

INTRA-ANNUAL SHIFTS IN ATLANTIC PUFFIN *FRATERCULA ARCTICA* DEPREDATION AND KLEPTOPARASITISM BY *LARUS* GULLS AT A MULTI-SPECIES SEABIRD COLONY

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ABSTRACT

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Great Black-backed Gulls *Larus marinus* and American Herring Gulls *L. argentatus smithsonianus* are considered dietary generalists at the population level: they consume a variety of prey types, including the adults and offspring of other seabirds, and they shift among prey types as availability varies. Atlantic Puffin *Fratercula arctica* adults, eggs, and chicks are often the target of depredation, and adults are also susceptible to kleptoparasitic attacks by large gulls during their summer breeding season in coastal Newfoundland, Canada. We investigated the depredation and kleptoparasitism of puffins by large gulls during July–August 2021/22 at a multi-species breeding colony on the northeast coast of Newfoundland. We hypothesized that both the inshore arrival of spawning Capelin *Mallotus villosus*, a key forage fish species in the region, and the onset of the puffin chick-rearing period, which typically coincide, influence puffin depredation and kleptoparasitism by large gulls. Shoreline transects on James Island revealed a decrease in new adult puffin carcasses during puffin chick-rearing and Capelin spawning, with most adult puffin depredation occurring before the inshore arrival of spawning Capelin in both years. Behavioural observations (i.e., focal animal, behavioural sampling, and instantaneous scan sampling) revealed that Great Black-backed Gulls were more often present within puffin burrow areas and spent a higher proportion of time in these areas relative to American Herring Gulls, especially during Capelin spawning and puffin chick-rearing. Within puffin burrow areas, Great Black-backed Gulls depredated chicks and kleptoparasitized adults. As only ~30% of followed individuals of both gull species entered puffin burrow areas, it is possible that only a few Great Black-backed Gulls were responsible for puffin depredation and kleptoparasitism.

Key words: depredation, kleptoparasitism, foraging behaviour, Atlantic Puffin, Great Black-backed Gull, American Herring Gull, Atlantic Canada

INTRODUCTION

Large gull species, including the Great Black-backed Gull *Larus marinus* and American Herring Gull *L. argentatus smithsonianus*, are dietary generalists at the population level. They consume a variety of prey types throughout the year, such as forage fish (e.g., Capelin *Mallotus villosus*, Sand Lance *Ammodytes* spp.), intertidal invertebrates (e.g., sea urchins, mussels), and the eggs, chicks, and adults of other seabird species (Harris 1965, Pierotti & Annett 1991, Russell & Montevecchi 1996, Regehr & Montevecchi 1997, Rodway *et al.* 1998, Steenweg *et al.* 2011, Veitch *et al.* 2016, Bond *et al.* 2023). In coastal Newfoundland, large gull species are important avian predators of other seabirds when the latter are rearing their chicks during the summer (late June–August; Harris 1980, Russell & Montevecchi 1996, Rodway *et al.* 1998, Stenhouse *et al.* 2000). Atlantic Puffins *Fratercula arctica* (hereafter ‘puffins’) are often the target of depredation by large gulls (Pierotti 1983, Russell & Montevecchi 1996, Rodway *et al.* 1998). Gulls catch adult puffins primarily in flight (Harris 1980) or when the puffins land near their burrows (Rodway *et al.* 1998), and gulls have been observed carrying injured birds, including puffins, to other locations to kill (e.g., to drown; Evans 1975, Harris 1980, Burger & Gochfeld 1984, Ingraham *et al.* 2020).

The larger Great Black-backed Gull (1300–2000 g; Good 2020) tends to feed on larger, higher trophic level prey than the smaller

American Herring Gull (600–1150 g; Weseloh *et al.* 2020, Maynard & Davoren 2020) and is more likely to attack large adult seabirds such as puffins (310–550 g; Lowther *et al.* 2020), the latter being a main prey source (Harris 1980, Pierotti 1983, Regehr & Montevecchi 1997, Westerberg *et al.* 2019). American Herring Gulls may attack adult seabirds of smaller species (Pierotti & Annett 1991, Bond *et al.* 2023), such as Leach’s Storm Petrels *Hydrobates leucorhous* (45–55 g in coastal Newfoundland; Pollet *et al.* 2021), but they tend to feed on smaller, lower trophic level prey than Great Black-backed Gulls (Steenweg *et al.* 2011, Washburn *et al.* 2013, Maynard & Davoren 2020). Therefore, American Herring Gulls are more likely to opportunistically prey on eggs, chicks, and fledgling seabirds than to attack adults of larger species (Pierotti 1983, Donehower *et al.* 2007). Despite being population-level dietary generalists, individuals of both large gull species may show contextual (fluctuating) or non-contextual (fixed) dietary specialization (McCleery & Sibly 1986, Araújo *et al.* 2011, Maynard *et al.* 2021).

Although a relatively high trophic level prey, adult puffins may not always be the preferred prey for gulls. Foraging theory predicts that the dietary composition of large gulls will shift with varying prey availability to maximize their rate of net energy intake (energy gained from consumption minus energy spent searching and handling). Thus, newly available prey types are incorporated when their addition

increases net energy intake (i.e., the new prey type is 'profitable'; MacArthur & Pianka 1966, McFarland 1977, Mangel & Clark 1986, Tome 1988, Bolnick 2001). Capelin is the dominant forage fish species in coastal Newfoundland when they migrate inshore to spawn during early to mid-July (Davoren 2013, Crook *et al.* 2017, Buren *et al.* 2019). Owing to the potential risk of injury during adult puffin depredation attempts, the dietary composition of large gulls may shift from puffin depredation to Capelin. In support, gull depredation pressure on other breeding seabird species in coastal Newfoundland typically decreases with increasing availability of Capelin (Regehr & Montevecchi 1997, Stenhouse & Montevecchi 1999, Massaro *et al.* 2000). Moreover, the population-level dietary niche breadth of chicks of large gulls typically narrows as parental gulls focus on Capelin during spawning (Gulka *et al.* 2017).

As surface feeders, however, gulls cannot access Capelin residing in deeper water (> 1 m; Regehr & Rodway 1999). Therefore, gulls often access these fish by kleptoparasitizing (i.e., stealing prey caught by others) other seabirds (e.g., pursuit-diving puffins; Harris 1965, Veitch *et al.* 2016, Lowther *et al.* 2020). Chick-rearing puffins carrying fish back to burrows in their bills ('bill load'; Lowther *et al.* 2020) are vulnerable to kleptoparasitic attacks. Gulls typically wait in puffin burrow areas and then run, lunge, or 'fly-jump' to intercept them as they land (Nettleship 1972, Pierotti 1983, Rodway *et al.* 1998, Veitch *et al.* 2016, Busniuk *et al.* 2020). Kleptoparasitizing puffins presents little danger to gulls, as puffins give up prey to escape potential harm or death. This allows gulls to successfully steal food in ~25%–50% of kleptoparasitic attacks with little risk of injury (Pierotti 1983, Busniuk *et al.* 2020). Therefore, kleptoparasitizing bill loads of puffins is likely more profitable than preying on adult puffins and may be a favourable foraging tactic when forage fish are inaccessible (Thompson 1986, Veitch *et al.* 2016, Busniuk *et al.* 2020). Additionally, chicks in shallow burrows or venturing to burrow openings also become available during chick-rearing and may be profitable, given their similarly lower risk of injury to gulls during capture and consumption. Indeed, gulls are known to prey on chicks of puffins (Nettleship 1972, Pierotti 1983) and other species (Donehower *et al.* 2007).

The main objective of this study was to investigate changes in the depredation and kleptoparasitism of puffins by large gulls under varying Capelin availability throughout the puffin breeding season in coastal Newfoundland. As puffins are long-lived seabirds with high annual adult survival (~80%–90%; Lowther *et al.* 2020) and low annual reproductive output (raising one chick per year, at most), adult mortality may have a high impact on their population dynamics (Harris 1980, Russell & Montevecchi 1996). We combined measures of gull presence and behaviour nearby and within puffin burrow areas with counts of new puffin carcasses throughout the puffin breeding season (July–August 2021/22). In this way, we assessed shifts in puffin adult/chick depredation and kleptoparasitism by Great Black-backed and American Herring gulls. We hypothesized that the inshore arrival of spawning Capelin and the onset of puffin chick-rearing, which typically coincide, influence adult puffin depredation by large gulls. We predicted that gulls shift from depredation on adult puffins to chick depredation and kleptoparasitism following the onset of puffin chick-rearing, when puffin chicks and chick-provisioning adults (susceptible to kleptoparasitic attacks) become readily available. We also predicted that this shift would be more pronounced in Great Black-backed Gulls relative to American Herring Gulls, as American Herring Gulls may rely more heavily on Capelin than other seabirds as

prey. Overall, we aimed to provide insight into factors influencing mortality of Atlantic Puffins, a protected species listed as globally threatened with the conservation status Vulnerable on the IUCN Red List of Threatened Species (BirdLife International 2023).

STUDY AREA AND METHODS

The largest puffin breeding colony on the northeast Newfoundland coast occurs on James Island (Fig. 1), a small island (< 0.150 km²) with a multi-species seabird breeding colony; it is home to ~17 000 puffin breeding pairs burrowing over an area of ~0.020 km² (Jenkins *et al.* 2018). James Island consists of a grassy interior and a shoreline of mostly bare rock and boulders (Fig. 1; Jenkins *et al.* 2018). Puffins build nests in sod burrows, and burrows are concentrated in multiple distinct 'burrow areas' (one burrow/m², 85% occupancy rate; Jenkins *et al.* 2018) that are separated by thick patches of waist-height vegetation. Most puffin burrows on James Island are found inshore of a boulder field along the southeastern coast and in large areas of sod along the western coast (Fig. 1). Other seabird species that breed alongside puffins on the island include Razorbills *Alca torda* (~2800 nests), Leach's Storm Petrels (~1600 nests), Common Murres *Uria aalge* (~23 nests), Great Black-backed Gulls (~8 nests), and American Herring Gulls (~30 nests; Jenkins *et al.* 2018). Gulls of both species also breed on two nearby (< 10 km) islands (~9 Great Black-backed and ~35 American Herring Gull nests; Jenkins *et al.* 2018).

In 2021, we made three visits to James Island to conduct research, for a total of 23 d during puffin incubation (07–12 July 2021) and chick-rearing (16–26 July 2021, 02–07 August 2021). In 2022, we made four visits, for a total of 21 d during puffin incubation (09–12 and 15–19 July 2022) and chick rearing (22–27 July 2022, 01–06 August 2022). Additionally, we made a final single-day visit in both years (13 August 2021, 12 August 2022) during the late stages of puffin chick rearing, when many puffin chicks were beginning to fledge. In both years, all gulls were rearing chicks and no longer guarded nests on the first colony visit. Although Russell and Montevecchi (1996) attributed all Atlantic Puffin carcasses at this colony to depredation by gulls, a recent analysis of regurgitated gull pellets from this colony did not detect adult puffin remains (Rieger 2022), likely because gulls primarily consume puffin breast muscle and other soft tissues, resulting in a lack of hard parts regurgitated in pellets (Holt & Schill 2002, Steenweg *et al.* 2011). As such, we used a combination of other methods to examine gull-based depredation and kleptoparasitism risk on puffins. First, we conducted a standardized transect throughout July–August 2021/22 to quantify the number of fresh adult puffin carcasses on the shoreline. Second, we conducted focal animal sampling on gulls from two locations ('vantage points' 1 and 2; Fig. 1) during 2021 to quantify the proportion of time spent by individual gulls in a variety of behaviours both within and outside of puffin burrow areas. Based on limited observations of depredation and kleptoparasitism during 2021, we shifted behavioural observations to instantaneous scan samples and behavioural sampling (following Martin & Bateson 2007) from a single location (vantage point 1; Fig. 1) during 2022. This shift in techniques allowed us to better meet our objectives by focusing on quantifying gull behaviour only while present in puffin burrow areas. In both years, behavioural observations were only performed during daylight as gulls are not typically present within puffin burrow areas at night (Rieger 2022).

To determine hatching dates of puffins (i.e., onset of the chick-rearing period), 44 active nests were monitored by hand-sampling

for the presence of an egg or chick every two to three days during colony visits in both years. The onset of the puffin chick-rearing period was defined as the date at which eggs in > 25% of monitored puffin burrows had hatched because both puffin chicks and parental puffins carrying bill loads of fish to their chicks would likely be abundant after this date.

To determine the date of arrival of spawning Capelin and define the spawning period, known intertidal and subtidal Capelin spawning sites within the study area were monitored every two to four days throughout the summer of 2021 and 2022, as part of a long-term Capelin monitoring program (Crook *et al.* 2017). Following Crook *et al.* (2017), sediment at spawning sites was sampled and examined for the presence of adhered Capelin eggs in early developmental stages, indicating spawning within the previous one to two days. Monitoring indicated the date of first spawning and the duration of spawning (i.e., date range when Capelin eggs in early developmental stages were first present to when spawning adult Capelin were no longer present).

All research was approved by the University of Manitoba Animal Care Committee (protocol number F20-017/1/2).

Atlantic Puffin carcass surveys

We repeated a transect to quantify the daily number of fresh adult puffin carcasses on the shoreline of James Island during July–August 2021/22, following a standard route (~0.660 km) along the west side of the island every two to four days during colony visits (Fig. 1). Locations of gull nests encountered along the transect route were recorded using a handheld GPS to determine whether puffin carcasses were clumped near gull nests. The grassy island interior was not surveyed to minimize disturbance to nesting birds and because few puffin carcasses were historically observed in this area (Russell & Montevecchi 1996). The east side of the island was avoided to minimize disturbance to Razorbill and Common Murre nesting areas near the shoreline. Each carcass transect was performed by a group of three to four researchers, where the number and locations of carcasses within 30 m on either side of the transect line (or the entire

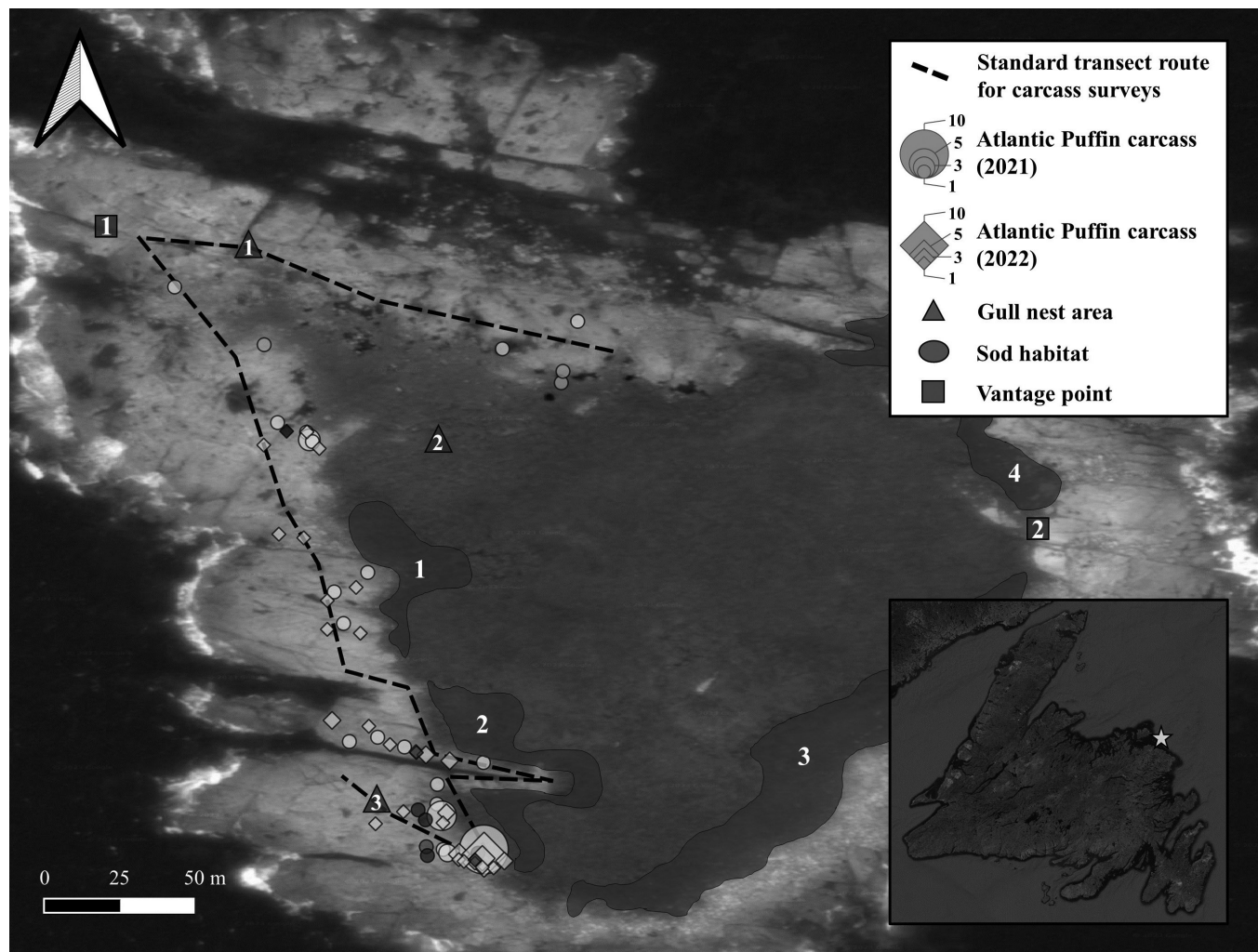


Fig. 1. Satellite image of James Island on the northeast Newfoundland coast, Canada, indicating Atlantic Puffin *Fratercula arctica* carcasses encountered during surveys following a standard transect route (black dashed line) during 2021 (circles sized by number of carcasses) and 2022 (diamonds sized by number of carcasses), with progression throughout the breeding season indicated by darker shading. Gull nest areas (triangles; 1 = 2 nests, 2 = ~30 nests, 3 = 6 nests), the approximate area of puffin sod burrow habitat (gray contours; Jenkins *et al.* 2018), and vantage points for gull behavioural observations (squares) are also indicated. Inset: location of James Island (star) relative to the Newfoundland mainland.

shoreline where it was narrower than 60 m) were recorded (modified strip transect). This resulted in ~0.029 km² surveyed, approximately half of the island's shoreline (~0.061 km²). The condition of each puffin carcass encountered was recorded to confirm it was killed by gulls (Thoresen 1964, Burger & Gochfeld 1984). Confirmation was indicated by intact head, breast, and wing feathers combined with peck holes and missing flesh around the breast, neck, and eyes (recent carcasses) or inverted and pulled back skin with much of the breast muscle, organs, and other soft tissue absent (older carcasses). Each puffin carcass encountered was marked with white yarn, and a spray-painted marking was made on the ground next to the carcass to differentiate carcasses encountered during previous transects (and years) from fresh carcasses.

Gull behavioural observations

During July–August 2021, we performed focal animal sampling ('focal observations') in 90-min periods during daylight to quantify the behaviour of individual gulls outside or inside of puffin burrow areas and time spent in each location. Focal observations involved following one gull for up to 10 min (or until it was lost from sight) and recording all behaviours observed (see Table 1), following Martin & Bateson (2007). Focal observations were performed using binoculars, and each bird was chosen using a random number generator, with the first number indicating the side of a standard field of view (odd = left, even = right) and the second indicating the gull to follow (e.g., '2-6' = sixth gull from the far-right side). During focal observations, we used a voice recorder (Olympus VN-541PC) to record the date and start time of the 90-min observation period, the starting location of the gull (i.e., inside or outside of a puffin burrow area), the starting behaviour, and then the time that the behaviour and/or location changed throughout the 10 min. Audio files were later transcribed and the time spent in each behaviour/location category was quantified for each individual gull.

We shifted behavioural observation techniques during July–August 2022 to instantaneous scan samples and behavioural sampling

(Martin & Bateson 2007) to quantify the presence and behaviour of Great Black-backed and American Herring gulls within puffin burrow areas. This shift increased the likelihood of observing rare events (i.e., kleptoparasitic attacks, adult/chick depredation) relative to focal animal sampling (Martin & Bateson 2007), allowing us to better meet our objectives. Behavioural observations were performed in ~30-min stints during daylight, which involved alternating between scan samples and 10-min behavioural sampling observations. Three scan samples were performed across an approximately 90° field of view during each observation stint to record the instantaneous behaviour (see Table 1) of each gull in three broadly categorized locations: grass/gull nest area, puffin burrow area, and shoreline. Scan sampling was performed first for American Herring Gulls and then Great Black-backed Gulls, and the duration of each scan was recorded. Two behavioural sampling observations were performed during each stint, during which we focused only on the puffin burrow areas visible from our vantage point (burrow area 1 and the northernmost portion of burrow area 2; Fig. 1) to record the number of gulls of each species in the burrow area, as well as the frequency of each behaviour (Table 1) performed by gulls in the area.

Statistical analysis

The number of newly encountered puffin carcasses on each survey day was used to calculate the cumulative number of puffin carcasses throughout the breeding seasons of 2021 and 2022. The location of each carcass was mapped in QGIS version 3.30.3 (QGIS Development Team 2023) to determine the dispersion pattern of carcasses along the transect route in relation to previously defined puffin burrow areas (Fig. 1; Jenkins *et al.* 2018), as well as gull nests recorded during carcass surveys and behavioural observations. Additionally, the cumulative number of carcasses in each year was combined with the transect area to determine carcass density (carcasses/m²). The area of bare shoreline, boulder field, grassy interior, and the total area of James Island were then combined with carcass density along the transect to estimate the cumulative number of puffins killed on the island for comparison with Russell and Montevecchi (1996).

All statistical analyses were performed in RStudio version 2023.03.0+386 (R Development Core Team 2023). During focal observations (2021), the total time each gull was observed varied, as some individuals were lost from sight before the end of the 10-min observation period. Therefore, the proportion of time spent in each behaviour was calculated to allow standardization among individuals. As gull presence within puffin burrow areas poses a higher risk of depredation and kleptoparasitism to puffins than presence outside of these areas, we summed the proportion of time spent inside burrow areas by each individual gull. Because many gulls did not enter the puffin burrow areas (i.e., there was a high number of individuals with zero time spent inside burrow areas), we examined whether presence of gulls within burrow areas differed across species and colony visits using a multiple logistic regression. We then subdivided the data and examined only focal gulls that entered burrow areas to determine whether the proportion of time spent in burrow areas differed among species and colony visits using a two-way ANOVA and subsequent Tukey's HSD post-hoc test. The non-normally distributed proportion data were arcsine square root-transformed before analysis. Behavioural observations occurred throughout the day (06h00–18h00 Newfoundland Daylight Time) during which time minimal differences in gull behaviour were observed (Rieger 2022). Thus, time of day was not analyzed.

TABLE 1
Behaviours of Great Black-backed Gulls *Larus marinus*
and American Herring Gulls *L. argentatus smithsonianus*
observed and recorded during behavioural observations in
July–August 2021/22 on James Island, Newfoundland, Canada

Behaviour
Depredation of adult Atlantic Puffin
Depredation of Atlantic Puffin chick
Kleptoparasitism of adult Atlantic Puffin
Hovering/circling or flying
Diving from flight at adult Atlantic Puffin
Fly-jumping at adult Atlantic Puffin
Walking or standing in place
Looking in Atlantic Puffin burrow
Sitting
Preening
Social/aggressive behaviour with another gull
Searching for/consuming other prey

We summarized the behavioural sampling data (2022) into the mean number of gulls of each species present within the puffin burrow areas and the mean proportion of each behaviour out of all behaviours recorded during each observation stint by averaging across the two 10-min behavioural samples conducted per stint. Using a two-way ANOVA and subsequent Tukey's HSD post-hoc test, we compared the mean number of gulls recorded within the burrow areas across species and colony visits. Additionally, we used a two-way ANOVA to examine whether the summed proportion (arcsine square root-transformed) of four 'aggressive' behaviours (looking in puffin burrows, depredation of chicks, and kleptoparasitism of and fly-jumping at adults) differed across species and colony visits. Using the scan sample data (2022), we calculated the mean number of gulls of each species in the burrow areas and the mean proportion of gulls in the burrow areas out of all gulls observed per observation stint by averaging across the three scans in each stint. We performed a two-way ANOVA and subsequent Tukey's HSD post-hoc test to compare the mean number of gulls in the burrows across species and colony visits. Additionally, we performed a two-way ANOVA on the transformed proportion of gulls within the burrows to compare between gull species and colony visits.

RESULTS

The onset of puffin chick-rearing was near the same day in both years (~17 July 2021; ~18 July 2022). The inshore arrival of spawning Capelin occurred ~17 July 2021, roughly coinciding with the onset of puffin chick-rearing. Large inshore spawning aggregations were no longer present after ~03 August 2021, marking the end of Capelin spawning and high inshore Capelin availability. During 2022, the onset of Capelin spawning occurred before our first colony visit, with Capelin eggs present at subtidal sites on or before 10 July 2022. Aggregations of spawning adult Capelin were last recorded on 16 July 2022, but newly spawned Capelin eggs were found at these sites until 22 July 2022. Thus, ~19 July 2022 represented the end of Capelin spawning and high inshore Capelin availability.

Atlantic Puffin carcass surveys

Carcasses were encountered throughout the transect in both years, although they appeared clumped near puffin burrows and a cluster of gull nests on the southwestern shore and in a grassy area on the northwestern shore (gull nest areas two and three; Fig. 1). During 2021, eight carcass surveys were performed and 44 adult carcasses were encountered along the transect over the breeding season (Fig. 2A). During 2022, we performed six surveys, recording 49 adult carcasses along the transect (Fig. 2B). All carcasses that were encountered matched descriptions of gull depredation. A total of 35 and 46 carcasses were recorded on the first surveys in 2021 and 2022, respectively. These numbers represent the accumulation of carcasses along the transect before our first colony visit in each year, as carcasses marked in 2021 were no longer present during 2022. A single new carcass was encountered during Capelin spawning in 2021 and none in 2022 (Fig. 2). An additional four and three new puffin carcasses were recorded following the end of the Capelin spawning period during 2021 and 2022, respectively (Fig. 2). In total, 11 and 10 gull nests were recorded along the transect in 2021 and 2022, respectively. The species of gulls using these nests was not determined, as neither parental nor juvenile gulls were observed in nests. Adult puffin carcass density along the transect was 0.0015

and 0.0017 carcasses/m² during 2021 and 2022, respectively. Based on these densities, we estimated 94 and 104 carcasses along the bare rock shoreline and boulder fields, with another estimated 25% in the unsurveyed grassy interior of the island (following Russell & Montevecchi 1996), for a total of 117 and 130 carcasses on James Island in 2021 and 2022, respectively.

Gull behavioural observations

During 2021, we performed 150 gull focal observations in 21 90-min observation periods (one to two periods per day, > 1 h apart) throughout the breeding season, observing similar numbers of Great Black-backed Gulls ($n = 72$) and American Herring Gulls ($n = 78$) across all colony visits. Given the low number of gulls nesting on James Island and other nearby islands, we likely observed the same gulls multiple times, but individuals were not banded or otherwise marked and, thus, could not be distinguished. Only ~30% of individuals of both gull species entered puffin burrow areas during focal observations (Fig. 3A). In general, Great Black-backed and American Herring gulls outside puffin burrow areas were frequently observed in behaviours not typically associated with depredation or kleptoparasitic attacks (e.g., sitting, preening, social behaviour with other gulls), whereas gulls within burrow areas were typically more alert and/or displaying behaviours associated with attacks

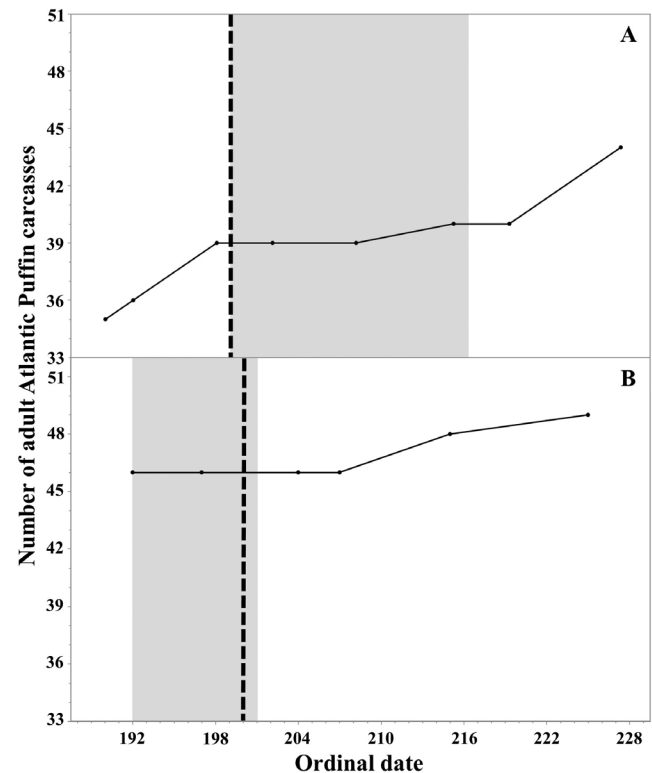


Fig. 2. Cumulative number of adult Atlantic Puffin *Fratercula arctica* carcasses (points) encountered throughout the breeding season (July and August) during (A) 2021 and (B) 2022 along a standard transect route on James Island (see Fig. 1 for route) on the northeast coast of Newfoundland, Canada. Capelin *Mallotus villosus* spawning periods (17 July–03 August 2021, 10–19 July 2022) are indicated by the shaded background; the onset of puffin chick-rearing (17 July 2021, 18 July 2022) is indicated by the dashed vertical line.

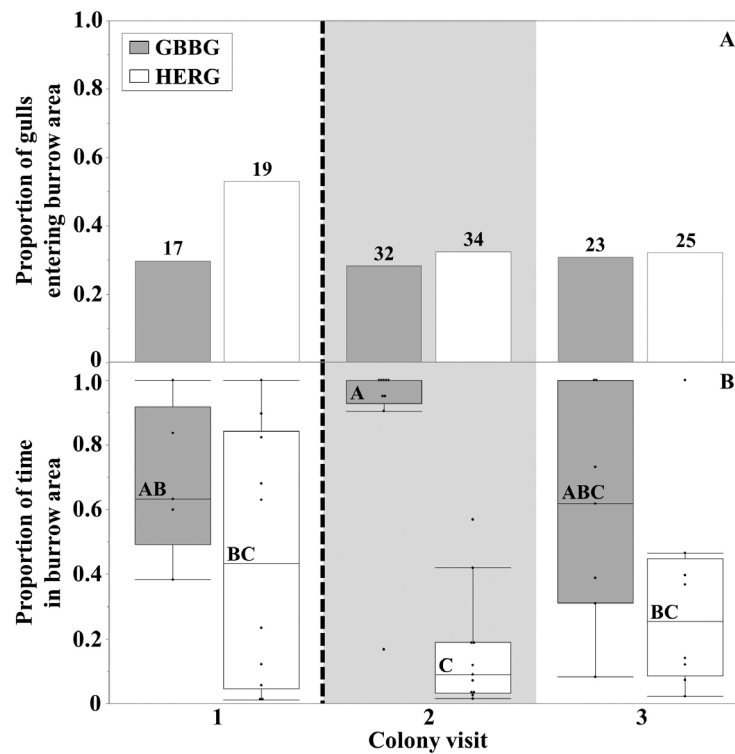


Fig. 3. The proportion of Great Black-backed Gulls *Larus marinus* (GBBG) and American Herring Gulls *L. argentatus smithsonianus* (HERG) that entered puffin burrow areas (A) and, when entering burrow areas, the proportion of time gulls spent in burrow areas (B) during focal observations across three colony visits: one (07–11 July 2021; puffin incubation, before Capelin *Mallotus villosus* spawning), two (17–25 July 2021; puffin chick-rearing, Capelin spawning), and three (03–06 August 2021; puffin chick-rearing, after Capelin spawning). The Capelin spawning period is indicated by the shaded background; the onset of puffin chick-rearing is indicated by the dashed vertical line. Sample sizes are indicated above bars in (A) and the results of a Tukey's HSD post-hoc test are indicated in (B), where factor levels not connected by the same letter differed significantly. Boxes in (B) show the median (center line), first, and third quartiles (top and bottom, respectively), and minimum and maximum values (whiskers).

(e.g., looking in puffin burrows, fly-jumping at adults, hovering in place). We did not observe attempted or successful adult or chick depredation events during focal observations and only observed one attempted and one successful kleptoparasitic attack, both performed by Great Black-backed Gulls. Gull presence within burrow areas did not differ significantly between species ($\chi^2_{1,144} = 1.460$, $P = 0.229$) or among colony visits ($\chi^2_{2,144} = 0.656$, $P = 0.520$) and there was no significant interaction between species and colony visit ($\chi^2_{2,144} = 0.623$, $P = 0.538$; Fig. 3A). For gulls that entered puffin burrow areas, the proportion of time in the burrow areas differed between species ($F_{1,44} = 21.375$, $P < 0.001$) but not among colony visits ($F_{2,44} = 0.280$, $P = 0.757$), and the interaction was significant ($F_{2,44} = 3.761$, $P = 0.031$). Overall, Great Black-backed Gulls spent a higher proportion of time than American Herring Gulls in the burrow areas, especially during the puffin chick-rearing period when Capelin were actively spawning (i.e., second colony visit; Fig. 3B).

During 2022, we performed 91 behavioural samples and 120 scan samples during 41 30-min stints (one to five stints per day, > 30 min apart). During behavioural sampling, the mean number of gulls per 30-min stint observed within the puffin burrow area differed between species ($F_{1,72} = 54.113$, $P < 0.001$) and colony visits ($F_{3,72} = 4.391$, $P = 0.006$), and the interaction was significant ($F_{3,72} = 3.760$, $P = 0.014$; Fig. 4). American Herring Gulls were virtually absent within the puffin burrow area throughout the summer, whereas more

Great Black-backed Gulls were present after Capelin spawning and puffin hatching relative to before, especially during late summer (i.e., fourth colony visit; Fig. 4). Scan samples revealed a similar pattern (Appendix 1, available online).

As American Herring Gulls were infrequently observed within puffin burrow areas during behavioural sampling (2022), especially during the second and third colony visits (Fig. 4), we focused our behavioural analyses on Great Black-backed Gulls. Great Black-backed Gulls were often observed performing 'aggressive' behaviours, including looking in puffin burrow openings (presumably searching for eggs or chicks within reach; Anthony 1906, Rodway *et al.* 1998), fly-jumping at adults returning to or standing outside their burrows, successfully kleptoparasitizing adults, and successfully preying on chicks from burrows. By contrast, only one American Herring Gull was observed fly-jumping at adult puffins. Great Black-backed Gulls were only observed preying on chicks and kleptoparasitizing adults later in the season (i.e., third and fourth colony visits; Fig. 5A). The summed proportion of these aggressive behaviours relative to non-aggressive behaviours (e.g., sitting, walking/standing in place, social/aggressive behaviour with another gull) by Great Black-backed Gulls when in burrow areas tended to be higher during the post-hatching and post-Capelin spawning period (i.e., third and fourth colony visits; Fig. 5B), but this was not significant ($F_{3,27} = 1.538$, $P = 0.228$).

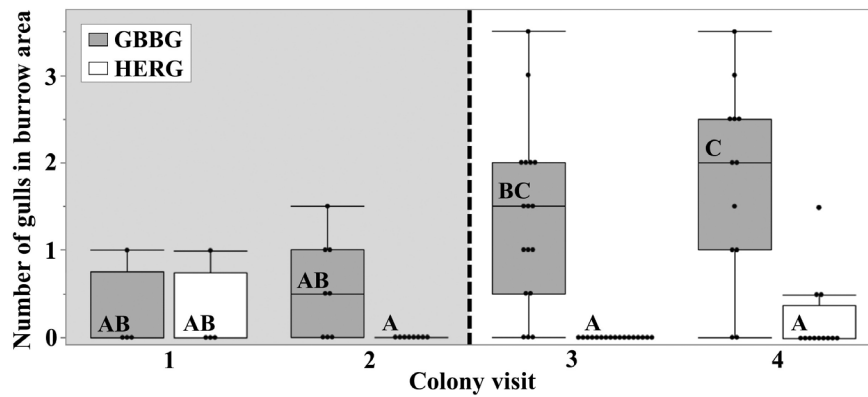


Fig. 4. Mean number of Great Black-backed Gulls *Larus marinus* (GBBG) and American Herring Gulls *L. argentatus smithsonianus* (HERG) observed within a puffin burrow area during behavioural samples in each 30-min observation stint by colony visits: one (09–12 July 2022), two (15–19 July 2022), three (22–27 July 2022), and four (01–06 August 2022). The Capelin *Mallotus villosus* spawning period is indicated by the shaded background; the onset of puffin chick-rearing is indicated by the dashed vertical line. The results of a Tukey's HSD post-hoc test are indicated, where factor levels not connected by the same letter differed significantly. Boxes show the median (center line), first and third quartiles (top and bottom, respectively), and minimum and maximum values (whiskers).

DISCUSSION

Our findings support the hypothesis that adult puffin depredation by large gull species is influenced by the inshore arrival of spawning Capelin and the onset of puffin chick-rearing. Findings that support this hypothesis include shifting gull behaviour and changes in the presence and time spent within puffin burrow areas as the availability of Capelin and puffin chicks varied across the breeding season. In both study years, most depredation on adult puffins occurred before Capelin spawning (and our first colony visit), with fewer new carcasses recorded following Capelin inshore arrival (Fig. 2), supporting our prediction that gulls shift away from adult puffins as prey when Capelin and puffin chicks become available. During and after Capelin spawning, Great Black-backed Gull presence, number, and proportion of time spent in puffin burrow areas were higher relative to American Herring Gulls (Figs. 3B, 4), supporting our prediction that Great Black-backed Gulls rely more on puffin adults and chicks than American Herring Gulls. This prediction was further supported by observations of Great Black-backed Gulls successfully preying on puffin chicks and kleptoparasitizing adults once puffins hatched (Fig. 5A), while American Herring Gulls were not observed displaying these behaviours. Together, these observations suggest that there is temporal separation of (i) depredation on adult puffins (which predominates before puffin hatching and near the end of chick-rearing), and (ii) chick depredation and adult kleptoparasitism (which predominates during Capelin spawning and puffin chick-rearing) by Great Black-backed Gulls on the northeast Newfoundland coast.

The low number of gulls found in puffin burrow areas in both study years suggests that only a small proportion of gulls on James Island actively prey on or kleptoparasitize puffins, possibly indicating individual dietary specialization. This inference might also be supported by the clumped distribution of puffin carcasses near a few gull nests in both years (Fig. 1). Other studies have identified individual specialization in large gull species. For example, only five Great Black-backed and American Herring gulls were responsible for chick depredation on Common Terns *Sterna hirundo* at a colony in one year (Guillemette & Brousseau 2001, see also

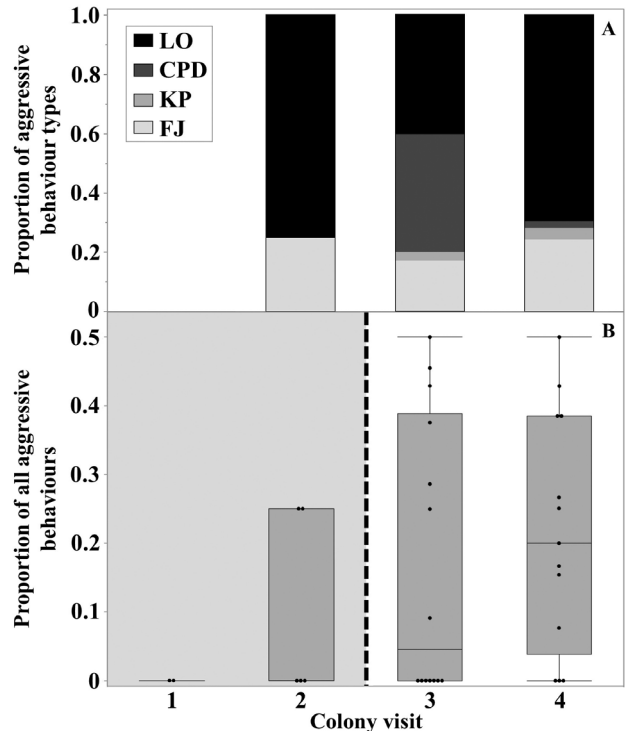


Fig. 5. Proportion of different types of aggressive behaviours (LO: looking in puffin burrow; CPD: depredation of puffin chick; KP: kleptoparasitism of adult puffin; FJ: fly-jumping at adult puffin) performed by Great Black-backed Gulls *Larus marinus* in a puffin burrow area during behavioural samples (A) and the summed proportion of aggressive behaviours relative to other behaviours performed by Great Black-backed Gulls (B) by colony visits: one (09–12 July 2022), two (15–19 July 2022), three (22–27 July 2022), and four (01–06 August 2022). The Capelin *Mallotus villosus* spawning period is indicated by the shaded background; the onset of puffin chick-rearing is indicated by the dashed vertical line. Boxes in (B) show the median (center line), first and third quartiles (top and bottom, respectively), and minimum and maximum values (whiskers).

Westerberg *et al.* 2019). Other studies have shown different degrees of specialization in diet and foraging behaviour by Great Black-backed Gulls (Maynard & Ronconi 2018, Maynard *et al.* 2021). If only a few gulls specialize on puffins, it may be misleading to rely on population-level observations alone (i.e., focal observations, scan sampling) to determine depredation and kleptoparasitism risk on puffins and other seabirds because the risk imposed by specialist gulls is diluted by most gulls focusing on other prey types. In contrast, behavioural sampling, which increases the likelihood of observing rare events (i.e., kleptoparasitic attacks, depredation; Martin & Bateson 2007) in puffin burrow areas may be a more accurate way to assess depredation risk at colonies. Future studies pairing behavioural sampling with marking gulls (e.g., Donehower & Bird 2005, Busniuk *et al.* 2020) could investigate dietary specialization and the impact of depredation by individual gulls at a colony.

Given the evidence suggesting some gulls specialized on depredation and/or kleptoparasitism of puffins, we attempted to explore our predictions with increased focus on these potential specialists by examining the proportion of time gulls spent inside puffin burrow areas only after entering (2021), and gull presence, number, and behaviour only within puffin burrow areas (2022). This focus allowed us to directly address our prediction that Great Black-backed Gulls feed more on puffins than American Herring Gulls. We found that Great Black-backed Gulls were more present in puffin burrows and in greater numbers compared to American Herring Gulls. Our findings are similar to Russell and Montevecchi (1996), who attributed all puffin carcasses on James Island to depredation by Great Black-backed Gulls, as only this species was observed successfully killing adult puffins (see also Harris 1980, Pierotti 1983, Regehr & Montevecchi 1997, Washburn *et al.* 2013).

Adult puffin depredation by Great Black-backed Gulls was highest prior to chick-rearing, whereas kleptoparasitism and chick depredation were recorded following the onset of chick-rearing in both years, suggesting a shift in foraging behaviour. This was indicated by the near-absence of new adult carcasses after puffin hatching, along with increased presence and numbers of Great Black-backed Gulls within burrow areas and an increased proportion of aggressive behaviour, including successful chick depredation and adult kleptoparasitism, during this period. Similar to our observations, gulls have been observed preying on puffin chicks, carrying live chicks back to their nest to provision their young (Anthony 1906, Thoresen 1964, Pierotti 1983) or swallowing chicks whole after catching them in burrow openings or outside burrows (Nettleship 1972, Rodway *et al.* 1998). Overall, these findings suggest that kleptoparasitism and chick depredation are more profitable foraging tactics relative to adult depredation for Great Black-backed Gulls when Capelin are abundant inshore and following puffin hatching. As Capelin spawning and puffin hatching did not overlap in 2022, further study in years of overlap is needed to compare the frequency of kleptoparasitic attacks and chick depredation when both prey types are readily available.

In contrast, American Herring Gulls preying on adult puffins and/or other food sources may have shifted to Capelin when they became highly available during spawning. American Herring Gulls tended to spend less time within puffin burrow areas during Capelin spawning (in 2021) compared to Great Black-backed Gulls and before, relative to after, Capelin spawning. Additionally, American Herring Gulls were consistently absent, or present in low numbers, within puffin burrow areas (in 2022), suggesting that American

Herring Gulls focused on other prey at the population level. Stenhouse & Montevecchi (1999) and Massaro *et al.* (2000) showed that Herring Gulls quickly switched from preying on other seabirds to Capelin following their inshore arrival to spawn. Alternately, the shift in American Herring Gull behaviour and the differences in behaviour between Great Black-backed and American Herring gulls may result from American Herring Gulls avoiding the pursuit of seabird prey in the presence of Great Black-Backed Gulls. Indeed, some Great Black-Backed Gulls may establish 'foraging territories' within puffin burrow areas, as reported in other *Larus* gull species (Spear 1993), and this may force smaller gulls (i.e., American Herring Gulls) to focus on alternative prey types. Great Black-backed Gulls are also aggressive toward other gull species, preying on their chicks (Pierotti 1983) and kleptoparasitizing adults (Donehower *et al.* 2007, Cotton 2009), and this may inhibit American Herring Gulls from foraging on high trophic level prey (Rome & Ellis 2004).

CONCLUSIONS

Overall, increased prey availability associated with the inshore arrival of spawning Capelin does not appear to result in specialist gulls shifting away from puffins as prey entirely (i.e., if they are non-contextual dietary specialists; Spear 1993, Maynard *et al.* 2021). Instead, specialist gulls may shift from preying on adult puffins to chicks and/or kleptoparasitizing adults, possibly reducing the impact on puffin population dynamics (Russell & Montevecchi 1996). Despite increased numbers in coastal Newfoundland relative to the 1970s (Regular *et al.* 2013), the Newfoundland puffin population may have plateaued (Wilhelm *et al.* 2015), and this species remains Vulnerable globally (BirdLife International 2023). Additionally, continued lower Capelin biomass and later spawning since the Newfoundland Capelin population collapsed in the early 1990s (Buren *et al.* 2014, 2019) could result in adult puffins being more vulnerable to depredation by dietary generalist or non-contextual specialist gulls that only target puffins under lower Capelin availability. While gull depredation in our study may have resulted in low adult puffin mortality on James Island (117–130 adults, or 0.004% of the population), greater numbers were killed by gulls on this island (908 adults or 0.023% of the population) in 1994, shortly after the 1991 Capelin population collapse (Russell & Montevecchi 1996). The higher number of puffins killed by gulls immediately after Capelin collapsed suggests that gull depredation may have a greater impact on puffin populations in years with decreased Capelin availability. Overall, our findings re-emphasize that future studies should identify and target individual gull dietary specialists to assess the response of gulls to shifting prey availability (e.g., Guillemette & Brousseau 2001, Westerberg *et al.* 2019, Maynard *et al.* 2021), as this will inform potential changes in colony-specific conservation efforts for Atlantic Puffins in coastal regions of the northwest Atlantic.

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REFERENCES

- ANTHONY, A.W. 1906. Random notes on Pacific Coast Gulls. *The Auk* 23: 129–137.
- ARAÚJO, M., BOLNICK, D. & LAYMAN, C. 2011. The ecological causes of individual specialization. *Ecology Letters* 14: 948–958.
- BIRDLIFE INTERNATIONAL. 2023. *Species factsheet: Fratercula arctica*. Cambridge, UK: BirdLife International. [Accessed at <http://datazone.birdlife.org/species/factsheet/atlantic-puffin-fratercula-arctica> on 24 June 2023].
- BOLNICK, D. 2001. Intraspecific competition favours niche width expansion in *Drosophila melanogaster*. *Nature* 410: 463–466.
- BOND, A.L., WILHELM, S.I., PIRIE-HAY, D.W., ROBERTSON, G.J., POLLET, I.L. & ARANY, J. 2023. Quantifying gull predation in a declining Leach's Storm-petrel (*Hydrobates leucorhous*) colony. *Avian Conservation Ecology* 18: 5.
- BUREN, A.D., KOEN-ALONSO, M., PEPIN, P. ET AL. 2014. Bottom-up regulation of Capelin, a keystone forage species. *PLoS One* 9: e87589.
- BUREN, A.D., MURPHY, H.M., ADAMACK, A.T. ET AL. 2019. The collapse and continued low productivity of a keystone forage fish species. *Marine Ecology Progress Series* 616: 155–170.
- BURGER, J. & GOCHFELD, M. 1984. Great black-backed gull predation on Kittiwake fledgelings in Norway. *Bird Study* 31: 149–151.
- BUSNIUK, K., STOREY, A.E. & WILSON, D.R. 2020. Herring gulls target profitable Atlantic puffins during kleptoparasitic attack. *Animal Behaviour* 166: 273–279.
- COTTON, J.F. 2009. Competition between Herring Gulls and Great Black-backed Gulls over natural and anthropogenic food sources in the Gulf of Maine. *Washington University Undergraduate Research Digest* 5: 17. [Accessed online at https://openscholarship.wustl.edu/vol5_iss1/17 on 21 March 2022.]
- CROOK, K.A., MAXNER, E. & DAVOREN, G.K. 2017. Temperature-based spawning habitat selection by Capelin (*Mallotus villosus*) in Newfoundland. *ICES Journal of Marine Science* 74: 1622–1692.
- DAVOREN, G.K. 2013. Distribution of marine predator hotspots explained by persistent areas of prey. *Marine Biology* 160: 3043–3058.
- DONEHOWER, C.E. & BIRD, D.M. 2005. A method for color-marking birds at resting sites. *Journal of Field Ornithology* 76: 204–207.
- DONEHOWER, C.E., BIRD, D.M., HALL, C.S. & KRESS, W.K. 2007. Effects of gull predation and predator control on tern nesting success at Easter Egg Rock, Maine. *Waterbirds* 30: 29–39.
- EVANS, P.G.H. 1975. Gulls and puffins on North Rona. *Bird Study* 22: 239–247.
- GOOD, T.P. 2020. Great Black-backed Gull (*Larus marinus*), version 1.0. In: BILLERMAN, S.M. (Ed.) *Birds of the World*. Ithaca, USA: Cornell Lab of Ornithology. [Accessed at <https://doi.org/10.2173/bow.gbbgul.01> on 24 June 2023.]
- GUILLEMETTE, M. & BROUSSEAU, P. 2001. Does culling predatory gulls enhance the productivity of breeding common terns? *Journal of Applied Ecology* 38: 1–8.
- GULKA, J., CARVALHO, P.C., JENKINS, E., JOHNSON, K., MAYNARD, L. & DAVOREN, G.K. 2017. Dietary niche shifts of multiple marine predators under varying prey availability on the northeast Newfoundland coast. *Frontiers in Marine Science* 4: doi:10.3389/fmars.2017.00324
- HARRIS, M.P. 1965. The food of some *Larus* gulls. *Ibis* 107: 43–53.
- HARRIS, M.P. 1980. Breeding performance of puffins (*Fratercula arctica*) in relation to nest density, laying date and year. *Ibis* 122: 193–289.
- HOLT, D.W. & SCHILL, L. 2002. Prey of Ring-billed Gulls in Lake County, Montana: Identification and quantification of prey and management implications. *Northwestern Naturalist* 83: 118–122.
- INGRAHAM, L.R., OSWALD, S.A., SON, E. & ARNOLD, J.M. 2020. Opportunistic predation of birds by breeding Herring Gulls (*Larus argentatus*). *PLoS One* 15: e0239180.
- JENKINS, E., GULKA, J., MAYNARD, L. & DAVOREN, G. 2018. *Seabird population update and trends from six colonies in Northeastern Newfoundland*. Technical Report prepared for Canadian Wildlife Service, Environment and Climate Change Canada. Winnipeg, Canada: University of Manitoba.
- LOWTHER, P.E., DIAMOND, A.W., KRESS, S.W. ET AL. 2020. Atlantic Puffin (*Fratercula arctica*), version 1.0. In: BILLERMAN, S.M. (Ed.) *Birds of the World*. Ithaca, USA: Cornell Lab of Ornithology. [Accessed at <https://birdsoftheworld.org/bow/species/atlpuff/cur/introduction> on 24 June 2023.]
- MACARTHUR, R. & PIANKA, E. 1966. On optimal use of a patchy environment. *The American Naturalist* 100: 603–609.
- MANGEL, M. & CLARK, C. 1986. Towards a unified foraging theory. *Ecology* 67: 1127–1138.
- MARTIN, P. & BATESON, P. 2007. *Measuring Behaviour: An Introductory Guide*. 3rd Edition. Cambridge, UK: Cambridge University Press.
- MASSARO, M., CHARDINE, J.W., JONES, I.L. & ROBERTSON, G.J. 2000. Delayed Capelin (*Mallotus villosus*) availability influences predatory behaviour of large gulls on black-legged kittiwakes (*Rissa tridactyla*), causing a reduction in kittiwake breeding success. *Canadian Journal of Zoology* 78: 1588–1596.
- MAYNARD, L.D. & RONCONI, R.A. 2018. Foraging behaviour of Great Black-backed Gull *Larus marinus* near an urban center in Atlantic Canada: Evidence of individual specialization from GPS tracking. *Marine Ornithology* 46: 27–32.
- MAYNARD, L.D. & DAVOREN, G.K. 2020. Inter-colony and interspecific differences in the isotopic niche of two sympatric gull species in Newfoundland. *Marine Ornithology* 48: 103–109.
- MAYNARD, L.D., GULKA, J., JENKINS, E. & DAVOREN, G.K. 2021. Different individual-level responses of great black-backed gulls (*Larus marinus*) to shifting local prey ability. *PLoS One* 16: e0252561.
- MCCLEERY, R.H. & SIBLY, R.M. 1986. Feeding specialization and preference in Herring Gulls. *Journal of Animal Ecology* 55: 245–259.
- MCFARLAND, D. 1977. Decision making in animals. *Nature* 269: 15–21.
- NETTLESHIP, D.N. 1972. Breeding success of the Common Puffin (*Fratercula arctica* L.) on different habitats at Great Island, Newfoundland. *Ecological Monographs* 42: 239–268.
- PIEROTTI, R. 1983. Gull-puffin interactions on Great Island, Newfoundland. *Biological Conservation* 26: 1–14.

- PIEROTTI, R. & ANNETT, C.A. 1991. Diet choice in the herring gull: Constraints imposed by reproductive and ecological factors. *Ecology* 72: 319–328.
- POLLET, I.L., BOND, A.L., HEDD, A., HUNTINGTON, C.E., BUTLER, R.G. & MAUCK, R. 2021. Leach's Storm-petrel (*Hydrobates leucorhous*), version 1.1. In: *Birds of the World*. Ithaca, USA: Cornell Lab of Ornithology. [Accessed online at <https://doi.org/10.2173/bow.lcspet.01.1> on 24 June 2023.]
- QGIS DEVELOPMENT TEAM. 2023. *QGIS Geographic Information System*. Chicago, USA: Open Source Geospatial Foundation Project. [Accessed online at <https://qgis.org> on 03 May 2023.]
- R DEVELOPMENT CORE TEAM. 2023. *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. [Accessed at <https://www.R-project.org/> on 19 April 2023.]
- REGEHR, H.M. & MONTEVECCHI, W.A. 1997. Interactive effects of food shortage and predation on breeding failure of black-legged kittiwakes: indirect effects of fisheries activities and implications for indicator species. *Marine Ecology Progress Series* 155: 249–260.
- REGEHR, H.M. & RODWAY, M.S. 1999. Seabird breeding performance during two years of delayed Capelin arrival in the northwest Atlantic: A multi-species comparison. *Waterbirds* 22: 60–67.
- RIEGER, G.M. 2022. *Larus Gull Predation and Kleptoparasitism on Breeding Atlantic Puffins (Fratercula arctica) Under Varying Forage Fish Availability*. BSc Honours thesis. Winnipeg, Canada: University of Manitoba. [Accessed online at <http://dx.doi.org/10.13140/RG.2.2.19239.62888> on 9 March 2023.]
- RODWAY, M.S., CHARDINE, J.W. & MONTEVECCHI, W.A. 1998. Intra-colony variation in breeding performance of Atlantic Puffins. *Waterbirds* 21: 171–184.
- ROME, M.S. & ELLIS, J.C. 2004. Foraging ecology and interactions between Herring Gulls and Great Black-backed Gulls in New England. *Waterbirds* 27: 200–210.
- RUSSELL, J. & MONTEVECCHI, W.A. 1996. Predation on adult puffins *Fratercula arctica* by great black-backed gulls *Larus marinus* at a Newfoundland colony. *Ibis* 138: 791–794.
- SPEAR, L.B. 1993. Dynamics and effect of Western Gulls feeding in a colony of Guillemots and Brandt's Cormorants. *Journal of Animal Ecology* 62: 399–414.
- STEENWEG, R.J., RONCONI, R.A. & LEONARD, M.L. 2011. Seasonal and age-dependent dietary partitioning between the Great Black-backed and Herring Gulls. *The Condor* 113: 795–805.
- STENHOUSE, I.J. & MONTEVECCHI, W.A. 1999. Indirect effects of the availability of Capelin and fishery discards: gull predation on breeding storm-petrels. *Marine Ecology Progress Series* 184: 303–307.
- STENHOUSE, I.J., ROBERSON, G.J. & MONTEVECCHI, W.A. 2000. Herring Gull *Larus argentatus* predation on Leach's Storm-petrel *Oceanodroma leucorhoa* breeding on Great Island, Newfoundland. *Atlantic Seabirds* 2: 35–44.
- THOMPSON, D.B. 1986. The economics of kleptoparasitism: optimal foraging, host and prey selection by gulls. *Animal Behaviour* 34: 1189–1205.
- THORESEN, A.C. 1964. Breeding behaviour of the Cassin Auklet. *The Condor* 66: 456–476.
- TOME, M. 1988. Optimal foraging: food patch depletion by ruddy ducks. *Oecologia* 76: 27–36.
- VEITCH, B.G., ROBERTSON, G.J., JONES, I.J. & BOND, A.L. 2016. Great black-backed gull (*Larus marinus*) predation on seabird populations at two colonies in eastern Canada. *Waterbirds* 39: 235–245.
- WASHBURN, B.E., BERNHARDT, G.E., KUTSCHBACH-BROHL, L., CHIPMAN, R.B. & FRANCOEUR, L.C. 2013. Foraging ecology of four gull species at a coastal-urban interface. *The Condor* 115: 67–76.
- WESELOH, D.V., HEBERT, C.E., MALLORY, M.L. ET AL. 2020. Herring Gull (*Larus argentatus*), version 1.0. In: BILLERMAN, S.M. (Ed.) *Birds of the World*. Ithaca, USA: Cornell Lab of Ornithology. [Accessed online at <https://doi.org/10.2173/bow.hergul.01> on 24 June 2023.]
- WESTERBERG, K., BROWN, R., EAGLE, G. & VOTIER, S.C. 2019. Intra-population variation in the diet of an avian top predator: generalist and specialist foraging in Great Black-backed Gulls *Larus marinus*. *Bird Study* 66: 390–397.