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ORIGINAL PAPER

Integrating behavior and physiology supports Storer-Ashmole's halo in a central place forager

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Abstract
Central place foraging may lead to local prey depletion as foragers select nearby prey ("Storer-Ashmole's halo"), causing individuals to forage progressively farther from the central place. We tested this idea by coupling GPS tracking (foraging behavior) and plasma metabolites (nutritional biomarkers) when studying thick-billed murres (*Uria lomvia*; $N = 237$), a colonial-nesting seabird where central place foraging constraints are expected to be particularly pronounced due to high transit costs. Foraging range decreased when birds were constrained to visit the central place several times per day (chick-rearing) compared to self-feeding (incubation), illustrating the constraint of central place foraging. Moreover, adult feeding frequency, as determined by plasma triglycerides, were higher during incubation, consistent with the longer fasts (incubation shifts) during that period. Transit time (foraging distance) increased with date during chick-rearing but not incubation, consistent with prey depletion due to central place foraging within the restricted chick-rearing foraging range. During late chick-rearing, when a diet switch to low-quality, smaller prey occurs, birds switched to foraging near the colony, consistent with the foraging range being overextended. Unlike other, smaller colonies where foraging success is higher due to a smaller halo, sexes had similar foraging behaviour in our study, except during early incubation when females foraged more (more flying, more swimming) as they overcame the cost of producing the egg. When we take our results with other lines of evidence (increased foraging distance with colony size, prey switching as birds "feed down the food chain"), we conclude that central place foraging seabirds may cause prey depletion at one of the world's largest murre colonies.

Keywords Thick-billed murre · Uria lomvia · Arctic seabird · Foraging theory · Resource depletion · Nutritional biomarkers

Introduction

Foraging is the process of searching for, capturing, handling, and digesting prey (Charnov 1976; Krebs and Davies 1989; Ydenberg et al. 1994). According to foraging theory, individuals are expected to optimize these foraging investments to maximize net energy gain per unit of time (MacArthur and Pianka 1966; Schoener 1971; Charnov 1976). Central place foraging theory proposes that predators moving to and from a central place (e.g., nesting birds) optimize their foraging by consuming prey closest to that place (Orians and Pearson 1979). If prey abundance or mobility is relatively high, predators that forage near the central place have a limited effect on local prey abundance over time since prey removal from patches would be limited (Orians and Pearson 1979; Pyke 1984). Then, foraging closest to the central place is always the best strategy (e.g.,

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mussels, antlions, spiders; Pyke 1984). By contrast, when prey removal occurs due to low abundance and mobility of prey, and/or the predator is numerous and associated prey intake high, central place foragers can deplete prey closest to the central place. In this context, 'Storer-Ashmole's halo' arises when predators cause patch quality to decline near the central place (Storer 1952; Ashmole 1963; Birt et al. 1987; Elliott et al. 2009). One direct effect of Ashmole's halo is that central-place foragers are expected to increase transit time (foraging distance) in exchange for decreased search time (exploration costs) and higher prey load (Orians and Pearson 1979; Krebs and Davies 1989). Although transit time to and from the central place to the area outside of Ashmole's halo where prey depletion is limited generates energy and time costs, they have the potential to outweigh the increased search costs of remaining close to the central place (Orians and Pearson 1979).

Many seabirds are central-place foragers, leaving breeding colonies to forage at sea. In addition to the effects of prey depletion, their colonial nature introduces intra-specific and inter-specific competition that may amplify Ashmole's halo over the breeding season (Davoren et al. 2003; Birt et al. 1987; Weber et al. 2021). These competitive effects may be exacerbated further when easily accessible benthic fish are eaten while schooling fish move away from the colony or deeper in the water column (Lewis et al. 2001; Elliott et al. 2009; Gaston et al. 2013). These compounded depletion costs are thought to play a predominant role in the population regulation of seabirds; as colony size grows, the zone of prey depletion increases at an accelerating rate, leading to reduced fitness, and may potentially regulate colony size (Patterson et al. 2022). Indeed, it has long been proposed that resource-based limitations may be the ultimate cause for the slow life-history strategies in seabirds, including delayed maturity, low fecundity, and high adult survival (Cairns 1989; Gaston 2004; Gaston et al. 2007).

Indirect evidence of prey depletion by seabirds has been deduced from positive correlations between colony size and reduced chick or adult physiological condition (reviewed by Lewis et al. 2001; Elliott et al. 2009; Ballance et al. 2009; Patterson et al. 2022), reduced size of neighboring colonies (Furness and Birkhead 1984; Ainley et al. 2004; Ford et al. 2007), and increased foraging trip duration through the season (Elliott et al. 2009). However, such correlations may be attributable to interference rather than exploitative competition (Ainley et al. 2004; Davoren et al. 2003). As the number of competitors (i.e., breeders) is likely to decline as individuals fail during reproduction, reduced foraging success through the breeding season is unlikely to represent interference competition. However, few studies have tested for a reduction in foraging success through the breeding season in wild animals foraging at large scales, including seabirds. More recently, technological advances in animal tracking support studies that link individual foraging movements in the wild to the physiological variables associated with them. These advances have opened the possibility of examining changes in foraging success consistent with Storer-Ashmole's halo (e.g., Goossens et al. 2020; Jackson et al. 2023).

Plasma metabolites that measure lipid mobilization may be particularly sensitive indicators of changes in individual state, as ~30% of mass loss during breeding in murres is due to loss of lipids (e.g., 17 g out of 52 g total lost between late incubation and chick-rearing; Jacobs et al. 2011). Flight relies on triglycerides (fat reserves) as fuel (Hennin et al. 2016; Sorenson 2016; Lamarre et al. 2017). For example, murres have higher plasma-neutral lipids during chick-rearing, consistent with mass loss due to lipid mobilization at that time (Jacobs et al. 2012; Eby et al. 2023). Lipid mobilization allows adults to transfer their reserves to their offspring via higher feeding rates (Gaston and Hipfner 2006a, b). Similarly, baseline levels of the glucocorticoid hormone corticosterone are associated with nutritional stress in seabirds (Kitaysky et al. 2001; Sorenson et al. 2017). Finally, beta-hydroxybutyrate is associated with increased fasting duration (Hennin et al. 2016; Lamarre et al. 2017; Morales et al. 2020; Eby et al. 2023). By integrating several plasma metabolites, behavior can be linked with the physiological status of individual birds, with lower food intake rate associated with low triglycerides and high corticosterone and beta-hydroxybutyrate, and vice-versa (Hennin et al. 2016; Sorenson 2016; Morales et al. 2020; Eby et al. 2023).

This study focuses on thick-billed murres (*Uria lomvia*; hereafter 'murres'), colonial seabirds facing high transit costs due to their (1) single prey loading to feed their offspring, (2) high wing-loading and associated flying costs, and (3) deep diving capabilities (over 200 m; Elliott et al. 2013). These constraints are expected to force murres to behave in ways that optimize energetic efficiency as predicted by central place foraging theory. The prey load brought back to their offspring increases with distance from the colony, featuring small prey caught throughout the dives and larger prey captured during ascent, indicating a focus on larger prey during exploration (Elliott et al. 2009; Brisson-Curadeau and Elliott 2019). During chick-rearing, murres invest more time in searching (diving) and transiting (flying), incurring higher energy costs associated with chick provisioning compared to incubation, likely leading to higher prey depletion at that time (Benvenuti et al. 2002; Ito et al. 2010; Elliott et al. 2014).

Our objective was to test the hypothesis that foraging behavior among murres adheres to the Ashmole's halo hypothesis at Digges Island, a large colony (~400,000 pairs) where prey depletion is expected to occur due to

high population size (density peaking at 130 birds per km^2 at 25 km distance) and a diet that includes both benthic prey (potential direct depletion) and pelagic prey (potential prey avoidance of the region; Gaston and Nettleship 1981; Patterson et al. 2022). Compared to murres at a nearby smaller colony (Coats), birds at our study site (Digges) foraged farther and longer but made fewer trips, resulting in a lower nutritional state, lower foraging success and stronger responses to changes in broad-scale conditions (sea ice regime) compared to birds at the smaller colony (Patterson et al. 2022, Eby et al. 2023), all suggesting a stronger impact of Ashmole's halo at our study site. We use an integrative approach, tracking murres at sea using GPS devices while simultaneously measuring changes in individual states (i.e. body mass and plasma metabolites). Based on the Ashmole's halo hypothesis, we predicted that search and transit costs would increase within the chick-rearing period, with a larger foraging range detected during incubation than in chick-rearing due to chick feeding constraints. Physiologically, longer foraging trips as chick-rearing progresses should result in a loss of adult body mass and therefore higher baseline stress (corticosterone), reduced energy intake (lower triglycerides) and higher lipid mobilization due to fasting (elevated high beta-hydroxybutyrate) as chick-rearing progresses. Finally, we also predicted no sex-specific variation in foraging behavior (unlike colonies with sex-stereotyped rhythms) because our study colony is so large that such rhythms cannot be maintained (Elliott et al. 2010; Elliott and Gaston 2015).

Methods

The study system

We performed our fieldwork at the thick-billed murre colony located in Digges Sound, Nunavut, Canada (Digges Island, 62.55°N, 77.73°W and Cape Wolstenholme, 62.55°N, 77.54°W; sampled from 2014 to 2016, referred to hereafter as Digges Island) which hosts 400,000 breeding pairs (Gaston et al. 2013; Sorenson 2016; Eby et al. 2023). Murres nest on rocky cliff ledges and the nesting locations on the 12 km of cliffs at Digges Island are not expected to be limiting colony size. The presence of Ashmole's halo is assumed to cause state-based changes in murres, such as variation in body mass and physiological condition due to the time and energy costs related to central place-foraging in the presence of diminishing resources. Body mass increases slightly during incubation before declining stepwise at the time of hatching when birds must return more often to the central place to feed chicks, which may be 'programmed' to reduce flight and dive costs (Croll et al. 1991; Gaston and Perin 1993a, b; Elliott et al. 2008). The stepwise mass loss is double at the Digges colony (~11% of incubation mass lost during chick-rearing) than when compared to the nearby Coats Island colony (~5%), where foraging radii are much smaller (Eby et al. 2023), supporting the idea that mass is lost to reduce flight costs (Croll et al. 1991; Gaston and Hipfner 2006a,b).

GPS field deployments and blood sampling

We captured breeding adult murres using noose poles at six different sites within the Digges Sound region separated by at most 10 km. We attached one GPS logger (either CatTraQ™, Catnip Technologies, 18 g; Uria-100™, Ecotone, 16 g; AXY-Depth™, Technosmart, 6.5 g; Table 1) to each bird's dorsal feathers using TESA© tape, glue and zip ties (adapted from Paredes et al. 2005, 2015). The sampling period of the GPS loggers was set to either one position every minute, every two minutes, or every five minutes based on the battery capacity of each device. Deployment efforts in 2014 and 2015 were spread over incubation and chick-rearing, whereas 2016 focused on chick-rearing only (Table 1). Following the device attachment, we released the birds at their capture site and recaptured them within 1 to 17 days (average 4.1 ± 0.16 days; mean ± sem). Data was collected remotely by a base station set adjacent to nesting

Table 1 Summary of GPS deployments on thick-billed murres at Digges Island across years and breeding stages, sorted by GPS types (CatTraQ, Uria-100, and AXY-Depth). GPS deployments format: deployed (recovered). "Trips" refer to the final number of foraging trips obtained by recovered devices

		CatTraQ		Uria-100		AXY-Depth	
		Deployed	Trips	Deployed	Trips	Deployed	Trips
2014	Incubation	11 (5)	19	21 (10)	55	0	0
	Early chick-rearing	17 (7)	26	32 (30)	238	0	0
	Late chick-rearing	0	0	0	0	0	0
2015	Incubation	18 (2)	2	31 (15)	34	0	0
	Early chick-rearing	22 (7)	15	45 (42)	125	0	0
	Late chick-rearing	0	0	0	0	0	0
2016	Incubation	0	0	0	0	0	0
	Early chick-rearing	0	0	41 (35)	159	43 (31)	98
	Late chick-rearing	0	0	17 (13)	82	32 (24)	86

ledges for Uria-100 devices but required direct unit recovery whenever possible for the remaining two unit types. At capture, we banded and weighed the birds (±5 g) with a spring balance. As body mass alone is the best predictor of lipid content in murres (Jacobs et al. 2012), we did not attempt to correct body mass by a size index (i.e., 'body condition'). We additionally collected a single drop of blood from the brachial vein for subsequent DNA sexing (details in Elliott et al. 2010).

In 2014 and 2015, we used 26-gauge needles and heparinized capillary tubes to collect an additional 1 to 2 mL of blood from the brachial vein (Eby et al. 2023). Of the 324 birds captured, 308 blood samples were collected. We attempted to collect blood twice per bird, once at initial GPS deployment and the second at recapture following return to the colony. All samples were collected within 3 min after capture to ensure baseline corticosterone levels could be measured (Romero and Reed 2008). Blood was kept on ice for up to 8 h (most often for 4 h), and then centrifuged at 10,000 rpm for 10 min. Plasma was separated, and both the plasma and red blood cells were stored in a dry-ice cryoshipper at -75 °C for the duration of the field season (up to a month). Upon return to the lab, samples were immediately transferred and stored in a -80 °C freezer.

Laboratory assays

All samples were assayed at the University of Windsor as described in Eby et al. (2023). For baseline corticosterone (CORT), plasma samples were extracted prior to assay (Eby et al. 2023). Tubes containing 20 uL of plasma, 1 mL of distilled water, and 5 mL of dichloromethane were vortexed and left to separate for two hours. The dichloromethane phase was removed into scintillation vials and left in a fume hood to evaporate. Samples were rehydrated with assay buffer and vortexed for 30 s to reconstitute the sample. Samples were assayed in triplicate at a dilution of 1:40 using a previously optimized protocol for seabirds (see Hennin et al. 2015) using a commercial EIA kit (Assay Designs Inc.). All samples were run with a control to obtain coefficients of intra- and inter-assay (plate) variation (2015: intra = 4.99%, inter = 8.52%, 2014: intra = 5.16%, inter 3.88%). Triglycerides (TRIG) and free glycerol were measured in duplicate with a commercially available kit (TRIG; #TR0100-1KT; Sigma Aldrich, USA; Williams et al. 2007; Eby et al. 2023). Each plate was run with a laying hen control plasma (Sigma-Aldrich, USA) and a standard curve of the kit-provided glycerol standard (Hennin et al. 2015), where the difference in total and free glycerol provides the total TRIG concentration ($mmol.L^{-1}$). All samples were run with a control to later obtain coefficients of variation for intra- and inter-assay (plate) variation (2015: intra = 2.94%, inter = 2.48%, 2014: intra = 3.27%, inter 3.30%). Beta-hydroxybutyrate (BOH) was measured by kinetic assay (SIGMA, Guglielmo et al. 2002; Lamarre et al. 2017). Samples were run in triplicate by reacting 11 uL of standard or plasma sample with 2 uL of BOH-butyrate dehydrogenase reagent and reagent buffer. The absorbance was then monitored by a spectrophotometer. Coefficients of variation for intra- and inter-assay (plate) variation were 2014: intra = 4.06%, inter = 3.50% and 2015: intra = 4.96%, inter = 5.12%.

Analysis of GPS data

We completed all data analyses using the program R 3.6.2 (Core Team 2019). Distances were calculated using the function *dist.Haversinae()* from the *'geosphere'* package (Hijmans 2019). Data was cleaned by removing duplicate GPS positions, GPS entries associated with an aberrant instantaneous speed (we assumed these to be caused by low GPS accuracy and/or precision), and/or when fewer than four satellites were available to provide the geographic position (when reported). Trips with substantial missing data were removed from analysis. The breeding stages were assigned as incubation or chick-rearing based on the status of the egg or chick at the time of capture and device retrieval. In rare instances, a bird incubated an egg during initial capture, and the chick hatched before recapture. These cases were removed from analyses because we did not know the exact hatching date. We divided each GPS deployment into resting (at the colony) or foraging phases. Each foraging phase (i.e., a foraging trip) was analyzed independently. We removed incomplete foraging trips from the analysis (those that began or ended farther than 10 km away from the colony or for which data were missing during more than half of the total trip duration). Foraging trips that contained data missing for more than two hours but less than half of the trip duration were kept unless the portion missing occurred at the farthest part of the foraging trip. This conservative approach was intended to eliminate the potential of miscalculating the maximum distance traveled from the colony.

GPS locations less than 100 m away from the colony were considered resting at the breeding site. When leaving the colony, after a change of brooding duty, birds typically glide to a 'splashdown area' typically directly below their breeding cliff (Gaston and Nettleship 1981; Burger and Piatt 1990; Davoren et al. 2003; Elliott et al. 2009). There, murres cleanse themselves for a few minutes and occasionally engage in social behaviors without foraging. After logger attachment, time spent at the splashdown area can extend to more than an hour before their first foraging trip is initiated (often as the bird responds to the new tag). Some birds can drift up to several km from the colony on tidal currents extending what is considered the splashdown area.

Table 2 Detailed list of all parameters extracted from GPS tracking of thick-billed murres at Digges Island in 2014-16

Abbreviation	Description	Unit
Duration	Duration of a foraging trip from leaving the splash-down area until coming back to the colony	h
FRI	Foraging Range Index: average foraging distance from the colony	km
MaximumDistance	Maximum Distance from colony	km
DistanceFlown	Total Distance flown in a foraging trip	km
TimeOnWater	Total time spent on/under the water	h
TotalDistance	Total distance traveled in a foraging trip	km
Time of departure/return	Time of the day of at which a bird departed/returned to the colony	h
Colony time before	Time spent at the colony before a foraging trip	h
Colony time after	Time spent at the colony after a foraging trip	h
Splashdown time	Time spent within the splashdown area before a foraging trip	h
Day number	Number of the day of the year, i.e. days since January 1st of each year	days
Median hatching date	Estimated date at which half of the eggs hatched	-
DaysRelHatchDate	Day number relative to median hatch date	days
Mass	Adult body mass	g
CORT	Plasma baseline corticosterone levels	ng/mL
BOH	Plasma β-hydroxybutyrate levels	mmol/L
TRIG	Plasma triglyceride levels	mmol/L
Energy expenditure	Estimated energy expenditure	kJ
NumberTripsPerDay	Number of foraging trips done per day, extrapolated from foraging activity around each foraging trip over a day	-
DistFlownPerDay	Distance flown per day, extrapolated from foraging activity around each foraging trip over a day	km/day
PropTimeOnWater	Proportion of time spent on the water, extrapolated from foraging activity around each foraging trip over a day	%
AverageEE	Average Energy Expenditure calculated over a day	l

We assume this time was spent preening, sometimes interacting with the newly deployed devices, but not foraging. In addition, we extrapolated depth from the pressure recorded every second by the AXY-Depth devices to delineate the area used by the birds without any diving activity below 1 m. Depth was not used for any other purpose in this study. GPS locations more than 100 m away from the colony and outside the splashdown area were considered foraging.

We further classified murre foraging behavior into flight or water activity (including swimming, diving, and resting on the sea). These categories were assigned based on differences in instantaneous speed between successive GPS positions. Based on the distribution of instantaneous speeds, we estimated the average flight ground speed S_F to be around 17.0 $m.s^{-1}$, and the average drifting and swimming speed on the water S_W around 0.6 $m.s^{-1}$. The speed threshold S_T at which half of the distance traveled between two GPS positions was covered by flight and half was covered on the water was calculated as:

$$S_T = \frac{2.S_F.S_W}{S_F + S_W} = 1.16m.s^{-1}$$

To be conservative (so that few resting periods were misassigned as flight), we considered any instantaneous flight speeds above 4 $m.s^{-1}$ to be mostly flight and everything else occurring on the water.

Calculating foraging metrics

For each foraging trip, we calculated four main foraging metrics: total distance flown, time spent on the water and underwater, entire trip duration, and Foraging Range Index (average foraging distance from the colony, abbreviated FRI, adapted from Gaston et al. 2013). FRI is the distance from the colony of the barycenter of all foraging behavior in a foraging trip; that is, it's the distance from the colony of the "average" location of the entire trip. Because its calculation considers all foraging locations, FRI is resilient to outliers. We used FRI as the primary measure of the foraging range to compare with other parameters. Additionally, we included the maximum distance from the colony, total distance traveled, time of the day of departure and return, and time spent in the splashdown area (Table 2).

Calculating foraging effort proxies

Foraging metrics describe foraging trips without accounting for effort or cost (energy expenditure). For example, shorter trips could be compensated for by a higher foraging frequency. To account for cost, we also calculated daily foraging effort proxies in addition to that of a single foraging

trip. To limit biases associated with diel cycles, we calculated all foraging activity within 12 h on either side of a foraging trip midpoint (based on duration) and then scaled those costs back to 24 h. We extended the observed period to entire trips and half the resting time before and after the first and last trips when applicable (when more than one trip was included). This step was particularly relevant for trips longer than a day. This approach allowed us to calculate the number of foraging trips per day, the distance flown per day, the proportion of time spent on the water over a day, and the average energy expenditure over a day for individual murres. Energy expenditure was extrapolated based on time spent flying, on the water, and resting at the colony using doubly labeled water energy expenditure data estimates from Elliott et al. (2013).

It is assumed that murres cannot assess food abundance in the water column while flying, and they must land on the sea and sample the water column by diving. Typically, murre flights are interrupted by short landings on the water, performing at least one dive (Elliott et al. 2009). Hence, in murres, transit is associated with flight and searching with dives. Therefore, we used total flight distance (cumulated distance flying during a single foraging trip) as a proxy to represent transit costs at the scale of the foraging trip. Similarly, we chose the distance flown per day to represent the transit part of the foraging effort. We chose flight distance over flight duration because birds could land briefly between GPS fixes without this being accounted for, which could affect calculations of total flight duration more than total flight distance. Conversely, we approximated search costs by total time spent on the water (cumulated time spent on the water surface or underwater – i.e., not flying – in a foraging trip) at the scale of the foraging trip. The proportion of time spent on water over a day will represent the exploration part of the foraging effort. We chose duration over the distance covered on water because (1) birds are drifting while on the water, and drifting speed might be affected by wind or current speed, artificially affecting distance traveled on the water, and (2) birds might quickly fly in between two GPS fixes without being accounted for, affecting total distance traveled more significantly than total duration on water.

Statistical analysis

To test for correlations among foraging parameters, we performed linear mixed-effects models with the *lme()* function from the *'nlme'* package (Pinheiro et al. 2020). Model construction and selection were done following Zuur et al. (2009) and Zuur et al. (2010). All foraging variables were log-transformed to address outliers and skewed distributions. The normality of model residuals was not always attained due to our large sample sizes. The homoscedasticity of the models was obtained by adjusting the variance structure and tested using a variation of Levene's test. To obtain the optimal models, we followed a top-down selection with a nested data structure, using REML and AIC to select random effects, and we dropped insignificant variables before refitting the models. All initial models included year and deployment ID (random intercepts) as nested random factors to deal with environmental differences between years and pseudo-replication from multiple foraging trips originating from a single GPS deployment. The initial models included the breeding stages and their interactions as fixed effects, as well as the above random effects. All log-transformed foraging metrics and effort parameters were correlated and plotted using basic linear models (X ~ Y) without random effects. We report Pearson's correlation coefficient using Pearson's product-moment correlation coefficient as the p-value. We performed a Principal Components Analysis (PCA) to explore the relationship between FRI, exploration costs (time on the water), transit costs (flight distance), and the other foraging metrics using *'corrplot'*, *'FactoMineR'*, and *'factoextra'* packages (Le et al. 2008; Wei and Simko 2017; Kassambara and Mundt 2019).

We determined the median hatch date for each year (ordinal day 211 in 2014, 215 in 2015, and 209 in 2016) and transformed the ordinal days to days relative to the median hatch date for each year (i.e., day 0 means median hatch day, day 1 means one day post median hatching, and so on) to standardize our time variable across years. We expected different stages to occur within the breeding period, separated by discrete breakpoints: incubation, chick-rearing, and late chick-rearing (after murres diet switches from fish to invertebrates). We adapted an automated breakpoint detection algorithm to find how each of our metrics and proxies behaved, how many breakpoints should be used to describe them best, and to determine whether and when chick-rearing should be split up into early and late stages (Kappel 2017). We also tested segmented regression with the R package *'segmented'* (Muggeo 2008). However, the automated breakpoint algorithm was always preferred based on BIC selection adapted for segmented regression models of post-hoc linear models (Hall et al. 2013). After applying a breakpoint analysis algorithm on the eight parameters (foraging metrics and effort) on 2016 chick-rearing data (see Table 2), five had a single significant breakpoint: all at 9.48 days relative to the median hatch date. From that finding, data before 9.48 days relative to the median hatching date were then considered as early chick-rearing (all 2014 and 2015 and part of 2016), and those occurring after were defined as late chick-rearing (only 2016 data, as that was the only year we stayed later). Days relative to median hatch date were then correlated with the foraging metrics (i.e.,

FRI, duration, distance flown, and time on the water), state-based metrics (body mass and plasma TRIG, CORT, and BOH), and foraging effort proxies (number of foraging trips per day, distance flown per day, proportion of time spent on water and average energy expenditure over a day). We used linear mixed-effects models using the same methods as foraging metric correlations. The exception was how we dealt with outliers. We did not log-transform the data and instead used Rosner's test for outliers from the *'EnvStats'* package (Millard 2013). We removed the longest and farthest foraging trip from our dataset, identified as an outlier by Rosner's test. For physiological metrics, we log-transformed plasma baseline corticosterone levels to achieve normality. We used deployment ID and year as nested random effects (random intercepts) and breeding stage and its interaction as fixed effects in all initial models.

Based on time of departure and return, foraging behavior did not show any periodicity with time of day or any stable patterns over time, both at the breeding pair and colony level, as also found previously (Elliott et al. 2010). Thus, we did not include the time of day in our models. Time of departure, time of return, time spent at the colony before and after a foraging trip, and time spent in the splashdown area were all uncorrelated to any other foraging parameters or metrics described earlier. These variables were excluded from further analysis, being irrelevant to our question. All model formulae, details, and results are in the Supplementary Materials. We performed linear mixed-effects models to investigate sex differences in foraging behavior and physiological and foraging effort metrics. The general formula used was Y ~ DaysRelHatchDate*Sex + 1|Year/ID, where Y is one of our dependent variables. Models were performed on each breeding stage separately but plotted together. Foraging behavior was graphically represented at each breeding stage using the *'adehabitatHR 0.4.14'* package (Calenge 2006). We used the ad hoc method *'href'* to estimate the smoothing parameter and then computed 50 and 95% utilization distribution kernel densities of foraging behavior for each year (locations associated with flight or at the colony were excluded). Chick-rearing was sub-divided into year and breeding stage groups: 2014 and 2015 incubation and early chick-rearing, and 2016 early and late chick-rearing.

Results

Foraging trip duration and range

The final dataset consisted of 237 GPS deployments and 1031 foraging trips, for an average of 4.4 ± 0.2 foraging trips per deployment (see Table 1). Within these, 154 first trips after deployment (58%) were associated with several hours of splashdown time immediately after the bird left the nesting site (3.30 ± 0.31 h). The at-sea distribution of thick-billed murres varied among breeding stages and years (Fig. 1). When all trips across the three study years were considered together, the foraging trip duration averaged 15.9 ± 0.4 h, and the maximum foraging distance averaged 52.4 ± 1.2 km. Murres traveled the farthest during the incubation period in 2015, with 71% of foraging trips extending beyond 60 km from the colony (Fig. 1A). By contrast, 75% occurred within 40 km of the colony during the late chick-rearing stage in 2016 (9.48 days after the median hatching date, Fig. 1D). The most distant trip occurred in the 2015 incubation period when a bird flew 305.3 km away from the colony over 5.3 days with a total trip distance of 719.9 km.

Foraging behavior

The metrics of foraging behavior (FRI, duration, distance flown, time on water, maximum distance, total distance, and total energy expenditure) were correlated with one another (Pearson's correlation coefficient: $r > 0.6$; Figs. 2 and 3), but only weakly with proxies of foraging effort, such as distance flown per day, proportion of time on the water and daily energy expenditure ($r < 0.45$; Fig. 2) and negatively with number of foraging trips per day ($r < -0.618$; Fig. 3). Murres flew farther away from the colony on longer trips, spending more energy and time on the water to rest and forage. The average length of the trips did not affect the distance flown per day, the overall proportion of the time spent on water, and the average energy expenditure as shorter trips were compensated by a higher trip frequency.

Most of the variation in foraging effort was represented by two axes within the overall PCA representing foraging effort proxies, with dim1 (major contributors: number of trips per day, proportion of time on water) and dim2 (distance flown per day and daily energy expenditure) representing 53.3% and 30.2% of the total variance, respectively (Fig. 4B). Switching from incubation to chick-rearing shifted the distribution along dim1 without any change along dim2. Thus, stage-related differences in the energy expended or distance flown per day were more limited than expected. Similarly, when considering only the metrics of foraging behavior, the first principal component (dim1) explained 87.2% of the total variance, dominated by colinear parameters representing foraging range and transit time: DistanceFlown, FRI, MaximumDistance, and TotalDistance (Fig. 4A). Indeed, dim2 only represented 8.8% of the total variance, with Duration and TimeOnWater contributing more than average towards dim2. Switching from incubation to chick-rearing caused a shift in dim1 (decreased transit) but not in dim2 (exploration). Thus, we separated foraging behavior along two axes: transit time (FRI) and

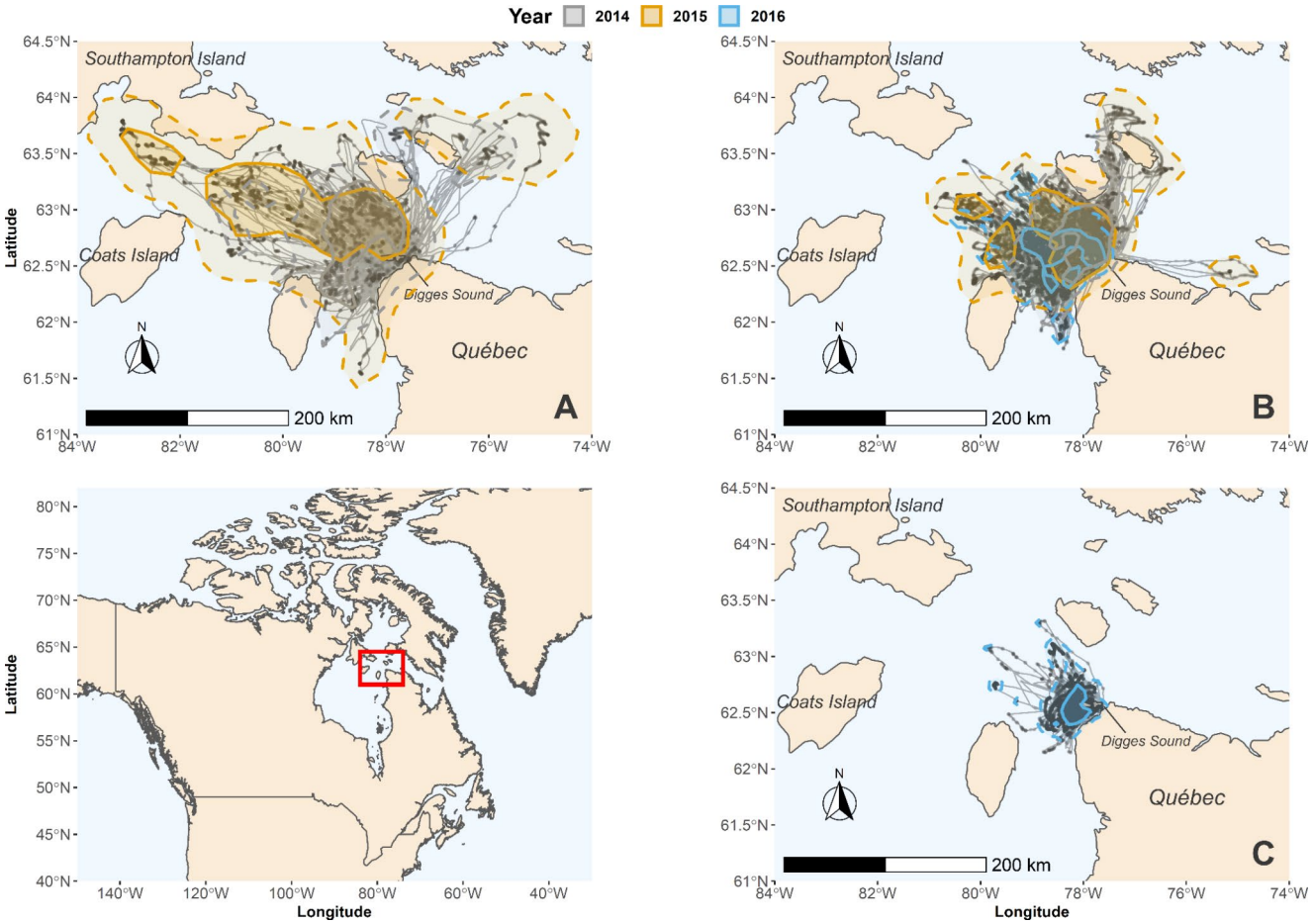

Fig. 1 Distribution of thick-billed murre foraging tracks around East Digges Island colony. A = Incubation 2014–2015; B = Early chick-rearing 2014 to 2016 (before 9.48 days since median hatching date); C = Late chick-rearing 2016 (after 9.48 days since median hatching date). Dashed and full lines represent 95 and 50% Utilization Distributions, respectively. Black lines and points represent all GPS data available, but only locations associated with water activities were used in the UDs

search time (TimeOnWater), with representative variables chosen due to their contributions to dim1 and dim2, respectively. As these PCAs suggest, the distance flown per day and energy expenditure remained constant and independent of the breeding stage. As adults transitioned from the incubation phase to the early and late chick-rearing phase, the trip frequency of adults increased while the proportion of time they spent on the water decreased. However, this is balanced by a decrease in foraging range and distance flown per trip (but not per day), which did not significantly affect the trip duration or time spent on water. Transit and rest time on water decreased, while search time was unaffected.

During incubation, only the time spent on the water declined over time from 12.6 to 2.9 h at the rate of -0.4 ± 0.1 h/day ($p < 0.0001$), while FRI (50.4 ± 5.6 km), trip duration (18.5 ± 2.2 h) and distance flown by murres (121.0 ± 12.6 km) did not change ($p > 0.3$; Fig. 5). The transition from incubation to the first nine days of early chick-rearing caused drops in FRI (-26.9 ± 5.4 km, $p < 0.0001$), trip duration (-10.4 ± 2.0 h, $p < 0.0001$), and the distance flown per foraging trip (-62.3 ± 12.6 km, $p < 0.0001$; Fig. 5). As the energetic demands of growing chicks increased throughout the chick-rearing phase, foraging behavior metrics increased over time (FRI: +1.1 ± 0.3 km/day, $p < 0.0001$; Duration: +0.5 ± 0.1 h/day, $p < 0.0001$; Distance flown: +3.6 ± 0.7 km/day, $p < 0.0001$; Fig. 5), but then remained stable in late chick-rearing ($p > 0.55$). The time murres spent on water increased during early chick-rearing (+0.1 ± 0.1 h/day, $p < 0.0001$) and declined in late chick-rearing (-0.1 ± 0.1 h/day, $p = 0.04$) without significant change in intercept. In other words, murres foraged in two rather stable circumstances during incubation and late chick-rearing, separated by early chick-rearing during which Ashmole's halo seems to apply.

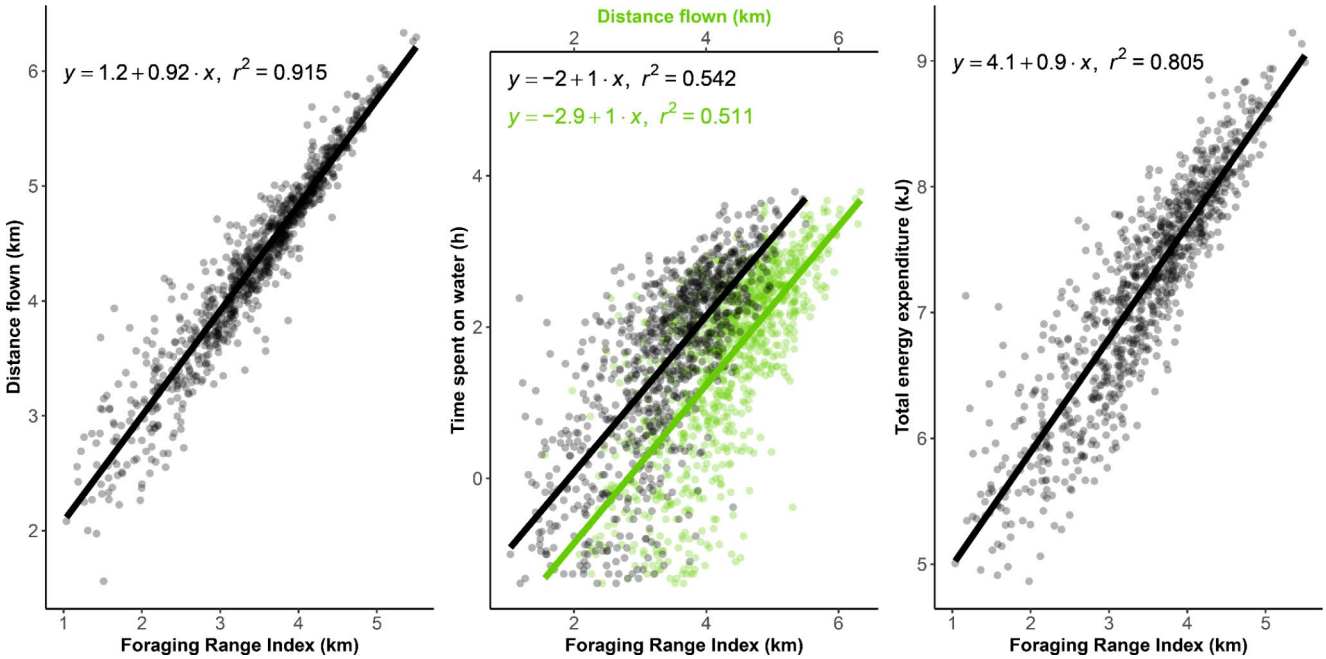

Fig. 2 Correlation between Foraging Range Index, cumulated flight distance, cumulated time spent on water and total energy expenditure for incubating and chick-rearing thick-billed murres at Digges Island in 2014-16. All data are log-transformed. Regression lines from linear models ($p < 0.0001$) account for years and GPS deployment repeated measures

Foraging effort

Murres flew 125.0 ± 6.1 km per day throughout the breeding season, independently of the breeding stage. All other proxies of foraging effort were stable during incubation (0.8 ± 0.2 number of trip/day, 52.1 ± 4.0% of time spent on the water, and 30.7 ± 2.0 W average energy expenditure over a day, $p > 0.29$; Fig. 7). Birds doubled their average number of foraging trips per day (1.5 ± 0.1, $p < 0.0001$) in early chick-rearing and then declined at the rate of − 0.08 ± 0.01 trip/day ($p < 0.0001$). Murres also reduced the proportion of time they spent on the water surface by one fifth (-9.2 ± 3.0%, $p = 0.002$), which then increased at the rate of + 1.2 ± 0.2% per day ($p < 0.0001$). The number of foraging trips stabilized again in late chick-rearing at 1.8 ± 0.5 trip/day ($p = 0.15$). The proportion of time spent on water did not significantly change between early and late chick-rearing (intercept: $p = 0.91$; slope: $p = 0.61$). The average energy expenditure intercept did not change between breeding stages (excluded in model selection), but it increased during early chick-rearing (+ 0.7 ± 0.2 W, $p < 0.0001$) and increased slowly in late chick-rearing (+ 0.2 ± 0.2 W, $p = 0.04$). Again, these results indicated that shorter trips coincided with a higher foraging frequency, meaning murres maintained a constant flight effort and rather constant daily energy expenditure. As such, the changes in the proportion of time spent on water suggest changes in foraging strategy between breeding stages.

State-dependent parameters

Overall, body mass (ignoring sex, see next section) of adult murres declined during both incubation (4.0 ± 1.9 g/day, $n = 48$, $p = 0.04$) and early chick-rearing (11.5 ± 2.3 g/day, $n = 234$, $p = 0.002$), before increasing in late chick-rearing (3.8 ± 3.1 g/day, $n = 86$, $p = 0.01$; Fig. 6). Log-transformed CORT did not significantly change over time during incubation ($n = 39$, $p = 0.3$) but did increase during early chick-rearing (0.08 ± 0.04 ng/mL/day, $n = 96$, $p = 0.03$; Fig. 6). Plasma BOH increased during incubation (0.04 ± 0.01 mmol/L/day, $n = 36$, $p = 0.002$) and then stabilized during early chick-rearing at 1.46 ± 0.08 mmol/L ($n = 93$, $p < 0.001$; Fig. 6). Plasma TRIG did not change over time (excluded in model selection) but did increase from 0.79 ± 0.06 mmol/L during incubation to 1.04 ± 0.08 mmol/L during early chick-rearing ($n = 95$, $p = 0.002$; Fig. 6). Fasting (higher BOH) increased during incubation as partners made longer foraging trips yet remained stable throughout early chick-rearing. Plasma TRIG increased between stages, while BOH was constant in early chick-rearing, suggesting higher feeding rates during early chick-rearing relative to incubation.

Sex differences

Both foraging behavior and effort varied by sex. Males began the incubation stage by making 50% shorter trips than females (13.1 h males, 28.2 h females), spending 50% less

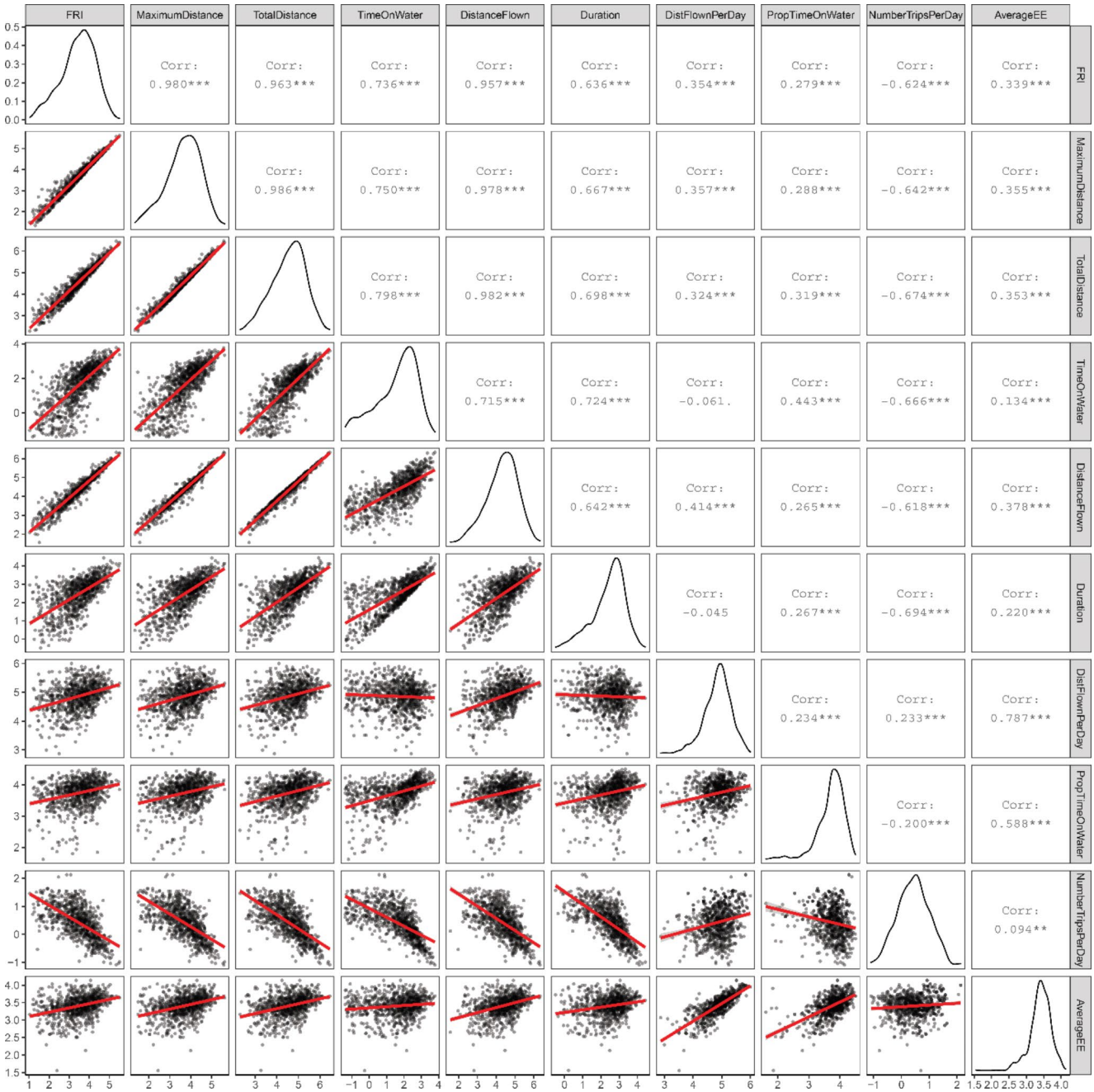

Fig. 3 Correlation of all foraging and foraging effort metrics of interest in thick-billed murres at Digges Island, all years combined. All variables were log-transformed. Descriptions of variables can be found in Table 2. The correlation index shown is Pearson's correlation coefficient. Significance is based on the result of Pearson's product-moment correlation coefficient (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$)

time on the water (8.6 h males, 15.3 h females) and flying 50% less (92.9 km males, 167.9 km females; Fig. 6). These behavioral decisions led to a decreased proportion of time spent on water and a consistently lower power consumption of 4.9 W for males (34.3 ± 1.1 W for females, 29.5 ± 1.4 W for males, $p = 0.003$; Fig. 6). Foraging range, number of trips per day, and distance flown per day, however, were similar between the sexes (Figs. 6 and 7). The foraging behavior metrics of males increased over the incubation stage and were on par with females right before early chick-rearing (Fig. 6). In other words, females appeared to forage at maximal foraging ranges throughout incubation, while males progressively increased foraging ranges from half to the same maximal range as females, adjusting other foraging metrics along the way, and saving daily energy expenditure in the process.

Females foraged 6.4 ± 2.7 km ($p = 0.02$) farther away from the nesting colony than males and flew 15.3 ± 6.4 km

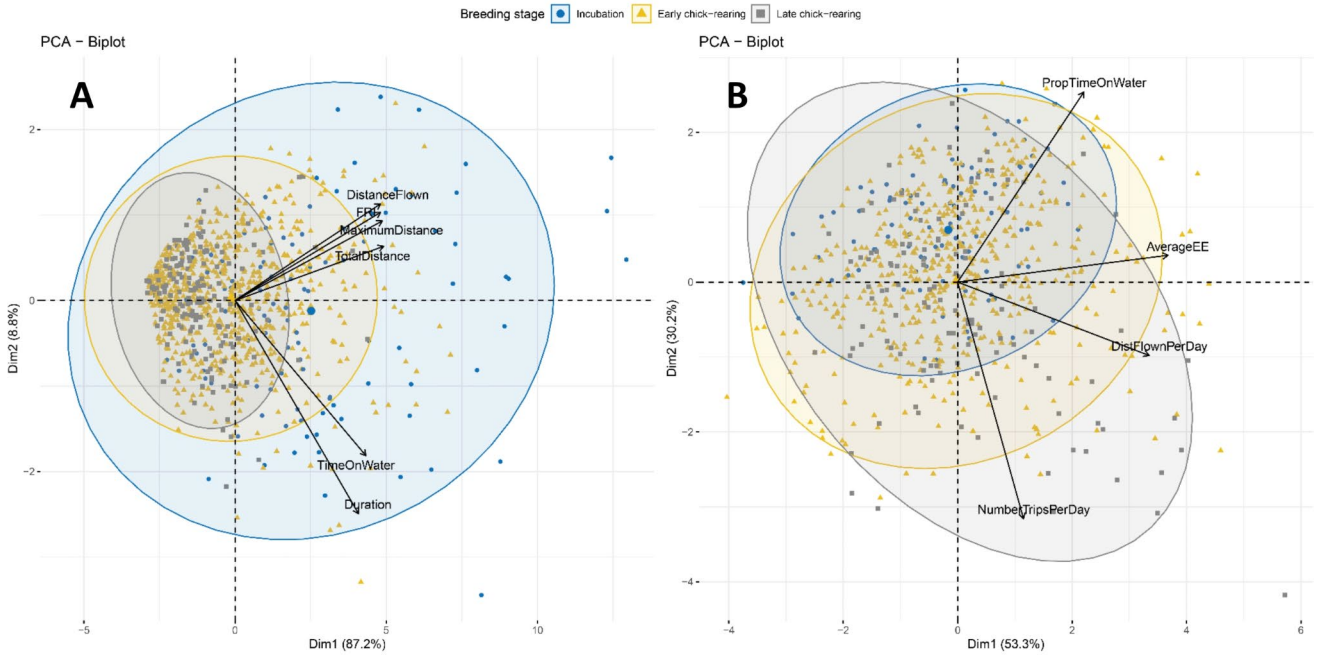

Fig. 4 Principal Component Analysis (PCA) of thick-billed murres foraging trips (blue and yellow dots) and their associated foraging parameters (black arrows, see Table 2). **A**: Foraging behavior metrics, dim1 had an eigenvalue of 5.23, and dim2 had an eigenvalue of 0.53. dim1 is dominated by parameters representing transit time, dim2 by parameters representing search time. **B**: Foraging effort proxies, dim1 had an eigenvalue of 2.13, and dim2 had an eigenvalue of 1.21. Dim1 is dominated by the number of foraging trips per day and the proportion of time spent on water, dim2 by distance flown per day, and average energy expenditure over a day. Centroids of the ellipses are represented by a larger colored point

more ($p = 0.02$) on average during early chick-rearing in all three years without differences in foraging effort (Figs. 5 and 7). Overall, the foraging effort appeared similar between sexes in early chick-rearing, despite males foraging slightly closer from the colony. In late chick-rearing, females made more (2.2 ± 0.2 trip/day females, 1.6 ± 0.3 trip/day males, $p = 0.05$) and shorter (4.9 ± 0.8 h females, 7.9 ± 1.2 h males, $p = 0.02$) foraging trips, and spent less time on water than males (3.9 ± 1.5 h females, 5.1 ± 0.5 h males, $p = 0.04$; Fig. 7). Females' distance flown per day increased into late chick-rearing ($+4.0 \pm 2.0$ km/day, $p = 0.03$), while male distances declined (-4.2 ± 4.1 km/day, $p = 0.05$). Despite shorter trips, the female foraging effort appeared maximal at this stage and much higher than males, particularly influenced by increases in foraging frequency and decreases in the proportion of time spent on water.

Finally, incubating males also had lower CORT and higher BOH levels than females (Fig. 7), while females had lower body mass and higher TRIG levels than males in early chick-rearing. Among females, CORT levels decreased over time, whereas CORT levels remained stable among males in early chick-rearing (Fig. 7).

Discussion

We used an integrative approach with multiple measures, including behavior recorded from GPS and nutritional physiology recorded from plasma metabolites, to test the idea that central place foraging constrains the foraging behavior of murres. Our work builds on the study of Eby et al. (2023), which used the same metrics, averaged across each year, to compare foraging behavior between a large and small colony, by examining trends within each year. In that study, we rather focused on the evolution of foraging behavior over the breeding season. Compared to murres at a nearby smaller colony (Coats), birds at our study site (Digges) foraged farther and longer but made fewer trips, resulting in a lower nutritional state, lower foraging success and stronger responses to changes in broad-scale conditions (sea ice regime) compared to birds at the smaller colony (Patterson et al. 2022, Eby et al. 2023), all suggesting a stronger impact of Ashmole's halo at our study site and consistent with stronger prey depletion (a larger Ashmole's halo) at the larger colony (Eby et al. 2023). Murres foraging range decreased when birds were constrained to visit the central place several times per day (chick-rearing) compared to self-feeding (incubation), illustrating the constraint of central place foraging. Transit time increased with date during chick-rearing but not incubation, consistent with prey depletion due to

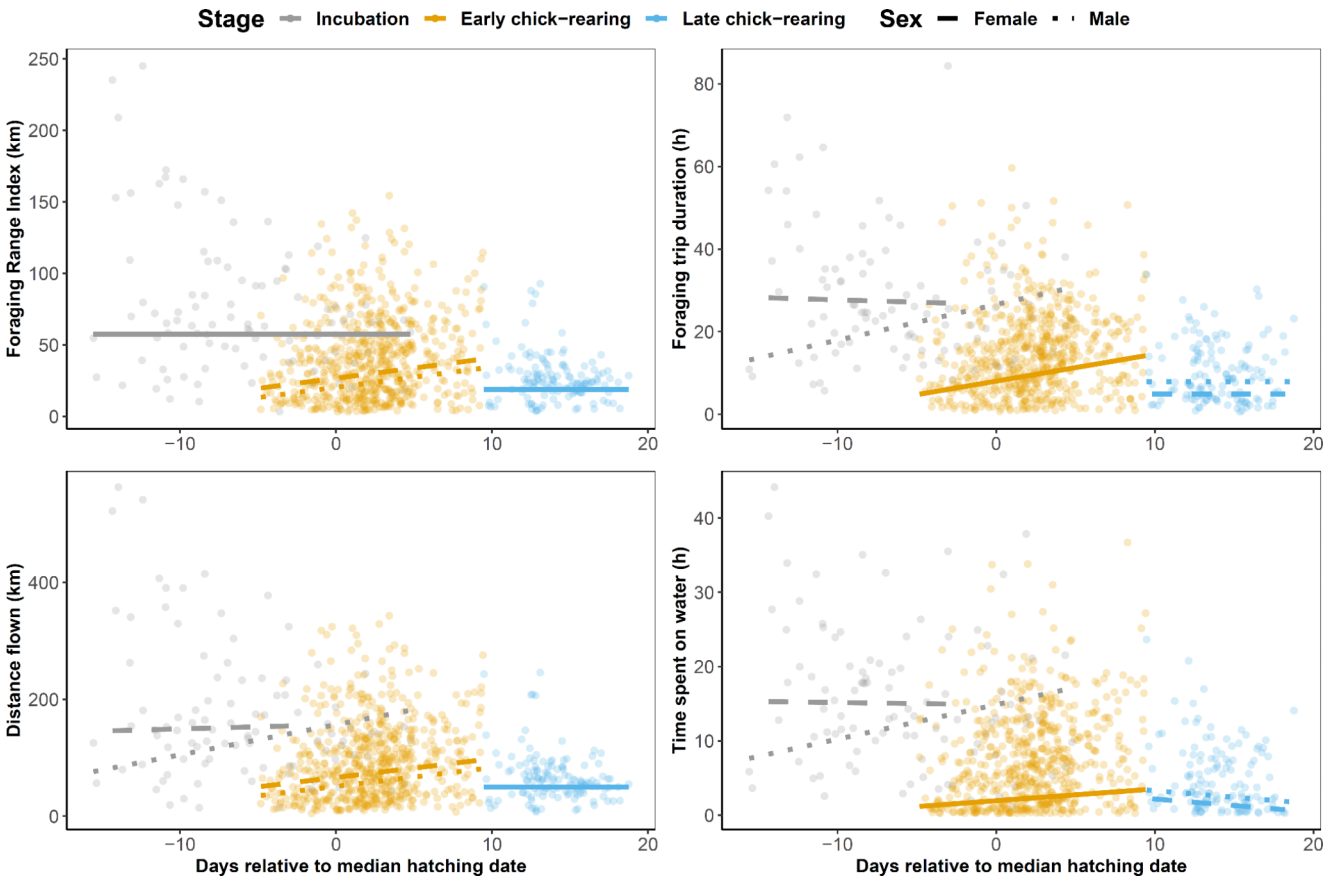

Fig. 5 Stage- and sex-dependent changes in foraging behavior in thick-billed murres at Digges Island during the 2014, 2015, and 2016 breeding seasons. Solid lines represent no sex differences. Early chick-rearing refers to prior to 9.48 days since the median hatching date, and Late chick-rearing refers to the past 9.48 days since the median hatching date. The 9.48 threshold was obtained using an automated breakpoint detection algorithm and has been set as the reference point. The lines represent linear mixed-effect model results, accounting for years and GPS deployment repeated measures. Individual models were performed for each breeding stage and combined into a single graph. Full model descriptions are available in supplementary material

central place foraging within the restricted chick-rearing foraging range—especially for benthic prey and Arctic cod that are resident at this scale over the ice-free period (Kessel et al. 2016). Together with Eby et al. (2023), we show strong evidence for central place foraging constraints and prey depletion among thick-billed murres.

Foraging range

As predicted, and consistent with central place foraging theory, the breeding stage of murres was the most important parameter influencing the foraging range, as represented by an index of foraging range (FRI). Murres flew farthest away from the colony (the 'central place') during the incubation period (average 77.9 kms) compared to chick-rearing (average 37.7 kms)—with 37 km being remarkably similar to the foraging range limit that has been modelled for congeneric common murres (Hentati-Sundberg et al. 2021). During incubation, birds are not constrained to return to the nest several times per day to feed chicks, which frees them to forage farther from the colony during incubation than chick-rearing. Hence, incubating birds may search for large schools of invertebrates (without the constraint of needing to bring a large prey back to the colony), as shown by stomach contents, allowing birds to maintain body mass (particularly females). Moreover, as predicted by Ashmole Halo's theory, the foraging range increased during chick-rearing until ~10 days where it reached a maximum of 33.7 km per trip. The leveling off in the foraging range occurred concurrently as a known diet switch by thick-billed murres in northern Hudson Bay from fish to invertebrates and small fish (Elliott et al. 2009). We also note that the change in distances flown at ~10 days corresponds to the age at which the energetic needs of chicks exceed the ability of both parents to provide enough fish to support their maximum growth rate (Gaston and Nettleship 1981; Elliott et al. 2017). That is, murres work at their maximum energy expenditure throughout the chick-rearing season, but by about ~10 days, they can no longer keep up with the growing needs of the chicks (Elliott et al. 2014, 2017). Thus, during a period of maximum

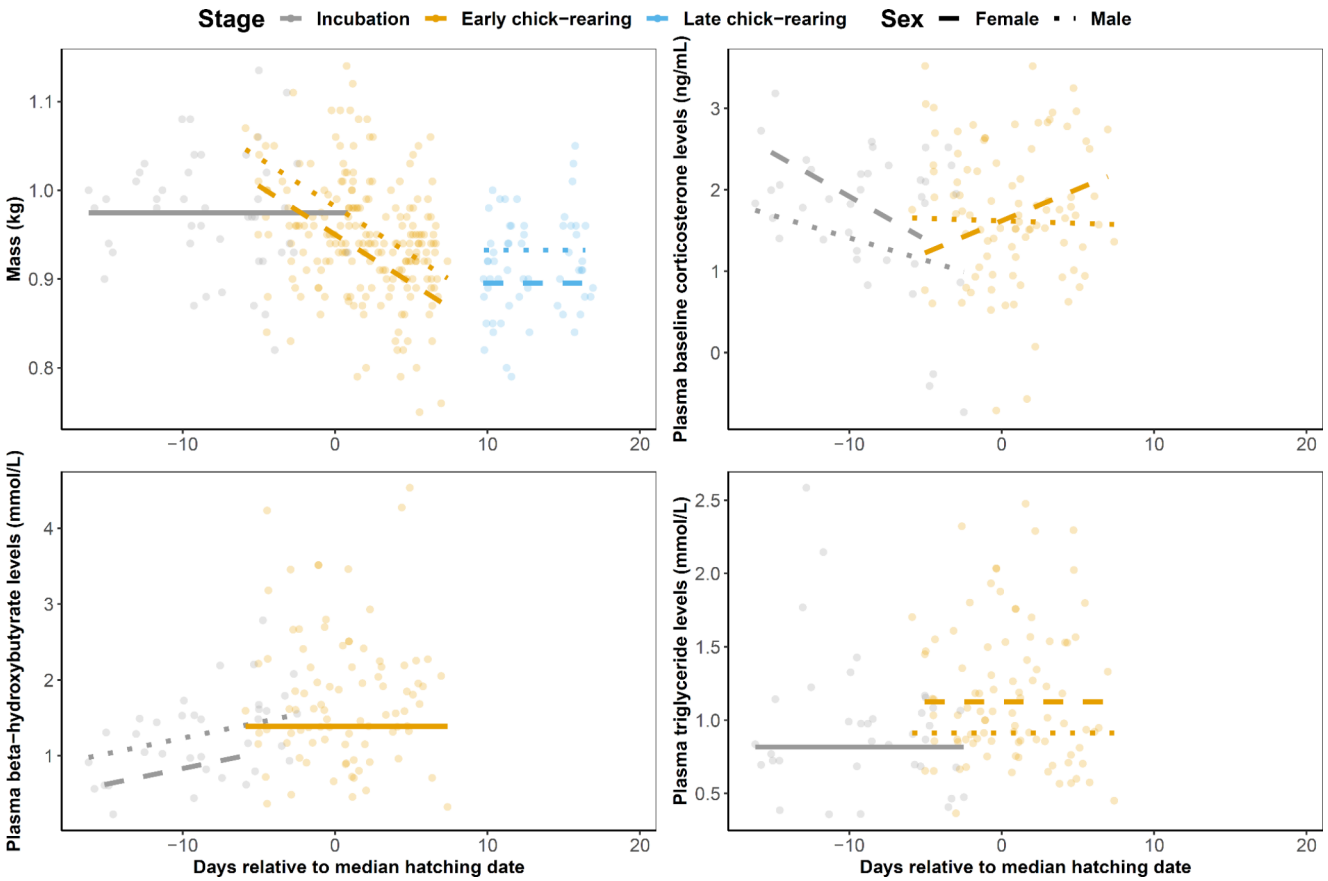

Fig. 6 Stage- and sex-dependent changes in state-based metrics in thick-billed murres at Digges Island during 2014, 2015 and 2016 breeding seasons. Solid lines represent no sex differences. Early chick-rearing refers to prior to 9.48 days since the median hatching date, and Late chick-rearing refers to the past 9.48 days since the median hatching date. The 9.48 threshold was obtained using an automated breakpoint detection algorithm and has been set as the reference point. The lines represent linear mixed-effect model results, accounting for years and GPS deployment repeated measures. Individual models were performed for each breeding stage and combined into a single graph. Full model descriptions are available in supplementary material

growth requirements, the parents switch to poorer quality prey near the colony as higher quality prey have apparently been depleted, and the benefits of long trips in search of fish are declining (Elliott et al. 2014). Our data support the finding that birds made shorter, more frequent foraging trips. In contrast, foraging effort (e.g., distance flown per day and average energy expenditure) was stable while breeding, as birds most likely foraged at or near their energetic ceiling regardless of reproductive stage.

As predicted by Ashmole's halo theory, thick-billed murres foraging around this immense colony in the Canadian Arctic flew to a maximum distance of over 300 km. As far as we are aware, this is the longest distance traveled during a single foraging bout recorded for this species (Gaston et al. 1986; Benvenuti et al. 1997; Eby et al. 2023). The large foraging distances by murres breeding at Digges Island and compared to previous studies conducted at smaller colonies (Eby et al. 2023) are consistent with prey depletion surrounding the large Digges Island colony (Lewis et al. 2001; Gaston et al. 2013; Patterson et al. 2022). Two birds sampled at another large colony at Latrabjorg, Iceland also traveled a total distance of 168 km) providing additional evidence that birds originating from large colonies travel the farthest (Patterson et al. 2022).

Sex differences

Despite the lack of sex-stereotyped nest attendance rhythms at the Digges colony that could lead to variation in central place foraging constraints (Elliott et al. 2010), murres demonstrated some small but statistically significant sex differences in foraging and nest attendance behavior. Female foraging behavior (i.e., search times, transit times) was more stable than males during incubation, with males investing less in transit and exploration. From early chick-rearing, females forage farther away from the colony and have higher daily energy expenditure balanced by a higher food ingestion rate (higher TRIG). These changes became even more pronounced during late chick-rearing, when females made more foraging trips per day while spending

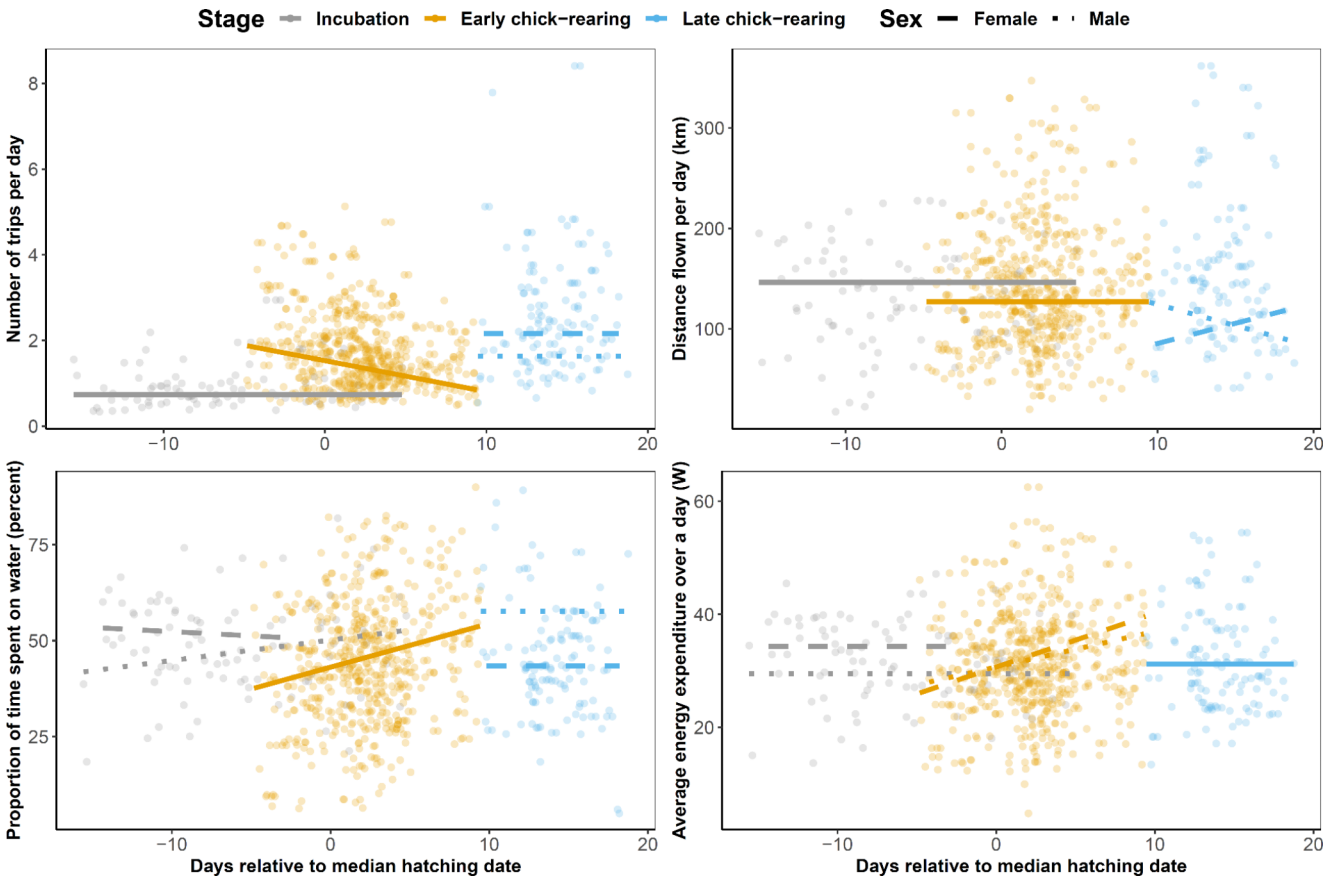

Fig. 7 Stage- and sex-dependent changes in foraging effort in thick-billed murres at Digges Island during 2014, 2015 and 2016 breeding seasons. Solid lines represent no sex differences. Early chick-rearing refers to prior to 9.48 days since the median hatching date, and Late chick-rearing refers to the past 9.48 days since the median hatching date. The 9.48 threshold was obtained using an automated breakpoint detection algorithm and has been set as the reference point. The lines represent linear mixed-effect model results, accounting for years and GPS deployment repeated measures. Individual models were performed for each breeding stage and combined into a single graph. Full model descriptions are available in supplementary material

proportionally less time on water. These differences in foraging behavior relative to sex likely have fitness benefits. After fledging, only the male takes care of the chick while the female becomes independent and free to forage with few constraints (Elliott et al. 2017). Perhaps the increased investment of females when feeding the chick that we detected could allow the male to feed itself more and spend more time at the colony to bond with the chick, increasing the survival of chicks immediately after fledging when the male parent and chick depart together.

Influence of foraging effort on state-based parameters

There was a sharp drop in both foraging range and trip duration in both sexes between the incubation and subsequent early chick-rearing periods, making the chick-rearing period more constrained. The shorter trips coincided with an increase in foraging trips taken per day. Combined, however, there was no difference in the overall distance traveled by a bird per day or daily energy expenditure between the two reproductive periods. Interestingly, foraging distance increased with date within the chick-rearing period, consistent with prey depletion and supporting Ashmole's halo hypothesis. When murres are more constrained in the chick-rearing period, the need to feed their chick increases search and transit times while the adults lose mass. A decline in body mass, with no change in energy expenditure, suggests that prey availability and/or quality declined closer to the colony.

Foraging distance suddenly fell after about 10 days post-hatch, coinciding with the age at which chick energetic needs begin to exceed the ability of parents to support chick growth at their maximum rate (Gaston and Nettleship 1981). As murres in this region of northern Hudson Bay are known to switch from fish to invertebrates at this time (Elliott et al. 2009), this may represent a sudden switch to more abundant but less valuable prey after larger fish have been depleted, which would provide support for Ashmole's halo hypothesis. More data in late chick-rearing, including

plasma CORT, BOH and TRIG, chick-growth, and isotopic data could help us to better understand this transition from early to late chick-rearing.

Rather than having distinct strategies reflecting possible prey types or foraging preferences, we found evidence for a continuum of strategies within the overall foraging space (as indicated by the foraging PCA). Specifically, most foraging variables we examined clustered along a single axis representing foraging distance (Foraging Range Index - FRI). Thus, we found that a single parameter, FRI (representing the average foraging distance from the colony), can be used to predict trip duration, maximal distance from the colony, distance flown, time spent on water, energy expenditure, and number of trips per day. The number of foraging trips and the proportion of time spent on water appear to be the adjustment variables that allow birds to transition between breeding stages and modulate body mass gains and losses. The number of foraging trips directly depends on the need for the parents to feed their chick regularly, which happens at the cost of the parent's ability to feed itself (proportion of time spent on water).

Body mass and plasma metabolites varied over the course of the breeding season. As expected, body mass showed a strong stepwise drop at the time of hatching (~11%, same as earlier studies), which may be 'programmed' to reduce flight and dive costs (Croll et al. 1991; Gaston and Perin 1993a, b; Elliott et al. 2008). Plasma TRIG was quite stable during each stage but increased between incubation and chick-rearing. The higher TRIG during chick-rearing may reflect more recent foraging (shorter incubation shifts; Jacobs et al. 2011, 2012; Eby et al. 2023). Similarly, in another charadriiform seabird, the brown skua (*Stercorarius antarcticus*), levels of very low-density and high-density lipoproteins are higher in chick-rearing than incubation, with the opposite true for low-density lipoproteins (Ibañez et al. 2021). Plasma levels of BOH increased from pre-breeding levels to chick-rearing levels throughout incubation, while CORT decreased throughout incubation only to increase again during early chick-rearing. The increasing baseline CORT in chick-rearing may reflect reduced foraging success as the halo is increasingly depleted (and foraging range increasing) during that period. Despite an accelerating mass loss over incubation and early chick-rearing, log-transformed CORT only increased during early chick-rearing, which is consistent with murres increasingly suffering from nutritional stress over the early chick-rearing period. Although we had expected the shift to shorter incubation shifts during chick-rearing to lead to decreased BOH and baseline CORT and higher TRIG during chick-rearing, perhaps due to the complicated lipid dynamics associated with mass loss during that period. Thus, some plasma metabolites (CORT/BOH) suggested that foraging success progressively decreased in each period, but much of the signal (mass/TRIG) was overwhelmed by the stepwise mass and lipid dynamics at the time of hatch. Plasma metabolites showed little to no evidence of a Storer-Ashmole's halo by themselves, reflecting the fact birds probably foraged at a constant foraging effort, with the increased foraging distance being compensated by lower feeding rates.

In conclusion, by coupling metrics of foraging behavior generated by GPS tracking technologies with metrics of individual state (i.e., body mass and plasma metabolites), we generated an integrated approach to explore the foraging ecology of thick-billed murres at one of the largest nesting colonies in Arctic Canada. Many of our results supported central place foraging theory: a reduction in foraging distance radius when feeding chicks, foraging distance explaining most of the variation in foraging behavior, and an increase in foraging distance within breeding stages that supports "Ashmole's Halo" of prey depletion over time. The colonial breeding strategy of thick-billed murres apparently constrained them to forage within about 50 km of this colony during chick-rearing, which generated the potential to deplete local fish stocks over time. This seems possible given that approximately one million adult murres are present in the Digges Sound region each summer (~400,000 breeding pairs with additional non-breeders). A conservative estimate suggests that each murre requires ~2200 kJ/d given a 70% assimilation efficiency and that this generates a daily population requirement of ~25 MW (Elliott et al. 2014), equivalent to a small hydroelectric dam and requires 640 t of fish consumed per day, or 12,800 t over the 20-day chick-rearing period. Such top-down control may play a key role in regulating predator and prey alike, demonstrating the ecological importance of seabird colonies in Arctic marine ecosystems, particularly within the foraging range of breeding seabirds.

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Author contributions Conceived study, field work and editing: All authors. Overseeing lab work: OPL. First draft: TL.

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Data availability Data are available at MoveBank: https://www.movebank.org/cms/movebank-content/arctic-animal-movement-archive.

Declarations

Conflict of interest The author declares no competing interest.

Ethical approval All work was conducted under a University of Windsor Animal Use Care permit (15 – 04), McGill animal care permit (2015–7599), and Environment and Climate Change Canada Animal Care and land use permits (NUN-SCI-14-11, EC-PN-14-017, EC-PN-15-017).

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