2023

Female and male Leach's Storm Petrels (Hydrobates leucorhous) pursue different foraging strategies during the incubation period

Robert A. Mauck
Kenyon College

Isabeau Pratte
Environment and Climate Change Canada

April Hedd
Environment and Climate Change Canada

Ingrid I. Pollet
Acadia University

Patricia L. Jones
Bowdoin College

See next page for additional authors

Recommended Citation

Mauck RA, Pratte I, Hedd A, Pollet II, Jones PL, Montevecchi WA, Ronconi RA, Gjerdrum C, Adrianowyscz S, McMahon C, Acker H, Taylor LU, McMahon J, Dearborn DC, Robertson GJ, & McFarlane Tranquilla LA. 2023. Female and male Leach's Storm Petrels (Hydrobates leucorhous) pursue different foraging strategies during the incubation period. Ibis (London, England), 165(1), 161–178.

Authors

Robert A. Mauck, Isabeau Pratte, April Hedd, Ingrid l. Pollet, Patricia L. Jones, William A. Montevecchi, Robert A. Ronconi, Carina Gjerdrum, Sarah Adrianowyscz, Colin McMahon, Haley Acker, Liam U. Taylor, Jennifer McMahon, Donald Dearborn, Gregory J. Robertson, and Laura A. McFarlane Tranquilla

IBIS
international journal of avian science
Ibis (2023), **165**, 161–178
doi: 10.1111/ibi.13112

Female and male Leach's Storm Petrels (*Hydrobates leucorhous*) pursue different foraging strategies during the incubation period

ROBERT A. MAUCK,*[1] ISABEAU PRATTE,[2] APRIL HEDD,[3] INGRID L. POLLET,[4] PATRICIA L. JONES,[5]
WILLIAM A. MONTEVECCHI,[6] ROBERT A. RONCONI,[2] CARINA GJERDRUM,[2] SARAH ADRIANOWYSCZ,[1]
COLIN MCMAHON,[1] HALEY ACKER,[1] LIAM U. TAYLOR,[5] JENNIFER MCMAHON,[1] DONALD C. DEARBORN,[6]
GREGORY J. ROBERTSON[3] & LAURA A. MCFARLANE TRANQUILLA[7]
[1]*Biology Department, Kenyon College, Gambier, OH, 42022, USA*
[2]*Canadian Wildlife Service, Environment and Climate Change Canada, 45 Alderney Drive, Dartmouth, NS, B2Y 2N6, Canada*
[3]*Wildlife Research Division, Environment and Climate Change Canada, Mount Pearl, NL, A1N 4T3, Canada*
[4]*Department of Biology, Acadia University, Wolfville, NS, B4P 2R6, Canada*
[5]*Biology Department, Bowdoin College, Brunswick, ME, 04011, USA*
[6]*Biology Department, Bates College, Lewiston, ME, 04240, USA*
[7]*Birds Canada, 43 Main Street, Sackville, NB, E4L 1G6, Canada*

Reproduction in procellariiform birds is characterized by a single egg clutch, slow development, a long breeding season and obligate biparental care. Female Leach's Storm Petrels *Hydrobates leucorhous*, nearly monomorphic members of this order, produce eggs that are between 20 and 25% of adult bodyweight. We tested whether female foraging behaviour differs from male foraging behaviour during the ~ 44-day incubation period across seven breeding colonies in the Northwest Atlantic. Over six breeding seasons, we used a combination of Global Positioning System and Global Location Sensor devices to measure characteristics of individual foraging trips during the incubation period. Females travelled significantly greater distances and went farther from the breeding colony than did males on individual foraging trips. For both sexes, the longer the foraging trip, the greater the distance. Independent of trip duration, females travelled farther, and spent a greater proportion of their foraging trips prospecting widely, as defined by behavioural categories derived from a hidden Markov Model. For both sexes, trip duration decreased with date. Sex differences in these foraging metrics were apparently not a consequence of morphological differences or spatial segregation. Our data are consistent with the idea that female foraging strategies differed from male foraging strategies during incubation in ways that would be expected if females were still compensating for egg formation.

Keywords: foraging behaviour, global location sensors, GPS, hidden Markov Model, incubation, seabirds, sex-specific, Storm Petrels.

Reproduction in procellariiform birds is characterized by a single egg clutch, slow development, a long breeding season and obligate biparental care. In these pelagic species, both sexes essentially perform the same behaviours during most of the reproductive season (Warham 1990). During incubation, parents alternate multi-day incubation bouts in which the adult at the nest fasts while its mate forages at sea. During chick-rearing, each parent forages independently and returns to the nest for brief visits to deliver food to the chick. Both parents sustain these behaviours across the several months required for successful incubation and chick provisioning. Extra-pair paternity rates are low for most procellariiform species (with the

*Corresponding author.
Email: mauckr@kenyon.edu

exception of some albatrosses; Jouventin *et al.* 2007). As a result, male and female parents in this clade are also expected to have similar genetic stake in their offspring.

Despite this broad biparental symmetry, underlying discrepancies in energetics, behaviour and morphology may cascade into sex differences in reproductive activity. In particular, breeding female procellariiforms build an egg that is between 10 and 25% of bodyweight (Warham 1990). In sexually monomorphic species, this fundamental energetic disparity may lead to reduced survival and offspring care of inexperienced female parents (e.g. *Hydrobates pelagicus*: Sanz-Aguilar *et al.* 2012), and sexual dimorphism in wing length or wing loading can affect lift and flight speed in open sea winds, ultimately resulting in different movement patterns as males and females travel and forage during the breeding season (e.g. *Diomedea exulans*: Shaffer *et al.* 2001; *Thalassarche impavida*: Sztukowski *et al.* 2018; *Hydrobates monteiroi*: Paiva *et al.* 2018). For both monomorphic and dimorphic procellariiforms, these reproductive differences can be 'context-dependent', with sex differences in breeding season behaviour emerging only in years of environmental stress or resource scarcity (e.g. *Calonectris borealis*: Paiva *et al.* 2017; *Oceanities oceanicus*: Gladbach *et al.* 2009).

Leach's Storm Petrels *Hydrobates leucorhous*, members of the family Hydrobatidae, the smallest members of the order Procellariiformes in North America, are nearly monomorphic and show no evidence of extra-pair parentage (Mauck *et al.* 1995, Dearborn *et al.* 2016). However, multiple lines of evidence suggest there are sex differences in reproductive behaviour. Leach's Storm Petrel eggs are 20–25% of adult bodyweight (Montevecchi *et al.* 1983, Bond & Hobson 2015, Pollet *et al.* 2020), possibly resulting in unique energetic or nutrient demands for females. Differences in male and female investment skew the opposite direction after egg-laying: compared with females, male Leach's Storm Petrels have been shown to incubate the egg for a greater proportion of time, to abandon a non-hatching egg less quickly and to maintain greater daily mean food deliveries to chicks (Mauck *et al.* 2011, Tyson *et al.* 2022). To date, it is unclear how these biases in offspring investment are tied to differences in the actual foraging activity of Leach's Storm Petrel parents.

Here, we used a combination of Global Positioning System devices (GPS) and Global Location Sensors (GLS) across five breeding colonies and six breeding seasons to examine the sex-specific characteristics of foraging behaviour in breeding Leach's Storm Petrels. We first ask whether individual foraging trips differ between the sexes in terms of total distance covered, maximum distance from the colony, trip duration and finer-grained behavioural characteristics of foraging flight (McClintock & Michelot 2018). To test for niche partitioning – which could further indicate sex differences in energetic demands, nutrient requirements or downstream differences in competitive foraging behaviour (Gladbach *et al.* 2009) – we ask whether females forage in spatially distinct regions that differ from those of males (Phillips *et al.* 2004b, 2011, Pinet *et al.* 2012). To determine whether sexual dimorphism impacts foraging behaviour (Shaffer *et al.* 2001, Paiva *et al.* 2017, 2018, Sztukowski *et al.* 2018) in this nearly monomorphic species, we test whether wing-length is a relevant predictor of foraging spatial metrics. In addition, we examine whether sex differences are consistent across years rather than context-dependent, appearing only in years of poor environment condition (Gladbach *et al.* 2009, Paiva *et al.* 2017). In this way, we examine how sex differences in Leach's Storm Petrel foraging behaviour may vary given the standing evidence for male-bias in incubation care and the fundamental energetic cost of egg formation to females.

METHODS

Global position system (GPS) data

We tracked foraging movements of 75 known-sex adult Leach's Storm Petrels during incubation across three breeding seasons (2016, 2017, 2019) from five colonies (Baccalieu Island (BA; 48°07′29.40"N, 52°48′2.99"W), Bon Portage Island (BP; 43°28′00″N, 65°45′00″W), Country Island (CI; 45°6′8″N × 61°31′35″W), Gull Island (GI; 47°15′42″N × 52°44′49″W) and Kent Island (KI; 44°34′48″N, 66°45′36″W)) in the Northwest Atlantic (Tables 1 and 2). Birds were chosen haphazardly for inclusion in the study at each colony in each year between mid-June and mid-July, which coincides with the bulk of the incubation period. All birds in the study completed

Table 1. Sample sizes by colony and sex.

	GLS						GPS					
	Females		Males		Total		Females		Males		Total	
Colony	*n*	Trips	*n*	Trips	*n*	Trips	*n*	Trips	*n*	Trips	*n*	Trips
BA	10	26	12	33	22	59	11	19	8	15	19	34
BI	7	15	3	9	10	24						
BP	5	9	2	4	7	13	8	14	5	6	13	20
CI	9	17	2	4	11	21	4	4	9	11	13	15
GI	9	30	11	38	20	68	9	10	9	10	18	20
KI	19	72	20	78	39	150	4	4	8	9	12	13
MLI	3	11	5	15	8	26						
TOTAL	62	180	55	181	117	361	36	51	39	51	75	102

n denotes number of individual birds and Trips represents the number of foraging trips by individuals in that column (Females, Males or Total). GLS devices were used in 2013–2015 and GPS devices were used in 2016–2019. Totals represent sample sizes for the modelling analyses and all years combined (BA = Baccalieu, BI = Bird, BP = Bon Portage, CI = Country, GI = Gull, KI = Kent, MLI = Middle Lawn).

Table 2. Foraging trips per year for all colonies combined.

Year	Females	Males	Total
2013	75	71	146
2014	83	64	147
2015	22	46	68
Total GLS	180	181	361
2016	16	19	35
2017	13	7	20
2019	22	25	47
Total GPS	51	51	102

Number of foraging trips recorded by sex for each year. GLS devices used in 2013–2015 and GPS devices in 2016–2019.

their foraging trips during the incubation stage of reproduction.

Upon capture by hand in their nesting burrows, nanoFix® GEO-Mini GPS devices (0.95 g, 20 × 12 × 4 mm, plus external whip antenna) from PathTrack Limited (www.pathtrack.co.uk) were attached to the inter-scapular region using sub-dermal suture after Pollet *et al.* (2014a). The location data collected for this study were a subset of a larger study funded by multiple governmental and non-governmental agencies with the aim of understanding threats to this pelagic species, which has recently been identified as a species of concern. The suture technique was needed to maximize the probability that the devices could be retrieved to support this important conservation effort. All procedures were reviewed and approved by the appropriate animal care authorities.

The GPS device with attachment weighed ~ 1.3 g, which is 2.5% of the mean weight of adult birds that have been caught on their first day of incubation at Kent Island (51.2 g ± 3.9 sd, $n = 593$, R. A. Mauck unpubl. data). Birds were returned to their nesting burrow within 15 min of attachment. Previous work using GLS devices of similar size and weight supported the reliability of suture attachments and showed no statistically significant effect on hatching success, fledging success, adult body mass or return rate, although there was some evidence for a small impact on chick growth (Pollet *et al.* 2014a, 2014b). Individuals in those GLS studies carried the device for multiple weeks; in this study, due to battery limitations, GPS devices were attached relatively briefly, typically for a single foraging trip (1.4 days ± 0.6 sd foraging trips, 3.6 days ± 1.8 sd per trip), with only four of the 75 birds in the study carrying the device for more than two foraging trips. Upon recapture, devices were removed by cutting the sutures and data were downloaded in the lab.

GPS devices were programmed to capture satellite data for location estimation every 2 h. Data stored included number of satellites obtained, date/time stamp in UTC, latitude, longitude and battery level. Initial screening of downloaded data identified location attempts with too few (< 4) satellite fixes for reliable estimation, which we assigned as unknown ('NA').

Individual trips were identified according to directional movement away from the colony location for a minimum of 2 h. A foraging trip was deemed completed when the bird returned to the colony.

Most foraging trips (65 of 102) were complete (i.e. had no missing locations). The other 37 trips had a first or last location that required an unrealistic flight speed (> 50 km/h) between that location and the colony, indicating a dying battery (end of trip) or a programmed delay in start time (beginning of trip), or simply a bad satellite acquisition. When calculating total distance for those trips, we assume a straight line connecting the known location of the colony to those first or last locations, and therefore total distance represents the minimum total distance travelled. Similarly, some isolated erratic locations also occurred in the data (33 of 4382 locations; 0.75%), probably the result of poor satellite acquisition (i.e. a location resulting in a step length that demanded an improbable flight speed). We assigned NA to those erratic coordinates and treated the previous and subsequent step lengths as a straight line.

Given the high spatial and temporal resolution provided by GPS, we were able to use state space modelling to associate each location to a behavioural state. We did so by implementing a hidden Markov Model (HMM) using the R package 'momentuHMM' (McClintock & Michelot 2018) to classify locations within each trip into behavioural categories based on step length and turning angle. Before implementing HMM, each trip trajectory was interpolated to regular 2-h intervals (the set interval of the GPS devices). This temporal scale provides less granularity than that provided by accelerometers but a useful estimation of general movement patterns. Note that interpolation and HMM model building are applied on the trajectory spanning from the first to the last observed locations without including assumed step length between first or last location of trip and the colony when those were missing (above). The final model was built with three states, and hour of the day was included as a covariate to account for potential effects of diel foraging strategies. Given the temporal resolution of the data (location every 2 h), we interpreted the three behavioural states as follows: 'Intensive search' (short steps and high tortuosity in trajectory), 'Extensive search' (lengthier steps and decreased tortuosity) and 'Transit' (travelling in a directional pattern with very little tortuosity). This terminology was suited to describing our telemetry data but should not be interpreted as perfect knowledge of a bird's behaviour. For example, the 'Intensive search' classification would probably include both foraging behaviour in a relatively small area of the ocean and resting behaviour, which could not be distinguished between here.

We further extracted bathymetry data at every search-related location in each trip using the R package 'marmap' (Pante & Simon-Bouhet 2013). We then calculated mean depth (DepthMean) and maximum depth (DepthMax) of searching locations for each foraging trip.

Spatial utilization

We used the *kernelUD* function from the R (R Core Development Team 2017) package 'adehabitatHR' (Calenge 2006) to calculate kernel utilization distributions (KUDs) of GPS locations for each sex at each colony using only locations identified as Intensive or Extensive searching. We used the same smoothing parameter (h) across sexes and colonies. This smoothing parameter corresponded to the average h found across all individuals (i.e. h was calculated using the *href* method from the *kernelUD* function for each individual and averaged between them (mean h = 67.7 km)). We then used the conditional estimate of Bhattacharyya's affinity (BhA; Fieberg & Kochanny 2005) to compare areas used by males and females within each colony.

Global location sensors (GLS)

We tracked 122 known-sex individuals for the GLS study from seven colonies (BA, Bird Island (BI; 44°52′12″N, 62°16′48″W), BP, CI, GI, KI and Middle Lawn (ML; 46°52′12″N, 55°37′12″W)) during incubation across three (2013–2015) breeding seasons (Tables 1 and 2). Field procedures for GLS were similar to those for GPS devices. GLS characteristics, calibration, deployment, data retrieval and the processing of raw location data have been described in detail by Hedd *et al.* (2018).

Because of the error associated with location estimates from GLS accuracy (Phillips *et al.* 2004a), we compared the calculated calibration error of devices (Lisovski *et al.* 2012) attached to males with those attached to females to rule out device bias in the results. We removed five devices for which the mean error (i.e. distance from known location) of all calibration points from the calibration site was >2 sd from the mean of all GLS devices. Median distance from the calibration reference points did not differ (Kruskall–Wallis, $H = 0.539$, $P = 0.46$) between devices on males (111.0 km) and on females (111.4 km) when pooling data across all colonies. Within all colonies, calibration did not differ ($P > 0.1$) between the sexes in terms of direction. The resulting 117 devices were then used in all GLS analyses.

Sex determination

We established the sex of adult Leach's Storm Petrels using a variation on the protocol for DNA-based sexing of non-ratite birds (Ellegren 1996). Birds from both datasets (GPS and GLS) were subsets of birds monitored for larger conservation-driven studies; information on sex was unavailable in 2018, resulting in more birds of known sex for the GLS dataset than for the GPS dataset (Table 1). Blood samples for sex-determination were collected upon recovery of the tracking device to reduce stress on individuals. We therefore had no instances of non-recovered devices to report for the investigation of sex differences in foraging. Across the larger conservation-driven studies (2013–2019), device recovery was ~ 76%, mainly due to egg abandonment by tagged individuals. This proportion is similar to historical hatching success in these colonies, which is also largely driven by egg abandonment (Pollet *et al.* 2020).

Trip metrics

For each dataset (GPS and GLS), we determined spatial characteristics of individual trips using the R packages 'adehabitatLR' and 'adehabitatHR' (Calenge 2006). We calculated total orthodromic distance (TotalD; km) covered on each foraging trip and the maximum orthodromic distance (MaxD; km) from the colony of each foraging trip. The duration (TDur) of each GPS foraging trip was calculated as the difference in time from the first to the last location recorded for each trip. For the GLS data, duration was calculated as the difference between the last day the bird was recorded at the colony before a foraging trip and the first day it was next recorded at the colony (Hedd *et al.* 2018). These variables were used to characterize sex differences in foraging behaviour at the level of individual foraging trips.

Statistical analyses

All statistical analyses were performed in R version 4.1.1 (R Core Development Team 2017). We used the 'lmerTest' package (Kuznetsova *et al.* 2017) in R to construct initial linear mixed-effects models (LMMs) with identity link and Gaussian error to explain variation in TotalD, MaxD and TDur of foraging trips for GPS data. For analysis of TotalD and MaxD, with both datasets, the initial model included fixed-effects of sex, TDur, Year, day of year (Julian day) of the trip departure date (DOY) and Wing Length (WL). The initial model also included the interactions between sex and Year, sex and DOY, as well as sex and TDur. We included trip duration to account for the positive effect of time on distance covered in any particular foraging trip. We included DOY to account for chronological changes through the season and the ~ 44-day incubation period, as we did not have egg-laying dates for most individuals. We included Year as a factor to determine whether results were overly influenced by conditions in a single year. We included Wing Length to determine the influence of morphology on foraging behaviour. In the initial models, we included Colony and Individual ID (ID) as random effects because some individuals in both datasets were recorded for more than one trip (Table 1), although only one individual (male) was used in more than one year. We used stepwise backward elimination from the 'lmerTest' package (Kuznetsova *et al.* 2017) to find the most parsimonious model from the variables included in the initial LMMs. An alpha of 0.05 was the threshold for removing fixed effects and 0.01 for random effects. We report the effect size, *t*-statistic and *P*-value of the significance of the fixed effects for the final variables included in the most parsimonious model. We repeated the procedure with the GLS dataset without including Wing Length, which was not available.

We used similar statistical procedures to analyse variation in TDur, as well as DepthMean and DepthMax for searching locations of foraging trips for the GPS dataset only. The initial models for these analyses contained variables directed by results of the distance models. Because the initial stepwise backward elimination in the TDur model dropped all random effects from the model, we had to use the R function 'step' on an initial model without the random effects for the stepwise elimination procedure. This function uses Akaike's information criterion (AIC) to determine the most parsimonious model (R Core Development Team 2017).

Using the dataset of behaviourally classified GPS locations derived from HMMs, we used multiple analysis of covariance (MANCOVA) to look at differences in the distribution of behaviours (Transit, Extensive search, Intensive search) per trip between males and females. To account for the portion of variance explained by potential colony differences and trip duration, we included those two variables as fixed terms in the MANCOVA model. Again, we included trip duration to adjust for the fact that the total number of categorized locations is dependent on time away from the burrow. This comparison was only possible for the GPS dataset, as GLS data suffer from much lower spatial and temporal resolution (Phillips *et al.* 2004a).

We examined the assumptions of all models, including evaluation of residuals for linearity and normal distribution. We tested for homogeneity of variance in the linear mixed-effects models relative to colony by calculating $F_{\max}$, which is derived from the variance of the dependent variable for each colony, then calculated as the ratio of the largest colony variance/smallest colony variance. An $F_{\max} < 10$ combined with an analogous ratio of sample size (largest colony sample size/smallest colony sample size) that is < 4 is considered acceptable (Tabachnick & Fidell 2013). For the MANCOVA, $F_{\max}$ was calculated from the variance ratios using ES, IS and TR. Unless stated otherwise in the Results, all models met assumptions.

To determine whether KUD overlap between the sexes in the GPS dataset was greater or lesser than expected by chance, we did a randomization procedure within each colony after Paiva *et al.* (2017). Briefly, for each of 1000 iterations, we randomly assigned sex (M or F) to all individuals in the colony maintaining the original sex ratio of birds studied in the colony. For each iteration, we then calculated BhA using the randomized individuals of each sex. No randomly assigned combination of males and females appeared more than once in the 1000 iterations. We then compared the BhA observed in the original data to the 1000 BhA values of the randomized data for each colony to determine the likelihood that the overlap observed was less than expected by chance.

We used the R package 'diptest' (Maechler 2021) to detect whether Leach's Storm Petrel trip distances showed the bimodal distribution of short and long foraging trips seen in some other seabird species (Weimerskirch *et al.* 1994, Wojczulanis *et al.* 2006, Welcker *et al.* 2009).

RESULTS

Populations

We obtained GPS locations for 102 foraging trips by 36 males and 39 females, and GLS locations for 360 foraging trips by 117 birds (65 females, 57 males) (Tables 1 and 2). The two datasets were analysed separately. Among the subset of GPS birds for which wing length was determined, female wing length adjusted for colony ($n = 17$, 160.8 mm ± 8.7 sd) and adjusted male wing length ($n = 28$, 159.3 mm ± 4.7 sd) were not significantly different ($t = 1.9$, df = 34.9, $P = 0.07$).

Foraging trip metrics

For TotalD and MaxD, the final models obtained following the backward stepwise elimination procedure of the initial LMM contained only the random effect of colony, and the fixed effects sex and TDur without interactions. This prevailed for both the GPS data and the GLS data for TotalD, whereas colony was not kept as a random effect for MaxD using the GLS data (Figs 1 and 2). Because WL was not included in any of the final models, we used the entire dataset ($n = 102$) to characterize the effects that were included in that final model.

Mean total distance of female foraging trips, calculated from GPS locations, exceeded that of males by 418.9 km ± 154 se ($t_{32.8} = 2.72$, $P = 0.01$; Fig. 1 and Table 3). Results from models derived from GLS locations showed the same tendency, with females covering on average 160.3 km ± 72.3 se more per trip than males ($t_{59.9} = 2.22$, $P = 0.03$; Table 3). Trip duration had the greatest effect on TotalD for both GPS (316 km/day ± 32.3 se, $t = 9.80$, $P < 0.0001$) and GLS (224 km/day ± 20.2 se, $t = 11.14$, $P < 0.0001$) data. Maximum distance from the colony reached during a foraging trip by females was 220.5 km ± 80.6 se greater than that reached by males when calculated using

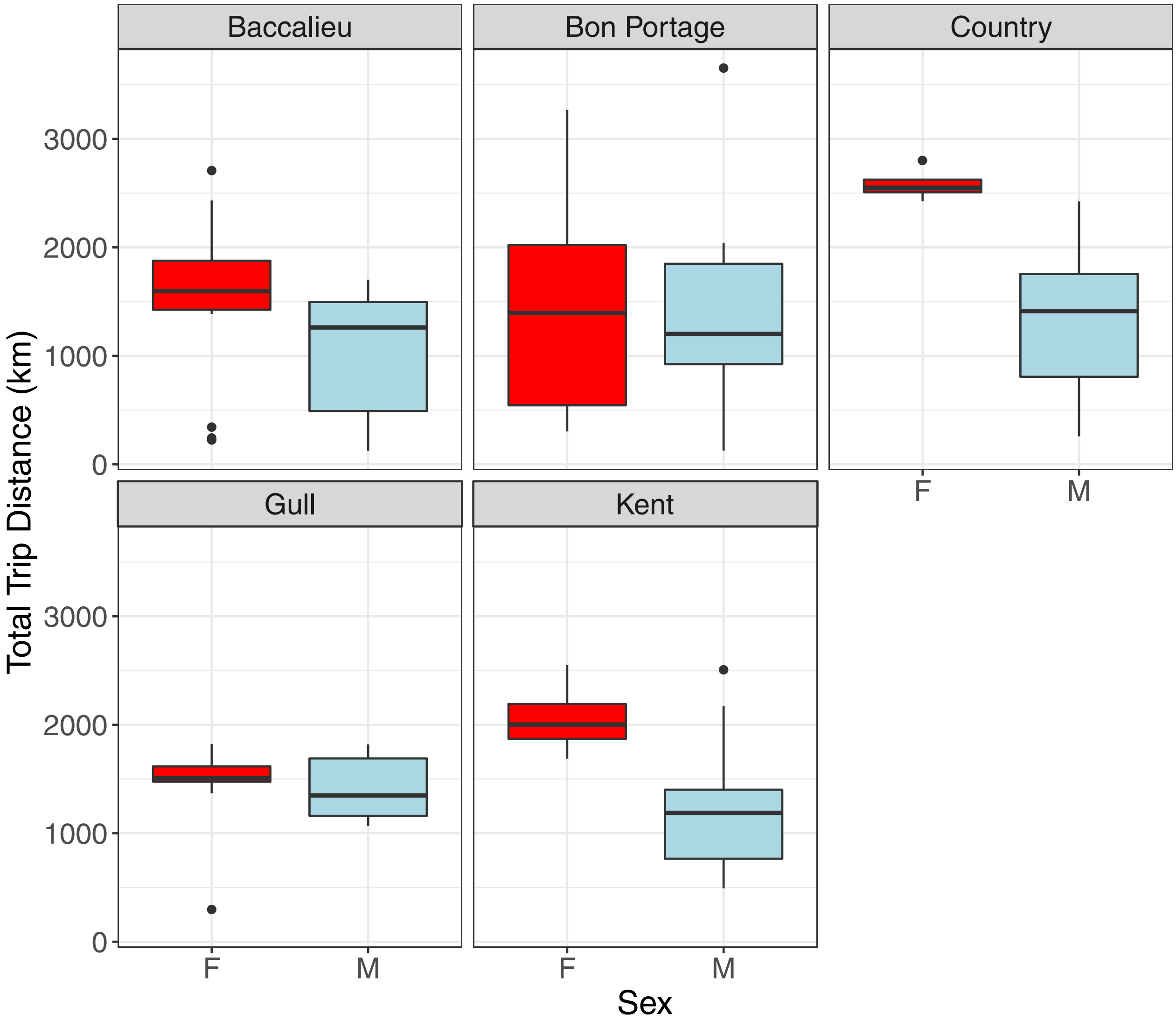

Figure 1. Total distance covered on foraging trips during the incubation period by Leach's Storm Petrels according to sex (dark = females, light = males) and nesting colony. Leach's Storm Petrels (n = 75) were tracked with GPS devices between 2016 and 2019 at five different colonies in eastern North America. [Colour figure can be viewed at wileyonlinelibrary.com]

GPS locations ($t_{66.7}$ = 2.74, $P < 0.01$; Fig. 2, Table 3). The same held true when considering GLS locations; female MaxD from the colony was 67.5 km/day ± 30.1 se greater than that of males ($t_{78.9}$ = 2.23, P = 0.03; Table 3). Trip duration, also, had the greatest effect on MaxD for both GPS (350.2 km/day ± 22.7 se; $t_{98.1}$ = 15.4, $P < 0.0001$) and GLS (53.5 km/day ± 6.5 se; $t_{247.7}$ = 8.18, $P < 0.0001$) data. Mean total distance and maximum distance from the colony were highly correlated (r = 0.93; Fig. 3).

The distribution of trip distances (GPS data) was not significantly different from unimodality across all colonies (D = 0.04, P = 0.28) or when viewing only the two Newfoundland colonies, Baccalieu and Gull, which had the largest sample sizes, relatively even sex ratios and similar trip metrics (D = 0.05, P = 0.25). However, visual inspection of TotalD distribution from these two colonies shows a cluster of short trips < 600 km (Fig. 4). These were equally split between the sexes (4 M, 4 F); male trips (185.1 km ± 65.2 sd)

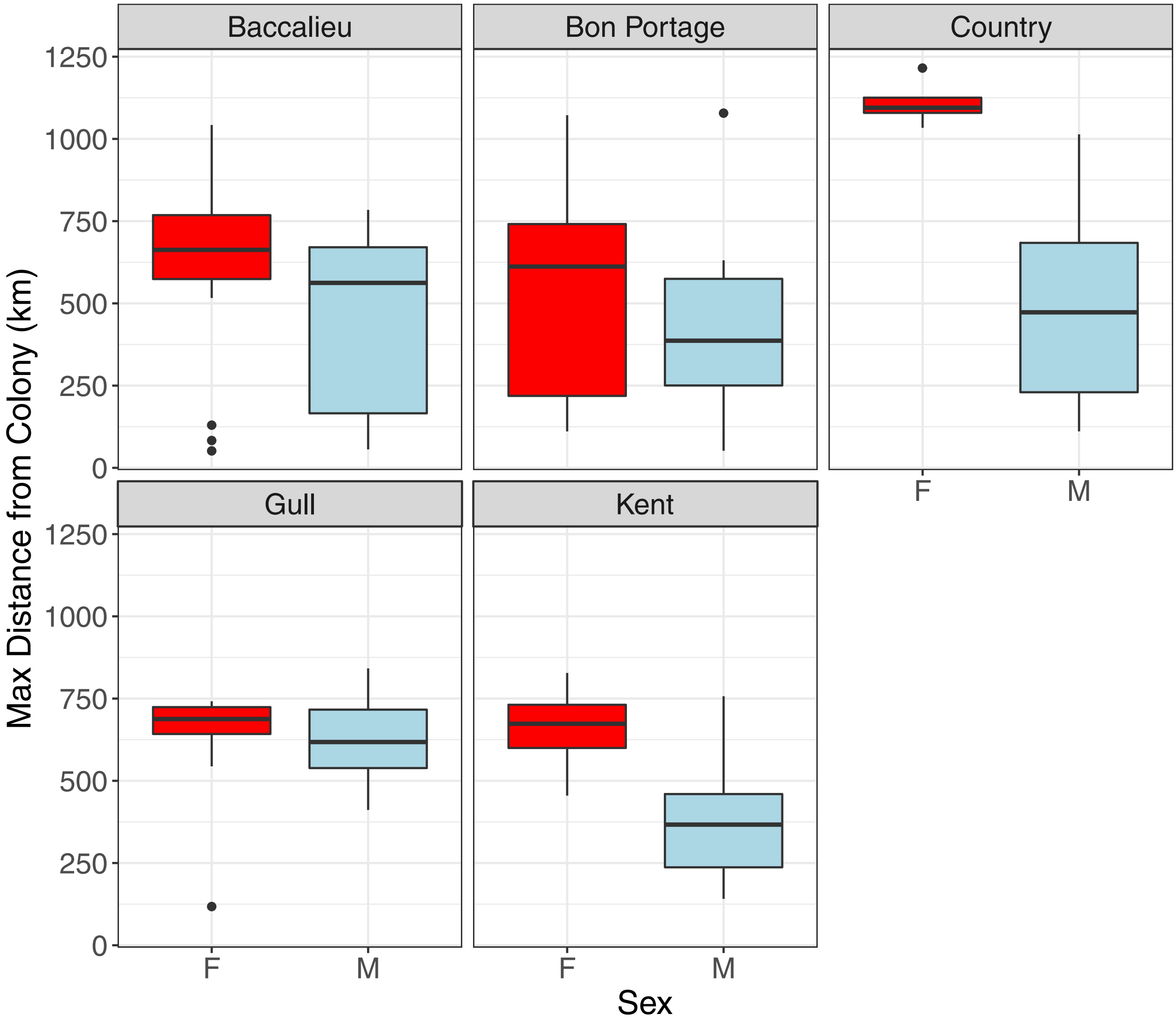

Figure 2. Maximum distance from the colony reached by Leach's Storm Petrels during foraging trips during the incubation period according to sex (dark = females, light = males) and nesting colony. Leach's Storm Petrels (n = 75) were tracked with GPS devices between 2016 and 2019 at five different colonies in eastern North America. [Colour figure can be viewed at wileyonlinelibrary.com]

and female trips (277.81 km ± 54.2 sd) were not significantly different (Wilcoxon test; $W = 14$, $P = 0.11$). The lower end distribution of trip lengths across all colonies showed similar characteristics. The Trip distances calculated from GLS data were not different from unimodal ($D = 0.02$, $P = 0.96$) and did not show a similar cluster at the lower end of the distribution.

The backward stepwise elimination procedure using the GPS dataset to model TDur eliminated all random effects. We therefore repeated the elimination procedure using linear models which resulted in a final model ($F_{5,96} = 5.92$, $P < 0.0001$) with the fixed effects of DOY ($t = -3.46$, $P < 0.001$) and sex ($t = 1.85$, $P = 0.07$) with their interaction (0.08 ± 0.05 day, $t = 1.78$, $P = 0.08$), along with a year effect ($t = 2.64$, $P = 0.01$) with no interaction. Females were away from the colony *c.* 15 h longer per trip than males (± 0.6 day; model adjusted; Table 3). Independent of sex, TDur declined throughout the breeding season (−1.2 days/DOY ± 0.04 se) but the interaction of DOY and Sex retained in the final model suggests that the decline across the

Table 3. Sex-specific trip metrics.

Measure	Sex	Trips	Mean	sd	Median
GPS: Total Distance (km)	F	51	1627.6	737.6	1639.62
	M	51	1273.0	688.0	1271.69
GPS: Maximum Distance (km)	F	51	638.7	280.0	676.62
	M	51	508.6	240.7	534.23
GPS: Trip Duration (days)	F	51	3.74	1.9	3.77
	M	51	3.39	1.6	3.76
GLS: Total Distance (km)	F	177	1738.3	722.0	1617.2
	M	181	1532.2	734.3	1427.9
GLS: Maximum Distance (km)	F	177	652.6	248.3	620.4
	M	181	573.1	249.0	540.7
GLS: Trip Duration (d)	F	177	4.22	1.42	4
	M	181	4.16	1.49	4

Summary of Trip Distance, Max Distance and Trip Duration raw values pooled across all colonies for males (M) and females (F). Trips = number of foraging trips.

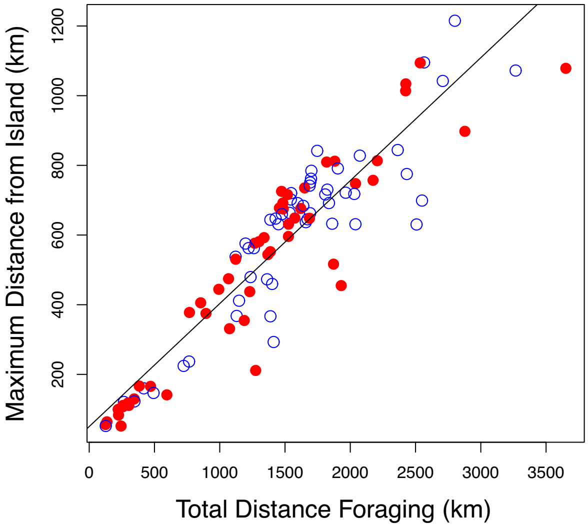

Figure 3. Relationship between Total Distance travelled on a foraging trip and the Maximum Distance reached from the colony on that trip. Filled circles are trips by male ($n = 51$) and empty circles are trips by female ($n = 51$) Leach's Storm Petrels. [Colour figure can be viewed at wileyonlinelibrary.com]

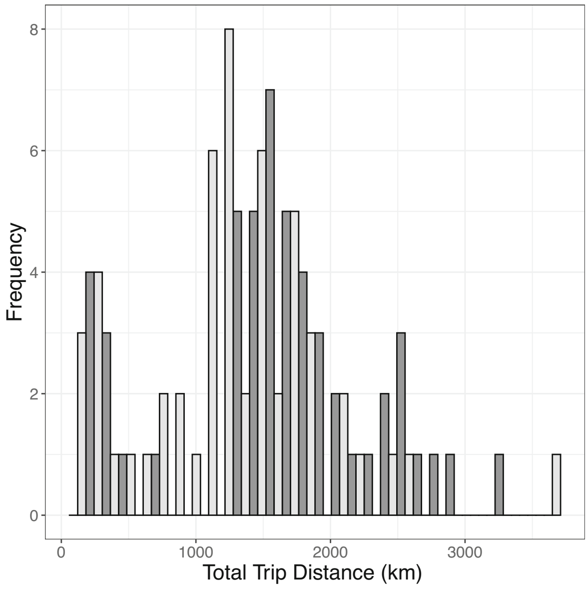

Figure 4. Distribution of total distance covered on foraging trips ($n = 102$) during the incubation period by male (light grey) and female (dark grey) Leach's Storm Petrels. Leach's Storm Petrels ($n = 75$) were tracked with GPS devices between 2016 and 2019 at five different colonies in eastern North America.

season was steeper for females than for males (Fig. 5). TDur in 2019 (4.1 days ± 0.3 se) was longer than TDur in 2016 (3.1 days ± 0.3 se) and 2017 (3.5 days ± 0.4 se). The final model for the GLS dataset contained the random effects of ID and Colony and the fixed effects of DOY (−0.55 day/DOY ± 0.01 se; $t_{194.1} = -5.56$, $P < 0.0001$) and Year such that TDur was generally longer in 2013 (4.6 days ± 0.3 se) than in either 2014 (3.99 days ± 0.3 se; $t_{58.4} = -2.57$, $P = 0.01$) or 2015 (3.6 days ± 0.3 se; $t_{59.3} = -3.77$, $P < 0.001$). No effect of sex on TDur was detected in the GLS dataset (Table 3).

Ocean depth at searching locations

Considering foraging trip MeanDepth and MaxDepth at searching locations, the final reduced models contained only the random factor of colony and the fixed effect of trip duration on both

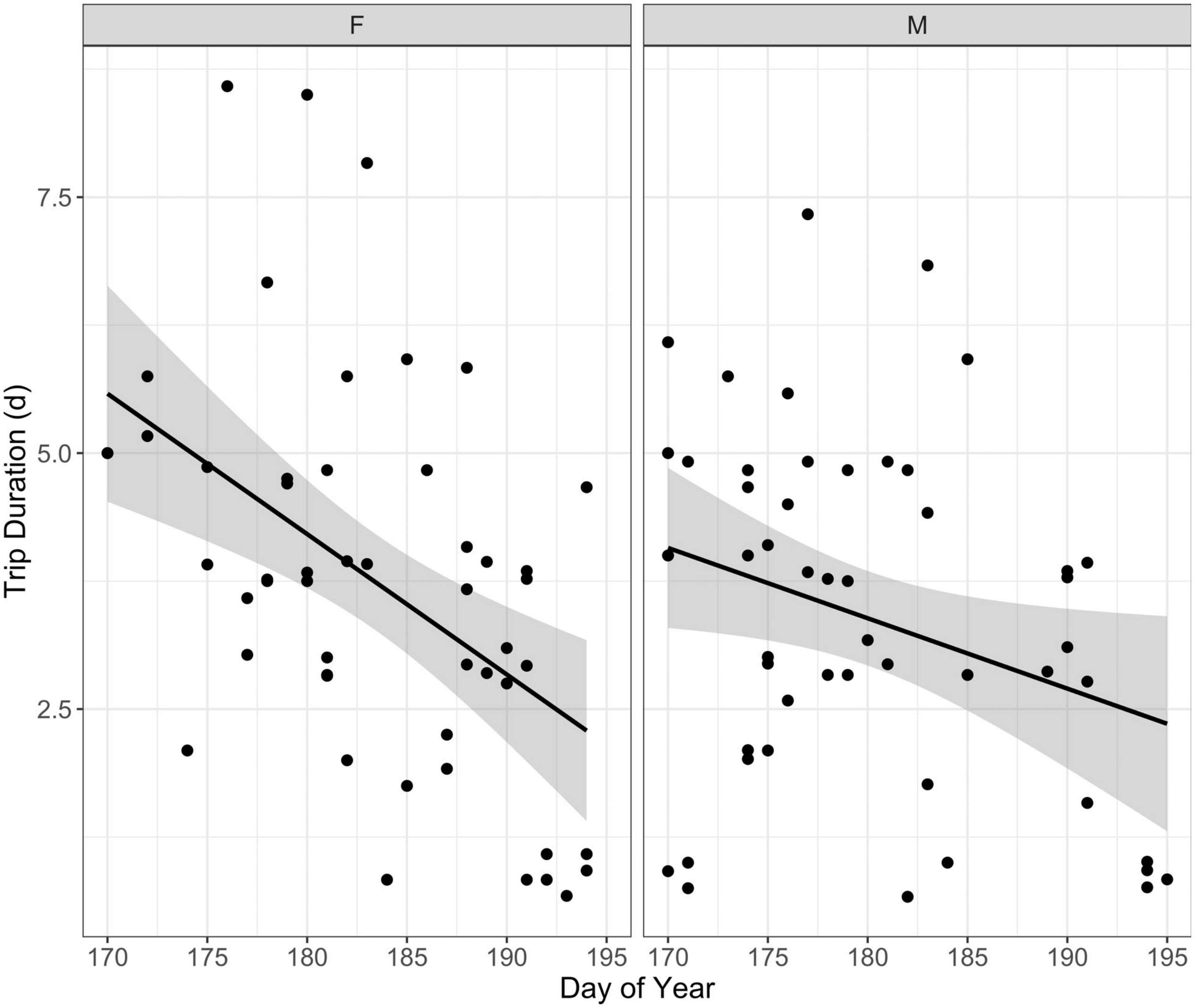

Figure 5. Leach's Storm Petrel foraging trip duration during the incubation period as a function of Day of Year and Sex (F = Females, M = Males). Day of Year represents the first day of an individual foraging trip (*n* = 102) and varied between 14 June (Day 170) to 14 July (Day 195) across years. Solid lines indicate the least squares fit and the shaded areas represent the 95% confidence interval of the fit. Leach's Storm Petrels (*n* = 75) were tracked with GPS devices between 2016 and 2019 at five different colonies in eastern North America.

MeanDepth (−1.31 m/km ± 0.13 se; $t_{95.2} = -10.4$, $P < 0.0001$) and MaxDepth (−1.96 m/km ± 0.14 se; $t_{95.2} = -14.0$, $P < 0.0001$). The degree to which ocean depth was influenced by trip duration varied across colonies for both measures ($\chi^2 > 14$, $P < 0.001$).

Utilization of space

Across colonies, Bhattacharyya's affinity (BhA) suggests a high degree of similarity in where the sexes foraged at the level of the 95% KUD (BhA = 0.70 ± 0.08 sd); however, core KUD (50%) shows much less overlap (BhA = 0.2 ± 0.08 sd) between the sexes (Fig. 6, Table 4). Randomization tests at both 95% and 50% KUD showed that the degree of overlap by monitored birds from Baccalieu, Gull and Kent is not less than expected by chance, whereas overlap of birds from Bon Portage and Country was less than expected (Table 4). Across colonies, the mean probability from the randomization tests weighted by sample size is not

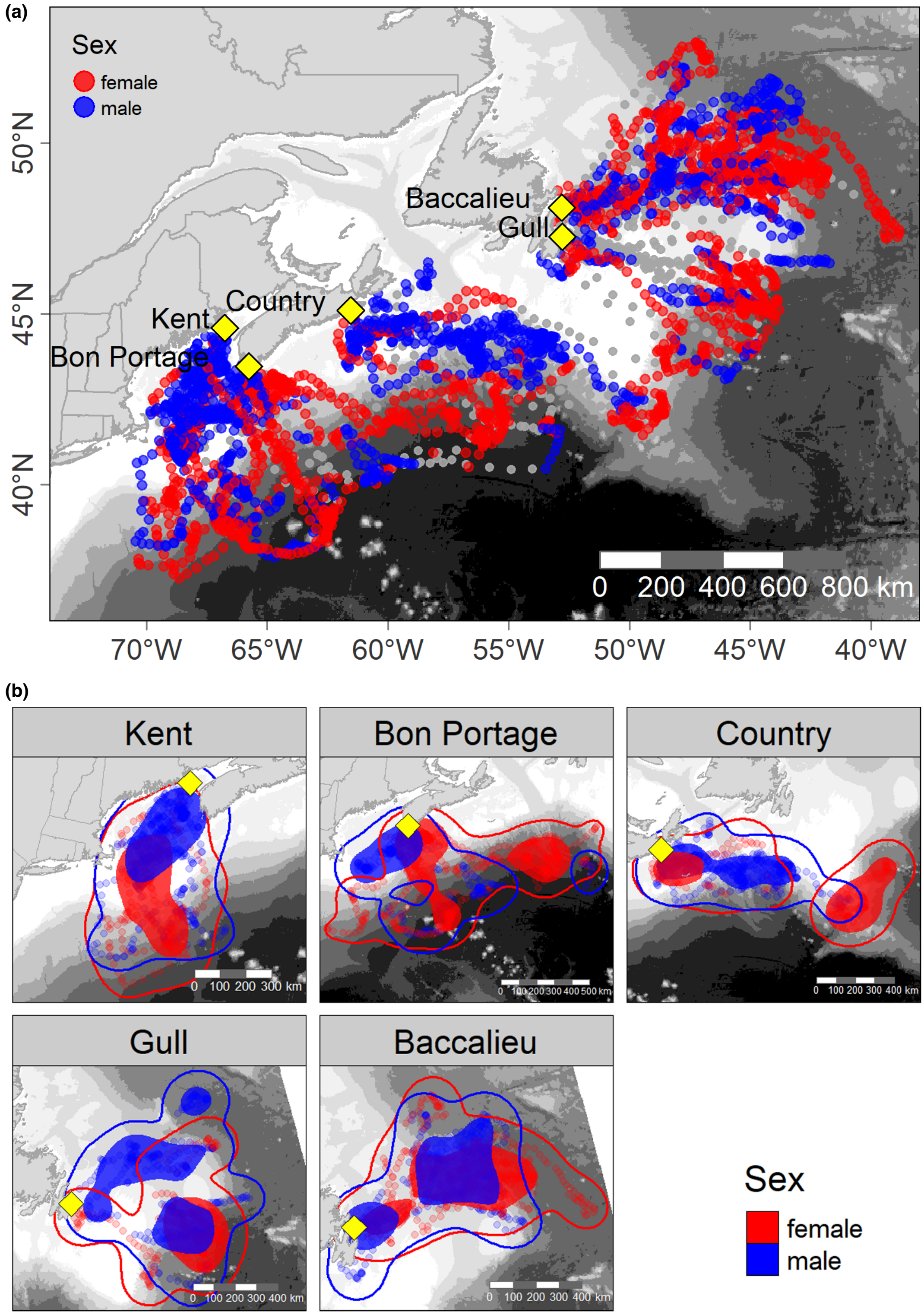

Figure 6. Leach's Storm Petrel (n = 75) were tracked with GPS during the incubation period from 2016 and 2019 at five different colonies in eastern North America (marked by yellow diamonds). (a) Locations (dots) classified as either extensive or intensive search for males (blue) and females (red) that were used to calculate kernel utilization distributions (KUD); grey dots show transit locations. (b) The 95% KUD (contour lines) and 50% KUD (solid polygons) by sex. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 4. Foraging area overlap.

Colony	BhA		Relative Size		Total	Randomization	
	KUD_{95}	KUD_{50}	$Area_{95}$	$Area_{50}$	$Area_{95}$	P_{95}	P_{50}
Baccalieu	0.82	0.32	0.92	1.02	562 078	0.43	0.47
Bon Portage	0.65	0.15	0.67	0.47	747 990	0.11	0.08
Country	0.60	0.16	0.78	0.82	548 741	0.00	0.02
Gull	0.68	0.23	1.39	2.15	558 622	0.60	0.42
Kent	0.73	0.14	0.96	0.77	269 837	0.12	0.10
Mean	0.70	0.20	0.94	1.05	537 454	0.29	0.25
sd	0.08	0.08	0.27	0.65	171 118		

Degree of overlap in searching locations between male and female Leach's Storm Petrels tracked with GPS at five different colonies in eastern North America between 2016 and 2019. BhA is the Bhattacharyya affinity, a measure of similarity in space use (0–1) between two independent groups. BhA columns show overlap at 95% and 50% KUDs between the sexes. Relative Size columns show the ratio (M/F) of the foraging areas (km^2) calculated from the KUDs. Total Area is the combined area for all foraging points by both sexes in a colony calculated from a 95% KUD for those pooled points. Randomization columns show the probability that the observed overlap (BhA) between the sexes is less than expected by chance, calculated from 1000 randomized trials for both the 95% KUD (P_{95}) and the 50% KUD (P_{50}).

different to expected by chance ($P_{50,95} > 0.05$; Table 4). Mean area of the 95% KUD for all Leach's Storm Petrels averaged across colonies was 537 454 km^2 ± 171 118. The mean ratios of coverage area (Male/Female) for the 95% KUD (0.94 ± 0.27) and the 50% KUD (1.05 ± 0.65) were similar (Table 4).

Activity pattern between sexes

Independent of colony differences and TDur, the distribution of behaviours within foraging trips differed strongly by sex ($F_{3,93} = 14.15$, $P < 0.0001$). Females spent more time than males in Transit ($F_{1,95} = 12.03$, $P = 0.0008$) and Extensive ($F_{1,95} = 10.86$, $P = 0.001$) searching mode, whereas males spent more time than females in Intensive search mode ($F_{1,95} = 8.71$, $P = 0.004$; Fig. 7).

DISCUSSION

Male and female Leach's Storm Petrels exhibited different spatial foraging strategies during the incubation period. Females covered significantly longer distances and foraged farther from their breeding colonies than did males on individual foraging trips, even controlling for the duration of the foraging trip. Accordingly, females spent more time in transit or extensively searching during foraging trips than males, and less time was spent intensively searching, suggesting that females travelled more widely than males when foraging during the incubation period.

Although GPS data provide more precise estimates of Leach's Storm Petrel movement patterns, it is an important confirmation that the GLS and the GPS spatial data qualitatively agreed. In fact, the inherent imprecision of GLS (Phillips *et al.* 2004a) may have biased against finding any differences between the sexes, as was probably the case with respect to trip duration. However, the error associated with GLS spatial data apparently was overcome by sample size. The congruence of spatial results between the two datasets across two different 3-year spans strongly suggests that the detected differences in foraging spatial characteristics between the sexes is a robust effect.

It is possible that the sex differences we see in foraging trips are driven by avoidance or resource partitioning, as has been found in some dimorphic procellariiform seabirds. For example, in Giant Petrels *Macronectes* spp., females and males apparently spatially partition the resources with diverging strategies that reduce competition (Granadeiro *et al.* 1998). In both Wandering Albatross and Giant Petrels, males and females seek different prey, causing them to segregate spatially (Phillips *et al.* 2011). While such sex-specific segregation may not be as common in monomorphic seabirds (Hedd *et al.* 2014), such segregation while raising chicks has been shown in the slightly dimorphic Scopoli's Shearwater *Calonectris diomedea* during environmentally challenging breeding seasons (Reyes-Gonzalez *et al.* 2021). Under such conditions, both sexes increased foraging effort, but females travelled farther and expanded their

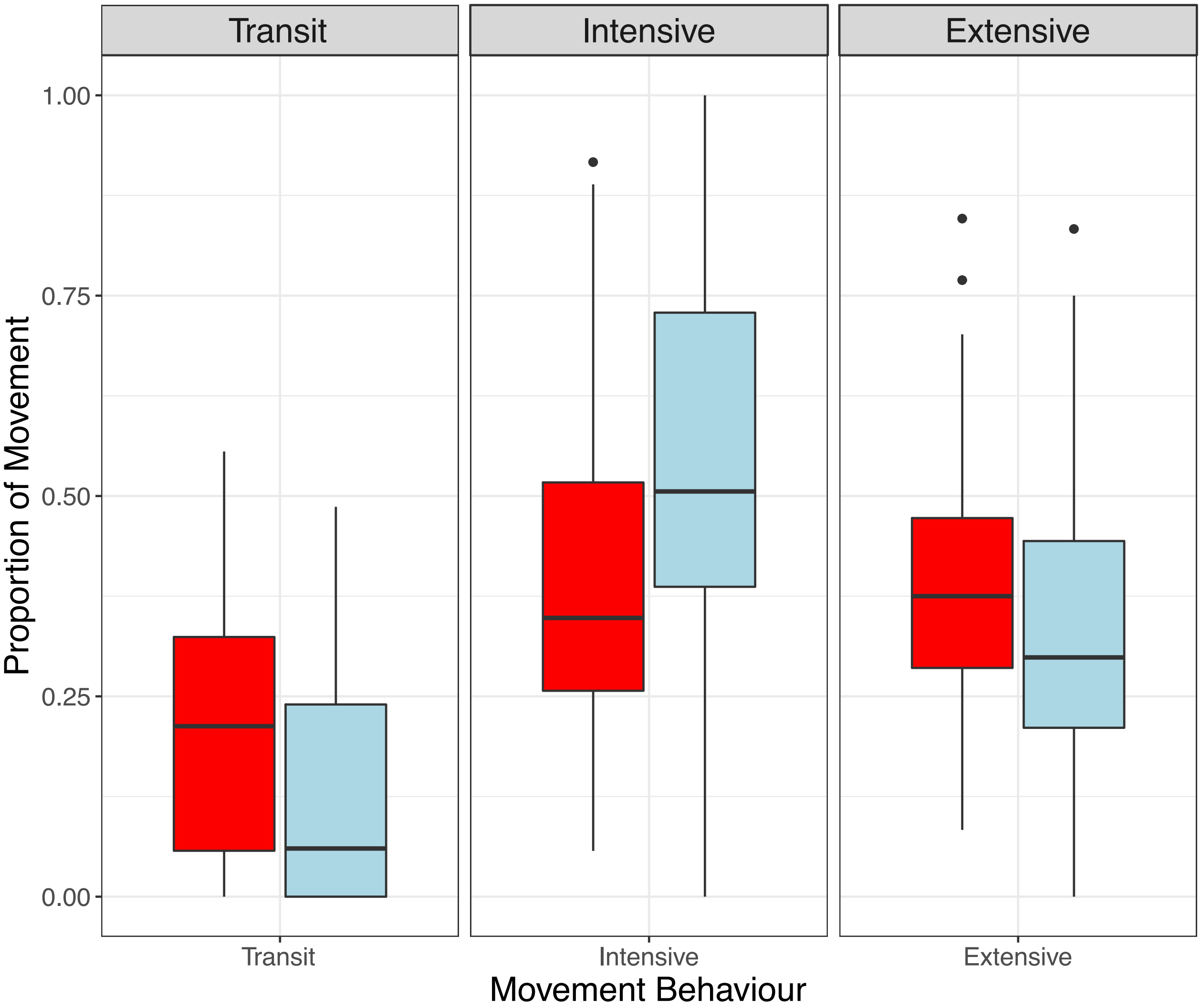

Figure 7. Distribution of the three behaviours during foraging trip according to sex (dark = females, light = males) for Leach's Storm Petrels ($n = 75$) tracked by GPS at five different colonies in eastern North America between 2016 and 2019. Data presented represent proportional distributions per foraging trip. [Colour figure can be viewed at wileyonlinelibrary.com]

foraging range beyond that of males, which the authors interpreted as competitive.

Our results do not support the segregation hypothesis for Leach's Storm Petrels. Although we found some inter-colony variation in overlap between the sexes in both the 50 and 95 KUDs, the weighted mean overlap was not less than expected by chance. Two colonies, Bon Portage and Country, showed signs of segregation, but these were the colonies with the smallest sample sizes and most skewed sex ratios of monitored birds. However, the two colonies with the largest sample sizes and balanced sex ratios (Baccalieu and Gull) showed no evidence of a sex difference in foraging area utilization. In addition, mean and maximum ocean depth during foraging were not significantly different between the sexes, which might be expected if resource partitioning drives differences in foraging distances. In general, therefore, we do not have evidence that spatial segregation drives the sex differences we found in foraging trip metrics.

Sex-specific differences in wing-loading have also been proposed to drive segregation and foraging behaviour. De Pascalis *et al.* (2020) found that female Scolpi's Shearwaters made longer trips, farther from the colony than males, a result similar to ours, which they determined was largely a function of higher wing-loading in males. Paiva *et al.* (2018) conclude that the longer wings of female Montiero's Storm Petrels *Hydrobates monteiroi* allowed them to forage more efficiently than males over longer distances, resulting in segregation, particularly during the incubation period, even though the female wings were only about 3% longer than males. In our sample, female wing length was not significantly longer than male wing length. The sex difference was about 1% and wing length cannot be used reliably to sex individuals (R. A. Mauck unpubl. data). Importantly, wing length was not included in the final models of TotalD and MaxD, whereas sex was retained. Apparently, the small inter-sexual difference in wing length is overwhelmed by other differences between the sexes and does not drive the observed sex differences in foraging trip metrics in Leach's Storm Petrels.

It was also possible that our results were a consequence of context, i.e. conditions in one particular year asymmetrically affecting the sexes, as has been shown during the chick-rearing period in some procellariaforms. This was the case for Scopoli's Shearwater during environmentally challenging breeding seasons (Reyes-Gonzalez *et al.* 2021), as well as Cory's Shearwaters *Calonectris borealis* over a 6-year period (Paiva *et al.* 2017). Similarly, female Wilson's Storm Petrel *Oceanites oceanicus* make longer foraging trips than males in years when krill is less available, allowing them to maintain chick-feeding rates comparable to males (Gladbach *et al.* 2009). While we found significant variation between years in both GPS and GLS datasets, we found no interaction with sex. Given that the sexes reacted similarly to conditions each year, we do not believe that the environmental context drives the sex differences we observed, perhaps because we examined behaviour during the incubation period.

In many seabird species, adults show a bimodal distribution of long and short foraging trips during the breeding season (Weimerskirch *et al.* 1994, Wojczulanis *et al.* 2006, Welcker *et al.* 2009). Such strategies are generally associated with feeding chicks when parental behaviour is not dependent on the partner's presence or absence on the egg, but it is still possible that our results can be explained by males prioritizing short trips more than females. Some bimodality has been shown in Leach's Storm Petrels from Gull Island during both incubation and chick-rearing periods (Collins *et al.* 2022). The overall distribution of trip lengths in our sample could not be distinguished from unimodal, though we observed a small cluster (17% of all trips) of trips with TotalD <600 km. In that cluster at the low end of the distribution, males and females were equally represented and mean trip length did not differ between the sexes. We might speculate that these were trips in which one partner returned to the nest before the incubating partner was ready to leave. While we cannot know the reason for these very short trips, it is doubtful that sex-specific differences in a bimodal strategy drive our results.

It may be useful to consider the initial disparity fundamental to petrel breeding; female Leach's Storm Petrels produce an egg that is 20–25% of their bodyweight (Pollet *et al.* 2020). Egg production in most birds depends on both female initial condition and resources gained during egg production (Nager 2006). Female procellariiforms commonly embark on a 'prelaying exodus' for this purpose (Gross 1935, Warham 1990). Some evidence suggests that seabird eggs require more resources than can be accrued by females strictly through such short-term 'income' (Hatch 1990, Sanz-Aguilar *et al.* 2012). Bond and Diamond (2010) used stable isotope analyses to demonstrate that Leach's Storm Petrel eggs comprised a combination of both locally derived nutrients and longer-term endogenous nutrients, with the yolk particularly dependent on stored resources. Further, in many species, egg formation degrades proteins associated with flight muscle, which then impacts flight characteristics (Veasey *et al.* 2001). Along the same lines, the simple fact that females carry an increased load over the 14–21 days of egg production should increase the mechanical costs of flight; using accelerometry, Whelan *et al.* (2021) showed that female Black-legged Kittiwakes *Rissa tridactyla* challenged with such a load significantly increased wing beat frequency while foraging. For a long-lived species such as Leach's Storm Petrels, in which current reproduction is a small proportion of lifetime reproductive potential, any dip in body condition should result in increased investment in self-maintenance at the cost of investment in offspring (Linden & Moller 1989, Mauck *et al.* 1999, Dearborn 2001). Thus, although foraging during egg formation may provide much of the resources needed by females, even a small toll on body condition should lead females to adjust their subsequent foraging strategies to compensate. It is therefore reasonable to think that female Leach's Storm Petrels bear some cost not experienced by males, either directly or indirectly, due to egg production.

Our results are consistent with the idea that females may compensate for the initial cost with a foraging strategy different from that of males. Specifically, females may compensate for decreased body condition not by flying less but by travelling more widely, perhaps to increase the likelihood of encountering more patches with enhanced prey availability or to adjust the balance between small fish and crustaceans in their diet (Hedd *et al.* 2009, Frith *et al.* 2020). Individual activity levels within each trip suggest that females spend more time prospecting compared with males; they spend a greater proportion of foraging trips either moving between patches (Transit) or prospecting more widely (Extensive search) compared with male Leach's Storm Petrels, which seem to spend more time in any particular patch (Intensive search). It is possible that Intensive search represents more time spent resting during a 2-h period rather than actively foraging in a restricted area. If this were the case, our data would suggest either (1) a sex-specific difference in foraging efficiency such that (1a) males are more efficient foragers than females and, therefore, have the 'luxury' of time to rest or (1b) females are more efficient foragers than males, allowing them to gather more food during extensive search and have less need of rest before returning to the colony, or (2) males need less food than females during incubation and do not need to spend as much time foraging. Although our data cannot rule out underlying differences between male and female foraging efficiencies, there are no biological indications that Leach's Storm Petrels harbour some fundamental sex-specific difference in sensory abilities or foraging skills. If Intensive search is, in fact, more reflective of resting than foraging – or the opposite is true and intensive search is somehow more costly than extensive search – parsimony might suggest that our data re-enforce the notion that the energetic needs of males are less than that of females during incubation.

If we think of females early in the incubation period as having a negative energy budget relative to males, then a mean level of energy intake sufficient for males may not be sufficient for females. If so, then risk-sensitive foraging theory (Caraco *et al.* 1980, Stephens 1981, Lim *et al.* 2015) predicts that females should pursue strategies with the prospect of greater reward than that needed by males, as Elliott *et al.* (2010) have shown for Thick-billed Murres *Uria lomvia* and a strategy employed by Black-legged Kittiwakes of both sexes under challenging environmental conditions (Chivers *et al.* 2012, Osborne *et al.* 2020). Put another way, it may be that females have a lower threshold at which they give up on a current prey patch (Brown 1988) and seek higher reward patches. Thus, we might expect females to cover greater distances than males, spend more time in transit and search more widely on average than males, spending less time in a more constricted area (Intensive search), all of which we found.

Under this hypothesis, we might expect females to travel more widely than males, at least until they have accrued enough resources to compensate for the original costs; the change in Leach's Storm Petrel foraging trip duration over time suggests this pattern. Trip duration early in the season is greater for females than for males but is essentially equal later in the season. For both sexes, trip duration decreased with date, as has been shown for other procellariiforms (Weimerskirch *et al.* 1993, Gonzalez-Solis 2004), but the best model of our data retained an interaction between DOY and Sex with a steeper negative slope for females than for males, though the interaction was not strong. The general decrease over time in foraging duration by both sexes could have been due to better foraging conditions, which may have improved as the season progressed (Brooke 1978). It is also possible that as females recovered from the cost of egg production, they were less likely to require a greater per-trip payoff than needed by males, resulting in a greater decrease over time than males.

We are confident that female foraging behaviour during the incubation period differs from male foraging behaviour in Leach's Storm Petrel, unlike other studies of larger monomorphic petrels and shearwaters (Pinet *et al.* 2012, Hedd *et al.* 2014, Ronconi *et al.* 2018). The fact that females cover more distance per unit time and spend more time in transit and foraging extensively is consistent with the idea that females move more than males. Perhaps, the most parsimonious explanation for this difference is that females are compensating for the cost of egg production by searching more widely for more, or higher quality, food.

While the observed differences in foraging behaviour are evident, additional data from individuals across the entire incubation period are needed to examine the relative costs and benefits of foraging between the sexes. Moreover, accelerometry data would provide relative energy expenditure by males and females on individual trips. Precise measures of mass before and after each trip would allow us to measure net energy intake, and sampling post-trip gut contents, faecal DNA or stable isotopes in blood might reveal sex differences in diet. One could also imagine monitoring change in physiological parameters throughout the period to assess costs beyond energetics. Such data would allow us to better understand the underlying drivers of the differing foraging behaviours we describe here, as well as better predict how changes in the ocean environment might influence sexes differently, and thus population foraging strategy, energetics, physiology and fitness.

This study was funded through Environment and Climate Change Canada, NSERC Discovery and CRD grants, the Environmental Damages Research Fund, Nova Scotia Habitat Conservation Fund and was supported by Birds Canada. Research reported in this publication was also supported by the National Institute of General Medical Sciences of the National Institutes of Health under Award Number P20GM103423. The content is solely the responsibility of the authors and does not necessarily represent the official views of the National Institutes of Health. R.A.M. was supported by the Max Planck Institute for Ornithology at Radolfzell while preparing the manuscript. R.A.M. was supported by a Newton Chun Award from Kenyon College. We thank Eli Bridge for comments on a very early draft of this paper and three anonymous reviewers, Richard Phillip, and Ruedi Nager for comments during the later stages. This is contribution #283 from the Bowdoin Scientific Station at Kent Island. Permission to handle study animals and attach devices was authorized under Canadian Wildlife Permits #SC2789, #02109, #10559, #10851, and Animal Care and Use Permits #ROC2008-2014, #IACUC2014-2015, #16GR01, #17GR01, #18GR01, #19GR01.

AUTHOR CONTRIBUTIONS

Robert A. Mauck: Conceptualization (lead); data curation (equal); formal analysis (lead); investigation (equal); methodology (equal); writing – original draft (lead). **Isabeau Pratte:** Conceptualization (supporting); data curation (lead); formal analysis (equal); software (equal); writing – review and editing (supporting). **April Hedd:** Data curation (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); writing – review and editing (equal). **Ingrid L. Pollet:** Data curation (equal); investigation (equal); methodology (equal); writing – review and editing (supporting). **Patricia L. Jones:** Data curation (equal); project administration (supporting); resources (supporting); writing – review and editing (supporting). **William A. Montevecchi:** Data curation (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal). **Robert A. Ronconi:** Data curation (supporting); formal analysis (supporting); investigation (supporting); methodology (supporting); resources (equal); supervision (supporting); writing – review and editing (supporting). **Carina Gjerdrum:** Data curation (equal); investigation (equal); methodology (equal); writing – review and editing (supporting). **Sarah Adrianowyscz:** Conceptualization (supporting); formal analysis (supporting); investigation (equal); writing – original draft (supporting). **Colin McMahon:** Investigation (equal). **Haley Acker:** Investigation (supporting). **Liam U. Taylor:** Conceptualization (supporting); investigation (equal); writing – review and editing (supporting). **Jennifer McMahon:** Investigation (supporting). **Donald C. Dearborn:** Conceptualization (supporting); investigation (supporting); resources (supporting); writing – review and editing (supporting). **Gregory J. Robertson:** Data curation (equal); funding acquisition (lead); project administration (lead); resources (supporting). **Laura A. McFarlane Tranquilla:** Data curation (equal); funding acquisition (lead); investigation (equal); methodology (equal); project administration (lead); resources (equal); writing – review and editing (supporting).

CONFLICT OF INTEREST

None.

FUNDING

Nova Scotia Habitat Conservation Fund, Kenyon College, National Institute of General Medical Sciences (Grant/Award Number: P20GM103423), Environment and Climate Change Canada Environmental Damages Research Fund.

ETHICAL NOTE

None.

Data Availability Statement

Data will be archived in Movebank (movebank.org).

REFERENCES

Bond, A.L. & Diamond, A.W. 2010. Nutrient allocation for egg production in six Atlantic seabirds. *Can. J. Zool.* **88**: 1095–1102.

Bond, A.L. & Hobson, K.A. 2015. Relaying propensity and characteristics of replacement clutches of Leach's Storm Petrels (*Oceanodroma leucorhoa*). *Can. J. Zool.* **93**: 181–185.

Brooke, M.D.L. 1978. Some factors affecting laying date, incubation and breeding success of Manx Shearwater, *Puffinus-puffinus*. *J. Anim. Ecol.* **47**: 477–495.

Brown, J.S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.* **22**: 37–47.

Calenge, C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Model.* **197**: 516–519.

Caraco, T., Martindale, S. & Whittam, T.S. 1980. An empirical demonstration of risk-sensitive foraging preferences. *Anim. Behav.* **28**: 820–830.

Chivers, L.S., Lundy, M.G., Calhoun, K., Newton, S.F., Houghton, J.D.R. & Reid, N. 2012. Foraging trip time-activity budgets and reproductive success in the black-legged kittiwake. *Mar. Ecol. Prog. Ser.* **456**: 269–277.

Collins, S.M., Hedd, A., Fifield, D.A., Wilson, D.R. & Montevecchi, W.A. 2022. Foraging paths of breeding Leach's Storm Petrels in relation to offshore oil platforms, breeding stage, and year. *Front. Mar. Sci.* **9** https://doi.org/10.3389/fmars.2022.816659

De Pascalis, F., Imperio, S., Benvenuti, A., Catoni, C., Rubolini, D. & Cecere, J.G. 2020. Sex-specific foraging behaviour is affected by wind conditions in a sexually size dimorphic seabird. *Anim. Behav.* **166**: 207–218.

Dearborn, D.C. 2001. Body condition and retaliation in the parental effort decisions of incubating great frigatebirds (*Fregata minor*). *Behav. Ecol.* **12**: 200–206.

Dearborn, D.C., Gager, A.B., Mcarthur, A.G., Gilmour, M.E., Mandzhukova, E. & Mauck, R.A. 2016. Gene duplication and divergence produce divergent MHC genotypes without disassortative mating. *Mol. Ecol.* **25**: 4355–4367.

Ellegren, H. 1996. First gene on the avian W chromosome (CHD) provides a tag for universal sexing of non-ratite birds. *Proc. R. Soc. B Biol. Sci.* **263**: 1635–1641.

Elliott, K.H., Gaston, A.J. & Crump, D. 2010. Sex-specific behavior by a monomorphic seabird represents risk partitioning. *Behav. Ecol.* **21**: 1024–1032.

Fieberg, J. & Kochanny, C.O. 2005. Quantifying home-range overlap: the importance of the utilization distribution. *J. Wildl. Manag.* **69**: 1346–1359.

Frith, R., Krug, D., Ronconi, R.A., Wong, S.N.P., Mallory, M.L. & Tranquilla, L.A.M. 2020. Diet of Leach's Storm Petrels (*Hydrobates leucorhous*) among three colonies in Atlantic Canada. *Northeast. Nat.* **27**: 619.

Gladbach, A., Braun, C., Nordt, A., Peter, H.U. & Quillfeldt, P. 2009. Chick provisioning and nest attendance of male and female Wilson's Storm Petrels *Oceanites oceanicus*. *Polar Biol.* **32**: 1315–1321.

Gonzalez-Solis, J. 2004. Sexual size dimorphism in northern giant petrels: ecological correlates and scaling. *Oikos* **105**: 247–254.

Granadeiro, J.P., Nunes, M., Silva, M.C. & Furness, R.W. 1998. Flexible foraging strategy of Cory's shearwater, *Calonectris diomedea*, during the chick-rearing period. *Anim. Behav.* **56**: 1169–1176.

Gross, A.O. 1935. The life history cycle of Leach's Storm Petrel (*Oceanodroma leucorhoa leucorhoa*) on the Outer Sea islands of the bay of fundy. *Auk* **52**: 382–389.

Hatch, S.A. 1990. Incubation rhythm in the fulmar *Fulmarus-glacialis* - annual variation and sex-roles. *Ibis* **132**: 515–524.

Hedd, A., Montevecchi, W.A., Davoren, G.K. & Fifield, D.A. 2009. Diets and distributions of Leach's Storm Petrel (*Oceanodroma leucorhoa*) before and after an ecosystem shift in the Northwest Atlantic. *Can. J. Zool.* **87**: 787–801.

Hedd, A., Montevecchi, W.A., Phillips, R.A. & Fifield, D.A. 2014. Seasonal sexual segregation by monomorphic sooty shearwaters *Puffinus griseus* reflects different reproductive roles during the pre-laying period. *PLoS One* **9**: e85572.

Hedd, A., Pollet, I.L., Mauck, R.A., Burke, C.M., Mallory, M.L., Tranquilla, L.A.M., Montevecchi, W.A., Robertson, G.J., Ronconi, R.A., Shutler, D., Wilhelm, S.I. & Burgess, N.M. 2018. Foraging areas, offshore habitat use, and colony overlap by incubating Leach's Storm Petrels *Oceanodroma leucorhoa* in the Northwest Atlantic. *PLoS One* **13**: e0194389.

Jouventin, P., Charmantier, A., DuBois, M.-P., Jarne, P. & Bried, J. 2007. Extra-pair paternity in the strongly monogamous wandering albatross *Diomedea exulans* has no apparent benefits for females. *Ibis* **149**: 67–78.

Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B. 2017. lmerTest package: tests in linear mixed effects models. *J. Stat. Softw.* **82**: 1–26.

Lim, I.S., Wittek, P. & Parkinson, J. 2015. On the origin of risk sensitivity: the energy budget rule revisited. *Anim. Behav.* **110**: 69–77.

Linden, M. & Moller, A.P. 1989. Cost of reproduction and covariation of life-history traits in birds. *Trends Ecol. Evol.* **4**: 367–371.

Lisovski, S., Hewson, C.M., Klaassen, R.H.G., Korner-Nievergelt, F., Kristensen, M.W. & Hahn, S. 2012. Geolocation by light: accuracy and precision affected by environmental factors. *Methods Ecol. Evol.* **3**: 603–612.

Maechler, M. 2021. *diptest: Hartigan's Dip Test Statistic for Unimodality - Corrected*. R package version 0.76-0. Available at: https://CRAN.R-project.org/package=diptest. Accessed 5 April 2021.

Mauck, R.A., Marschall, E.A. & Parker, P.G. 1999. Adult survival and imperfect assessment of parentage: effects on male parenting decisions. *Am. Nat.* **154**: 99–109.

Mauck, R.A., Waite, T.A. & Parker, P.G. 1995. Monogamy in Leach's Storm Petrel: DNA-fingerprinting evidence. *Auk* **112**: 473–482.

Mauck, R.A., Zangmeister, J.L., Cerchiara, J.C., Huntington, C.E. & Haussmann, M.F. 2011. Male-biased reproductive effort in a long-lived seabird. *Evol. Ecol. Res.* **13**: 19–33.

McClintock, B.T. & Michelot, T. 2018. momentuHMM: R package for generalized hidden Markov models of animal movement. *Methods Ecol. Evol.* **9**: 1518–1530.

Montevecchi, W.K., Kirkham, I.R., Roby, D.D. & Brink, K. 1983. Size, organic composition, and energy content of Leach's Storm Petrel (*Oceanodroma leucorhoa*) eggs with reference to position in the precocial-altricial spectrum and breeding ecology. *Can. J. Zool.* **61**: 1457–1463.

Nager, R.G. 2006. The challenges of making eggs. *Ardea* **94**: 323–346.

Osborne, O.E., O'Hara, P.D., Whelen, S., Zandbergen, P., Hatch, S.A. & Elliott, K.H. 2020. Breeding seabirds increase foraging range in response to an extreme marine heatwave. *Mar. Ecol. Prog. Ser.* **646**: 161–173.

Paiva, V.H., Pereira, J., Ceia, F.R. & Ramos, J.A. 2017. Environmentally driven sexual segregation in a marine top predator. *Sci. Rep.* **7**: 1–11.

Paiva, V.H., Ramos, J.A., Nava, C., Neves, V., Bried, J. & Magalhaes, M. 2018. Inter-sexual habitat and isotopic niche segregation of the endangered Monteiro's Storm Petrel during breeding. *Fortschr. Zool.* **126**: 29–35.

Pante, E. & Simon-Bouhet, B. 2013. Marmap: a package for importing, plotting and analyzing bathymetric and topographic data in R. *PLoS One* **8**: e73051.

Phillips, R.A., McGill, R.A.R., Dawson, D.A. & Bearhop, S. 2011. Sexual segregation in distribution, diet and trophic level of seabirds: insights from stable isotope analysis. *Mar. Biol.* **158**: 2199–2208.

Phillips, R.A., Silk, J.R.D., Croxall, J.P., Afanasyev, V. & Briggs, D.R. 2004a. Accuracy of geolocation estimates for flying seabirds. *Mar. Ecol. Prog. Ser.* **266**: 265–272.

Phillips, R.A., Silk, J.R.D., Phalan, B., Catry, P. & Croxall, J.P. 2004b. Seasonal sexual segregation in two Thalassarche albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proc. R. Soc. B Biol. Sci.* **271**: 1283–1291.

Pinet, P., Jaquemet, S., Phillips, R.A. & Le Corre, M. 2012. Sex-specific foraging strategies throughout the breeding season in a tropical, sexually monomorphic small petrel. *Anim. Behav.* **83**: 979–989.

Pollet, I.L., Bond, A.L., Hedd, A., Huntington, C.E., Butler, R.G. & Mauck, R. 2020. Leach's Storm Petrel (*Oceanodroma leucorhoa*), version 1.0. In Billerman, S.M., Keeney, B.K., Rodewald, P.G. & Schulenberg, T.S. (eds) *Birds of the World*. Ithaca, NY, USA: Cornell Lab of Ornithology. https://doi.org/10.2173/bow.lcspet.01

Pollet, I.L., Hedd, A., Taylor, P.D., Montevecchi, W.A. & Shutler, D. 2014a. Migratory movements and wintering areas of Leach's Storm Petrels tracked using geolocators. *J. Field Ornithol.* **85**: 321–328.

Pollet, I.L., Ronconi, R.A., Jonsen, I.D., Leonard, M.L., Taylor, P.D. & Shutler, D. 2014b. Foraging movements of Leach's Storm Petrels *Oceanodroma leucorhoa* during incubation. *J. Avian Biol.* **45**: 305–314.

R Core Development Team 2017. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Reyes-Gonzalez, J.M., De Felipe, F., Morera-Pujol, V., Soriano-Redondo, A., Navarro-Herrero, L., Zango, L., Garcia-Barcelona, S., Ramos, R. & Gonzalez-Solis, J. 2021. Sexual segregation in the foraging behaviour of a slightly dimorphic seabird: influence of the environment and fishery activity. *J. Anim. Ecol.* **90**: 1109–1121.

Ronconi, R.A., Schoombie, S., Westgate, A.J., Wong, S.N.P., Koopman, H.N. & Ryan, P.G. 2018. Effects of age, sex, colony and breeding phase on marine space use by great shearwaters *Ardenna gravis* in the South Atlantic. *Mar. Biol.* **165**: 58.

Sanz-Aguilar, A., Minguez, E. & Oro, D. 2012. Is laying a large egg expensive? Female-biased cost of first reproduction in a petrel. *Auk* **129**: 510–516.

Shaffer, S.A., Weimerskirch, H. & Costa, D.P. 2001. Functional significance of sexual dimorphism in wandering albatrosses, *Diomedea exulans*. *Funct. Ecol.* **15**: 203–210.

Stephens, D.W. 1981. The logic of risk-sensitive foraging preferences. *Anim. Behav.* **29**: 628–629.

Sztukowski, L.A., Cotton, P.A., Weimerskirch, H., Thompson, D.R., Torres, L.G., Sagar, P.M., Knights, A.M., Fayet, A.L. & Votier, S.C. 2018. Sex differences in individual foraging site fidelity of *Campbell albatross*. *Marine Ecol.* **601**: 227–238.

Tabachnick, B.G. & Fidell, L.S. 2013. *Using Multivariate Statistics*, 6th edn. Boston, MA: Pearson Education, Inc.

Tyson, C.W., Jennings, S.L., Hoover, B.A. & Miles, A. 2022. Energetic constraints drive sex-specific parental care in the monomorphic Leach's Storm Petrel *Hydrobates leucorhous*. *J. Avian Biol.* **2022**: e02904.

Veasey, J.S., Houston, D.C. & Metcalfe, N.B. 2001. A hidden cost of reproduction: the trade-off between clutch size and escape take-off speed in female zebra finches. *J. Anim. Ecol.* **70**: 20–24.

Warham, J. 1990. *The Petrels: Their Ecology and Breeding Systems*. London: Academic Press, Ltd.

Weimerskirch, H., Chastel, O., Ackermann, L., Chaurand, T., Cuenot-Chaillet, F., Hindermeyer, X. & Judas, J. 1994. Alternate long and short foraging trips in pelagic seabird parents. *Anim. Behav.* **47**: 472–476.

Weimerskirch, H., Salamolard, M., Sarrazin, F. & Jouventin, P. 1993. Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. *Auk* **110**: 325–342.

Welcker, J., Harding, A.M.A., Karnovsky, N.J., Steen, H., Strom, H. & Gabrielsen, G.W. 2009. Flexibility in the bimodal foraging strategy of a high Arctic alcid, the little auk *Alle alle*. *J. Avian Biol.* **40**: 388–399.

Whelan, S., Hatch, S.A., Benowitz-Fredericks, Z.M., Parenteau, C., Chastel, O. & Elliott, K.H. 2021. The effects of food supply on reproductive hormones and timing of reproduction in an income-breeding seabird. *Horm. Behav.* **127**: 104874.

Wojczulanis, K., Jakubas, D. & Walkusz, W. 2006. Differences in food delivered to chicks by males and females of little auks (*Alle alle*) on South Spitzbergen. *J. Ornithol.* **147**: 543–548.

Received 15 June 2021;
revision accepted 5 July 2022.
Associate Editor: Philllips, Richard.