



## Foraging movements of Leach's storm-petrels *Oceanodroma leucorhoa* during incubation

Ingrid L. Pollet, Robert A. Ronconi, Ian. D. Jonsen, Marty L. Leonard, Philip D. Taylor and Dave Shutler

I. Pollet ([ipollet@yahoo.com](mailto:ipollet@yahoo.com)), M. L. Leonard, Dept of Biology, Dalhousie Univ., Halifax, NS B3H 4R2, Canada. – I. D. Jonsen, Ocean Tracking Network, Dept of Biology, Dalhousie Univ., Halifax, NS B3H 4R2, Canada. – R. A. Ronconi, P. D. Taylor and D. Shutler, Dept of Biology, Acadia Univ., Wolfville, NS B4P 2R6, Canada.

Knowledge of foraging movements during the breeding season is key to understanding energetic stresses faced by seabirds. Using archival light loggers (geolocators), a Bayesian state–space model, and stable isotope analysis, we compared foraging movements of Leach's storm-petrels *Oceanodroma leucorhoa* during their incubation periods in 2012 and 2013. Data were collected from two colonies, Bon Portage Island and Country Island, which are 380 km apart along the coast of Nova Scotia, Canada. Based on allometry for procellariiform mass, predicted foraging ranges for Leach's storm-petrels are 200 km; however, observed maximum distances from the colony were 3 to 5 times that. Storm-petrels from Country Island travelled  $1015 \pm 238$  km southeast to the Laurentian fan and south of the Grand Banks whereas storm-petrels from Bon Portage Island travelled  $613 \pm 167$  km southeast, beyond the continental slope, east of Georges Bank. The average distance travelled in a return trip was  $2287 \pm 603$  km and  $1303 \pm 351$  km for Country Island and Bon Portage Island, respectively. There were no differences between years in cumulative distances travelled within islands, but foraging trips did not last as long in 2013 ( $4.7 \pm 1.5$  d) as they did in 2012 ( $6.2 \pm 2.1$  d). Stable isotope analyses indicated that, during the incubation period, prey items from Country Island were from higher trophic levels and possibly had higher energy content than those from Bon Portage Island, perhaps explaining the more distant and longer foraging trips for Country Island birds.

Pelagic seabirds spend most of their time at sea (Warham 1990). Determining how marine habitat is used is key to understanding many of the threats they face (Weimerskirch et al. 1997). Knowing at-sea distributions of seabirds is also critical for understanding their role in ocean ecosystems and for identifying sites for the establishment of marine protected areas that are vital to population persistence (Ronconi et al. 2012, Maxwell and Morgan 2013, McGowan et al. 2013). At-sea distributions for most seabirds are strongly linked to the distribution of their prey, which in turn are influenced by physical characteristics of the ocean such as temperature, wind, current and salinity (Franks 1992, Nogueira et al. 2012). Those characteristics are heterogeneous both spatially and temporally (Hunt and Schneider 1987, Donaghay et al. 1991, Mahadevan and Campbell 2002) which means that prey distribution varies accordingly, and seabirds must adjust their foraging movements daily, seasonally and annually (Weimerskirch et al. 1993, Quillfeldt et al. 2010a, Garthe et al. 2011).

Until recently, seabird movements have been difficult to track on open oceans. The earliest studies of at-sea distribution consisted of observations carried out from ships that could identify birds to species (Brown 1979, Griffiths and Sinclair 1982), but usually provided little information on breeding

status, sex, age, foraging behavior, or distance from a colony (Burger and Shaffer 2008). In recent years, development of electronic tracking devices has made it possible to track some bird species at sea (Weimerskirch et al. 2005, Shaffer et al. 2006, Egevang et al. 2010, Harris et al. 2010, Bridge et al. 2011, Guilford et al. 2012). Tracking devices have provided information about sex-specific foraging behavior (Pinet et al. 2012), intraspecific avoidance of competition (Grémillet et al. 2004), and migration routes (Egevang et al. 2010) that was previously impossible to gather. Miniaturisation of archival light loggers (geolocators) has enabled researchers to gain valuable knowledge about foraging and migratory movements of an increasing number of seabird species that weigh less than 500 g (Rayner et al. 2012, Navarro et al. 2013). Stable isotope analysis has also been used to study geographic movements (Cherel et al. 2000) and changes in diet associated with movements for many birds, including seabirds (Mallory et al. 2010, González-Solís et al. 2011). For instance,  $^{13}\text{C}$  tends to be depleted towards the poles (Cherel and Hobson 2007, Quillfeldt et al. 2010b), so differences in carbon signature can provide information about north–south movement. Similarly, stable isotopes of carbon have lower proportions of  $^{13}\text{C}$  in oceanic particulate organic matter compared to benthic environments, indicating whether

a bird had foraged closer to shore versus in more pelagic waters (Rubenstein and Hobson 2004). Finally, proportions of  $\delta^{15}\text{N}$  increase in a stepwise manner at each trophic level (Kelly 2000) and so can be used to infer trophic position at which birds feed.

Leach's storm-petrels *Oceanodroma leucorhoa* are small, abundant seabirds of the western North Atlantic. Populations at many surveyed colonies have declined in the past 50 yr, and some colonies have been abandoned (Robertson et al. 2006). Several processes are thought to be related to these declines including mammalian and avian predation at breeding colonies (Bicknell et al. 2009), collisions with large man-made offshore structures (Wiese et al. 2001), and exposure to oil contamination (Leighton 1993). Probabilities of encounter with the latter threats increase with increasing foraging range.

Based on allometry for other procellariiforms, Leach's storm-petrels are thought to forage within 200 km of their colony during the breeding season (Ricklefs and Schew 1994, Huntington et al. 1996, Thaxter et al. 2012) but there are no empirical data to evaluate this expectation. The goals of our study were to determine at-sea distributions and movements of Leach's storm-petrels during their incubation periods. Here, we used geolocators (GLS) to map foraging ranges of incubating Leach's storm-petrels in two different breeding seasons, at two geographically separated breeding colonies in Nova Scotia, Canada. We compared foraging movements from two colonies to determine if there were colony-specific differences in foraging behaviours and ranges, and whether these differences were reflected in diets, as determined by stable-isotope signatures.

## Methods

### Study sites and species

Leach's storm-petrels are small ~45-g sexually monomorphic procellariiforms. They arrive at island breeding sites in Nova Scotia in early May, reunite with their partner to breed, and then depart. Females return to their colony to lay a single egg in June. Incubation is shared between sexes, with a 3- to 5-d rotation between adults (Huntington et al. 1996). During incubation, adults may lose 4–7% of their body mass daily, which they regain on their next foraging trip (Ricklefs et al. 1986). Incubation lasts ~45 d. After hatching, adults brood their chick for several days, after which the chick is left alone with both parents returning independently at night to feed them. Fledging occurs after ~65 d spent as a nestling (Huntington et al. 1996).

This study was conducted during the summers of 2012 and 2013 on Country Island (45°06'N, 61°32'W) and Bon Portage Island (Outer Island on some maps, 43°28'N, 65°44'W) in Nova Scotia, Canada. Country Island is situated along the eastern shore of Nova Scotia. The island is roughly circular, ~500 m in diameter, and has an estimated 8700 breeding pairs of Leach's storm-petrels (S. Wilhelm pers. comm.). Bon Portage Island is situated approximately 380 km southwest of Country Island, off the southwest coast of Nova Scotia. It is ~3.0 × 0.5 km and has an estimated 50 000 breeding pairs of Leach's storm-petrels (Oxley 1999).

On Country Island, our study plot consisted of 62 randomly selected nesting burrows and on Bon Portage Island, we monitored ~250 burrows, distributed among twelve 12 × 12 m plots. On both islands, occupied burrows were labelled with uniquely numbered metal tags. Burrows were visited no more than twice during incubation to reduce desertion (Blackmer et al. 2003). When first handled, adults were fitted with a uniquely numbered Canadian Wildlife Service metal band. The Acadia Univ. Animal Care Committee approved all animal handling procedures (Protocol no. 06-09).

### Foraging movements during incubation

We used MK5740, British Antarctic Survey (BAS) GLS, which weighed 0.9 g and measured 21.9 × 7.9 × 3.8 mm with a light sensor stalk of 6.8 mm. GLS and attaching material weighed 1.3 g, which represents less than 3% of an average adult Leach's storm-petrel's mass (e.g. average adult mass on Bon Portage Island in 2012 was 46.1 g). GLS were equipped with an internal clock and battery, measured light levels every 60 s, and recorded maximum levels in 10-min intervals (full details in Afanasyev 2004).

To determine foraging locations in 2012, we deployed 21 GLS on Leach's storm-petrels on Country Island between 8 and 9 July, during early stages of incubation. We also deployed 17 GLS on Leach's storm-petrels on Bon Portage Island between 19 July and 22 August, during late stages of incubation. Leach's storm-petrels were randomly selected to be fitted with GLS on Country Island and distributed (1 or 2 per plot) amongst the twelve plots on Bon Portage Island.

On Country Island, nine of the 21 GLS were deployed using a modified leg-loop harness following Haramis and Kearns (2000). Of those nine Leach's storm-petrels, only one bird was recovered and it had lost the GLS. None of those birds was relocated in 2013. The remaining GLS (n = 12) on Country Island and all GLS on Bon Portage Island were deployed using a combination of tape and glue. An 8 × 22 mm strip of Tesa tape (4651) was cut to fit the length of the device. Two 5 × 50 mm strips were cut and stuck perpendicular to the first one. GLS were attached to this frame of tape before being glued to the back feathers. We first lifted a few contour feathers from the back. Two drops of glue (Loctite 402) were placed on a few feathers on the back of the bird along the spine and the tape was pressed on the glue, sticky side up, with a GLS on top of it. Feathers were flattened back against the body and side strips of tape were closed over these feathers. The ends of the tape were trimmed to reduce mass. Individuals were returned to their burrows immediately after GLS were affixed. Of the 29 Leach's storm-petrels fitted with GLS using the tape and glue technique, 17 were recaptured using one-way traps (Mauck and Grubb 1995). Five GLS (total of 9 foraging tracks) were recovered from Country Island and another 5 GLS (total of 6 foraging tracks) were recovered from Bon Portage Island. The remaining 7 birds were recaptured without a GLS. All individuals from which we recovered GLS were still incubating at the time of recovery. Individuals were weighed upon recovery. For logistical reasons, we could not determine how long they had been incubating on a given incubation bout at the time that they were weighed. Weight can vary across the incubation bout

(Ricklefs et al. 1986), and we treated control birds and GLS birds in the same manner.

To determine foraging locations in 2013, we deployed 15 GLS on Leach's storm-petrels on Country Island between 3 and 4 July, and 15 GLS on Bon Portage Island between 6 and 10 July, during early stages of incubation. Another 5 GLS on Bon Portage Island were deployed on 2 August, during late stages of incubation. All GLS deployed in 2013 were attached with sub-dermal sutures (Ethicon Prolene 4-0, FS-2 19 mm) to the backs of birds (MacLeod et al. 2008). We used 70% ethanol to sterilize suture sites. Alcohol also helped to part feathers and expose each bird's skin. Skin was lifted to avoid muscles and sutures were threaded in between the scapulae and 2 cm below, to attach to the front and back of the GLS. Double square knots were used to tie sutures. Between each deployment, all equipment was sterilized with 70% alcohol. Leach's storm-petrels were returned to their burrows immediately after GLS were affixed, usually within 10 min. Eleven individuals were recovered from Country Island (total of 21 foraging tracks) and 14 individuals were recovered from Bon Portage Island (total of 32 foraging tracks). Individuals were weighed upon recovery. The remaining 4 individuals on Country Island and 6 individuals on Bon Portage Island were not recaptured within the breeding season.

### Seasonal difference in foraging movements during incubation

To test for changes in foraging patterns relative to stage of incubation, on the day of the GLS deployment, we candled eggs to estimate stage of development on a scale of 0 to 22 using Weller's criteria (1956). Stage 0 corresponds to a freshly laid egg; stage 22 corresponds to when the bill of the chick is pressed against the inner shell membrane; chicks at the latter stage hatch within 24 h. We then monitored burrows for hatching date. With this information, we were able to estimate egg stage development at the beginning of each foraging trip. We preferred this metric of stage of the season over day of the year because Leach's storm-petrels do not breed synchronously (Huntington et al. 1996).

### Impacts of geolocators on Leach's storm-petrels

To test for impacts of GLS, we compared changes in mass of recaptured adults, hatching and fledging rate, and chick growth rate, measured by the slope of mass gain between days 5 and 30, between GLS-birds (tape and glue method and suture methods) and a random set of control birds ( $n = 15$  on Country Island and  $n = 100$  on Bon Portage Island). Chi-square tests were used to compare hatching success and fledging rate between GLS birds (tape and glue method and suture methods) and control birds; ANOVAs were used to compare mass change and chick growth between GLS birds (tape and glue method and suture methods) and control birds.

### Diet inferred from stable isotopes

To test for differences in diet between individuals from each island,  $\sim 100 \mu\text{l}$  of blood was drawn from a subset of incubating Leach's storm-petrels in 2012 ( $n = 15$  and  $n = 10$  for

Country Island and Bon Portage Island, respectively) for carbon and nitrogen stable isotope analysis. A drop of 10% ethanol was used to mat feathers over brachial veins. A puncture was made with a 26-gauge needle. Blood was collected with capillary tubes and stored in centrifuge tubes. Samples were kept on ice for  $< 2$  h in the field before being transferred to liquid nitrogen. Every 7 to 14 d, samples were transferred to a  $-80^\circ\text{C}$  freezer. Blood samples were dried at  $60^\circ\text{C}$  for 3 d, then ground up using a metal probe. Samples were analysed at the Stable Isotopes in Nature Laboratory at the Univ. of New Brunswick, Fredericton, NB, Canada for simultaneous determination of carbon and nitrogen stable isotope values. Stable isotopes are quantified as the deviation from a standard following the equation:  $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ , with X being either  $^{13}\text{C}$  or  $^{15}\text{N}$  and R being the corresponding  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$  ratio.

### Data processing and statistical analysis

Data obtained from GLS were decompressed using BAS Trak software (Biotrack, Dorset, UK). From pre-deployment calibration on Acadia Univ. Campus, we chose the threshold that led to the closest calibration position with the least variation. Times of sunrise and sunset using that threshold were determined from light curves using TransEdit2 software (Biotrack).

We used a light level threshold of 12 and calculated a sun elevation of  $-3.7^\circ$  for Country Island and  $-4.0^\circ$  for Bon Portage Island (angle corresponding to sunrise and sunset based on pre-deployment calibration). Accuracy, calculated from the calibration period, was  $170 \pm 88$  km, with a magnitude of  $1.06 \pm 1.16^\circ$  for latitude and  $0.86 \pm 0.47^\circ$  for longitude. This is similar to a calibration study of GLS on black-browed albatrosses *Thalassarche melanophrys* where error was  $186 \pm 114$  km (Phillips et al. 2004).

From these estimated day lengths and time of local noon, we obtained latitude and longitude using Locator software (BAS; Ekstrom 2004). This method gave us two locations per day (midnight and noon). We excluded positions associated with Leach's storm-petrels being in burrows where they spent several days in complete darkness. Light-level based locations can have high errors due to effects of cloud cover, feather or body shading of the light sensor, and high daily travel rates, all of which interfere with recording of local sunrise and sunset events (Phillips et al. 2004, Block et al. 2011). We used a Bayesian state-space model to filter location data (Jonsen et al. 2013), accounting for location errors and yielding sets of locations at regular 12-h time intervals. The model is a modification of the first-difference correlated random walk model described in Jonsen et al. (2005) to account for light-level GLS data (as per Winship et al. 2012), with the following process equation:

$$\mathbf{d}_t = \gamma \mathbf{T} \mathbf{d}_{t-1} + \eta_t \quad (1)$$

where  $\mathbf{d}_t = \mathbf{x}_t - \mathbf{x}_{t-1}$  and  $\mathbf{x}_t$  is a vector of length 2 representing the true longitude and latitude of a petrel at time  $t$ . The transition matrix  $\mathbf{T}$  is parameterized by the mean turning angle  $\theta$  and gives the average change in direction between movements  $\mathbf{d}_t$  and  $\mathbf{d}_{t-1}$ . The degree of correlation or persistence in movements is controlled by  $\gamma$ , where values approaching

1 imply highly correlated, straight-line movements and values approaching 0 imply uncorrelated, tortuous movements. Stochastic deviations in movement  $\eta_t$  are assumed to be normally distributed with mean 0 and variance-covariance  $\Sigma$ .

Observed states  $\mathbf{x}_t$  were linked to GLS data via the following observation equation:

$$\mathbf{y}_i = \boldsymbol{\mu}_i + \boldsymbol{\varepsilon}_i \quad (2)$$

where  $\mathbf{y}_i$  is the  $i$ th pair of longitude and latitude observations,  $\boldsymbol{\mu}_i$  is the corresponding estimated locations and  $\boldsymbol{\varepsilon}_i$  are normally distributed, serially independent observation errors in longitude and latitude. True locations  $\boldsymbol{\mu}_i$  were derived from observed states  $\mathbf{x}_t$  that were regular in time according to the following interpolation:

$$\boldsymbol{\mu}_i = (1 - j_i)\mathbf{x}_{t-1} + j_i\mathbf{x}_t \text{ for } i \in I_t \quad (3)$$

where  $I_t$  is the set of observations that occurs between times  $t-1$  and  $t$ , and the scalar  $j_i$  is the proportion of this time step that elapsed prior to  $\boldsymbol{\mu}_i$ . See Winship et al. (2012) for further details.

Because foraging trips were relatively short, we used a hierarchical state-space formulation that facilitated improved location estimates by simultaneously fitting to multiple track datasets (Jonsen et al. 2003). The model described in Eq. (1) through (3) was fit hierarchically by estimating movement parameters  $\gamma$ ,  $\theta$ , and  $\Sigma$  across all tracks rather than individually (Block et al. 2011). Models were fit to tracking data using open source JAGS software (ver. 3.3.0; Plummer 2003). A total of 100 000 samples were taken as an adaptive sampling and burn-in phase and an additional 100 000 joint posterior samples in each of two Markov Chain Monte Carlo chains were generated after convergence was assumed. These latter samples were thinned by a factor of 100 to reduce sample autocorrelation, yielding a final set of 2000 joint posterior samples. Convergence was assessed visually by examining: 1) trace plots of model parameters for signs of non-stationarity and poor mixing of the chains; 2) density plots of the chains overlaid to ensure posterior distributions were unimodal; 3) autocorrelation function plots of each chain to ensure that sample autocorrelation was not unduly large after thinning.

We used program R (ver. 2.15.2) for all subsequent analyses. We determined: 1) duration of foraging trip as the number of days an individual was at sea, 2) maximum range as the farthest point from the colony during a foraging trip, and 3) cumulative distance as the total distance travelled during a foraging trip. Maximum distance from a colony and cumulative distance travelled for each foraging trip were calculated from the set of locations produced by the state-space model, using the package 'sp'. To study the distribution of foraging positions during the incubation period, we created a kernel density map using the `kde2d` function in R. Coordinates representing tracks start and endpoints (i.e. colony locations) were removed to avoid over-representation of that area. We calculated distances from colonies to the maxima of their respective kernel density surface.

From candling, we estimated egg-stage development (scale of 0 through 22) for the start of each foraging trip. We fit a linear mixed-effects model to each foraging measure

using 'lmer' in the package 'lme4', with individual birds fitted as random effects. Egg stage was included in all models, and we used likelihood ratio tests to assess effects of each of the remaining terms in the set of nested models. Stable isotope data were compared between islands using ANOVA. Results are presented as means  $\pm$  SD.

## Results

### Impacts of geolocators

Mass change was not significantly different between control birds and those with GLS affixed with tape ( $F_{1,5} = 0.4$ ,  $p = 0.56$ ), or between control birds and those with sutured GLS ( $F_{1,80} = 0.8$ ,  $p = 0.36$ ). Because of likely predation by meadow voles *Microtus pennsylvanicus*, fledging success was very low on Country Island for both GLS (7%) and control birds (15%), so only results from Bon Portage Island are presented here. GLS affixed with tape are for year 2012, and sutured GLS are for year 2013. Hatching success did not differ significantly between control birds and those with GLS affixed with tape ( $\chi^2_1 = 1.7$ ,  $p = 0.19$ ), or between control birds and those with sutured GLS ( $\chi^2_1 = 1.4$ ,  $p = 0.23$ ). Similarly, fledging success did not differ significantly between control birds and those with GLS affixed with tape ( $\chi^2_1 = 0.1$ ,  $p = 0.73$ ) or between control birds and those with sutured GLS ( $\chi^2_1 = 0.6$ ,  $p = 0.44$ ). Chick growth did not differ significantly between control birds ( $1.67 \pm 0.57 \text{ g d}^{-1}$ ) and those affixed with tape ( $1.30 \pm 0.44 \text{ d}^{-1}$ ,  $F_{1,54} = 3.0$ ,  $p = 0.08$ ). However, chick growth was higher for control birds ( $1.57 \pm 0.59 \text{ d}^{-1}$ ) than for sutured GLS birds ( $1.19 \pm 0.63 \text{ d}^{-1}$ ,  $F_{1,128} = 5.0$ ,  $p = 0.03$ ).

### Spatial difference in foraging movements during incubation

All recovered GLS yielded data. For Country Island, 9 foraging trips were recorded from 5 individuals in 2012, and another 21 foraging trips were recorded from 11 individuals in 2013. For Bon Portage Island, a total of 6 foraging trips was recorded from 5 individuals in 2012, and another 33 foraging trips from 16 individuals were recorded in 2013.

Foraging trips initiated on Country Island tracked southeast, on or past the continental shelf. Foraging trips initiated from Bon Portage Island also tracked southeast, usually past the continental shelf (Fig. 1). There was very little geographical overlap in foraging range between the two colonies (Fig. 1). Individuals on Country Island had almost twice the maximum range ( $\chi^2_1 = 26.8$ ,  $p < 0.001$ , Table 1, 2) and travelled almost twice the cumulative distance compared to individuals from Bon Portage Island ( $\chi^2_1 = 15.7$ ,  $p < 0.001$ , Table 1, 2). Distances from colonies to the maximum of a bird's respective kernel density surface was 699.3 km and 249.5 km for Country Island and Bon Portage Island, respectively (Fig. 2). Individuals from Country Island gained significantly more mass ( $+0.23 \pm 0.18 \text{ g d}^{-1}$ ) while carrying GLS than did individuals from Bon Portage Island ( $+0.02 \pm 0.21 \text{ g d}^{-1}$ ;  $F_{1,26} = 6.7$ ,  $p = 0.02$ ).

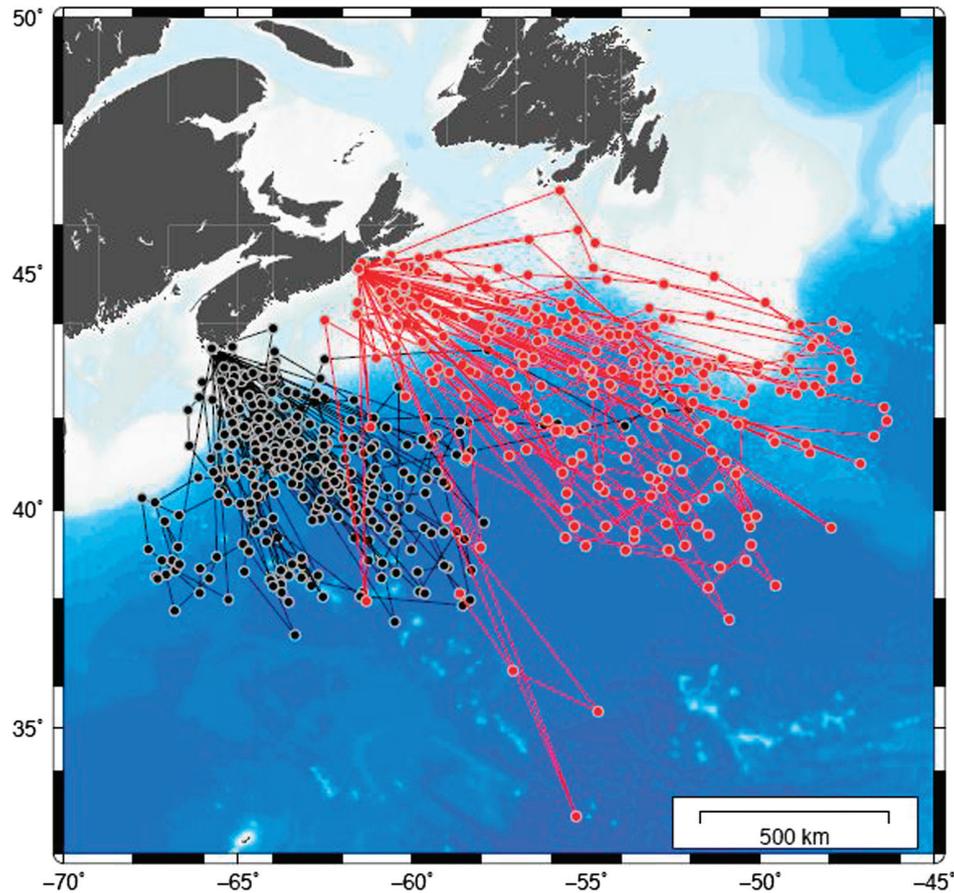


Figure 1. Tracks of Leach's storm-petrels with noon and midnight locations from Bon Portage (BP, black dots) and Country Island (CI, red dots).

### Seasonal and inter-annual difference in foraging movements during incubation

Durations of foraging trips were not correlated with stage of incubation ( $\chi^2_1 = 0.7$ ,  $p = 0.41$ ). Foraging movements (maximum and cumulative distance) did not differ between the two years ( $\chi^2_1 = 0.5$ ,  $p = 0.48$  for maximum distance and  $\chi^2_1 = 0.8$ ,  $p = 0.37$  for cumulative distance), but foraging trip duration was shorter in 2013 compared to 2012 ( $\chi^2_1 = 6.8$ ,  $p = 0.009$ , Table 1, 2).

### Diet inferred from stable isotopes

Blood samples of Leach's storm-petrels on Country Island were significantly more depleted in  $^{13}\text{C}$  than samples from birds on Bon Portage Island (Country Island:  $-19.5 \pm 0.2$ ,

Bon Portage Island:  $-19.1 \pm 0.2$ ;  $F_{1,23} = 20.7$ ,  $p < 0.001$ , Fig. 3), suggesting that birds from Country Island foraged further north, and/or in more pelagic waters than birds from Bon Portage Island. Blood samples of Leach's storm-petrels on Country Island were more enriched in  $^{15}\text{N}$  than samples from Leach's storm-petrels on Bon Portage Island (Country Island:  $13.8 \pm 0.3$ , Bon Portage Island:  $12.6 \pm 0.3$ ;  $F_{1,23} = 86.3$ ,  $p < 0.001$ , Fig. 3), indicating that birds from Country Island fed at a higher trophic level.

### Discussion

Our data show that Leach's storm-petrels from colonies 380 km apart have distinct foraging locations and foraging ranges. Leach's storm-petrels from Country Island

Table 1. Summary of foraging trip characteristics of Leach's storm-petrels from Country Island (CI) and Bon Portage Island (BP) during 2012 and 2013 incubation.

Metric	Year			
	2012		2013	
	CI	BP	CI	BP
Deployment duration (d)	17 ± 6	9 ± 4	20 ± 12	31 ± 17
Number of foraging trips	1.8 ± 0.4	1.2 ± 0.4	1.9 ± 0.3	2.3 ± 0.8
Foraging trip duration (d)	6.2 ± 0.5	6.3 ± 1.2	4.9 ± 0.3	4.6 ± 0.3
Maximum distance from colony (km)	1086 ± 220	684 ± 209	983 ± 249	587 ± 149
Cumulative distance (km)	2659 ± 615	1013 ± 159	2117 ± 541	1371 ± 379

Table 2. Fixed effects means and standard errors of linear mixed effect models, with maximum distance from colony, cumulative distance, and foraging duration as response variables. Variables with no value had no significant effect in models.

Model	Egg stage	Island	Year
Maximum ~ egg + island + year + 1 Bird		368.0 ± 63.5	
Cumulative ~ egg + island + year + 1 Bird		729.0 ± 174.4	
Forage ~ egg + island + year + 1 Bird			-1.38 ± 0.53

travelled ~1000 km, with a maximum kernel density 700 km from the colony. They travelled southeast to the Laurentian fan and deep waters beyond, south of the Grand Banks of Newfoundland. In contrast, Leach's storm-petrels from Bon Portage Island travelled ~ 500 km southeast, with a maximum kernel density 250 km from the colony. They travelled east of Georges Bank and into areas of deep water beyond the continental slope, including western portions of the New England Seamount chain. For other seabirds, colony-specific segregation of foraging grounds may be influenced by regional wind patterns and foraging site fidelity (Grémillet et al. 2004), or intra-specific competition among colonies (Wakefield et al. 2013).

Previous estimates of foraging distance for Leach's storm-petrels at other colonies were less than 200 km (Ricklefs and Schew 1994, Huntington et al. 1996, Thaxter et al. 2012). Our study shows that foraging distances can be 3–5 times higher than that estimate ( $1015 \pm 238$  km,  $612 \pm 166$  km, for Country Island and Bon Portage Island, respectively). Because of the extreme foraging range compared to what was

previously thought for this species, we decided to compare foraging range relative to body mass for this species with that of other procellariiforms. We used ISI Web of Knowledge to search for studies reporting foraging range of seabirds during incubation (i.e. we excluded studies that provided data for the nestling stage). We calculated a foraging range (in km per trip) to mass (in g) index from procellariiform species during incubation (Table 3). The index for other procellariiform species ranged from 0.1 for black-browed albatrosses to 10.5 for Chatham petrels *Pterodroma axillaris*; the index for Leach's storm-petrel was 24.1. Foraging range for species similar in size to Leach's storm-petrels have yet to be published and might provide similar ratios.

The long trips observed in this study may only be possible during incubation when parents do not have to make frequent trips back to the colony to feed their chick. During chick-rearing, foraging must provide both chicks' and adults energy requirements, and adults' may reduce trip lengths to meet demands of rearing young. Many procellariiforms accommodate this demand by alternating long foraging trips when individuals build up their own body reserves with shorter foraging trips used to provision chicks (Weimerskirch 1998).

Despite travelling longer distances during the incubation period, individuals from Country Island gained more weight during GLS deployment than those from Bon Portage Island. Differences in geographic locations and ocean depth at their foraging areas likely have important implications for food availability. Hedd et al. (2009) estimated that Leach's storm-petrel diets in Newfoundland consisted mainly of fish with high energy content, including mature lanternfish (myctophids; *Benthosema glaciale*, *Protomyctophum arcticum*) and sand lance (genus *Ammodytes*), with euphausiid and hyperiid

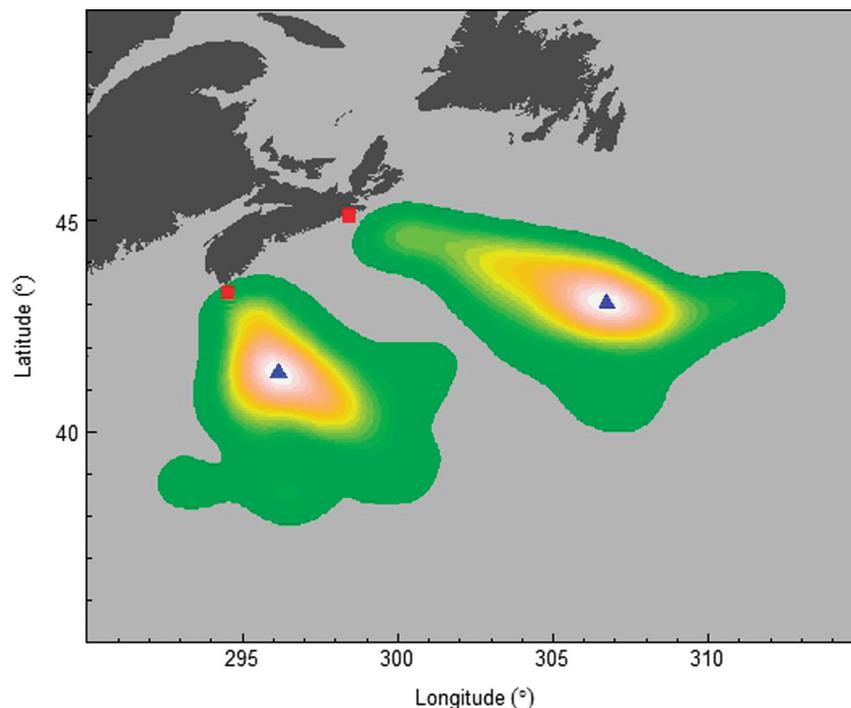


Figure 2. Map showing colour gradient of the upper 0.90 quartile of the kernel density surface for each island, with maximum kernel density (blue triangles) and source islands (red squares).

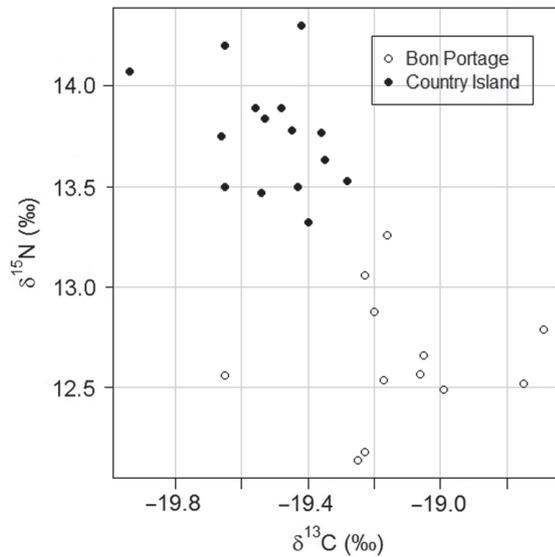


Figure 3. Blood  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  from Leach's storm-petrels from Bon Portage (open circles) and Country Island (solid circles).

crustaceans of lower energy content accounting for a smaller proportion. Our data suggest that prey items of Leach's storm-petrels from Country Island are at a higher trophic level than they are for Leach's storm-petrels from Bon Portage Island. There is evidence that concentrations of some essential fatty acids may be positively correlated with trophic level in marine food webs (Connelly et al. 2013) so that foraging at higher trophic levels may be associated with higher quality prey, but this hypothesis requires further evaluation.

Foraging seabirds may travel for many days during incubation and some species decrease the duration of foraging trips towards the end of incubation periods (Weimerskirch et al. 1986, 1993, González-Solís 2004). This behavior ensures that chicks can be fed soon after hatching. In this study, we could not confirm this behavior in Leach's storm-petrel, partly because our tracking ended before the end of incubation for most individuals. It could also be that foraging trip durations are not variable enough in this species to detect decreases during incubation.

Despite not observing a seasonal change in foraging distance, we observed an inter-annual decrease in foraging duration between 2012 and 2013 for individuals from both islands. This difference could be the result of better foraging conditions in 2013. Seabirds can adjust characteristics of their foraging with favorable foraging conditions (Quillfeldt et al. 2010b). Via coordinated transitions of incubation shifts between mates, shorter foraging trip durations during incubation would result in more continuous incubation of eggs, and hence faster embryo development (Boersma 1982). However, we observed no differences in duration of egg development between years ( $F_{1,117} = 0.2$ ,  $p = 0.66$ ). Similarly, if the same trends persisted through chick-rearing, this could result in greater chick provisioning and faster chick growth. However, we observed no differences between years in chick growth ( $F_{1,184} = 0.8$ ,  $p = 0.35$ ).

To our knowledge, our study is the first to successfully deploy GLS on a seabird as small as Leach's storm-petrel (45 g). We used three different techniques of attachment. At this point, we discourage researchers from using the leg-loop harness method on storm-petrels (0% recovery rate). The tape and glue method (34% recovery rate) is quick and

Table 3. Maximum range, mass, and the ratio of foraging range to mass from published data (ISI web of Knowledge) for species of procellariiforms during the incubation period. Methods include geolocators (GLS), platform terminal transmitters (PTT), global positioning systems (GPS), or a combination of tracking devices (Various).

Species	Mass (g)	Range (km)	Range: Mass index	Method	Reference
Leach's storm-petrel <i>Oceanodroma leucorhoa</i>	45	1086	24.13	GLS	This study
Chatham petrel <i>Pterodroma axillaris</i>	200	2095	10.47	GLS	Rayner et al. (2012)
Barau's petrel <i>Pterodroma baraui</i>	375	2336	6.23	GLS	Pinet et al. (2012)
Thin-billed prion <i>Pachyptila belcheri</i>	130	670	5.15	GLS	Quillfeldt et al. (2013)
Antarctic prion <i>Pachyptila desolata</i>	163	824	5.05	GLS	Navarro et al. (2013)
Blue petrel <i>Halobaena caerulea</i>	187	834	4.46	GLS	Navarro et al. (2013)
Short-tailed shearwater <i>Puffinus tenuirostris</i>	600	2877	4.80	PTT	Einoder et al. (2011)
Great shearwater <i>Puffinus gravis</i>	850	3813	4.49	PTT	Ronconi et al. (2010)
Grey-faced petrel <i>Pterodroma macroptera</i>	572	2208	3.86	PTT	MacLeod et al. (2008)
Cory's shearwater <i>Calonectris diomedea</i>	535	1819	3.40	PTT	Magalhães et al. (2008)
Manx shearwater <i>Puffinus puffinus</i>	450	1191	2.65	GPS	Dean et al. (2012)
South Georgian diving petrel <i>Pelecanoides georgicus</i>	124	240	1.93	GLS	Navarro et al. (2013)
Common diving petrel <i>Pelecanoides urinatrix</i>	147	261	1.77	GLS	Navarro et al. (2013)
White-chinned petrel <i>Procellaria aequinoctialis</i>	1279	2100	1.64	GLS	Phillips et al. (2006)
Streaked shearwater <i>Calonectris leucomelas</i>	500	645	1.29	GLS	Yamamoto et al. (2012)
Laysan albatross <i>Phoebastria immutabilis</i>	2780	2356	0.84	PTT	Kappes et al. (2010)
Westland petrel <i>Procellaria westlandica</i>	1200	961	0.80	GLS	Landers et al. (2011)
Northern fulmar <i>Fulmarus glacialis</i>	600	400	0.67	Various	Thaxter et al. (2012)
Black-footed albatross <i>Phoebastria nigripes</i>	3150	1782	0.56	PTT	Kappes et al. (2010)
Black petrel <i>Procellaria parkinsoni</i>	700	332	0.47	GLS	Freeman et al. (2010)
Grey-headed albatross <i>Thalassarche chrysostoma</i>	3507	1211	0.34	Various	Phalan et al. (2007)
Light-mantled sooty albatross <i>Phoebastria palpebrata</i>	2785	970	0.34	Various	Phalan et al. (2007)
Northern giant petrel <i>Macronectes halli</i>	3700	1226	0.33	PTT	González-Solís et al. (2000)
Wandering albatross <i>Diomedea exulans</i>	7650	1483	0.19	Various	Phalan et al. (2007)
Black-browed albatross <i>Thalassarche melanophrys</i>	3800	474	0.12	Various	Phalan et al. (2007)

could be improved by inserting a layer of chiffon material between GLS and the tape (R. Mauck pers. comm). Subdermal suturing gave us the best GLS recovery rate (71%) but previous experience with suturing and very steady hands are mandatory to work on such a small bird. Neither the tape and glue method nor the suture method had an impact on hatching success or fledging success. At this point, we cannot evaluate long-term impact of such devices and attachment methods on the physiology and survival of Leach's storm-petrels, but we recognize there may be potential consequences (Barron et al. 2010, Quillfeldt et al. 2012).

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