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Benoît Sittler, Adrian Aebischer, Olivier Gilg. Post-breeding migration of four Long-tailed Skuas (*Stercorarius longicaudus*) from North and East Greenland to West Africa. *Journal für Ornithologie* = *Journal of Ornithology*, 2011, 152 (2), pp.375-381. 10.1007/s10336-010-0597-6 . hal-00637799

HAL Id: hal-00637799

<https://hal.science/hal-00637799>

Submitted on 3 Nov 2011

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

3

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11

12 **Abstract**

13 The Long-tailed Skua is a specialist predator of lemmings during summer and hence an important
14 component of the Tundra ecosystems, but most of its life cycle takes place offshore and remains
15 largely unknown outside of the breeding season. Using 9.5g solar-powered satellite transmitters, we
16 could document for the first time the post-breeding movements of the Long-tailed Skua, from its high-
17 Arctic breeding- grounds in North and Eastern Greenland, to the tropical waters of West Africa. The
18 birds travelled the ca. 10.000 km of this migration in only 3-5 weeks, covering 800-900 km/day during
19 active migration, which also occurred during night time. Leaving their breeding areas in August
20 (except for one failed breeder), the Long-tailed Skuas first moved south along the coast of East
21 Greenland towards a staging area off the Canadian Great Banks where they stayed for 1-3 weeks.
22 From there, they crossed the Atlantic Ocean eastwards in just one week and entered the African waters
23 near the Madeira Archipelago in September. Although we only monitored four birds for 1.5 to 3
24 months, migration routes were relatively similar between birds breeding in different locations and in
25 different years.

26

27 **Keywords**

28 Satellite tracking, post-breeding migration, staging area, upwelling, rates of travel, Long-tailed Skua,
29 *Stercorarius longicaudus*, Greenland.

30

31

32 **Zusammenfassung**

33

34 **Der Zug von vier Falkenraubmöwen (*Stercorarius longicaudus*) von den Brutgebieten**
35 **in Nord- und Ostgrönland bis nach Westafrika.**

36

37 Falkenraubmöwen ernähren sich während der Brutzeit hauptsächlich von Lemmingen und
38 stellen somit ein wichtiges Glied in Tundren-Ökosystemen dar. Da sie aber den Großteil ihres
39 Lebens auf hoher See verbringen, ist über ihre Lebensweise außerhalb der Brutsaison nur
40 wenig bekannt. Mit Hilfe von 9.5 g schweren, solarbetriebenen Satellitensendern konnten
41 nun erstmals die Zugbewegungen von den hocharktischen Brutplätzen in Nord- und
42 Ostgrönland bis in die tropischen Gewässer vor der westafrikanischen Küste dokumentiert
43 werden. Innerhalb von 3 bis 5 Wochen legten die Vögel etwa 10000 km zurück. Die
44 Tagesetappen betragen 800 bis 900 km, wobei die Vögel auch nachts zogen. Nach dem
45 Verlassen der Brutgebiete im August flogen die Vögel zunächst entlang der
46 ostgrönländischen Küste bis zum Festlandsockel vor Neufundland, wo sie 1 bis 3 Wochen
47 blieben. Sie überquerten anschließend in nur einer Woche den Atlantik in südöstlicher
48 Richtung und gelangten über Madeira und die Kanaren bis in die Nähe der Kapverdischen
49 Inseln. Bisher konnten wir nur 4 Vögel über einen Zeitraum von 1.5 bis 3 Monate verfolgen,
50 jedoch wiesen die Zugrouten aus unterschiedlichen Brutgebieten in beiden
51 Untersuchungsjahren ähnliche Muster auf.

52

53 **Introduction**

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

62 Conditions experienced by seabirds during migration and on their wintering grounds are
63 assumed to impact their subsequent reproductive performance (Furness et al. 2006). De Korte (1985)
64 has shown that Long-tailed Skuas breeding in Northeast Greenland arrive with maximal fat reserves in
65 spring. The pelagic habitats they use during the non-breeding period (9-10 months of the year) must
66 hence provide them with sufficient food resources to initiate breeding but are also, in turn, indirectly
67 impacting the lemming population dynamics. Little is known, however, about the flyways and
68 wintering grounds used by the species, the most pelagic of all Skuas (Furness 1987; Olsen and Larsson
69 1997). With the exception of some local concentrations reported from the Benguela upwelling
70 (Lambert 1980; Ryan 1989), a cold nutrient rich current off the coasts of Namibia and South-Africa,
71 there are nearly no ring recoveries for the species during the non-breeding period and flyways have
72 been inferred from only a limited number of offshore observations.

73 Recent developments in satellite telemetry, with transmitters weighing less than 10g, have
74 opened new perspectives for the study of medium sized bird (between 300 and 500g). Because it
75 breeds in remote Arctic areas and spends the rest of the year in similarly remote offshore waters, the
76 Long-tailed Skua is a perfect candidate species for these new research techniques. The present study
77 presents the timing, duration, and flyways of four Greenlandic Long-tailed Skuas during their post-
78 breeding migration, as part of a comprehensive long-term research of terrestrial vertebrates in
79 Northeast Greenland (Gilg et al. 2003; Sittler 1995).

80

81 **Material and methods**

82 Four Long-tailed Skuas were captured and fitted with satellite transmitters (PTTs) in 2006 and 2007 in
83 the “North and East Greenland National Park” (Table 1). All birds were breeding. In 2007 we captured
84 the birds on the nest using a bow net, while in 2006 they were captured within a few meters of the

85 nest, using a small mist net (ca. one square meter) fixed on two handhold poles and rapidly raised in
86 front of attacking birds.

87 All birds were equipped with 9.5g solar-powered PTTs from Microwave Telemetry Inc
88 (Columbia, USA). Transmitters were attached to the birds as a backpack using Teflon ribbon and four
89 silver rings to build the harness. The PTT and harness (ca. 2g) weighted less than 12g, which was on
90 average 3.9% (± 0.15 SD) of the body mass of the birds. The PTTs fitted on the two birds in 2006 were
91 set to a constant duty cycle of 7/38h (on/off, respectively), the two PTTs attached in 2007 had a
92 constant duty cycle of 7/25h on/off.

93 PTTs were located using the Argos positioning system (CLS 2008) that provides positions in
94 seven precision classes. The location errors of the classes called LC3, LC2, LC1 and LC0 follow a
95 normal distribution with a standard deviation of <150, <300, <1000 and >1000 m respectively. There
96 is no accuracy estimate associated with the remaining classes (i.e. LCA, LCB and LCZ) but LCA have
97 been shown to have the same accuracy as LC1 (Hays et al. 2001; Vincent et al. 2002). We used
98 orthodromic distances to estimate the “daily rates of travel” of the birds (Imboden and Imboden 1972;
99 James et al. 2005) for time scales of 45 ± 7 hours (in 2006) and 32 ± 7 hours (in 2007). For these
100 calculations, we used successive “best daily location” (i.e. in order of preference: LC3, LC2, LC1,
101 LCA, LC0) produced during the 7 hour transmitting period. We never used LCB and LCZ in the
102 calculations. We also estimated “hourly rates of travel” using successive high accuracy fixes (LC3,
103 LC2 and LC1) for time periods between 0.5-2 hours (for more details see Gilg et al. 2010).

104

105 **Results**

106 Altogether, the four PTTs produced 1019 Argos positions and the birds could be monitored for 45 to
107 86 days (mean 66 days; Table 1). Only one third (i.e. 376) of these locations were LC3, LC2, LC1 or
108 LCA, but more than 70% of the “best daily positions” (i.e. 93 out of 131) were high accuracy fixes
109 (LC3, LC2 and LC1).

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

116 Hence, the start of the fall migration (i.e. the date of departure from the breeding grounds)
117 occurred between July 19th and August 15th, in line with previous studies (Korte 1984; Wiley and Lee
118 1998; Benoît Sittler and Olivier Gilg, unpublished data).

119 After departure, all birds moved southward following the outer coast (note that “Blissy” did
120 not take the shortest route over the Greenland icecap), passing between southeast Greenland and
121 Iceland, towards a large (ca. 500.000 km²) staging area located off the Great Banks of Newfoundland
122 in Canada (Figure 1). The first bird (Lucy) arrived there by the end of July, the others by the end of
123 August. With the exception of Blissy, which was lost 20 days after it had started its migration (i.e.
124 shortly before reaching this area), it took the birds 1-2 weeks to travel the 3.000 km from their
125 breeding grounds in Northeast Greenland to this staging area (Figure 1). The three birds then stayed in
126 this area for 8-20 days.

127 Two of the remaining birds could be further followed while they crossed the Atlantic Ocean
128 towards North-West Africa. It took them one week to travel the 2500-3000 km from the staging area to
129 the African waters, north of the Madeira Archipelago, where they arrived on September 12th (Papikk)
130 and 23rd (Niilar), i.e. 21 and 39 days respectively after they had left their breeding grounds. From
131 there, the last bird we monitored (Papikk) continued to move south, flying a few 100’s of km offshore,
132 and was finally lost one week later and 2500 km further south, off the coast of Guinea (ca. 10° Lat. N).

133 After they had left their breeding grounds, the rate of travel of the birds was usually between
134 100-400 km/day, with maximum rates of 800-900 km/day (Figure 2: upper panel). When adding
135 together the daily legs of this route, the length of the post-breeding flyway, from Greenland to Guinea
136 (through the Canadian waters -off the Great Banks- and the Madeira Archipelago) is about 10.000 km
137 (Figure 2: central panel), and is 1500 km longer for birds like “Blissy” breeding in North Greenland.
138 The remaining distance to the main known wintering grounds (see Discussion) off South Africa is
139 about 5000 km on a direct route crossing the Gulf of Guinea (according to Lambert (2006), some
140 migrating Long-tailed Skuas follow the coast of Angola while other cross the Gulf of Guinea
141 offshore).

142 The hourly rate of travel calculated during migration with 63 successive pairs of high accuracy
143 fixes was 14 km/h on average (maximum values: 53, 56 and 61 km/h). In several instances, we also
144 found evidence of active nocturnal migration, as already suspected by Lambert (1988). Two such cases
145 presented in detail in Table 2 (using four and six LC0 fixes) indicate that distances travelled during
146 such events (i.e. >200 km), are not anecdotal when compared with the mean daily rate of travel
147 (Figure 2: upper panel).

148

149 **Discussion**

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

160 From this staging area, Long-tailed Skuas head eastward, crossing the Atlantic Ocean north of
161 the Azores Islands and reaching Northwest Africa between mid August and late September. Only few
162 autumn observations have been made from the coasts of West Africa, probably because the migrating
163 birds pass far offshore (see Papikk and Niilar on Figure 1), but seawatching from the Cape Verde
164 Peninsula in Senegal has provided an average of 18 birds per day in October between 1995 and 2008
165 (111 days of monitoring and 1988 birds counted; Dubois et al. 2009), with a maximum of 123 birds on
166 27 October 2007 (Nilsson 2008). Numbers are probably even higher in late August and September
167 (e.g. 69 Long-tailed Skuas counted in a single day the 31st of August 1990; Baillon and Dubois 1991;
168 see also Fig. 2 lower panel) but no regular monitoring has yet been undertaken during this period
169 (Dubois et al. 2009).

170 At first glance, our results would suggest that the Greenland birds migrate to the South-
171 African wintering zone, where large concentrations of this species have been reported in the past,
172 rather than to South-America, as previously thought by some authors (Harrison 1989; Olsen and
173 Larsson 1997; but see below). Lambert (1980) for example found great numbers of Long-tailed Skuas
174 off the coast of Namibia (> 200 birds some days) and Ryan (1989), working off the South African
175 coast, gave an estimate of 75.000 Long-tailed Skuas wintering between 34 and 44° Lat. S. (see also
176 observations from Lambert (2006) who counted up to 26 birds per day in October/November off the
177 coast of Angola). Whether overestimated or not, these figures are at least suggesting that this region, a
178 highly productive marine area due to the Benguela upwelling system (Hutchings 1992), is a key
179 wintering area for the species. It probably hosts birds from many different origins, and possibly most if
180 not all of the western Palaeartic populations.

181 However, we can't yet rule out the possibility that some at least of the Greenland birds
182 continue their migration towards the other main wintering area reported in the Southern Atlantic
183 Ocean: the Falkland current off Argentina. Up to 1500 birds were seen daily in this region in early
184 November 1920 (Cramp 1985; Olsen and Larsson 1997), though later visits always provided much
185 smaller numbers (Brown et al, 1975; Murphy 1936; Veit 1985; Wetmore 1926) or even failed to record
186 the species at all (see e.g. Orgeira 2001; Tuck 1985). Among all known wintering areas for this
187 species, the remaining ones only host small numbers of wintering birds and are less likely to be used
188 by Greenland Long-tailed Skuas. For example the east coast of Africa (Lambert 2005) and the south-
189 western coast of South America (Harrison 1989; Howell and Webb 1995; Johnson 1965; Tuck and
190 Heinzel 1985), another region with productive upwelling zones, are thought to host birds originating
191 from central Siberia (Lambert (2005) suggested that these birds use overland migration) and from
192 eastern Siberia-Alaska, respectively. A few additional wintering areas may exist, e.g. off Australia and
193 New Zealand, as suggested by irregular but repeated observations (Harrison 1989; Lewis 1991;
194 Marchant and Higgins 1996; Melville 1985; Olsen and Larsson 1997; Wood 1989), and the species
195 may even winter in the sub-Antarctic region where it has been seen from boats (Kampp 2001).

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

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

213 Unfortunately, and for reason that are still unknown, the PTTs we used were only working for
214 a few weeks. Overcoming these difficulties, for example using geolocators (Egevang et al. 2010),
215 would open new perspectives and may also shed new light on the spring migration which, according to
216 Lambert's (1980) observations (he still noticed adult birds off Namibia in early May, i.e. one month
217 only before they arrive on their breeding grounds), could be much faster than the autumn migration
218 (i.e. ≥ 12.000 km in only one month).

219

220 **Acknowledgments**

221 We are grateful to the Groupe de Recherche en Ecologie Arctique and the Musée d'histoire
222 naturelle de Fribourg for financial support, to Pascal Grand, Brigitte Sabard and Luc Hardy for their
223 help in the field, to the Government of Greenland (Ministry of Domestic Affairs, Nature and
224 Environment) for granting access and research permits in the "North and East Greenland National
225 Park", and to Ross Bartley for his comments on an earlier draft of the manuscript.

226

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329

330

331 **Table 1:** Summary data for the four studied Long-tailed Skuas and timing of their post-breeding
 332 migration
 333
 334

<i>Birds' names (mass)</i>	<i>Trapping location (deg. Lat.N / Long. W)</i>	<i>Release date</i>	<i>Duration of tracking</i>	<i>Start date of fall migration in Greenland¹</i>	<i>Duration of staging off Canada</i>	<i>Arrival off NW Africa</i>
Papikk (300g)	Karupelv Valley (72.50°/24°)	30-6-2006	81 days	5-12 August	8 days	12-9-06
Niilar (280g)	Karupelv Valley (72.50°/24°)	3-7-2006	86 days	14-15 August	16 days	23-9-06
Lucy (278g)	Mestersvig (72.25°/24°)	2-7-2007	45 days	19 July ²	20 days	n.d.
Blissy (295g)	Bliss Bugt (83.57° /30°)	8-7-2007	52 days	8 August	n.d.	n.d.

335 ¹ the earliest and latest possible departure dates from breeding grounds are given when the exact data could not
 336 be documented
 337 ² this bird left its breeding territory on the 9th of July but remained within 50-100km of this area until July 18.
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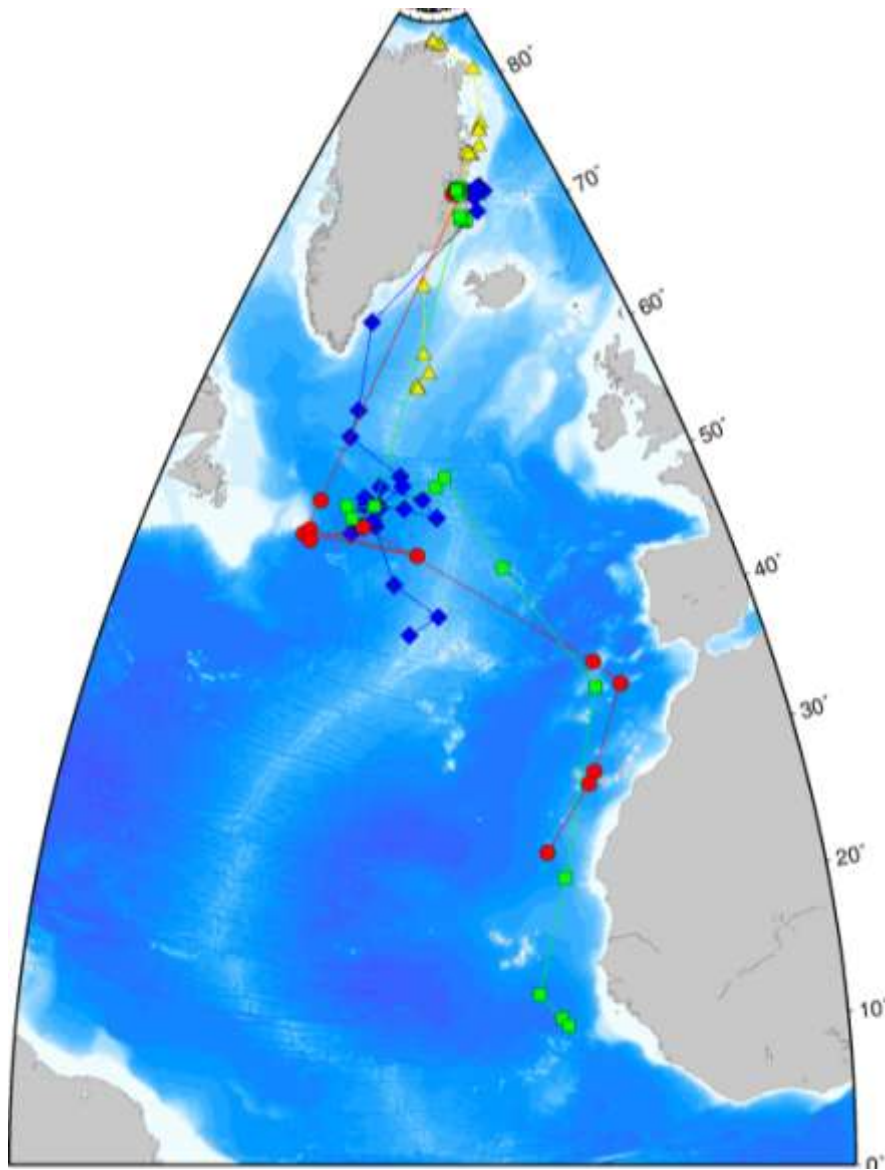
339 **Table 2:** Evidences for nocturnal migration of Long-tailed Skua.

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Bird	Date	Latitude (deg. N)	Longitude (deg. W)	Solar time	Solar angle (deg./horizon)	Distance (km)	Speed (km/h)
Papikk	12-13/09/06	35.29°	15.16°	22:12:37	-43		
		34.87°	15.33°	23:51:30	-51	50	30
		34.10°	15.06°	01:33:29	-46	89	53
		33.30°	14.70°	03:07:38	-32	96	62
Lucy	14-15/08/07	43.63°	33.28°	19:59:43	-10		
		43.23°	32.74°	21:41:41	-24	62	37
		43.17°	32.62°	22:00:59	-26	12	37
		42.84°	32.00°	23:26:00	-32	62	45
		42.76°	31.84°	23:44:34	-33	16	55
		42.58°	31.19°	01:20:42	-30	57	36

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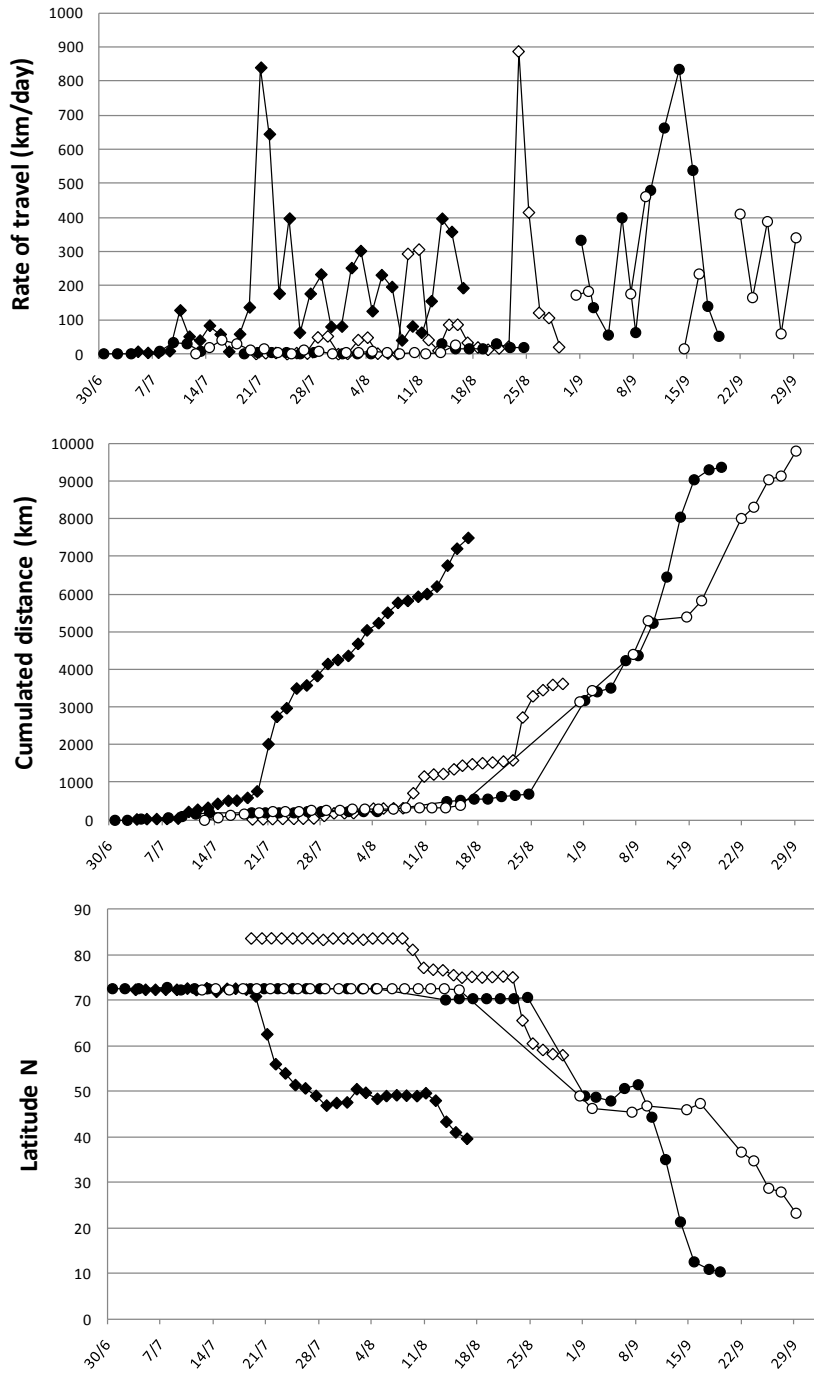
342 **Fig. 1:** Post-breeding flyway of four Long-tailed Skuas from North and East Greenland to West Africa (Papikk:
343 square; Niilar: circle; Lucy: diamond and Blissly: triangle; details in Table 1). The background map is a
344 transverse mercator projection between 0-85° Lat. North and 0-60° Long. West
345 (www.seaturtle.org/maptool; Coyne and Godley 2005). Only the best daily locations (i.e. one position per
346 day per bird) presented on the tracks (see Methods).
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352 **Fig. 2:** Movements of four Long-tailed Skuas (Papikk: black circle; Niilar: open circle; Lucy: black diamond and
 353 Blissly: open diamond) between Greenland and Africa. Time scales used for the calculations are 45 ± 7
 354 hours (in 2006; circles) and 32 ± 7 hours (in 2007; diamonds; see Methods).
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