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Seasonal movements of Gyrfalcons *Falco rusticolus* include extensive periods at sea

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Little information exists on the movements of Gyrfalcons *Falco rusticolus* outside the breeding season, particularly amongst High Arctic populations, with almost all current knowledge based on Low Arctic populations. This study is the first to provide data on summer and winter ranges and migration distances. We highlight a behaviour previously unknown in Gyrfalcons, in which birds winter on sea ice far from land. During 2000–2004, data were collected from 48 Gyrfalcons tagged with satellite transmitters in three parts of Greenland: Thule (northwest), Kangerlussuaq (central-west) and Scoresbysund (central-east). Breeding home-range size for seven adult females varied from 140 to 1197 km^2 and was 489 and 503 km^2 for two adult males. Complete outward migrations from breeding to wintering areas were recorded for three individuals: an adult male which travelled 3137 km over a 38-day period (83 km/day) from northern Ellesmere Island to southern Greenland, an adult female which travelled 4234 km from Thule to southern Greenland (via eastern Canada) over an 83-day period (51 km/day), and an adult female which travelled 391 km from Kangerlussuaq to southern Greenland over a 13-day period (30 km/day). Significant differences were found in winter home-range size between Falcons tagged on the west coast (383–6657 km^2) and east coast (26 810–63 647 km^2). Several Falcons had no obvious winter home-ranges and travelled continually during the non-breeding period, at times spending up to 40 consecutive days at sea, presumably resting on icebergs and feeding on seabirds. During the winter, one juvenile female travelled over 4548 km over an approximately 200-day period, spending over half that time over the ocean between Greenland and Iceland. These are some of the largest winter home-ranges ever documented in raptors and provide the first documentation of the long-term use of pelagic habitats by any falcon. In general, return migrations were faster than outward ones. This study highlights the importance of sea ice and fjord regions in southwest Greenland as winter habitat for Gyrfalcons, and provides the first detailed insights into the complex and highly variable movement patterns of the species.

Keywords: breeding home-range, Greenland, outward migration, return migration, sea ice, winter home-range.

The Gyrfalcon *Falco rusticolus* is the largest falcon and breeds in the circumpolar High Arctic to Subarctic zones, some individuals migrating south as far as northern temperate zones during the late autumn and winter (Cade 1982, Cade *et al.* 1998, Ferguson-Lees & Christie 2001, Potapov & Sale 2005). Individuals breeding in the High Arctic are believed to be wholly migratory (Salomonsen 1950), and those breeding in the Low Arctic and Subarctic zones are largely year-round residents or partial migrants (Cade 1960, Platt 1977, Kuyt

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1980, Nielsen & Cade 1990). Although Gyrfalcons have been studied throughout their range during the breeding season, little information exists on their movements during the non-breeding season (Booms *et al.* 2008), apart from a few ring recoveries and observations of birds on migration (Potapov & Sale 2005).

In Greenland, Gyrfalcons breed from as far north as 82°N (Johnsen 1953) to as far south as approximately 60°N (Rafn 1933, Salomonsen 1950), encompassing both the High and the Low Arctic zones over a latitudinal span of approximately 2650 km. Because only limited amounts of ice-free land exist in Greenland, the majority of breeding sites are coastal, the largest ice-free inland area being in the central-west (Fig. 1). Along the coast seabirds are the most numerous prey items while Rock Ptarmigan *Lagopus muta* and passerines are more common inland.

From 1948 to 1992, there were only 14 recoveries of ringed Gyrfalcons in Greenland (Lyngs 2003), and none outside, although the 'white' Gyrfalcons seen in Iceland in winter are assumed to come from Greenland because white birds do not breed in Iceland (O. Nielsen, pers. comm.). The High Arctic population in Greenland is believed to be migratory while the Low Arctic population is thought to be resident (Salomonsen 1950). Knowledge on seasonal movements and timing of migration of Gyrfalcons in Greenland is based mainly on observations of individuals passing through particular localities (Salomonsen 1950).

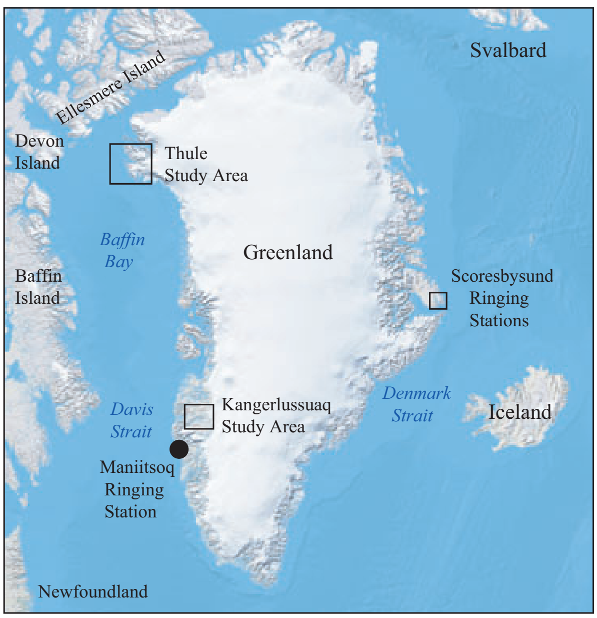

Figure 1. Map of Greenland and neighbouring areas showing the Thule and Kangerlussuaq study areas and Scoresbysund and Maniitsoq ringing stations.

The aims of our study were to assess the extent to which High and Low Arctic populations of Gyrfalcons in Greenland differ in migratory strategy and to document their movements. Furthermore, we assessed whether coastal populations of nesting Gyrfalcons have smaller breeding home-ranges than inland populations, as a result of higher prey abundance on the coast. This is the first study of the year-round movements of adult and juvenile Gyrfalcons from both Low and High Arctic populations on the west and east coasts of Greenland.

STUDY AREAS

We studied populations of breeding Gyrfalcons in the Thule (75.9–77.6°N) and Kangerlussuaq (66.5–67.5°N) areas from 2000 to 2004 (Fig. 1). In Thule, the population was coastal and fed primarily on Little Auks *Alle alle* and Rock Ptarmigan (Burnham 2008), while the Kangerlussuaq population was situated inland and fed mainly upon Rock Ptarmigan and passerines (Burnham & Mattox 1984, Booms & Fuller 2003). On average, Gyrfalcons in the Kangerlussuaq area began egg-laying on 22 April, incubation on 26 April, hatching on 30 May and the young fledged on 16 June (Burnham 2008). In Thule, the process was delayed approximately 17 days, with the equivalent dates being 9 May, 13 May, 17 June and 2 August (Burnham 2008).

In autumn 2004, capture and ringing stations were established in central-east Greenland in the Scoresbysund area (Kap Tobin, 70.4°N; Constable Pynt, 70.8°N), which effectively sampled Gyrfalcons breeding locally and to the north (Fig. 1). The three locations were separated by approximately 1170 km (Thule to Kangerlussuaq), 1175 km (Kangerlussuaq to Scoresbysund) and 1550 km (Scoresbysund to Thule). Scoresbysund was separated from the two west coast study areas by the Greenland ice cap, which comprised approximately 1200 and 850 km of the respective distances between the locations.

Additional capture and ringing stations were operated during the autumns of 2000 and 2002 at Maniitsoq (65.4°N), central-west Greenland, and in the Thule area in the autumn of 2002 and 2003 (Fig. 1). The Maniitsoq site was slightly south of the Kangerlussuaq area and nearer the coast. The

Gyrfalcons captured at the Thule ringing station were probably from the local population while those captured at the Maniitsoq site were probably from further north in Greenland, possibly including the northeastern Canadian Arctic.

METHODS

During 2000–2004, 56 platform transmitter terminals (PTTs; Microwave Telemetry Inc., Columbia, MD, USA, and North Star Science and Technology, LLC, Baltimore, MD, USA) were fitted to Gyrfalcons in the Kangerlussuaq, Thule, Scoresbysund and Maniitsoq study areas, units weighing either 18 or 30 g. Falcons were captured using a bow net, dho-gaza net or a lure pole/bow net combination (for further description see Meredith 1961, Bub 1978). All PTTs were battery powered and attached as backpacks using Teflon ribbon (Fuller *et al.* 1995). Duty cycles were programmed to transmit from as frequently as 4 h on/27 h off to 7 h on/106 h off, depending on battery life. GPS locations were taken at all nest-sites or capture locations where birds were tagged. Each PTT recorded information on location, battery voltage, temperature and activity. Location data were used for tracking falcons, while temperature, battery voltage and activity sensor data were used to determine whether the PTT was functioning correctly.

Of the 56 PTTs, 29 were placed on adult Gyrfalcons (one adult was recaptured and fitted with a new unit, so $n = 28$ adults tagged), 22 on juveniles and four on nestlings (Table 1). In Kangerlussuaq, all units were placed on individuals at the nest in June and July. In Thule, all juveniles were tagged at a ringing station, while some adults were tagged at the nest and others at a ringing station between July and September. At Scoresbysund and Maniitsoq, all individuals were captured at ringing stations between September and November while presumably on outward migration. All PTTs weighed <3% of the body weight of the Gyrfalcons tagged. Individuals were identified by their five-digit Argos PTT ID numbers.

Falcon movements were followed using the Argos satellite system (http://www.argos-system.org), which provides locations with an associated estimate of accuracy (location class, LC) based on the quality of the signal. Location class is divided into seven categories (in descending order of accuracy, LC = 3, 2, 1, 0, A, B and Z), Argos suggesting estimated accuracies of < 150, 150–350, 350–1000 and > 1000 m for LC 3, 2, 1 and 0, respectively. However, accuracy levels appear to be less than reported (Britten *et al.* 1999, Hays *et al.* 2001). In their study, Burnham (2008) collected data from a stationary PTT in Thule for 13 consecutive months and found average accuracy levels of: LC 1 = 0.9 km, LC 2 = 1.3 km, LC 3 = 2.3 km and LC 0 = 11.0 km. Data from PTTs were analysed using ArcView GIS 3.3 and Spatial Analyst (Environmental Systems Research Institute, Redlands, CA, USA) and the Animal Movement Extension designed for it (Hooge & Eichenlaub 2000). Sea ice maps were provided by the National Ice Center, National Oceanic and Atmospheric Administration, and figures were produced in ArcGIS 9.2. Maximum sea ice extent is shown in all sea ice figures. Areas along the ice edge commonly ranged from 10 to 50% ice cover, with the percentage usually increasing nearer land. Individual locations from PTTs were visually inspected to verify likely accuracy based on other locations from the same day (Fuller *et al.* 1998).

When adults were tagged at the nest-site, breeding home-ranges included all points obtained from PTT attachment, usually during rearing of young, until departure for a pre-migration home-range or

Table 1. Number of PTTs deployed and the location, sex and age of individual Gyrfalcons tagged in Greenland during 2000–2004.

	Males			Females		
	Adults	Juveniles	Nestlings	Adults	Juveniles	Nestlings
Kangerlussuaq	1	0	1	5*	0	1
Maniitsoq	4	0	0	8	0	0
Thule	1	8	1	5†	10	1
Scoresbysund	3	2	0	3	2	0

*Includes one adult female first tagged at Maniitsoq, which later bred in the Kangerlussuaq area and was captured and had its PTT replaced.
†Includes two sub-adults, or second-year birds, that were grouped with adults.

for outward migration (Ganusevich *et al.* 2004). For adults tagged with PTTs during outward migration or while already on winter home-range, breeding home-ranges included all points obtained the following breeding season between the completion of return migration to the nest-site and departure for outward migration. Although in some instances it was not possible to verify that individuals bred, based on movements and dates it was possible to make inferences. Breeding home-ranges were estimated for Gyrfalcons with > 20 locations with LC 3–1 and described using 90% minimum convex polygons (MCPs) and fixed 50 and 95% kernels. We calculated a 36.6-km^2 90% MCP 'home-range' size for the stationary PTT in Thule (LC 3–1 = 1006 locations), suggesting that PTT accuracy using LC 3–1 is sufficient to provide estimates of home-range size. If breeding home-range estimates included areas that encompassed glaciers or the Greenland Ice Cap, these areas were included because prey species have been shown to cross the Greenland Ice Cap both during migration and in the breeding season (Alerstam *et al.* 1986).

The start of migration was defined as the date at which Gyrfalcons began continuous movement from the breeding home-range in the general direction of likely wintering areas or vice versa (Berthold 2001). Migration distances were measured as Great Circle Distances (GCDs; WGS 84 datum) and the total length of routes taken by Gyrfalcons was calculated by summing the lengths of the individual flight segments along the migration route, beginning at the location of the nest, capture site or pre-migration area, depending upon the individual. Although not suitable for breeding home-range estimation, LC 0 was included for description of migratory movements and time spent on winter home-range based on the long distances travelled and time intervals (Britten *et al.* 1999, Green *et al.* 2002). The starting points for flight segments were chosen by taking the location with the highest quality location class, LC 3–0, from each duty cycle/transmission period (Fuller *et al.* 1998). If multiple locations with the same LC were available, the first to occur in the transmission cycle was used (Fuller *et al.* 1998). The overall speed of outward and return migration was determined by dividing the total of the segment lengths by the number of days spent on migration. Data from Falcons which appeared still to be on outward migration when their PTTs stopped functioning have been included as 'incomplete migrations' if they either completed more than 10 days of outward migration or travelled more than 250 km.

Departure dates from breeding areas could be determined accurately only for those Gyrfalcons tagged at the nest (n = 13) or which departed the nest after being earlier tagged at a ringing station. Falcons captured and tagged at ringing stations in Maniitsoq and Scoresbysund were possibly from further north and already on migration. Several Gyrfalcons that were tagged at ringing stations appeared to be already on their winter home-range, and partial outward migrations were not recorded. Additionally, two individuals tagged at ringing stations continued to have long-distance movements throughout the entire winter period, and were not included with outward migration data.

RESULTS

The periods for which PTTs on individual Gyrfalcons operated varied from 5 to 392 days, with a median of 37 days (mean = 95, sd = ± 108.8, n = 49 PTTs) (Table 2). Seven PTTs stopped functioning shortly after attachment and no data from these units were included in the analysis. A total of 15 013 locations were received from the 49 units, with a mean of 306 per unit (median = 150, sd = ± 374, range = 9–1726). Locations with LC 3–0 comprised an average of 64.1% of the data (median = 64.7, sd = ± 13.9). The two most accurate locations, LC 3 and 2, comprised an average of 6.1% of all data collected (n = 49, median = 4.0, sd = ± 5.2) while LC 1 comprised 16.7% (n = 49, median = 16.7, sd = ± 8.0).

The number of days of operation for PTTs varied significantly between adults and juveniles (t = 4.4225, P < 0.0001, df = 45), with an average of 147 days of data received for adults and 31 for juveniles (Table 2). No differences were found

Table 2. Number of days 49 PTTs operated correctly and transmitted data on Gyrfalcons tagged in Greenland during 2000–2004.

	n	Median	Mean	sd	Range
All Gyrfalcons	49	37	95	± 109	5–392
Adults	27	101	147	± 121	5–392
Juveniles	21	24	31	± 39	5–193
Nestlings*	1	51	na	na	na

*Data from a single individual, and therefore no mean, standard deviation or range.

between males and females either for adults or for juveniles ($t = 0.6838$, $P = 0.5007$, df = 24, and $t = 1.1535$, $P = 0.2630$, respectively).

Breeding home-range

Breeding home-range size was estimated for seven females and two males (Table 3). Of those, five were tagged at the nest while rearing young and four were captured at ringing stations, with breeding home-ranges calculated in the subsequent spring/summer. One Gyrfalcon (ID 11988) that was initially captured at the Maniitsoq ringing station was tracked to a nest-site in the Kangerlussuaq area, where during nesting it was captured and had its PTT replaced. Data from these units were combined to calculate breeding home-range size.

Based on 90% MCPs, adult female Gyrfalcons had an estimated average breeding home-range size of 571 km^2 ($n = 6$, median = 430, sd = ± 442), varying from 140 to 1197 km^2. The two females with the largest home-range size (IDs 10095 and 11988) spent long periods away from the nest, probably hunting, and travelled up to 35 km each way. Two further females (ID 35243 and 35253) also frequently travelled approximately 25 and 31 km away from the nest, respectively; however, each trip was to the same location (a large seabird colony), and because of this their home-range size was smaller than those of the other two individuals. Fixed 95% and fixed 50% kernels gave an average calculated breeding home-range size of 457 km^2 ($n = 6$, median = 504, sd = ± 228) and 53 km^2 ($n = 6$, median = 61, sd = ± 25), respectively. Breeding home-ranges were obtained for two adult male Gyrfalcons, with an average of 503 km^2 (sd = ± 19) when using 90% MCP and 280 km^2 (sd = ± 88) and 28 km^2 (sd = ± 11), respectively, when using 95 and 50% fixed kernels. Although no overlap of ranges occurred in the Kangerlussuaq area, in Thule in 2002, two had overlapping home-ranges as they both appeared to hunt frequently at the same seabird colony.

Data were received for one adult male and one female for the entire breeding cycle and home-range size varied by month for each bird. The adult male, which probably bred in northwest Ellesmere Island at 80.7°N, had a relatively small home-range in May, but the size approximately doubled in June when, based on information on breeding chronology for the Thule area, the chicks are likely to have hatched. After June, range size generally decreased through to September (Fig. 2). A female that bred in Thule showed the reverse pattern, and home-range size increased each month from May to September (Fig. 2).

Outward migration

Timing

Departure dates for Gyrfalcons could be determined accurately only for those individuals leaving a nest-site. Gyrfalcons tagged at the Thule ringing station were included because these birds were probably from the local area. The ringing station was close to large seabird colonies, providing a rich food source. It appeared to be an important pre-migration area for juvenile Gyrfalcons, with up to 10 observed there at one time.

Departure dates for outward migration were obtained for two Gyrfalcons from the Kangerlussuaq area. An adult male departed the nest vicinity

Table 3. Mean breeding home-range sizes for seven adult female and two adult male Gyrfalcons calculated using 90% minimum convex polygons (MCPs), 95% fixed kernels and 50% fixed kernels. For definitions, see text.

Breeding location	Sex	PTT ID	90% MCP (km^2)	95% Kernel (km^2)	50% Kernel (km^2)	Days of data	Total LC 3–1
Kangerlussuaq, Greenland	M	10112	516	342	35	50	129
	F	11988	1035	546	73	142	81
	F	35245	192	462	57	47	23
Thule, Greenland	F	10095	1197	738	72	52	151
	F	35243	140	88	8	132	76
	F	35249*	407	829	183	63	66
	F	35252	434	590	64	43	50
	F	35253	426	316	44	63	73
Ellesmere Island, Canada	M	35248	489	218	20	156	203

*This individual probably did not breed based on arrival and departure dates and known breeding chronology, and is excluded from analysis.

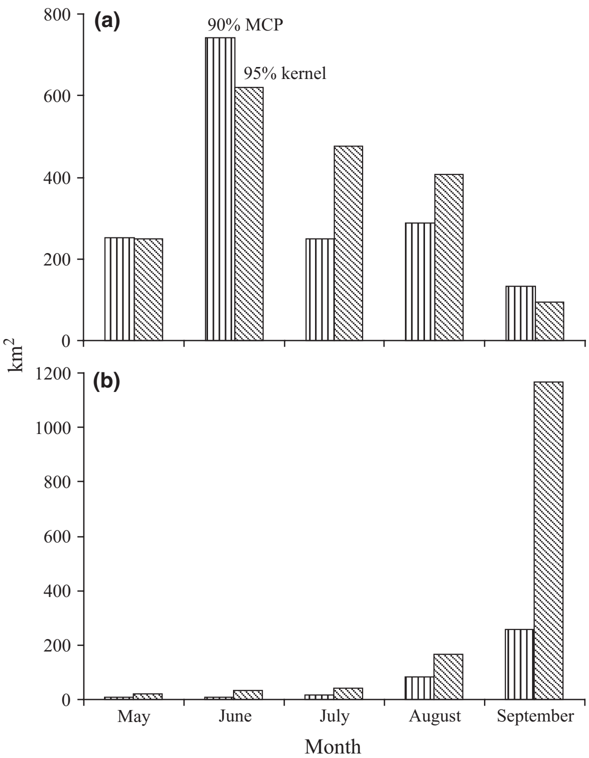

Figure 2. Breeding home-range size by month for an adult male (a) (Ellesmere Island, Canada) and female (b) (Thule, Greenland). Home-range size was calculated as 90% minimum convex polygons (MCPs) and 95% fixed kernels.

on 27 August and then returned on two occasions, 5 September and 11 October, with the time between spent up to 140 km away. The last location received for the adult male was on 15 October, approximately 26 km north of the nest-site at which it bred. An adult female departed the nest area on 12 August to the southwest. Two additional adult females continued to stay in the area around their respective nest-sites until their PTTs failed, with the last signals received on 6 and 29 September.

During 2001–2003, six adult female Gyrfalcons tagged in Thule departed on outward migration on dates from 19 August to 4 October (mean = 19 September, median = 27 September, including one individual in two successive years). Another non-breeding female left on 19 August. Two individuals initially flew west to Ellesmere Island, then returned to Greenland, before leaving again after a few days for Ellesmere Island, a round trip of 400 km. A single adult male Gyrfalcon that was observed feeding young at the ringing station departed Thule on 5 October, and another adult male left Greely Fjord, northwest Ellesmere Island, on 7 October.

Average departure dates for juvenile male and female Gyrfalcons tagged at the ringing station in Thule were 24 September (n = 5, median = 20 September, range = 15 September–16 October) and 23 September (n = 5, median = 20 September, range = 18 September–9 October), respectively.

In total, three individuals were tracked for their complete outward migration from their breeding home-ranges while seven were tracked for complete outward migrations from ringing stations. For an additional 23 individuals, data on the recorded outward migration were apparently incomplete. For individuals initially tagged at the Maniitsoq ringing station which were subsequently tracked to their breeding areas, data from the autumn when they were initially tagged were grouped in with Maniitsoq data, while outward migration data from the following year were grouped by breeding area.

Distance, direction and speed

Data were available for two birds from Kangerlussuaq (one adult male and one adult female), 16 birds from Thule (seven adult females, one adult male, and four female and four male juveniles), seven birds from Scoresbysund (three adult males, three

Table 4. Distances travelled by adult and juvenile Gyrfalcons during 15 incomplete outward migrations and a single complete outward migration (adult female) from Thule, Greenland, 2001–2003. Distance travelled is in kilometres and speed of travel is in km/day. See Methods for definition of incomplete migration.

	Distance travelled (km; mean ± sd, range, median)	Days of travel (mean ± sd, range, median)	Speed of travel (km/day; mean ± sd, range, median)
Adult females, n = 6	1399 ± 1112, 643–3495, 910	46 ± 41, 12–122, 28	37 ± 16, 15–58, 33
Adult male, n = 1	647	9	72
Juvenile females, n = 4	690 ± 572, 177–1490, 546	19 ± 10, 11–32, 17	33 ± 14, 14–47, 35
Juvenile males, n = 4	918 ± 459, 329–1361, 991	18 ± 11, 8–34, 16	57 ± 32, 27–99, 52
Complete outward, n = 1	4234	71	60

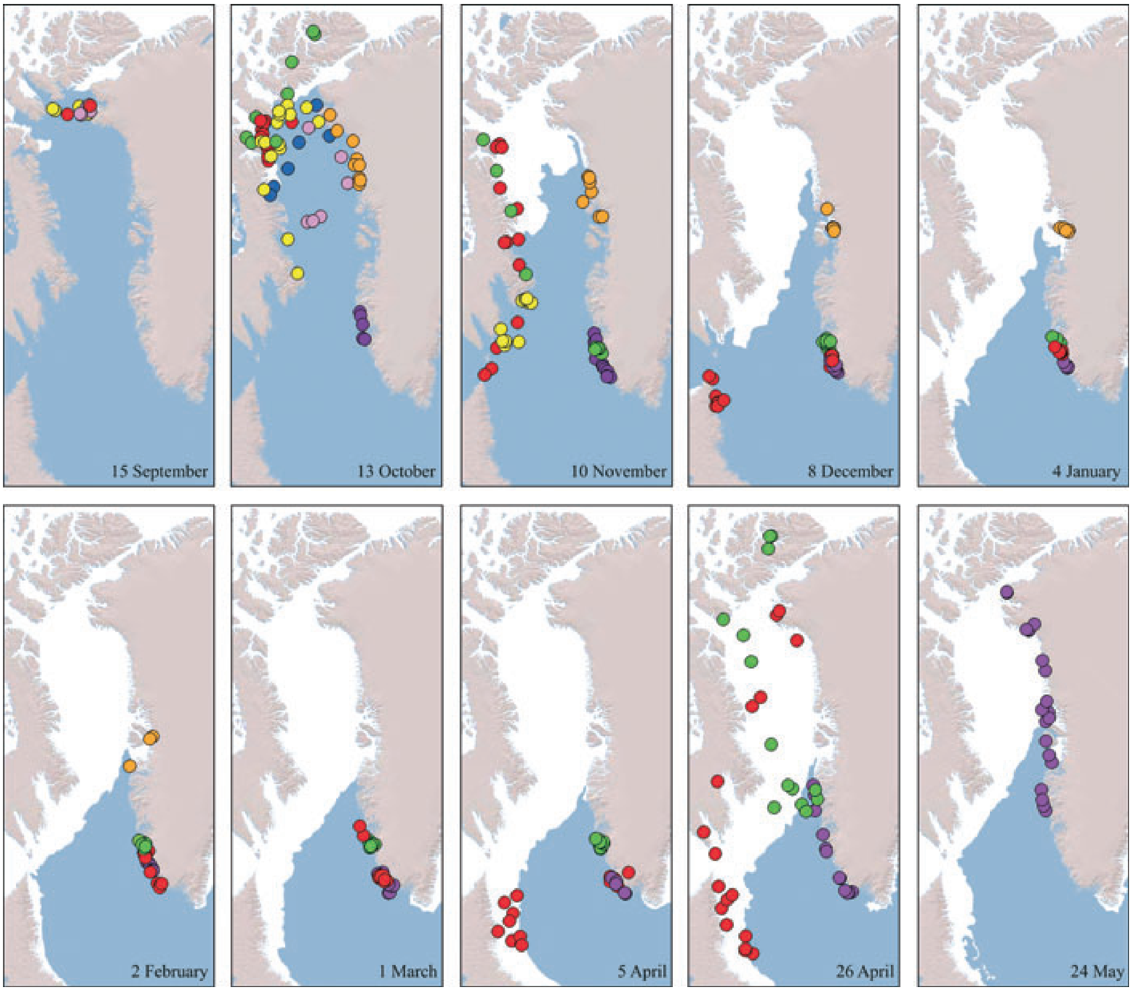

Figure 3. Migration routes and wintering areas (approximately every 28 days) of Gyrfalcons from the Thule area, Greenland, and Ellesmere Island, Canada, tagged from 2001 to 2003. Green (ID 35248) and purple (ID 35249) initially tagged in the Maniitsoq area in autumn. No more than one location (LC 3–0) has been included per Falcon per day. Locations are from 2 weeks before and after individual map dates. Maximum sea ice extent shown for each map and sea ice data are from 2003/2004. Pink (ID 35242), blue (ID 35241), yellow (ID 35252) and orange (41444) are examples of incomplete outward migration paths, red (ID 35243) and green show winter home-ranges and complete outward and return migrations, and purple shows winter home-range and return migration.

adult females and one juvenile male), seven birds from Maniitsoq (five adult females and two adult males) and one adult male from Ellesmere Island.

Table 5. Outward migration paths used by 15 Gyrfalcons from the Thule area, northwest Greenland, 2001–2003.

	East Canada route	Ocean route	West Greenland route
2001	ad ♀	–	–
2002*	3 ad ♀, 2 juv ♂	2 juv ♂	–
2003*	ad ♀, juv ♀	ad ♂, 3 juv ♀	2 ad ♀

*Female 35243 included for both 2002 and 2003; east Canada route used both years.

From Kangerlussuaq, the adult male had incomplete data on outward migration and travelled at least 805 km over a 50-day period, including several trips from the breeding home-range to the coast and back and a large clockwise circle to the north. He later returned to a location 26 km north of the nest-site where he was captured and where the last signal was received from the PTT. The adult female completed outward migration and travelled approximately 391 km over a 13-day period to southwest Greenland, at a mean speed of 30 km/day (see Supporting Information, Fig. S1, for examples of movement patterns of birds tagged in Kangerlussuaq).

From Thule, the data included one female for which two outward migrations were recorded, in 2002 and 2003. All these 16 journeys were incomplete except the 2002 journey of this female. The six incomplete outward migrations made by adult females covered an average of 1399 km at an average speed of 37 km/day, with a mean of 46 days of data received for each bird (Table 4). The adult male travelled 647 km during the 9 days that data were received, at a speed of 72 km/day. Four juvenile females travelled an average of 690 km at 33 km/day (Table 4). Juvenile males flew an average of 918 km at 57 km/day, with data received for an average of 18 days per individual (Table 4). The only complete journey recorded for a adult female covered 4234 km at a speed of 60 km/day over 71 days (Table 4, see Fig. 3 for map). Of the 16 outward migration routes documented for Gyrfalcons from the Thule area during 2001–2003, eight travelled directly from Greenland to Canada (Table 5). Once in Canada birds proceeded south following the east coast of Ellesmere Island, Devon Island and Baffin Island, one individual going as far south as the northeast coast of Labrador (Fig. 3). The Falcon with complete data on outward migration used this route and crossed back into southwest Greenland at the end of outward migration.

Six of the 16 individuals departed Thule to the south, travelling hundreds of kilometres and spending many days over the open ocean, at times several hundred kilometres from land, before turning west toward central-west Baffin Island (Fig. 3). The other

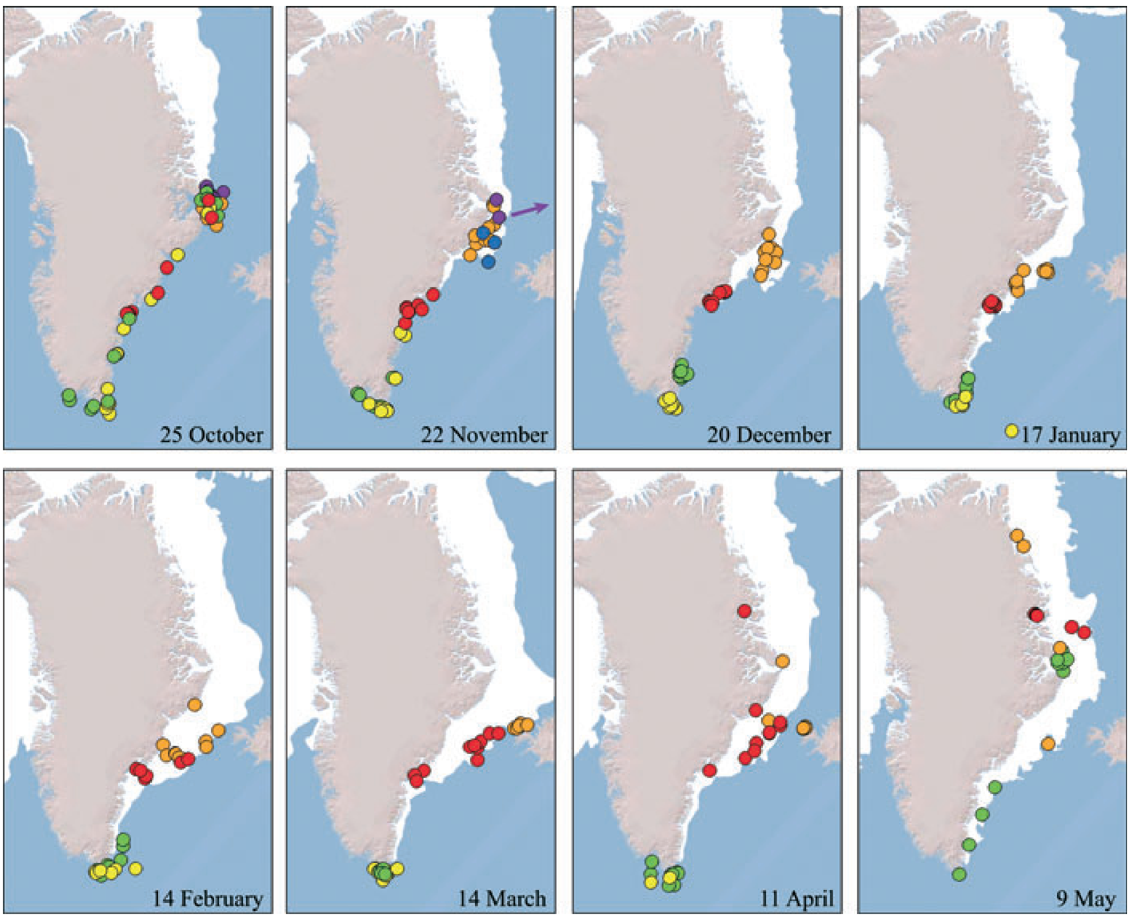

Figure 4. Distribution (every 28 days) of Gyrfalcons tagged in the Scoresbysund area, east Greenland, in autumn 2004. No more than one location (LC 3–0) has been included per Falcon per day. Locations are from 2 weeks before and after individual map dates. Maximum sea ice extent show for each map and sea ice data are from 2004/2005. Purple (ID 49761) and blue (ID 49769) show incomplete outward migrations, while red (ID 49771), orange (ID 49768), yellow (ID 49764) and green (ID 49762) show entire winter period. PTTs 49764 and 49768 stopped before completing return migration while IDs 49771 and 49762 appeared to reach breeding areas.

Table 6. Winter home-range sizes for adult Gyrfalcons calculated using 90% minimum convex polygons (MCPs), 95% fixed kernels and 50% fixed kernels. Unless otherwise noted, days on range is the entire time period Gyrfalcons spent on winter home-range.

Location PTT was attached or breeding area, and year	Sex	PTT ID	90% MCP (km^2)	95% Kernel (km^2)	50% Kernel (km^2)	Days on range	Total LC 3–1
Kangerlussuaq, 2000/2001	F	11988	945	1566	160	139	52
Kangerlussuaq, 2002/2003	F	35245	383	357	59	197	100
Thule, 2002/2003	F	35243	4931	14 398	2067	115	65
Thule, 2002/2003	F	35249	6657	18 443	1984	168	79
Scoresbysund, 2004/2005	M	49762	54 683	78 151	9559	189	30
Scoresbysund, 2004/2005	M	49764	26 810	104 896	26 157	162	16
Scoresbysund, 2004/2005	F	49771	63 647	172 007	24 594	185	46
Maniitsoq, 2000/2001	F	05707	5160	7675	1647	194	68
Maniitsoq, 2002/2003*	F	35259	708	1694	348	86	46
Maniitsoq, 2002/2003	F	36318	1163	1153	53	169	162
Ellesmere Island, 2002/2003	M	35248	816	1292	187	171	64

*PTT stopped functioning part way through the period spent on winter home-range.

two documented outward migrations from Thule were along the west coast of Greenland (Fig. 4). Although we have attempted to define and generalize routes taken by Gyrfalcons during outward migration from Thule, variation was great and some individuals used a combination of routes.

From Scoresbysund ringing station, three of seven birds had completely recorded outward migrations. These birds, two adult males and an adult female, continued down the east coast of Greenland and travelled an average of 1564 km (median = 1664, sd = ± 543, range = 978–2050) during outward migration at an average speed of 50 km/day (median = 47, sd = ± 9, range = 42–60) (Fig. 4). However, based on the continued movements of all three Falcons, there was no specific end to their outward migration and no obvious winter home-range. The four individuals, one adult male, two adult females and one juvenile male, that had incompletely recorded outward migrations travelled an average of 603 km (median = 590, sd = ± 596, range = 53–1342) over an average of 21 days (median = 19, sd = ± 10, range = 12–33), giving an average speed of 29 km/day (median = 36, sd = ± 17, range = 4–41). Two of the individual PTTs stopped working in the Scoresbysund area, while one juvenile female continued on outward migration to the southeast and travelled 824 km before the last location was received approximately halfway between Greenland and Iceland (Fig. 4). The juvenile male, ID 49761, spent almost the entire next month in the Scoresbysund area, but then travelled east, with the last signal from approximately 425 km northeast of Iceland and approximately 475 km north of the Faeroe Islands (Fig. 4).

From the Maniitsoq ringing station, three adult females and an adult male completed outward migration and flew an average of 505 km (median = 551, sd = ± 195, range = 254–664) over an average of 12 days (median = 14, sd = ± 9, range = 6–26), giving an average speed of 43 km/day (median = 45, sd = ± 21, range = 17–66). All four continued to travel down the southwest coast of Greenland, each stopping in a

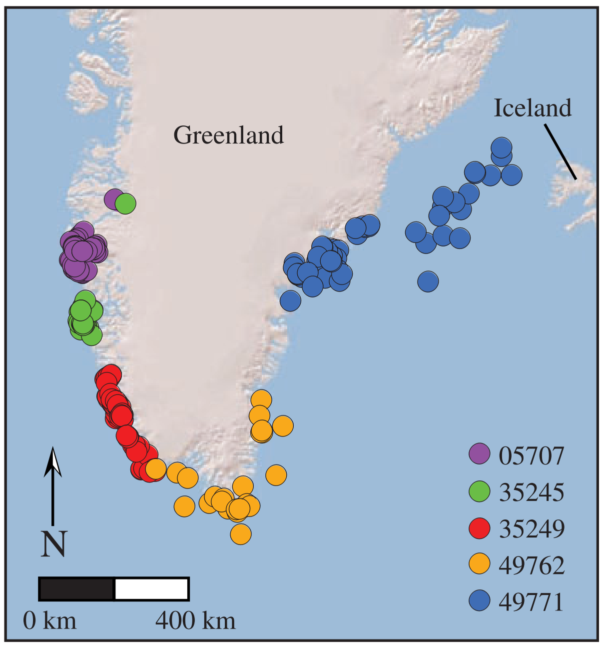

Figure 5. Winter home-ranges for five adult Gyrfalcons tagged in Greenland during 2000–2004. Points included are locations received from PTTs with location classes 3–1 during the time period individual Falcons spent on winter home-range. Only a single location was included for each day.

different location; however, ID 35258 frequently travelled up and down the coast (see supporting Figs S1 and S2). Within 1 month of completing outward migration, the PTT on ID 36319 stopped functioning, leaving open the possibility that the Falcon may have continued to move throughout the winter. The two adult females and one adult male that had incomplete outward migrations travelled an average of 624 km (median = 678, sd = ± 241, range = 360–833) over an average of 30 days (median = 27, sd = ± 6, range = 26–36), giving a speed of 23 km/day (median = 19, sd = ± 7, range = 19–31). All three individuals continued moving south along the coast, but one male and one female stopped and returned north, and both PTTs failed near the ringing station.

The adult male from northwest Ellesmere Island, ID 35248, travelled 3137 km on outward migration at an average speed of 83 km/day. It spent 38 days on outward migration and travelled southwest to the southeast corner of Ellesmere Island from where it continued south along the coast of Baffin Island before crossing into southwest Greenland (Fig. 3).

In total, complete outward migrations were documented on 10 occasions, with ID 35248 completing an outward migration in both 2002 and 2003 to the same area. Three individuals completed outward migrations from breeding home-ranges and seven completed outward migration after being tagged at a ringing station. A single adult female, ID 35245 from Kangerlussuaq, completed outward migration from her breeding home-range and arrived in her winter range on 24 August. From Thule, a single adult female, ID 35243, arrived at her winter range on 7 December. Three adults completed outward migration after being tagged in Scoresbysund, two females (IDs 49762 and 49764) and a male (ID 49771), and finished outward migration on 22 and 19 September and 8 October, respectively. Four adult Gyrfalcons completed outward migration from the Maniitsoq ringing station, three females (IDs 11988, 35248 and 36319) and a male (ID 35248), with an average completion date of 26 October (range = 14 October–5 November) for the females and 24 October for the lone male. Outward migration completion dates were difficult to determine and several Falcons made sustained movements throughout the winter period.

Winter home-range

Gyrfalcons wintered on the same coast in Greenland at which they were initially tagged. Only over a section of coastline approximately 200 km long, along the southern tip of Greenland, did individuals from both coasts overlap in winter. The furthest north that any individual was recorded while on winter home-range was approximately 67.9°N, where twilight in mid-winter would have extended to almost 6 h. However, an adult female (ID 41444) tagged in Thule and which did not complete outward migration was at approximately 70.6°N during the winter solstice (21 December), at which point only 3.5 h of twilight were available each day.

Winter home-range sizes were calculated for eight female and three male adult Gyrfalcons using locations with LC 3–1 (Table 6). Following log transformation, 90% MCPs winter home-range sizes were significantly larger on the east coast than west ($t = 7.18$, $P < 0.001$, df = 8). No differences between sexes and years were evident, although samples were small. Within the range of values

Table 7. Return migration data from adult Gyrfalcons that spent the winter non-breeding season in southern Greenland (distances given as Great Circle Distances).

Breeding home-range, PTT, age and sex	Start and end date of migration	Total distance (km)	Speed of travel (km/day)	Number of days	Number of days with locations (%)	Range of distances travelled per day (km)	Location classes used for daily calculations* (LC 3, 2, 1, 0)
Kangerlussuaq 11988/ad♀	13 March–22 March	848	85	10	8 (80.0)	5–276	1, 0, 1, 4
Thule 35243/ad♀	30 March–8 May	4502	113	40	28 (70.0)	11–536	2, 4, 12, 8
Thule 35249/ad♀	20 April–13 June	2763	50	55	34 (61.8)	1–143	0, 9, 15, 8
Scoresby. 49762/ad♂	3 May–27 May	1657	66	25	9 (36.0)	27–148	0, 0, 3, 4
Scoresby. 49771/ad♀	20 April–4 May	1576	105	15	6 (40.0)	31–223	0, 0, 4, 0
Ellesmere 35248/ad♂	11 April–2 May	2792	127	22	14 (63.6)	15–320	0, 5, 4, 3

*Location for start and end date of migration not included.

obtained, estimated home-range sizes were not correlated with the number of locations on which they were based, nor were any relationships apparent between arrival dates on winter home-range and range size. Winter home-range values for individual Falcons are given in Table 6.

For adults on the west coast of Greenland, the average 90% MCP winter home-range size was 2595 km^2 (n = 8, sd = ±2533, median = 1054, range = 383–6657). Fixed 95 and 50% kernels gave an average size of 5822 km^2 (n = 8, sd = ±7006, median = 1630, range = 357–18 443) and 813 km^2 (n = 8, sd = ±912, median = 268, range = 53–2067), respectively. Adults on the east coast had an average 90% MCP winter home-range size of 48 380 km^2 (n = 3, sd = ±19 210, median = 54 683, range = 26 810–63 647), and on 95 and 50% fixed kernels, 118 351 km^2 (n = 3, sd = ± 48 353, median = 104 896, range = 78 151–172 007) and 20 103 km^2 (n = 3, sd = ±9165, median = 24 594, range = 9559–26 157), respectively.

Figure 5 shows the highly variable sizes and locations of Gyrfalcon winter home-ranges. Considerable overlap existed between individuals on both coasts: some individuals had very large ranges completely overlapping individuals with smaller ranges (Figs 3 and 4). Some winter home-ranges were clearly defined, such as those of Falcons 05707 and 35245, while the much larger home-ranges documented for Falcons such as 49762 and 49771 were more open to subjective interpretation (Fig. 5).

Falcons 49762 and 49771 did not use their entire winter home-range each month, only large portions of it. Both spent periods in areas with sea ice and along the ice edge. In particular, bird 49771 spent almost a month along the ice edge between Greenland and Iceland from February to March (Fig. 3). Although individuals on both coasts used areas over the ocean, only on the east coast did Falcons spend long periods far from land. This behaviour largely accounted for their very large home-ranges, relative to birds on the west coast.

An adult male tagged at Maniitsoq (ID 35258) continued to migrate down the southwest coast of Greenland throughout the entire winter and did not stop moving southward until late April, after which it began moving north in early May (see supporting Figs S1 and S2). Throughout the winter period, Falcon 35258 appeared to have four home-ranges or use areas, each occupied for 1–3 months (Figs S1 and S2). If this period had been classed as a winter home-range, calculated range sizes would have been 15 364 km^2 (90% MCP), 39 840 km^2 (95% kernel) and 9419 km^2 (50% kernel).

After being tagged in Scoresbysund, a juvenile female (ID 49768) moved continually, travelling over 4548 km during a 200-day period, an area that included portions of the east coast of Greenland and northwest Iceland (Fig. 3). During this period, the bird spent well over half of its time over open ocean, sea ice and along the ice edge, a period of 40 days away from land, more than that of any other Falcon. Using the same methods as above to calculate winter home-range size, Falcon 49768 had a range size of 160 225 km^2 (90% MCP), 265 547 km^2 (95% kernels) and 84 143 km^2 (50% fixed kernel).

On the west coast, an adult female from Thule (ID 41444) and two adult males tagged in Maniitsoq (IDs 35250 and 35257) moved throughout the entire period that their PTTs functioned. Although their movements could have been considered nomadic, their PTTs certainly failed too early. Falcon 35248, from northwest Ellesmere Island, had data collected for one entire winter period and for the start of another, appearing to winter in the same fjord area in both years.

Return migration

Eight adult Gyrfalcons departed on return migration on dates between 7 March and 3 May (mean = 4 April, median = 5 April) from southern Greenland (Table 7), and six were tracked until they had completed their entire journey. Four probably bred, while the other two appeared to establish summer home-ranges, but did not breed (based on dates). Of the other two adults that appeared not to have completed return migration, one travelled approximately 450 km north before she returned south to her winter home-range, where her PTT then failed. The other briefly visited the nest-site where she was originally tagged and then also returned to her winter range, then continued 150 km south down the coast to where her PTT stopped. A single juvenile female began return migration on 5 May after being tagged in Scoresbysund, but her PTT failed before she established a summer home-range. Of the three adults that probably bred after completing return migrations on the west coast, the further north each individual bred the later it departed on return migration. The female that bred in Kangerlussuaq departed on 13 March, the female which bred in

Thule departed on 30 March, and the male which summered (and probably bred) in northwest Ellesmere Island departed on 11 April.

In general, return migrations were faster than outward ones, with three individuals travelling at more than 100 km/day, while during outward migration the fastest speed was 99 km/day, but for an incomplete journey. Two Falcons that had complete outward migrations also had complete return migrations, and in both the return was faster. The shortest distance travelled on return migration was for Falcon 11988, which spent 10 days on return migration and travelled 848 km at a mean speed of 85 km/day (Table 7). From Thule, Falcon 35249, which did not breed, travelled 2763 km over 55 days, a speed of only 50 km/day, while Falcon 35243 spent 40 days on return migration and travelled over 4502 km at a speed of 113 km/day. Falcon 35243 travelled further on return migration than on outward migration, 4502 km compared with 4234 km, but spent almost half as many days on return migration (40 days compared with 71 days) and travelled at almost double the speed (113 km/day compared with 60 km/day), with the last 12 days of return migration at a mean speed of 165 km/day. Individuals initially tagged in Scoresbysund travelled 1657 and 1576 km on return migration, spending 25 (66 km/day) and 15 (105 km/day) days on return migration, respectively (Table 7). The adult male which travelled to northwest Ellesmere Island spent 22 days on return migration, and travelled 2792 km at a speed of 127 km/day (Table 7). This compared with an outward migration that lasted 38 days and covered 3137 km at a speed of only 83/km day. For the last 8 days of return migration the adult male travelled at an even faster speed of 232 km/day.

Routes used during return migration were similar to those used during outward migration, albeit with slight variations. Falcon 35243 from Thule, which departed west to Canada during outward migration, crossed over Baffin Bay from Baffin Island during return migration, a slightly more direct route (Fig. 3). Additionally, after crossing from Greenland into Canada, Falcon 35243 spent almost a month along the ice edge off Labrador, a pattern not seen during outward migration. (Fig. 3). Additionally, Falcon 35248, which travelled down the east coast of Canada during outward migration, travelled almost exclusively over sea ice during return, appearing to spend 15 consecutive days over the ocean while travelling a minimum of 2370 km during that period (Fig. 3). Individuals initially tagged in Scoresbysund that completed return migration travelled along the east coast of Greenland, at times using the ice edge (Fig. 4).

DISCUSSION

Previous research using PTTs on Gyrfalcons is limited. Klugman *et al.* (1993) calculated an MCP breeding home-range size of 589 km^2 for an adult female in Kangerlussuaq and McIntyre *et al.* (2009) described the dispersal patterns of 15 juveniles from nest-sites in Alaska. Data from our study provide the first detailed examination of movement patterns of both adults and juveniles outside the breeding season. The results revealed the first records of Gyrfalcons leaving Greenland, to both Canada and Iceland, and documented the largest winter home-ranges sizes ever calculated for raptors, including large areas over the open ocean and sea ice, far from land.

Home-range sizes of breeding Gyrfalcons in Kangerlussuaq, Thule and Ellesmere Island appeared to be similar, with no apparent differences between areas or sexes despite apparent differences in prey availability. In Thule, tens of millions of seabirds (Salomonsen 1950, Boertmann *et al.* 1996, Egevang *et al.* 2003) were available as prey within kilometres of almost all Falcon nest-sites, and a small breeding home-range was expected as a result. In Kangerlussuaq, limited numbers of land-based prey were observed close to Gyrfalcon nests, and a larger home-range was expected as a result of Falcons having to travel generally further for food. However, Rock Ptarmigan numbers have been shown to fluctuate cyclically throughout the Arctic (Gudmundsson 1960, Weeden & Theberge 1972, Watson *et al.* 1998, Moss & Watson 2001), including Greenland (Salomonsen 1950, Vibe 1967), and we do not know at what point in this cycle the local population was during our study. If marked changes in Rock Ptarmigan densities occurred in the Kangerlussuaq area, the size of Gyrfalcon breeding home-ranges could have been affected.

Data were recorded for two individuals for the entire approximate 5-month period they were on their breeding home-ranges. The range size for adult female 35243, which bred in Thule, increased in size each month, probably as a result of the growth and level of independence of young, as described by Newton (1979, 1986) for other raptor species. However, for adult male 35248 from northwest Ellesmere Island, range size decreased through the breeding period. Based on PTT locations the nest was located in a large fjord. Early in the season prey were probably scarce in this area, with adult Ptarmigan and adult Hares *Lepus arcticus* the only food sources, but as pack ice broke up other land-birds and seabirds would have become increasingly available, allowing the male to make shorter and closer foraging trips from the nest.

On average, adult Gyrfalcons departed Thule on outward migration on 21 September ($n = 8$) while juveniles departed on 23 September ($n = 10$). Using a calculated average fledging date of 2 August, juveniles spent a post-fledging period of approximately 7 weeks in the Thule area before departure (Burnham 2008). In Alaska, McIntyre *et al.* (2009) calculated an average departure date of 27 August for 15 juveniles tagged with PTTs, almost a month earlier than in Thule, with an average post-fledging period of 6 weeks, again shorter than in Thule. Part of the difference in departure dates of juveniles between the two areas results from latitudinal variation in timing of breeding, with the Alaska study being more than 12° further south. In addition, the high late season abundance of prey near where the juveniles were captured in Thule may have allowed them to further delay migration by up to several weeks. In particular, large numbers of Black Guillemots *Cepphus grylle* were observed, which Salomonsen (1950) considered to be the last bird species to depart the High Arctic on outward migration, remaining until sea ice formed in October or November.

Although it appears that adults departed within days of juveniles, there was no evidence that adults and young travelled together on outward migration. Even though large numbers of juveniles congregated and were observed together at the ringing station in Thule (up to 10), PTT data suggest that they travelled individually. However, at the Scoresbysund ringing station up to 13 different juveniles were caught in a single day, with several caught within an hour. Similar occurrences were reported by Manniche (1910) for northeast Greenland, who reported, 'Often 4 to 5 individuals would appear at one time…circling around the mast-heads…watching for pigeons'. Whether this was a result of juveniles travelling in groups is unknown, and it is equally possible that large numbers of Falcons were travelling through the area independently of one another and were attracted to the ringing station by other individuals stooping/diving at the decoys.

Gyrfalcons tagged in Kangerlussuaq, Thule and Scoresbysund all migrated in a southward direction. Several individuals tagged in Maniitsoq appeared already to be on winter home-range, and it was not possible to determine if they were migrants. In Thule, Gyrfalcons most frequently crossed the ocean to Canada before turning south, although routes over the ocean and along the west coast of Greenland were also used. This was the first documentation of Gyrfalcons from Greenland migrating along the east coast of Canada. Todd (1963) described Gyrfalcons migrating annually along the east coast of Labrador, but believed that these birds were from Canada, doubting that they regularly crossed the ocean. Falcons crossing to Canada and travelling south along the east coast of Ellesmere Island, Devon Island and Baffin Island probably preyed upon the large number of seabirds that occur throughout this area (McLaren & Renaud 1982, Lepage *et al.* 1998). The lone Falcon that did not depart to the south was a juvenile male from Scoresbysund, which flew to the east, the last location being nearly equidistant between Iceland and the Faeroe Islands.

Falcons from Thule frequently made reverse migrations or even stopped for weeks at a time while on outward migration, with one individual reversing its migration over 550 km northwards. Although reverse movements or migration have been documented and described in a number of bird species (Åkesson *et al.* 1996, Berthold 2001), these are probably the longest recorded. In the Kangerlussuaq, Scoresbysund and Maniitsoq areas Falcons similarly travelled up and down the coast for many hundreds of kilometres.

The average speed of outward migration for Gyrfalcons ranged from 4 to 99 km/day ($n = 33$). However, these numbers include incomplete outward migrations and might represent only small portions of longer journeys. For the three individuals that completed outward migrations from their breeding home-ranges, the speed of travel decreased with latitudinal nesting location, from 83 to 60 to 30 km/day. With so few complete outward migrations documented, it is difficult to make any general statements comparing one area with another. In the Thule area, and based on limited samples, it appears that males migrated faster than females irrespective of age, although further research in this regard is needed.

Distances travelled by the three Gyrfalcons with completely recorded outward migrations from breeding home-ranges in Ellesmere Island, Thule and Kangerlussuaq varied from 391 to 4234 km. Although the Falcons from Ellesmere Island and Thule wintered only about 125 km apart, the Falcon from Ellesmere Island took a more direct route, and despite nesting over 500 km northwest of Thule, it travelled approximately 1100 km less than the Thule bird on outward migration. Furthermore, the Thule bird spent almost twice as many days on outward migration (71 vs. 38) than the Ellesmere Island bird, despite having less far to travel. Although both these birds completed outward migration from the most northern study areas, they did not spend the most days on outward migration. An adult female tagged in Thule spent 122 days on outward migration with her PTT failing while still travelling south. This pattern was also apparent in other individuals for which we recorded incomplete outward migrations, and it appears that the number of days spent on outward migration and the distance travelled were not correlated, although too few data were collected to be sure.

Winter home-ranges of Gyrfalcons varied widely within Greenland, with birds tagged in Scoresbysund having significantly larger winter home-ranges than those on the west coast. Gyrfalcons tagged in Scoresbysund used extensive areas over the open ocean, sea ice and along the ice edge during winter months, with one Falcon spending up to 40 days offshore. Similar behaviour was not observed in west coast birds except during migration. On both coasts, movements while on winter range were not always in one direction, and could have been described as 'pursuing' or weather-related behaviour, as found in other migrants (Berthold 2001).

On the west coast, Gyrfalcon movement patterns varied from individuals having small and stationary winter home-ranges to continually moving up and down the coast for hundreds of kilometres. Some Falcons had large winter home-ranges that completely overlapped those with much smaller ranges. Additionally, some individuals had up to four winter ranges, spending between a few weeks and 3 months in an area before moving on.

Winter home-range sizes for Gyrfalcons on the east coast of Greenland were the largest so far documented for raptors, with only the Lesser Spotted Eagle *Aquila pomarina* having a reported winter home-range (25 000 km^2) that approached the size of our estimated ranges for Gyrfalcons (Meyburg *et al.* 1995, 2004). Although ranges of individual Falcons frequently overlapped on the east coast, they did not use their entire winter home-range each month, but they did continually travel over long distances. Calculated minimum distances travelled by three Falcons while on winter home-range on the east coast were 5201 km for Falcon 49762 and 3864 km for Falcon 49773, with average daily speeds of travel of 28 and 21 km/day, respectively. Falcon 49764 travelled an even greater average distance each day, at 30 km/day. If data were available for every day these distances may have been much greater, as demonstrated for the Ivory Gull *Pagophila eburnea* (Gilg *et al.* 2010).

Two Gyrfalcons did not have typical winter ranges and were not included in winter home-range analyses. A juvenile female that was tagged in Scoresbysund spent most of the winter over the ocean and sea ice, almost continually moving, and occasionally used the east coast of Greenland and northwest coast of Iceland. An adult male tagged in Maniitsoq continued to move south along the coast throughout the entire winter, with multiple winter ranges or use areas.

It is likely that prey availability determines the movements of Gyrfalcons both during migration and while on winter home-range. While conducting surveys for 'sea-associated' birds in the Davis Strait and southern Baffin Bay during March 1981 and 1982, Mosbech and Johnson (1999) observed 16 Gyrfalcons on the sea ice. Falcons were observed along the coast and up to 300 km out to sea, frequently perched on or flying near large icebergs, with open water in the vicinity. They speculated that the Falcons were hunting Black Guillemots, which were using the open water around large icebergs to feed. It seems probable that Gyrfalcons regularly use sea ice and icebergs to rest on and hunt from during migration and while on winter home-range.

Many millions of seabirds and sea ducks winter or pass through the fjords and offshore areas of southwest Greenland and Iceland (Salomonsen 1950, Brown 1984, Durinck & Falk 1996, Merkel *et al.* 2002, Boertmann *et al.* 2004, Barrett *et al.* 2006). When compared with data from wintering Harlequin Ducks *Histrionicus histrionicus* and Common Eiders *Somateria mollissima* tagged with PTTs, Gyrfalcons tagged during this study overlapped within the same fjord regions in southwest Greenland (Mosbech *et al.* 2006, Chubbs *et al.*

2008). This combination of an abundance of seabirds and sea ducks provides wintering Gyrfalcons with a potentially rich food source, especially with their apparent ability to spend long periods of time living on the sea ice.

The large observed differences in winter range size amongst Gyrfalcons on the west coast probably result from some birds being territorial there. Individuals with small winter home-ranges, which probably have an abundance of food, are dominant and drive off other Falcons. Individuals that are not able to establish small winter home-ranges are left to wander, possibly being pushed from one area to another and relying upon a wider variety of prey, and thereby achieving larger winter home-ranges. In particular, juveniles may face more frequent movements than adults; with the single juvenile which provided data all winter covering a larger area than any of the adults, a pattern similar to that described by Marquiss and Newton (1982) for adult and juvenile Eurasian Sparrowhawks *Accipiter nisus*. In extreme situations, juveniles may even be forced out over the open ocean or sea ice (depending upon time of year), or even longer distances, such as to Iceland (e.g. Fig. 4, tag ID 49768). Although the ocean is home to large numbers of seabirds, these populations are likely to be scattered, with Falcons having to frequently make long daily flights. When compared with individuals with small home-ranges along the coast, which appear to forage over short distances and rest on protected cliff faces, these Falcons probably expend much more energy. It could be such individuals that occasionally turn up well south of the usual range in winter, including the northeastern USA and the British Isles.

The extreme difference in winter home-range size between Gyrfalcons on the east and west coast is probably a result of prey abundance and movement patterns. As can be seen in Figures 2 and 3, southwest Greenland remains ice-free throughout the winter, allowing seabirds and sea ducks continuous access to the shore and fjords to feed. On the east coast, sea ice gradually builds throughout the winter, eventually to encompass the entire coastline all the way to the southern tip of Greenland. As a result, seabirds are pushed towards the ice edge and sea ducks are probably driven to open coastline elsewhere (e.g. southwest Greenland or Iceland). As the amount of sea ice on the east coast increases, seabirds and Gyrfalcons are pushed greater distances from shore. Furthermore, as sea ice conditions are continually changing, sea birds must continually move along the ice edge, with Falcons accompanying them over long distances. Gilg *et al.* (2010) reported a similar pattern for Ivory Gulls, which followed the ice edge along the east coast of Greenland from July to December.

Perhaps the only other predator to behave in this way is another arctic nester, the Snowy Owl *Bubo scandiacus*, in which some satellite-tracked individuals spent up to 3 months on the sea ice (Therrien *et al.* in press). Snowy Owls also frequently travel long distances in winter, probably facing many of the same difficulties as Gyrfalcons in this harsh environment (Fuller *et al.* 2003, Therrien *et al.* in press). Individual Falcons probably adjust to environmental conditions as they find them, their daily movements reflecting a continually shifting prey supply.

Complete return migrations were recorded for six Gyrfalcons and generally appeared to be faster than outward migrations. Falcons commonly used the ice edge, probably as a result of the greater density of prey, with the timing and route of return migration for Falcons 35243 and 35248 very similar to those of other seabirds along the east coast of Canada (Tuck 1971, McLaren 1982, Renaud *et al.* 1982). The rapid speed of return migrations is probably influenced by the narrow breeding window available for Gyrfalcons in the Arctic, with Falcons that nest further north generally travelling faster and having a shorter breeding window than those that nest further south (e.g. Peregrine Falcons *Falco peregrinus*, Burnham 2008). A similar difference between spring and autumn migration speeds has been recorded in some other bird species, but not in all raptors (Newton 2008).

With limited light, at times as little as a few hours per day, and temperatures frequently below −20 °C, winter months in the Arctic are severe. To survive, Gyrfalcons must have a continual food supply that can be depended upon and captured in a relatively short period of time. While during the breeding season Falcons can spend numerous hours hunting in an area (24 h of daylight), periodic long-distance pursuing movements are necessary during winter in order to find large and abundant food sources that can be captured quickly. Although written to describe other migrants, Newton's (2003) statement that migrants 'mobile lifestyle enables them to exploit short-lived food-supplies at different places at different times, as they occur' seems to fit the situation in Gyrfalcons. This 'mobile lifestyle' is probably the key factor that enables Gyrfalcons to survive the harsh winter weather during the non-breeding season in the Arctic.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Migration routes and wintering areas (approximately every 28 days) of Gyrfalcons tagged in Kangerlussuaq and Maniitsoq, Greenland. No more than one location (LC 3–0) has been included per falcon per day.

Figure S2. Area used by Gyrfalcon 35258 while on winter home-range with locations from each individual month represented by a different colour and symbol.

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