HATCHING SUCCESS OF COMMON MURRES *URIA AALGE* IS LINKED TO THE NUMBER OF NEIGHBOURS AND RESOURCE AVAILABILITY

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ABSTRACT

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When breeding within densely populated colonies, seabirds benefit from increased offspring protection from predators, but intraspecific competition for resources may outweigh these benefits. We tested whether the number of breeding-site neighbours and days of predator presence influenced the breeding performance of Common Murres *Uria aalge* at two different-sized colonies off the northeastern Newfoundland coast: Cabot Island (10000 breeding pairs; < 10 km offshore) and Funk Island (500000 breeding pairs; ~60 km offshore). Gulls, the main predators of murre eggs/chicks, inhabit both islands in similar numbers. During July–August 2018, camera traps placed at topographically similar plots on each colony recorded breeding performance metrics (i.e., hatching, fledging, reproductive success), number of breeding-site neighbours, and daily presence of gulls. Hatching success was lower at Funk Island (64.7%) than Cabot Island (96.2%), but nearly all hatched chicks fledged at both colonies. Lower hatching success at Funk Island was due to higher egg abandonment and predation. It was also associated with fewer breeding-site neighbours, including non-brooding mates and non-breeders, along with higher gull presence (96.6% of all gull sightings at both colonies). Fewer neighbours at Funk Island may have resulted from mates and non-breeding murres spending more time at sea due to longer distances to predictable foraging sites and higher conspecific densities relative to Cabot Island. In turn, with fewer breeding-site neighbours at Funk Island, parents appeared less able to defend against or deter gull predation. Although Funk Island has special conservation status, protection of Cabot Island may also be important for the long-term conservation of murres in Newfoundland.

Key words: hatching, breeding, resource availability, conservation, *Uria aalge*

INTRODUCTION

Group living occurs commonly across many species, both large (e.g., lions *Panthera leo*; Coulson 2007) and small (e.g., Cape ground squirrels *Xerus inauris*; Waterman 1997), offering both potential benefits and costs (Alexander 1974). Most seabirds breed colonially, with high nest densities occurring at sites without terrestrial predators (Coulson 2001). For seabird species with low conspecific aggression, nesting in areas of high density is often associated with improved reproductive success (Birkhead 1977, Stokes & Boersma 2000) and offspring survival (Greenwood 1964), as there are more eyes to detect threats ('collective detection' effect; Powell 1974, Lima 1995). This nesting strategy allows for collective predator defense and repulsion (Wittenberger & Hunt 1985). Collective defense is a more effective deterrent than solitary or paired defensive attacks (Tinbergen 1964, Gilchrist & Gaston 1997), as the cost of physical harm to or energy lost by a predator in a failed attack may outweigh the potential foraging opportunity (Gilchrist *et al.* 1998, Gilchrist 1999). Despite protection benefits, there are costs of living with many conspecifics. As colony-nesting seabirds are central-place foragers (Orians & Pearson 1979), parental birds are restricted to foraging within a maximum range from the nest to adequately provision themselves and chicks. Many conspecifics foraging within this limited range can lead to competition near the colony (Storer 1952, Ashmole 1963, Birt *et al.* 1987), resulting in increased distances to foraging sites and energy expenditure to collect food for their offspring (Ainley *et al.* 2003, Ballance *et al.* 2009, Elliott *et al.* 2009). These longer foraging trips not only affect energy expenditure of adults, but they may also lead to decreases in offspring feeding rates (Gaston *et al.* 2007, Ainley *et al.* 2018), defense, and survival (Ashmole 1963, Boersma & Rebstock 2009). Thus, there is a fitness trade-off between the costs and benefits of high-density colonial breeding.

The Common Murre *Uria aalge* is a long-lived, pursuit-diving seabird that breeds in large, dense colonies on headlands and islands. Common Murres and closely related Thick-billed Murres *Uria lomvia* form monogamous pairs, have a clutch size of one, and raise no more than one offspring per year. Parents share parental care during incubation (32 days) and chick rearing (about 21 days; Birkhead & Nettleship 1987, Boekelheide *et al.* 1990), whereby one parent typically guards the egg/chick while the other parent is foraging at sea. This continues until the flightless chick leaves the colony at ~25% of adult body mass with the male parent (Harris & Birkhead 1985). Murres do not construct nests, but rather lay a single egg directly on open cliff ledges or flat ground (Tuck 1960), and parents at neighbouring breeding sites are often in direct contact. In addition to brooding birds, non-brooding mates and non-breeding individuals also attend the colony (Harris *et al.* 2015). Non-breeding birds include immature birds (Halley *et al.* 1995) and mature birds currently without a mate (Harris & Wanless 1995) who are potentially prospecting for future breeding sites and mates (Gaston & Nettleship 1981). With minimal conspecific aggression (Gaston & Nettleship 1981), the presence of these non-breeding/non-brooding birds may be beneficial for breeders via predator detection or defense. Gulls, one of the primary egg/chick predators at many murre colonies (Johnson 1938, Veitch *et al.* 2016), often target areas of low breeding density because space is available for gulls to land and steal exposed eggs (Johnson 1938, Gaston & Nettleship 1981); a similar situation occurs in penguin colonies (Young 1994). Additionally, murres breeding at low densities tend to respond to predators by abandoning their breeding sites (Johnson 1938), and previous studies on murres have recorded higher egg predation rates at breeding sites with fewer neighbours (Johnson 1938, Birkhead 1977, Gilchrist & Gaston 1997).

Two colonies of Common Murres (hereafter 'murres') located ~65 km apart on the northeastern Newfoundland coast vary substantially in the number of breeding pairs and distance to inshore foraging areas, but they occupy similar, flat-ground breeding habitat at similar densities (18–37 breeding pairs/m^2; Wilhelm *et al.* 2015). Approximately 10 000 pairs breed on South Cabot Island (hereafter 'Cabot Island'), located < 10 km from shore, whereas ~500 000 pairs breed on Funk Island Seabird Ecological Reserve (hereafter 'Funk Island'), located ~60 km from shore (Fig. 1; Wilhelm *et al.* 2015). Both colonies mainly forage inshore (Fig. 1). Combined, these murres represent > 75% of the population in the Northwest Atlantic (Cairns *et al.* 1989). The main predators of murre eggs at these colonies appear to be American Herring Gulls *Larus smithsonianus* and Great Black-backed Gulls *Larus marinus*, which breed in or near both colonies in similar numbers (~50–100 breeding pairs per species on each island; E. Jenkins pers. comm.). Murre productivity at both colonies has only recently been quantified (Gulka *et al.* 2020), as human presence is a substantial disturbance to breeding birds due to the remoteness of the colony and the flat-ground topography. This recent study compared murre productivity at Funk and Cabot islands and found similar fledging success at both colonies. However, hatching success was lower on the large offshore colony, relative to the small inshore colony (Gulka *et al.* 2020). It was proposed that predation risk and proximity to resources explained the difference, as gulls breeding on Funk Island appeared to focus more on seabird prey relative to alternative prey at inshore colonies (Maynard & Davoren 2020). Chick-rearing murres from the large offshore colony travelled farther to coastal foraging areas relative to breeders at the small inshore colony (Gulka *et al.* 2020). Increased foraging distances, likely related to proximity to predictable abundant patches of their main prey fish, capelin *Mallotus villosus* (Davoren 2013), may reduce colony attendance and thus the number of neighbours available for defense against predators (see also Zador & Piatt 1999). However, the mechanisms driving these colony-level differences in reproductive success have not been explored.

Our objective here was to conduct an in-depth comparison of breeding performance (i.e., hatching, fledging, and reproductive success) on these two colonies, with a focus on examining the mechanisms underlying differences in hatching success. Although murres breed at similar densities on these colonies (Wilhelm *et al.* 2015), the amount of gull predation and the number of non-breeding neighbours at each are unknown. We hypothesize that gull predation and the number of breeding-site neighbours will influence murre hatching success. Specifically, we predict that breeding sites on Funk Island will have fewer neighbours, as non-breeding murres and non-brooding/incubating mates must spend more time at sea due to longer commutes to distant predictable foraging areas (with greater intraspecific competition), leading to higher vulnerability of eggs to predation by gulls. As the study area hosts a regionally and internationally significant breeding population of Common Murres, an understanding of the mechanisms influencing reproductive success at these colonies will be important for determining target colonies for protection and management.

METHODS

To quantify the breeding performance of Common Murres, cameras traps were deployed on Cabot Island (Bushnell Agressor no-glo, n = 4) and Funk Island (Bushnell Agressor no-glo, n = 3; Reconyx PC 800, n = 1) during incubation and retrieved near the end of chick rearing (Cabot Island: 04 July to 09 August 2018; Funk Island: 16 July to 12 August 2018). As egg laying was not observed, we estimated that cameras were deployed during mid to late incubation on each colony, based on the number of days to hatch relative to camera deployment dates. We used camera traps rather than direct observations to minimize the possible effects of human disturbance on gull predation (Johnson 1938, Schauer & Murphy 1996). Camera traps were mounted on wooden towers (~2.5 m high, base ~0.25 m^2), with each camera angled 45° down and away from each other to ensure each camera covered a different plot containing 15–30 breeding sites. Two towers with two cameras each were established at different locations on each colony, resulting in four possible plots per colony. Towers were placed 2–5 m outside of the breeding area in regions that could be approached with minimal disturbance to breeding birds. The plots represented typical and similar breeding habitats and densities across plots and colonies. Bushnell cameras were set to take one photograph every 30 minutes during daylight (05h00–21h00 local time), while photographs at night were taken only when the camera's motion sensor was triggered. The Reconyx camera was programmed to take two photographs at 15-minute intervals from 09h00–10h00 and 17h00–18h00 daily. Once the towers and cameras were established, visits to the colony were limited to minimize human disturbance. At Funk Island, 41 focal breeding sites could be consistently monitored in four separate plots, while 29 breeding sites were monitored from only two plots at Cabot Island, due to failure of two cameras. All research was conducted in agreement with the approved Animal Care Protocol from the University of Manitoba (F016–17/1/2).

Breeding performance metrics

Pictures were processed for hatching success, fledging success, and overall reproductive success at both colonies starting on 16 July, despite different camera deployment dates, to ensure similar observation periods on both colonies. Timing of egg laying differed by about a week (see Results). The first three days of photographs from each camera were viewed to identify and label breeding sites with eggs; breeding sites were chosen based on site visibility (Fig. 2A). During this initial period, we observed a few chicks in plots. While these were excluded from consideration, they supported our estimate that analyses encompassed mid to late incubation through chick rearing on both colonies. We assessed the progress of breeding sites from all pictures on each day by classifying each focal breeding site into one of the following categories: (1) adult with an egg or chick; (2) egg or chick without an adult; (3) adult sitting, potentially incubating an egg or brooding a chick; (4) adult standing, with no egg or chick visible; (5) adult visible but breeding site was obstructed (e.g., conspecifics around the breeding site, adult was behind a ledge); or (6) breeding site no longer in field of view, due to accidental movement of the camera. Visible eggs and chicks were distinguished from one another, and potential eggs and chicks were coded when the parental murre stood up and shifted its posture (i.e., sitting with body lifted off the

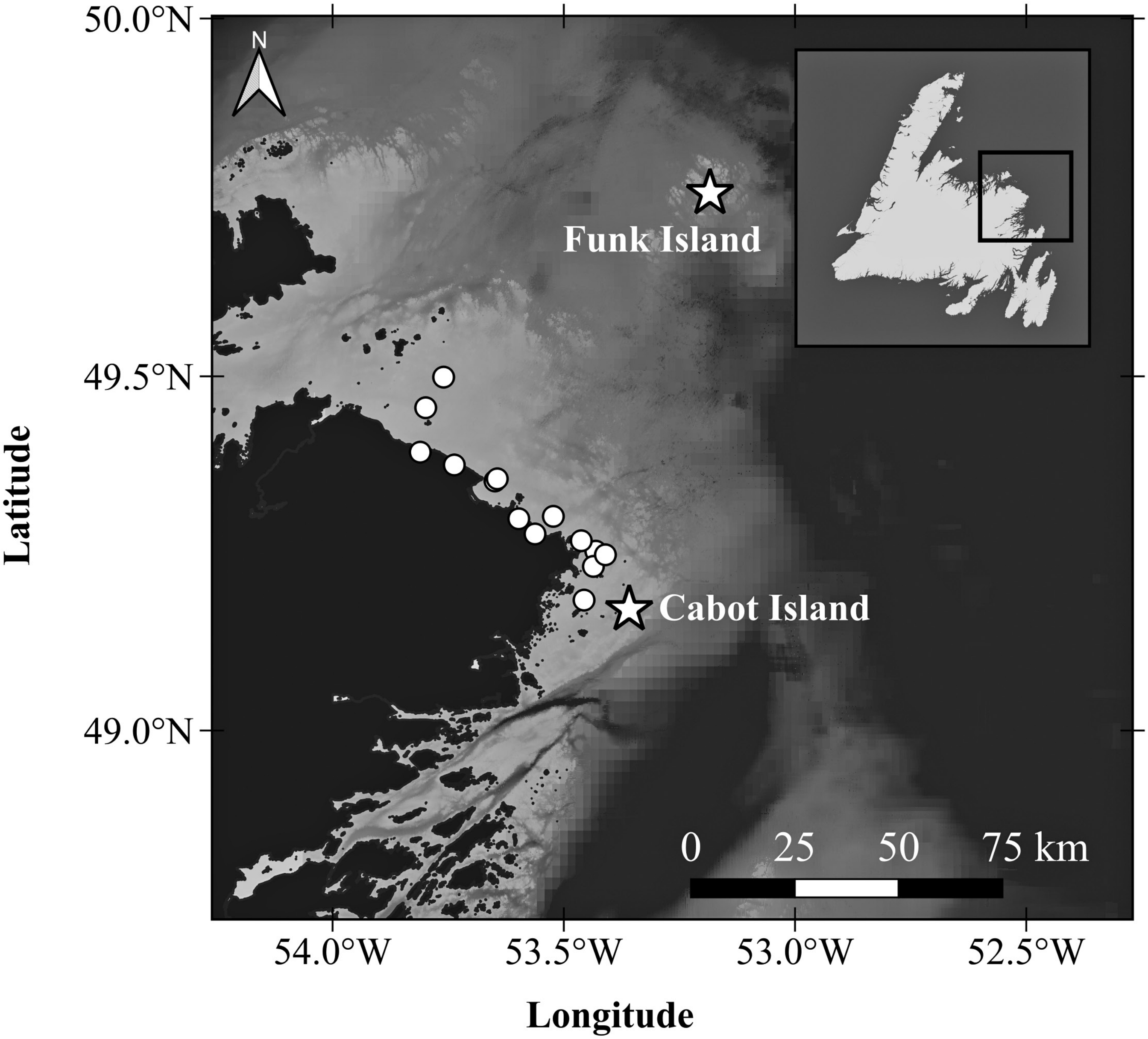

Fig. 1. A map of the study area on the northeastern Newfoundland coast, indicating Common Murre *Uria aalge* colonies (stars) and spawning sites of their prey (capelin; circles), which represents key foraging areas for murres.

ground slightly; Tuck 1960, Murphy & Schauer 1994), such that raised abdominal feathers revealed either brown/green (potential egg) or black (potential chick). Image quality was recorded for each photograph to indicate instances of low visibility due to ambient conditions (e.g., rain, fog) or lens obstruction (e.g., dirt, moisture). In addition, inadvertent changes in camera position and malfunctioning/battery issues led to different usable date ranges by plot (Table 1).

At the end of camera deployment, each breeding site was classified as having either successful or unsuccessful hatching and fledging. For unsuccessfully hatched breeding sites, the site was classified as either egg without adult (indicating abandonment) or adult without egg (indicating egg loss/predation). If an egg was still being incubated at the end of deployment, the breeding site was removed from analysis. The date of a successful hatch was recorded as the first date the chick was directly observed. A breeding site was classified as having successfully fledged a chick if it reached ≥ 15 days old (Gaston & Nettleship 1981, Murphy & Schauer 1994). Chicks that were < 15 days old and still present at the breeding site upon camera retrieval were excluded from the fledging success and reproductive success analyses.

Hatching success, fledging success, and reproductive success per focal breeding site are binary (success/fail) dependent variables. Thus, a linear mixed model with a binomial distribution and logit link was used to test whether these metrics varied between colonies (fixed, independent factor), while accounting for variation among plots within each colony (random effect). Due to unbalanced sample sizes and a categorical predictor variable with no interactions, a Type II ANOVA on a linear model with a normal distribution was used to examine if hatch dates differed between colonies with plot as a random effect (Quinn & Keough 2002). All statistical analyses were performed in R version 3.5.1 (R Core Development

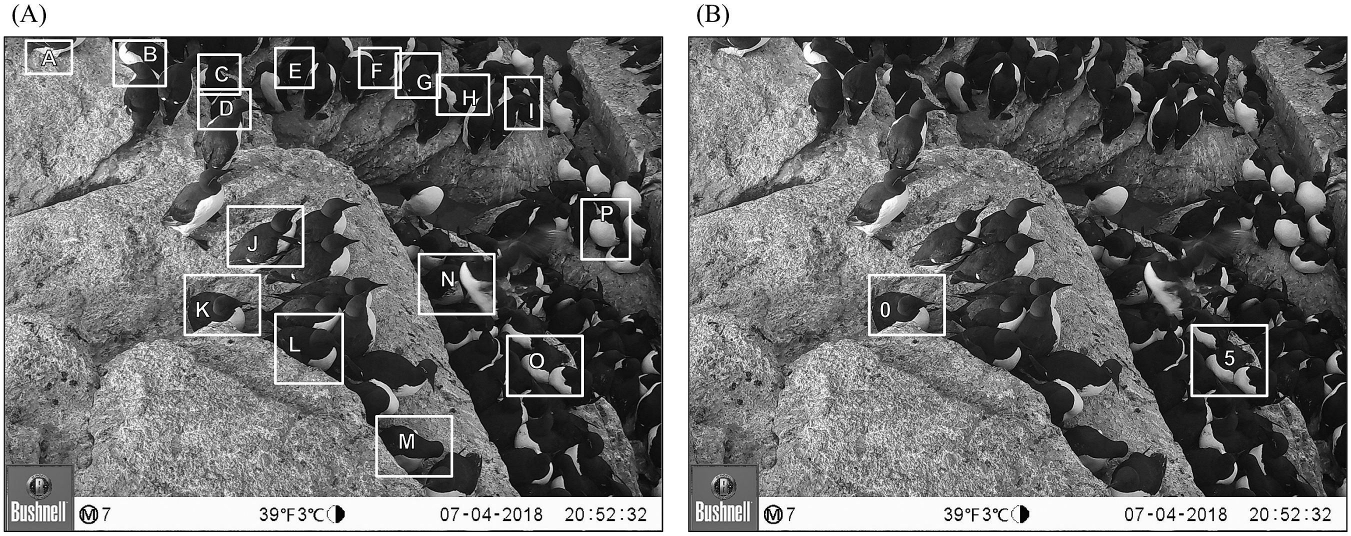

Fig. 2. A photograph of breeding and non-breeding Common Murres *Uria aalge* at plot E on Cabot Island during July 2018. In (A), breeding sites are labelled (n = 16, A–P). In (B), the number of neighbours (i.e., nests directly touching) for breeding sites O and K is indicated.

Team 2018) using the "lme4" (Bates *et al.* 2015) and "car" (Fox & Weisberg 2019) packages; α was set to 0.05 and means are reported as ± standard error.

Breeding-site vulnerability

Picture processing for breeding-site vulnerability at both colonies began the day after deployment at each, to minimize the impacts of human disturbance. For each photograph, the presence or absence of a gull was recorded. When a gull was present, we also recorded the date, time, gull species, and number of gulls. As predation attempts or events were not captured in photographs, the presence or absence of gulls (all species combined) at each plot on each day during the camera deployment period was used as a proxy of predation risk. We conducted a generalized linear mixed model with a binomial distribution and logit link to test whether daily gull presence/absence (binary, dependent variable) differed between colonies (fixed, independent factor), while accounting for variation among plots (random effect) within each colony. Similarly, we tested whether gull presence (binary, dependent variable) differed between gull species and two time categories: daylight (05h00–21h30) and night (21h31–04h59).

TABLE 1
Breeding-site monitoring data for Common Murres *Uria aalge* at each plot on Funk Island (plots A–D) and Cabot Island (plots E–F) during July–August 2018

	Funk Island					Cabot Island		
Plot	A	B	C	D	**Total**	E	F	**Total**
Monitored breeding sites[a]	12 (3)	6 (1)	6	10 (3)	**34 (7)**	12	14 (3)	**26 (3)**
Hatched eggs[b]	10 (7)	4 (1)	0	8 (6)	**22 (14)**	11 (6)	14 (11)	**25 (17)**
Fledged chicks	2	3	N/A	2	**7**	4	3	**7**
n[c]	5	5	6	4	**20**	6	3	**9**
Hatching success (%)	83.3	66.7	0	80.0	**64.7**	91.7	100.0	**96.2**
Fledging success (%)	66.7	100.0	N/A	100.0	**87.5**	80.0	100.0	**87.5**
Reproductive success (%)	40.0	60.0	0	50.0	**35.0**	66.7	100.0	**77.8**
Deployment date range	16 Jul–12 Aug					04 Jul–09 Aug		
Usable date range	16 Jul–12 Aug					04 Jul–09 Aug	15 Jul–02 Aug	

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[a] Breeding sites with eggs that were used to determine hatching success; the number in parentheses is the number of breeding sites removed from analysis, i.e., parents were still incubating upon camera retrieval.

[b] Successfully hatched eggs; the number in parentheses is the number of chicks that were removed from analysis, i.e., chicks were not observed for ≥ 15 days.

[c] The number of breeding sites where chicks were observed for ≥ 15 days and could be used for measures of reproductive success.

To test whether the number of neighbours influenced hatching success, we produced a 10-day data set to quantify the number of neighbours associated with breeding sites. We counted the number of murres directly touching the incubating/brooding bird at each focal site from photographs at three times per day (morning, afternoon, night) for 10 days, spaced every 2–3 days (Funk Island) or every 3–4 days (Cabot Island) throughout the camera deployment period for each plot (Fig. 2B). The interval between days differed between colonies due to different camera deployment duration and to avoid days of low image quality. The number of neighbours included other incubating/brooding birds, non-incubating/brooding mates, and non-breeders. Photographs representing morning and afternoon were taken at 09h30 and 16h30, respectively. Due to the different camera settings during daylight and darkness, photographs representing night were from 23h00 if available; when unavailable, we used the next available photograph after 23h00 during the night or dawn but before full daylight (i.e., before 05h45). We summarized the modal number of neighbours per focal breeding site across all 10 days to reflect the typical number of neighbours at each site throughout the entire breeding period over all times per day and for each time of day. We conducted generalized linear mixed models with a binomial distribution and logit link to test whether hatching success (binary, dependent variable) was influenced by the modal number of neighbours (continuous, independent factor) across all times of day and within each time of day. Additionally, we conducted a generalized linear mixed model with a Poisson distribution and logit link function to test whether the modal number of neighbours (count data) differed between colonies and among the three time-of-day categories, with plot included as a random effect. As our data set included unbalanced sample sizes among predictor variables and an interaction, we used a Type III ANOVA with a Wald chi-squared test (Quinn & Keough 2002). Tukey HSD pairwise tests were used to compare differences among factor categories.

To further examine diel temporal patterns in the number of neighbours per breeding site, we quantified the number of neighbours per focal breeding site for every photograph (~30-minute intervals) throughout each day on three of the 10 days (10-day data set). The three days were chosen from early, mid, and late deployment to reflect the typical number of neighbours per focal breeding site throughout the entire breeding period. The same three days were used across plots when possible, but if unusable photographs were taken on those dates for a plot, the nearest possible date was chosen. For four photographs per day—representing peaks (13h00, 20h00) and lows (01h00, 09h30) in the number of breeding-site neighbours—each neighbour was classified as either (1) an incubating/brooding individual or (2) a non-incubating/non-brooding mate or non-breeding bird (hereafter referred to as ‘non-breeders/non-brooders’), as the latter two could not be distinguished. We then quantified the proportion of neighbours that were non-breeders/non-brooders versus breeders to distinguish which neighbour type was responsible for shifts in the number of neighbours at breeding sites throughout the day. To determine whether the proportion of non-breeders/non-brooders per breeding site differed between colonies and among the four time-of-day categories, we arcsine square-root transformed the proportions to meet the underlying assumption of parametric statistics (Quinn & Keough 2002) and applied a linear mixed model with both colony and time of day as fixed factors and plot as a random effect. A Type III ANOVA with a Wald chi-squared test was used again due to unbalanced sample sizes (Quinn & Keough 2002), with a Tukey HSD pairwise test performed to compare among the factor categories. All analyses were performed in R (R Core Development Team 2018) using the “car” (Fox & Weisberg 2019), “lme4” (Bates *et al.* 2015), and “emmeans” (Lenth 2020) packages.

RESULTS

Breeding performance metrics

At the end of camera deployment, breeding sites with eggs that were still being incubated (Funk Island: $n = 7$; Cabot Island: $n = 3$) were removed from analysis (Table 1). Hatching success differed significantly between colonies ($Z = 2.02$, $P = 0.044$; Fig. 3A): all plots on Funk Island had lower hatching success (0%–83%) than those on Cabot Island (92%–100%; Fig. 3A), with 22 out of 34 breeding sites (64.7%) hatching at Funk Island, compared with 25 out of 26 breeding sites (96.2%) hatching at Cabot Island (Table 1). Owing to the hatching failure of all focal breeding sites in plot C at Funk Island, we re-ran the analysis without this plot. While eggs still tended to be more likely to hatch on Cabot Island (8.3 times), this difference between colonies was no longer significant ($Z = 1.91$, $P = 0.06$). The 12 unsuccessfully hatched breeding sites at Funk Island were equally classified as an adult without an egg (i.e., depredated) or an egg with no adult (i.e., abandoned). Specifically, we recorded one depredated and one abandoned egg at both plots A and D; two depredated eggs at plot B; and two depredated and four abandoned eggs at plot C. At Cabot Island, the

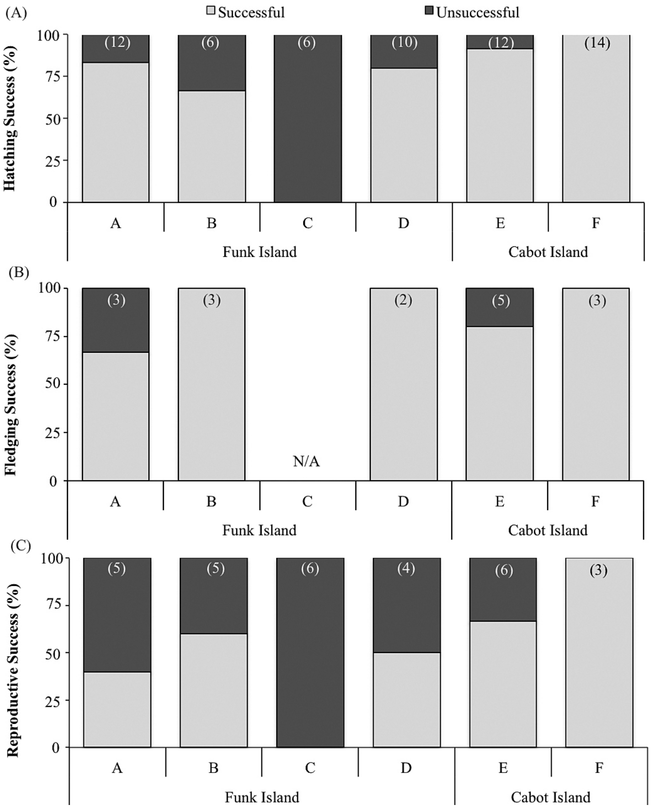

Fig. 3. Breeding performance metrics of Common Murres *Uria aalge* per plot (A–F) at Funk Island and Cabot Island throughout July and August 2018, including (A) hatching success, (B) fledging success (i.e., chick ≥ 15 days old), and (C) reproductive success. The total number of breeding sites is in parentheses.

one unsuccessfully hatched egg was classified as an adult without an egg (i.e., depredated) at plot E. Although Cabot Island had an earlier mean hatching date (25 July) compared to Funk Island (31 July), mean hatching dates did not differ significantly between colonies ($\chi_1^2 = 1.05$, $P = 0.31$).

In contrast, fledging success did not differ significantly between colonies ($Z = 0.00$, $P = 1.00$). Of the 22 and 25 breeding sites that successfully hatched chicks at Funk Island and Cabot Island, respectively, eight sites were included in the analysis of fledging success at each colony, as they were observed for ≥ 15 days (Table 1). Of these eight sites, seven at each colony (87.5%) were considered successfully fledged (Fig. 3B). Overall, the reproductive success did not differ significantly between colonies ($Z = 1.83$, $P = 0.07$), but tended to be lower at Funk Island, where only seven breeding sites successfully fledged chicks out of the 20 sites with an egg (35%), compared to Cabot Island where seven breeding sites successfully fledged a chick out of nine sites with an egg (77.8%; Fig. 3C, Table 1).

Breeding-site vulnerability

The two gull species observed near breeding sites were American Herring Gulls (adults: 31% of all gulls; immatures: 24%) and Great Black-backed Gulls (adults: 45%). All gull sightings ($n = 29$ in 12 027 images) occurred before each colony's peak hatch date. Most gull sightings across both colonies occurred at Funk Island (96.6%; 2 at plot B, 26 at plot C). We removed six gull observations at plot C from analysis, as they were observed after all breeding sites at this plot had failed (27 July). At Cabot Island, the only gull sighting was one American Herring Gull observed at plot E. Overall, the daily gull presence did not differ between colonies ($Z = -0.57$, $P = 0.57$), but gulls were present at plot C on Funk Island on all 11 consecutive days from camera deployment to the date when all breeding sites had failed at this plot (16–26 July); gulls were often observed multiple times per day (range: 1–6 gulls). As most gulls were observed at plot C on Funk Island, we examined whether the number of gulls of each species at this plot differed significantly among daylight and dark periods. Although the majority of Great Black-backed Gulls (9 of 12 sightings; 75%) and American Herring Gulls (9 of 14 sightings; 64.3%) were observed during the day, the presence of gulls did not differ between day and night ($Z = -0.88$, $P = 0.38$) nor between gull species ($Z = 0.85$, $P = 0.40$), and the interaction between time of day and gull species was not significant ($Z = -0.25$, $P = 0.80$).

One parent was not brooding its egg during the times of neighbour assessment and was removed from the 10-day data set. Hatching success from the remaining 59 breeding sites at both colonies combined was not significantly influenced by the modal number of neighbours per focal breeding site in the 10-day data set for all time categories combined ($Z = 1.74$, $P = 0.08$; Fig. 4) or for the afternoon (16h30: $Z = 1.47$, $P = 0.14$). However, higher hatching success was associated with more neighbours near breeding sites in both the morning (09h30: $Z = 2.96$, $P = 0.003$) and at night (23h00: $Z = 2.88$, $P = 0.004$). Additionally, the modal number of neighbours per breeding site differed significantly between colonies ($\chi_1^2 = 7.30$, $P = 0.007$) and time categories ($\chi_2^2 = 14.60$,

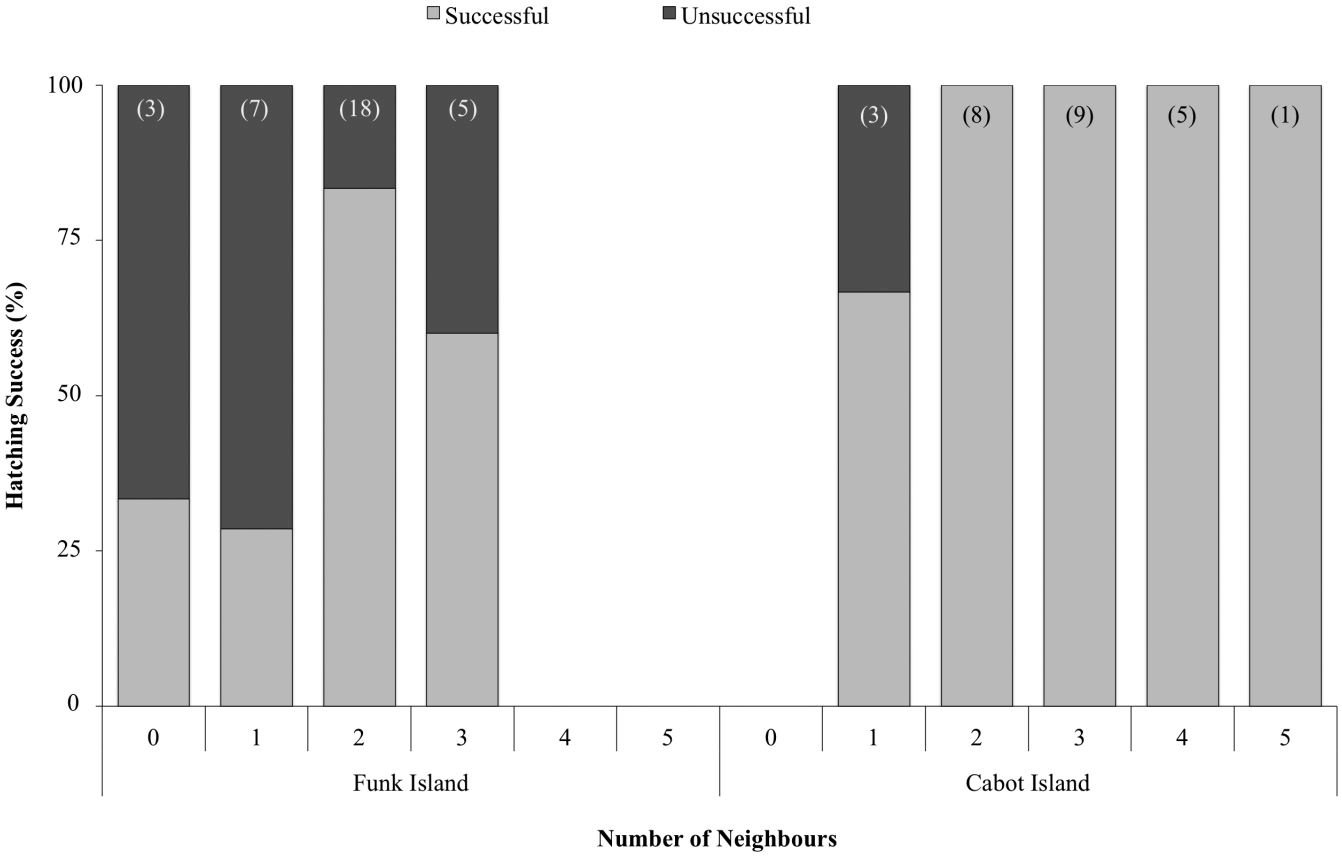

Fig. 4. Hatching success of Common Murres *Uria aalge* across all plots (A–F) at Funk Island and Cabot Island throughout July and August 2018, in relation to the modal number of neighbours across all three time-of-day categories (09h30, 16h30, 23h00) combined.

P = 0.0007); the interaction was also significant (χ_2^2 = 6.24, *P* = 0.044; Fig. 4). Post-hoc tests revealed that the number of neighbours was significantly lower at Funk Island during the night (23h00) relative to Cabot Island during all time categories (*P* = 0.006 at 09h30; *P* = 0.002 at 16h30; *P* = 0.014 at 23h00), but it did not differ between colonies throughout the rest of the time categories (*P* values = 0.23–0.99). The number of neighbours at Funk Island was also significantly lower at night than during the afternoon (16h30; *P* = 0.002), but did not differ among other time categories at Funk Island (*P* values = 0.15–0.53) and did not differ between any time categories at Cabot Island (*P* values = 0.96–0.99).

Using three days from the 10-day data set, we examined which neighbour type was responsible for shifts in the number of neighbours at breeding sites throughout the day. The percentage of non-breeding/non-brooding neighbours differed significantly among times of day (χ_3^2 = 68.99, *P* ≤ 0.0001) but not between colonies (χ_1^2 = 2.89, *P* = 0.09), although Cabot Island tended to have a higher proportion of non-breeding neighbours at all time categories (Fig. 5); the interaction was not significant (χ_3^2 = 6.95, *P* = 0.07). A Tukey post-hoc test showed that the percentage of non-breeding/non-brooding neighbours at 01h00 was significantly lower relative to all other times at each colony (*P* values ≤ 0.041), but the percentage

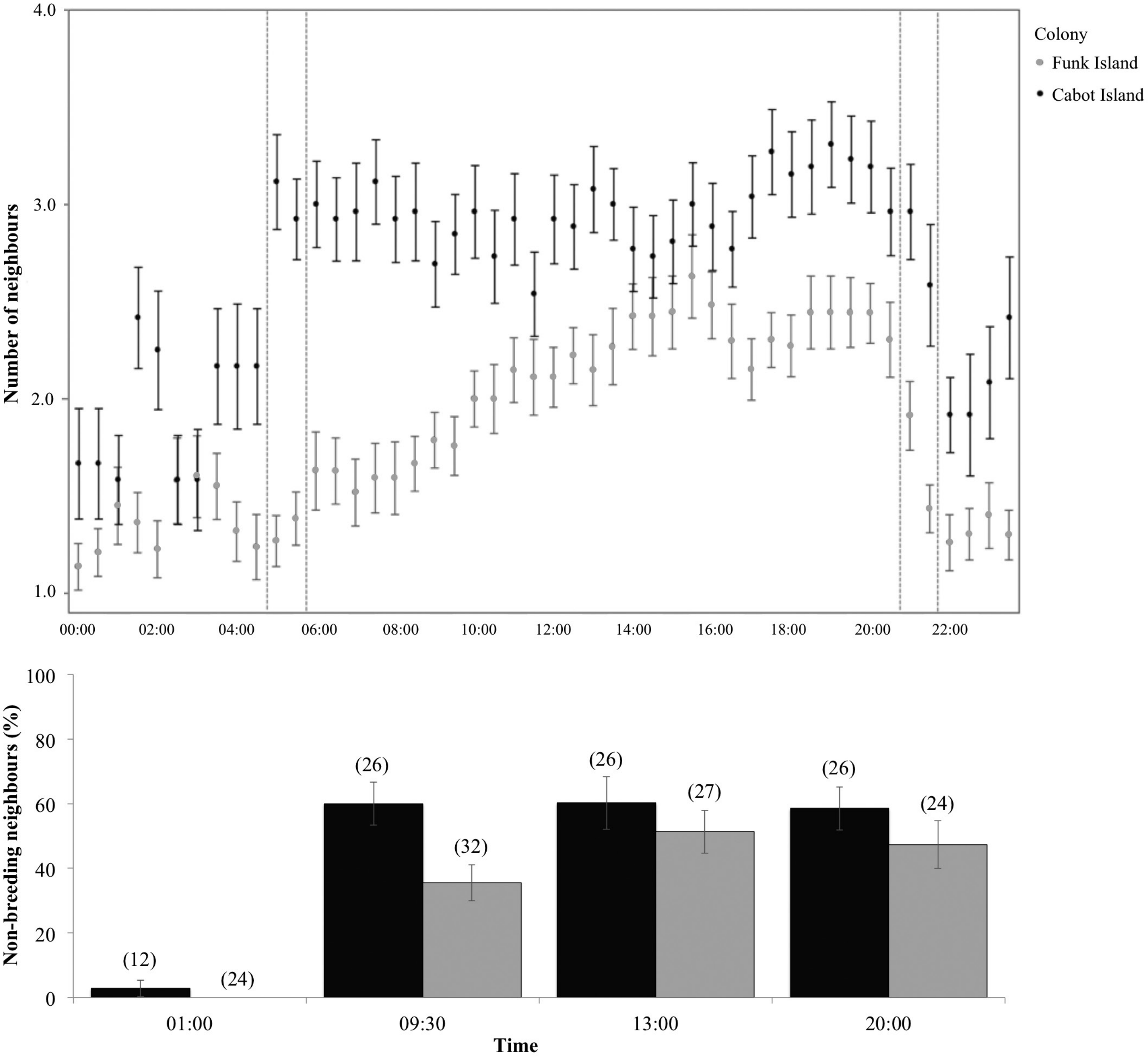

Fig. 5. Upper panel: Number of neighbours (mean ± standard error (SE)) for 59 focal breeding sites of Common Murres *Uria aalge* across all plots at Funk Island (grey) and Cabot Island (black) during three days in July–August 2018, where dawn (05h00–05h45) and dusk (20h50–21h30) are shown within the dotted lines to indicate day and night periods. Lower panel: The mean ± SE percentage of non-breeding/non-brooding neighbours at four times of day (01h00, 09h30, 13h00, 20h00) was averaged over three days at each colony (Funk Island (grey) and Cabot Island (black)), with the sample size indicated in parenthesis.

of non-breeding/non-brooding neighbours did not differ among other times of day during daylight hours (P values > 0.17; Fig. 5).

DISCUSSION

As we did not observe the entire incubation period at each colony and sample sizes were low (n = 70 breeding sites monitored), we acknowledge that we likely overestimated hatching success because eggs were probably lost prior to our observation period and therefore, hatching success may not be representative across the entire colony. This study, however, provides the first contemporary quantitative estimates of phenology and productivity at these two key colonies, representing > 75% of the Northwest Atlantic population of Common Murres. Consistent with previous findings using the same data set (Gulka *et al.* 2020), hatching success was lower at Funk Island (64.7%) than at Cabot Island (96.2%), resulting in lower reproductive success at Funk Island (35%) relative to Cabot Island (77.8%). Because lower hatching success was associated with fewer breeding-site neighbours (morning, night) and because Funk Island had both fewer neighbours (night) and tended to have a lower percentage of non-breeding/non-brooding neighbours relative to Cabot Island, the lower hatching success at Funk Island may be related to higher vulnerability of eggs to gull predation. Although gulls were only present in 0.24% of all pictures, one study reported similarly few sightings of gull predation events in the colony yet recorded high feeding rates of murre eggs/chicks to gull offspring (Gaston *et al.* 1985). This indicates that predation events are rapid, difficult to detect, and likely require continuous observations to document (Hatchwell 1991, Schauer & Murphy 1996). All gull observations occurred before peak hatching, which suggests that gulls might preferentially depredate eggs over chicks; this is consistent with the divergent hatching success but similar fledging success between the colonies.

Our observations of lower hatching success and breeding sites with fewer neighbours (primarily non-breeders/non-brooders) at Funk Island indicated higher predation risk at this colony. In support, higher egg predation of murres has been previously associated with fewer neighbours (Johnson 1938). Egg predation attempts by gulls are more successful in areas of low breeding densities, possibly because high neighbour densities deter gulls from attacking breeding sites (Birkhead 1977, Gaston & Nettleship 1981). For example, 44% of predation attempts by Glaucous Gulls *Larus hyperboreus* on Thick-billed Murre eggs were unsuccessful in areas of high breeding density, whereas only 24% of gull predation attempts were unsuccessful in sparsely populated breeding areas (Gilchrist & Gaston 1997). At colonies with high breeding densities, many murres lunging toward approaching gulls can deter their attacks and reduce the time during which murres need to be alert (Birkhead 1977), which is consistent with the "collective detection" effect (Powell 1974, Lima 1995). In contrast, when breeding at low neighbour densities, both Great Black-backed and American Herring gulls have been observed pulling adult murres by the wing or tail feathers, then lunging for the exposed egg, but this is infrequently observed at high breeding densities (Birkhead 1977). Lower hatching success with fewer neighbours at night, together with fewer non-breeder/non-brooding neighbours at night, indicate that eggs may be especially vulnerable to predation during dark periods. Although we did not observe higher gull presence at night, possibly due to our camera settings resulting in lower observation effort relative to the daytime, previous studies of gull predation on murres also lack observation effort at night (Hatchwell 1991, Parrish 1995, Veitch *et al.* 2016). Future studies investigating nocturnal gull predation at murre colonies may improve our understanding of predation risk during the dark hours.

Murres breeding at low densities may also be more likely to abandon their egg in the presence of a predator. This may explain the apparently equal egg abandonment and predation rates at Funk Island, which combined to result in lower hatching success. Indeed, previous studies have described higher probabilities of parental murres standing up and exposing their egg to gulls in areas of low breeding density, relative to areas of high density (Birkhead 1977). In fact, murres at lower breeding densities have been observed to alarm call, flap their wings, and abandon their breeding site in response to a predation attempt by gulls, likely resulting in the development of a conditioned fear response to gull presence after multiple predation attempts (Johnson 1938). This fear response includes rapid head bobbing (i.e. alarm-bowing) and repetitive calling ("owka"; Tuck 1960, Birkhead 1976, Gaston & Nettleship 1981), and the response from one breeder can lead to an area-wide fear response and additional egg abandonments (Johnson 1938, Birkhead 1977, Parrish 1995). Such a fear response may explain the complete failure of plot C on Funk Island, which had the lowest average number of neighbours and four egg abandonments after 26 gull sightings at this plot (90% of all sightings in this study). Overall, egg predation and abandonment appeared to be higher when murres had fewer neighbours available to watch and collectively defend breeding sites from gulls. This was likely the reason for lower hatching success at Funk Island (Birkhead 1977, Schauer & Murphy 1996).

Predation risk at Funk Island may also be exacerbated by an increased dietary reliance on seabirds by gulls. Gulls breeding on islands farther from shore have fewer options, owing to more limited access to coastal resources (e.g., intertidal invertebrates) relative to those breeding closer to shore. These offshore gulls have exhibited different dietary composition from inshore breeding gulls, as diet relates to proximate available resources (Enners *et al.* 2018, Maynard & Davoren 2020). In particular, the large murre colony (~500 000 breeding pairs; Wilhelm *et al.* 2015) on Funk Island provides an abundant resource, and both Great Black-backed and American Herring gulls breeding at Funk Island appeared to provision their chicks at higher trophic levels (i.e., seabirds) relative to gulls breeding on inshore colonies in the study area; murre chicks have been observed as part of the gull chick diet (Maynard & Davoren 2020).

Consistently higher numbers of neighbours at Cabot Island breeding sites compared to Funk Island sites, despite similar reported breeding densities of murres at both colonies (18–37 breeding pairs/m^2; Wilhelm *et al.* 2015), may be explained by non-breeding/non-brooding neighbours spending less time at sea to provision themselves and their chicks. In support, murres at Cabot Island during the study year (2018) travelled shorter distances (< 10 km) to predictable inshore prey patches than those at Funk Island (~60 km) and also likely experienced lower conspecific densities within foraging ranges relative to Funk Island (Gulka *et al.* 2020). Previous studies showed that the number of neighbours near breeding sites varied among murre colonies (Harris *et al.* 2015), often due to differences in food availability. Indeed, food shortages result in less time spent at colonies by non-brooders (i.e., 'paired time' with mates; Zador & Piatt 1999), non-breeders (Gaston & Nettleship 1981, Harding *et al.* 2007), and in one instance, both breeding adults simultaneously (Ashbrook *et al.* 2008). In turn, during times of seasonally high prey availability, non-breeders/non-brooders spend less time foraging at sea and more time at colonies, resulting in higher neighbour densities (Gaston & Nettleship 1981). The presumably greater time that non-breeding/non-brooding murres at Funk Island spent foraging at sea may have been further increased during incubation because high abundance aggregations of the main prey species (capelin) were typically not yet present within colony foraging ranges (Davoren *et al.* 2012). This lower resource availability during incubation would be exacerbated at larger seabird colonies, where the foraging ranges of a higher number of conspecifics overlap (Lewis *et al.* 2001), resulting in higher intraspecific competition near the colony (Ronconi & Burger 2011, Gaston *et al.* 2013). As lower resource availability is known to cause higher stress levels in breeding murres (Kitaysky *et al.* 2007)—resulting in delayed egg laying (Gaston & Nettleship 1981, Shultz *et al.* 2009), poor hatching success (Kitaysky *et al.* 2007, Shultz *et al.* 2009), and possibly egg abandonment (Groscolas *et al.* 2008)—it might also explain lower hatching success at Funk Island. Overall, a combination of factors likely influenced the divergent number of neighbours near breeding sites at Funk Island relative to Cabot Island, which likely influenced hatching success.

Divergent foraging conditions (i.e., distance to foraging sites, conspecific densities) within the ranges of both colonies may also explain the colony-specific differences in neighbour densities throughout the diel cycle. Previous studies of murres have found lower neighbour densities at night relative to daytime (Birkhead 1978, Slater 1980, Gaston & Nettleship 1981), due to non-brooding mates usually spending nights at sea (Wanless & Harris 1986). Similarly, we found that non-brooders/non-breeders likely spent nights at sea, as most breeding-site neighbours at both colonies during the night were brooding birds. Therefore, higher numbers of neighbours throughout the day likely indicates the accumulation of non-breeding/non-brooding birds at the colony, as non-breeders appear to mimic the arrival time of breeders (Birkhead 1978, Gaston & Nettleship 1981). The steep increase in the number of neighbours at dawn on Cabot Island compared to the gradual increase throughout the morning on Funk Island again indicates that non-breeding/non-brooding birds arrive at the Cabot Island colony faster from nearby foraging sites (Gaston & Nettleship 1981) and that mates remain together longer at Cabot Island due to the presumably less time spent at sea relative to Funk Island (Birkhead 1978).

Interestingly, fledging success did not appear to be affected by the divergent foraging conditions within the foraging ranges of each colony, although small sample sizes for fledged breeding sites may have influenced these conclusions. While previous studies found that chick-rearing murres who spend more time foraging at sea are known to provision chicks at a lower rate (Davoren & Montevecchi 2003, Piatt *et al.* 2007), fledging success may not be affected (Harris & Wanless 1988, Piatt *et al.* 2007) but may instead result in lower fledging body condition (Davoren & Montevecchi 2003). As flightless murre chicks leave the breeding site with the male parent at ~25% of adult body mass (Harris & Birkhead 1985), these long-lived parents may favour their own survival over offspring survival to maximize their lifetime reproductive success (Schaffer 1974, Parrish 1995). Thus, they preferentially provision the chick at sea rather than at the colony due to the high energetic costs of flight among murres (Elliott *et al.* 2013). This strategy might explain why body condition at fledging does not appear to influence first-year survival (Hedgren 1981, Harris *et al.* 2007), and it suggests that fledging success may not be the best colony-based metric of reproductive success for Common Murres.

CONCLUSIONS

Overall, shorter distances to foraging areas by murres at Cabot Island combined with lower conspecific densities at foraging sites may have led to non-breeding/non-brooding individuals spending less time at sea and consequently more time at the colony. This may explain the higher number of neighbours at Cabot Island relative to Funk Island, which likely deterred gull predators, leading to only a single depredated breeding site and no egg abandonments and, thus, higher hatching success relative to Funk Island. As most breeding-site failures and all gull sightings occurred before hatching, the effect of better breeding-site defense from gulls with an increased number of neighbours may be most important during the incubation period, thereby acting as a limitation on breeding performance. Although we cannot preclude the impact of human disturbance during camera deployment, whereby gulls are attracted to murre breeding sites after adults have fled in response to human disturbance (Johnson 1938, Birkhead 1976), we would have expected our impact to be similar across colonies.

Together, based on these findings, we suggest that Cabot Island may be more productive than Funk Island and that the higher number of non-breeding/non-brooding neighbours also indicates greater competition for higher-quality breeding sites (Kokko *et al.* 2004). It is important to understand colony productivity. Although the murre population at Funk Island is growing, growth is minimal (i.e., 0.3% per year, 1972–2009; Wilhelm *et al.* 2015) and likely results from the population rebounding after regional-scale removal of gillnets deployed to capture Atlantic cod *Gadus morhua* in 1992, which caused significant murre bycatch during 1950–1992 (Regular *et al.* 2013). While Funk Island is an Important Bird and Biodiversity Area, a designation that establishes the island as a distinct area for implementing conservation action, the surrounding water and Cabot Island remain unprotected. Although population trends of murres on Cabot Island are currently unknown, Cabot Island may also be a key priority for protection if the higher reproductive success is consistent at this colony over time. Indeed, protection of both colonies may ensure long-term conservation of the Common Murre population in the region, which represents > 75% of the Northwest Atlantic population (Cairns *et al.* 1989), while protection of only Funk Island may not.

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