Different individual-level responses of great black-backed gulls (*Larus marinus*) to shifting local prey availability

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Short title: Individual response differ between prey availability

Abstract

To grow, survive and reproduce under anthropogenic-induced changes, individuals must respond quickly and favourably to the surrounding environment. A species that feeds on a wide variety of prey types (i.e. generalist diet) may be comprised of generalist individuals, specialist individuals that feed on different prey types, or a combination of the two. If individuals within a population respond differently to an environmental change, population-level responses may not be detectable. By tracking foraging movements of eight great black-backed gulls (*Larus marinus*), a generalist species, we compared group-level and individual-level responses to an increase in prey biomass (capelin; *Mallotus villosus*) during the breeding season in coastal Newfoundland, Canada. As hypothesized, shifts in prey availability resulted in significantly different individual responses in foraging behaviour and space use, which was not detectable when data from individuals were combined. Some individuals maintained similar foraging areas, foraging trip characteristics (e.g., trip length, duration) and habitat use with increased capelin availability, while others shifted foraging areas and habitats resulting in either increased or decreased trip characteristics. We show that individual specialization can be non-contextual in some gulls, whereby these individuals continuously use the same feeding strategy despite significant change in prey availability conditions. Findings also indicate high response diversity among individuals to shifting prey conditions that a population- or group-level study would not have detected, emphasizing the importance of examining individual-level strategies for future diet and foraging studies on generalist species.

Keywords: foraging behaviour, plasticity, individual, prey availability, capelin

Introduction

With exponential growth of the human population over the last century, wildlife faces reduced availability of pristine habitats and rapidly changing environmental conditions [1]. Individuals must respond quickly and favourably to these anthropogenic-induced changes for populations to persist. Phenotypic plasticity, or the variation in expression of a trait (i.e., physiological, morphological, behavioural) across environmental gradients [2], allows individuals to express traits that maximize fitness under varying environmental conditions [3,4] and in turn can help populations or species buffer against environmental change [5–8]. Alternately, plasticity may be limited, whereby there is a relatively stable expression of a trait by individuals across environmental gradients (i.e. specialization) [9]. Specialization may be favorable in stable environments and help to reduce intra-specific competition, whereby individuals only compete against others with similar trait expressions [6,10], but can also result in lower responsiveness to environmental change at the population level. Therefore, examining plasticity at the population level may mask important individual responses [11]. Studying plasticity at the individual level allows a greater understanding of the response diversity within a population and degree to which it can tolerate varying environmental conditions [12].

A species that feeds on a wide variety of prey types (i.e. generalist diet) may be comprised of generalist individuals, specialist individuals that feed on different prey types, or a combination of the two [13]. Under an increase in prey availability, generalist individuals would modify their foraging behaviour to take advantage of newly abundant resources, while the behaviour of specialist individuals should be unaffected [4,14]. Specialization, however, can be contextual, whereby a individual may be a specialist under stable conditions, but shifts to a

generalist strategy when conditions change (released from competition, increase in prey availability) [5,15]. Alternately, the behaviour of a non-contextual specialist would remain unaffected under shifting environmental conditions [5]. Many large gull species are dietary generalists at the population level [16,17] and prey availability has been shown to affect the diet and foraging behaviour of several gull species. For instance, previous studies have shown that gulls shift their diet to be primarily comprised of fish from other prey types [18–20], including fisheries offal [21], when natural fish prey abundance increases in the surrounding environment. Despite known flexibility in large gulls at the population level, individual-level differences in diet and foraging behaviour is also evident in many species [22–24], suggesting that gull populations are comprised of a combination of specialist and generalist individuals that respond to changing prey availability differently [11,25]. Given rapid anthropogenic-induced changes in marine environments, the degree of plasticity in marine predators, such as seabirds, in response to varying prey resources can have important conservation consequences.

The great black-backed gull (*Larus marinus*), commonly found on the coast of northeastern North America, is considered a dietary generalist species [17]. While great black-backed gulls mainly forage in marine environments by surface-feeding on pelagic fish [26,27], they also kleptoparasitize other seabirds, capture benthic invertebrates in coastal environments, and consume food waste at landfills [17,28,29]. great black-backed gulls also depredate seabird eggs, chicks and adults, resulting in low breeding performance of other seabird species [30,31]. Most studies of great black-backed gull resource use have focused at the population level [28,32,33], though a few studies have examined inter-individual differences in diet [25] and foraging movements [22,24,34]. The degree to which individual great black-backed gulls alter their foraging behaviour and diet in response to changing resource availability, however, is

unknown. In Newfoundland, Canada, a key forage fish, capelin (*Mallotus villosus*), migrates into coastal areas to spawn during the seabird breeding season, causing the inshore prey biomass to double upon arrival at inshore spawning sites [4,35,36]. This dramatic shift in prey availability results in population-level dietary shifts of other seabirds [4,20,21] and reduced seabird predation by gulls [30,31]. These prey dynamics also provide natural experimental conditions to improve our understanding of individual-level responses of great black-backed gull foraging behaviour and habitat use to changes in resource availability.

The goal of this study is to examine the degree to which studying population-level behavioural responses to changing prey biomass in Larids can mask important individual responses. To do this, we compare group-level and individual-specific responses in the foraging movements of great black-backed gulls to a 125% increase in prey biomass (capelin) during July-August, 2018 on the northeast coast of Newfoundland, Canada. We hypothesize that the foraging behavior responses of great black-backed gull to shifting prey (capelin) availability will vary among individuals, owing to inter-individual differences in foraging tactics shown previously for this species [22,25,34], but that a population-level response will be undetectable. Indeed, we predict that changing prey availability will result in divergent habitat use (i.e., marine, terrestrial/coastal, island) and foraging trip characteristics (i.e., trip length, distance from colony, duration) among individuals, whereby these measures may increase, decrease or remain unchanged to varying degrees, while the group-level response will show no statistical differences. As reduced fisheries activities and, thus, reduced supplemental food, have resulted in gull population declines in eastern North America [37,38], understanding individual responses of gulls to changes in natural prey availability will help better understand population-level responses to future changes in fisheries activities [39] as well as shifts in predation pressure on

other seabird populations, thereby informing population conservation and management of large gulls and other seabirds in coastal Newfoundland.

Methods

Study area and field work

During 2018, we captured adult great black-backed gulls during incubation ($n = 7$, June 10-11) and chick-rearing ($n = 1$, July 8, LGM02) from different nests using drop traps on North Cabot Island ($49^{\circ}10'30.67''\text{N}$; $53^{\circ}21'57.57''\text{W}$; Fig. 1) on the northeast coast of Newfoundland, Canada. This colony is located nearby localized areas of high density prey, including < 400 m from a colony of Common Murres (*Uria aalge*) on South Cabot Island ($\sim 10\,000$ pairs) [40], where gulls have been observed to depredate eggs and chicks, and < 10 km from a cluster of annually-persistent capelin spawning sites (Fig. 1) [41] and 9.9 km from shore. Upon capture, we recorded bill depth at gonys and total head length (mm) to determine sex based on a discriminant function analysis [42], and we deployed solar-paneled GPS loggers (Ecotone® HARRIER-M, $\sim 20\text{g}$) using a leg-loop harness made of 6.5 mm Teflon tape [43]. Anesthesia or euthanasia was not necessary for this study and birds were safely released after handling. Devices weighed between 0.8-1.3% of body mass. GPS loggers recorded latitude and longitude at 15 min intervals and data from loggers were downloaded remotely via UHF to a base station set up near nest sites on the colony. As researchers were not resident on the colony throughout the tracking period, they recorded the breeding status of nests of tagged individuals when possible (June 11, July 5, July 21).

Fig. 1. Location of the breeding colony of GPS-tagged Great Black-backed Gulls (*Larus marinus*; orange) as well as a nearby Common Murre (*Uria aalge*) colony (pink), known subtidal

and intertidal capelin spawning sites (yellow), and the hydroacoustic survey track (red) used to quantify capelin biomass during July-August, 2018 in coastal Newfoundland, Canada.

To determine shifts in prey availability within foraging range of the gull colony (i.e. ~50 km) [22,34,44], we monitored capelin presence at known and persistently used beach (intertidal) and subtidal capelin spawning sites in 15-40 m every 2-5 days throughout July and August 2018 (Fig. 1), following [45]. In brief, we monitored spawning sites for evidence of spawning (i.e., presence of capelin eggs, dead capelin, spawning capelin). We considered capelin availability as ‘high’ when capelin spawning was initiated at one or several spawning sites until capelin spawning had finished and we considered it ‘low’ outside of this period. Although capelin biomass peaks near the start of spawning [35,36,46], we further corroborated capelin availability periods using published data [36] from a ship-based hydroacoustic survey that quantified capelin biomass (g/m²) over a cluster of subtidal spawning sites (Fig. 1). The low capelin availability period included gull movement data both at the start and the end of the study period (July-August), thus shifts in trip characteristics between periods should relate to changes in resources rather than changes due to breeding stage [34]. Research protocols has been reviewed and approved by University of Manitoba Animal Care Committees in adherence with the Canadian Council of Animal Care (F16-017/1) and was conducted under a Canadian Scientific Permit to Capture and Band Migratory Birds (10873).

Data analysis

We first quantified GPS locations as either on or off the breeding island using the intersect function in QGIS [47]. As birds roosting on the edge of the breeding island may be considered ‘off island’ due to GPS error (± 20 m) and inaccuracy of base maps, we conservatively defined a foraging trip as trips off the breeding island > 2 hours [34,48]. Within

each trip, we considered point locations under 4 km/h foraging/roosting locations, following [48] and [34]. For each foraging trip, we quantified a number of foraging trip parameters, including mean distance from shore over the complete trip (km), mean distance from the colony over the complete trip (km), total trip distance (km) and total number of foraging/roosting locations per habitat. During data exploration, mean and maximum distance parameters were similar and, thus, we only present the mean distance. We also assigned habitat type to each foraging/roosting location using open-source polygons (open.canada.ca). Habitats included marine (indicating pelagic foraging), coastal/terrestrial (indicating foraging intertidally and at anthropogenic sources), and island (indicating presence at seabird breeding colony, i.e. likely predation).

To compare individual- and group-level foraging responses to prey availability, we examine space use at both the group and individual level. We first calculated 50% utilization distributions (UD) of foraging/roosting GPS locations using the *adehabitatHR* package [49] in R [50] at two temporal scales to represent core foraging areas. First, we calculated the 50% UD at the scale of the individual (all foraging trips combined) and group (all trips from all individuals combined) by capelin availability period (low, high). We compared the size of core foraging areas for each individual between capelin availability periods using a paired t-test. Second, we calculated 50% UD at the scale of each foraging trip by individual and we quantified the spatial overlap of foraging trips using Bhattacharyya's affinity index (BA) [51], where a value of 0 indicates no spatial similarity and a value of 1 indicates complete spatial similarity. To investigate the spatial consistency of foraging space of each individual within a prey period, we calculated the pairwise BA of all foraging trips made by an individual during low and high capelin availability periods separately. We then calculated the mean spatial overlap within a capelin availability period for all individuals combined, and then for each individual. These

mean BA values represent consistency in foraging space use by each individual or the group within a capelin availability period. We then conducted two analyses of variance on the BA values: (1) individual-level model, with individual and capelin availability as fixed predictor variables, including their interaction; (2) group-level model, with capelin availability only. These ANOVAs allowed us to investigate whether some individuals were more spatially consistent (i.e. high mean BA) within a capelin availability period than other individuals (individual-model), and whether the group (all individuals combined) were more spatially consistent within a capelin availability period. If the predictor was significant, post-hoc Tukey tests were performed.

To investigate the spatial consistency of foraging trips across prey periods, we calculated the pairwise spatial overlap (BA) of foraging trips made by an individual during high prey period with foraging trips during the low prey period. We then calculated the mean spatial overlap across prey periods for each individual and then all individuals combined. These mean BA values represent consistency in foraging space use across capelin availability periods, whereby a high (scale 0-1) BA would indicate that an individual or the group (all individuals combined) used the same foraging areas in both capelin availability periods. An analysis of variance was then performed on the BA values of each individual, with individual as the fixed predictor variable, allowing us to investigate whether some individuals were more consistent in space use across capelin availability periods (i.e. high mean BA) than other individuals. These mean BA values of each individual were then qualitatively compared to the mean BA of all individuals combined.

We also compared foraging responses to shifting prey availability by examining changes in foraging trip characteristics (i.e. distance and habitat use) between capelin availability periods. We used two analysis of variance models: (1) individual-level model, with capelin (prey)

availability period (i.e. high, low), sex, individual, and capelin availability period x individual as fixed factors; and (2) group-level model, with only capelin availability period and sex as predictors. In our first model (individual-level model), we included individuals as a fixed effect rather than a random effect, which is often used with repeated measures [52], because our primary goal was to compare responses to shifting capelin availability among individuals. We conducted both ANOVAs for each foraging trip characteristic (mean distance from shore, mean distance from colony, total trip distance; six models total). For habitat use, we used a similar method where fixed predictor variables were the same as stated above, except that the response variables were square-root transformed proportions of foraging points within marine, coastal/terrestrial and island habitat per foraging trip (six additional models, total of 12). For all individual-level models, when the interaction between capelin availability and individual was significant, we used *a priori* contrasts to compare means between individuals to evaluate individual differences between low and high capelin periods. Additionally, due to the small sample size, we did not consider the results about sex differences in the models, but kept this predictor in the model to account for any potential sex-related variation.

Results

GPS loggers were deployed on six male and two female great black-backed gulls, which recorded data for 5-65 days (285 foraging trips total) from June 10 - August 14 (Table 1). Capelin began spawning on July 10 and remained present at spawning sites until August 10, and, thus, capelin availability was classified as high from July 11 - August 9 (89 foraging trips; 8 individuals tracked) and classified as low from June 10 – July 10 and August 10 - 14 (196 foraging trips; six individuals tracked). Five hydroacoustic surveys (July 9, 18, 24, 28, August 7) corroborated these prey availability periods, with capelin biomass peaking on July 28 (0.239

g/m²; see Berard & Davoren 2020 for details) with a mean density of 0.0138 g/m² during low capelin availability. Nest failure occurred in six of the initial seven tracked individuals between June 8 - July 7. The tracked individual with a successful nest had two chicks on July 5, but had lost its GPS logger after 10 days (LMG07; Table 1). The GPS logger deployed on July 8 (LMG02) was lost after 5 days during which the nest site had already two chicks. Therefore, GPS loggers from breeding individuals (i.e., LMG02, LMG07) recorded for 5-11 consecutive days (7-9 foraging trips per individual) and failed breeders for 12-65 days (10 - 88 foraging trips per individual, Table 1), though the exact date of nest failure is unknown. Owing to variation in the number of tracking days per individual, we explored the impact of tracking duration by conducting all analyses on the first 10 days of tracking as well as tracking days 10-20 and all tracking days. As the results did not differ based on the study period used, we present results using all tracking days.

Table 1. Deployment information and foraging characteristics of eight GPS-tracked great black-backed gulls (*Larus marinus*) during June-August, 2018 in coastal Newfoundland. Deployment information includes deployment date, sex, breeding status, and number of days tracked. Foraging characteristics include number of foraging trips and sizes of core foraging areas (50% utilization distributions) in both low (June 10-July 10, August 10-14) and high (July 11-August 9) capelin availability periods. Note that LMG03 and LMG07 were not tracked during high capelin availability.

Individual	Deployment				No. Trips		Core Foraging Areas (km ²)	
	Date	Sex	Status	Days	Low	High	Low	High
LMG01	June 10	M	Failed	54	28	19	631.28	592.91
LMG02	July 8	M	Breeding	5	3	4	277.95	188.51
LMG03	June 10	M	Failed	11	10	-	125.01	-
LMG04	June 10	M	Failed	60	44	19	142.82	540.68

LMG05	June 10	M	Failed	41	13	11	175.23	607.21
LMG06	June 10	M	Failed	65	58	30	6.17	1.99
LMG07	June 10	F	Breeding	10	9	-	1.13	-
LMG08	June 11	F	Failed	39	31	6	24.48	45.47
<i>All individuals</i>				285	196	89	137.39	227.17

248

249 The size of core foraging areas of individuals increased between low and high capelin
250 availability periods for some individuals but decreased for others (Table 1; Fig. 2). Although the
251 group-level core foraging area was 89 km² smaller during low compared to high capelin
252 availability (Table 1), this difference was not statistically significant (Table 1; $t_5 = -1.27$; $p =$
253 0.26). When examining the spatial overlap of foraging trips made by individuals within each
254 prey availability period, the individual-level model showed a significant interaction between
255 individual and capelin availability ($F_5 = 42.87$; $p < 0.001$), and contrasts showed that two
256 individuals exhibited higher spatial overlap of foraging trips during high capelin availability
257 compared to low capelin availability, while three individuals exhibited the opposite pattern (Fig.
258 3). The group-level model, however, showed no significant differences in spatial overlap of
259 foraging trips between capelin availability periods ($F_1 = 1.67$; $p = 0.196$; Fig. 3). When
260 examining spatial overlap of foraging trips made by individuals across capelin availability
261 periods, the amount of overlap differed significantly among individuals ($F_5 = 53.38$; $p < 0.001$;
262 Fig. 4), while group-level overlap was higher (0.27 ± 0.28) than all individuals except one (Fig.
263 4). Although spatial overlap of foraging trips made by individuals across capelin availability
264 periods was generally low, one individual (LMG06) had a significantly higher overlap (mean BA
265 = 0.34) than the other individuals (mean BA = 0.14-0.24; Fig. 4).

266 **Fig. 2.** Core foraging areas (i.e. 50% utilization distributions) for each great black-backed gull (n
267 = 8) as well as all individuals combined, during low (orange) and high (purple) capelin

availability periods in coastal Newfoundland during June-August 2018. Black dots indicate capelin spawning sites and the star indicates the gull colony. Note that LMG03 and LMG07 were not tracked during high capelin availability, and spatial scale of LMG06 and 07 are different than the other six individuals.

Fig. 3. Mean ($\pm$ SE) spatial overlap (Bhattacharyya's index) of foraging trips of each individual great black-backed gull and all individuals combined within capelin availability periods (low=orange, high=purple) in coastal Newfoundland during June-August 2018. Note that LMG03 and LMG07 were not tracked during the high capelin availability period. Asterisks indicates significance level: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Fig. 4. The mean ($\pm$ SE) spatial overlap (Bhattacharyya's index) of foraging trips made by individual great black-backed gull **across** low and high capelin availability periods in coastal Newfoundland during June-August 2018. Asterisks indicates significance level: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Foraging trip characteristics and habitat use differed between individuals and capelin availability periods in the individual-level model, but did not differ between capelin availability periods in the group-level model (Table 2; Fig. 5-6). Three gulls (LMG06, LMG01, LMG08) exhibited different foraging behaviour (Fig. 5) and habitat use (Fig. 6) under varying capelin availability, while two other gulls (LMG04, LMG05) did not exhibit any significant changes. Of those exhibiting differences in behaviour, with a shift from low to high capelin availability, one individual (LMG06) increased trip length, utilized areas closer to shore, and decreased use of island habitat relative to coastal/terrestrial and marine habitats. Another individual (LMG01) also foraged closer to shore, and decreased marine habitat use during high capelin availability, but did

not significantly increase use of coastal/terrestrial or island habitats. Lastly, a third individual (LMG08) showed an opposite response compared with the other two individuals by foraging farther from shore and increasing island habitat use during high relative to low capelin availability. Responses of two gulls (i.e., LMG03, LMG07) could not be evaluated as they were not tracked across both capelin availability periods.

Fig. 5. Comparing foraging trip characteristics between capelin availability periods (low, high) for all great black-backed gull during June-August 2018 in coastal Newfoundland for all individuals combined (boxplot with median indicated by the horizontal line), as well as for each individual separately (mean of each individual indicated by color). Trip characteristics included a) mean distance from shore (km); b) mean distance from colony (km); c) total trip length (km). Asterisks indicate significance level (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). Note that LMG03 and LMG07 were not tracked during the high capelin availability period and that y-axes differ by panel.

Fig. 6. Proportions of foraging/roosting locations per habitat type by capelin availability period for all great black-backed gull individuals (mean indicated by the horizontal line in the box plot), as well as each individual separately (mean of each individual indicated by color) during June-August, 2018 in coastal Newfoundland. Habitat types included a) marine b) island and c) coastal and terrestrial habitats. Asterisks indicate significance level (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). Note that LMG03 and LMG07 were not tracked during the high capelin availability period.

310 **Table 2.** Summary results of analysis of variances for foraging trip characteristics, including total trip distance (km), mean distance
311 from shore (km), mean distance from the colony (km), along with the proportion of foraging/roosting locations per habitat type of
312 GPS-tracked Great Black-Backed Gulls (*Larus marinus*) during June-August, 2018 in coastal Newfoundland. Habitat types included
313 marine (pelagic foraging), coastal/terrestrial (intertidal foraging and foraging at anthropogenic sources), or island (seabird colony).

	Foraging trip characteristics						Habitat use					
	Trip Distance		Dist. from Shore		Dist. from Colony		Marine		Island		Coastal/Terrestrial	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>P</i>
<i>Individual-level model</i>												
Sex	15.93	< 0.001	3.52	0.06	13.211	< 0.001	0.69	0.41	4.07	0.04	1.33	0.25
Individual	7.12	< 0.001	4.56	< 0.001	12.26	< 0.001	15.25	< 0.001	26.48	< 0.001	6.87	< 0.001
Capelin availability	0.94	0.33	2.68	0.1	0.84	0.36	5.31	0.02	0.38	0.54	2.67	0.1
Individual:Capelin	5.17	< 0.001	4.62	< 0.001	3.39	0.005	0.005	< 0.001	4.18	0.001	2.79	0.02
<i>Group-level model</i>												
Sex	3.12	0.08	13.27	< 0.001	10.29	0.001	0.51	0.48	1.16	0.28	2.55	0.11
Capelin availability	2.16	0.14	1.65	0.2	0.14	0.71	3.05	0.08	2.89	0.09	0.3	0.58

Discussion

As predicted, shifts in capelin availability resulted in different individual responses by great black-backed gulls in foraging behaviour and space use, whereas group-level differences were undetectable. Indeed, some individuals maintained similar foraging areas, movement patterns (i.e. foraging trip characteristics) and proportional habitat use under varying capelin availability, while others shifted foraging areas and either increased or decreased movement and proportional use of certain habitat types. These results suggest the presence of individual specialization, both contextual and non-contextual, and that these responses to varying resource availability would have gone undetected if focused at the population level.

As the great black-backed gull is a generalist species in both diet and foraging behaviour [17,26], we expected that some individuals within the population might modify their foraging behaviour under shifting prey regimes [9]. Indeed, individuals appeared to use different foraging areas in each prey period, as evidenced by the low spatial overlap ($BA < 0.25$) of foraging areas for most tracked gulls across capelin availability periods. Specifically, four of the six individuals (LMG01, LMG02, LMG06, LMG08) altered movement patterns and/or habitat use, likely in response to the increase in capelin availability. These differences in foraging behaviour were not evident at the group-level, whereby the size of core foraging areas and mean spatial overlap of foraging trips were similar across periods. This lack of group-level response was expected but still surprising as the arrival of spawning capelin in coastal Newfoundland is known to affect population-level seabird diet [20,35,53] including the great black-backed gull [21,30,31]. For generalist and opportunist species, changes in prey availability may have different effects on individuals [11,54]. Indeed, during the high capelin availability period, capelin was readily available at wharfs (from fisheries activities) as well as in coastal and marine habitats where

capelin spawn [4,55], and at seabirds colonies, where provisioning seabird parents, such as common murre (*Uria aalge*), are targets for kleptoparasitism [21,56]. Although gulls had access to capelin from different sources and habitats, individuals responded differently to this sudden increase in prey availability, possibly due to variation in temperament [14], that were disguised when examining at the group-level. While small sample sizes (i.e. number of individuals tracked) may play a role in the lack of group-level patterns observed in this study, we highlight the importance of individual-level differences in behaviour and space use of six individuals that were tracked across prey periods. Although higher sample sizes would likely improve understanding of the amount of individual variation present in the population, we predict that combining data across a larger sample would likely still result in undetectable changes at the group level. Additionally, targeting these individual-level responses highlights the diversity of responses among individuals, which will play an important role in understanding the population dynamics and persistence of this and other generalist populations.

In our study, three of the six individuals tracked during both prey periods showed minimal behavioural and/ or spatial response to varying capelin availability, indicative of individual specialization. These individuals had slightly higher spatial overlap across prey periods, as well as similar foraging trip characteristics and habitat use between prey periods. For instance, one individual (LMG06) foraged in the same area during high and low capelin availability, illustrated by the smallest core foraging area and the highest spatial overlap across periods. This individual could be considered a non-contextual specialist, i.e., an individual that remains specialized despite changes in prey availability [5]. Contextual specialization may occur in situations when some individuals are restricted to a portion of their niche due to competitive interactions [57], but these specialists may show higher plasticity when released from

competition [5,15]. For instance, a study on Cory's shearwater (*Calonectris diomedea*) [58] showed that consistency of diet and space use of individual shifted over time, likely in relation to prey changing conditions. Alternately, specialization over time and conditions (non-contextual specialization) was observed in dolphin gulls (*Leucophaeus scoresbii*) [54] and yellow-legged gulls (*Larus michahellis*) [11]. While individual specialization has been reported multiple times in great black-backed gulls [22,24,25], these studies did not quantify gull behaviour under varying resource conditions. Therefore, it is unknown if individual specialization in these previous studies was contextual [5,9]. We show that individual specialization in great black-backed gulls behaviour can be non-contextual in some individuals, whereby these individuals continuously use the same foraging behaviour despite changing prey conditions. Future studies should explore the prominence of non-contextual specialization as well as the link between behavioural and dietary specialization.

As the majority of our individuals were male failed breeders, we are confident that most of the behavioural variation is due to increase in prey availability. We unfortunately lacked the sample size to infer additional potential sources of behavioural variation, such as sex and breeding status [59,60]. For instance, male lesser black-backed gulls travel further from the colony and spend more time offshore than females [61]. Breeding status can also affect behavioural consistency [14,62]. Indeed, a study [14] showed that female brown-nosed albatross (*Thalassarche melanophrys*) had more variable behaviour and wider foraging ranges than males, which stayed closer to the colony. In contrast, another study [62] showed that northern gannets (*Morus bassanus*) with unsuccessful nests had an intermediate fidelity to foraging sites relative to immatures and active breeders. This avenue of research should be further studied in gulls.

Conclusion

This study provided novel information on foraging behaviour plasticity of individual great black-backed gulls, while exemplifying the potential to mask important individual-level responses when focusing foraging ecology studies solely at the population level. While a small sample size limits our ability to make population-level conclusions on the response of a generalist species to changes in prey availability, we show a diversity of individual responses and therefore highlight the importance of individual-level studies in generalist species. High response diversity allows populations to buffer against environmental change [8], which may explain why gull species persist and often thrive in rapidly changing environments, such as urban habitats [38]. Gull species may also thrive in changing environments because different responses to environmental change among individuals can also reduce intraspecific competition and, thus, individuals only compete within others that behave similarly [10,63]. Such a strategy to minimize intraspecific competition may be particularly important in highly competitive species, such as large gulls, which are known to defend food resources and act aggressively, depriving other conspecifics or heterospecifics access to resources [21,28]. Finally, the results of this study exemplify the importance of measuring individual responses to changing resources and/or environmental conditions, to examine the degree to which specialization is contextual. This distinction informs the ecological mechanism of specialization and a population's capacity to adjust to environmental change.

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Declarations

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Conflict of interest The authors declare that they have no conflict of interest.

Data availability statement The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Ethical approval Research protocols has been reviewed and approved by University of Manitoba Animal Care Committees in adherence with the Canadian Council of Animal Care (F16-017/1). All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which studies were conducted. Research was conducted under a Canadian Scientific Permit to Capture and Band Migratory Birds (10873). Anesthesia or euthanasia was not necessary for this study and birds were safely released after handling.

References

1. Marzluff JM. Worldwide urbanization and its effects on birds. *Avian Ecol Conserv an Urban World*. 2001; 19–47. doi:10.1007/978-1-4615-1531-9_2
2. Danchin É, Giraldeau L-A, Cézilly F. *Écologie Comportementale*. Paris: Dunod; 2012.
3. Erikstad K, Fauchald P, Tveraa T, Steen H. On the cost of reproduction in long-lived birds : the influence of environmental variability. *Ecology*. 1998;79: 1781–1788.

- 429 4. Gulka J, Davoren GK. High individual flexibility in the foraging behavior of a marine
430 predator, the common murre. *Mar Biol.* 2019;166: 83. doi:10.1007/s00227-019-3530-4
- 431 5. Araújo MS, Bolnick DI, Layman CA. The ecological causes of individual specialisation.
432 *Ecol Lett.* 2011;14: 948–958. doi:10.1111/j.1461-0248.2011.01662.x
- 433 6. Dall SRX, Bell AM, Bolnick DI, Ratnieks FLW. An evolutionary ecology of individual
434 differences. *Ecol Lett.* 2012;15: 1189–1198. doi:10.1111/j.1461-0248.2012.01846.x
- 435 7. Schindler DE, Armstrong JB, Reed TE. The portfolio concept in ecology and evolution.
436 *Front Ecol Environ.* 2015;13: 257–263. doi:10.1890/140275
- 437 8. Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, et al. Why
438 intraspecific trait variation matters in community ecology. *Trends Ecol Evol.* 2011;26:
439 183–192. doi:10.1016/j.tree.2011.01.009
- 440 9. Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, et al. The ecology
441 of individuals: incidence and implications of individual specialization. *Am Nat.* 2003;161:
442 1–28. doi:10.1086/343878
- 443 10. Shaffer SA, Cockerham S, Warzybok P, Bradley RW, Jahncke J, Clatterbuck CA, et al.
444 Population-level plasticity in foraging behavior of Western Gulls (*Larus occidentalis*).
445 *Mov Ecol.* 2017;5: 27. doi:10.1186/s40462-017-0118-9
- 446 11. Navarro J, Grémillet D, Ramirez FJ, Afán I, Bouten W, Forero MG. Shifting individual
447 habitat specialization of a successful predator living in anthropogenic landscapes. *Mar*
448 *Ecol Prog Ser.* 2017;578: 243–251. doi:10.3354/meps12124
- 449 12. Réale D, Gallant BY, Leblanc M, Festa-Bianchet M. Consistency of temperament in
450 bighorn ewes and correlates with behaviour and life history. *Anim Behav.* 2000;60: 589–
451 597. doi:10.1006/anbe.2000.1530

- 452 13. Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H. Determining trophic niche
453 width: A novel approach using stable isotope analysis. *J Anim Ecol.* 2004;73: 1007–1012.
- 454 14. Patrick SC, Weimerskirch H. Consistency pays: Sex differences and fitness consequences
455 of behavioural specialization in a wide-ranging seabird. *Biol Lett.* 2014;10: 20140630–
456 20140630. doi:10.1098/rsbl.2014.0630
- 457 15. Bolnick DI, Ingram T, Stutz WE, Snowberg LK, Lau OL, Pauli JS. Ecological release
458 from interspecific competition leads to decoupled changes in population and individual
459 niche width. *Proc R Soc B Biol Sci.* 2010;277: 1789–1797. doi:10.1098/rspb.2010.0018
- 460 16. Pierotti R, Good TP. Herring Gull (*Larus argentatus*). In: Poole A, Gill F, editors. *The*
461 *Birds of North America*. Academy of Natural Sciences, Philadelphia, Pennsylvania;
462 American Ornithologists' Union; 1994. p. No. 124.
- 463 17. Good TP. Great Black-backed Gull (*Larus marinus*). In: Poole A, Gill F, editors. *The*
464 *Birds of North America*. Cornell Lab of Ornithology; 1998. p. No 330.
- 465 18. Pierotti R, Annett CA. Diet and reproductive output in seabirds. *Bioscience.* 1990;40:
466 568–574. doi:10.2307/1311297
- 467 19. Bukacinska M, Bukacinski D, Spaans A. Attendance and diet in relation to breeding
468 success in Herring Gulls (*Larus argentatus*). *Auk.* 1996;113: 300–309. Available:
469 <http://www.jstor.org/stable/10.2307/4088896>
- 470 20. Gulka J, Carvalho PC, Jenkins E, Johnson K, Maynard L, Davoren GK. Dietary niche
471 shifts of multiple marine predators under varying prey availability on the northeast
472 Newfoundland coast. *Front Mar Sci.* 2017;4: 1–11. doi:10.3389/fmars.2017.00324
- 473 21. Maynard LD, Carvalho PC, Davoren GK. Seabirds vary responses to supplemental food
474 under dynamic natural prey availability and feeding aggregation composition. *Auk.*

- 2019;137: 1–13. doi:10.1093/auk/ukz062
22. Maynard LD, Ronconi RA. Foraging behaviour of Great Black-backed Gull *Larus marinus* near an urban center in Atlantic Canada: Evidence of individual specialization from GPS tracking. Mar Ornithol. 2018;46: 27–32.
23. Juvaste R, Arriero E, Gagliardo A, Holland R, Huttunen MJ, Mueller I, et al. Satellite tracking of red-listed nominate Lesser Black-backed Gulls (*Larus f. fuscus*): Habitat specialisation in foraging movements raises novel conservation needs. Glob Ecol Conserv. 2017;10: 220–230. doi:10.1016/j.gecco.2017.03.009
24. Borrmann RM, Phillips RA, Clay TA, Garthe S. High foraging site fidelity and spatial segregation among individual Great Black-backed Gulls. J Avian Biol. 2019;50: jav.02156. doi:10.1111/jav.02156
25. Westerberg K, Brown R, Eagle G, Votier SC. Intra-population variation in the diet of an avian top predator : generalist and specialist foraging in Great Black-backed Gulls *Larus marinus*. Bird Study. 2019; 1–8. doi:10.1080/00063657.2019.1693961
26. Washburn BE, Bernhardt GE, Kutschbach-Brohl L, Chipman RB, Francoeur LC. Foraging ecology of four gull species at a coastal–urban interface. Condor. 2013;115: 67–76. doi:10.1525/cond.2013.110185
27. Hunt GLJ, Hunt MW. Habitat partitioning by foraging gulls in Maine and Northwestern Europe. Auk. 1973;90: 827–839. doi:10.1016/j.cognition.2008.05.007
28. Steenweg RJ, Ronconi R a., Leonard ML. Seasonal and age-dependent dietary partitioning between the Great Black-backed and Herring gulls. Condor. 2011;113: 795–805. doi:10.1525/cond.2011.110004
29. Cotton JF. Competition between Herring Gulls and Great Black-backed Gulls over natural

and anthropogenic food sources in the Gulf of Maine. Washington University. 2009.

Available: https://openscholarship.wustl.edu/wushta_spr2009/51

30. Massaro M, Chardine JW, Jones IL, Robertson GJ. Delayed capelin (*Mallotus villosus*) availability influences predatory behaviour of large gulls on Black-legged Kittiwakes (*Rissa tridactyla*), causing a reduction in kittiwake breeding success. Can J Zool. 2000;78: 1588–1596.
31. Stenhouse IJ, Montevecchi W a. Indirect effects of the availability of capelin and fishery discards: Gull predation on breeding storm-petrels. Mar Ecol Prog Ser. 1999;184: 303–307. doi:10.3354/meps184303
32. Gilliland SG, Ankney CD, Hicklin PW. Foraging ecology of Great Black-backed Gulls during brood-rearing in the Bay of Fundy, New Brunswick. Can J Zool. 2004;82: 1416–1426. doi:10.1139/Z04-124
33. Veitch BG, Robertson GJ, Jones IL, Bond L. Great Black-backed Gull (*Larus marinus*) predation on seabird populations at two colonies in Eastern Canada. Waterbirds. 2016;39: 235–245. doi:10.1675/063.039.sp121
34. Maynard LD, Davoren GK. Sea ice influence habitat type use by Great Black-backed Gulls (*Larus marinus*) in coastal Newfoundland, Canada. Waterbirds. 2018;41: 449–456.
35. Carvalho PC, Davoren GK. Niche dynamics of sympatric non-breeding shearwaters under varying prey availability. Ibis (Lond 1859). 2020;162: 701–712. doi:10.1111/ibi.12783
36. Berard MT, Davoren GK. Capelin (*Mallotus villosus*) availability influences the inshore summer diet of Atlantic cod (*Gadus morhua*) in coastal Newfoundland. Environ Biol Fishes. 2020;103: 771–782. doi:10.1007/s10641-020-00982-9
37. Chapdelaine G, Rail JF. Relationship between cod fishery activities and the population of

- Herring Gulls on the North Shore of the Gulf of St Lawrence, Quebec, Canada. ICES J Mar Sci. 1997;54: 708–713. doi:10.1006/jmsc.1997.0248
38. Anderson JGT, Shlepr KR, Bond AL, Ronconi RA. Introduction: A historical perspective on trends in some gulls in Eastern North America, with reference to other regions. Waterbirds. 2016;39: 1–9. doi:10.1675/063.039.sp106
39. Grémillet D, Charmantier A. Shifts in phenotypic plasticity constrain the value of seabirds as ecological indicators of marine ecosystems. Ecol Appl. 2010;20: 1498–1503. doi:10.1890/09-1586.1
40. Wilhelm SI, Mailhiot J, Arany J, Chardine JW, Robertson GJ, Ryan PC. Update and trends of three important seabird populations in the Western North Atlantic using a Geographic Information System approach. Mar Ornithol. 2015;43: 211–222.
41. Penton PM, Davoren GK. Physical characteristics of persistent deep-water spawning sites of capelin: Importance for delimiting critical marine habitats. Mar Biol Res. 2012;8: 778–783. doi:10.1080/17451000.2012.678858
42. Mawhinney K, Diamond T. Sex determination of Great Black-backed Gulls using morphometric characters. J F Ornithol. 1999;70: 206–210.
43. Mallory ML, Gilbert CD. Leg-loop harness design for attaching external transmitters to seabirds. Mar Ornithol. 2008;36: 183–188.
44. Shlepr KR, Ronconi RA, Hayden B, Allard KA, Diamond AW. Estimating the relative use of anthropogenic resources by Herring Gull (*Larus argentatus*) in the Bay of Fundy, Canada. Avian Conserv Ecol. 2021;16. doi:10.5751/ace-01739-160102
45. Crook KA, Maxner E, Davoren GK. Temperature-based spawning habitat selection by capelin (*Mallotus villosus*) in Newfoundland. ICES J Mar Sci. 2017.

doi:10.1093/icesjms/fsx023

46. Gulka J, Ronconi RA, Davoren GK. Spatial segregation contrasting dietary overlap: niche partitioning of two sympatric alcids during shifting resource availability. *Mar Biol.* 2019;166: 115. doi:10.1007/s00227-019-3553-x
47. QGIS Development Team. QGIS Geographic Information System. Open Source Geospatial Foundation Project; 2021. Available: <http://qgis.osgeo.org>
48. Shamoun-Baranes J, Bouten W, Camphuysen CJ, Baaij E. Riding the tide: Intriguing observations of gulls resting at sea during breeding. *Ibis (Lond 1859)*. 2011;153: 411–415. doi:10.1111/j.1474-919
49. Calenge C, Dray S, Royer-Carenzi M. The concept of animals' trajectories from a data analysis perspective. *Ecol Inform.* 2009;4: 34–41. doi:10.1016/j.ecoinf.2008.10.002
50. R Core Development Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2021. Available: <https://www.r-project.org/>
51. Fieberg J, Kochanny CO. Quantifying Home-Range Overlap: the Importance of the Utilization Distribution. *J Wildl Manage.* 2005;69: 1346–1359. doi:10.2193/0022-541x(2005)69[1346:qhotio]2.0.co;2
52. Quinn GP, Keough. Experimental design and data analysis for biologists. New York: Cambridge University Press; 2002.
53. Montevecchi WA, Benvenuti S, Garthe S, Davoren GK, Fifield D. Flexible foraging tactics by a large opportunistic seabird preying on forage-and large pelagic fishes. *Mar Ecol Prog Ser.* 2009;385: 295–306. doi:10.3354/meps08006
54. Masello JF, Wikelski M, Voigt CC, Quillfeldt P. Distribution patterns predict individual

specialization in the diet of Dolphin Gulls. PLoS One. 2013;8.

doi:10.1371/journal.pone.0067714

55. Davoren GK. Distribution of marine predator hotspots explained by persistent areas of prey. Mar Biol. 2013;160: 3043–3058.

56. Spencer R, Russell YI, Dickins BJA, Dickins TE. Kleptoparasitism in gulls Laridae at an urban and a coastal foraging environment: an assessment of ecological predictors. Bird Study. 2017;64: 12–19. doi:10.1080/00063657.2016.1249821

57. Roughgarden J. Evolution of niche width. Am Nat. 1972;106: 683–718.

doi:10.1086/282892

58. Ceia FR, Paiva VH, Garthe S, Marques JC, Ramos JA. Can variations in the spatial distribution at sea and isotopic niche width be associated with consistency in the isotopic niche of a pelagic seabird species? Mar Biol. 2014;161: 1861–1872.

59. Pons J-M. Feeding strategies of male and female Herring Gulls during the breeding season under various feeding conditions. Ethol Ecol Evol. 1994;6: 1–12.

doi:10.1080/08927014.1994.9523003

60. Phillips RA, Lewis S, González-solís J, Daunt F. Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. Mar Ecol

Prog Ser. 2017;578: 117–150. doi:10.3354/meps12217

61. Camphuysen KCJ, Shamoun-Baranes J, Van Loon EE, Bouten W. Sexually distinct foraging strategies in an omnivorous seabird. Mar Biol. 2015;162: 1417–1428.

doi:10.1007/s00227-015-2678-9

62. Votier SC, Fayet AL, Bearhop S, Bodey TW, Clark BL, Grecian J, et al. Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator.

- 590 Proc R Soc B Biol Sci. 2017;284: 20171068. doi:10.1098/rspb.2017.1068
- 591 63. Shaw AK. Causes and consequences of individual variation in animal movement. Mov
- 592 Ecol. 2020;8: 12. doi:10.1186/s40462-020-0197-x

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