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FACULTY OF BIOSCIENCES, FISHERIES AND ECONOMICS
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Space use by South Polar Skua during the breeding season at Svarthammaren, Antarctica

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Abstract

South Polar Skua is a seabird feeding on both marine resources and on other seabirds' egg and chicks. There are few studies investigating South Polar Skua space use during breeding season and how it is affected by sex or phenology. This study was carried out during the breeding season 2012-2013 at Svarthammaren in Dronning Maud Land (71° 53′ S, 05° 10′ E). 56 GPS loggers were used to track 48 individuals during incubation and chick rearing period of skua and petrel. At Svarthammaren, South Polar Skua use petrels as their only available food resource with no competitors. We investigated how sex and phenology (skua and petrel incubation and chick rearing periods) affected South Polar Skuas main activities, such as hunting effort (i.e., area used in the petrel colony), time spent on nest defense, and bathing activity. Indeed, petrels defend themselves by spitting oil on their attackers, which affects feathers and flight ability of skua. Skua time budgets depended on prey phenology and differed between sexes. During petrel incubation time, females spent more time around the nest area than males and both skua partners had higher bathing activity during petrel chick-rearing period. Both sexes invested more in hunting effort during the chick-rearing period compared to incubation. The results were mostly in line with previous studies, that skua chick phenology affects their hunting effort and skua had higher bathing activity when they were more exposed for oily attacks. However, we also found that prey phenology affected on skua nest attendance to higher degree than expected, which we believed were based on prey availability.

Keywords: Space use, South Polar Skua breeding season, phenology, predator-prey, Antarctica

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Tromsø, November 2014

Johan Nils Swärd

Table of Contents

Introduction

Understanding animals' movements is important when we want to get insight about their behavioral and population ecology or understand ecological processes influencing different components of individual fitness (Rubenstein and Hobson 2004, Horne and Garton 2006, Horne et al. 2007, Spencer 2012). This knowledge can be important for population management (William 1943, Rubenstein and Hobson 2004) by understanding, for example, how populations are affected by habitat loss or environmental changes. Analyzing animals' movements with respect to ecological mechanisms implies that we relate them to activities such as feeding, mating, and taking care of the young (William 1943, Powell and Mitchell 2012). Studies of movement based on such activities can be defined as the animals' *space use*.

Space use can be affected by many factors, such as inter- or intra- specific competition (Minta 1992), distribution of resources (Powell 2000 in Horne and Garton 2006), and interactions between predators and their prey (Stamps 1995, Williams and Flaxman 2012). For example, when resource (i.e., prey) levels are high, the area used by predators tends to be smaller (Ford and Glenn 1983, Mitchell and Powell 2012), whereas when the resource levels are low, the predator has to travel more and increase its feeding or foraging area (Schoener 1968). In addition, animals with high energy demand, for example due to their larger size, may need to use a larger space than smaller animals with lower energy demand (Schoener 1968). Animals with pronounced sexual size dimorphism can often display differences in space use (Mysterud et al. 2001, Weimerskirch et al. 2006), as for example, a larger partner can better defend an home area (Catry and Furness 1999) or travel longer distances for foraging (Weimerskirch et al. 2006).

Among altricial birds, space use strongly depends on their breeding phenology (Weimerskirch et al. 1997, Sakshaug et al. 2009), as they need to gain enough resources while taking care of their young and / or defending their young against predators

(Shaffer et al. 2003, Frederiksen et al. 2004, Wakefield et al. 2013). Predation can be a common cause of offspring mortality during the incubation and chick rearing period (Trillmich 1978). Birds pairs often share duties, with one bird attending the nest while the other is gathering food (Wiggins and Morris 1986). Foraging effort by the breeding adults can be constrained by the need for protecting their chick (Caldow and Furness 2000), which is demanding for birds, as they have to spend more time foraging to fill the energy need of the offspring (Shaffer et al. 2003, Carneiro et al. 2014). Seabirds preferences for food resources can therefore change with phenology, to cover the chick's energy demand, and resources with higher energy content are preferred later during the breeding season (Navarro et al. 2006, Williams and Flaxman 2012).

Skuas of the southern hemisphere species (*Catharacta spp)*(Ritz et al. 2008) are seabirds that breed around coastal Antarctica and adjacent islands (Kopp et al. 2011). They are regarded as top predators which can prey upon chicks and eggs of other seabirds, such as penguins or petrels (Steel and Cooper 2012) as well as on marine prey, like fish and cephalopods (Steel and Cooper 2012). Skuas are long lived-species, with a maximum lifespan of ~30-40 years (Ainley 1974). They should therefore abort breeding when risk level becomes too high (Cairns 1987), for example when food gathering involves high risk or when the resources become scarce. The main risk associated with predation on petrels is associated with the oil spitting behavior of petrels. Oil exposure on feathers can effect flying capability and water repellency (Warham 1977) and also most likely thermoregulation. Skuas have been recorded to bath and clean themselves after they have been exposed to oil from petrels (Murphy 1936, Pietz 1986, Brooke et al. 1999). Both adults and chicks of petrels are able to use oily defense mechanism; young petrels can discharge oil attacks several days after their last meal (Murphy 1936). Parental attendance of the petrel chick decreases with chick size, i.e., larger chicks can spit more oil and defend themselves better (Weidinger 1998). The prey phenology (i.e., petrel) is most likely an important factor for South Polar Skua foraging behavior in terms of both energy content (i.e., egg or chick) and in terms of the risk associated with predation (i.e., oily attacks).

A breeding site for the South Polar Skua (*Catharacta maccormicki*) is Svarthammaren (described in Mehlum et al. 1988), located 200km inland on Dronning Maud Land on the Antarctic continent (71° 53′ S, 05° 10′ E). About 100 pairs of South Polar Skuas breed in association with Antarctic Petrels (~150 000 – 250 000 pairs) and Snow Petrels (~500 pairs) and skuas are the only predator of petrels. At Svarthammaren, petrels are the only food resource available in the area and South Polar Skuas feed exclusively on Antarctic petrels eggs, chicks and adults (Brooke et al. 1999, Varpe and Tveraa 2005). Predation on adults is rare but apparently occur only when adult petrels are in poor condition (pers. obs.). Therefore, South Polar Skua space use is restricted to Svarthammaren during the whole breeding season and skuas only leave the area if breeding ends or fails. One previous study has recorded South Polar Skua behavior at Svarthammaren and was done by Brooke et al. (1999). Their main conclusion, based on direct observations (78h between 28 Dec – 13 Jan 1996-1997), was that South Polar Skua breeding success at Svarthammaren is limited by the availability of petrels and the most constrained period was during late incubation of the petrel. They recorded that activities by South Polar Skua was exclusively based on three behaviors: (i) hunting in the colony, and a large part of hunting was by actively flying and to little extent sitting and watching, (ii) protecting their nest area, as incubating the egg, brooding, or feeding the chick, and (iii) bathing activity, as they observed South Polar Skuas visiting water ponds to clean themselves from the petrels oily attacks They also recorded that skua pairs divided their nest attendance and hunting in the petrel colony, however, Brooke et al. (1999), did not investigate if sex or breeding phenology affected hunting effort, defense of the nest, or their bathing activity. In addition, Brooke et al. (1999) observations were based on a time period during petrel incubation and they did not provide any information for skua behavior during petrel chick rearing time. We know from studies in coastal Antarctic breeding sites, where South Polar Skuas breed in association with other skuas (Brown Skua *Catharacta*) and where they have access to terrestrial and marine resources, that their foraging behavior is affected by their breeding phenology. During incubation the smaller males invested more time in hunting and the larger females stayed more at the nest to defend the egg, but during chick rearing, females increased their hunting effort to equal that of the males (Trivelpiece et al. 1980, Pietz 1984). We are not aware of studies of the South Polar Skua behavior and possible effect from of prey phenology.

The simple food web at Svarthammaren, where South Polar Skuas have only access to terrestrial resources and where they have no competition from other predators, makes it a good study system for the analysis of space use by South Polar Skua during breeding season. In contrast to the study by Brooke et al. (1999) we used telemetry (GPS) to investigate the space use of South Polar Skua. The use of GPS offers a better understanding of animals movement (Amstrup et al. 2004, Horne and Garton 2006) because it allowed us to record the birds continuously over long periods. My main aims were to 1) describe the behavior of South Polar Skuas and compare the sexual size dimorphism behavior with other breeding sites and 2) investigate their activities. I divided skua activity into three categories; (i) hunting effort, (ii) nest attendance, and (iii) bathing activity, with regard to the effect of sex and / or phenology (both predator phenology and prey phenology) on these activities. The prey phenology (i.e. breeding phenology of the Antarctic Petrel) may be interpreted in terms of resource availability, as petrel chicks likely have higher energy content than petrel eggs (Brooke et al. 1999). South Polar Skua phenology may be interpreted in terms of energy demand, as breeding South Polar Skuas need more energy during chick rearing. The following predictions where tested: (i) South Polar Skuas have higher hunting effort in the chick rearing period because they need to bring back more food items for both their young and themselves; (ii) no sex difference should be found in nest attendance, with possible exception of the skuas' incubation period, when females should defend the nest area more compared to males; (iii) breeding South Polar Skuas need to visit water ponds to clean themselves and this behavior should occur more frequently when skuas have higher hunting effort or are exposed to higher risk of oil attacks.

Material and Method

Study area

Svarthammaren is the world largest known Antarctic petrel colony. The Antarctic Petrel is the dominant species (between 150 000 and 250 000 breeding pairs) together with Snow petrels (~500 pairs) and South Polar Skua (~100 pairs). Most South Polar Skuas breed at the bottom of the main petrel colony, confined on a small area between the petrel colony and the glacier (Mehlum et al. 1988) and the nests were often not more than 15 – 20m from each other (pers. obs.). South Polar Skua breed from November to March and hatching is spread over several weeks (from 12 December to 19 of January in the season 2012-2013).

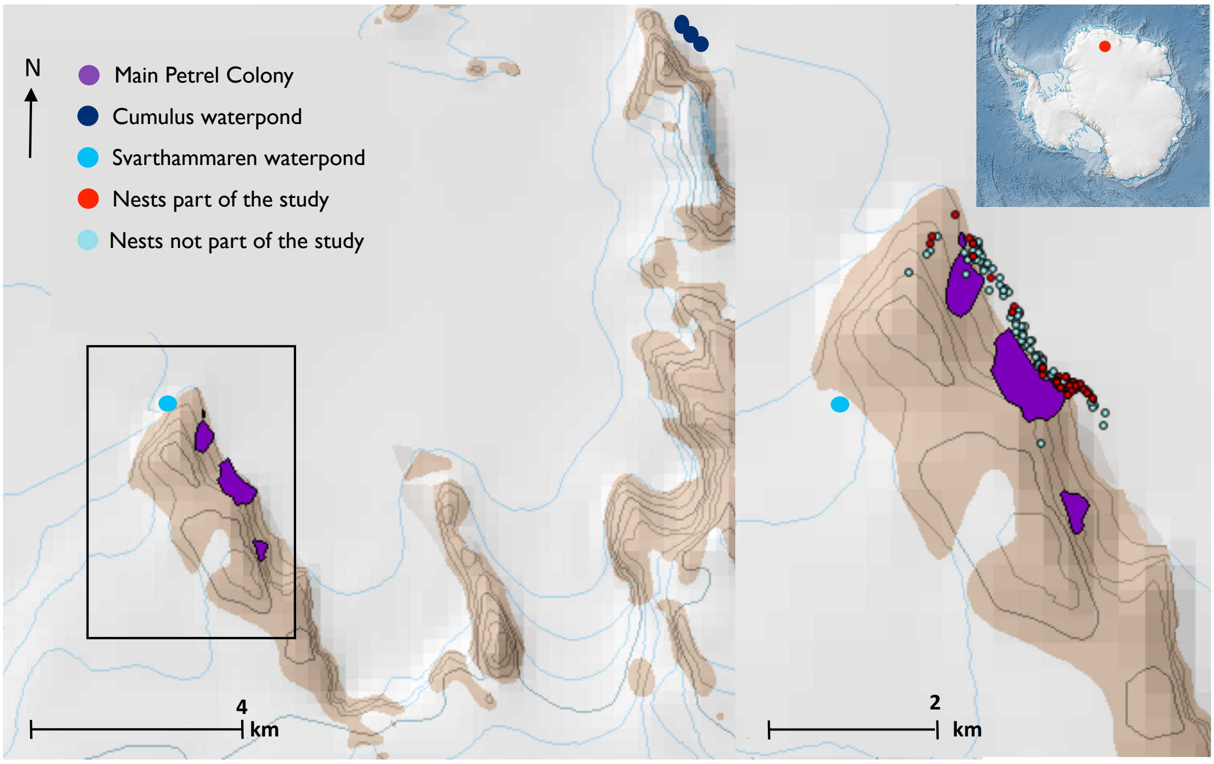

Fig. 1: The area of Svarthammaren and its location on the Antarctic continent. The Antarctic Petrel colony consisted of two main areas and a smaller third area, and in addition, one minor Snow Petrel area (both Antarctic and Snow Petrel marked with purple color). The main figure shows the two water ponds (See method for details), Svarthammaren and Cumulus water pond. The bottom right figure, represents a close-up on Svarthammaren Mountain and locations of South Polar Skua nests (n=90). The red dots are the position of South Polar Skua nests where we equipped birds with GPS loggers.

Logger deployment and capture method

The South Polar Skua nests were located below the Antarctic petrel colony and were spread along approximately 2 km. In total, 90 nests were found in the breeding season 2012-2013. Nests were monitored every 5 days on average. In total, 56 GPS loggers were deployed and retrieved on 48 individuals from 30 nests (8 individuals have had two logger deployments, during two separate time periods, see figure 2). The 30 nests were evenly spread in the monitored area. Among the GPS equipped birds, 23 were females, 23 males and 2 birds with unknown gender. Gender selection was based on both previous ringing information (Bustnes et al. 2007) and observations during our fieldwork 2012 -2013. We sexed South Polar Skuas based on larger mass and body weight, as well as, higher pitch voice in females than males (Pietz 1985).

We used different methods to capture South Polar Skuas. The first method was to use a large hand net. The second method involved a radio-controlled trap, which was placed on the nest. When the trap was triggered, it caught the bird, by tightening a nylon loop around its legs (note that eggs were replaced by fake eggs during captures). The third method was to use a net gun that captured the bird with a large net. The GPSs deployed were from *Cattrack* company. They weighted 25 grams and were attached on the birds' two tail feather with tape and glue. Human disturbance around nest sites was minimized after GPS deployment and field workers avoided walking through the breeding area. GPS deployment occurred between December 2012 and February 2013. Loggers were set at 5 and 10 minutes interval and deployed on birds from 3 to 21 days (average 10 days). Number of GPS locations for the tracking period between individuals varied from 432 to 3871 locations (mean=2216). Figure 2 gives an overview of the distribution of logger deployment. See Appendix I for example of the South Polar Skuas movement in the Svarthammaren area.

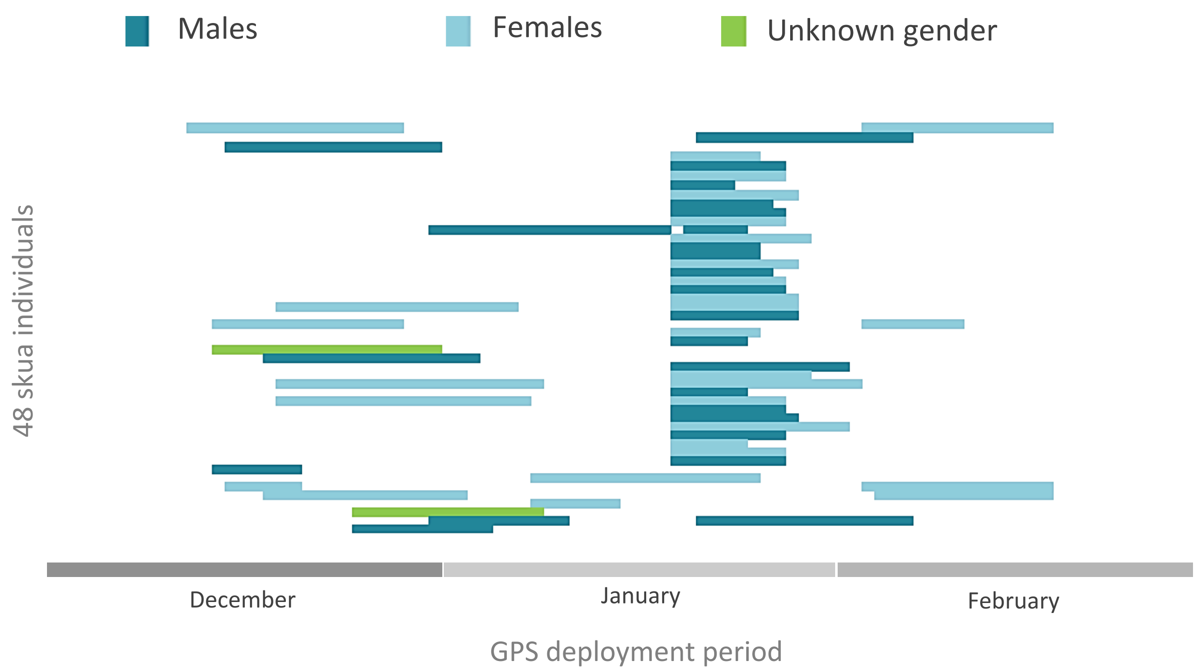

Fig. 2: GPS deployment in period December 2012 to February 2013. The different colors represent bird sex.

Data sets and Home range calculation

The South Polar Skua space use was interpreted as a function of our field observations and the previous study by Brooke et al. (1999). Antarctic petrels have a highly synchronized reproduction and hatching occurs within 10 days. In this study, I considered that the Antarctic Petrels were incubating until the 15th of January (i.e., average day) and chick rearing occurred thereafter. Two South Polar Skuas were tracked both before and after the 15th of January; I considered that one of the individual was tracked to during the petrel chick rearing period (tracking date: 8 Jan – 25 Jan) and the other skua tracked during petrel incubation period (tracking date: 30 Dec – 18 Jan).

<u>Hunting effort</u>

To test my first prediction concerning South Polar Skua hunting effort and the effect of sex, skua- and petrel phenology, I assumed that if South Polar Skua used a larger area in the petrel colony, they also have higher hunting effort. I wanted thereby to know how much of the South Polar Skua daily movement was located within the petrel colony. I estimated a daily movement by using a kernel density estimator and then estimated how much of the kernel area overlapped with the petrel colony area. When I estimated movements using the kernel density estimator, I used the average area for each of their daily movement (i.e., kernel estimate for each day and then taking the average of the daily values), because I wanted to compare the use of petrel colony among all individuals while taking into account differences in tracking time. Second, I removed all locations further away then 2 kilometers from the nest. The 2 kilometers threshold represented the estimated maximum distance from the skua nest to the petrel colony (i.e., total area of the petrel colony). When South Polar Skua traveled outside the colony area, the estimated area (i.e., kernel density estimator) became overly sensitive to these observations far away from the nest (examples on kernel estimates in appendix II).

The kernel density estimator is a well-known method to estimate space use (Worton 1987, Seaman et al. 1998). The method is non parametric and is based on a bivariate probability density function. It places a utilization distribution model over each tracking location. The kernel estimation of the density function is given by:

$$\hat{f}(\mathbf{x}) = \frac{1}{nh^2} \sum_{i=1}^{n} K\left\{\frac{1}{h}(\mathbf{x} - \mathbf{X}_i)\right\}$$

‘

where x is a location (a 2 dimensional vector), *h is* bandwidth or smoothing parameter, *n* is number of relocations, and X_i is the i^{th} relocation of the sample (Seaman et al. 1998). Formally, one would need to integrate the resulting density over a given area to get probability of use. The higher the value for the smoothing parameter, the bigger the area will be around each location. A 95 % kernel estimate represents the area within which there is a 95 % probability to relocate the animal (Worton 1989).

The "95 percent probability" was selected by plotting different values (30 % - 99%) for each individual and then evaluating the space use area. Individuals spent most of their time within a 50m radius from the nest, and I needed to have a high percent value to get movements also outside the nest area. For example, if I selected a 50% kernel, the plotted area was just around the nest itself, but if I selected 90 – 99%, the estimated movement area covered the petrel colony (example in appendix II). However, because the main goal was to compare the use of the petrel colony and test differences between sexes and different breeding stages, the exact value was not of primary importance as long as it was the same for all individuals. Kernel estimates are sensitive to the selection of the smoothing parameter. There is no agreement regarding how to choose an optimal smoothing parameter and several methods exist (Laver and Kelly 2008). I selected *href,* which refers to a *reference bandwidth* and uses the "theoretical optimal value, which is based on the assumption that the true distribution is normally distributed" (Silverman 1986). It is given by:

$$h = \sigma * n^{-1/6}$$

where

$$\sigma = 0.5 * (\sigma_x + \sigma_y)$$

σ_x and σ_y are the standard deviations of the x and y coordinates of relocations respectively.

The grid function controls the number of cells in which the model divides the area used by the tracked skua. A grid value of 500 means the model divides the total area (i.e., covering the included GPS positions) with 500 cells, where in each cell, the model estimates the kernel probability to relocate the animal, and all cells combine represents the total kernel density estimator area. A small value (thereby large and few cells) could mean the kernel is estimated with low resolution and is then less precise. However, the exact value does not influence the estimates largely (Silverman 1986), as long as the value is "within the range of valid estimates" (Seaman et al. 1998). The value of 500 gave enough resolution to describe the use of the petrel colony. The *extent* function controls the coverage of the grid value, which we could basically describe as the size of the area the function grid is based on (i.e., total area which we divided into 500 cells). A small *extent* value could possibly exclude locations if they are located outside the cells, and since I wanted to include possible locations outside the cells, I selected a larger value than the default. Based on these described options (i.e., *95 %, href, grid and extent*), I made a polygon using the kernel density estimator and a function called *getverticeshr* (in *adehabitatHR* package) to display the area the bird has used. The area of the petrel colony was based on a *shapefile* made by The Norwegian Polar Institute and represented both Snow and Antarctic Petrel areas at Svarthammaren. From the polygon, I could calculate the overlap with *shapefile* representing the petrel colony. The overlap with the petrel colony was done for each bird and for each day during the tracking period.

Nest attendance

To answer my second predictions concerning nest attendance and the effects of sex and phenology of skuas and petrels, I wanted to estimate time spent at the nest site by South Polar Skua. I therefore selected a radius of 50m around the nest and selected all locations the South Polar Skua had within this area. Then the number of locations for each bird within the 50m radius was divided with the total number of GPS positions. The final index was given in percent time the bird spent within the 50m radius from the nest.

Water Ponds

For the third prediction concerning the bathing activity and the effect of sex and prey- or skua phenology, I wanted to estimate the number of trips the South Polar Skuas preformed to water ponds during their tracking time. During the fieldwork two different water ponds were discovered at Svarthammaren (Fig 1: Svarthammaren- and Cumulus water pond) and South Skuas regularly visited these two water ponds. In addition, there was a third water pond, 100km east of Svarthammaren that was used twice by one South Polar Skua breeding at Svarthammaren in February 2013. Since there were only two cases where one individual visited this remote water pond during our study period, it was not included in our study. To estimate how the South Polar Skua used the Svarthammaren and Cumulus water pond, I calculated the average number of visits per day for each individual by taking the number of trips to each pond, divided by the total number of tracking days (i.e., two estimates, one for Svarthammaren and one for Cumulus pond (appendix III for examples). I considered that a bird visited the Cumulus pond when one position was located within 500m around the cumulus pond: for Svarthammaren pond, I considered that a bird visited the pond when one position was located within 50m around the pond. The Cumulus water pond was located ~9 km from the Svarthammaren breeding area, behind a large mountain, and consisted of several smaller ponds. I plotted all South Polar Skua GPS positions and based on the distribution of the total movement in the area, I could assume that there were no other reasons to travel to Cumulus Mountain than for bathing activity. I selected the most centered point among the Cumulus water ponds and selected 500m around it as the radius to reflect if the South Polar Skua visited the Cumulus water pond. The second water pond, Svarthammaren, was located close to South Polar Skua nest area (north of the colony). This water pond was smaller than Cumulus and, depending on the temperature, consisted of one or two open ponds. From the most centered point within these two ponds, I selected a radius of 50m to represent an area to describe if a bird visited the pond or not. Two South Polar Skua individuals were nesting around 100 to 150m from the Svarthammaren water pond and it is possible that I have interpreted movement from these two individuals around their nest area to be due to bathing activity.

Statistics

For the three activities considered here (use of the petrel colony, nest attendance and trips to water ponds), the effect of sex and phenology (and their interactions) were tested using linear mixed models where *Nest* was included as a random factors to take into account the dependency among individuals from the same nest. I also used a linear model with the frequency of the use of Cumulus water ponds as a predictor and the frequency to use the Svarthammaren as a response to investigate if the use of the two water ponds differed among individuals. Results are presented as a contrast (e.g., effect of sex is given as the difference Male-Female). I assumed that the results were not affected by the 5 or 10 minutes logger (explaination in "*Logger deployment and capture method" section*) interval, because the number of locations for each individual was high, I did not sub sample or used two different logger intervals in the analyses. For all statistical calculations, I used ´R program version 3.0.2. with package adehabitatHR, *gIntersection, nlme*, gplot, and gArea (included in Rgeos). For possible bias or sources of error see appendix IV.

Results

Hunting effort

Overlap with the Antarctic and Snow Petrel colony (i.e., proxy for hunting effort) varied between 0 and 25 percent for all individuals, with an average value of 6.4 % (SE=0.7 %)

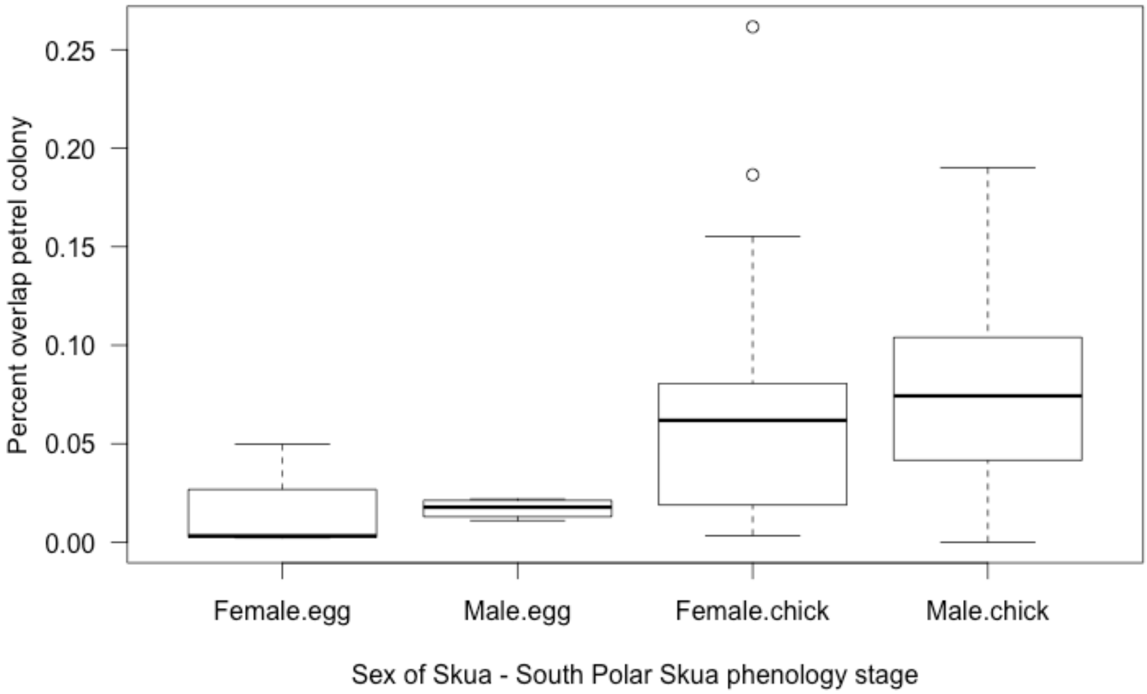

Fig. 3. Boxplot showing the distribution of percentage overlap with the petrel colony by sex and South Polar Skua phenology stage. Female/Male.Egg=Skua sex and Skua incubation period. Female/Male.chick=skua sex and Skua chick rearing period.

Based on a linear mixed model with Nest as a random factor, there was no evidence for an interaction between the fixed factors Sex and Petrel phenology (t=-0.39, n=54, P=0.70) or an effect of Petrel phenology, but evidence for an effect of Skua phenology (full model [n=54]: Male-Female b=0.007 [SE=0.015], Petrel phenology; Chick-Egg 0.002 [0.020], Skua phenology; Chick-Egg 0.057 [0.025], Figure 3). South Polar Skua used more of the petrel colony when they had chicks. The standard deviation of the random effect Nest was estimated as 0 indicating that males and females from the same nest did not use the petrel colony in a similar way.

Nest attendance

South Polar Skua individuals spent between 50 to 90 percent of their time within a radius of 50m from the nest (mean=53%, [SE=4%])

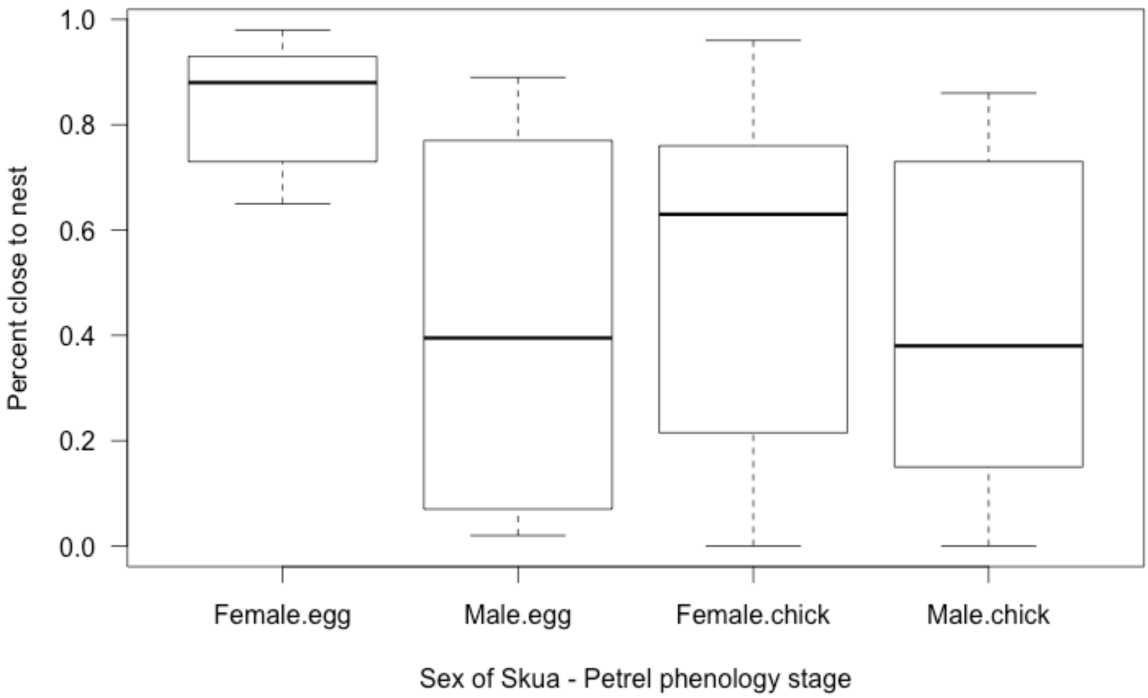

Fig. 4. Boxplot showing the distribution of proportion of time spent within 50m from the nest by sex and petrel phenology stage. Female/Male.Egg= Skua sex and petrel incubation period, Female/Male.chick= skua sex and petrel chick rearing period.

Based on a linear mixed model with nest as a random factor, there was evidence for an interaction between the fixed factors Sex and Petrel phenology (t=-2.40, n=54, P=0.026), but no effect of skua phenology (full model [n=54]: Male-Female during the egg phase: b=-0.26 [SE=0.09], Male-Female during the chick phase: -0.04 [0.03], Skua Phenology; Chick-Egg -0.02 [0.07]). Females were much more present at the nest than the males during the egg-laying phase of the petrel, but this difference disappeared during the chick-rearing phase (Figure 4). The standard deviation of the random effect Nest was large compared to the residual standard deviation (SD[Nest]=0.30 vs SD[Res]=0.09) indicating that males and females from the same nest stayed close to the nest with a high degree of consistency.

Use of the water ponds

During the logging period for South Polar Skua, 28 of 56 tracking periods included skua (48 skua individuals and 56 GPS loggers) visiting the Cumulus water pond (~9k away) and 46 of 56 tracking periods included skuas visiting Svarthammaren pond (close to colony). On average, the South Polar Skuas made 0.2 trips / logging day (± of 0.56 SD) and for Svarthammaren pond 0.97 (SD=0.11, figure 5).

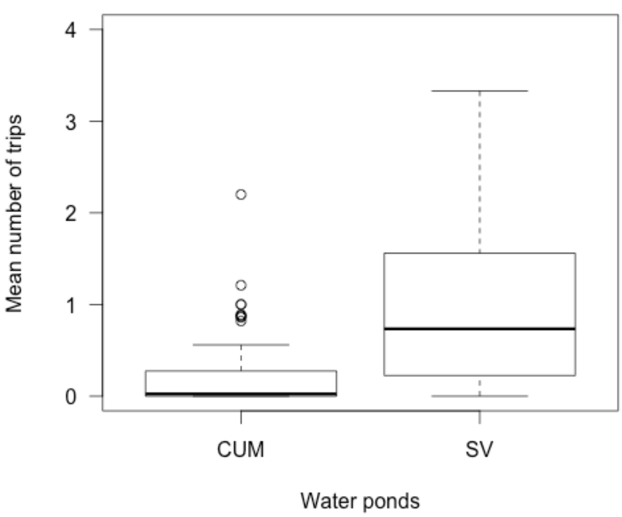

Fig. 5. Boxplot showing the distribution of number of trips made by the 56 tracking periods (48 individuals) to Cumulus water pond (CUM) and Svarthammaren water pond (SV)

Based on a linear mixed model with nest as a random factor, there was no evidence for effect of the fixed factors; Sex, Petrel phenology and Skua phenology, on the use of Cumulus water pond (full model [n=54]: Male-Female: b=0.04 [SE=0.11], Skua phenology; Chick-Egg 0.19 [0.20], Petrel Chick-Egg -0.19 [0.15]; Model with Petrel phenology only [n=56]: Chick-Egg: -0.08 [0.11]). The standard deviation of the random effect Nest was relatively large compared to the residual standard deviation (SD [Nest]=0.24 vs SD [Res]=0.35) indicating that males and females from the same nest used Cumulus water pond with some degree of similarity.

Fig. 6. Boxplot showing the distribution of number of trips to Svarthammaren water pond divided up by sex and petrel phenology stage. Female/Male.egg=Skua Sex and petrel incubation period, Female/Male.chick=skua sex and petrel chick rearing period

For the Svarthammaren water pond, petrel phenology did influence use with South Polar Skua using this water pond more often when petrels had chicks (Figure 6). There was no evidence for an effect of the other variables (full model [n=54]: Male-Female: -0.10 [0.22], Skua phenology; Chick-Egg -0.33 [0.37], Petrel phenology; Chick–Egg 0.80 [0.29]; Model with Petrel phenology only [n=56]: Chick-Egg: 0.91 [0.22], P=0.0004). There was little similarity among the birds from the same nest (model with petrel phenology as fixed factor; SD[Nest]=0.0001, SD[Res]=0.77). Also, that there was no interaction between Sex and Skua phenology, Sex*Phenology (P=0.97). Based on the linear mixed model with Nest as random factor, there was a negative relationship between the frequency of use of Svarthammaren pond and of Cumulus pond (b=-0.84 [SE=0.27] P=0.05), indicating that birds using the Cumulus water ponds used the Svarthammaren pond to a lesser extent.

Discussion

This study indicated that differences in South Polar Skuas space use at Svarthammaren area are related to sex and affected mostly by prey breeding phenology (i.e., petrel). Indeed, skua females spent more time at the nest during petrel incubation period and both sexes visited water ponds more often during petrel chick rearing period, probably because they were more exposed to oily attacks. However, hunting effort was affected by skua phenology, when both female and male invested more in hunting during chick rearing period than during their incubation.

Hunting effort

As in previous studies (Pietz 1984) and in line with our predictions, South Polar Skuas had higher hunting effort during the chick-rearing period than during incubation. This is most likely explained by the higher energy demand during chick rearing (Navarro et al. 2006, Williams and Flaxman 2012). Antarctic Petrel phenology did not affect the hunting effort of skuas, meaning that availability of petrel eggs or chicks did not affect the skuas' foraging. This result, combined with the lack of synchronization in skua breeding phenology (i.e., hatching is spread over >1 month), suggests that contrary to many other predator-prey system (Hipfner 2008, Borcherding et al. 2010) there is no strong fitness advantage for skuas to match their own reproduction to the one of their prey.

Nest attendance

Our results indicated that South Polar Skua spent most of their time (mean=53%) within 50m from their nest and skua pairs stayed in the nest area consistently during the study period. Nest attendance has been considered as a good measurement for describing the tradeoff between a birds need for nest defenses and foraging allocation (Catry and Furness 1999). Indeed, South Polar Skua need to defend their nest at Svarthammaren from other skuas as interspecific aggressive behavior has been recorded between skuas and predation on eggs at other breeding sites (Trillmich 1978, Pietz 1987, Young 1963). Other studies have concluded that skuas that defend their home area, have higher breeding success compared to non defending skuas (Trillmich 1978). The findings that skuas spend a high percent of time within their nesting area with great consistency could indicate the need to defend their nest at Svarthammaren.

We predicted that during the skuas chick-rearing stage, we would detect differences in nest defense depending on sex of skua together with stage of the offspring. The females are larger than the males and could better defend the nest whereas males are more suited for hunting activity (Catry and Furness 1999). Interestingly, we found that nest defense in skuas was affected by petrel phenology and sex of the skua. During the petrel incubation period, female skuas spent more time defending their nest, and during petrel chick rearing, both skuas' sexes invested more time in hunting. Brooke et al. (1999) recorded high access to petrel eggs available for predation by skuas during early petrel phenology. Most likely South Polar Skua spend more time around the nest during this time, as they can hunt close to the nest or they need to spend less effort on hunting in the petrel colony. Predation on petrel chicks could possible influence skuas' other activities, such as bathing and hunting, and could explain the spatial pattern we found. It is possible that hunting a chick requires more effort (i.e., longer handling time) compared to predations on eggs. Further more, the hunting effort may increase as prey becomes less available. Petrels' nest location is affected by the predation rate from skua, as petrel are more predated on exposed nest sites (Varpe and Tveraa 2005), therefore, it is possible that the most exposed petrel nests are predated early and skuas need to cover a larger area to find predation opportunities.

Use of water ponds

Almost all individuals used the water ponds, which can indicate the importance of access to water for the birds. The closest pond, Svarthammaren was the most used (average 0.97 trips / day for all individuals). The use of the water ponds was similar for both sexes and did not vary as a function of skua phenology. However, the petrel phenology did affect the use of Svarthammaren pond and the use of this pond increased during petrel chick rearing. When South Polar Skua predates on petrel chicks, they are most likely more exposed to oily attacks. Petrel chicks are known to spit large amounts of oil on predators as a defense mechanism (Franeker et al. 2001). Indeed, when a South Polar Skua is exposed to more frequent oliy attacks, they need to clean themselves more often to decrease the detrimental impact of stomach oil on their feathers (Warham 1977). As South Polar Skuas at Svarthammaren only feed upon petrels and not upon marine resources, the need for water ponds is likely more important as compared to other breeding sites in Antarctica.

I found South Polar Skuas preferred different water ponds, as different individuals visited either the Cumulus or the Svarthammaren pond. Furthermore, I found out that partners from the same nest used Cumulus with similar frequency. Therefore, the reason behind South Polar Skuas flying the ~9km travel to Cumulus water pond (compare to ~1km to Svarthammaren) could be explained by intra-specific competition and monopolization by some dominant individuals. By using a more distant pond they could avoid or minimize the competition to use the open water and therefore access it more easily. As animals with high mobility can have large space use (Ford and Glenn 1983), the cost for South Polar Skua to travel such distance is likely small as compared to the benefit of accessing more easily open waters due to lower competition.

Conclusion

Space use by South Polar Skua at Svarthammaren in Antarctica has been described using telemetry. I have concluded that, in this simple food web, South Polar Skua display space use similar to our predictions and compared to other breeding sites. Prey breeding stages had stronger effects on skua use of their nest area than skua breeding stages. This study gave a description of the skua space use at Svarthammaren but more detailed analyses are possible. To include individual quality factors like mass and breeding success could let us investigate possible links between skua activities and fitness and its determinants. The results given in this study are based on one field season and to better understand the system we would need data from more seasons. For example, inter annual differences in space use are common for seabirds (Pettex et al. 2012). Therefore, to link changes in petrel breeding success as well as abiotic factors (such as temperature and precipitation) to space use of South Polar Skua, we would need data covering several seasons. This study contributes to a better understanding of ecological interactions in a predator and prey system at a remote breeding area on the Antarctic Continent. Such knowledge can contribute to understanding of species population dynamics and with more research, can help us in future management and conservation of a species like South Polar Skua.

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Appendix I

Examples from the results of 5 tracked South Polar Skua and their movement (Figure 7). The Cumulus water pond was ~9km from the Colony and Svarthammaren water pond located ~500m north of the Petrel Colony.

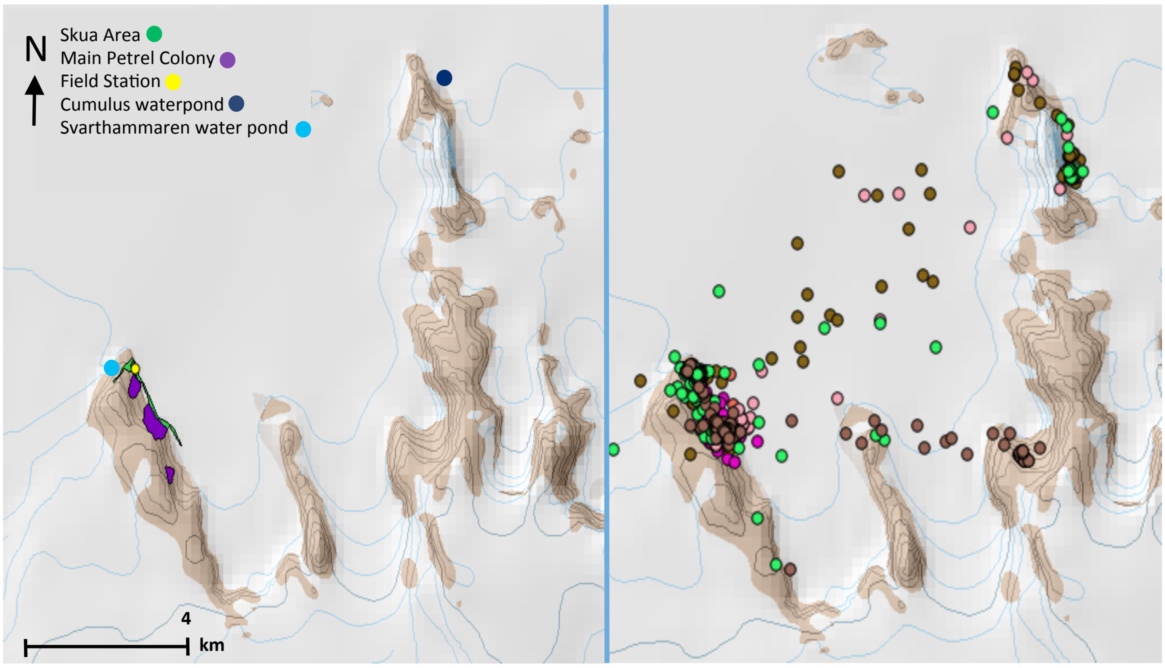


Fig. 7: The left figure shows the area over Svarthammaren, the surroundings and Svarthammaren- and Cumulus water ponds (marked with dark blue and light blue). The field station is marked with yellow. Skua nest are is marked with green. The figure to the right shows a small selection of result from GPS tracking of 5 Skua individuals. The different colors represents the 5 different individuals.

Appendix II

A plot with kernel density estimator values in km^2 for the 56 GPs loggers (48 individuals) (Figure 8) shows the output from kernel estimates was a gradually increasing with the size of the area from South Polar Skua movements. Above 95 percent, this area increases rapidly and is believed to do so because Skua may travel to Cumulus water pond or to other areas. When I included all locations it gave circular kernel images (Figure 9), compared to when I removed the movement outside colony area, it gave more detailed movement in the petrel colony (Figure 10).

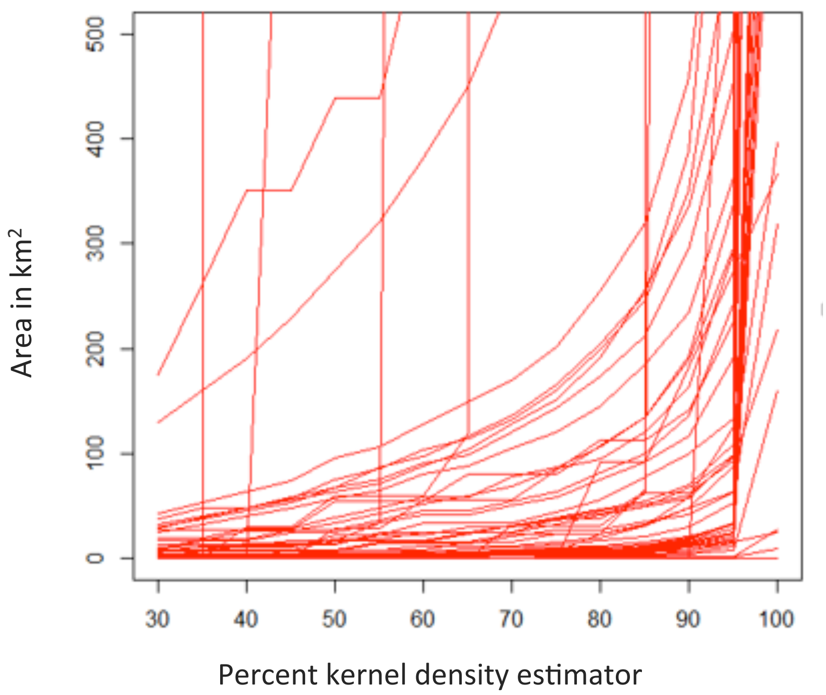
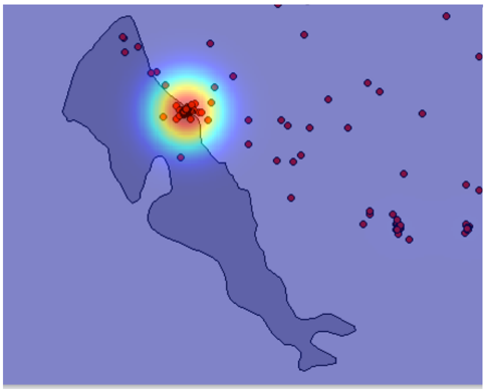


Fig. 8. The X-axis is kernel density estimate 0 – 100 percent (h = href) and Y-axis the km² area estimated. All 56 GPS loggers (48 individuals) are included.

Kernel density estimate area



%	km²
30	38.58954
35	46.87814
40	55.98201
45	65.90115
50	77.04320
55	89.54404
60	104.08306
65	121.06789
70	141.72145
75	168.08191
80	204.22563
85	262.65346
90	395.81455
95	846.11645
100	30776.51775

Fig. 9. To the left: A kernel image from the movement of one South Polar Skua with all locations included. To the right is two column table with different percent values of kernel density estimator and estimated area in km^2

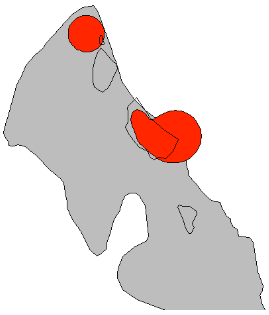


Fig. 10. A polygon representing 95 percent Kernel density estimator (marked with red), where only locations within 2km radius are included. The grey area is the Svarthammaren Mountain and the non-colored polygons represent the Antarctic and Snow Petrels nest area. The overlap between the Getverticeshr polygon and the Petrel area was used as index when describing the use of the Petrel colony.

Appendix III

Figures 11 to 14 are examples to demonstrate how I estimated the amount of trips to the water ponds.

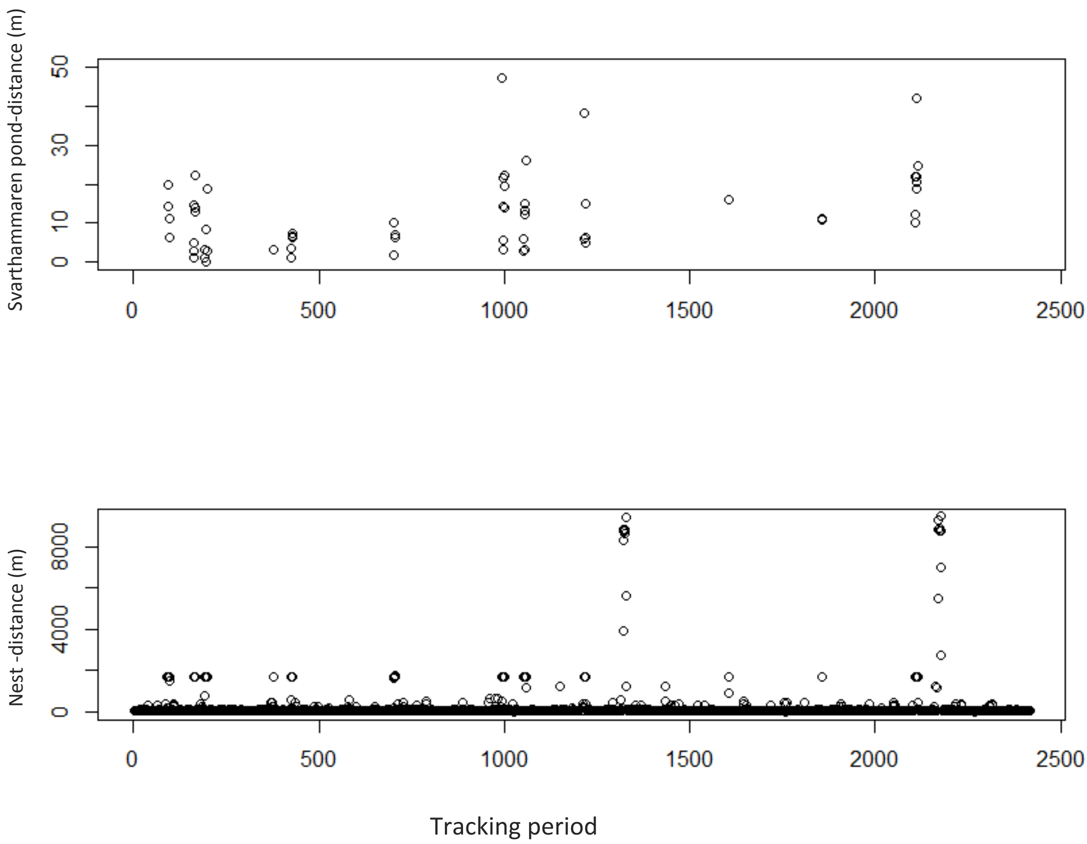


Fig. 11. The above figures displayed the distance from a random selected South Polar Skua individual. The X-axis is the distance to the Svarthammaren water pond where only distance between 0 and 50m is displayed. The Y-axis is the nr of locations during the tracking period. The bottom figure is the distance to the nest. The number of trips was estimated by separating one trip from another. In this given example, I estimated 10 trips to Svarthammaren water pond.

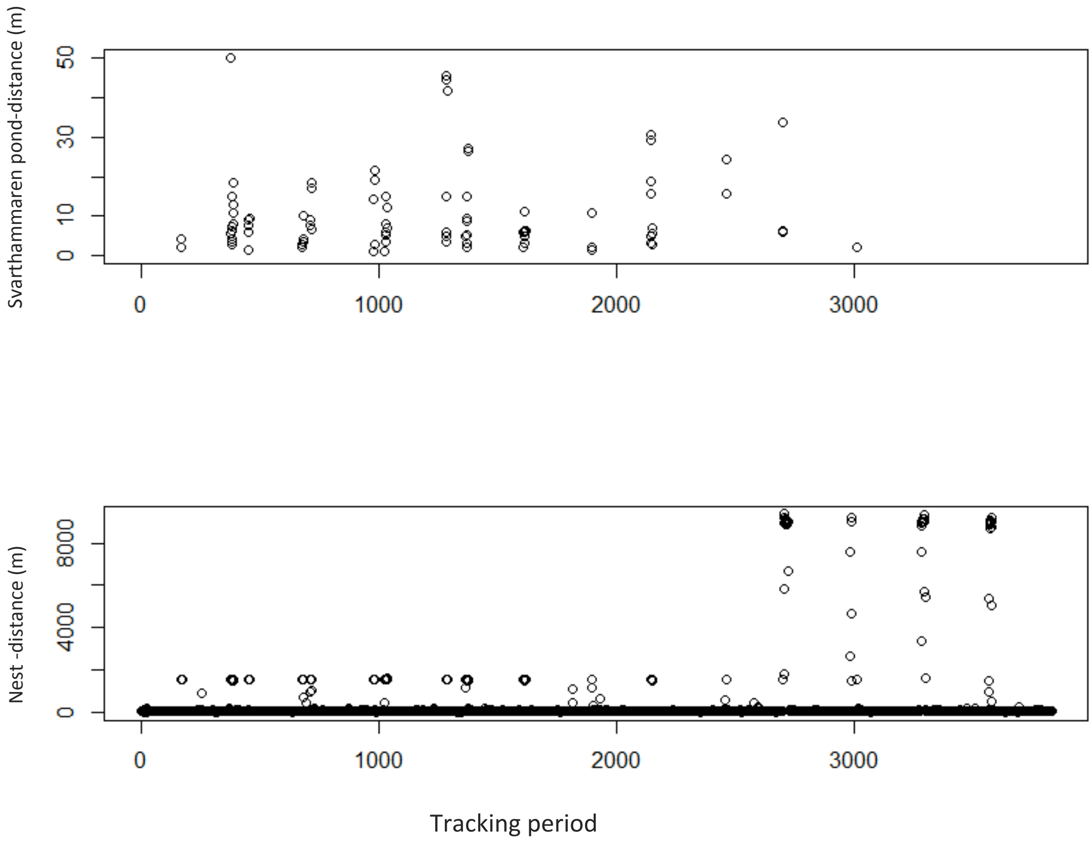


Fig. 12. The above figures displayed the distance from a random selected South Polar Skua individual. The X-axis is the distance to the Svarthammaren water pond where only distance between 0 and 50m is displayed. The Y-axis is the nr of locations during the tracking period. The bottom figure is the distance to the nest. The number of trips was estimated by separating one trip from another. In this given example, I estimated 11 trips to Svarthammaren water pond.

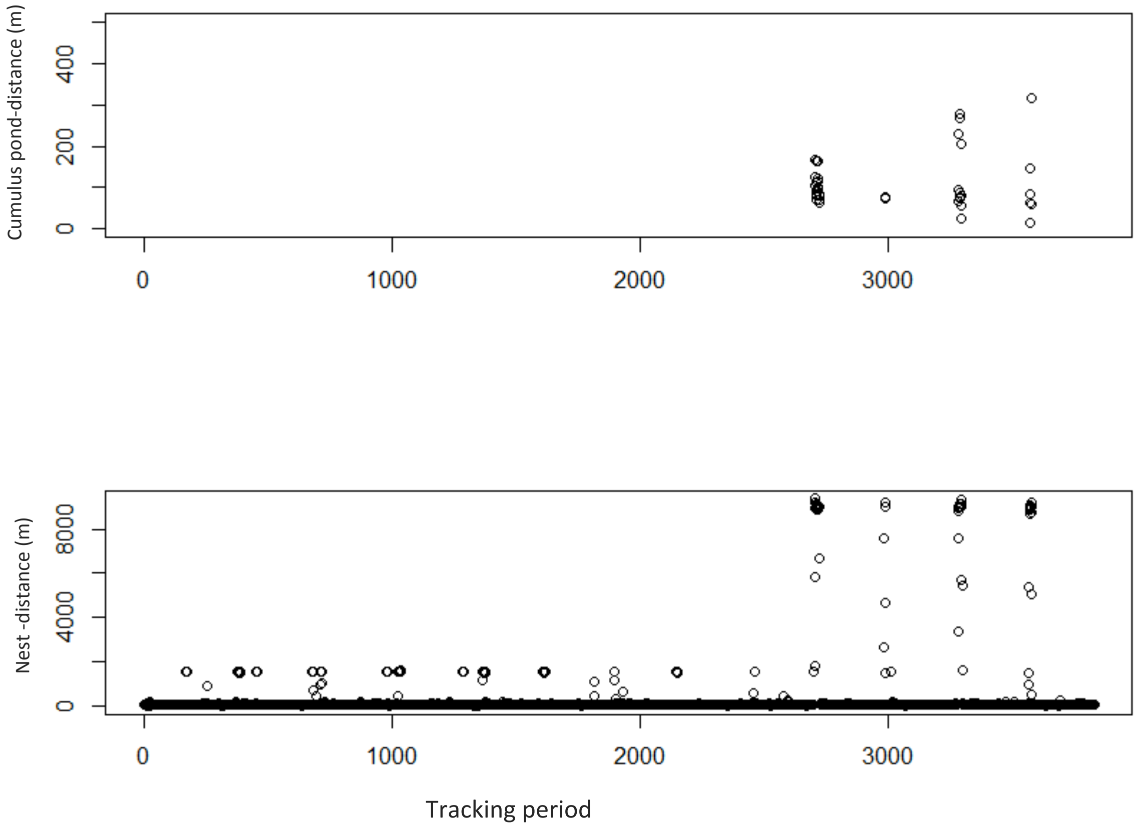
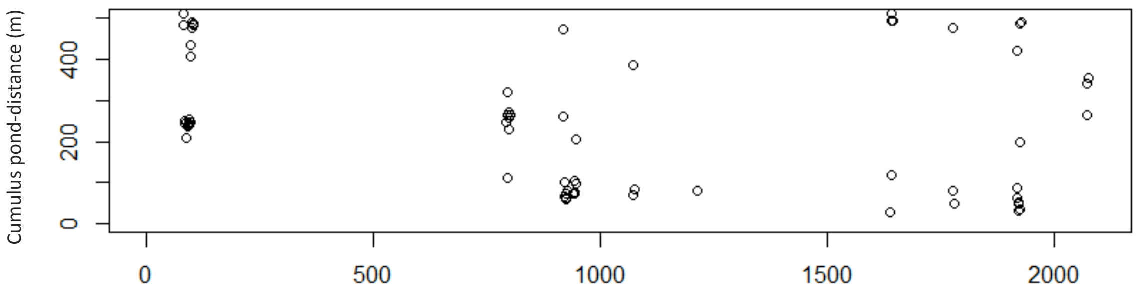


Fig. 13. The above figures displayed the distance from a random selected South Polar Skua individual. The X-axis is the distance to the Cumulus water pond where only distance between 0 and 500m is displayed. The Y-axis is the nr of locations during the tracking period. The bottom figure is the distance to the nest. The number of trips was estimated by separating one trip from another. In this given example, I estimated 4 trips to Cumulus water pond.



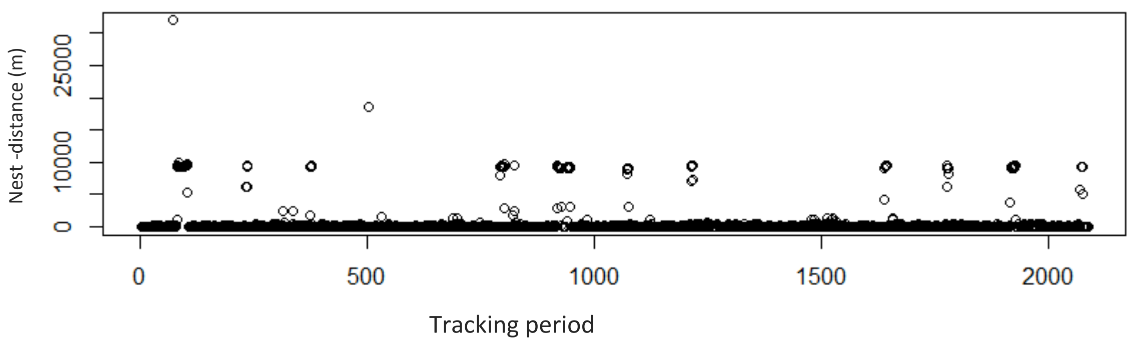


Fig. 14. The above figures displayed the distance from a random selected South Polar Skua individual. The X-axis is the distance to the Cumulus water pond where only distance between 0 and 500m is displayed. The Y-axis is the nr of locations during the tracking period. The bottom figure is the distance to the nest. The number of trips was estimated by separating one trip from another. In this given example, I estimated 11 trips to Cumulus water pond.

Appendix IV

Possible bias or sources for error

I assumed that the 50m radius reflected South Polar Skua activity related to their nest area. South Polar Skua breeding success has been linked to a short distance from the nest to the prey (Pietz 1987) and it is possible that in this study the selection of the 50m radius from the nest also includes skua hunting activity. A suggestion for a better solution could be to describe how the distance from the nest changes throughout the season during chick rearing and take this into account for the analyses. I also assumed that the size for the area the Skua used in the petrel colony reflected their hunting effort. To better describe and understand the hunting effort and foraging behavior we could quantify the time spent in the petrel colony and combine this with the area overlap used in this study.