

Post-breeding migration of four Long-tailed Skuas (*Stercorarius longicaudus*) from North and East Greenland to West Africa

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Abstract The Long-tailed Skua (*Stercorarius longicaudus*) is a specialist predator of lemmings during the summer and hence an important component of the tundra ecosystems, but most of its life cycle takes place offshore and remains largely unknown outside of the breeding season. Using 9.5-g solar-powered satellite transmitters, we were able to document for the first time the post-breeding movements of the Long-tailed Skua, from its high-Arctic breeding-grounds in North and Eastern Greenland to the tropical waters of West Africa. The birds traveled the approximately 10,000 km of this migration in only 3–5 weeks, covering 800–900 km/day during active migration, which also occurred during nighttime. Leaving their breeding areas in August (except for one failed

breeder), the Long-tailed Skuas first moved south along the coast of East Greenland towards a staging area off the Canadian Great Banks where they stayed for 1–3 weeks. From there, they crossed the Atlantic Ocean eastwards in just 1 week, entering African waters near the Madeira Archipelago in September. Although only four birds were monitored for 1.5–3 months, the data reveal that the migration routes between birds breeding in different locations and in different years were relatively similar.

Keywords Satellite tracking · Post-breeding migration · Staging area · Upwelling · Rates of travel · Long-tailed Skua · Greenland

Zusammenfassung Falkenraubmöwen ernähren sich während der Brutzeit hauptsächlich von Lemmings und stellen somit ein wichtiges Glied in Tundren-Ökosystemen dar. Da sie aber den Großteil ihres Lebens auf hoher See verbringen, ist über ihre Lebensweise außerhalb der Brutsaison nur wenig bekannt. Mit Hilfe von 9.5 g schweren, solarbetriebenen Satellitensendern konnten nun erstmals die Zugbewegungen von den hocharktischen Brutplätzen in Nord- und Ostgrönland bis in die tropischen Gewässer vor der westafrikanischen Küste dokumentiert werden. Innerhalb von 3 bis 5 Wochen legten die Vögel etwa 10,000 km zurück. Die Tagesetappen betragen 800 bis 900 km, wobei die Vögel auch nachts zogen. Nach dem Verlassen der Brutgebiete im August flogen die Vögel zunächst entlang der ostgrönländischen Küste bis zum Festlandssockel vor Neufundland, wo sie 1 bis 3 Wochen blieben. Sie überquerten anschließend in nur einer Woche den Atlantik in südöstlicher Richtung und gelangten über Madeira und die Kanaren bis in die Nähe der Kapverdischen Inseln. Bislang konnten wir nur 4 Vögel über einen Zeitraum von 1.5 bis 3 Monate verfolgen, jedoch wiesen

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die Zugrouten aus unterschiedlichen Brutgebieten in beiden Untersuchungsjahren ähnliche Muster auf.

Introduction

The Long-tailed Skua (*Stercorarius longicaudus*) is an important component of the Arctic terrestrial vertebrate community. Across most of its breeding range, it depends on cyclic lemming densities to breed (Andersson 1971, 1976, 1981; Larson 2007; Maher 1970; Meltofte and Høye 2007), and there is a strong interaction between these two species (Gilg et al. 2003). Along with a few other predators, the Long-tailed Skua regulates the Collared Lemming (*Dicrostonyx groenlandicus*) dynamics in Northeast Greenland (Gilg et al. 2006; Schmidt et al. 2008), especially during the peak phase of the lemming cycle when, along with the Snowy Owl (*Nyctea scandiaca*) and the Arctic Fox (*Alopex lagopus*), it is responsible for the rapid summer decline in lemming numbers (Gilg 2002).

Conditions experienced by seabirds during migration and on their wintering grounds are assumed to impact their subsequent reproductive performance (Furness et al. 2006). De Korte (1985) has shown that Long-tailed Skuas breeding in Northeast Greenland arrive with maximal fat reserves in the spring. The pelagic habitats they use during the non-breeding period (9–10 months of the year) must therefore provide them with sufficient food resources to initiate breeding but are also, in turn, indirectly impacting the lemming population dynamics. Little is known, however, about the flyways and wintering grounds used by the species, the most pelagic of all Skuas (Furness 1987; Olsen and Larsson 1997). With the exception of some local concentrations reported from the Benguela upwelling (Lambert 1980; Ryan 1989), a cold, nutrient-rich current off the coasts of Namibia and South Africa, ring recoveries for the species during the non-breeding period have been exceedingly rare, and flyways have been inferred from only a limited number of offshore observations.

Recent developments in satellite telemetry, with transmitters now weighing <10 g, have opened new perspectives for the study of medium-sized birds (between 300 and 500 g). Because it breeds in remote Arctic areas and spends the rest of the year in similarly remote offshore waters, the Long-tailed Skua is a perfect candidate species for these new research techniques. We report here the post-breeding movements (timing and duration of migration and flyways) of four Greenlandic Long-tailed Skuas, as part of a comprehensive long-term research of terrestrial vertebrates in Northeast Greenland (Gilg et al. 2003; Sittler 1995).

Materials and methods

Four Long-tailed Skuas were captured and fitted with satellite transmitters [platform transmitter terminals (PTTs)] in 2006 and 2007 in the “North and East Greenland National Park” (Table 1). All birds were breeding. In 2007, we captured the birds on the nest using a bow net, while in 2006 they were captured within a few meters of the nest, using a small mist net (approx. 1 m²) fixed on two handhold poles and rapidly raised in front of attacking birds.

All birds were equipped with 9.5-g solar-powered PTTs from Microwave Telemetry (Columbia, MD). The transmitters were attached to the birds as a backpack using Teflon ribbon and four silver rings to build the harness. The PTT and harness (approx. 2 g) weighed <12 g, which was on average 3.9% (± 0.15 standard deviation) of the body mass of the birds. The PTTs fitted on the two birds in 2006 were set to a constant duty cycle of 7/38 h (on/off, respectively), while the two PTTs attached in 2007 had a constant duty cycle of 7/25 h (on/off).

PTTs were located using the Argos positioning system (CLS 2008) that provides positions in seven precision classes. The location errors of classes LC3, LC2, LC1 and LC0 follow a normal distribution with a standard deviation of <150, <300, <1,000, and >1,000 m, respectively. There

Table 1 Summary data for the four studied Long-tailed Skuas and timing of their post-breeding migration

Birds' names (mass)	Trapping location (deg. Lat. N/Long. W)	Release date	Duration of tracking (days)	Start date of fall migration in Greenland ^a	Duration of staging off Canada (days)	Arrival off Northwest Africa
Papikk (300 g)	Karupelv Valley (72.50°/24°)	30 June 2006	81	5–12 August	8	12 September 2006
Niilar (280 g)	Karupelv Valley (72.50°/24°)	3 July 2006	86	14–15 August	16	23 September 2006
Lucy (278 g)	Mestersvig (72.25°/24°)	2 July 2007	45	19 July ^b	20	n.d.
Blissy (295 g)	Bliss Bugt (83.57°/30°)	8 July 2007	52	8 August	n.d.	n.d.

n.d., Not determined

^a The earliest and latest possible departure dates from breeding grounds are given when the exact data could not be documented

^b This bird left its breeding territory on 9 July but remained within 50–100 km of this area until 18 July

is no accuracy estimate associated with the remaining classes (i.e., LCA, LCB and LCZ), but LCA has been shown to have the same accuracy as LC1 (Hays et al. 2001; Vincent et al. 2002). We used orthodromic distances to estimate the “daily rates of travel” of the birds (Imboden and Imboden 1972; James et al. 2005) for time scales of 45 ± 7 h (in 2006) and 32 ± 7 h (in 2007). For these calculations, we used successive “best daily location” (i.e., in order of preference: LC3, LC2, LC1, LCA, LC0) produced during the 7-h transmitting period; LCB and LCZ were never used in the calculations. We also estimated “hourly rates of travel” using successive high accuracy fixes (LC3, LC2, and LC1) for time periods of between 0.5 and 2 h (for more details, see Gilg et al. 2010).

Results

Altogether, the four PTTs produced 1,019 Argos positions, and the birds could be monitored for 45–86 days (mean 66 days; Table 1). Only one-third (i.e., 376) of these locations were LC3, LC2, LC1, or LCA, but more than 70% of the “best daily positions” (i.e., 93/131) were high-accuracy fixes (LC3, LC2, and LC1).

Since 2006 and 2007 were 2 years with very low lemming densities in Mestersvig and in the Karupelv Valley, no Long-tailed Skuas bred successfully at either of these study sites during these years (Gilg et al. 2009; B. Sittler, unpublished data). The three birds monitored from this region left their breeding grounds 36–43 (Papikk), 42–43 (Niilar), and 12 days after they had been released (Table 1). The bird from Bliss Bugt (Blissy), the only bird that had possibly raised young (considering a fledging period of 25 days; Cramp and Simmons 1983), left its territory 31 days after release.

Hence, the start of the fall migration (i.e., the date of departure from the breeding grounds) occurred between 19 July 19 and 15 August, which is in line with observations made in previous studies (de Korte 1984; Wiley and Lee 1998; B. Sittler and O. Gilg, unpublished data).

After departure, all birds moved southward following the outer coast (note that “Blissy” did not take the shortest route over the Greenland icecap), passing between the southeastern part of Greenland and Iceland, towards a large (approx. 500,000 km²) staging area located off the Great Banks of Newfoundland, Canada (Fig. 1). The first bird (Lucy) arrived there by the end of July; the others by the end of August. With the exception of Blissy, which was lost 20 days after it had started its migration (i.e. shortly before reaching this area), it took the birds 1–2 weeks to travel the 3,000 km from their breeding grounds in Northeast Greenland to this staging area (Fig. 1). The three birds then stayed in this area for 8–20 days.

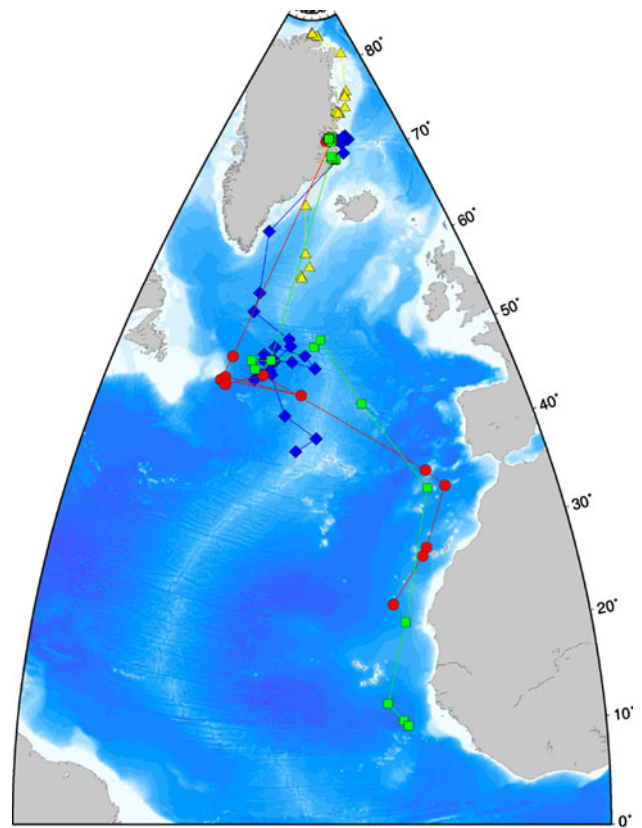
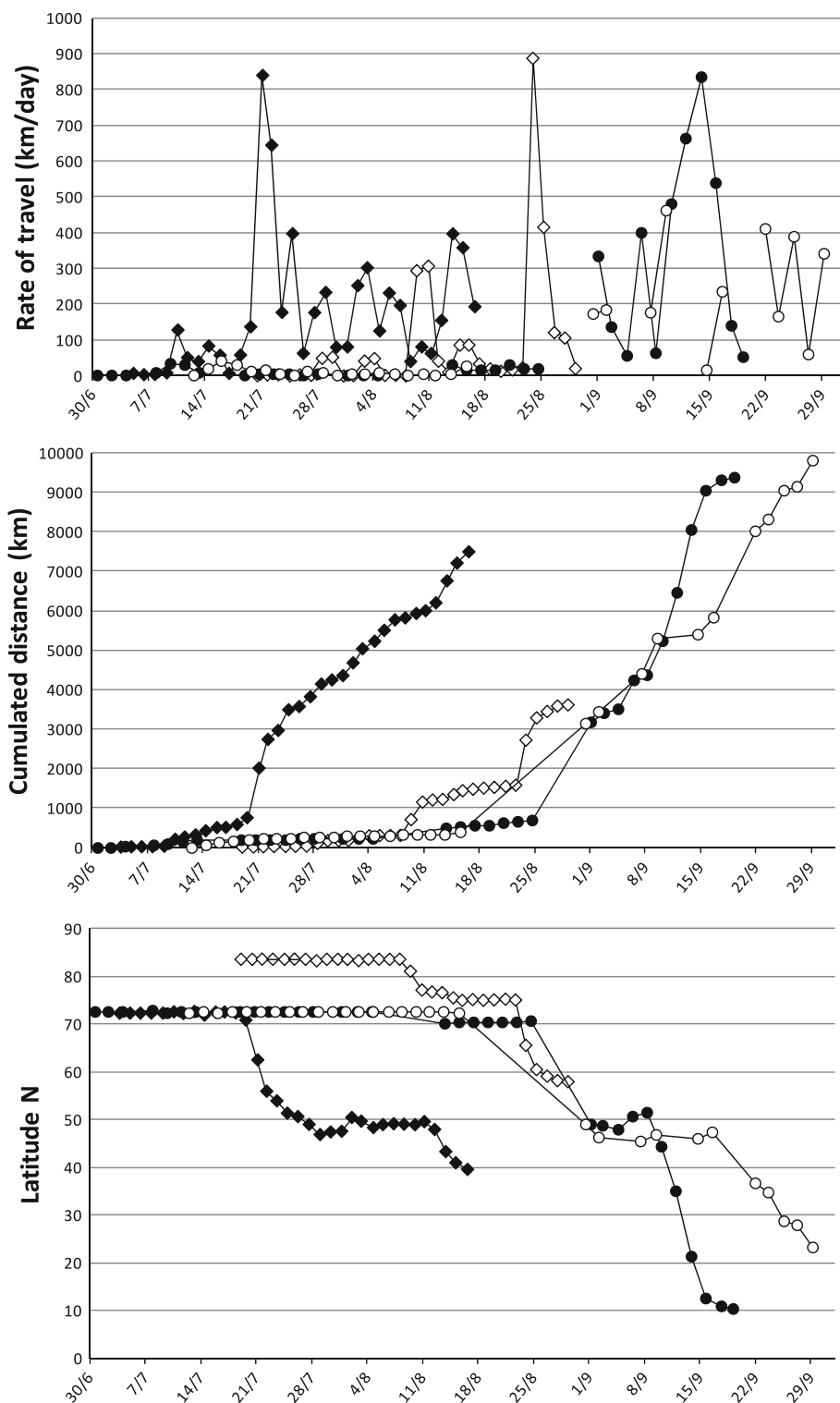


Fig. 1 Post-breeding flyway of four Long-tailed Skuas from North and East Greenland to West Africa: *square* Papikk, *circle* Niilar, *diamond* Lucy, *triangle* Blissy. See Table 1 for details. The background map is a transverse Mercator projection between 0–85° Lat. North and 0–60° Long. West (www.seaturtle.org/maptool; Coyne and Godley 2005). Only the best daily locations (i.e., one position per day per bird) are presented on the tracks (see “Methods”)

Two of the remaining birds could be further followed while they crossed the Atlantic Ocean towards Northwest Africa. It took them 1 week to travel the 2,500–3,000 km from the staging area to the African waters, north of the Madeira Archipelago, where they arrived on 12 (Papikk) and 23 September (Niilar), i.e., 21 and 39 days, respectively, after leaving their breeding grounds. From there, the last bird we monitored (Papikk) continued to move south, flying a few hundred kilometers offshore, finally being lost 1 week later and 2,500 km further south, off the coast of Guinea (approx. 10° Lat. N).

After they had left their breeding grounds, the rate of travel of the birds was usually between 100 and 400 km/day, with maximum rates of 800–900 km/day (Fig. 2, upper panel). The summation of the daily legs of this route revealed that the length of the post-breeding flyway—from Greenland to Guinea (through Canadian waters off the Great Banks to the Madeira Archipelago)—is about 10,000 km (Fig. 2, central panel), and about 1,500 km longer for birds like “Blissy” breeding in North Greenland.

Fig. 2 Movements of four Long-tailed Skuas between Greenland and Africa: *filled circle* Papikk, *open circle* Niilar, *filled diamond* Lucy, *open diamond* Blissy. Time scales used for the calculations are 45 ± 7 h (in 2006; *circles*) and 32 ± 7 h (in 2007; *diamonds*; see “Methods”)



The remaining distance to the main known wintering grounds (see “Discussion”) off South Africa is about 5,000 km on a direct route crossing the Gulf of Guinea [according to Lambert (2006), some migrating Long-tailed Skuas follow the coast of Angola, while other cross the Gulf of Guinea offshore].

The average hourly rate of travel calculated during migration based on 63 successive pairs of high-accuracy fixes was 14 km (maximum values: 53, 56, and 61 km/h). In several instances, we also found evidence of active nocturnal migration, as already suspected by Lambert (1988). Two such cases presented in detail in Table 2

Table 2 Evidence for nocturnal migration of Long-tailed Skua

Bird	Date	Latitude (deg. N)	Longitude (deg. W)	Solar time	Solar angle (deg./horizon)	Distance (km)	Speed (km/h)
Papikk	12–13 September 2006	35.29°	15.16°	22:12:37	−43	50	30
		34.87°	15.33°	23:51:30	−51	89	53
		34.10°	15.06°	01:33:29	−46	96	62
		33.30°	14.70°	03:07:38	−32		
Lucy	14–15 August 2007	43.63°	33.28°	19:59:43	−10	62	37
		43.23°	32.74°	21:41:41	−24	12	37
		43.17°	32.62°	22:00:59	−26	62	45
		42.84°	32.00°	23:26:00	−32	16	55
		42.76°	31.84°	23:44:34	−33	57	36
		42.58°	31.19°	01:20:42	−30		

(using four and six LC0 fixes) indicate that distances traveled during such events (i.e., >200 km) are not anecdotal when compared with the mean daily rate of travel (Fig. 2, upper panel).

Discussion

Although our results are inferred from only four individuals, the consistency in the routes followed by these birds, and the fact that they originated in three different locations over two different years, supports the idea that the Long-tailed Skuas breeding in East and North Greenland use a specific post-breeding flyway that includes a staging area off the Canadian Great Banks (between approx. 48–51° Lat. N; Figs. 1 and 2: see plateau on lower panel). This staging area is a pelagic region that is well known for its high productivity (see, for example, <http://www.oceancolor.gsfc.nasa.gov/SeaWiFS>) and has also recently been suggested as a “hot-spot” for other seabird species (Egevang et al. 2010; see also historical data in Wynne-Edwards 1935). Staging in this area probably allows the Long-tailed Skuas to restore fat reserves after the demanding breeding season prior to heading to the southern hemisphere through the low-productive tropical waters off West Africa.

From this staging area, Long-tailed Skuas head eastward, crossing the Atlantic Ocean north of the Azores Islands and reaching Northwest Africa between mid August and late September. Only few autumn observations have been made from the coasts of West Africa, probably because the migrating birds pass far offshore (see Papikk and Niilar on Fig. 1), but seawatching from the Cape Verde Peninsula in Senegal has provided an average of 18 birds per day in October between 1995 and 2008 (111 days of monitoring and 1,988 birds counted; Dubois et al. 2009), with a maximum of 123 birds on 27 October 2007 (Nilsson 2008). The numbers are probably even higher in late

August and September [e.g., 69 Long-tailed Skuas counted in a single day (31 August 1990); Baillon and Dubois 1991; see also Fig. 2 lower panel], but no regular monitoring has yet been undertaken during this period (Dubois et al. 2009).

At first glance, our results would suggest that the Greenland birds migrate to the South African wintering zone, where large concentrations of this species have been reported in the past, rather than to South America, as previously thought by some authors (Harrison 1989; Olsen and Larsson 1997; but see below). Lambert (1980), for example, found great numbers of Long-tailed Skuas off the coast of Namibia (>200 birds on some days), and Ryan (1989), working off the South African coast, gave an estimate of 75,000 Long-tailed Skuas wintering between 34 and 44° Lat. S. [see also observations from Lambert (2006) who counted up to 26 birds per day in October/November off the coast of Angola]. Whether these numbers are overestimations or not, they do suggest that this region, a highly productive marine area due to the Benguela upwelling system (Hutchings 1992), is a key wintering area for the species. It probably hosts birds from many different origins, and possibly most if not all of the western Palearctic populations.

However, we can not yet rule out the possibility that at least some of the Greenland birds continue their migration towards the other main wintering area reported in the Southern Atlantic Ocean: the Falkland current off Argentina. Up to 1,500 birds were seen daily in this region in early November 1920 (Cramp 1985; Olsen and Larsson 1997), although subsequent observers always provided much smaller numbers (Brown et al. 1975; Murphy 1936; Veit 1985; Wetmore 1926) or even failed to record the species at all (see, for example, Orgeira 2001; Tuck 1985). Among the known wintering areas for this species, the remaining ones only host small numbers of wintering birds and are less likely to be used by the Greenland Long-tailed Skuas. These include the east coast of Africa (Lambert 2005) and the south-western coast of South America (Harrison 1989;

Howell and Webb 1995; Johnson 1965; Tuck and Heinzel 1985), the latter being another region with productive upwelling zones, which are thought to host birds originating from central Siberia [with Lambert (2005) suggesting that these birds use overland migration routes] and from eastern Siberia–Alaska, respectively. A few additional wintering areas may exist, such as off Australia and New Zealand, as suggested by irregular but repeated observations (Harrison 1989; Lewis 1991; Marchant and Higgins 1996; Melville 1985; Olsen and Larsson 1997; Wood 1989), and the species may even winter in the sub-Antarctic region where it has been seen from boats (Kampp 2001).

Both in terms of migration routes and wintering grounds, the Long-tailed Skua is often associated with the Sabine's Gull (*Larus sabini*; Olsen and Larsson 1997), which has a similar circumpolar breeding range. It is also interesting to note that the post-breeding flyway of the East Greenland Long-tailed Skuas greatly overlaps with the one recently documented for 11 Arctic Terns (*Sterna paradisaea*) originating from the same region (Egevang et al. 2010). While most of these birds ($n = 7$) moved along the African Coast heading to South Africa, four of these Terns crossed the Atlantic using an alternate flyway towards the coast of Brazil. Such a bi-directional migration pattern might also exist for the Long-tailed Skuas originating from the North Atlantic sector and would explain the records made off South America (see above). Indeed, and as suggested above, after reaching the tropical waters off West Africa, some birds could make use of favorable easterly winds to continue westward (see Felicísimo et al. 2008), hence following a “S-shape” flyway from breeding to wintering grounds.

Based on this study and given our limited knowledge of the migration patterns and wintering areas of the Long-tailed Skua, it is obvious that if we want to document the different flyways and assess the exact borders and respective importance of the different wintering grounds, we should continue our efforts and initiate sister projects over the entire breeding range of the species. To date, Southwest Africa and southeastern South America appear to be the two main wintering grounds for this species, but the relative importance of these areas is still unclear.

Unfortunately, and for reasons that are still unknown, the PTTs we used in our study functioned for only a few weeks. Overcoming these difficulties, for example, using geolocators (Egevang et al. 2010), would open new perspectives and may also shed new light on the spring migration which, according to Lambert's (1980) observations (he still noticed adult birds off Namibia in early May, i.e., only 1 month before they arrive on their breeding grounds), could be much faster than the autumn migration (i.e., $\geq 12,000$ km in only 1 month).

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