Movement Ecology

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Spatial and temporal predictability drive foraging movements of coastal birds

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Abstract

Background Temporal and spatial predictability of food resources are critical to the foraging efficiency of central place foragers. While site fidelity is often assessed in this context, route fidelity, or the repeated use of the same path while traveling, and temporal aspects of habitat predictability have received less attention. We examined how the use of urban, coastal, and offshore habitats influenced spatiotemporal predictability in the foraging patterns of herring gulls (*Larus argentatus*) and great black-backed gulls (*L. marinus*). Since gulls show higher site fidelity when foraging in urban habitats, we predicted that these trips would also show higher route fidelity. Similarly, we predicted that gulls foraging in coastal habitats would adapt the timing of foraging trips relative to tides.

Methods We analyzed GPS tracks of herring gulls (n = 79) and great black-backed gulls (n = 37)—between 2016–2022 from four nesting colonies whose surrounding areas varied in their degree of urbanization. Fréchet distance, which is defined as the repeated use of the same path while traveling, was used to assess route fidelity, within colonies and between habitat types. We also compared the consistency of foraging trip timing relative to tidal stage and day of week, respectively, across habitat types.

Results Neither herring nor great black-backed gulls showed higher route fidelity in urban habitats. Herring gulls showed direct travel between urban foraging sites but revisited sites in different orders, suggesting that a mosaic map may be used to navigate between known urban foraging sites. Herring and great black-backed gulls that foraged at coastal sites exhibited patterns in trip timing in relation to the tidal cycle, with foraging primarily occurring at or around low tide. Herring gulls in urban environments foraged more on Fridays and weekends, possibly due to increased or altered human activities on these days.

Conclusions Our results demonstrate the importance of spatial memory and spatiotemporal predictability of gull foraging habitats and highlight the extent to which gulls adjust their movements based on their foraging habitats.

Keywords GPS tracking, Fréchet distance, Great black-backed gull, Herring gull, *Larus argentatus*, *Larus marinus*, Route fidelity, Seabirds, Tidal patterns

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Background

Resource availability is a major driver of animal movement across taxa and ecosystems [9, 33, 49]. Marine resources in particular are often distributed in heterogeneous patches in space and time [64, 95], though more permanent features such as reefs, steep bathymetric gradients, and tidally- or bathymetry-driven fronts can create predictable foraging areas for marine predators [17, 21, 53, 58, 61, 98]. Returning to predictable foraging areas can increase foraging efficiency by allowing animals to minimize the energetic costs of foraging, thus positively influencing their survivorship and reproductive success [54, 76]. A range of marine predators show site fidelity to foraging habitats [57, 82, 99], with higher fidelity occurring in more spatially predictable sites [7, 53, 75]. However, the role of route fidelity, defined here as the repeated use of the same path while traveling, in maintaining foraging efficiency is less clear. Assessing the extent to which route fidelity occurs in animals could provide insights into the cues, features, and mechanisms used to navigate landscapes and the energetic benefits of foraging in predictable areas.

Studies of route fidelity in animals have largely focused on the flexibility of migratory movements and how route fidelity can be impacted by individual learning [13, 18], visual landmarks [4], or the spatial heterogeneity of the area an individual is traveling through [5, 42, 43]. Individual migrating birds often use similar flight paths across trips that is distinct from other migrating individuals [25, 105], suggesting individuals develop their own preferred path [105]. In resident bird species, such as homing pigeons (*Columba livia domestica*), route fidelity can occur on a localized scale of up to several kilometers [6, 33, 59, 72]. Individuals use consistent routes between foraging areas [40, 61, 71] and animals may use visual cues to navigate between spatially or temporally dependable foraging areas [100, 104]. During high-energy investment periods like the breeding period, repeatably using the same foraging route could decrease energetic costs for adults [74] but could also reduce the ability to search for new foraging areas.

In seabirds, temporal predictability in foraging habitats can also allow birds to optimize their time spent time foraging to reduce energetic costs [19]. Variations in tidal height and tidal currents can create temporally predictable fish and zooplankton aggregations which can be exploited by foraging seabirds [22, 41, 44, 91, 107]. Further, urbanized and industrialized areas create foraging habitats that are fixed in space and can be highly predictable in time [34, 50–52, 86]. Assessing how seabirds optimize the timing of foraging trips and routes taken to travel to foraging areas could further our understanding of the implications of predictability for foraging ecology and energetics, and for adaptation in the face of rapid urbanization.

Gulls (genus *Larus*) present ideal species for assessing how predictable foraging areas across various habitat types, including littoral, urban, and offshore habitats, influence route fidelity during the breeding season [20, 29, 50, 86]. The ability of gulls to navigate through urban environments can be assessed, as birds are known to return to the same locations repeatedly when foraging [24, 40, 50, 86, 97, 100]. Foraging in urban environments may influence route fidelity, as birds may increase foraging efficiency by taking the same path repeatedly to and from predictable resources. However, since many gulls forage in both coastal and urban areas [50, 86, 97], the timing of foraging trips may also reflect the predictability of different sites, as seabirds foraging in tidally driven areas focus foraging efforts during times of high prey accessibility [44, 46, 60, 96, 107, 108].

We assessed whether spatial and temporal consistency in foraging patterns vary with habitat type. We predicted that (i) there is a greater degree of route fidelity in urban foraging sites than in coastal and pelagic ones; and (ii) the timing of gull foraging trips depends on tide cycles, when birds are foraging in coastal and pelagic habitats, and on day of the week, which can influence human activities.

Methods

Species

Herring and great black-backed gulls (*Larinus argentatus and L. marinus*, respectively) are central place foragers (when birds are spatiotemporally constrained to a nesting site, and so return to the same place after every foraging trip) during the breeding season, making them ideal for exploring the effects of spatial and temporal predictability within their foraging areas. Herring gulls are widely distributed throughout North America [101], while great black-backed gull distributions are restricted to the east coast of North America [38]. Both species breed from April to June and can nest in a variety of coastal and urban habitats [66]. Herring and great black-backed gulls feed on fish, crustaceans and mollusks, and urban sources of food such as refuse from landfills or dumpsters [38, 95]. However, herring gulls primarily rely on anthropogenic food sources in urban areas and feed on coastal and pelagic food sources at more remote colonies, while great black-backed gulls feed primarily on coastal and pelagic food sources at both urban and more remote colonies [50, 51]. Herring gulls exhibit higher foraging site fidelity in urban environments than those that forage in coastal or pelagic habitats [34, 50, 51].

Study sites

Herring and great black–backed gulls were tracked from four colonies located on coastal islands along an urban gradient in the northeast United States: Little Egg Island in Jamaica Bay Wildlife Refuge, Young's Island, Muskeget Island, and Tuckernuck Island (Fig. 1). Jamaica Bay and Young's Island are the most urbanized of the four colonies, as they are either within or directly adjacent to highly urbanized areas [34]. Little egg Island in Jamaica Bay is located within the largest city in the US, New York City in the Brooklyn borough, which has a human

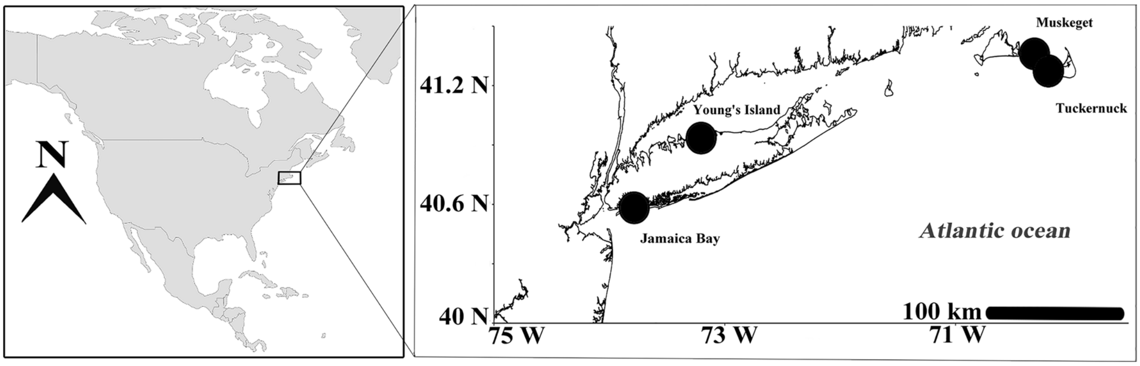

Fig. 1 Location of four study colonies In New York and Massachusetts on the east coast of the United States. The extent of the detailed map is shown within North America on the left

population of 2,641,052 people and a human population density of 39,437 people per square mile [94]. Young's Island is a 21-acre island within Suffolk County, NY which has a human population of 1,525,465 and a human population density of 1647 people per square mile [94]. Muskeget and Tuckernuck are the least urban of the four study sites and are located off the coast of Nantucket Island; Muskeget is an uninhabited island. Tuckernuck, located 1.6 km from Muskeget, is partially comprised of a land trust, and has a small number of vacation homes (approximately 35) which are unoccupied for most of the year. While both herring and great black–backed gulls nest at all four study sites, great black–backed gull data were only collected from Muskeget and Young's Island. There was no overlap in foraging areas used from Young's Island and Jamaica during incubation, but habitats used by gulls foraging from Muskeget and Tuckernuck did show some overlap given the close proximity of these study sites. Previous studies have highlighted species- and colony-level differences in foraging behavior between these colonies [18, 50, 51].

Tag deployments

Gulls were captured at study colonies with noose carpets and bow-net traps from late April to early June, coinciding with the incubation period. IgotU GT-120 (Mobile Action technologies, Taiwan) and Catlog Generation 2 (Catnip Technologies, Hong Kong) GPS loggers were used to track foraging movements of gulls. GPS loggers were attached with Tesa Tape (Tesa Tape, Inc., NC) to the central 3–4 tail feathers. Every device was equivalent to 1 – 2% of the tagged individuals body mass, well below the 3% threshold above which device effects can become apparent in pelagic seabirds [73]. Tags were programmed to take positional data (latitude and longitude) at an interval of 2 min and were deployed for at least 5 days (with an average 7.5 days ± 3.39 days) prior to recapture.

All animal handling and sampling were approved by Stony Brook University's Institutional Animal Care and Use Committee (IACUC number 875550). GPS tagging was conducted with State (New York State Department of Environmental Conservation number 2035; Massachusetts Wildlife number 018.22BB) and Federal (Federal Bird Banding number 22795 all to R.R. Veit) banding permits. Approval to access Jamaica Bay was given by the National Park Service (Permit number GATE-2017-SCI-0020) and Young's Island access was approved by the New York Department of Environmental Conservation (Temporary Revocable Permit numbers 2018–001; 2019–002; 2020–01; 2021–01; 2022–01). We received approval from the land owner to access the study site Muskeget.

Analysis of foraging trips

Foraging trips were defined as trips of at least 30 min in duration that extended at least 0.5 km away from the colony to avoid including within–colony movements in analyses [104]. We included individuals with six or more foraging trips in our analyses to ensure that individual variability in habitat use was sufficiently represented [89].

Foraging locations were identified by quantifying ARS (Area Restricted Search) behavior using First Passage Time (FPT) analysis, which is the amount of time required for an animal to cross a circle with a given radius [30]. To reduce autocorrelation, we sequentially identified the GPS point with the maximum FPT value for a given radius and excluded all points within 2 × the radius until the entire trackline was adjusted [87]. After adjusting for autocorrelation, points with the upper quartile of FPT values along each track line were considered ARS locations. We observed some individual trips (n = 4 individuals; n = 8 foraging trips) where a small subset of foraging points was observed moving slowly in a straight line, appearing to result from either natural drifting of the bird on the surface of the water or from sitting on a moving boat. In these instances, only the first coordinate point of that sequence was used.

Satellite imagery from ArcGIS (ESRI version 10.61) was used to classify foraging points as urban, coastal, or offshore. All points that occurred in urban habitats (e.g. shopping centers, landfills) were classified "urban", points that occurred in beaches, inlets or in coastal marshes were classified "coastal", and all points at least 10 m from the shoreline were classified as "offshore". All foraging trips were classified as either urban, coastal, or offshore if all foraging points during that trip occurred in only that habitat type (e.g., if all foraging points occurred in urban habitats, then the trip was considered "urban"). If a trip's foraging points occurred in more than one habitat type, then the trip was classified as occurring in multiple habitat types.

We calculated the total distance traveled (in kilometers) of every trip for every individual, and then averaged across individuals to find the colony average. The average total trip duration (in minutes) was calculated by averaging the total duration of trips for every individual, and then averaging across individuals to find the colony average. Previous studies conducted using these data have found that year did not significantly impact habitat use or diet [50, 51], and we therefore pooled data from all years in analyses.

Habitat use relative to tidal cycles and day of week

We assessed whether the timing of gull foraging trips in different habitats is influenced by the tidal cycle using data taken from the closest tidal station (National Oceanic and Atmospheric Administration, Washington, DC) for each trip. We used tidal data from Port Jefferson station 8514560 and Norton Point station 8516891 [67] to approximate time of high tide for Young's Island and Jamaica Bay, respectively. The Nantucket Sound has a complicated geography that leads to temporal lags in tidal cycles. Thus, for Tuckernuck and Muskeget trips, four tidal array stations were used: Boston station 8443970, Wasque Point station 8448683, Hyannis Port station 8447605 and Nantucket Island station 8449130 [67]. Fine scale differences in tides were estimated by adjusting time of high tide for foraging points based on their location around Tuckernuck and Muskeget using tidal array information from Limeburner & Beardsley [55]. Tidal data were used to bin foraging points relative to high tide within two hour periods that were defined as follows: low tide = 1 h before and after low tide; flood tide 1 = 1–3 h after low tide; flood tide 2 = 3–5 h after low tide; high tide = 1 h before and after high tide; ebb tide1 = 1–3 h after high tide; and ebb tide 2 = 3–5 h after high tide.

To assess tidal patterns in habitat use, we examined the average proportion of foraging points across individuals occurring throughout the tidal cycle for different habitat types. We then constructed rose plots showing the number of foraging points occurring both relative to tidal time and to time of day. Rose plots were constructed using the R package `*circular*` [2] to account for the circular shape of the data, as tides and time of day occur cyclically. Rose plots along with assessments of mean values of the proportion of foraging points occurring in each temporal period were used to determine which times of day and tidal times were preferentially used by herring and great black-backed gulls across colonies.

To examine whether gulls showed temporal variability in foraging behavior that might be related to changes in human activities, we calculated the average proportion of foraging points across individuals occurring on each day of the week. However, the number of GPS tracking points for each day of the week may have been biased based on the timing of tag deployments (e.g., often multiple tags were deployed on the same day). To account for this potential bias, we used a Chi-square test for each species and colony to assess whether the distribution of foraging events by day of the week differed from the distribution of tracking data by day of week. We compared the average number of foraging points observed across individuals on each day of week and habitat type to the number that would be expected if the distribution of foraging points followed the distribution of GPS points by day of week.

Analysis of Fréchet distance

We used Fréchet distance [23] to quantify route fidelity using tracks along entire foraging trips. The Fréchet distance is a metric that measures the similarity between two curves and can compare curves of different lengths and durations. The Fréchet distance is calculated by continuously measuring across two different curves to generate many maximum distance values, and the smallest of these maximum values is the Fréchet distance [27]. This method is useful for assessing route fidelity because it can compare the trajectories (paths through space and time) of birds, whose movements are often complex and varied in length [56, 85]. Further, Fréchet distance considers the directionality of a path, making this metric suitable for assessing the relationship between route fidelity and site fidelity.

Fréchet distance is sensitive to the start and endpoint of a trajectory [11]. We standardized all foraging trips to remove any bias from slight deviations in start and end points of trips within the colony by averaging the nest location coordinates that were recorded upon initial capture to calculate the nest centroid.

Fréchet distances were then calculated using the R package '*Similarity Measures*' [91]. Higher Fréchet values indicated lower route fidelity while lower Fréchet values reflected higher route fidelity [11]. Fréchet distances were calculated for all possible combinations of pairs of trips. It is logical that longer trip distances could result in higher Fréchet values, since trips to multiple distant sites can inherently differ more in distance than those to more proximate sites. To remove the effect of distance on the Fréchet value, the Fréchet distance was divided by the average of two trip distances. Justification and effectiveness of this method can be found in supplementary Table 1.

Distance-standardized Fréchet distances (hereafter Fréchet distances) were compared within- versus between-individual gulls using a permutation approach as in Ramellini et al. [74], as Fréchet values were not normally distributed. Permutations were run in the *Permuco* package in R [32] with 2000 iterations. Between-individual variability was calculated by randomly selecting six trips from every bird within a colony so that each individual was equally represented. Within-individual variability was calculated by comparing all trips within a bird to each other. To assess whether Fréchet distances differed significantly within- versus between- individuals for specific habitat types, we assessed within- versus between-individual route fidelity within each habitat type (Multiple habitats, Coastal, Urban and Offshore) for both herring and great black-backed gulls using the permutation approach. To account for four multiple comparisons we used the Bonferroni correction factor, given the four different habitat types (alpha threshold was set to $1.25e-2$).

In addition, we compared all Fréchet distances across habitat types using analysis of variance models (AOVs), in which each data point reflected a pair of trips. AOVs were constructed separately for the two species. Since pairs of trips could not be assumed to be independent (e.g., high route fidelity in a habitat type would infer similarity between all trips in that habitat type), we compared mean Fréchet distance across habitat types using the individual mean in each habitat type. Fréchet values were square root transformed to achieve a normal distribution and homoscedastic variance. We also compared mean trip distance and duration between habitat types to assess whether route fidelity was associated with lower search effort. Since foraging is often dominated by a particular habitat type at a given colony [34, 50, 51] (Supplementary Table 3), foraging across all habitat types cannot be observed within colonies. It was therefore necessary to pool data from across colonies in order to examine the effect of habitat type on route fidelity or trip metrics across all habitat types. We note that while colony influences the extent to which birds are using different habitat types, this does not infer that predictability of foraging trips *within* these habitats is different between colonies. For all AOVs, we conducted a post-hoc comparison of marginal means using a post – hoc Tukey correction to account for multiple comparisons, given the six different habitat type combinations. All analyses were conducted using R (version 2023.03.1).

Results

Foraging trip metrics of herring and great black-backed gulls during nesting

Herring and great black-backed gulls across all colonies typically took 1–2 foraging trips (1.70 ± 0.71) per day during incubation (trip metrics by colony shown in Supplementary Table 3). At the two colonies where both species were tracked (Young's Island and Muskeget), herring gulls generally took foraging trips that were longer in duration than great-blacked backed gulls, though trip distances were similar between species (Supplementary Table 3). Foraging trips had similar trip distances across urban colonies but were longer in duration on average at the less urban colonies (Tuckernuck and Muskeget) for herring gulls.

Use of coastal, urban, and offshore habitats

At Young's Island and Jamaica Bay, a high proportion of herring gull foraging trips were in urban habitats (Supplementary Table 2). At Tuckernuck and Muskeget, nearly half of herring gull trips took place in offshore habitats (Supplementary Table 2). Great black-backed gulls at Young's Island used a variety of habitats compared to great black-backed gulls at Muskeget, where almost all foraging trips took place in offshore areas (Supplementary Table 2).

Within vs. between individual comparisons of route fidelity

For both herring and great black-backed gulls at all colonies, Fréchet distances were significantly lower within- vs. between-individuals when considering all trips (Table 1). Herring and great black-backed gulls showed significant differences in Fréchet distances within- vs. between-individuals across most habitat types. However, foraging trips in offshore and multiple habitat trips were variable; for offshore foraging trips, gulls at Muskeget showed significant differences in Fréchet distances within- vs. between-individuals, but those at Young's Island and Tuckernuck did not. For foraging trips using multiple habitat types, Fréchet distances were significantly different within- vs. between-individuals at Young's Island, and for herring gulls at Tuckernuck and Muskeget. However, Fréchet distances for trips using multiple habitat types did not differ significantly within vs. between individuals for great black-backed gulls at Muskeget, and were of borderline

Table 1 Summary of results of the permutation ANOVA assessing within vs. between individual Fréchet distances

Comparison	Number of Birds	Number of Trips	T-statistic	*P*-value
Herring gulls				
Young's Island				
All Trips	38	17766	7.41	<< **0.0001**
Urban Trips	37	5460	7.23	< **0.001**
Coastal Trips	21	528	4.49	< **0.001**
Offshore Trips	2	6	0.24	0.81
Trips Using Multiple Habitats	38	11772	3.81	< **0.001**
Jamaica Bay				
All Trips	21	4950	8.37	<< **0.0001**
Urban Trips	15	595	1.91	0.056
Coastal Trips	10	105	3.65	< **0.001**
Offshore Trips	2	1	NA	NA
Trips Using Multiple Habitats	20	4249	1.94	0.05
Tuckernuck				
All Trips	7	528	3.66	< **0.001**
Urban Trips	NA	NA	NA	NA
Coastal Trips	NA	NA	NA	NA
Offshore Trips	6	105	1.75	0.08
Trips Using Multiple Habitats	7	423	2.14	< **0.001**
Muskeget				
All Trips	14	1770	7.07	< **0.001**
Urban Trips	NA	NA	NA	NA
Coastal Trips	NA	NA	NA	NA
Offshore Trips	11	496	3.62	< **0.001**
Trips Using Multiple Habitats	13	1274	6.62	< **0.001**
Great black-backed gulls				
Young's Island				
All Trips	23	6105	11.49	< **0.0001**
Urban Trips	3	45	4.04	< **0.001**
Coastal Trips	15	300	2.01	< **0.001**
Offshore Trips	10	190	1.49	0.14
Trips Using Multiple Habitats	23	5570	9.56	< **0.001**
Muskeget				
All Trips	14	1830	4.91	**< 0.001**
Urban Trips	NA	NA	NA	NA
Coastal Trips	NA	NA	NA	NA
Offshore Trips	14	1653	4.64	**< 0.001**
Trips Using Multiple Habitats	13	177	0.88	0.38

"All trips" represents the total number of birds tracked, and the total number of foraging trips observed across all habitats. Each test involved 2000 permutations. To calculate the test statistic, the numerator is 1 for all tests, and the denominator is n – 2. Colonies that had ≤ 2 individuals and ≤ 5 trips in a particular habitat did not have sufficient data for comparisons and are marked with NA. Multiple comparisons were corrected using the Bonferroni inequality as (0.05/4) and values shown in bold were significant at $p < 0.0125$

significance ($p = 0.50$) for herring gulls at Jamaica Bay. While trips in urban habitats generally showed differences in Fréchet distances within- vs. between-individuals, differences were not significant for herring gulls foraging in urban habitats at Jamaica Bay ($p = 0.056$). Due to random sampling of six trips from each individual and the limited number of trips using certain habitats, some habitat types could not be assessed using this approach. These included trips occurring in offshore habitats at Jamaica Bay, trips occurring in urban and coastal habitats at Tuckernuck and Muskeget for herring gulls, and trips occurring in urban and coastal habitats at Muskeget for great black-backed gulls (shown as Nas in Table 1).

Route fidelity and trip metrics relative to habitat type

We found limited evidence of differences in route fidelity between habitat types. For herring gulls, Fréchet distances were significantly higher on trips using multiple habitats than in trips using exclusively offshore, coastal or urban habitat types, reflecting lower route fidelity (Fig. 2, Table 2). Great black-backed gulls showed no difference in Fréchet distance between the habitat types, reflecting similar route fidelity across habitats (Fig. 2, Table 2). In contrast, we found that coastal habitats showed lower trip distance and duration for both species; for herring gulls, these metrics were significantly lower in coastal habitats than in all other habitats, while for great black-backed gulls, these metrics were lower in coastal habitats than in mixed habitats (Supplementary Fig. 1).

Timing of foraging trips by habitat type relative to tides

Herring gulls foraged in coastal habitats from Young's Island most frequently during and after low tide (Fig. 3). Coastal foraging trips of herring gulls at Jamaica Bay occurred most frequently before and during low tide. Herring gulls foraging in coastal habitats at Tuckernuck and Muskeget did not show clear patterns relative to tides. Herring gulls foraging in offshore habitats at Muskeget foraged somewhat more often during and around high tide, while those at Tuckernuck foraged most often during flood tide 2 and ebb tide 2 (Fig. 3). Foraging trips in urban habitats at Young's Island occurred most often at and around high tide, while those at other colonies did not appear to show tidal patterns at any of the study colonies.

Great black-backed gulls at Young's Island foraged in coastal habitats most frequently at and around low tide (Fig. 4), as did those foraging in offshore habitats. At Muskeget, offshore foraging dominated foraging trips of great black-backed gulls and occurred most frequently from flood tide through high tide (Fig. 4). Other foraging trips for great black-backed gulls did not show a clear pattern relative to tides.

Timing of foraging trips by habitat type relative to day of week

Herring gulls showed variability in the timing of foraging trips relative to day of week (Supplementary Fig. 2). Herring gulls tracked from urban colonies (Young's Island and Jamaica Bay) foraged in urban habitats more often on Fridays and weekends. Herring gulls at Jamaica Bay also foraged in coastal habitats more often on Fridays and weekends. Trends in herring gull habitat use relative to day of week were less evident at the more remote colonies (Muskeget and Tuckernuck), although there was some evidence for increased foraging in offshore habitats on weekends at these colonies (Supplementary Fig. 2). The results of the Chi – Squared test reflected these results, as the number of observed foraging points differed significantly from the expected if the observed number of foraging points followed the distribution of GPS points based on day of week.

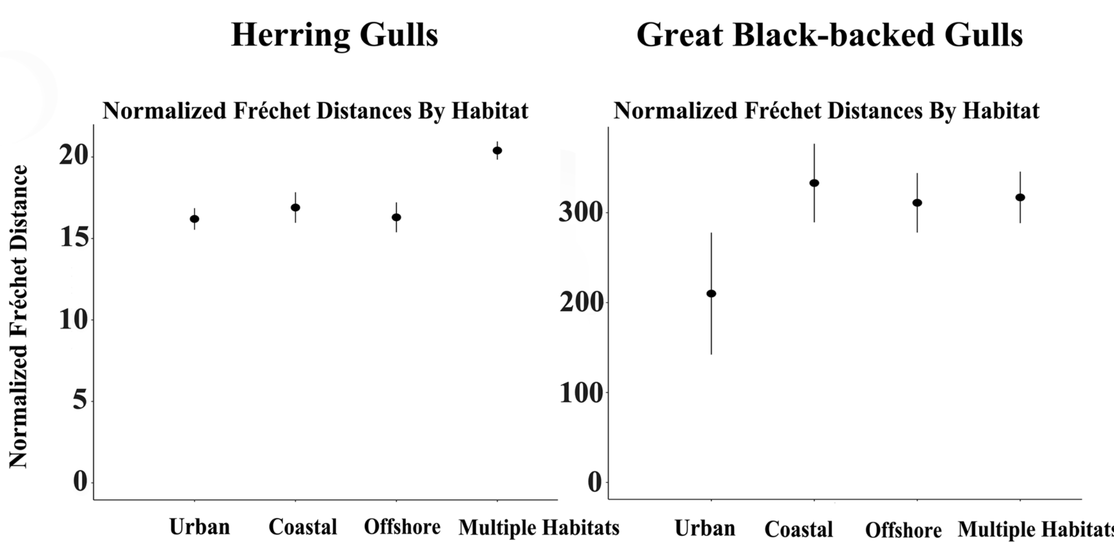

Fig. 2 Fréchet distances for herring gulls (left) and great black-backed gulls (right) foraging in different habitats from AOVs accounting for colony effects. Values reflect means ± standard error. Urban (coastal/offshore) habitats reflect foraging trips in which birds were exclusively foraging in urban (coastal/offshore) habitats, while multiple habitats reflect foraging trips in which birds used multiple habitats. Note that lower Fréchet distances reflect higher route fidelity

Table 2 Results of a Tukey post – hoc multiple comparisons test of an AOV analysis comparing Fréchet distances for herring and great black-backed gulls foraging in different habitats

	Comparison	Value	Standard error	Degrees freedom	t-value	*P*-value
Herring gulls						
Fréchet Distance	Urban-Offshore	0.15	1.13	174	0.13	0.99
	Urban-Coastal	0.72	1.15	174	0.63	0.92
	Urban-Multiple	4.18	0.87	174	4.83	< **0.001**
	Coastal-Offshore	0.58	1.31	174	0.44	0.97
	Coastal-Multiple	3.45	1.09	174	3.17	< **0.01**
	Offshore-Multiple	4.03	1.07	174	3.76	< **0.01**
Trip Duration	Urban-Offshore	−13.30	19.20	990	−0.69	0.89
	Urban-Coastal	−69.20	15.10	990	−4.57	< **0.001**
	Urban-Multiple	82.10	11.80	990	6.95	< **0.001**
	Coastal-Offshore	−55.90	20.70	990	−2.70	< **0.001**
	Coastal-Multiple	151.30	13.80	990	10.96	< **0.001**
	Offshore-Multiple	95.40	16.70	990	5.69	< **0.001**
Trip Distance	Urban-Offshore	−5.99	3.46	990	−1.73	0.308
	Urban-Coastal	−19.16	2.72	990	−7.05	< **0.001**
	Urban-Multiple	14.12	2.12	990	6.53	< **0.001**
	Coastal-Offshore	−13.18	3.72	990	−3.54	< **0.001**
	Coastal-Multiple	33.28	2.48	990	13.42	< **0.001**
	Offshore-Multiple	20.11	3.01	990	6.69	< **0.001**
Great black-backed gulls						
Fréchet Distance	Urban-Offshore	100.86	75.40	62	1.34	0.54
	Urban-Coastal	122.49	80.70	62	1.52	0.43
	Urban-Multiple	106.72	73.60	62	1.45	0.47
	Coastal-Offshore	21.62	54.80	62	0.39	0.98
	Coastal-Multiple	−15.77	52.30	62	−0.30	0.99
	Offshore-Multiple	5.86	43.70	62	0.13	0.99
Trip Duration	Urban-Offshore	30.01	21.2	363	1.41	0.49
	Urban-Coastal	27.00	20.00	363	1.35	0.53
	Urban-Multiple	76.73	17.90	363	4.28	< **0.001**
	Coastal-Offshore	−3.01	17.50	363	−0.17	0.99
	Coastal-Multiple	49.73	13.20	363	3.78	< **0.001**
	Offshore-Multiple	46.72	14.10	363	3.30	< **0.001**
Trip Distance	Urban-Offshore	−1.30	4.17	363	−0.31	0.99
	Urban-Coastal	−5.99	3.93	363	−1.52	0.43
	Urban-Multiple	10.43	3.52	363	2.96	< **0.001**
	Coastal-Offshore	−4.69	3.43	363	−1.37	0.52
	Coastal-Multiple	−16.42	2.59	363	6.35	< **0.001**
	Offshore-Multiple	11.73	2.78	363	4.22	< **0.001**

Urban (coastal/offshore) habitats reflect foraging trips in which birds were exclusively foraging in urban (coastal/offshore) habitats, while multiple habitats reflect foraging trips in which birds used multiple habitats. Values shown in bold were significant ($p < 0.05$)

Great black-backed gulls showed less variability in the timing of foraging trips relative to day of the week than herring gulls (Supplementary Fig. 3), although at Young's Island coastal habitat use appeared to be higher on Sunday and Mondays. At Muskeget, herring and great black-backed gulls appeared to show contrasting patterns of habitat use relative to day of week; herring gulls primarily took offshore foraging trips from Sunday through Tuesday, while great black-backed gulls primarily took offshore foraging trips in the middle of the week (Supplementary Figs. 2, 3). The results of the chi-squared test broadly reflected these results; for all urban colonies,

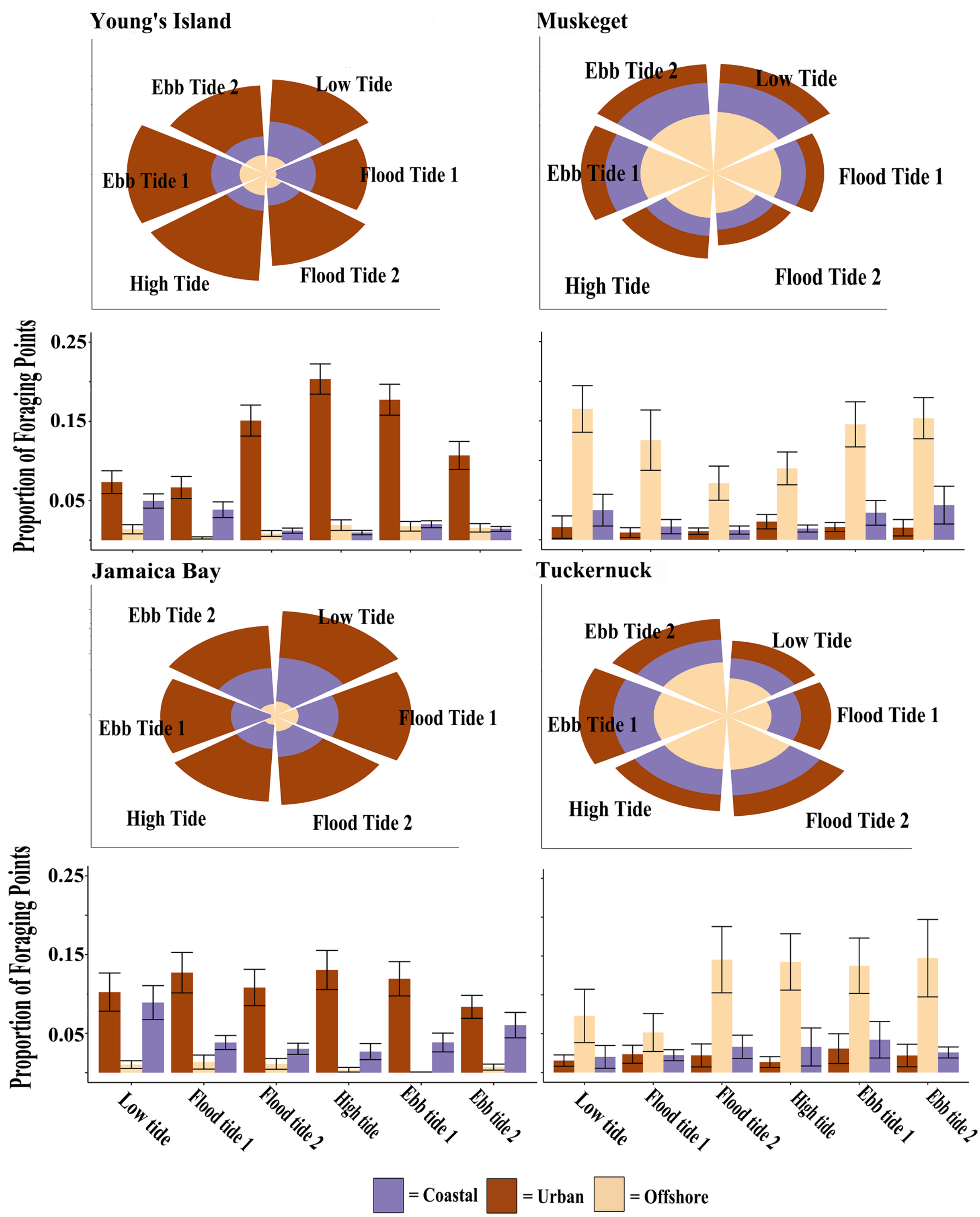

Fig. 3 Bar plots and stacked rose plots showing the average proportion of herring gull foraging points (± SE for bar plots) across individuals in each habitat type and tide time, and frequency of occurrence of foraging points in each two-hour tidal period within urban, coastal and offshore habitats across all individuals at Young's Island, Jamaica Bay, Muskeget and Tuckernuck, respectively. The tidal cycle is broken up into 2-h periods, low tide, flood tide 1, flood tide 2, high tide, ebb tide 1, ebb tide 2

the number of observed foraging points by habitat type differed significantly from that expected if the observed number of foraging points followed the distribution of GPS points based on day of week. In more remote colonies, differences between observed and expected distributions relative to day of week were only consistently significant for offshore habitats (Supplementary Table 5).

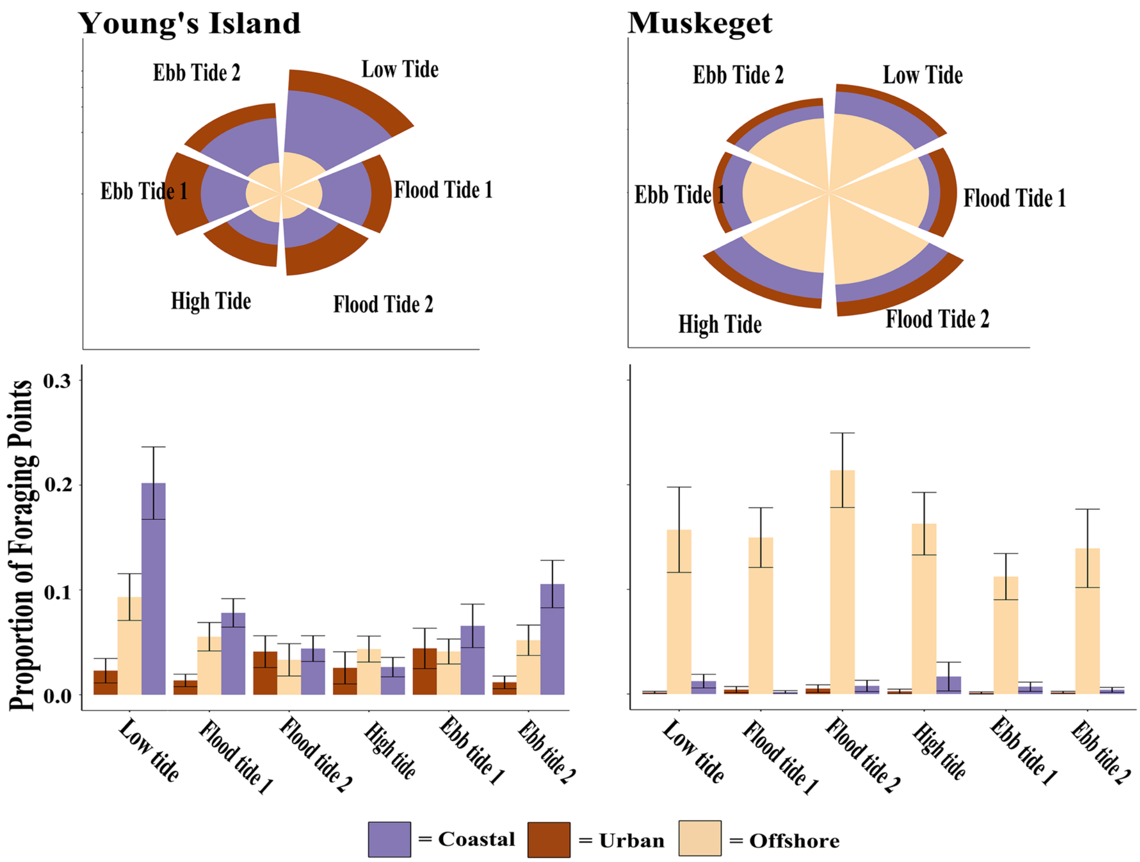

Fig. 4 Bar plots and stacked rose plots showing the average proportion (±SE) of great black-backed gull foraging points across individuals in each habitat type and tide time, and frequency of occurrence of foraging points in each two-hour tidal period within urban, coastal and offshore habitats across all individuals at Young's Island and Muskeget, respectively. The tidal cycle is broken up into 2-h periods, low tide, flood tide 1, flood tide 2, high tide, ebb tide 1, ebb tide 2

Discussion

Environmental predictability in space and time plays an important role in animal foraging ecology [26, 62, 78]. Using consistent routes to successful foraging areas may decrease the energetic costs of searching for prey [105]. Such route fidelity may be particularly beneficial during breeding when birds are spatially and temporally constrained to the breeding colony [75, 79, 98]. However, the relationship between predictability and route fidelity in foraging gulls was not consistent with our predictions. We expected to see the highest route fidelity in urban habitats, where herring gulls revisit fixed urban foraging sites such as malls or landfills [36, 53]. Instead, we found limited differences in route fidelity between habitat types and no evidence that gulls showed higher route fidelity in urban habitats. Herring gulls frequently used urban habitats during foraging trips from Jamaica Bay and Young's Island but showed limited route fidelity during these foraging trips. While individual herring gulls repeatedly visited specific urban foraging areas [34, 51], we found that individual birds sometimes revisited sites in different orders, and therefore use markedly different routes between foraging trips (Fig. 5). Further, while gulls foraging in other habitats (e.g., coastal habitats) often foraged in a few distinct regions (e.g., within two spatially separate inlets or beaches), urban foraging gulls often visited a larger number of spatially separated regions. The spatial predictability of urban habitats may allow gulls more flexibility in their foraging paths by taking more exploratory trips between spatially discrete sites. This, combined with the fact that gulls sometimes visited urban sites in different orders, could explain the fact that birds did not show high route fidelity in urban habitats despite showing high site fidelity [34, 51].

While great black-backed gulls also did not show evidence of higher route fidelity in urban habitats, only a small number of great black-backed gulls (N = 3) used urban habitats, with most great black-backed gulls foraging in offshore and multiple habitat types. In contrast, herring gulls had a comparable number of trips across trip types. Thus, comparisons of trip metrics and Fréchet

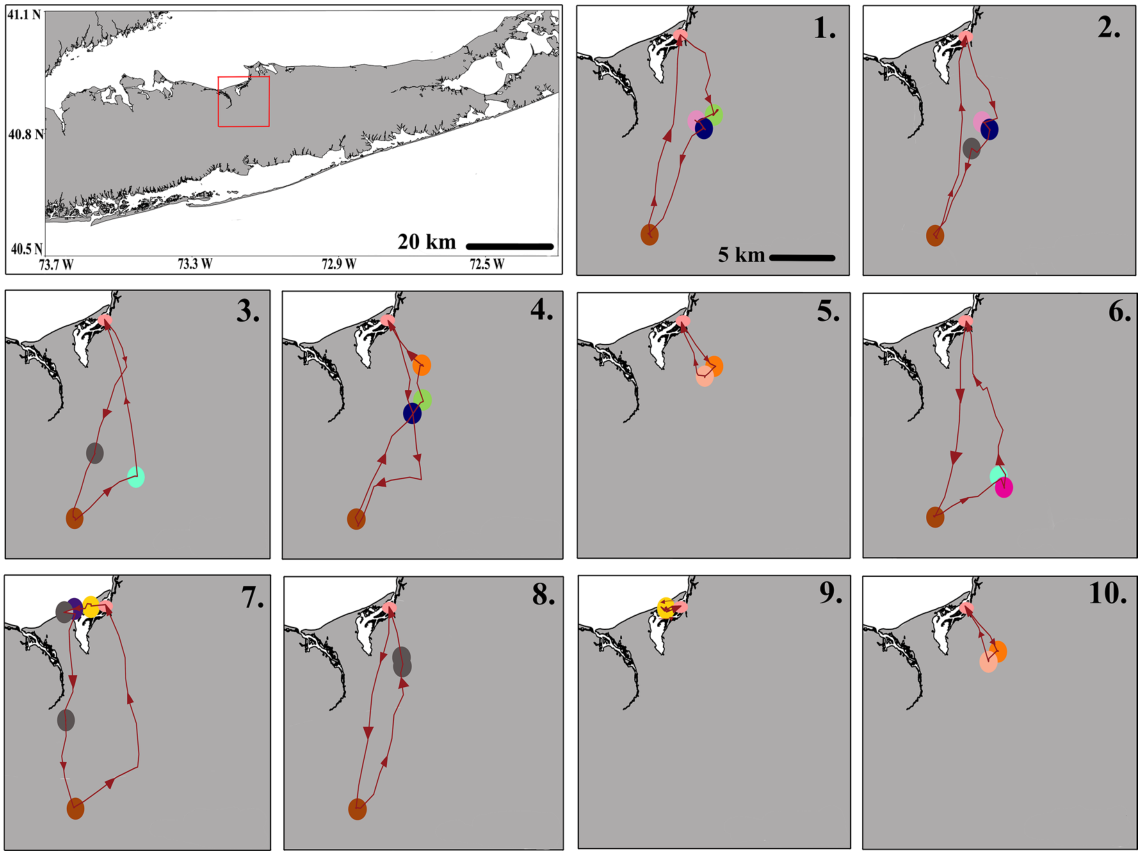

Fig. 5 Example of consecutive foraging trips (numbered 1–10) of a herring gull tracked at the Young's Island study colony. The extent of the foraging trip plots is shown in the map of Long Island, New York in the upper left of the figure. The tagged bird made repeat visits to several urban foraging spots, shown with colored circles. Foraging areas that were not visited repeatedly are shown in gray. Colony point colored pink. Arrows along tracks show the direction of travel

distances across habitat types for great black-backed gulls may be limited by sample size for this species.

In both herring and great black-backed gulls, individual birds used similar routes and showed directional travel to urban sites, despite visiting sites in different orders. Flexible foraging strategies may allow herring and great black-backed gulls to navigate effectively between urban foraging sites. Some seabirds, such as tube-nosed seabirds, are thought to heavily rely on olfactory cues for navigation [10, 13, 35] and sometimes locate foraging areas by following a gradient of olfactory cues [45, 64, 65]. It is unlikely that gulls use olfactory cues or stimulus gradients to navigate between urban foraging areas as gulls are not known to have a well-developed olfactory sense or rely on it for navigation of well-known areas [8, 31, 103], and usually navigate much smaller foraging areas than procellariforms. Gulls may instead be using visual landmarks to navigate urban foraging areas, potentially using piloting, or following a sequence of familiar landmarks to orient towards a goal [1, 12, 100]. Directional travel between urban foraging sites and the fact that herring gulls revisited sites in different orders and traveled in different directions to and from these sites suggests an understanding of spatial relationships of the landscape in relation to their colony—referred to as a mosaic map [1]. There is evidence for the presence of mosaic maps in birds and bats. Bats take shortcuts to areas they consistently use and navigate back to their home range after displacement [84, 92] and Rufous hummingbirds, dark—eyed juncos and black—capped chickadees return regularly to the same foraging sites, but appear to rely little on spatial cues, route-based navigation, or piloting to do so [14, 15, 88]. Mosaic maps are not often assessed in seabirds [48], but our results suggest that herring gulls foraging in urban habitats may navigate between discrete foraging locations using a mosaic map. Spatial predictability of urban areas may facilitate an understanding of spatial relationships between foraging sites.

We found some evidence that foraging trips using offshore and multiple habitat types showed lower route fidelity. Offshore habitats are not static environments and prey resources are often patchy in space and time [63, 95], which may lead to lower predictability. When comparing across colonies, herring gulls showed lower route fidelity in foraging trips using multiple habitat types. Herring gulls may alter their foraging paths to take advantage of different habitat types if they experience limited foraging success in a given location or habitat type. However, the specific habitat types used during trips occurring in multiple habitats could influence route fidelity. For example, if a foraging trip primarily uses urban habitats but includes a small proportion of foraging in coastal habitats, it may have higher route fidelity than a trip that primarily uses offshore habitats and uses urban or coastal habitats to a lesser degree.

Gulls often showed more similarity in their individual routes in comparison to routes of other individuals within a colony. Even when overall route fidelity values were low, birds showed higher within- vs. between-individual route fidelity (e.g., significant within- vs. between- Fréchet values for trips using multiple habitats for herring gulls at all colonies aside from Jamaica Bay, even though Fréchet values were highest for trips using multiple habitats than for other habitat types). This highlights that even if individuals are showing comparatively low route fidelity in a particular habitat (relative to that observed in other habitat types), they may still show some consistency in their routes.

Repeatedly following similar paths while foraging may allow birds to increase foraging efficiency by decreasing search effort in space and time. However, we did not find a clear relationship between route fidelity and the distance or duration of foraging trips in different habitat types. Trip distance and duration were lower in coastal habitats in both species, though coastal habitats showed similar route fidelity to urban and offshore habitats. While herring gulls showed lower route fidelity in trips using multiple habitat types, foraging trips using multiple habitat types made up 33–50% of all foraging trips across colonies (Supplementary Table 4), highlighting the importance of these trips to the overall foraging strategy of this species. Importantly, a shorter foraging trip, or one with higher route fidelity, isn't necessarily a more successful one. Additionally, broad metrics of trip distance or duration might not accurately reflect time spent actively searching for resources. The availability of different habitat types at each colony would need to be assessed along with foraging success and search effort to more thoroughly understand the role of route fidelity in foraging efficiency.

In both coastal and offshore habitats at the more urban study sites, gulls showed associations with tides, broadly supporting our prediction. Associations were clearest in coastally feeding herring and great black-backed gulls from Young's Island, which often foraged at or around low tide. Both herring and great-blacked back gulls in our study areas eat intertidal organisms such as bivalves and crabs [6], and these species are likely easier to access around low tide. Similarly, in other regions, great black-backed gulls, Saunder's gulls, Olrog's gulls, glaucous-winged gulls and herring gulls have been recorded to concentrate their coastal foraging efforts at and around low tide, likely due to higher availability of prey like mussels or crabs in intertidal areas during low tide [28, 36, 47, 106, 107].In addition, tidally driven aggregations of prey in the water column could influence these foraging patterns [16, 44]. Tidal currents create foraging opportunities through upwelling, mixing areas or eddies [80, 83], which aggregate prey items near the surface at particular times of the tidal cycle [3, 16, 44, 90].

The timing of offshore foraging trips relative to tides varied between species and colonies. The presence of fishing vessels at certain times of day may influence offshore foraging, as gulls frequently feed on fisheries discards [18, 19, 37, 69, 93]. At Muskeget, herring and great-blacked backed gulls showed contrasting patterns of habitat use relative to tides; herring gulls primarily foraged offshore from ebb tide through low tide, while great black-backed gulls foraged offshore least often during ebb tide to low tide. Timing differences in trips relative to tides could be an example of resource partitioning in two species that share foraging grounds. Lato et al. [53] found that Muskeget herring gull regurgitants were dominated by longfin squid, and great black-backed gull regurgitants contained no squid despite similar spatial habitat use, and temporal differences in foraging could provide a mechanism for maintaining differences in diet. In addition, analyses of foraging trips relative to day of week suggested that these herring and great black-backed gulls may also be maximizing foraging effort on different days of the week. Temporal resource partitioning in seabirds can be on the scale of breeding seasons, where one species' season starts at the end of another species' season to avoid overlap [81] or when foraging at different times of day in the same area, seen in sympatric cormorants [59]. Resource partitioning can reduce antagonistic intraspecific interactions and competition for available prey. This is also seen in tidal features, as different prey types (Euphausiids, forage fish & zooplankton, among others) can be aggregated in different locations are exploited by different seabird species [16, 44].

We found that herring gulls in urban environments forage more often on Fridays and weekends, possibly due to increased or altered human activities on these days. For example, birds feeding at shopping malls might take advantage of increased refuse available during busy weekend shopping days. Previous studies have found that yellow-legged gulls, lesser black-backed gulls, and herring gulls time foraging behavior depending on day of week, with weekend foraging occurring in anthropogenically—influenced habitats like landfills and parks and weekday foraging coinciding with commercial fishing vessel trips and school recesses [39, 70, 86, 93]. It is possible that to increase foraging efficiency in urban habitats, gulls are coordinating foraging times with human activity when not foraging in tidally—driven areas. This further emphasizes the ability of herring and great black-backed gulls to adjust their foraging strategy and schedule in accordance with habitat type.

Our analyses included some limitations. We did not collect data on the sex of tagged birds, which could have influenced our results. Previous studies have highlighted differences in trip distances and durations varied based on sex [77, 98], as well as differences in habitats used between sexes [68, 102]. We assumed that trips more than a half kilometer outside of the colony and lasting >20 min were foraging trips, and shorter, inter-colony movements were not considered. Thus, any fine-scale foraging patterns occurring in close proximity to the colony, were not included in our analysis. Additionally, when conducting the AOV analysis comparing Frechet distances across habitat types, we had to pool data from across colonies as there were no colonies in which all habitat types were well represented. However, it is possible that route fidelity may vary between colonies, and this represents a potential limitation that could not be addressed within the present study. Lastly, while our results highlight the presence of route fidelity and foraging behavior during incubation, but may not reflect the foraging behavior of gulls after chicks hatch, or outside of the breeding season.

Our results highlight how animal cognition, movement abilities, and predictability of foraging habitats in both space and time together can influence movement patterns [80]. Gulls repeatedly returned to the same foraging areas in urban habitats and foraged consistently relative to tides in coastal habitats. However, tracks of consecutive herring gull foraging trips in urban habitats highlighted a mismatch between site fidelity and route fidelity; birds appear to have learned spatial relationships between urban foraging sites and transit directly between them, though often not in the same order, and thus showed similar route fidelity to birds foraging in other habitats in spite of higher site fidelity. Spatial memory and the predictability of foraging habitats play an important role in the foraging efficiency of birds when spatially constrained during breeding. For species that can adapt to urbanization, the use of fixed urban foraging areas may facilitate navigation between multiple foraging areas and can create novel movement patterns.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40462-025-00531-y.

Supplementary Material 1.

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Author contributions
MF and LT conceived of the study. LT, MF and KL led field studies. RV assisted with field studies. MF conducted analyses and prepared Figs. 1–5 with support from LT and KL. RC contributed to statistical analyses. All authors contributed to the preparation, review and editing of the manuscript.

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Availability of data and materials
GPS data used in this study are available from Open Science Framework: https://doi.org/https://doi.org/10.17605/OSF.IO/N68XA. Fréchet data used in this study are available from Open Science Framework: https://doi.org/https://doi.org/10.17605/OSF.IO/XF29P.

Declarations

Ethics approval and consent to participate
All animal handling and sampling were approved by Stony Brook University's institutional Animal Care and Use Committee (IACUC number 875550).

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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