The influence of multiple industries on the behaviour of breeding gulls from four colonies across the eastern Gulf of Maine, Canada

Authors: Gutowsky, Sarah E., Studholme, Katharine R., Ronconi, Robert A., Allard, Karel A., Shlepr, Katherine, et al.

Source: Wildlife Biology, 2021(2)

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.00804

Wildlife Biology 2021: wlb.00804
doi: 10.2981/wlb.00804

Subject Editor: Sonja Christine. Editor-in-Chief: Ilse Storch. Accepted 16 February 2021

The influence of multiple industries on the behaviour of breeding gulls from four colonies across the eastern Gulf of Maine, Canada

Sarah E. Gutowsky, Katharine R. Studholme, Robert A. Ronconi, Karel A. Allard, Katherine Shlepr, Anthony W. Diamond, Jessie McIntyre, Shawn R. Craik and Mark L. Mallory

S. E. Gutowsky (https://orcid.org/0000-0003-1711-4744) ✉ (sarahegutowsky@gmail.com), J. McIntyre (https://orcid.org/0000-0001-5762-8593) and M. L. Mallory (https://orcid.org/0000-0003-2744-3437), Dept of Biology, Acadia Univ., Wolfville, NS, Canada. – K. R. Studholme (https://orcid.org/0000-0003-0921-4745), Dept of Biology, Dalhousie Univ., Halifax, NS, Canada. – R. A. Ronconi (https://orcid.org/0000-0002-3635-7162), Canadian Wildlife Service, Environment and Climate Change Canada, Dartmouth, NS, Canada. – K. A. Allard (https://orcid.org/0000-0002-7571-9365), Canadian Wildlife Service, Environment and Climate Change Canada, Sackville, NB, Canada. – K. Shlepr (https://orcid.org/0000-0001-6046-5131), Dept of Biological Sciences, Florida Atlantic Univ., Boca Raton, FL, USA. – A. W. Diamond, Atlantic Laboratory for Avian Research, Univ. of New Brunswick, Fredericton, NB, Canada. – S. R. Craik (https://orcid.org/0000-0003-2649-2747), Dépt des Sciences, Univ. Sainte-Anne, Pointe-de-l'Église, NS, Canada.

Opportunist gulls use anthropogenic food subsidies, which can bolster populations, but negatively influence sensitive local ecosystems and areas of human settlement. In the eastern Gulf of Maine, Canada, breeding herring gulls *Larus argentatus* have access to resources from aquaculture, fisheries and mink farms, but the relative influence of industry on local gull populations is unknown. Our objectives were to 1) assess use of natural and anthropogenic habitats by herring gulls from multiple colonies, 2) evaluate variation among colonies in use of distinct resource types within these habitats and 3) highlight areas of high gull:industry interaction. Using GPS devices on 39 gulls from four colonies, we identified visitation behaviour (slow, localized movements) and assigned visits to nine resource types. To evaluate the spatial distribution of visits, we created a use intensity index, reflecting both fidelity (i.e. repeated visits) and time spent in specific areas. All four anthropogenic resource types were heavily used (56 ± 11% of visiting time across colonies), notably, fish plants and mink farms. Despite large distances among three colonies, birds overlapped at particular distant, inland mink farms. In contrast, birds from close colonies overlapped in visitation to specific nearby resources (e.g. fish plants and human settlement), and otherwise diverged in distribution and use of offshore and coastal areas. Birds from three colonies also made frequent, long visits to uninhabited islands. Industry is clearly influencing the behaviour of breeding gulls in the eastern Gulf of Maine, Canada, where birds are travelling great distances or spending large proportions of time interacting with anthropogenic resources, while otherwise paying lengthy visits to nearby coastal islands. Studies have shown that concentrations of gulls can have harmful direct and indirect ecological and societal impacts. Our findings have implications for the management and regulation of industry to mitigate detrimental effects on local ecosystems and humans.

Keywords: animal husbandry, anthropogenic influence, aquaculture, fish processing, movement ecology, seabirds, urban

The impacts of worldwide industrialization on birds are widespread and complex, but are often negative (Marzluff 2001). However, for flexible, opportunist species like the *Larus* gulls, anthropogenic food subsidies have often led to rapid population growth and range expansions, particularly near human settlements (Ramos et al. 2011, Oro et al. 2013, Anderson et al. 2016). Such responses can have detrimental impacts on local ecosystems (Vidal et al. 1998, Donehower and Bird 2008, Kickbush et al. 2018, Scopel and Diamond 2018), and human well-being (Burger 2001, Winton and River 2017, Desjardins et al. 2019, Navarro et al. 2019).

The herring gull *Larus argentatus* is the most widespread Larid in the Northern Hemisphere. Like many seabird species, these gulls depend on isolated islands (or rooftops) that offer protection from predators to raise young (Weseloh et al. 2020). Within the Canadian portion of the eastern Gulf of Maine including coastal southwest Nova Scotia and the outer Bay of Fundy (herein referred to as the 'eastern Gulf of Maine'; Fig. 1), suitable nesting areas are abundant. In this region, the herring gull is thus one of two common, large, breeding gull species (the second being the great black-backed gull *Larus marinus*), with dozens of colonies

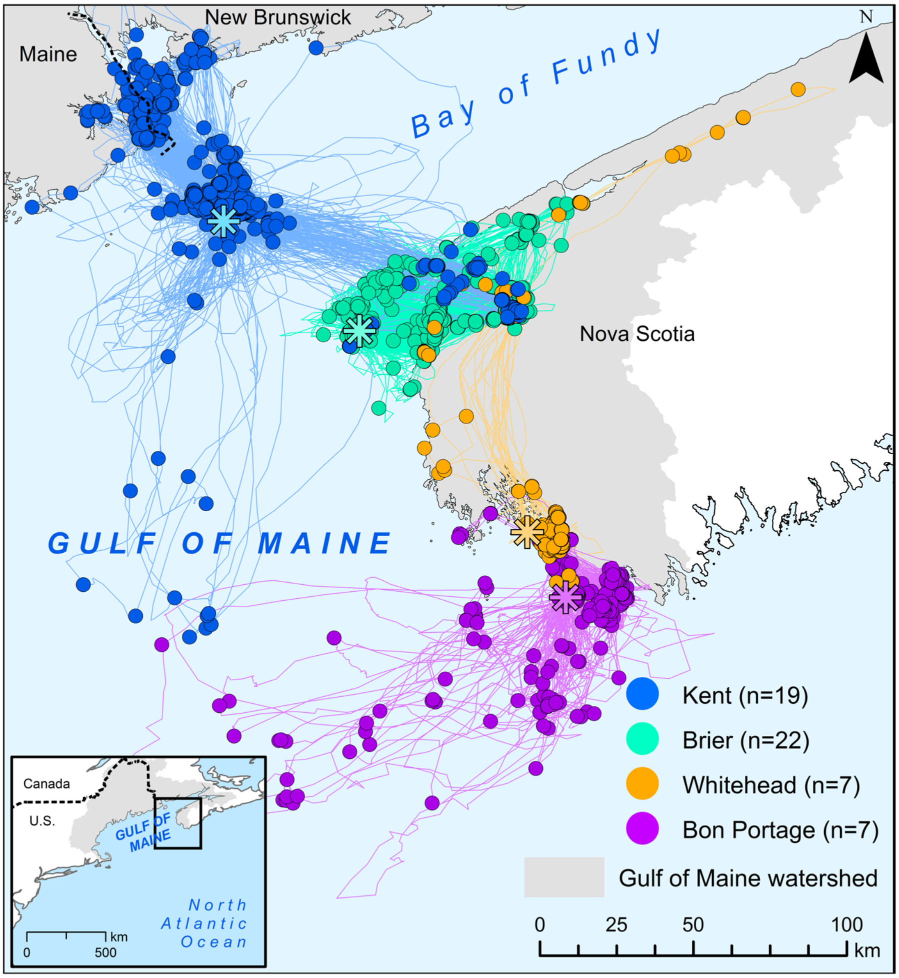

Figure 1. Movements of 39 breeding herring gulls equipped with GPS devices at four island colonies in the eastern Gulf of Maine, Canada. Sample sizes indicate the number of bird-years contributing data for each colony (some individuals were tracked in multiple breeding seasons, n = 55 bird-years, Table 1). Transits (continuous lines) are shown between identified visits (filled circles, representing the centroid of visit resources) on trips for all bird-years combined.

ranging in size from 10 to 5000 pairs (Cotter et al. 2012). Here, breeding birds derive resources from habitats offering a diverse array of natural and human-influenced (i.e. anthropogenic) foraging opportunities within offshore, coastal and inland areas of the eastern Gulf of Maine marine and watershed ecosystem. Their 'generalist scavenger' foraging strategy, along with their inherent neophilia and boldness, means they are well adapted to discover and access diverse food resource options (Goumas et al. 2020). Indeed, fluctuations in herring gull populations over the last century have been linked to substantial changes in anthropogenic food subsidies from various industries (Farmer and Leonard 2011, Cotter et al. 2012, Wilhelm et al. 2016).

Some local herring gull populations are large enough to negatively influence coastal island ecosystems in southeastern Atlantic Canada, presenting challenges to wildlife managers (Farrow and Nussey 2013). Southwest Nova Scotia and southern New Brunswick boast productive local economic activity from various fisheries-based industries (including fin-fish aquaculture operations, active wharfs and harbours, and fish processing plants targeting American lobster *Homarus americanus* and groundfish), as well as an American mink *Neovison vison* farming industry. Despite the shared ubiquity of these predictable industrial food sources and gulls in the eastern Gulf of Maine ecosystem, the extent of the influence of each industry on local gull populations is not well understood. Yet it has been suggested that gull populations pose concerns for human health and industry, and threaten native biodiversity (Whittam and Leonard 1999, Donehower and Bird 2008, Environment and Climate Change Canada 2018). Effective mitigation, including interventions to mitigate problematic responses of wildlife such as gulls to human activities, necessitates identifying causal mechanisms to inform management priorities and planning.

In this study, we used GPS devices to examine breeding season movements and behaviour of herring gulls nesting at four island colonies in relation to natural and anthropogenic habitats and potential associated food resources available on the landscape. Specifically, our objectives were to: 1) evaluate the overall relative use of natural versus anthropogenically-influenced habitats by herring gulls in the eastern Gulf of Maine, Canada; 2) examine variation among colonies in the use of distinct landscape features or 'resource types' within these two broad habitat categories; and 3) identify localized areas of most intense gull:industry interaction. Ultimately, our examination of breeding gull activity allowed us to make inferences regarding the relative influence of different industrial activities on local gull populations. These results have important implications for the management of sensitive local ecosystems, highlighting where potential changes and regulation of industry practices may help mitigate detrimental effects of human-induced pressures.

Material and methods

Study sites and data collection

In 2014, 2015 and 2019, we deployed GPS devices on 45 incubating herring gulls at four colonies with access to resources within the Canadian portion of the eastern Gulf of Maine marine and watershed ecosystem: three island colonies in Nova Scotia: Bon Portage (43°47'N, 65°75'W), Whitehead (43°66'N, 65°87'W), Brier (44°26'N, 66°38'W) and one island colony in New Brunswick: Kent (44°58'N, 66°76'W) (Table 1, Fig. 1). The nearest distance between colonies was 22 km (Whitehead and Bon Portage) and the furthest was 145 km (Kent and Bon Portage; Fig. 1). Birds were captured with drop traps over nests, and devices were attached with a teflon ribbon leg-loop harness (Mallory and Gilbert 2008). The majority of devices deployed were solar-powered models Harrier-M or Harrier-L, Kite-M and URIA 240 from Ecotone Telemetry (Gdynia, Poland) which upload data to a colony base station over UHF radiowaves when within 0.2–8.0 km. Five i-GotU retrieval-based devices (MobileAction Technology, New Taipei City, Taiwan) were also deployed at Brier in 2014. Devices were programmed with duty cycles to record at 5, 10 or 15 min sampling intervals for periods roughly coincident with the breeding season (realized median intervals 5–18 min). Tracking duration varied among equipped individuals from 10 to 820 days, identified herein as independent bird-years; eight birds from each of Kent and Brier contributed data from multiple breeding seasons (Table 1). Some device duty cycles were remotely programmed to switch to 1 or 24 h sampling intervals in mid-July and to switch back to higher resolution sampling the following breeding season. Longer intervals and complete data gaps also occurred sporadically for some devices, likely due to temporary battery depletion, or device or ground station error.

Data preparation

To assess spatial resource use during breeding, we used data within a time window of 14 May to 29 July in each year, approximating the local reported breeding phenology with peak laying 14 May, incubation period of 30–32 days and peak fledging ~29 July (Weseloh et al. 2020). We also removed the first three days following deployment to avoid residual effects of capture and handling (Shlepr et al. 2021). For birds with unknown lay dates (second or third year of tracking), we removed data before 25 May to minimize the potential of including behaviour prior to clutch initiation.

Data manipulation, visualization and analyses were conducted using R 3.6.1 (<www.r-project.org>) and ArcGIS 10.5 (ESRI, Redlands, California, USA). We quality-controlled each bird-year positional dataset using the R package *SDLfilter* (Shimada et al. 2012). Temporal duplicates were removed with duplicates defined as positions with intervals less than the programmed duty cycle interval for each device (e.g. 5, 10 or 15 min). We removed positions associated with unrealistic movement rates using a maximum of 100 km h^{-1} for herring gulls (Rock et al. 2016). Quality-controlled datasets were plotted and examined for evidence of early fall migration or consistently erroneous positions (three bird-years were removed). Finally, we interpolated each remaining quality-controlled bird-year dataset to 15 min intervals using the *interpolateTime* function in R package *move* (Kranstauber et al. 2019). We did not interpolate over data gaps > 45 min. To maintain consistency across bird-years, those with ≥7 d of complete data (i.e. 96 positions; days defined relative to 00:00 Atlantic Daylight Time), each containing at least one complete trip, were retained for further analyses. One bird-year met these criteria but exhibited atypically long and variable trip durations starting early in the breeding season and was removed as a likely failed breeder. This resulted in a final dataset of 55 bird-years, each with consistent interpolated positions at 15-min intervals for 7–74 complete days falling between 17 May and 29 July (Table 1). This dataset is available on the Dryad Digital Repository (Gutowsky et al. 2021). Overall, the filtering process removed 8.9 ± 8.8 (mean ± SD) tracking days with incomplete data (i.e. days without a complete trip) for each bird-year retained in the final dataset. All subsequent data analyses were performed on the filtered and interpolated positions.

Behavioural metrics

For each bird-year, we identified complete 'at-colony' periods and 'trips' based on entry and exit from 1 km colony buffers (Shaffer et al. 2017). To qualify as a trip, duration outside the colony buffer had to be ≥ 1 h (four positions). Within each trip, we identified periods of distinct behavioural states of either 'visits' or 'transits' based on movement rates between positions, calculated using the R package 'move' with a Lambert Azimuthal Equal Area projection. Following Shaffer et al. (2017) and Maynard and Ronconi (2018), a clear breakpoint in the histogram of movement rates was identified at 2 km h^{-1}. Visits were differentiated from transits along a trajectory as periods of ≥ 30 min (i.e.

Table 1. Overview of herring gull GPS device deployments from four island colonies in the eastern Gulf of Maine, Canada. Total days tracked with (+) indicates some devices still transmitting at end of 2019 breeding season. Means are reported with standard deviation (± SD).

Colony	Deploy years	Deploy dates	Total days tracked per bird	Birds equipped	Birds used	Bird-years used	Breeding season days per bird-year
Kent	2015	3–4 June	386 ± 113	14	11	19	48 ± 9
Brier	2014, 2015	13–16 May	390 ± 380	14	14	22	46 ± 23
Whitehead	2019	28 May	59 ± 13(+)	8	7	7	31 ± 14
Bon Portage	2019	25–27 May	59 ± 14(+)	9	7	7	39 ± 14

movement between three sequential positions) with movement rates continuously ≤ 2 km h^{-1}, while transits were identified as periods with movement rates > 2 km h^{-1}. We could not distinguish between foraging, circling and roosting, thus visits may represent any combination of these behaviours. We summarized duration- and frequency-based behavioural metrics for trips and visits for each bird-year and colony, and for all colonies combined (Table 2).

To identify habitat as either anthropogenic or natural resource types for each visit, we examined positions relative to temporally-matched historical satellite imagery in Google Earth (Google Earth Pro ver. 7.3.2.5776) and used its Google Maps quick-link function for street-view. Nine resource types were considered in this study: four anthropogenic types associated with human infrastructure and industrial activity (mink farm, human settlement, fisheries processing plant (herein 'fish plant'), aquaculture) and five ostensibly natural types without documented and/or visible human infrastructure (freshwater, natural terrestrial, uninhabited island, coastal/nearshore and offshore). For a resource type to be assigned to a visit, the majority of positions in that visit were required to meet the criteria outlined in Table 3. Priority was given to the assignment of anthropogenic resource types, with 'natural' resource types being assigned when the criteria for anthropogenic resource assignment were not met. Similarly, because human settlements consistently co-occurred with mink farms and fish plants, and because these industries can provide larger and more predictable food subsidies, the human settlement resource type was only assigned if the criteria for mink farm or fish plant were not met. Buffer sizes for qualification of each resource type were chosen based on visual examination of movements during visits. Resource types and visit durations were recorded along with the centroid of each visit (average coordinates of all positions), facilitating further examination of consistency in resource assignments across all bird-years and colonies.

We evaluated overall visitation behaviour to each resource type for each bird in a given breeding season by summarizing at the bird-year level. This approach allowed us to assess the general use of different resource types by each bird during breeding, while avoiding issues from uneven sampling across bird-years. We determined for each bird-year the proportion of total visiting time spent at each resource type. To assess whether the proportion of visiting time differed according to the type of habitat (Anthropogenic or Natural) or by colony, we used a beta family (logit link) generalized linear mixed model with Bird ID as a random effect using R package *glmmTMB* (Brooks et al. 2017). Model fit was examined using R package *DHARMa* (Harting 2020), including tests for outliers, dispersion and uniformity which yielded no significant deviations. Significance of model terms was determined using ANOVA (type III sum of squares), and post hoc analyses were performed using pairwise comparisons of estimated marginal means and the Tukey method for p-value adjustment (R package *emmeans*; Lenth 2020).

We also determined for each bird-year the mean distance between colony and visit centroids and the mean visit duration for each resource type. For trips including the most frequently visited anthropogenic resource types (mink farm and fish plant), we also calculated the trip composition (mean number of visits to each resource type across qualifying trips for each bird-year) to examine potential differences in behaviour between these two trip types. In addition, we examined more closely trips exhibiting offshore behaviour (any position > 1000 m from high tide line of any land) and trips with offshore visits, as engagement with natural or anthropogenic resources in the pelagic environment could manifest differently relative to movements rates used to identify visits.

Spatial metrics

To quantify the distribution and intensity of space use at the level of individual bird-years and colony, we used ArcGIS to create a use intensity index (UII) which reflected both fidelity to specific areas (i.e. repeated visits) and total time spent in specific areas, and accounted for uneven sampling across birds and colonies. For each bird-year, visit centroids were overlaid on a 250 × 250 m grid covering the study area, and the following two metrics were evaluated for each grid cell: fidelity (proportion of total visits made to a given cell) and time spent (proportion of total time spent visiting in a given cell). Bird-year UII was then calculated for each grid cell as fidelity × time spent. Colony-level UII was then calculated for each grid cell as proportional colony UII (sum of bird-year UIIs for a given cell/sum of bird-year UIIs across all cells) × proportional colony visitation (number of bird-years from that colony found visiting in a given cell/total number of bird-years from colony). The resource type represented by each grid cell was identified, as per individual visit criteria (above). We then visualized colony UII across space in relation to visit resource type and identified specific sites of particularly intense visitation.

Results

Overall breeding season movement patterns

Our final dataset, following quality control, captures movement information for 39 individuals from four island colo-

Table 2. Summary of breeding season movement patterns of 39 GPS-tracked herring gulls (n = 55 bird-years) from four colonies. Data are reported for all birds combined and for each colony independently. Means are across bird-years and reported with standard deviation (± SD).

Colony	Total trips	Total visits	Trips per day	Visits per trip	At-colony duration (h)	Trip duration (h)	Visit duration (h)	Distance traveled per trip (km)	Max. distance from colony (km)
Overall	75 ± 40	119 ± 11	1.7 ± 0.6	1.7 ± 0.9	8.6 ± 3.6	6.3 ± 2.8	1.7 ± 0.5	55 ± 22	22 ± 9
Kent	85 ± 33	111 ± 59	1.8 ± 0.7	1.4 ± 0.8	9.0 ± 3.5	5.4 ± 2.6	1.7 ± 0.6	46 ± 19	19 ± 8
Brier	70 ± 39	112 ± 69	1.5 ± 0.4	1.7 ± 0.7	9.9 ± 3.9	6.7 ± 2.6	1.7 ± 0.6	71 ± 14	29 ± 5
Whitehead	68 ± 55	136 ± 77	2.1 ± 1.0	2.4 ± 1.3	6.2 ± 2.3	6.9 ± 4.1	1.7 ± 0.3	31 ± 13	11 ± 3
Bon Portage	69 ± 44	117 ± 48	1.7 ± 0.6	2.0 ± 0.8	5.7 ± 1.3	6.9 ± 2.2	1.5 ± 0.2	51 ± 19	18 ± 7

Table 3. Description of nine resource type criteria for assignment of breeding herring gull visits on trips from four colonies during the breeding season.

Classification	Resource type	Assignment criteria
Anthropogenic	Mink farm	Within 500 m of mink farms and associated facilities.
Anthropogenic	Fish plant	Within 500 m of a plant that processes fish for food (seafood wholesalers, packers, holding facilities) or feed (mink farm feed suppliers).
Anthropogenic	Human settlement	Within 500 m of populated areas from small groupings of dwellings to urbanized areas, attached agricultural lands, and associated infrastructure including roadways, parking lots, parks, golf courses, buildings, piers, breakwaters or wharfs (without fish plants).
Anthropogenic	Aquaculture	Within 250 m of floating fin-fish aquaculture pens.
Natural	Freshwater	Within 250 m of freshwater lakes or non-coastal streams and wetlands.
Natural	Natural terrestrial	Over 500 m inland from nearest high tide line, forested areas without identifiable anthropogenic or industrial activity.
Natural	Uninhabited island	Positions on an uninhabited island that is either vegetated or >150 m across.
Natural*	Coastal and nearshore	Between 500 m inland and 1000 m offshore, measured from nearest high tide line.
Natural*	Offshore	> 1000 m from high tide line of any land.

* Presence/absence of vessels unknown.

nies. The 39 birds were tracked over 55 bird-years for a total of 4106 trips and 6371 visits during the breeding season study period (Table 1, 2). Birds from Whitehead generally made more trips per day and more visits per trip relative to the other three colonies (Table 2). The average amount of daily time spent at the colony varied among bird-years from 3.2 to 18.8 h, but was generally higher for birds from Kent and Brier than birds from Whitehead and Bon Portage (Table 2). Similarly, the average trip duration varied among bird-years from 2.7 to 14.2 h and was similar across colonies (Table 2), however the longest trips lasted up to 4 d. On each trip, the average proportion of time spent in transit was 70 ± 26% and ranged from 3 to 100% (some trips did not present visitation behaviour). Individual visits lasted between 0.5 and 18.25 h but were similar on average across colonies (Table 2). On each trip, birds travelled total distances ranging from 1.8 to 647 km, with birds from Brier travelling farthest (on average 40 km farther than birds from Whitehead, Table 2). Similarly, average maximum distances reached from the colony were farthest for Brier birds and closest for Whitehead, ranging overall from 1.4 to 161 km (Table 2, Fig. 1).

Visits to natural versus anthropogenic habitats

Using our criteria to characterize visits, herring gulls from all colonies split their time evenly between natural and anthropogenic habitats (mean proportion of total visiting time spent was 44 ± 26% and 56 ± 26%, respectively), but with variation between birds both within and among colonies (Fig. 2). Both colony and the interaction of colony and habitat type were significant predictors of the proportion of visiting time in our model, while bird identity as a random effect was not (Supplementary material Appendix 1 Table A1). Birds from Whitehead spent significantly more time visiting in anthropogenic than natural habitat (Fig. 2; pairwise comparisons of estimated marginal means, Tukey's HSD, df = 100, t-ratio = −6.36, $p < 0.01$), and spent more time in anthropogenic habitat (and less time in natural habitat) than birds from the other three colonies (Whitehead–Kent: t-ratio = −4.07, $p < 0.01$; Whitehead–Brier: t-ratio = −3.07, $p = 0.05$; Whitehead–Bon Portage: t-ratio = −3.99, $p < 0.01$). Time spent visiting in the two habitat types varied more widely among individuals from Kent and Brier than Bon Portage but, for all three colonies, time spent visiting in natural and anthropogenic habitats was not significantly different (Fig. 2; Kent: t-ratio = 0.27, $p = 1.00$; Brier: t-ratio = −2.96, $p = 0.07$; Bon Portage: t-ratio = 1.39, $p = 0.86$).

Comparative use of resource types across colonies

Birds attended all nine resource types at varying frequencies across colonies. For all birds, the natural inland resource types of freshwater and terrestrial were infrequently visited, while the natural marine resource types of uninhabited island and coastal/nearshore were highly frequented (Fig. 3, 4). Offshore areas were the least frequently visited natural marine resource overall, although birds from Bon Portage and Kent spent more time visiting at this resource type than birds from other colonies (Fig. 1). However, birds from all colonies made transitory movements offshore on 22–100% of trips (see colony specific results below for more detail). All four anthropogenic resource types were heavily used, but fish plants were most consistently frequented, with all but one bird visiting a fish plant at least once, spending 28 ± 11% of their time on visits lasting 1.6 ± 0.1 h (Fig. 3, 4).

For Kent birds, the majority of total visiting time was spent associating with coastal/nearshore resources, in addition to aquaculture, fish plant and uninhabited islands. Only Kent birds regularly visited aquaculture, with 74% of birds visiting aquaculture at least once, visits lasting around 1.6 h (Fig. 4), within 3–45 km of the colony (Fig. 5). All Kent birds visited fish plants at least once, with visits occurring on average < 20 km from the colony (Fig. 5). Nearly all Kent birds (95%) visited uninhabited islands and coastal/nearshore. Visits to uninhabited islands lasted over 2.5 h on average and were relatively close to the colony while visits to coastal/nearshore were shorter, at varying but farther distances from the colony (Fig. 4, 5). Visits offshore were made on 6 ± 12% of trips (range 0–53%) for each bird, while transit movements offshore (any positions > 1 km from shoreline) were made on 85 ± 10% of trips (range 57–100%). Visits from the Kent colony to the coastal regions of mainland New Brunswick and Maine and to mink farms on mainland Nova Scotia required offshore transits (Fig. 1, 6). For the 37% of Kent birds which visited mink farms, these visits lasted on

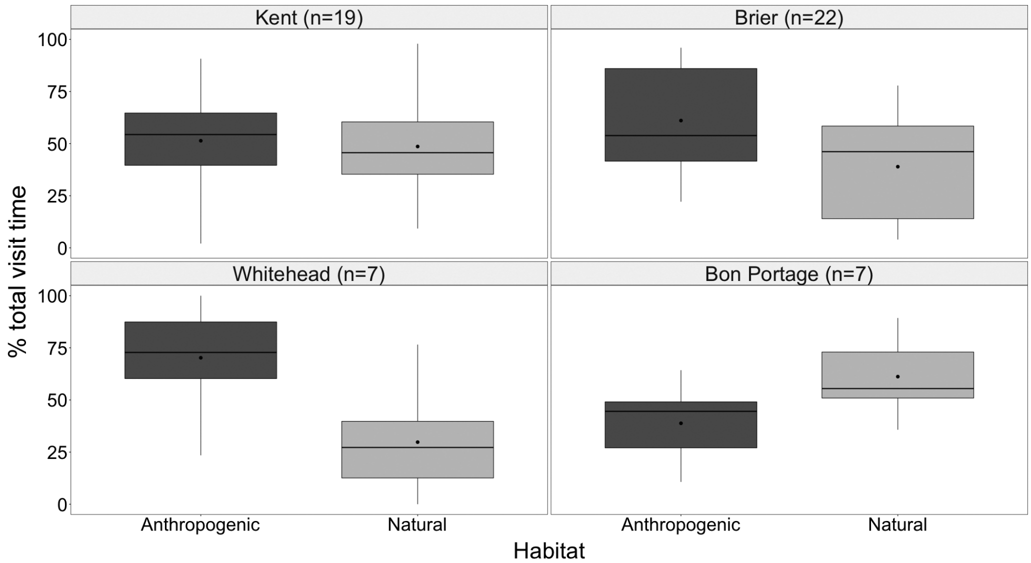

Figure 2. Proportion of total time spent visiting within natural and anthropogenic habitats by breeding herring gulls tracked from four colonies. Each data point is a bird-year mean value.

average 1.4 h (ranging from 0.5 to 6.5 h) and were all 65–75 km from the colony (Fig. 4, 5).

In contrast, all birds from Brier visited mink farms at least once, where they spent on average 40 ± 26% of their total visiting time (Fig. 3), with 1 h long visits (Fig. 4) taking place within ca 40 km of the colony (Fig. 5). Like Kent birds, visits to mink farms from the Brier colony required offshore transits (Fig. 1, 6). Accordingly, 87 ± 13% of trips (range 65–100%) included positions > 1 km from shore, while visits offshore were only made on 3 ± 7% of trips (range 0–30%). All Brier birds also visited coastal/nearshore resources, but spent only 11 ± 10% of their time at mean distances ranging from 3 to 43 km from the colony (Fig. 3, 5). Nearly all Brier birds (91%) visited fish plants at least once, spending between 0–87% of total visit time (Fig. 3), with 2 h long visits within ≤ 25 km of the colony (Fig. 4, 5). Uninhabited islands close to the colony were also frequently visited and for long durations; 86% of Brier birds visited uninhabited islands at least once, spending 0–59% of total visit time for average durations of 4.4 h at a time (ranging from 0.5 to 12.5 h), mostly within ≤ 5 km of the colony (Fig. 3–5).

Birds from Whitehead also made long visits to uninhabited islands close to the colony, where 86% of birds visited at least once, spending 0–50% of total visit time for durations of over 3.5 h at a time (ranging from 0.5 to 11 h), mostly within ≤ 10 km of the colony and < 1 km of other land (Fig. 3–5). No Whitehead birds made offshore visits, but all birds had transits offshore, with 42 ± 11% of trips (range 22–54%) having at least one transit position > 1 km from shore. All Whitehead birds visited fish plants and human settlements, spending the most cumulative time at fish plants (43 ± 30%; Fig. 3) close to the colony (Fig. 5). One third

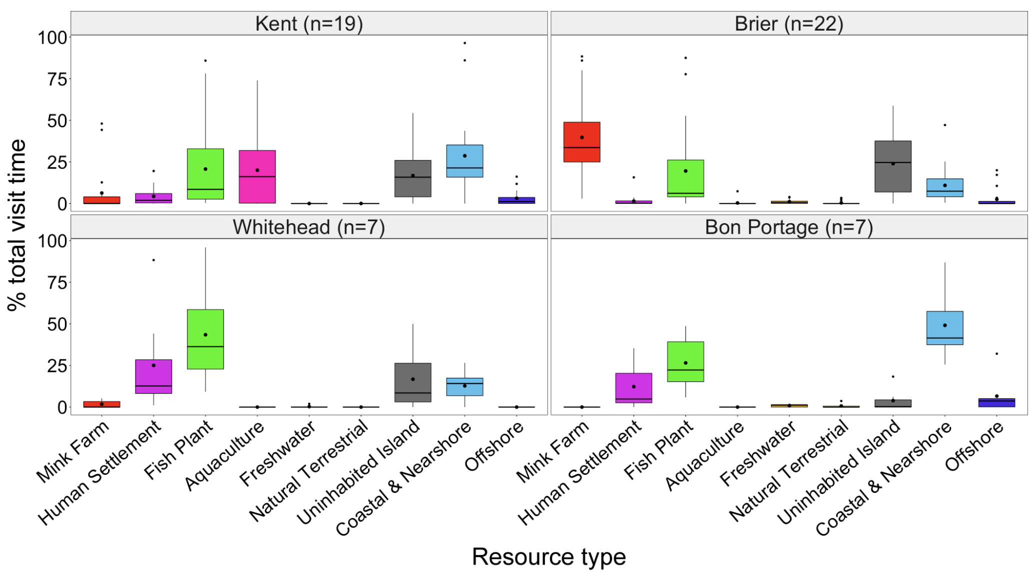

Figure 3. Percentage of total visit time spent at each resource type by breeding herring gulls tracked from four colonies. Data from all bird-years from each colony are shown.

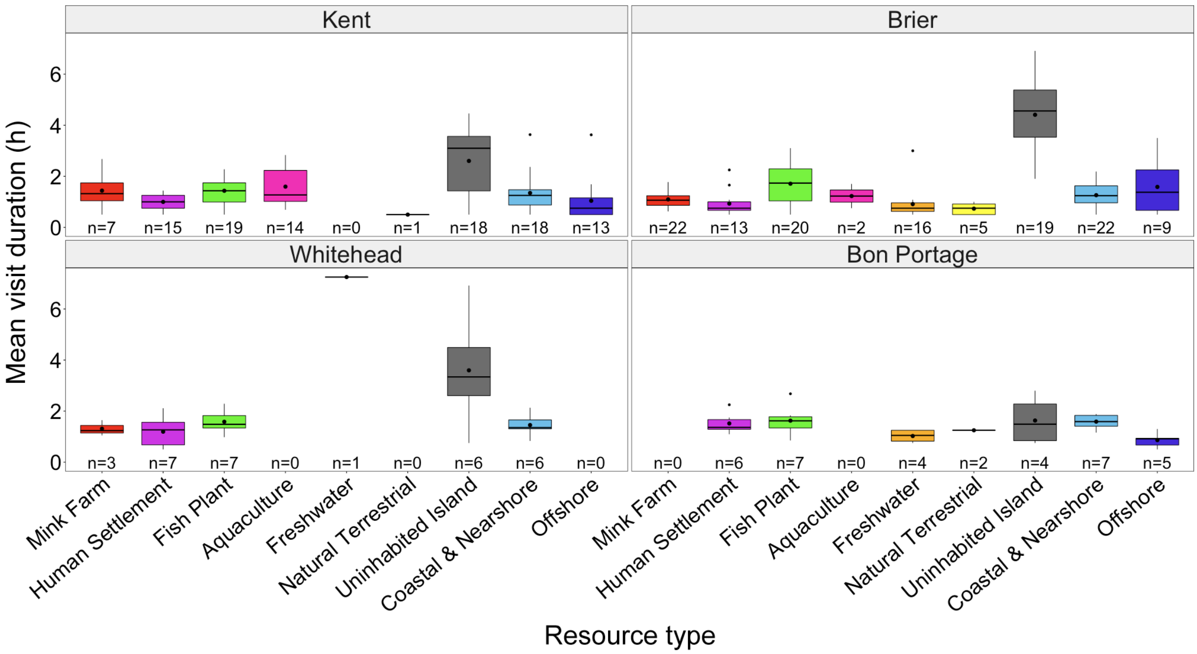

Figure 4. Mean duration of time (h) spent visiting at each resource type by breeding herring gulls tracked from four colonies. Only data from bird-years with visits to a given resource type are shown, resulting in different sample size for each colony-resource combination. Each data point is a bird-year mean value.

(37%) of Whitehead birds made infrequent visits to mink farms, where they spent 1–5% of their time visiting at distances of 68–77 km from the colony (Fig. 3–5).

Despite the relatively close proximity between Whitehead and Bon Portage (23 km; Fig. 1), there were important differences in behaviour of birds between the two colonies. Birds from Bon Portage did not visit mink farms and did not commonly make visits to uninhabited islands (Fig. 3). Instead, Bon Portage birds spent 49 ± 21% of their total visiting time at coastal/nearshore resources close to the colony (3–20 km, Fig. 5). Visits offshore were made on 8 ± 9% of trips (range 0–24%) for each bird, and transit movements offshore were made on 51 ± 12% of trips (range 38–80%). All Bon Portage birds visited fish plants, spending 9–49% of total visit time for durations ranging from 0.5 to 9 h, mostly within ≤ 10 km of the colony (Fig. 3–5). Human settlement

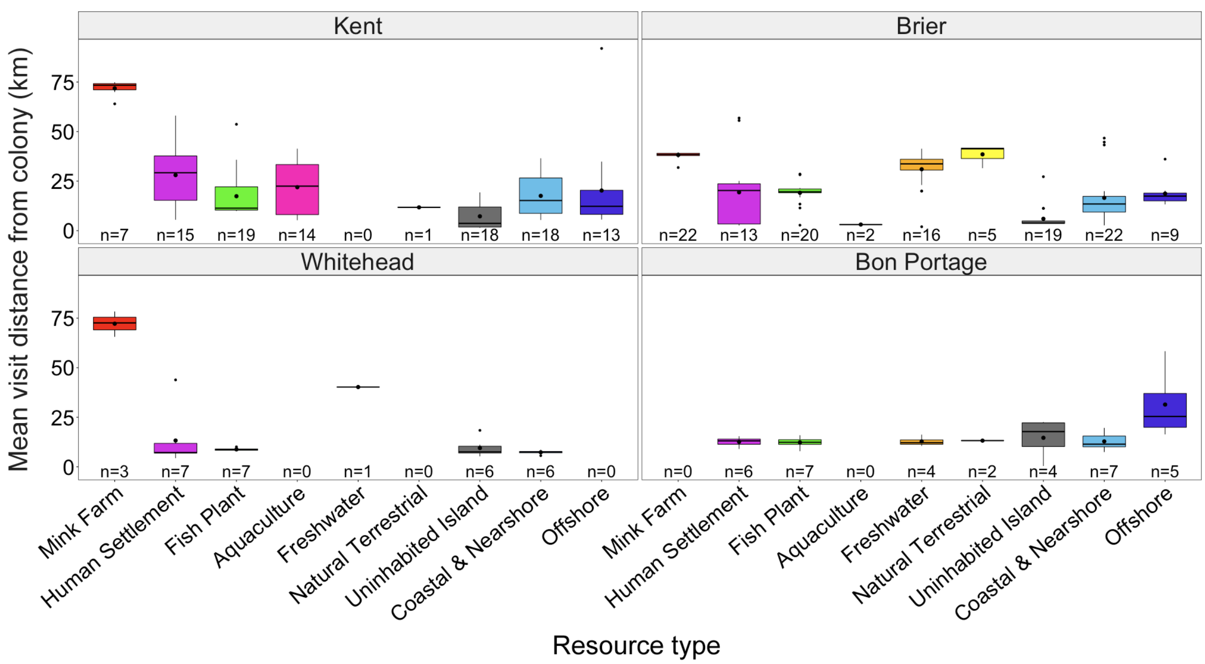

Figure 5. Mean distance travelled (km) from colony to each resource type by breeding herring gulls tracked from four colonies. Only data from bird-years with visits to a given resource type are shown, resulting in different sample size for each colony–resource combination. Each data point is a bird-year mean value.

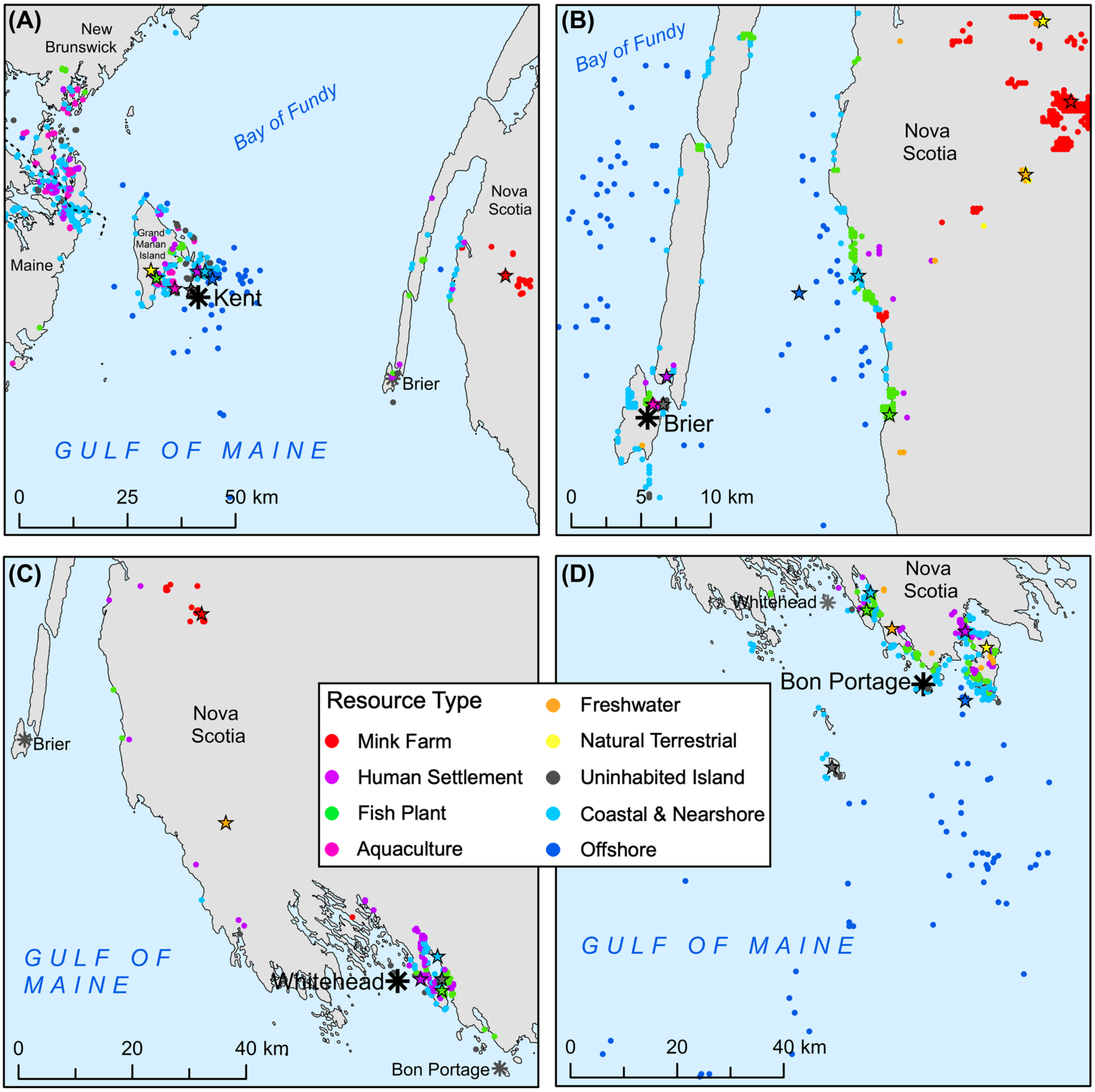

Figure 6. Spatial distribution of visits to nine distinct resource types by breeding herring gulls tracked from four colonies (A) – Kent, (B) – Brier, (C) – Whitehead, (D) – Bon Portage. For each colony, points depict locations with at least one visit (250 × 250 m resolution) and stars depict locations with the highest use intensity index (UII; see Methods for details) by resource type. More detailed figures of visits and relative UII for each colony are provided in Supplementary material Appendix 1 Fig. A1–A4.

and offshore resources were also visited at least once by most Bon Portage birds (86 and 71%, respectively).

Colony-specific sites of visitation

Birds from each colony exhibited specific sites of more intense visitation, with a small number of sites shared by multiple colonies (Fig. 6, Supplementary material Appendix 1 Fig. A1–A4). For example, most mink farm visits made by birds from Brier, Kent and Whitehead occurred in the inland region of Digby County, Nova Scotia. This area was particularly heavily used by Brier birds, with a concentrated region of high UII around a large-scale, mink-farming operation. Birds from Kent and Whitehead tended to use consistent direct travel routes from their respective colonies to reach these mink farms, more than 70 km away (Fig. 1). In contrast, long-distance transits and visits by Bon Portage birds were only made offshore to the south (Fig. 6, Supplementary material Appendix 1 Fig. A4). Overlap in high UII between birds from Whitehead and Bon Portage occurred mostly around nearby fish plants (Fig. 6, Supplementary material Appendix 1 Fig. A3, A4). Whitehead birds also heavily used a small, uninhabited island (just 70 m across and 165 m long) to the northeast, as well as human settlement and coastal/nearshore resources primarily to the northwest. Bon Portage birds instead spent more time to the east, around coastlines, fish plants and nearby communities (Fig. 6, Supplementary material Appendix 1 Fig. A4).

In addition to inland mink farms, birds from Brier also exhibited relatively high UII on a small, uninhabited island just 1.5 km northeast of the colony called 'Peter Island' as well as a small, uninhabited island (150 m across) at the end of a narrow, long rock shoal to the south of Brier Island (Fig. 6, Supplementary material Appendix 1 Fig. A2). On Brier itself, nearby fish plants and human settlements were important areas (Fig. 6, Supplementary material Appendix 1 Fig. A2). Brier birds also travelled northeast to the mainland shoreline, with high UII around more distant fish plants (Fig. 6, Supplementary material Appendix 1 Fig. A2). Offshore visits were made primarily to the northwest or east of the colony, between 1 and 7 km offshore. Despite being tracked concurrently, birds from Kent Island transited over these same offshore areas of high visitation by Brier birds and did not slow their movements to indicate visitation behavior (Fig. 1, 6).

Kent birds exhibited high UII around fish plants near the colony, as well as aquaculture operations ranging from 5.5 to 55 km distant (Fig. 6, Supplementary material Appendix 1 Fig. A1). Birds from Kent also demonstrated particularly high UII in a coastal/nearshore region on the southeast coast of White Head Island, as well as nearby offshore areas (Fig. 6, Supplementary material Appendix 1 Fig. A1). Birds from Kent travelled ≥ 30 km northwest of the colony to an area on the border of Maine and New Brunswick, where they visited aquaculture, human settlement, coastal/nearshore and uninhabited island resources (Fig. 6, Supplementary material Appendix 1 Fig. A1).

Resource-specific trip composition

For the two most frequently visited anthropogenic resource types (mink farm and fish plant), we investigated trip composition. On most trips where birds visited a mink farm, multiple independent mink farm visits were made, with birds transitioning between visit and transit states (Supplementary material Appendix 1 Fig. A5). For birds from Kent and Brier, trips to mink farms were made almost exclusively for that resource type, whereas birds from Whitehead were more likely to visit other resource types on the same trip, particularly human settlement. Similar to mink farm trips, on most trips where birds visited fish plant resources, multiple distinct visits to fish plants were made, as well as visits to other resource types (Supplementary material Appendix 1 Fig. A6).

Discussion

Our study examined the breeding season movements of herring gulls tracked from four colonies in the eastern Gulf of Maine in relation to their use of natural and anthropogenically-influenced habitats. The proximity of colonies to one another and relative access to the various resource types was expected to influence patterns of movement and visitation at the colony-level. Despite large distances between some breeding sites (e.g. Kent, Brier and Whitehead; up to 145 km), birds from these locations made long-distance trips, converging on the same distinct areas offering particular resources (e.g. a concentration of mink farming operations). In contrast, despite only small distances between some sites (e.g. Whitehead and Bon Portage), breeding birds from these colonies overlapped only in their visitation to specific nearby resources (e.g. a concentration of fish processing plants), while they otherwise diverged markedly in both their distribution and relative use of different resource types. Thus, the influence of varying anthropogenic infrastructure and industry differed significantly among colonies but was high overall. Although not assessed here, this has possible implications for relative influence on breeding success and subsequent population establishment, growth and persistence for gulls throughout the eastern Gulf of Maine and southeastern Atlantic Canada in general.

Accessibility and attraction to different resources

Fur farms influence the behaviour of breeding *Larus* gull species, as shown in Finland (Juvaste et al. 2017) and Russia (Zelenskaya and Khoreva 2006). Gulls are attracted by the substantial volume of waste produced in fur farming and processing, including manure, waste food, carcasses and animal fat (Verschuren Centre 2017). In Russia, breeding slaty-backed gulls *Larus schistisagus* obtained > 30% of their food from mink farms, leading to exponential growth and concomitant impacts on the flora of the island breeding site (Zelenskaya and Khoreva 2006). In contrast, lesser black-backed gull *Larus fuscus* populations in Finland are in decline and red-listed, but fox and mink fur farming operations are important anthropogenic food sources that are sustaining the population (Juvaste et al. 2017). Like these gulls in Russia and Finland, herring gulls breeding in Nova Scotia and New Brunswick made dedicated, long trips to specific preferred fur farms. These trips involved relatively short visits to the region of southwest Nova Scotia where over 80% of ca 40 currently operating mink farms in the province are located, containing > 100 000 domestic mink (Statistics Canada 2020). Over the course of our study, the number of active mink farms in Nova Scotia declined from 116 in 2014 to 43 in 2019 (Statistics Canada 2020), yet birds tracked in 2019 from Whitehead also made trips to the same farms as birds tracked from Kent and Brier in 2014 and 2015, albeit with visits to other resource types en route. Based on optimal foraging theory for central-place foragers, repeated visits to distant resources indicate predictable and profitable resources, as these would be required to recover travel costs (Shaffer et al. 2017) – as shown by lesser black-backed gulls travelling tens of kilometres to access predictable sources of fisheries discards in the North Sea (Sommerfeld et al. 2016). In the eastern Gulf of Maine, this would suggest that herring gulls from various colonies preferentially rely on distant mink farm subsidies, despite reductions over time in the number of farms and farmed animals in the province. If the Nova Scotia mink farming industry continues to decline, herring gulls from these colonies will likely adjust to alternative resources, perhaps more similar to those from Bon Portage in 2019 where tracked birds did not visit mink farms.

Aquaculture operations, namely open-pen fin-fish farms, attract *Larus* gulls elsewhere, such as the silver gull *Larus novaehollandiae* in Tasmania and Australia (Pemberton et al. 1991, Harrison 2009). In Australia, food subsidies from fish food at southern bluefin tuna *Thunnus maccoyii* ranching pens allowed the local population of silver gull to expand its breeding season (which now parallels the ranching season), increase its reproductive output, and exponentially increase its local breeding population (eight-fold increase in six years; Harrison 2009). In our study, aquaculture operations were heavily used by three-quarters of tracked herring gulls from the New Brunswick colony (Kent), notably foraging at large, open, circular pens stocked primarily with Atlantic salmon *Salmo salar* and rainbow trout *Oncorhynchus mykiss*. Interestingly, gulls from Kent regularly visited aquaculture resources both near and far from the colony, ranging 3–45 km distant, whereas birds from the Nova Scotia colonies did this rarely, if ever, despite multiple accessible operations close to their breeding sites and en route to frequently visited areas. Our data suggest that either the few accessible aquaculture sites near the study colonies in Nova Scotia are less profitable relative to other locally available food sources than those in New Brunswick, or that gulls in southwest Nova Scotia do not yet appear to regularly recognize aquaculture sites as potential food sources, at least for the colonies we monitored.

Despite the maritime nature of the breeding colony islands in this study, our tracked gulls spent little time visiting more than 1 km offshore. They did however frequently exhibit movements at this distance from land, thus spending considerable time on trips within the offshore environment. While many of these more pelagic trips without offshore visits were clearly en route to land-based resources, others were not. Seabirds foraging in the unpredictable open ocean environment often employ an area-restricted search strategy in response to patchy resources, alternating between high speed, direct movements and reduced speed, tortuous movements as they encounter natural prey and then carry on searching (Weimerskirch 2007). Similarly, if birds encounter fishers, their movement patterns should reflect both ship-following and attempts to access ship-based resources by matching vessel speeds and increasing tortuosity, as exhibited for example by lesser black-backed gulls when within 5 km of fishing vessels (Sommerfeld et al. 2016). Indeed, research from our study region has shown that herring gull diets can comprise a high proportion of offshore prey including forage fish and krill *Meganyctiphanes norvegica* (Steenweg et al. 2011, Shlepr et al. 2021), that gulls are often observed following fishing vessels, and that egg size and productivity of gulls are influenced by fisheries landings (Bennett et al. 2017). Thus, visits identified by travel rates of ≤ 2 km h^{-1} for periods of ≥ 30 min could fail to detect interactions with either natural or fisheries-based resources offshore, and more likely represent resting or preening than active foraging. Future work will determine the relative influence of natural and anthropogenic resources in the offshore environment by assessing overlap between gull and vessel monitoring system tracking data in space and time, and gull movement responses.

The attraction of seabirds to various activities within the fishing industry is well-documented worldwide (Montevecchi 2001), however the use of land-based fish plants in particular, has received less attention (but see Navarro et al. 2017). Fish plants were easily accessible and frequently used by gulls tracked from the entire study region. All but one bird visited a fish plant at least once, spending on average 28% of their total visiting time, with some individuals spending > 90% of their time. Visits to human settlements were also likely influenced by fishing-related activity as many of these locations were coastal, including piers and wharfs where fishers process their own catch and dispose of leftover bait and offal. The birds are likely attracted by the potential for discards at plants and offal from nearby effluent pipes discharging into shallow, nearshore waters. Indeed, a study that conducted stable-isotope analysis of blood samples from a sub-sample of the Brier and Kent birds in the present study found that high trophic marine prey (Atlantic herring *Clupea harengus*, Atlantic mackerel *Scomber scombrus*) and crabs (*Cancer borealis*, *Carcinus maenas*) sourced from known fish plants and wharfs were among the gulls' top prey categories (Shlepr et al. 2021). The gregarious nature of gulls also attracts birds to spend time in the vicinity of locations like fish plants and wharfs where high concentrations of conspecifics occur, where they roost and preen communally rather than actively forage (Clark et al. 2016). We cannot determine whether tracked breeding gulls were foraging or resting during visits, but it is clear that birds from each colony mainly visited the easily accessible fish plants and ports nearest to their breeding site, where both the potential availability of resources and social interactions incentivize birds to spend a great deal of their time when away from the colony. Further observational studies would help to elucidate the nature of the gulls' attraction to these locales.

Tracked herring gulls from three of the four colonies also exhibited high use intensity of uninhabited islands, away from direct anthropogenic influence. Specific coastal islands close to each colony were targeted by the locally breeding birds, and these sites were visited for the longest continuous durations of any resource type. This may be cause for concern, as large gulls have been identified to pose a significant threat to coastal island biodiversity in the region (Farrow and Nussey 2013). These relatively ecologically-intact islands provide refugia from land-based predators and human threats and offer high productivity intertidal areas. Herring gulls can pose significant predation pressure in these systems, preying on other breeding seabirds in addition to offshore, intertidal and terrestrial prey (Pierotti and Annett 1991, Steenweg et al. 2011). High population levels of gulls, potentially sustained by anthropogenic food subsidies, are known to affect other breeding seabirds at uninhabited islands in Nova Scotia and New Brunswick, including species-at-risk. For example, predation by large gulls is considered a key factor in population declines in several tern colonies in the region (Scopel and Diamond 2018), notably on endangered roseate terns (*Sterna dougallii*; Leonard et al. 2004, Environment Canada 2015). Loafing gulls may also occupy significant space on non-nesting islands and possibly dissuade other birds from nesting in suitable habitat. Future work should investigate how visiting gulls are dividing their time between loafing and foraging, and what they are feeding on, as these cannot presently be distinguished. While it is suspected that the tracked gulls could have detrimental impacts on sensitive island ecosystems, further research is needed to investigate their behaviour while visiting the uninhabited islands identified in this study.

Research and management recommendations

Our tracking data revealed clear, colony-level tendencies for the use of particular habitats and resource types, but also suggested varying levels of individual variation amidst the colonies (Supplementary material Appendix 2 Fig. A7). Such variation can arise from different foraging strategies in relation to sex, age and true individual specialization (Bolnick et al. 2003, Ceia and Ramos 2015). Dietary findings from Newfoundland revealed that only one quarter of herring gull pairs had generalist diets, while three quarters specialized on either intertidal (mostly blue mussel *Mytilus edulis*), seabird (mostly adult Leach's storm-petrel *Oceanodroma leucorhoa*) or human refuse resources (Pierotti and Annett 1991). Throughout Europe, some individual lesser black-backed and yellow-legged gulls *Larus michahellis* specialize in the use of resources from anthropogenic habitats such as mink farms, fisheries discards or fish farms, while other individuals use more generalist strategies (Tyson et al. 2015, Juvaste et al. 2017, Navarro et al. 2017). Such divergent and complex foraging strategies among individuals could be expected for species that breed in dense aggregations with high intraspecific competition, as well as potential sexual segregation from differences in morphology, parental roles or nutritional requirements, all combined with an environment offering temporally and spatially predictable food sources (Bolnick et al. 2003, Ceia and Ramos 2015). For kelp gulls *Larus dominicanus* in Argentina, the degree of sexual segregation in use of anthropogenic food subsidies differed greatly among three colonies, likely reflecting differing environmental pressures and availability of local food resources (Kasinsky et al. 2021). Specialization on the most profitable or available resources can provide a reproductive advantage; herring gulls in the United Kingdom with generalist diets had smaller egg size than those more specialized on either terrestrial or marine diets (O'Hanlon et al. 2020). We could not examine age- or sex-effects in our study, and quantification of individual specialization was beyond our scope, however, our data did suggest distinct resource preferences for some individuals from each colony (Supplementary material Appendix 1 Fig. A7). We recommend that future studies investigate sex- and individual-based variation in the trophic ecology of gulls in the eastern Gulf of Maine, particularly in regard to consistency in the use of specific anthropogenic food subsidies over the course of a single breeding season and over multiple years, as well as subsequent influences on reproductive output.

From our findings, it is clear that industrial activity influences the behaviour of breeding gulls throughout the region, with birds spending at least half of their time attending anthropogenic rather than natural habitats. This in turn is likely influencing breeding success, relative distribution and population persistence (Bennett et al. 2017, O'Hanlon et al. 2020). Such anthropogenic subsidies can result in adverse impacts to local ecosystems and human communities, and warrant further study in order to identify opportunities for effective management interventions. Given the extent to which gulls currently interact with industrial activity within our study region, reducing available anthropogenic food subsidies (regulation, enforcement, best practices) will have direct impacts on local gull populations. Provincial governments have already taken some regulatory steps to reduce the attraction of predators to certain sites, including mink farms in Nova Scotia (Verschuren Centre 2017), and aquaculture in New Brunswick (Government of New Brunswick 2019). Given the distances that herring gulls move to access specific anthropogenic resource types in combination with their heavy use of particular island sites, we suggest that consistent, broad, regional efforts informed by further research and monitoring will be required, if local-scale reductions of gull populations to limit gull impacts on sensitive local ecosystems or human well-being are deemed necessary.

Gulls are abundant seabirds found throughout the world that can exploit a wide variety of food sources due to their opportunistic nature and dietary flexibility. In the Canadian portion of the Gulf of Maine, the contribution of various anthropogenic food subsidies to gull diet varies among colonies and individuals, but is likely substantial overall given the movement behaviour we recorded. Despite the reduction in open landfills and fisheries discards in the region, various other industries including mink farming, fin-fish aquaculture and fish processing are highly influential for breeding herring gulls. These findings have important implications for the management of both local ecosystems and industries, specifically in terms of mitigating pressures on local ecosystems and humans stemming from particular industrial practices.

Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.d2547d82b> (Gutowsky et al. 2021).

Acknowledgements – The Kespukwitk/Southwest Nova Scotia Priority Place Coastal Islands Working Group contributed significantly to the project through participation in a collaborative planning process that identified the impacts of problematic native species as a threat to coastal islands biodiversity and species at risk in Southwest Nova Scotia. We greatly appreciate help from the many assistants who participated in gull capture, tag deployment, equipment checks and data retrieval, namely Zoe Chrysler, James Kelley, Laurie Maynard, Brad Toms, Sarah Wong and Miko Wongconi on Brier, Damon Gannon, Patty Jones, Ian Kyle, Claire Schollaert and Bowdoin College students on Kent, Raphaël Blais, Matthew Deagle, Bertin D'Eon, Ted D'Eon, Natalie Thimot, and especially Alix d'Entremont on Whitehead, and Julia Baak and Rielle Hoeg on Bon Portage. Thanks to Sabina Wilhelm and Greg Robertson for support and equipment loans for work carried out on Brier, to Bowdoin Scientific Station for support on Kent, and to Ben Morton for transportation to Whitehead. Gary Leblanc repaired drop traps.

Funding – Funding was provided by Environment and Climate Change Canada (Atlantic Ecosystem Initiatives and Stewardship Unit of the Canadian Wildlife Service), New Brunswick Wildlife Trust Fund, Nova Scotia Habitat Conservation Fund, Natural Sciences and Engineering Research Council of Canada Strategic and Discovery grants to MLM, and University of New Brunswick.

Ethics statement – This study was undertaken as a large collaboration between multiple primary investigators and institutions. Work was carried out principally under Canadian Wildlife Service Banding Permits 10480, 10694, 10851 and 19851, and Animal Care Permits from Acadia University (Permit 04-18) and University of New Brunswick (Permit 14027).

Author contributions – SEG led the analysis and wrote the manuscript. KRS assisted with data processing, analysis and visualization. JM, RAR and KS led the collection of field data. MLM, SRC, KAA, RAR and AWD facilitated inception and collaboration of the study. All authors inputted to the manuscript and gave final approval for publication.

Conflict of interest – We confirm there are no financial interests, connections or other situations that might raise the question of bias in the work reported or any of the conclusions reached in this manuscript for any of the authors.

References

Anderson, J. G. T. et al. 2016. Introduction: a historical perspective on trends in some gulls in eastern North America, with reference to other regions. – Waterbirds 39: 1–9.

Bennett, J. L. et al. 2017. Variability in egg size and population declines of herring gulls in relation to fisheries and climate conditions. – Avian Conserv. Ecol. 12: 16.

Bolnick, D. I. et al. 2003. The ecology of individuals: incidence and implications of individual specialization. – Am Nat 161:1–28.

Brooks, M. E. et al. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. – R J. 9: 378–400.

Burger, J. 2001. Landfills, nocturnal foraging and risk to aircraft. – J. Toxicol. Environ. Health A 64: 273–290.

Ceia, F. R. and Ramos, J. A. 2015. Individual specialization in the foraging and feeding strategies of seabirds: a review. – Mar. Biol. 162: 1923–1938.

Clark, D. E. et al. 2016. Roost site selection by ring-billed and herring gulls. – J. Wildl. Manage. 80: 708–719.

Cotter, R. et al. 2012. Population status, distribution and trends of gulls and kittiwakes breeding in eastern Canada, 1998–2007. – Can. Wildl. Serv. Occas. Pap. No. 120.

Desjardins, C. F. et al. 2019. Is the urban-adapted ring-billed gull a biovector for flame retardants? – Environ. Pollut. 244: 109–117.

Donehower, C. and Bird, D. 2008. Gull predation and breeding success of common eiders on Stratton Island, Maine. – Waterbirds 31: 454–462.

Environment and Climate Change Canada 2018. Action plan for the eastern mountain avens *Geum peckii* in Canada. Species at risk act action plan series. – Environment and Climate Change Canada, Ottawa, ON, Canada.

Environment Canada 2015. Action plan for the roseate tern *Sterna dougallii* in Canada. Species at risk act action plan series. – Environment Canada, Ottawa, ON, Canada.

Farmer, R. G. and Leonard, M. L. 2011. Long-term feeding ecology of great black-backed gulls *Larus marinus* in the northwest Atlantic: 110 years of feather isotope data. – Can. J. Zool. 89: 123–133.

Farrow, L. and Nussey, P. 2013. Southwest Nova Scotia habitat conservation strategy. – Mersey Tobeatic Research Inst. Report to Environment and Climate Change Canada, Kempt, NS, Canada, <www.merseytobeatic.ca/projects-habitat-conservation-priorities.php>.

Goumas, M. et al. 2020. Urban herring gulls use human behavioural cues to locate food. – R. Soc. Open Sci. 7: 191959.

Government of New Brunswick 2019. Dept of Agriculture, Aquaculture and Fisheries. – <www2.gnb.ca/content/gnb/en/departments/10/news/news_release.2019.11.0633.html>.

Gutowsky, S. E. et al. 2021. Data from: The influence of multiple industries on the behaviour of breeding gulls from four colonies across the eastern Gulf of Maine, Canada. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.d2547d82b>.

Harrison, S. J. 2009. Interactions between silver gulls *Larus novaehollandiae* and southern bluefin tuna *Thunnus maccoyii* aquaculture in the Port Lincoln area. – PhD thesis, Flinders University of South Austrlia, Adelaide, SA, Australia.

Harting, F. 2020. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. – R package ver. 0.3.0. <https://CRAN.R-project.org/package=DHARMa>.

Juvaste, R. et al. 2017. Satellite tracking of red-listed nominate lesser black-backed gulls *Larus f. fuscus*: habitat specialisation in foraging movements raises novel conservation needs. – Global Ecol. Conserv. 10: 220–230.

Kasinsky, T. et al. 2021. Geographical differences in sex-specific foraging behaviour and diet during the breeding season in the opportunistic kelp gull *Larus dominicanus*. – Mar. Biol. 168: 14.

Kickbush, J. C. et al. 2018. The influence of avian biovectors on mercury speciation in a bog ecosystem. – Sci. Total Environ. 637–638: 264–273.

Kranstauber, B. et al. 2019. move: visualizing and analyzing animal track data. – R package ver. 3.2.2. <https://bartk.gitlab.io/move/index.html>.

Lenth, R. 2020. emmeans: estimated marginal means, aka least-square means. – R package ver. 1.4.4. <https://CRAN.R-project.org/package=emmeans>.

Leonard, M. et al. 2004. Status and management of roseate terns *Sterna dougallii* in Nova Scotia. – Proc. Nova Scotian Inst. Sci. 42: 253–262.

Mallory, M. L. and Gilbert, C. D. 2008. Leg-loop harness design for attaching external transmitters to seabirds. – Mar. Ornithol. 36: 183–188.

Marzluff, J. M. 2001. Worldwide urbanization and its effects on birds. – In: Marzluff, J. M. et al. (eds), Avian ecology and conservation in an urbanizing world. Springer, pp. 19–47.

Maynard, L. D. and Ronconi, R. A. 2018. Foraging behaviour of great black-backed gulls *Larus marinus* near an urban centre in Atlantic Canada: evidence of individual specialization from GPS tracking. – Mar. Ornithol. 46: 27–32.

Montevecchi, W. 2001. Interactions between fisheries and seabirds. – In: Schreiber, E. and Burger, J. (eds), Biology of marine birds. CRC Press, Washington, DC, USA, pp. 527–558.

Navarro, J. et al. 2017. Shifting individual habitat specialization of a successful predator living in anthropogenic landscapes. – Mar. Ecol. Prog. Ser. 578: 243–251.

Navarro, J. et al. 2019. Pathogen transmission risk by opportunistic gulls moving across human landscapes. – Sci. Rep. 9: e10659.

O'Hanlon, N. J. et al. 2020. Landscape-mediated variation in diet is associated with egg size and maculation in a generalist forager. – Ibis 162: 687–700.

Oro, D. et al. 2013. Ecological and evolutionary implications of food subsidies from humans. – Ecol. Lett. 16: 1501–1514.

Pemberton, D. et al. 1991. Predators on marine fish farms in Tasmania. – Pap. Proc. R. Soc. Tasmania 125: 33–35.

Pierotti, R. and Annett, C. 1991. Diet choice in the herring gull: constraints imposed by reproductive and ecological factors. – Ecology 72: 319–328.

Ramos, R. et al. 2011. Insights into the spatiotemporal component of feeding ecology: an isotopic approach for conservation management sciences. – Divers. Distrib. 17: 338–349.

Rock, P. et al. 2016. Results from the first GPS tracking of roof-nesting herring gulls *Larus argentatus* in the UK. – Ring. Migrat. 31: 47–62.

Scopel, L. C. and Diamond, A. W. 2018. Predation and food–weather interactions drive colony collapse in a managed metapopulation of arctic terns *Sterna paradisaea*. – Can. J. Zool. 96: 13–22.

Shaffer, S. A. et al. 2017. Population-level plasticity in foraging behavior of western gulls *Larus occidentalis*. – Move. Ecol. 5: 27.

Shimada, T. et al. 2012. Improving data retention and home range estimates by data-driven screening. – Mar. Ecol. Prog. Ser. 457: 171–180.

Shlepr, K. R. et al. 2021. Estimating the relative use of anthropogenic resources by herring gull *Larus argentatus* in the Bay of Fundy, Canada. – Avian Conserv. Ecol. 16: 2.

Sommerfeld, J. et al. 2016. Combining bird-borne tracking and vessel monitoring system data to assess discard use by a scavenging marine predator, the lesser black-backed gull *Larus fuscus*. – Mar. Biol. 163: 16.
Statistics Canada 2020. Table 32-10-0116-01 Supply and disposition of mink and fox on fur farms. – <https://doi.org/10.25318/3210011601-eng>.
Steenweg, R. J. et al. 2011. Seasonal and age-dependent dietary partitioning between the great black-backed and herring gulls. – Condor 113: 795–805.
Tyson, C. et al. 2015. Individual specialization on fishery discards by lesser black-backed gulls *Larus fuscus*. – ICES J. Mar. Sci. 72: 1882–1891.
Verschuren Centre. 2017. Resolution of Mink Waste Management – fermentation and digestion methods to resolve mink waste management issues. – Verschuren Centre for Sustainability in Energy and the Environment, Cape Breton Univ., Sydney, NS, Canada.
Vidal, E. et al. 1998. Is the yellow-legged gull a superabundant bird species in the Mediterranean? Impact on fauna and flora, conservation measures and research priorities. – Biodiv. Conserv. 7: 1013–1026.
Weimerskirch, H. 2007. Are seabirds foraging for unpredictable resources? – Deep-Sea Res. II Top. Stud. Oceanogr. 54: 211–223.
Weseloh, D. V. et al. 2020. Herring gull *Larus argentatus*, ver. 1.0. – In: Billerman, S. M. (ed.), Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA.
Whittam, R. M. and Leonard, M. L. 1999. Predation and breeding success in roseate terns *Sterna dougallii*. – Can. J. Zool. 77: 851–856.
Wilhelm, S. I. et al. 2016. Large-scale changes in abundance of breeding herring gulls *Larus argentatus* and great black-backed gulls *Larus marinus* relative to reduced fishing activities in southeastern Canada. – Waterbirds 39: 136–142.
Winton, R. S. and River, M. 2017. The biogeochemical implications of massive gull flocks at landfills. – Water Res. 122: 440–446.
Zelenskaya, L. A. and Khoreva, M. G. 2006. Growth of the nesting colony of slaty-backed gulls *Larus schistisagus* and plant cover degradation on Shelikan Island (Taui Inlet, the Sea of Okhotsk). – Russ. J. Ecol. 37: 126–134.

Supplementary material (available online as Appendix wlb-00804 at <www.wildlifebiology.org/appendix/wlb-00804>). Appendix 1.