2007, Phillips *et al.* 2008, Mackley *et al.* 2011). However, there are reports of Great Skuas hunting other seabirds at night during the breeding season, and they may take particular advantage of moonlit nights (Mougeot & Bretagnolle 2000, Votier *et al.* 2006,

Miles *et al.* 2013). Nevertheless, conditions may be quite different during the non-breeding period where the opportunity to catch small avian prey might be rare over the open sea.

There was no notable difference in activity patterns between male and female Great Skuas, although the sample size was relatively small, with only 2 males among the 17 site-faithful birds. Nevertheless, this is consistent with recent studies of several species of albatross and shearwater that also found no apparent differences between the sexes (Catry *et al.* 2009, Mackley *et al.* 2010). Harris *et al.* (2013) mention in their study of Imperial Shags *Phalacrocorax atriceps*, that even though there was a small difference between sexes in timing of wet bouts during the breeding period, there was no detectable sex effect during the winter.

The obvious motivation for birds to travel between wintering areas might be to find places offering better feeding opportunities to reduce their total energy expenditure. However, most of the tracked Great Skuas did not reduce their foraging effort after changing wintering area. In theory, they would have incurred a higher energy cost from the long-distance commute than if they had remained resident; however, the distances between wintering areas were modest, so this would be minor. For example, the trip across the Atlantic Ocean by Bird 5769 took about seven days, including feeding stop-overs along the way. Only one bird (#5749) showed a significant reduction in flight activity after moving site (from Iberia to northwest of Africa). Nevertheless, it is not clear whether travellers are able to predict the feeding conditions they will encounter at the next wintering area, or if the migration has a different motivation. For example, while percentage of time spent foraging or searching for food can indirectly provide quantitative information on food availability, it does not reveal the energetic or other nutritional quality of different prey. Moreover, our study reports the activity of birds over a single winter, and it would therefore be interesting to obtain activity data for travellers in multiple years to see if they keep the same migration pattern or change strategy, for example remaining in the same area in some years. Magnusdottir *et al.* (2012) showed that the two Great Skuas tracked for two years did return to the same region in successive winters.

In conclusion, the deployment of global location sensing loggers allowed us to study the proportion of time spent in flight, which we assumed was spent searching for food so was a proxy for foraging activity of Great Skuas on their wintering grounds. We highlighted differences in apparent foraging effort between the five main wintering areas. It remains to be determined whether these differences had an influence on body condition, and whether these differences affect the outcome of the following breeding season or the survival of individuals (i.e. represent carry-over effects).

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