Population ecology of Long-tailed Skuas *Stercorarius longicaudus* at Ammarnäs, Swedish Lapland

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Abstract

Breeding densities of Long-tailed Skuas show a strong response to rodent densities. At intermediate rodent abundances, only a subset of pairs manages to breed. It is not understood how in such years some pairs manage to breed while others pairs do not. Possibly, these breeding pairs may be more experienced and effective hunters, and/or occupy higher quality territories than non-breeding pairs. A first step in evaluating the latter hypothesis was done in this study. Territories with high or low occupancy in years with low breeding numbers were spatially clustered, whereas territory occupancy did not show spatial clustering in years with high breeding numbers. It is unlikely that this is the result of different survey intensities. Indeed, this supports the idea that certain areas hold less favorable territories. However, no further evidence was found in habitat, but this was probably due to the low resolution of the vegetation map. However, territory occupancy showed a positive correlation with elevation, suggesting that higher elevation provided better circumstances for breeding. This may be caused by good arthropod hunting conditions.
Introduction

The Long-tailed Skua *Stercorarius longicaudus* is a long-distance migrant, with a circumpolar breeding range in the (sub)arctic areas from sea level to inland mountainous tundra, wintering on the oceans of the southern hemisphere ([Cramp1983]; [Glutz1982]). For several areas, aspects of its breeding ecology have been described (e.g. [Andersson1971]; [Korte1984]; [Maher1974]; [Meltofte2007]). This manuscript discuss the population at Ammarnäs, Swedish Lapland, using nest locations collected during breeding bird surveys in 1985-2008.

Upon arrival at the breeding grounds in the last week of May, Long-tailed Skuas occupy large all-purpose territories ([Cramp1983]; [Glutz1982]). Territory and nest density shows marked temporal and geographical variation. Several studies have shown a strong linkage of Long-tailed Skua breeding densities to population cycles of their major prey: rodents ([Maher1974]; [Andersson1976]; [Korte1988]; [Meltofte2007]). In many areas, skuas may even refrain from breeding in years with no or very few rodents (e.g. [Maher1974]; [Korte1988]). At intermediate rodent levels, only part of the pairs breed, an ability which has been attributed to the utilisation of alternative resources ([Andersson1981]; [Aunapuu2004]). However, it is unclear how some pairs do manage to produce eggs while others do not. Possibly, the breeding pairs occupy higher quality territories than non-breeding pairs (cf [Sergio2003]) or are more experienced and effective hunters ([Andersson1976]). As Long-tailed Skuas show high site tenacity (e.g. [Andersson1981]; [Maher1970]; [Larsson2007]), it is difficult to differentiate between these hypotheses when only nest locations are known. A first step to understand the ability to breed in rodent-poor years and if this can be explained by habitat quality, is to test if territory occupancy is spatially clustered. In absence of detailed data food abundance and distribution, I here explore whether territory occupancy changes with vegetation cover, elevation, slope and aspect.

Figure 1 - The distribution of recorded nests (circles) in the study area from 1985-2008. Nests are clustered into territories by nearest neighbour joining. Territory boundaries at 600m from nests delimit the analysed areas.
Methods

Study area
The study area consists of a tundra plateau of 12.9 km$^2$, located WNW of Ammarnäs, Swedish Lappland (centred at approximately 66°0'N; 15°55'E [Svensson 2007]).

Surveys
A long-term breeding bird survey project has been carried out by the University of Lund, Sweden, from 1984 onwards ([Svensson 2007]). The study has been interrupted several times, leaving gaps for 1992, 1994 and 1996-2004. During surveys, found nests have been marked on paper maps, which have later been digitized. During 2007 and 2008, nest positions have also been recorded by GPS. Long-tailed Skuas are relatively easy to record, owing to the pale underparts. As most pairs aggressively defend their nesting areas, nests are in general easy to locate. There are, however, pairs that only start attacking human territory intruders when these are at a range of approximately 50m. Furthermore, nest figures could be underestimated as a result of loss to depredation before they were found. However, this was not observed during 2007-2008. In a few cases, breeding was only discovered after young chicks had been found.

Densities, clustering and occupancy
The distance to the nearest neighbour was calculated and averaged for each year (figure 2). Ripley's K-function was used to assess whether the nest locations and territory centres showed clustered, random or regular pattern. K(r) is defined as the expected number of nests within distance r of an arbitrary nest divided by the mean density of nests (Ripley 1981). Here, a square root transformation of the Ripley's K function, called the L-function, was used, which removes the scale dependence of the K statistic for independent patterns and stabilizes the variance (Besag 1977). Territories were defined as the largest cluster of nests from different years, clustered by joining the nearest neighbours first and subsequently joining (sets of) nests to its closest cluster. Subsequently, territory centres were approximated by calculating the central point the nests. Non-breeding but territorial pairs were not considered. To quantify the extent to which nests are translocated within a territory from one year to the next, the distance from each nest to the closest nest from the previous year was calculated. To test if the frequency of the number of nests in a territory differed from expected, the frequency distribution was compared to a poisson distribution. To test for spatial correlation of territory occupancy Moran's I Index (Moran 1950) was calculated for years with either more or less than half of the territories occupied.

Topography and vegetation
Within the plot, altitudinal differences are moderate (820-940masl) but the area is bordered by steep cliffs to the north and approaches the treeline of the birch zone to the south. Topographical data was obtained by digitizing a map (Lantmäteriet, Gävle, August 2002) with elevational isolines (resolution of 20m). From this, a tin-layer was created, allowing the estimation of elevation, slope and aspect of nest locations.

Similar tundra habitat as in the study area continues to the west and east. Just over half of the 78ha open water (c 6% of the plot) is contained in four larger lakes (25, 7 and 5 and 4ha); the remaining part is distributed over 64 smaller water bodies. Using the vegetation classification tool in the Leica Image Analysis extension for the ArcGIS 9.2 software package, two vegetation classes could be identified from a Landsat satellite image with a spectral resolution of 100m/pixel. The first comprised dry heath, with bilberry and grasses. The second class included willow heath but also mires. Lakes and rocky areas were digitalized by an unsupervised classification in the Image Analysis extension, which uses the Isodata algorithm to assign pixels to classes (Saghri et al 2000).

According to Maher (1974), Long-tailed Skua pairs heavily defend a core area around the nest of 400-600yards in diameter (366-549m; cited incorrectly as in meters by Wiley & Lee (1998) and [Cramp1983]); the remaining area is less aggressively defended, but is used for foraging. Andersson (1971) reported that Long-tailed Skuas hunt mostly up to a distance of 600-700m from the nest. Therefore, both an analysis of the cover within 600m from all nests in a territory and of a core area up to 275m from the nest was analysed. In both analyses, I assigned overlapping areas to the closest territory centre. Whether in years with less than half of the territories occupied territory occupancy changed with vegetation cover, elevation,
slope and aspect, a Generalized Linear Model was used. As territory occupancy concerns count data, errors were assumed to follow a poisson distribution. Vegetation cover data was first arcsine transformed before tested. The maximal model was simplified stepwise, excluding high order interaction and the least significant terms first. These statistical tests were conducted using the R statistical package (R DCT 2008).

Figure 2 - Upper panel: number of recorded territories and the number in which nests were found. Middle panels: mean distance to the nearest neighbouring nest in the current year (grey circles and bars) and apparent displacement within a territory relative to previous years' nest location (closed circles and black bars). Overall frequencies are shown in the panels to the right. Numbers indicate sample sizes for the previous year comparison. Sample sizes for the current year measurements are the number of nests, which is depicted in the upper panel. In the lower panel, black bars represent the fraction of the territories of previous year that held a nest again in the present year.
Results

In total, 90 nests of Long-tailed Skuas were found. Since 1984, the number of Long-tailed Skua nests has varied from zero (1984, 1988, 1993 and 2006) to 15 (in 2008) (figure 2). Number of nests and territories were slightly higher than those earlier reported by Svensson (2007): 14 instead of 12 territories in 1990, and 11 located nests instead of 10 in 1995. The first two years with no recorded nests (1985 and 1988) were separated by three years with nests, the second and third (1988 and 1993) by four years of which at least three with nests, and the third and fourth by 13 years, of which at least two with nests. In five years (1987, 1995, 2005, 2007 and 2008), nests were found in eleven or more territories. These were classified as years with high breeding densities. In the remaining five years (1985, 1986, 1989, 1990 and 1991), 4-7 nests were found. These were classified as having low breeding densities.

The average difference between GPS-measured nest locations and map-read nest locations for 2007 and 2008 was 88m (SD=50; range=7-187; n=25) for the two years combined. The inaccuracy did not differ between these years (t=0.5015; df=22.871; p=0.6208).

In years with low breeding densities, the distance to the nearest neighbouring was in the order of 900m, whereas it was about 600m in high density years (figure 2).

Using nearest neighbour joining of nests from different years, 20 territories were identified (figure 1). Ripley's K statistics showed that Long-tailed Skua nests are clustered up to a distance of about 1km (figure 3), but territory centres are regularly spaced up to a distance of about 600m. Above this value, the locations of territory centres do not differ from a random pattern (figure 3). Although the nest is not necessarily the center of the territory ([Maher1970]), the central point of the nests in a territory is a fairly accurate estimate of the territory centre. The nest locations within a territory were on average at a distance of 159m from the calculated territory centre (n=90; SD=117). The distance to the nearest nest from the year before in the same territory averaged in most years between 200 and 400m, with even lower figures in 1991 (figure 2). Using GPS-measured nest locations, nests were translocated on average 236m between 2007 and 2008 (SD=95.87; range=72-371; n=11).

Territory occupancy, split for years with more or with less than half of the territories occupied, is depicted in figure 4. A single territory held only nests in years with low breeding densities. The remaining 13 territories held nests in years with low and high densities. Most territories held more nests in high density years than in low density years (figure 5). The frequency of number of nests per territories did not differ from a poisson distribution in both low ($\chi^2=2.869; \text{df}=4; \ p=0.580$) and high density years ($\chi^2=5.895; \text{df}=4; \ p=0.207$). However, Moran's I statistics showed that in years with less than half of the territories occupied, territories with similar rates of occupancy were more clustered than expected (Moran's I=0.026; Expected I=-0.053; Var=0.021; Z=0.598). In years with a higher number of breeding pairs, the spatial pattern of occupancy did not differ from expected (Moran's I=0.026; Expected I=-0.053; Var=0.021; Z=0.594).

Elevation, slope and aspect

In years with low breeding numbers, territory occupancy did not significantly change with any of the vegetation cover attributes (figure 6). Nor did territory occupancy change with slope or aspect. However, territory occupancy showed a significant positive relation with elevation (figure 5; $Z=2.451; \text{df}=18; \ p=0.014$).
Figure 3 – Second-order spatial analysis of the distribution of Long-tailed Skua nest or territory centres using a modification of Ripley’s K function, L(r). Shaded areas represent confidence intervals for complete spatial random-ness of 90% (dark grey, nine permutations) and 95% (pale grey, 99 permutations). When the observed pattern (line) is above these areas, it is considered clustered, whereas below it is considered regularly spaced. **Upper left:** all nests of all years show a clustered pattern over distances of up to 1000m. **Upper right:** territory centres are more equally separated than expected up to a distance of about 600m. Above this distance, the pattern does not differ from randomness.

Figure 4 – The number of years in which a nest was found in a territory, for years in which less than half (upper panel) or more than half (lower panel) of the territories held nests.
Discussion

Population dynamics
The variation in number of breeding pairs as encountered in Ammarnäss, with no or very few breeding birds in some years, is in accordance with earlier studies in North Sweden ([Andersson1971]; [Andersson1981]; [Larsson2007]), Greenland ([Korte1988]; [Meltofte2007]) and Alaska ([Maher1970]; [Maher1974]). These fluctuations have generally been attributed to rodents density cycles ([Andersson1976]; [Maher1974]; [Andersson1981]; [Meltofte2007]; [Korte1988]; [Larsson2007]). At Ammarnäss, after a lemming peak in 1982, microtine rodent densities have reportedly remained at intermediate or low levels. It was not until 2007 and spring 2008 that high rodent densities reoccurred (Sören Svensson, Martin Green pers comm; [Hornfeldt2008]). The numbers of Norwegian Lemming and Grey-sided Vole at Ammarnäss as reported by Hornfeldt (2008) for 1995-2007 correspond well with the high number of Long-tailed Skua nests in 2007 and the absence of nests in 2006, but not to the high number of breeding Long-tailed Skuas during 1995 and 2005, when spring and autumn densities of rodents were low. For 1985-1993 there is no quantitative data on rodent densities from Ammarnäss, but lowland rodent populations at Umeå, northern Sweden (including Grey-sided Vole but lacking Norwegian Lemming; [Hornfeldt2004]), are in agreement with what has reportedly happened in Ammarnäss: a change from three or four-year cycles up to 1985 into yearly, small fluctuations at low population levels. During this period, several years with no nests of Long-tailed Skuas appeared in the study area. Apparently, rodent densities were below a certain threshold under which Long-tailed Skuas are unable to produce any eggs ([Maher1974]; [Meltofte2007]; [Aunapuu2004]). These non-breeding years did not occur in a regular pattern, further corrobating the view that regular cycles were absent. Assuming that in 1985-2006 rodent densities never reached levels comparable to those in peak years as 2007, 2008 and prior to 1985, it is remarkable that the numbers of Long-tailed Skua nests did reach levels approaching the high numbers found in 2007-08. It has been argued that Long-tailed Skuas are able to breed at low rodent densities thanks to the utilisation of alternative resources, such as insects, berries and young birds ([Maher1974]; [Aunapuu2004]).

Site tenacity
Long-tailed Skuas are known for their high site tenacity ([Maher1970]; [Maher1974]; [Andersson1981]; [Meltofte2007]; [Larsson2007]), although a minority of individuals have been reported to shift to nest locations up to 9km away from an earlier nest site ([Andersson1981]). Returning to a well-known territory and partner may allow a rapid onset of breeding, which seems advantageous as lemming...
numbers often drop during summer, and may also allow more effective hunting and predator avoidance ([Andersson1981]). Site tenacity at Ammarnäs was shown by the observation of several breeding birds in 2008 – wearing rings – very near or at the same location were individuals had been ringed at the nest in 2007. Moreover, one of these was identified with certainty as the same individual as previous year (pers obs). This bird had been ringed at the very same spot in 1997. In most years, more than half of the territories with a nest in the previous breeding year held a nest again (figure 2). Obviously, it has not been ascertained that these were the same individuals returning. Within these territories, nests were located 200-400m from previous years’ nest location, which is slightly lower than the figures reported by Meltofte & Hoye (2007); a difference that may be attributed to the fact that they did not identify territories, but merely measured the distance to the nearest nest in the previous year.

**Nest locations and territory occupancy**

The regular spacing of nests within a year illustrate the intraspecific aggression shown by Long-tailed Skuas. Only in a single case, nests were closer to each other than 275m, which is the distance stated by Maher (1970) to which breeding pairs heavily defend a core area around the nest against territory intruders, whereas the majority were 400m or more apart. This is in accordance with earlier studies (e.g. [Andersson1971]; [Maher1974]).

The mean distance to the nearest neighbour is in between figures reported from Northeast Greenland, where nests were mostly 450-600m apart ([Meltofte2007]) and those from Alaska, where they were on average about 1,5km apart ([Maher1974]). Remarkably, another study from Sweden, only about 125km from Ammarnäs, also reported higher values ([Larsson2007]).

Four out of five years with low breeding numbers showed a much larger variation in inter-nest distances than did years with many nests. Instead of breeding further away from each other when allowed by the number of nests, this was caused by a few nests in the north-western territories isolated from an aggregation of nests in the south-eastern part of the study area. Indeed, in low density years, non-occupied territories clustered in the north-western parts of the study area, whereas territories occupied in up to four years clustered in the eastern part. No such clustering was apparent in years with high breeding numbers. It seems unlikely that this pattern is caused by lower survey intensities in the northwestern parts, as there is no proof of clustering in high density years and there is no reason to assume different survey intensities between years with high and low breeding pairs. Rather, this supports the idea that occupancy of territories in years with low breeding numbers reflects territory quality, with those not occupied being the least favorable. If pairs managed to breed thanks to their high experience, a spatial clustering with territory occupancy would not necessarily be shown. Detailed data on food density per territory may provide insights in the validity of this hypothesis, but unfortunately, this data is missing for the study area. An indirect approach, analysing habitat coverage, did not indicate any relation with occupancy, but this analysis was probably hampered by the low level of detail of the habitat maps.

There was, however, a positive correlation between elevation and territory occupancy in years with low breeding numbers. This suggest the higher areas provide better circum-stances to breed in rodent-poor years. As snow generally dissappears earlier at lower elevations than at higher (Rychetnik 1987), feeding opportunities for Long-tailed Skuas may be better at the higher areas of the study areas, facilitating breeding. The availability of food may be two-fold. First, the few rodent present in rodent-poor years may be concentrated in areas with more snow-cover, as this protects them from predators. Second, and possibly more significant when rodents are scarce, wind-blown arthropods can easily be caught when immobilized and made conspicuous by snow (Edwards 1972). Therefore, snow may provide good forage opportunities for Long-tailed Skuas. Meltofte & Hoye (2007) advocated the importance of arthropods in the pre-laying diet, possibly triggering egg-laying.
Figure 6 – Cover of territories within 600m (upper panel) and 275m from the nest (middle panel), ordered from left to right by the number of nests in poor years and good years (lower panel). No cover variable significantly correlated with territory occupancy in years with less than half of the territories occupied.
Acknowledgements

I especially thank Martin Green and Sören Svensson (Lund University), for allowing me to spend two field seasons in Ammarnas. Jim de Fouw introduced me to the Long-tailed Skuas of Ammarnas by inviting me to spend the 2007 field season there and provided the nest locations for 2007. Fer van der Lans joined me during the fieldwork in 2008 and Johannes Hungar provided positions and elevations of several nests in 2008.

Also, thanks go out to all who developed the free, open source software I used for creating this report: RLPlot (Reinhard Lackner, University of Innsbruck), R (R development team), OpenOffice and Linux Ubuntu Intrepid.

References