**Foraging behaviour and habitat use by brown skuas *Stercorarius lonnbergi* breeding AT South Georgia**

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**Abstract**

Top predators are critical to ecosystem function, exerting a stabilising effect on the food web. Brown skuas are opportunistic predators and scavengers. Although skuas are often the dominant land-based predator at seabird colonies, this is the first detailed study of their movements and activity during breeding. The study was carried out at Bird Island, South Georgia (54°00’S, 38°03’W) in the austral summer of 2011/12, and included GPS data from 33 breeding adults tracked during the late incubation and early chick-rearing periods. Brown skuas spent on average more than 80% of time in the territory, and it was extremely rare for both partners to leave the territory simultaneously. Much more time was spent foraging at the coast than in penguin colonies and, based on saltwater immersion data, adults never foraged at sea. None of the tracked birds appeared to specialise in catching small petrels at night. Fewer foraging trips were made per day, and hence more time was spent in the territory, during incubation than chick-rearing. Despite the pronounced sexual size dimorphism, there were no effects of sex on territorial attendance, foraging time or habitat use. Skuas at Bird Island show higher territorial attendance and are less likely to leave the territory unattended than those breeding elsewhere, suggesting closer proximity to more diverse or abundant food resources than at other colonies. The results tie in with previous diet studies indicating that brown skuas at this site feed mostly on seal placentae and carrion; and that birds may rely on a broader range of food resources as the season progresses.

**Introduction**

Top predators can exert an important stabilising effect on the food web, keeping prey species in check and preventing the loss of inferior competitors (Paine 1966; Soulé et al. 2003). The decline of top predators can therefore have dramatic knock-on effects, affecting multiple trophic levels within the local community (Paine 1966; Soulé et al. 2003; Österblom et al. 2006; Heithaus et al. 2008). Simple communities with relatively few trophic linkages are particularly susceptible to such top-down cascades, as the limited number of species implies a lack of redundancy within the system (Soulé et al. 2003). The Antarctic provides a clear example of the fragility of these communities; over the last few decades, the synergistic effects of global climate change and human activities have impacted a number of key top predators, leading to large changes in abundance, distribution and phenology of different species across multiple trophic levels (Jenouvrier et al. 2005; Österblom et al. 2006; Hahn et al. 2007; Ainley and Hyrenbach 2010; Péron et al. 2010).

If studies of the foraging ecology and distribution of top predators are to provide useful insights into changes in food resources in the wider environment, several factors need to be taken into consideration. Feeding habits can vary considerably over the course of the breeding season, as a result of seasonal fluctuations in the availability of prey as well as changes in the nutritional demands of offspring (Shaffer et al. 2003; Navarro et al. 2009; Hipfner et al. 2013). Thus, the number, duration and distance of foraging trips probably also vary substantially. However, the extent that parents adjust their foraging effort when breeding is poorly understood in seabirds, particularly the behavioural changes sometimes associated with the transition from incubation to provisioning the chick (Annett and Pierotti 1989; Shaffer et al. 2003). Foraging behaviour and distribution can also vary according to sex, often thought to be related to the influence of sexual size dimorphism on sex-specific parental roles during breeding, inter-sexual competition, or habitat specialisation (González-Solís et al. 2000; Phillips et al. 2004b; Quillfeldt et al. 2008; Quillfeldt et al. 2011; Stauss et al. 2012).

Skuas are top predators in marine ecosystems. They display a remarkable variety of feeding tactics - aerial or terrestrial hunting, fishing, scavenging and kleptoparasitism - which enable them to exploit a wide range of food resources, according to their temporal and spatial availability (Furness 1987; Moncorps et al. 1998; Mougeot et al. 1998). Small skuas breeding on the Arctic tundra hold large terrestrial feeding territories that they defend against intra- and inter-specific competitors, although Arctic skuas *Stercorarius parasiticus* can also feed by kleptoparasitism in the southern part of their range (Maher 1974; Phillips et al. 1996). Northern hemisphere skuas will take fish, marine invertebrates, offal and carrion, fledgling and adult passerines, other birds, eggs of many species, and occasionally insects and berries (Furness 1987). Southern hemisphere skuas, although also opportunistic, usually depend on fewer prey types; primarily seal carcasses and placentae, or eggs, chicks or adults of seabirds nesting in nearby colonies (Pietz 1987; Reinhardt et al. 2000), and there are individuals that specialise on catching small petrels at night (Young et al. 1988; Ryan and Moloney 1991; Moncorps et al. 1998; Mougeot et al. 1998; Ryan et al. 2009). In several Antarctic populations, some birds establish feeding territories in areas adjacent to penguin or petrel colonies, whereas others forage over a wide area that they do not defend (Trivelpiece et al. 1980; Pietz 1987; Hahn and Peter 2003). South polar *S. maccormicki* and brown skuas *S. lonnbergi* share a predilection for penguin and other seabird prey, but in areas of sympatry, brown skuas tend to dominate over south polar skuas, forcing the latter to forage almost exclusively at sea (Trivelpiece and Volkman 1982; Hemmings 1984; Pietz 1987).

Brown skuas are widely distributed on islands from the subantarctic south to the Antarctic continent, and although few populations are monitored closely, the total number is thought to be broadly stable at c. 7-9,000 breeding pairs; however, there is considerable variation in trends among sites (Skira 1984; Furness 1987; Woehler and Croxall 1997; Mougeot et al. 1998; Phillips et al. 2004a). On Bird Island, South Georgia, this species appears to have benefited from an increase in the local population of Antarctic fur seals *Arctocephalus gazella* which has recovered since the 1930s from over two centuries of overexploitation. Seal carrion is now the main component of skua diet during the incubation period (Phillips et al. 2004a; Anderson et al. 2009). With 467 breeding pairs and an additional 312 non-breeders present at club-sites in summer 2003/04, Bird Island holds ca. 5-7% of the global population and is probably the most densely populated colony of brown skuas in the world, with 132 pairs per km2 of suitable habitat (Phillips et al. 2004a).

Although the diet of brown skuas has been characterised at a number of sites (Mougeot et al. 1998; Reinhardt et al. 2000; Phillips et al. 2004a; Ryan et al. 2009; Grilli and Montalti 2012), little is known about their movements, foraging behaviour and habitat selection during the breeding season. Using the first fine-scale tracking data for brown skuas during breeding, the aims of the present study were to: 1) examine changes in habitat use, foraging and bathing activity during late incubation and early chick-rearing, and; 2) test for differences in foraging strategies of males and females. The results are discussed in the context of reproductive constraints, and spatial and seasonal prey availability. Particularly given the very high density of brown skuas at Bird Island and their potential impact on other seabirds (Phillips et al. 1999; Votier et al. 2004), a better understanding of the ecological parameters that can be monitored during breeding (breeding performance, diet, foraging effort, chick growth, survival rate, pollution levels) will improve their usefulness as indicators of the health of the wider marine ecosystem (Furness and Camphuysen 1997).

**Materials and methods**

*Field deployments*

Fieldwork was carried out on brown skuas at Bird Island, South Georgia (54°00’S, 38°03’W) during the austral summer of 2011/12. A total of 36 GPS loggers (IgotU; Mobile Action Technology Inc., Taiwan) and 22 immersion (activity) loggers (Mk 18L; British Antarctic Survey, Cambridge) were deployed on breeding adults for 4-6 days during late incubation and early chick-rearing. Skuas were captured on the ground by hand, or using a hand net or noose pole. GPS loggers weighed 25 g including waterproof packing and were attached to the dorsal feathers with TESA® tape. Immersion loggers weighed 1.5 g and were fitted with a cable-tie to the British Trust for Ornithology metal ring on the tarsus. Total instrument load including the tape was c. 32 g, equivalent to 1.7% of the mean mass of adults, which was well below the threshold of 3% at which device effects tend to become apparent in other flying seabirds (Phillips et al. 2003; Vandenabeele et al. 2012). Negative effects associated with handling and the additional weight of tracking devices may be difficult to avoid entirely (Barron et al. 2010). However, attachment of the GPS and immersion loggers took only 5-8 mins, and after release, the bird either returned to the nest within a few minutes (if the partner was not present), or flew off and landed elsewhere on the territory. There were no instances of nest desertion associated with device deployment. In addition, tracked birds were weighed at capture and recapture, and the weight change compared with the seasonal trend from a larger sample that included a control group of untracked birds (*N* = 75) that were weighed only once. Although mean body mass of tracked birds differed significantly between capture (1878.0 ± 32.7 g, range = 1600-2240) and recapture (1832.8 ± 31.5 g, range = 1570-2240) (Paired t test, *t*24 = 2.5, *P* = 0.021), a seasonal decline in body mass is expected, given the higher energetic costs to adults of feeding chicks compared with incubating eggs. Indeed, the mean estimated rate of mass change just of the individuals that were tracked was not significantly different from the slope of the regression of log body mass at first capture of tracked and untracked birds vs. the number of days since the beginning of the season (One sample t test, *t*24 = 1.6, *P* = 0.116). This indicated that the decline in body mass of birds fitted with loggers was in line with that of the wider population. The GPS loggers were programmed to acquire a fix every 10 or 20 min, which ensured the battery lasted for the 4-6 days deployment period. A sampling interval of 20 min might have been too long to detect short trips during the breeding season. However, visual observations of brown skuas feeding at the coast or penguin colonies, and bathing indicated that these activities usually lasted >30 min, suggesting that this sampling interval did not compromise the ability to detect foraging or bathing trips. The activity loggers tested for saltwater immersion every three seconds, and logged the number of positive tests at the end of each 10 min period, i.e., values from 0 (continuously dry) to 200 (continuously wet). Study birds were sexed by morphometric measurements or by analysis of DNA extracted from a blood sample taken from the tarsal vein (Fridolfsson and Ellegren 1999).

*Tracking data processing*

Habitat use by individual skuas was assessed in terms of the time spent per day undertaking different activities during the breeding season. This was based on the overlap between GPS locations of tracked birds and: 1) a buffer of 100 m radius from the nest, indicating time spent on the territory; 2) penguin colonies, indicating time spent foraging on this resource; 3) the coast (defined as the area between mean high water mark and the 50 m contour on Bird Island and mainland South Georgia), indicating time spent foraging on seal carrion or placentae, and; 4) lakes and ponds, indicating time spent at potential bathing sites (Fig. 1). The spatial extent of all breeding colonies of macaroni *Eudyptes chrysolophus* and gentoo *Pygoscelis papua* penguins on Bird Island was mapped by walking the perimeters with a handheld GPS. On the Willis Islands, the penguin colonies were considered to include the area between the mean high water mark and the 50 m contour, as there are many colonies around the coast of those islands and very few fur seals breed on the steep, rocky terrain (Fig. 1). GPS locations of tracked birds considered to be feeding (i.e., overlapping with penguin colonies or the coast) were categorised as day or night using civil twilight as the threshold (Phalan et al. 2007), and used to calculate the proportion of time spent foraging in daylight or darkness.

Time spent off territory was split into separate trips, corresponding to each series of successive fixes outside the 100 m radius around the nest. For each trip, the following information was derived: 1) duration (elapsed time from the beginning to end of the trip); 2) total distance (summed great circle distances between fixes), and; 3) maximum range (great circle distance to the furthest location). As skuas perform different types of trip during the breeding season (Oswald et al. 2008), we calculated the time spent either foraging or bathing within each individual trip. Foraging trips refer to those that overlapped penguin colonies or the coast, whereas bathing trips were to lakes or ponds. The small number of dual-purpose trips, which included time spent on both activities, were combined with foraging trips in further analyses because the great majority of the time was devoted to foraging. For breeding pairs (*N* = 14) where both adults were fitted concurrently with GPS loggers, the total time the territory was unattended was calculated by comparing timing of trips by each partner. To ensure results were comparable between breeding stages etc., GPS data collected originally at 10 min intervals were sub-sampled at 20 min intervals before statistical analysis. All the preceding analyses were run on raw GPS locations (i.e. uninterpolated data).

To produce a density map all tracks were interpolated linearly at two min intervals using the ‘adehabitatLT’ package (Calenge 2012) in R (R Development Core Team 2008). Interpolated locations were overlaid on a vector grid with a cell size of 500 x 500 m, with Z giving the percentage of the total fixes per unit area (Grémillet et al. 2004). In order to examine at-sea activity patterns in more detail, the duration and proportion of time spent on the water was calculated for all birds fitted with immersion loggers. ArcGIS 10 and scripts written in R were used for all analyses. Unless indicated otherwise, all data are presented as means ± SE.

*Statistical analysis*

Linear mixed-effect models were used when analysing data on trip characteristics because individuals were tracked for several successive trips; otherwise, linear models were used. Bird identity was included as a random factor to account for repeated measures in the linear mixed-effect models built using the lme4 package in R (Pinheiro et al. 2013). Models with either (i) stage of the breeding cycle (incubation and chick-rearing), or (ii) calendar date (number of days from the first deployment of the season) were compared using ΔAIC; however, as they had equivalent explanatory power, only the analyses with breeding stage are presented in the results. The initial full model included sex and stage of the breeding cycle, and second order interactions; location of each habitat type (penguin colonies and coast) was included in the initial full model for the time spent feeding, and light level (day and night) was included for the proportion of time foraging during daylight and darkness hours. A backwards stepwise elimination process was used until the minimal model was reached by removing fixed terms that did not have a significant effect. The statistics and *P* values of the significant terms (i.e. those retained in the minimal model) were obtained by removing the relevant term from the minimal model, and the statistics and *P* values for the non-significant terms by adding the term to the minimal model. The robustness of the results was confirmed by using AIC for model selection and by sampling the posterior MCMC distributions obtained from the lme4 package in R (Bates et al. 2013); in all cases, the conclusions did not differ irrespective of which model selection approach was used. The results of non-significant interactions, AIC values and MCMC are not presented. Data were square root or arcsine square-root transformed if necessary to achieve normality and satisfy model assumptions. There were too few records of saltwater immersion for a comparison of at-sea activity patterns between sexes and breeding stages.

**Results**

A total of 12,843 fixes at 20 min intervals (389 ± 12.6, range = 292-565 per bird) were obtained from 33 birds (7 males and 10 females in incubation, 7 males and 9 females in chick-rearing) tracked for 4-6 days between 24 December 2011 and 10 January 2012. Five loggers were detached by the birds before recapture, although three were subsequently found on the ground, 1 day to 9 months later; fixes from these loggers were included up until the time that the device became stationary (one of the loggers was excluded from the analysis because fixes were all from the nest site). Birds were tracked on average for 122.7 ± 2.0 h (range = 97.6-144.7). Data from a total of 734 trips (22.2 ± 1.2, range = 10-34 per bird), corresponding to 14.5 ± 1.0 (range = 5-28, *N* = 479) foraging trips and 3.6 ± 0.5 (range = 0-11, *N* = 119) bathing trips per bird were obtained. The remaining 136 trips (18.5% of the total) did not fit in any of the classifications (i.e. they were not to bathing sites, penguin colonies or the coast) and were excluded from further analysis.

*Habitat use*

The territory locations of the study birds and extent of each habitat type, and the density distribution of the tracked birds are shown in Figs. 1 and 2, respectively. Brown skuas spent on average more than 80% of time in the territory (Table 1). All tracked skuas visited the coast of Bird Island, which was the main foraging area, and 23 (70%) also visited the coast of mainland South Georgia. Nineteen birds (57.6%) visited penguin colonies. Although one individual travelled as far as 25 km, the majority of the tracked birds remained within 3 km of their nests during the 4-6 day tracking periods.

The time spent in the territory per day was affected marginally by breeding stage (i.e. borderline statistical difference between incubation and chick-rearing: ANOVA, $F\_{(1,31)} $= 3.7, *P* = 0.063), and unaffected by sex (ANOVA, $F\_{(1,31) }$= 0.1, *P* = 0.761). On average, time spent foraging on the coast was longer than time foraging on penguin colonies (Likelihood ratio test, $χ\_{1}^{2} $= 36.7, *P* < 0.001), with no difference between the sexes (Likelihood ratio test, $χ\_{1}^{2}$ = 0.7, *P* = 0.392) nor, in this case, an effect of breeding stage (Likelihood ratio test, $χ\_{1}^{2} $= 0.2, *P* = 0.635). Time spent bathing did not differ between sexes (ANOVA, $F\_{(1,31)} $= 0.8, *P* = 0.392) or breeding stages (ANOVA, $F\_{(1,31)} $= 0.3, *P* = 0.596).

Study birds spent a higher proportion of time foraging during daylight than darkness (10.5% vs. 5.2%; Likelihood ratio test, $χ\_{1}^{2} $= 4.3, *P* = 0.038). Of the 33 study birds, 21 (63.6%) foraged solely during daylight and 12 (36.4%) foraged both during daylight and darkness; no bird foraged exclusively during darkness. Although the effect of sex was not significant (Likelihood ratio test, $χ\_{1}^{2} $= 1.4, *P* = 0.239), the majority of birds that foraged during darkness were males (75%). Time spent foraging during daylight and darkness did not differ between breeding stages (Likelihood ratio test, $χ\_{1}^{2} $= 0.9, *P* = 0.346).

*Trip analysis*

Most trips away from the nest were for foraging rather than bathing (Table 2). All 33 study birds performed at least five feeding trips during the study period, whereas during incubation and chick-rearing, just 14 (42%; five males and nine females) and 14 (42%; seven males and seven females) birds, respectively, travelled to bathing sites.

Fewer foraging trips were made per day during incubation than chick-rearing (ANOVA, $F\_{(1,31)} $= 5.7, *P* = 0.023). There was no effect of sex on the number of foraging trips per day (ANOVA, $F\_{\left(1,30\right)}$ = 0.7, *P* = 0.419). Mean trip duration, total travel distance and maximum range did not differ between males and females (Likelihood ratio test, $χ\_{1}^{2} $= 0.4, *P* = 0.552, $χ\_{1}^{2} $= 0.0, *P* = 0.893 and $χ\_{1}^{2}$ = 0.0, *P* = 0.965, respectively), nor between incubation and chick-rearing (Likelihood ratio test, $χ\_{1}^{2} $= 1.6, *P* = 0.205, $χ\_{1}^{2} $= 0.0, *P* = 0.911 and $χ\_{1}^{2} $= 0.1, *P* = 0.804).

Travel distance and maximum range during bathing trips were greater during chick-rearing than incubation (Likelihood ratio test, $χ\_{1}^{2}$ = 7.2, *P* = 0.007 and $χ\_{1}^{2}$ = 7.5, *P* = 0.006). There was no effect of sex on the mean total travel distance, nor the maximum range (Likelihood ratio test, $χ\_{1}^{2} $= 1.3, *P* = 0.249 and $χ\_{1}^{2} $= 1.5, *P* = 0.226). The number of bathing trips per day and their mean duration did not differ between sexes (ANOVA, $F\_{(1,31)} $= 0.1, *P* = 0.790 and Likelihood ratio test, $χ\_{1}^{2} $= 0.0, *P* = 0.918), nor between breeding stages (ANOVA, $F\_{(1,31)} $= 0.8, *P* = 0.388 and Likelihood ratio test, $χ\_{1}^{2}$ = 1.7, *P* = 0.188).

From a total of 14 nests where both partners were tracked concurrently, only seven pairs (three in incubation and four in chick-rearing) left the territory completely unattended at any time, and this was for extremely brief periods; 6-16 min during incubation and 3-29 min during chick-rearing, respectively, representing on average of just 0.22% and 0.38% of the concurrent tracking period for all 14 pairs.

*Immersion activity*

The study birds spent very little time in saltwater. The 22 skuas equipped with immersion loggers spent on average only ca. 11 ± 3.1 min (range = 0 to 55.7 min) in saltwater, representing a mean of 0.14% (range = 0-0.78%) of the 4-6 day tracking periods.

**Discussion**

Although skuas are often the dominant land-based predator at seabird colonies in the Southern Ocean, as far as we are aware, the only previous tracking studies of any skua species during breeding involved deployments of small numbers of radio-transmitters on brown skuas at the Chatham Islands, New Zealand (Young et al. 1988), and great skuas *S. skua* at Hermaness, Shetland, UK (Votier et al. 2004) and St Kilda, Outer Hebrides, UK (Votier et al. 2006). Although this technology has drawbacks for following movements because locations are relatively inaccurate and only available intermittently when transmitters are in line-of-sight of a radio-receiver, the results indicated that brown skuas at the Chathams and great skuas at St Kilda regularly foraged at night to catch petrels, as did some of the brown skuas tracked in our study at South Georgia. In addition, the great skuas at Hermaness which fed on fish had the largest home ranges, followed by specialist bird predators with feeding territories, and bird predators that did not defend a feeding territory. In contrast, none of the brown skuas at Bird Island travelled to sea to feed on fish, and there was no clear evidence for specialist bird predators, as all the tracked birds spent considerable time scavenging on the coast. This underlines the variability in foraging strategies among breeding colonies of these adaptable and highly opportunistic predators.

Although brown skuas at Bird Island foraged mostly during daylight hours, some individuals were active at night. These were mostly males, perhaps because their smaller size and greater manoeuvrability is an advantage when feeding on petrels at night, or during kleptoparasitism (Phillips et al. 2002). However, none of the tracked birds fed exclusively at night and it seems therefore that a potential feeding specialisation involving the capture of small petrels at night is uncommon at this colony. This is despite the very high abundance of Antarctic prions, blue petrels, common and South Georgian diving petrels on the island, which occur regularly in the diet of the skuas, particularly of some pairs (Hunter et al. 1982; Phillips et al. 2004a). This contrasts with previous studies of brown skuas at other subantarctic islands, which showed high levels of activity at night, mostly targeted at catching petrels (Young et al. 1988; Ryan and Moloney 1991; Moncorps et al. 1998; Mougeot et al. 1998; Ryan et al. 2009).

Time spent away from the territory by adult skuas is frequently used as an index of foraging effort, and hence is potentially indicative of local resource abundance (Catry et al. 1998; Ratcliffe and Furness 1999; Caldow and Furness 2000; Phillips et al. 2004a). The study birds spent on average 83.2% of the time within their own nesting territories, and it was extremely rare for both partners to leave the territory simultaneously; this lasted just 3-29 min on the few occasions it was recorded (Table 1). The proportion of time on territory was very similar in brown skuas breeding much farther south around Palmer Station on Anvers Island, Antarctic Peninsula (81.5%; Pietz 1987). In contrast, south polar skuas usually spend less time on the nesting territory than brown skuas, 50%and72.5%; Pietz (1987) and Young (1963), respectively, as do great and Arctic skuas in the northern hemisphere (Hamer et al. 1991; Phillips et al. 1996; Caldow and Furness 2000). The one exception seems to be the south polar skuas breeding at Svarthamaren, Dronning Maud Land, where the largest known colony of Antarctic petrels *Thalassoica antarctica* is found and the mean overall nest attendance was 93% (Brooke et al. 1999). Regardless, the high attendance rates found at Bird Island suggest a high proximity of abundant food resources available at least until mid chick-rearing or efficient foraging by the adults (Catry and Furness 1999; Caldow and Furness 2000; Hahn and Peter 2003; Votier et al. 2004). This is also reinforced by the lower number of joint absences from the territory when compared with other studies (Catry and Furness 1999; Caldow and Furness 2000).

It is difficult to make a direct comparison of feeding trip duration and effort *per se* with skuas elsewhere because of the considerable spatial and seasonal variation in diet and foraging strategies. In addition, there are no other published data on foraging range or travel distances for skuas breeding in the subantarctic or Antarctic. However, average trip duration of brown skuas at Bird Island and those breeding around Palmer Station that did not defend feeding territories were very similar (1.5 ± 0.2 vs. 1.0 ± 0.2 h) (this study, Pietz 1986; Pietz 1987). Although our tracked birds foraged for longer periods than skuas at other sites with feeding territories in seabird colonies (Young 1963; Burton 1968; Pietz 1986; Pietz 1987; Brooke et al. 1999), their trip durations were shorter than skuas elsewhere that do not defend feeding territories (Young 1963; Hemmings 1984; Votier et al. 2004), which is the more revealing comparison given the lack of evidence for consistent feeding territories at Bird Island. Hence, the comparison in trip characteristics tends to confirm the conclusions based on territorial attendance, which is that feeding conditions are comparatively good at Bird Island.

Brown skuas breeding in Bird Island spent more time per day foraging on the coast than in penguin colonies (1.9 ± 0.2 vs. 0.3 ± 0.1 h). These results tie in with previous diet studies indicating that brown skuas at this site feed mostly on seal placentae and carrion on the coast (Phillips et al. 2004a; Anderson et al. 2009). Although the differences were not statistically significant, the time spent feeding per day in penguin colonies increased from incubation to chick-rearing, whereas the time spent on the coast decreased, indicating that birds have to rely on a broader range of resources as the season progresses. During incubation, fewer foraging trips were made per day, and hence more time was spent in the territory attending the nest. By mid January, fur seal pupping is long finished, pup survival is higher now that the vulnerable neonatal period has passed, and fur seal bulls are no longer dying from injuries sustained in territorial conflict (Phillips et al. 2004a). It is possible then, that the brown skuas still foraging on the coast for seal carrion during chick-rearing are the more aggressive birds, and that the poor competitors have switched to feeding further afield. More trips during chick-rearing might also reflect the increased energy demand associated with chick provisioning (Catry and Furness 1999; Caldow and Furness 2000), which can precipitate dietary switches in gulls (Annett and Pierotti 1989). It is hard to determine whether the increase in foraging effort in our study resulted from a seasonal decline in food resources or a switch in behaviour associated with the demands of feeding a growing chick. Indeed, the effect of calendar date and stage were impossible to disentangle in the models. At Bird Island, however, this switch seems to coincide with the decline of seal carrion available on the beaches. Very large numbers of other prey (seabirds) were present on Bird Island during the whole study period, yet skuas were much more likely to target these species from January onwards (Phillips et al. 2004).

The GPS tracking in combination with concurrent deployment of the immersion loggers indicated that the tracked skuas spent very little or no time foraging at sea. Indeed, the very short periods of saltwater immersion that were recorded may be indicative of bathing rather than feeding behaviour. That birds feed so little at sea is surprising given that brown skuas are highly pelagic during the winter (Phillips et al. 2007). Even after hatching when foraging effort increased and food availability presumably declined, skuas still preferred to forage on land, suggesting that marine resources are not profitable within an economical travel distance of Bird Island. Prey movements, either horizontally or vertically, may also make marine resources less temporally and spatially predictable for skuas (Pietz 1986; Pietz 1987; Votier et al. 2004).

*Sex-role specialisation*

There was little evidence of sex differences in foraging strategies among the tracked birds despite well-defined sexual size dimorphism at Bird Island, where females on average are considerably larger and heavier than males (Phillips et al. 2002). Pronounced sexual size differences in skuas and other species can lead to the larger female spending more time on the territory to defend the eggs or young, while the smaller male undertakes the bulk of food provisioning (Catry et al. 1999; Catry and Furness 1999; Käkelä et al. 2006; Oswald et al. 2008). As the season advances, female great skuas progressively increase their contribution in terms of foraging effort, and by the beginning of chick-rearing, they spend almost as much time gathering food as their mates (Catry et al. 1999). However, as female skuas are larger, they may also have an advantage in competitive interactions over food resources (Hahn and Bauer 2008). If so, the degree of size dimorphism between sexes might be more pronounced where there is a high level of competition (Catry et al. 1999). If this is correct, at Bird Island, where most birds appear not to defend feeding territories and food resources seem to be reasonably abundant, body size and hence sex may not be a key influence on foraging strategies. This would explain the lack of any clear differences between males and females in attendance or feeding trip characteristics in the present study.

*Bathing behaviour*

Although skuas spend time bathing in freshwater, possibly to reduce heat stress, the implications of this activity for their time budgets remains little investigated (Oswald et al. 2008). The tracked skuas used 19 different ponds and lakes for bathing, of which five were located on Bird Island and the other 14 on mainland South Georgia, the furthest of which was 9.5 km from the bird’s territory. Bathing sites located on Bird Island were used with the same frequency as those on the mainland (50.3% vs. 49.7%, respectively). However, the use of sites on the mainland doubled from incubation to chick-rearing, which explains the increase in travel distance and maximum range (Table 2). Brown skuas at Bird Island spent on average 1.8% of each day on bathing trips, which is consistent with a previous study that reported bathing was rare and sporadic among this species breeding near Palmer Station, Antarctica (Pietz 1986). Similarly, bathing is very infrequent in the south polar skua (Pietz 1986; Brooke et al. 1999). In great skuas, there was a negative relationship between time spent foraging and time spent bathing in years of poor food availability (Oswald et al. 2008). This might imply that the small proportion of time that the brown skuas at Bird Island spent on bathing sites reflected lower food availability or higher competition for resources. Alternatively, the much lower ambient temperature in the subantarctic may mean that bathing is less necessary for keeping cool.

In conclusion, skuas breeding at Bird Island have access to locally abundant food resources, as they show higher territorial attendance and fewer joint absences compared with skuas elsewhere. During incubation, they feed mainly on the coast, almost certainly on seal placentae and carrion (based on a previous diet study; Phillips et al. 2004a), but time spent foraging in penguin colonies increases after the chicks hatch as they presumably exploit a broader range of food resources. However, more studies should be carried out during the later breeding season, when the availability of resources further decreases, to determine the responses of these highly opportunistic species. Further tracking work could also usefully target the pre-laying period when there is very little carrion available from fur seals, and most burrowing petrels have yet to return, such that resources for skuas are likely to be even more limiting. A previous study found that 2 of 3 tracked skuas carried out a long (8-9 days) pre-laying exodus in late October to early November, shortly after their first return, to waters 500 to 1000 km from South Georgia (Phillips et al. 2007). Further work with a larger sample size would reveal whether this is the typical pattern and at what point birds switch to exploiting prey obtained exclusively on land, as they do in incubation (this study).

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**Table 1** Time spent per day in different activities by brown skuas tracked at Bird Island, South Georgia in summer 2011/12. Values are average (in h) ± SE, with the overall percentages in parentheses.

|  |  |  |  |
| --- | --- | --- | --- |
|   | All birds (*N* = 33) | Incubation | Chick-rearing |
| Male (*N* = 7) | Female (*N* = 10) | Male (*N* = 7) | Female (*N* = 9) |
| *Nest attendance* |  |  |  |  |  |
| Territory | 20.0 ± 0.3 (83.2) | 20.5 ± 0.2 (85.6) | 20.3 ± 0.5 (84.7) | 19.2 ± 0.7 (80.0) | 19.7 ± 0.5 (82.0) |
| *Feeding* |  |  |  |  |  |
| Penguin colonies | 0.3 ± 0.1 (1.3) | 0.2 ± 0.1 (0.8) | 0.1 ± 0.0 (0.3) | 0.7 ± 0.5 (2.7) | 0.4 ± 0.2 (1.7) |
| Coast  | 1.9 ± 0.2 (8.0) | 1.7 ± 0.3 (7.0) | 2.2 ± 0.4 (9.3) | 1.5 ± 0.4 (6.2) | 2.1 ± 0.5 (8.8) |
|  Bird Is | 1.3 ± 0.2 (5.5) | 1.1 ± 0.4 (4.6) | 1.5 ± 0.5 (6.1) | 1.3 ± 0.4 (5.3) | 1.4 ± 0.5 (5.7) |
|  Mainland | 0.6 ± 0.1 (2.5) | 0.6 ± 0.3 (2.4) | 0.8 ± 0.3 (3.2) | 0.2 ± 0.1 (0.9) | 0.7 ± 0.2 (3.1) |
| *Bathing* |  |  |  |  |  |
| Ponds and lakes | 0.4 ± 0.1 (1.9) | 0.4 ± 0.1 (1.8) | 0.4 ± 0.1 (1.7) | 0.4 ± 0.1 (1.5) | 0.6 ± 0.1 (2.4) |
| Othera | 1.4 ± 0.2 (5.7) | 1.1 ± 0.2 (4.8) | 1.0 ± 0.1 (4.0) | 2.3 ± 0.7 (9.7) | 1.2 ± 0.2 (5.1) |
| aOther: locations that were outside the selected habitat types.  |

**Table 2** Characteristics of foraging and bathing trips by brown skuas tracked at Bird Island, South Georgia in summer 2011/12. Values are the overall mean ± SE, calculated from the mean value per individual, with the range in parentheses indicating the minimum to maximum recorded for any bird.

|  |  |  |  |
| --- | --- | --- | --- |
|   | All birds | Incubation | Chick-rearing |
| Male | Female | Male | Female |
| *Foraging trips* |   |   |   |   |   |
| Trips per day | 2.8 ± 0.2 (1.0-5.7) | 2.4 ± 0.4 (1.0-3.6) | 2.4 ± 0.3 (1.1-4.0) | 3.0 ± 0.4 (2.0-4.7) | 3.5 ± 0.4 (2.4-5.7) |
| Trip duration (h) | 1.5 ± 0.2 (0.3-7.1) | 1.6 ± 0.3 (0.5-4.9) | 1.6 ± 0.2 (0.4-5.4) | 1.5 ± 0.3 (0.3-7.1) | 1.2 ± 0.1 (0.3-3.9) |
| Travel distance (km) | 7.4 ± 1.6 (0.0-52.4) | 9.0 ± 1.9 (0.1-28.5) | 6.0 ± 1.2 (0.0-24.6) | 6.5 ± 1.4 (0.0-37.3) | 8.5 ± 1.9 (0.2-52.4) |
| Maximum range (km) | 3.3 ± 0.7 (0.0-25.4) | 3.8 ± 0.8 (0.1-12.4) | 2.6 ± 0.5 (0.0-9.0) | 2.9 ± 0.5 (0.0-10.0) | 4.0 ± 0.9 (0.1-25.4) |
| *Bathing trips* |   |   |   |   |   |
| Trips per day | 0.7 ± 0.1 (0.0-2.0) | 0.8 ± 0.3 (0.0-1.9) | 0.5 ± 0.1 (0.0-1.3) | 0.7 ± 0.2 (0.4-1.5) | 0.9 ± 0.3 (0.0-2.0) |
| Trip duration (h) | 1.1 ± 0.2 (0.5-3.2) | 1.1 ± 0.1 (0.5-1.9) | 1.1 ± 0.2 (0.5-1.9) | 1.2 ± 0.2 (0.5-2.7) | 1.2 ± 0.2 (0.6-3.2) |
| Travel distance (km) | 8.0 ± 2.9 (0.1-44.3) | 7.2 ± 1.9 (0.2-19.1) | 3.7 ± 2.7 (0.2-20.2) | 11.2 ± 3.3 (0.7-21.6) | 11.0 ± 3.3 (0.1-44.3) |
| Maximum range (km) | 3.8 ± 1.3 (0.1-20.8) | 3.4 ± 0.9 (0.1-9.3) | 1.7 ± 1.2 (0.1-8.9) | 5.3 ± 1.5 (0.4-9.5) | 5.2 ± 1.6 (0.1-20.8) |



**Fig. 1** Study area and ArcGIS coverages used to classify GPS fixes of skuas tracked at Bird Island, South Georgia in summer 2011/12



**Fig. 2** Density distribution of time spent off territory (foraging or bathing) by brown skuas tracked at Bird Island, South Georgia in summer 2011/12. Map based on GPS fixes interpolated at 2 min intervals