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Foraging on anthropogenic food predicts problem-solving skills in a seabird

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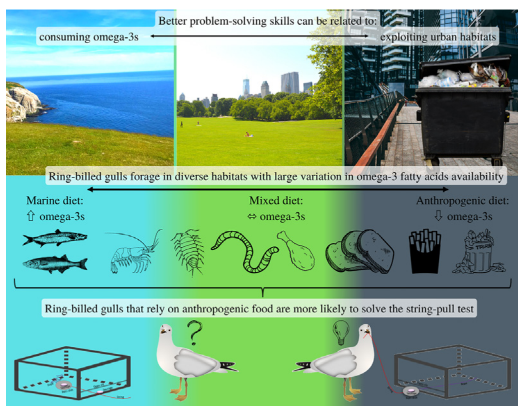
HIGHLIGHTS

- Urban nesters living by the ocean favour anthropogenic foods deficient in omega-3s.
- High reliance on anthropogenic food predicts better problem-solving skills.
- Low omega-3 intake did not constrain the problem-solving skills of incubating birds.

GRAPHICAL ABSTRACT



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ABSTRACT

Species and populations with greater cognitive performance are more successful at adapting to changing habitats. Accordingly, urban species and populations often outperform their rural counterparts on problem-solving tests. Paradoxically, urban foraging also might be detrimental to the development and integrity of animals' brains because anthropogenic foods often lack essential nutrients such as the long-chain omega-3 fatty acids eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), which are important for cognitive performance in mammals and possibly birds. We tested whether urbanization or consumption of EPA and DHA are associated with problem-solving abilities in ring-billed gulls, a seabird that historically exploited marine environments rich in omega-3 fatty acids but now also thrives in urban centres. Using incubating adults nesting across a range of rural to urban colonies with equal access to the ocean, we tested whether urban gulls preferentially consumed anthropogenic food while rural nesters relied on marine organisms. As we expected individual variation in foraging habits within nesting location, we characterized each captured gulls' diet using stable isotope and fatty acid analyses of their red blood cells. To test their problem-solving abilities, we presented the sampled birds with a horizontal rendition of the string-pull test, a foraging puzzle often used in animal cognitive studies. The isotopic and fatty acid profiles of urban nesters indicated a diet comprising primarily anthropogenic food, whereas the profiles of rural nesters indicated a high reliance on marine organisms. Despite the gulls' degree of access to urban foraging habitat not predicting solving success, birds with biochemical profiles reflecting anthropogenic food (less DHA and a higher carbon-13 ratio in their red blood cells) had a greater

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probability of solving the string-pull test. These results suggest that experience foraging on anthropogenic food is the main explanatory factor leading to successful problem-solving, while regular consumption of omega-3s during incubation appears inconsequential.

1. Introduction

Species and populations with larger brain sizes are more successful at adapting to changing habitats, colonizing new environments, and avoiding extinction or extirpation (Fristoe et al., 2017; Sayol et al., 2016; Shultz et al., 2005; Sol et al., 2008), presumably because larger brain sizes support greater cognitive performance associated with problem-solving skills, behavioural flexibility, and innovation rates (Benson-Amram et al., 2016; Sol, 2009; Sol et al., 2005, but see Logan et al., 2018). Species and populations with larger brain sizes also tend to be better at evading predators (Møller and Erritzøe, 2014; Samia et al., 2015), surviving harsh environments (Wagnon and Brown, 2020), and finding and exploiting new food sources (Lefebvre et al., 1997). Animals with superior problem-solving skills tend to be more attractive (Cauchard et al., 2013; Mateos-Gonzalez et al., 2011) and have better reproductive success (Cauchard et al., 2013; Cole et al., 2012; Preiszner et al., 2017). Differences in cognitive abilities among species and individuals are generally explained by disparities in relative brain size (Lefebvre and Sol, 2008; Sol et al., 2016), neuronal density (Herculano-Houzel, 2017; Olkowicz et al., 2016), and the brain's fatty acid composition (Pilecky et al., 2021; Roy et al., 2020). Cognitive abilities, reflected by innovation potential, can be tested non-invasively by presenting animals with novel problem-solving tasks (Audet, 2020; Griffin et al., 2017; Griffin and Guez, 2014; Roth and Dicke, 2005).

Environmental pressures can enhance certain aspects of cognition by selecting for larger brain sizes or greater behavioural flexibility (Sayol et al., 2016; Sol et al., 2013). A clear example is the urbanization of natural habitats, which leads to an altered or anthropogenic food resource base (Lowry et al., 2013; Shochat et al., 2006; Sol et al., 2013). Species and populations that thrive in urban environments generally have larger relative brain sizes, higher innovation rates, and superior problem-solving skills (Audet et al., 2016; Grunst et al., 2020; Møller, 2009; Papp et al., 2015; Preiszner et al., 2017; Sayol et al., 2020; Sol et al., 2005). A possible reason for this urban effect is that more innovative and behaviourally flexible individuals can survive the challenges of the urban environment and successfully exploit its ever-changing nature (Maklakov et al., 2011; Snell-Rood and Wick, 2013; Sol et al., 2013).

A possible disadvantage of urban diets is that they lack omega-3 long-chain polyunsaturated fatty acids (n3-LCPUFA; Simopoulos, 2002). N3-LCPUFAs are important for the brain's structure and function in mammals (reviews by Bauer et al., 2014; Bazinet and Layé, 2014; Dyall, 2015; Hoffman et al., 2009; Joffre et al., 2014; Luchtman and Song, 2013; Pilecky et al., 2021; Weiser et al., 2016) and, possibly, in birds (Lamarre et al., 2021; Price et al., 2018) and fish (Benítez-Santana et al., 2014; Ishizaki et al., 2001; Roy et al., 2020), notably by optimizing and preserving the brain's size during development and throughout the lifespan (McNamara et al., 2018; Ogundipe et al., 2018; Pottala et al., 2014; Zou et al., 2021). The main n3-LCPUFAs providing these benefits are eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA; Hixson et al., 2015), which are thought to benefit cognition through their neurogenesis and anti-inflammatory properties, in addition to DHA being integral to neuronal membranes (Bazinet and Layé, 2014; Calder, 2015; Hoffman et al., 2009). As a result, individuals with greater intake of EPA and DHA tend to show better cognitive abilities, including better memory and learning abilities (Barnes et al., 2021; Chung et al., 2008; Fedorova et al., 2007; Kuratko et al., 2013), processing speed (Duchaine et al., 2022; Øyen et al., 2018; Sørensen et al., 2015), and problem-solving skills (Braarud et al., 2018; Judge et al., 2007).

These fatty acids are found in aquatic ecosystems, where they are produced by phytoplankton and bioaccumulate in zooplankton, aquatic invertebrates, and fish (Barrett et al., 2007; Calder, 2015; Colombo et al., 2016; Kainz et al., 2004; Parrish, 2013). Except for land-dwelling herbivores that can convert α-linolenic acid (ALA) from plants into n3-LCPUFAs, most species rely on dietary consumption of n3-LCPUFAs to meet their nutritional demands (Gladyshev et al., 2016; Speake and Wood, 2005). In addition to lacking n3-LCPUFAs, terrestrial and anthropogenic environments are rich in arachidonic acid (ARA) and its precursor linoleic acid (LA), which are both essential omega-6 polyunsaturated fatty acids (n6-PUFAs; Colombo et al., 2016; Gladyshev et al., 2016; Gladyshev and Sushchik, 2019). Although ARA is necessary for optimal cognitive development in vertebrates (de Haas et al., 2017; Hadley et al., 2016; Marszalek and Lodish, 2005), its encephalic concentration is less important for cognition than that of DHA (Bazan, 2009; Price et al., 2018; SanGiovanni and Chew, 2005). Furthermore, n6-PUFAs and n3-LCPUFAs compete metabolically, consequently reducing the absorption and action of whichever one is less abundant (Brenna et al., 2009; Saini and Keum, 2018). Consuming a balance of n6-PUFAs and n3-LCPUFAs is therefore important for optimal cognitive performance (Elkin et al., 2021), yet is difficult to achieve for animals consuming anthropogenic diets rich in n6-PUFAs and deficient in n3-LCPUFAs (de Faria et al., 2021; Meyer et al., 2003; Williams and Buck, 2010).

In the current study, we tested the competing hypotheses that either urbanization or consumption of n3-LCPUFAs, a type of fatty acid scarce in anthropogenic diets, are associated with better problem-solving abilities in ring-billed gulls (*Larus delawarensis*), a historically aquatic forager that now also thrives in and around urban centres (Giroux et al., 2016; Pollet et al., 2012). We tested our hypotheses using more urbanized and more rural (hereafter 'urban' and 'rural') breeding colonies surrounded by marine waters and thus having easy access to the marine environment. We expected rural nesting birds to forage primarily on marine foods rich in n3-LCPUFAs. In contrast, we expected urban nesters to forage primarily on anthropogenic foods deficient in n3-LCPUFAs (e.g. heavily processed foods found in human and agricultural wastes), as seen in other urban gull species with access to the marine environment (e.g. de Faria et al., 2021; Langley et al., 2021). Since differences in foraging habits have been reported in ring-billed gulls, even when nesting at the same colony (Caron-Beaudoin et al., 2013; Marteinson and Verreault, 2020), we used fatty acid and stable isotope analysis of their red blood cells to more precisely characterize their diet at the individual level. We tested problem-solving skills using a modified string-pull test, which is commonly used to assess problem-solving abilities in mammals and birds. The test requires an animal to pull on a string to retrieve a food item that is visible but otherwise inaccessible (review by Jacobs and Osvath, 2015). Animals are thought to require insight and means-end understanding in order to pull on a string with no inherent value to obtain a food reward, although learning through trial-and-error that pulling on the string moves the food towards them might also play a role in solving success (Heinrich, 1995; Jacobs and Osvath, 2015; Taylor et al., 2010). We previously showed that approximately 25 % of wild nesting ring-billed gulls can solve the string-pull test, making them one of the few non-passerine, non-psittacine species to do so (Lamarre and Wilson, 2021). Our first objective was to use stable isotope and fatty acid analyses of red blood cells to characterize the diets of gulls breeding across a rural-urban gradient. Our second objective was to test whether performance on the string-pull test was related to colony-level differences in urbanization and individual-level differences in foraging environment and n3-LCPUFA consumption. We predicted that either urbanization or consumption of EPA and DHA would be associated with better problem-solving abilities in ring-billed gulls.

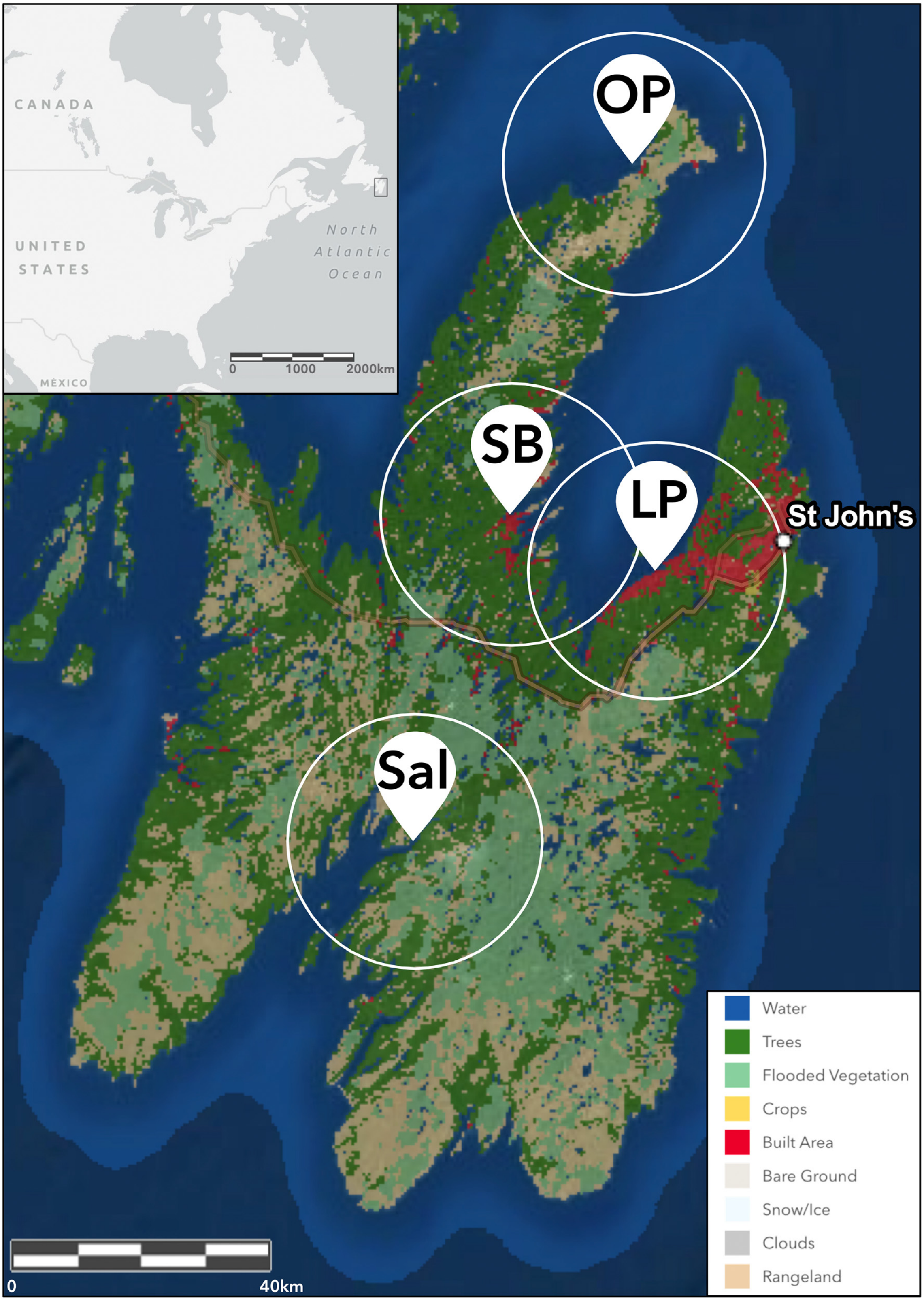

Fig. 1. Locations of the four coastal colonies studied in Newfoundland, Canada (including the 20 km radius range around each colony), and the surrounding land cover showing in red the areas comprising anthropogenic structures (land cover map from Karra et al., 2021). The Long Pond (LP; 47°31′09.8″N, 52°58′33.6″W) and Spaniard's Bay (SB; 47°35′51.8″N 53°16′48.7″W) colonies are considered to be situated in urban environments, whereas the Old Perlican (OP; 48°05′15.7″N 53°01′20.6″W) and Salmonier (Sal; 47°08′11.0″N 53°28′48.6″W) colonies are considered to be rural. The Long Pond, Spaniard's Bay, and Salmonier colonies are connected to the mainland by a sandbar, whereas the Old Perlican colony is on an island 600 m from shore.

2. Methods

2.1. Study sites and subjects

The study was conducted in 2020 at four ring-billed gull breeding colonies located along marine coastlines in Newfoundland, Canada (Fig. 1). We classified these four colonies as urban or rural based on their degree of urbanization, which we determined by calculating the percentage of area covered by anthropogenic structures within a 20 km radius around each site (breeding ring-billed gulls typically forage within 20 km of their colony: Caron-Beaudoin et al., 2013; Patenaude-Monette et al., 2014). We used a land cover map produced by Karra et al. (2021), onto which a 2 × 2 km grid (Suarez-Rubio and Krenn, 2018) was superimposed to measure the area within which anthropogenic structures (impervious structures, buildings, houses and lawns, and city parks) were present compared to the total area covered by the grid (see Fig. S1). We scored quadrats as either containing anthropogenic structures or not (0, absent; 1, present), and then calculated the percentage of quadrats with structures present (similar to Liker et al., 2008). Our urban colonies showed degrees of urbanization of 33.10 % (Long Pond) and 24.51 % (Spaniard's Bay) while our rural colonies had degrees of urbanization of 6.05 % (Old Perlican) and 4.46 % (Salmonier). Although birds from all four colonies had equal access to a marine diet rich in n3-LCPUFAs, more urbanized birds would also have had access to heavily processed anthropogenic foods in the form of household and restaurant refuse, and landfills. Although the rural colonies are located adjacent to small human settlements, the local production of garbage accessible to wildlife is restricted to a few houses around both sites and to small landfills located 3.5 km from the Old Perlican colony and 8.5 km from the Salmonier colony (https://easternregionalserviceboard.com/residents/waste-recovery-facilities/). Thus, their access to anthropogenic foods deficient in n3-LCPUFAs is expected to be limited compared to urban nesters.

We tested adult ring-billed gulls at the end of their respective colonies' incubation period, when they are reluctant to leave their nest and thus easier to capture (Brown and Morris, 1995; Chardine, 1978; Conover and Miller, 1979). We estimated when the end of incubation would occur by visiting the colonies at the beginning of their breeding season and recording the date of clutch initiation. Based on an incubation period of 26 days (Pollet et al., 2012), we returned to the colonies to conduct our study on the following dates: Long Pond, 7–14 June; Spaniard's Bay, 17–21 June; Old Perlican, 22–26 June; Salmonier, 27–30 June.

We targeted gulls haphazardly and captured them on the nest with a hand net or noose trap over a period of two (Old Perlican, Spaniard's Bay, Salmonier) or three (Long Pond) days. We intended to capture one or both mates from 40 nests per colony, but the gulls quickly learned to avoid us, making continued capture efforts less effective and increasingly disruptive. Our final sample was 133 adults, including 46 adults from 43 nests at Long Pond, 40 adults from 40 nests at Spaniard's Bay, 22 adults from 22 nests at Old Perlican, and 25 adults from 25 nests at Salmonier. The urban colonies were larger (>300 breeding pairs each) than the rural colonies (<150 pairs each), which likely explains the difference in sample size between urban and rural colonies.

We attached a metal Canadian Wildlife Service band to the left leg of each captured bird for permanent identification, and a plastic colour band (green, blue, pink, purple, or yellow) to the right leg for identification during subsequent string-pull test trials. During banding, we weighed each gull with a Pesola spring-scale (precision: ±5 g) and used a hypodermic syringe to draw up to 1.2 mL of blood from the brachial vein. The blood was stored on ice in 600-uL lithium-heparin coated tubes (BD Microtainers with plasma separator; BD, Canada, cat# B365985) for up to 12 h before being centrifuged at 2000*g* for 4 min to separate the plasma and cell fractions. The plasma phase was transferred into an Eppendorf tube and both plasma and cell fractions were stored at −20 °C until analysis. All methods were performed under appropriate permits (Canadian Wildlife Service Scientific Permit, number SC4049; Environment and Climate Change Canada Scientific Permit to Capture and Band Migratory Birds, numbers 10890 and 10890B) and were approved by Memorial University of Newfoundland and Labrador's Animal Care Committee (number 19-03-DW).

Immediately after capturing and banding an individual, we installed a burlap fence around its nest (1.3 × 1.3 m) to minimize the risk of social learning between neighbors and to provide privacy from thieves during string-pull tests (Fig. 2). We initially kept the burlap at ground level to minimize the visual disturbance at the site and encourage parents to return quickly to their nest. After the parents returned, we gradually unrolled the burlap over the next two days to a height of 50 cm.

2.2. Problem-solving test

As detailed in Lamarre and Wilson (2021), we designed and administered a horizontal rendition of the string-pull test (Danel et al., 2019; Jacobs and Osvath, 2015) to assess gulls' problem-solving skills. We used a transparent plastic box (32 × 19 × 11.5 cm) with a removable lid and a 2 cm high slit cut across the base of the front panel (Fig. 2). A Petri dish containing 5 g of sausage was placed inside the box, and a string attached to the Petri dish extended through the open slit. To solve the test, a gull had to pull on the string to retrieve the sausage (Fig. 2). The testing procedure for any given individual began within 3 days of when that individual was captured, banded, and blood sampled.

We conducted five habituation trials at each target nest to create an association between a lidless version of the string-pull box and the food reward. During each of the first four habituation trials, we placed 2 pieces of sausage (5 g each) at the edge of each box's open slit, where they were easily visible and accessible to the incubating gull. The gulls were given 30 min to return to their nests and consume the food while the investigators remained hidden from the colony. The habituation trials ran twice a day for the first two days. The fifth and final habituation trial was conducted during the morning of the third day and was shortened to 15 min because parents had returned quickly during the previous habituation trials. This trial was recorded with a video camera (Canon VIXIA HF R800 video recorder; 1920 × 1080 resolution, 35mbps using MP4 compression, 60fps) to ensure that a parent, rather than a neighbor, had returned to the nest and consumed the sausage. During this fifth habituation trial, we added a Petri dish containing 5 g of sausage to the centre of the floor of the box. It was attached to a red string that extended through the open slit and rested on the rim of the nest 10 cm beyond the box (Fig. 2). Another piece of sausage was placed next to the string at the edge of the box to encourage the gulls to investigate the string. For this last habituation trial, the gulls could obtain the sausage in the Petri dish directly through the lidless top or by pulling on the string.

We administered the first string-pull test trial in the afternoon following the last habituation trial, then two more test trials the following day for a total of three test trials per nest (one conducted in the morning, two conducted in the afternoon). Test trials were shortened to 10 min and the lids were fastened to the boxes so that gulls could only retrieve the sausage from the Petri dish by pulling on the string. As in the habituation trials, another piece of sausage was also placed at the edge of the box's open slit. We discontinued trials at a nest only if the eggs or chicks were depredated or had disappeared. Since we could not control which parent returned to the nest during a trial, individual gulls could have been exposed to the test between zero and three times. Once all tests were completed, we moved our equipment to the next colony.

2.3. Fatty acid analysis

We analyzed the fatty acid composition of red blood cells because they have a 2–4 week turnover rate (Bearhop et al., 2002) and therefore should reflect the fatty acids consumed throughout incubation. Details of the fatty acid analysis are in Lamarre et al. (2021), but we provide a brief overview here. We extracted lipids from 300 μL of the red blood cell fraction following Folch et al. (1957), then transmethylated them and extracted the resulting fatty acid methyl esters (FAMEs) according to Chechi et al. (2010). The FAMEs extract was dried under nitrogen, dissolved in 50 mL of carbon

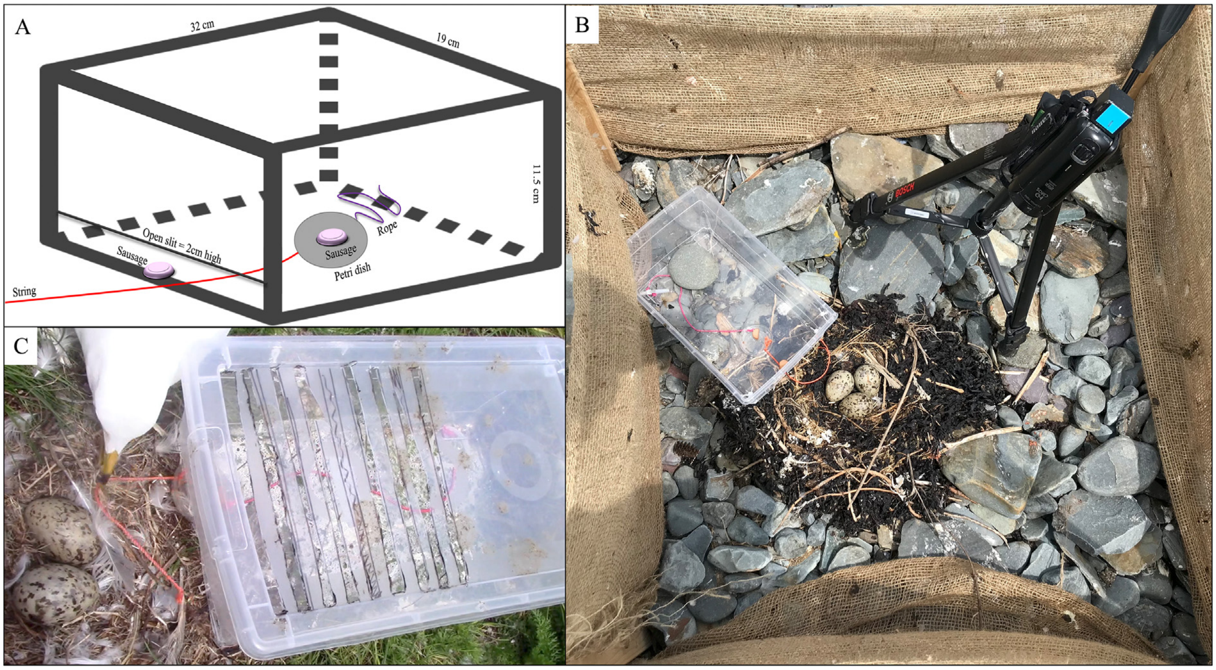

Fig. 2. Design of the string-pull test used to assess the problem-solving skills of ring-billed gulls. (A) Horizontal rendition of the string-pull test, in which food (sausage) is placed on a Petri dish inside the transparent box; to obtain the sausage, the bird must pull on a string that is tied to the Petri dish and which extends out of the box through a slit at the base of the front panel. (B) Nests were surrounded by a burlap fence. The string-pull test box is next to the nest with its lid removed. The box contains a sausage in a Petri dish and a rock used to secure the box in place. (C) A gull identified in a previous video frame by its purple band successfully solves the test by pulling on the string (pictured).

disulfide, and run in a gas chromatograph for 45 min on an Omegawax X 320 (30 m × 0.32 mm) column from Supelco (Sigma-Aldrich, Canada) using a flame ionization detector (Chechi et al., 2010). We used fatty acid standards (PUFA-2, -3, and Supelco 37 component FAME mix; Sigma-Aldrich, Canada) to identify the fatty acids by retention time. Before transmethylation, we added an internal standard (nonadecanoic acid C19:0, Sigma-Aldrich, Canada) of known concentration to calculate the concentration of each fatty acid. Results are expressed as relative concentration using percentage of total identified fatty acids.

2.4. Stable isotope analysis

The stable isotope ratios of carbon ($^{13}C/^{12}C$, expressed in delta notation as $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$, expressed as $\delta^{15}N$) are dietary tracers found in the tissues of consumers. They originate from the foods consumed by an animal and indicate the type of ecosystem ($\delta^{13}C$) and trophic level ($\delta^{15}N$; Hobson et al., 1994; Perkins et al., 2014) exploited at the time the tissue was produced. Given the 2–4 week turnover rate of red blood cells, their stable isotope ratios should reflect the gulls' diets during the same timeframe (Bearhop et al., 2002). Here, we used stable isotope analysis to corroborate our expectation that rural nesters foraged primarily in the marine ecosystem. Marine food webs and, to a lesser extent, freshwater food webs, are typically longer than terrestrial and anthropogenic food webs and thus are characterized by enriched $\delta^{15}N$ (an increase of 2–4 ‰ with each increasing trophic level; Chisholm et al., 1982; Hobson, 1987; McCutchan et al., 2003; Minagawa and Wada, 1984; Schoeninger et al., 1983). In North America, $\delta^{13}C$ also tends to be higher in marine ecosystems than in terrestrial ecosystems because of differences in the source of inorganic carbon incorporated by primary producers (Chisholm et al., 1982; Schoeninger and DeNiro, 1984). We also used the stable isotope analysis to estimate the degree to which gulls fed on anthropogenic food. Gulls foraging in urban centres primarily consume garbage, which is characterized by the heavy presence of corn and sugarcane, as well as proteins derived from livestock consuming corn (Chesson et al., 2008; Nakamura et al., 1982). Compared to the natural terrestrial food web of North America, these two plants are highly enriched in $\delta^{13}C$ (Smith and Epstein, 1971; O'Leary, 1981; van der Merwe, 1982). Thus, in generalist predators such as ring-billed gulls, individuals feeding primarily on anthropogenic foods should have high $\delta^{13}C$ and low $\delta^{15}N$ (owing to the lower number of trophic levels in anthropogenic food webs; Chisholm et al., 1982; Hobson, 1987; Schoeninger et al., 1983), in combination with low levels of n3-LCPUFAs. In contrast, gulls feeding on natural food sources are expected to have highly variable levels of $\delta^{15}N$ owing to their generalist nature, with the lower end of the $\delta^{15}N$ distribution expected in individuals specializing on exploiting terrestrial ecosystems and the higher end in those specializing on fish. In addition, gulls exploiting terrestrial ecosystems should have low $\delta^{13}C$, those feeding in freshwater ecosystems should have intermediate $\delta^{13}C$, and those feeding in marine ecosystems should have high $\delta^{13}C$ (Chisholm et al., 1982; Hebert et al., 1999; Hobson, 1987; Schoeninger et al., 1983).

A 100 μL subsample of each red blood cell fraction was freeze-dried for 48 h and then homogenized. Lipids were not extracted owing to their low content in the red blood cell fraction (elemental C:N < 3.5; Post et al., 2007). The subsamples were sent to the Stable Isotope Laboratory at Memorial University of Newfoundland and Labrador for analysis. After being weighed in tin capsules (range: 0.84 to 1.10 mg), their $\delta^{13}C$ and $\delta^{15}N$ content was quantified simultaneously using a Delta V Plus (Carlo Erba) continuous-flow isotope ratio mass spectrometer. The isotope ratios are expressed as parts per thousand (‰) relative to the international standards Vienna Pee Dee Belemnite (VPDB) for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$ following the equation: $\delta^{15}N$ or $\delta^{13}C = [(R_{sample} / R_{standard}) - 1] \times 1000$, where $R = {}^{15}N/{}^{14}N$ or ${}^{13}C/{}^{12}C$, respectively. B2155 protein was used as a reference standard and EDTA #2 and USGS62 were used for isotopic calibration. Replicates ($N = 78$) using these certified materials were spaced throughout runs and indicated average standard deviations of ±0.11 ‰ for $\delta^{15}N$ and ± 0.03 ‰ for $\delta^{13}C$. Due to an insufficient amount of red blood cell fraction, four banded birds from Long Pond and one banded bird from Salmonier were not included in the stable isotope analysis.

2.5. Molecular sexing analysis

Male and female ring-billed gulls could not be distinguished in the field. We therefore determined sex genetically using the red blood cell fraction of the centrifuged blood samples following the methods of Fridolfsson and Ellegren (1999). Sex was determined by counting the number of bands appearing in the gel. One band (approximately 650 bp) indicates a male, whereas two bands (approximately 650 and 450 bp) indicate a female (Fridolfsson and Ellegren, 1999; Indykiewicz et al., 2019).

2.6. Video analysis

We used BORIS event recording software (version 7.9 RC1; Friard and Gamba, 2016) to score the gulls' behaviours during the string-pull test trials. First, we identified which mate was present during a given trial based on the presence or absence of a specific colour band. Each parent was given a unique identifier to account for their presence during multiple trials. There were five instances where a pilfering gull entered a fenced nest and stole the easily accessible sausage from the edge of the box, but it was always possible to distinguish these thieves from legitimate parents. The thieves arrived and departed very rapidly and never attempted to retrieve the sausage from the Petri dish, whereas parents tended to resume incubation after returning to their nest. Once the parent was identified, we noted whether it ate the easily accessible sausage left at the rim of the box and then recorded any subsequent interactions with the string-pull test, including the number of pecks made to the box or to the string before solving the test or the test ending. We considered any interactions with the testing apparatus beyond eating the easily accessible sausage as an indicator that the gull was interested in solving the test, and the number of those interactions as a measure of its effort towards obtaining the food reward. A gull successfully solved the test if it retrieved and consumed the sausage from the Petri dish.

2.7. Statistical analysis

All statistical analyses were performed in R (version 4.1.0, R Core Team, 2021). Models were validated using diagnostic Q-Q plots and plots of residuals versus fitted values to ensure that there were no patterns observed in the residuals and, for appropriate models, that they were normally distributed. We simulated the responses of all models and plotted the simulated and raw data as semi-transparent layers on the same histogram to ensure an appropriate overlap between the two. We tested for zero-inflation using the *DHARMa* package in R (Hartig, 2022) and we found that the number of zeros in the real data was similar to that of the simulated datasets ($p > 0.05$ in all cases), suggesting that zero-inflation was not a problem in our models. The models' goodness of fit (R^2) was computed using the *performance* package in R (Lüdecke et al., 2021). Interactions were kept only when statistically significant, otherwise they were dropped and the model refitted. We did not find evidence of collinearity in our models with multiple continuous predictors as the variance inflation factors were consistently below 5.0. Significance thresholds were set at $\alpha = 0.05$.

2.7.1. Stable isotope differences between urban and rural colonies

Possible differences in $\delta^{13}C$ and $\delta^{15}N$ were investigated as a function of the colonies' urbanization (urban versus rural) using linear models (LM). We included sex and mass as covariates in each model because heavier males might outcompete smaller individuals for high-value food resources (Phillips et al., 2011; Ronconi et al., 2014). We then determined the isotopic niche breadth of each colony and of rural and urban nesters using bivariate means with one standard deviation and standard ellipse areas (SEA) encompassing 95 % of the raw data points around the groups' means, which equate to two standard deviations beyond the mean (Jackson et al., 2011). Using the *SIBER* package (Jackson et al., 2011), we accounted for our small sample sizes by calculating the SEA with a correction factor (SEAc). We also computed Bayesian ellipses (SEAb; 10,000 model iterations and the default priors to generate confidence intervals) for comparison with the SEAc. Stable isotope signatures of potential prey items were drawn from the existing literature (Table S1) and plotted alongside the ring-billed gulls' signatures to help identify the foods the gulls might be consuming at each colony. A diet-tissue discrimination factor based on the blood of ring-billed gull chicks (-3.10 for $\delta^{15}N$, $+0.30$ for $\delta^{13}C$, as per Hobson and Clark, 1992) was applied to the gulls' $\delta^{13}C$ and $\delta^{15}N$ values to allow comparisons with $\delta^{13}C$ and $\delta^{15}N$ values from potential prey. Comparisons between these adjusted $\delta^{13}C$ and $\delta^{15}N$ values and the isotopic profiles of prey should be interpreted with caution because a gull's isotopic signature can be derived in multiple ways. For example, values similar to the stable isotope values for shrimp could be derived by eating a diet comprising mainly shrimp, or by consuming multiple other foods (e.g., amphipods, beef from fast-food restaurant, and Atlantic cod) that, together, yield an average isotopic signature similar to that of shrimp. To strengthen our understanding of the foraging habits of the gulls sampled, we also extracted isotopic signatures of comparable avian species with known foraging niches from the literature (Table S1) and plotted them alongside the ring-billed gulls' unadjusted $\delta^{13}C$ and $\delta^{15}N$ values.

2.7.2. Fatty acid differences between urban and rural colonies

We tested whether gulls consumed different levels of EPA and DHA based on their urbanization (urban versus rural) using general linear models (GLMs) that included sex and mass as covariates. Since neither sex nor mass showed a relationship with the n3-LCPUFAs, we removed these variables from our models and compared the entire fatty acid profile of urban and rural nesters using non-parametric Mann Whitney *U* tests to account for the non-normality of the fatty acid data. Linear regressions were then performed to investigate possible relationships between the stable isotope values and the n3-LCPUFA concentrations.

2.7.3. Success at solving the string-pull test

We focused our analysis on trials in which the subjects showed an interest in solving the test (i.e. they pecked the box or inserted their bill into the box's open slit after eating the easily accessible sausage left at the edge of the slit). Our intention was to limit the analyses to trials in which subjects were hungry and recognized the sausage inside the box as food. This was important because several parents ignored the box upon returning to their nests, suggesting that they were either indifferent to the presence of food at their nest or they did not recognize it as food. Since it is possible that urban foragers would have encountered sausage before and thus been more likely to recognize it as food, we tested whether urbanization influenced the birds' likelihood of showing an interest in solving the test. Although we deployed the string-pull test three times at each nest, each parent was typically present and showing interest in solving the test during only one trial ($N = 63$), whereas few parents undertook a second ($N = 29$) or third trial ($N = 12$). We restricted our analyses to the gulls' performance during their first attempt at solving the test to remove potential confounding effects of experience from individuals whose repeated attempts could have influenced their solving success during later trials. However, additional analyses exploring the gulls' performance over repeated trials are available in the supplementary material.

We used a GLM with a binomial distribution to test whether the urbanization of the gulls' colonies (urban versus rural) predicted whether the birds showed an interest in solving the test during the first trial for which they were present.

We then used the entire sample of parents that showed an interest in solving the string-pull test ($N = 104$, including $N = 47$ banded parents (Long Pond = 19, Spaniard's Bay = 17, Old Perlican = 6, Salmonier = 5) and $N = 57$ unbanded parents (Long Pond = 25, Spaniard's Bay = 19, Old Perlican = 10, Salmonier = 3)) to investigate the effect of urbanization on string-pull test performance. We used a GLM with a binomial distribution to test whether urbanization (urban versus rural) predicted whether they solved the string-pull test during their first solving attempt. We also included in the model the number of pecks made to the box ahead of either solving the test or the test ending to test whether the gulls' effort influenced their probability of solving success. The interaction between urbanization and effort was not significant and therefore was dropped from the model.

Focusing on the subset of parents that we had captured and from which we obtained a blood sample, we then tested whether their n3-LCPUFA consumption and trophic niche predicted their performance on the string-pull test. Once again, we restricted this analysis to the subjects' performance during the first trial in which they showed an interest in solving the string-pull test ($N = 43$ gulls: 10 solvers and 33 non-solvers). Analyses exploring their performance over repeated trials are available in the supplementary material. We used a GLM with a binomial distribution. We included urbanization, DHA, EPA, $\delta^{13}C$, and $\delta^{15}N$ as predictors and whether the subject solved the test as the dependent variable. We kept only the significant fixed effects from a preliminary version of this GLM and then added the predictors ARA, LA, and the number of pecks made to the box during the solving attempt (proxy for solving effort) to further explore the relationship between the type of fatty acid consumed (n3-LCPUFAs or n6-PUFAs), their persistence towards obtaining the food reward, and their success at solving the string-pull test. Using our most parsimonious model, we tested whether there were interactions between urbanization and the biochemical predictors of our most parsimonious model and found them to be non-significant, therefore they were dropped and the model refitted.

3. Results

3.1. Stable isotope differences between urban and rural colonies

There were significant differences in the stable isotope signatures of the red blood cells of ring-billed gulls based on the urbanization of their colony (Type III; $\delta^{13}C$: $F_{1,126} = 118.56$, $p < 0.001$; $\delta^{15}N$: $F_{1,126} = 158.92$, $p < 0.001$). On average, gulls nesting in the urban colonies had significantly lower values of $\delta^{13}C$ (Long Pond: mean ± SD = −22.98 ± 0.71 ‰, range −24.24 to −21.26 ‰; Spaniard's Bay: mean ± SD = −21.91 ± 1.26 ‰, range −25.02 to −19.20 ‰) and $\delta^{15}N$ (Long Pond: mean ± SD = 9.45 ± 1.52 ‰, range 7.09 to 12.96 ‰; Spaniard's Bay: mean ± SD = 10.23 ± 1.50 ‰, range 7.62 to 13.29 ‰) than rural nesters (Old Perlican: $\delta^{13}C$ = −20.65 ± 0.66 ‰ (mean ± SD), range −22.50 to −19.05 ‰; $\delta^{15}N$ = 12.62 ± 0.81 ‰ (mean ± SD), range 10.58 to 13.60 ‰; Salmonier: $\delta^{13}C$ = −20.09 ± 0.74 ‰ (mean ± SD), range −22.49 to −19.32 ‰; $\delta^{15}N$ = 13.35 ± 0.64 ‰ (mean ± SD), range 12.02 to 14.49 ‰). Neither stable isotope was related to sex or mass ($p > 0.05$).

The isotopic niche breadths of rural and urban colonies were distinct from each other (Figs. 3 and S2). Urban gulls exploited large foraging niches (SEA_c: Long Pond = 3.50; Spaniard's Bay = 4.43), whereas rural nesters showed much narrower niche breadths (SEA_c: Old Perlican = 1.49; Spaniard's Bay = 1.39).

Gulls nesting in rural environments (Old Perlican and Salmonier) fed at a higher trophic level than urban nesters (Long Pond and Spaniard's Bay) and tended to exploit food sources enriched in $\delta^{13}C$ (Fig. 3). Their adjusted isotopic signatures align with the $\delta^{15}N$ and $\delta^{13}C$ values reported for some marine invertebrates and fish found in Newfoundland's marine ecosystem (Fig. 3a, Table S1). We note that the gulls' adjusted isotopic signatures are most closely aligned with those of shrimp, and that we observed large amounts of shrimp exoskeletons throughout their colonies. Although the gulls' adjusted isotopic values are consistent with a diet of shrimp, such values could also be derived by consuming multiple other foods that together yield a similar average stable isotope signature. The unadjusted signatures of the gulls (i.e. no tissue-discrimination factor applied) are also comparable to those of other birds that specialize on marine food sources, including common murres (*Uria aalge*), razorbills (*Alca torda*), and herring gulls (*Larus argentatus*) and great black-backed gulls (*Larus marinus*) from populations that are known to forage primarily at sea (Fig. 3b, Table S1). In contrast, the adjusted $\delta^{15}N$ and $\delta^{13}C$ values of urban nesters are bordered by the isotopic signatures of mainly freshwater and terrestrial prey and anthropogenic food (Fig. 3a). This includes freshwater fish and terrestrial and freshwater invertebrates on the $\delta^{13}C$-depleted side of their isotopic niche, and anthropogenic food sources (mink farm wastes, refuse, fast food meats) on the $\delta^{13}C$-enriched side (Fig. 3a). Their diet might also include some marine prey such as copepods (Fig. 3a). Their non-adjusted isotopic values more closely resemble those of bird species that prey on freshwater and terrestrial invertebrates (American robins, *Turdus migratorius*; tree swallows, *Tachycineta bicolor*; song sparrow, *Melospiza melodia*), as well as those of ring-billed gulls nesting away from marine environments and foraging on anthropogenic foods and freshwater fish (Fig. 3b, Table S1).

3.2. Fatty acid differences between urban and rural colonies

As predicted, the fatty acid profiles of gulls differed significantly between urban and rural colonies (Table 1). Compared to gulls nesting at the rural colonies Old Perlican and Salmonier, the urban nesters of Long Pond and Spaniard's Bay had higher levels of n6-PUFAs (ARA, LA) and lower levels of n3-LCPUFAs (DHA, EPA), resulting in a mean n6:n3 ratio more than three to five times greater than that of rural nesters (Table 1). Large variations in the fatty acid profiles of gulls with similar degrees of urbanization still existed, particularly among urban nesters in accordance with their larger trophic niche (Table 1). Levels of EPA and DHA in urban nesters ranged from 0.36 to 20.0 % and 0.94 to 11.0 % respectively, whereas levels of EPA and DHA in rural nesters ranged from 3.59 to 19.80 % and 4.32 to 19.80 % respectively.

3.3. Success at solving the string-pull test

String-pull tests typically began with a parent returning to their nest within 2.7 ± 2.3 (mean ± SD) minutes of the researcher's departure and either resuming incubation immediately or shortly after investigating the testing apparatus. Those that investigated the box usually started by eating the easily accessible sausage left beside the string at the open slit. They then either ignored the box for the remainder of the trial or interacted with it further by pecking at the box, inserting their bill into the open slit, or pulling on the string. The urbanization of the gulls' colonies (urban versus rural) did not influence their probability of expressing an interest in solving the test (i.e., interacting with the testing apparatus beyond eating the easily accessible sausage) during the first trial for which they were present (Table 2 model 1). Out of 104 banded and unbanded parents that interacted with the box, 21 of them solved the test during their first solving attempt by pulling on the string and extracting and consuming the sausage (16 of 80 urban nesters and 5 of 24 rural nesters; Movie S1). Gulls from all four colonies solved the test, and their probability of success was not predicted by their effort at obtaining the food reward (number of pecks to the box) or by urbanization, whether the analyses were restricted to the gulls' first attempt at solving the test, (Table 2 model 2; Fig. S3) or whether their performance over repeated trials was taken into account (Supplementary Analyses, Table S1).

Contrary to our prediction, gulls with less DHA and more $\delta^{13}C$ in their red blood cells during the incubation period were more likely to solve the test during their first solving attempt (Table 3 model 1, Figs. 4 and 5). Similar results were obtained when repeated trials were considered (Supplementary Analyses, Table S1). It is noteworthy that DHA and $\delta^{13}C$ are positively correlated (Pearson $r = 0.64$, $p < 0.001$; subset of 43 gulls that attempted to solve the test), yet show opposite relationships with the gulls' probability of solving the test (Fig. 5). Levels of EPA and $\delta^{15}N$ in the red blood cells did not predict whether subjects solved the test, and neither did their urbanization (Table 3 model 1, Fig. 4). Whether or not subjects solved the test was not significantly related to the interactions between urbanization of the gulls' colonies and either their DHA levels ($p = 0.834$, odd ratio = 12.0, CI [0.23, 95.60])) or C13 levels ($p = 0.194$ odd ratio = 0.18, CI [0.0, 29.30]); these interactions were thus dropped from the final model.

When added to a reduced model containing DHA and $\delta^{13}C$ as predictors, ARA, LA, and solving effort (the number of pecks on the box during their

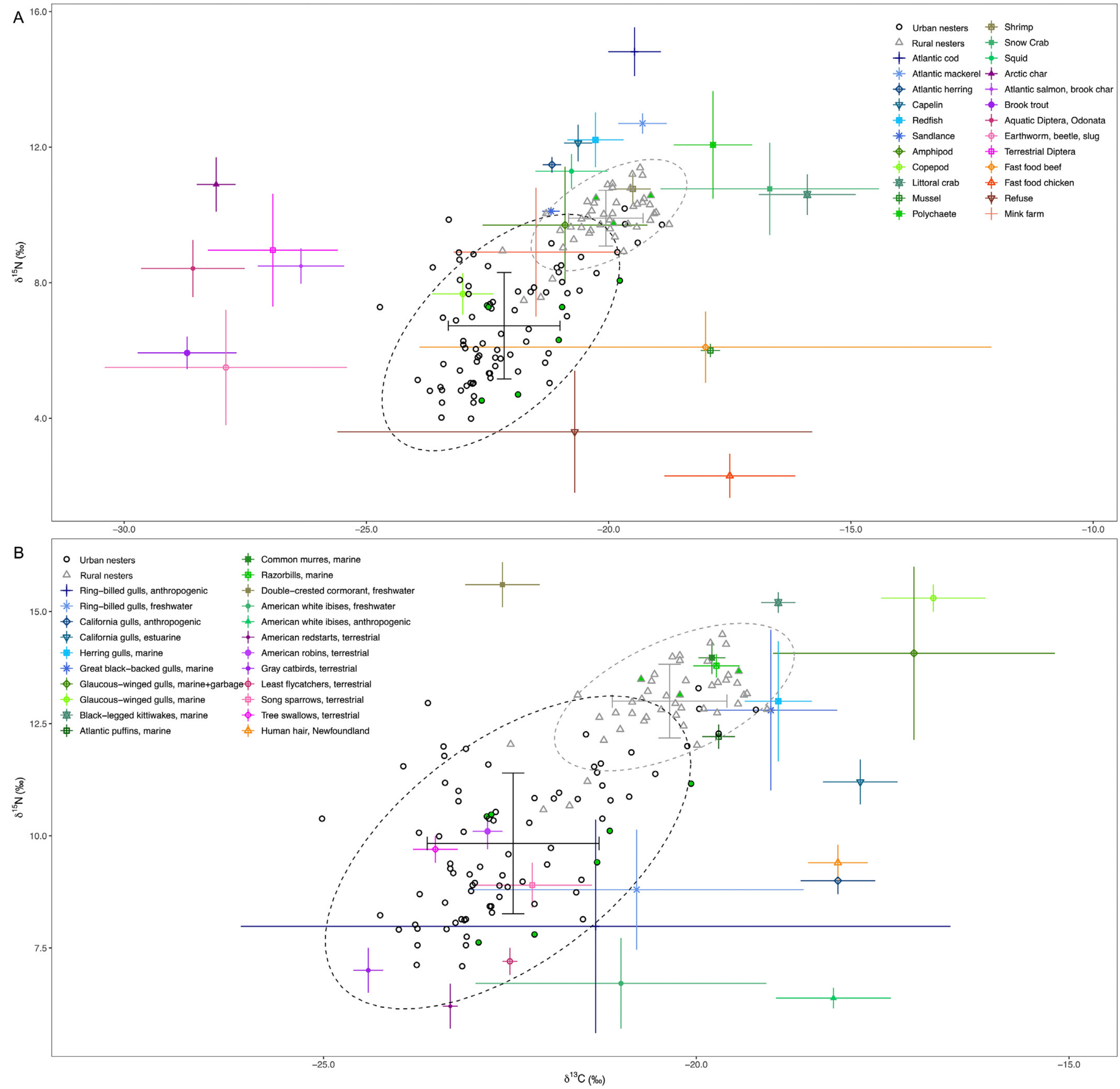

Fig. 3. Stable isotope signatures ($\delta^{15}N$ and $\delta^{13}C$ (‰)) of ring-billed gulls nesting in urban (Long Pond, Spaniard's Bay; black circles, $N = 82$) and rural colonies (Old Perlican, Salmonier; grey triangles, $N = 47$) with fill colour corresponding to their performance at the string-pull test during their first solving attempt (green = solved the test, white = failed to solve the test), in relation to (A) their possible food sources or (B) other avian species with comparable foraging niche. The bivariate means (±SD, connected lines) and the 95 % ellipse areas (dashed lines) from urban and rural colonies are included for comparison. (A) The bivariate means (±SD) of potential food sources were drawn from the literature (Table S1). To allow for comparisons between consumers and their potential prey, the stable isotope values of the gulls' red blood cells (RBC) were adjusted with a diet-tissue discrimination factor (−3.10 for $\delta^{15}N$, +0.30 for $\delta^{13}C$, as per Hobson and Clark, 1992). (B) The bivariate means (±SD) of comparable avian species were drawn from the literature (Table S1) and represent the isotopic values of these species' RBC or whole blood (Table S1). Here, the unadjusted isotopic values from our subjects' RBC are plotted for direct comparison with the isotopic values of other predatory birds exploiting parts of the ring-billed gull's forging niche.

first solving attempt) failed to predict whether a gull solved the string-pull test, though these models continued to show that gulls with less DHA and more $\delta^{13}C$ were significantly more likely to solve the test (Table 3 model 2, Fig. 4E). Our most parsimonious model containing only DHA and $\delta^{13}C$ show them both remaining as significant predictors of the gulls' probability to solve the test (Table 3 model 3).

4. Discussion

Ring-billed gulls nesting at rural locations (Old Perlican and Salmonier) fed at a higher trophic level and within a narrower trophic niche on marine foods rich in n3-LCPUFAs, whereas gulls nesting in urban locations (Long Pond and Spaniard's Bay) fed at a lower trophic level and across a broader

Table 1
Fatty acid profiles of the red blood cells of ring-billed gulls nesting at urban and rural colonies. The fatty acid concentrations are medians with their interquartile range (IQR) and are expressed as relative concentration (percentage of total identified fatty acids). Asterisks (*) indicate the fatty acids that differ significantly between urban and rural colonies based on Mann-Whitney *U* tests. Data are presented for all gulls from which a blood sample was drawn ($N = 133$).

Fatty acid (%)	Rural ($N = 47$)	Urban ($N = 86$)	Mann-Whitney U Statistic	*p*
C14:0	0.60 (0.19)	0.38 (0.15)	605	<0.001*
C14:1	0.06 (0.05)	0.10 (0.11)	1251	<0.001*
C16:0	16.40 (2.95)	15.40 (2.03)	1442	0.006*
C16:1*n*−7	2.45 (1.21)	1.02 (0.78)	647	<0.001*
C16:2*n*−4	0.26 (0.14)	0.40 (0.29)	1027	<0.001*
C17:0	0.33 (0.08)	0.49 (0.27)	785	<0.001*
C18:0	15.60 (2.22)	18.0 (2.44)	847	<0.001*
C18:1*n*−9	16.40 (4.72)	17.10 (5.16)	1940	0.705
C18:1*n*−7	3.58 (1.26)	2.33 (1.0)	656	<0.001*
C18:2*n*−6 (LA)	2.48 (0.59)	7.93 (4.58)	212	<0.001*
C18:3*n*−6	0.11 (0.17)	0.10 (0.19)	1922	0.631
C18:3*n*−3 (ALA)	0.34 (0.24)	0.38 (0.26)	1430	0.005*
C20:0	0.22 (0.08)	0.30 (0.15)	1262	<0.001*
C18:4*n*−3	1.24 (0.91)	0.30 (0.41)	608	<0.001*
C20:2	0.22 (0.13)	0.33 (0.30)	1384	0.003*
C20:4*n*−6 (AA)	13.40 (5.27)	21.30 (5.73)	425	<0.001*
C20:5*n*−3 (EPA)	9.63 (4.58)	1.85 (2.56)	326	<0.001*
C22:0	0.28 (0.13)	0.37 (0.19)	1397	0.003*
C22:1*n*−9	0.44 (0.55)	0.20 (0.21)	1109	<0.001*
C22:5*n*−6	0.37 (0.13)	1.02 (0.50)	103	<0.001*
C22:5*n*−3	1.52 (0.36)	1.61 (0.90)	1734	0.177
C22:6*n*−3 (DHA)	8.74 (2.54)	2.96 (3.61)	283	<0.001*
Σ SFAs[a]	33.80 (3.01)	35.30 (2.76)	1539	0.023*
Σ MUFAs[b]	23.20 (6.9)	21.0 (5.33)	1499	0.014*
Σ PUFAs[c]	39.90 (4.22)	39.90 (3.86)	1862	0.456
Σ *n*6 FAs[d]	16.70 (6.27)	31.10 (4.11)	184	<0.001*
Σ *n*3 FAs[e]	22.10 (5.16)	8.03 (6.33)	252	<0.001*
Ratio *n*6/*n*3	0.73 (0.41)	4.06 (2.67)	175	<0.001*

[a] Sum of saturated fatty acids: C14:0 + C16:0 + C17:0 + C18:0 + C20:0 + C22:0.
[b] Sum of monounsaturated fatty acids: C14:1 + C16:1n7 + C18:1n9 + C18:1n7 + C22:1n9.
[c] Sum of polyunsaturated fatty acids: C16:2n4 + C18:2n6 + C18:3n6 + C18:3n3 + C18:4n3 + C20:2 + C20:4n6 + C20:5n3 + C22:5n6 + C22:5n3 + C22:6n3.
[d] Sum of omega-6 polyunsaturated fatty acids: C18:2n6 + C18:3n6 + C20:2 + C20:4n6 + C22:5n6.
[e] Sum of omega-3 polyunsaturated fatty acids: C18:3n3 + C18:4n3 + C20:5n3 + C22:5n3 + C22:6n3.

Table 2
The urbanization of ring-billed gulls' colonies (urban versus rural) was not related to their probability of showing interest in solving the string-pull test during their first exposure to it, nor to their success at solving it during their first solving attempt. The effort put towards solving the test (measured as the number of times the bird pecked the box during the solving attempt) was also not associated with the birds' likelihood of solving the test.

Model	Response	Predictors	Estimates	Standard error	df	LR χ^2	*p*
	Interest towards	Intercept	0.27	0.33			
1[a]	solving the string-pull test (Yes/No)	Urbanization (Urban)	0.48	0.40	1	1.47	0.225
		R^2	0.01[c]				
	Solved the	Intercept	−1.31	0.62			
2[b]	string-pull test (Yes/No)	Urbanization (Urban)	−0.04	0.58	1	0.01	0.943
		Effort	<0.01	0.03	1	<0.01	0.945
		R^2	<0.01[c]				

The responses were modeled using general linear models with a binomial distribution.
[a] This model included all banded and unbanded gulls during their first exposure to the test; $N = 138$ gulls.
[b] This model included all banded and unbanded gulls during their first attempt at solving the test; $N = 104$ gulls.
[c] Marginal R^2.

Table 3
Ring-billed gulls consuming foods with less DHA and higher $\delta^{13}C$ during incubation had a greater probability of solving the string-pull test during their first solving attempt. The concentrations of docosahexaenoic acid (DHA), eicosapentaenoic acid (EPA), arachidonic acid (ARA), and linoleic acid (LA), and the stable isotopic values of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), were measured in the red blood cells of banded adult ring-billed gulls that continued to interact with the string-pull test box beyond eating the easily accessible sausage placed at the slit of the box ($N = 43$ colour banded birds). Solving effort was measured as the number of times the bird pecked the box during their first solving attempt and urbanization is a binary variable classifying Long Pond and Spaniard's Bay as urban and Old Perlican and Salmonier as rural. DHA, EPA, ARA, and LA are expressed as relative concentrations (percentage of total identified fatty acids) and $\delta^{13}C$ and $\delta^{15}N$ are expressed as parts per thousand (‰).

Model	Response	Predictors	Estimates	Standard error	df	LR χ^2	*p*
	Solved the	Intercept	53.60	23.50			
1	string-pull test (Yes/No)	Urbanization (Urban)	−2.95	2.49	1	1.94	0.164
		DHA	−1.0	0.49	1	7.11	0.008*
		EPA	−0.35	0.264	1	2.34	0.125
		$\delta^{13}C$	2.18	0.90	1	10.0	0.002*
		$\delta^{15}N$	0.11	0.49	1	0.05	0.826
		R^2	0.68[a]				
	Solved the	Intercept	46.36	19.11			
2	string-pull test	DHA	−0.63	0.40	1	3.89	0.049*
	(Yes/No)	$\delta^{13}C$	2.08	0.82	1	12.33	<0.001*
		ARA	0.02	0.13	1	0.02	0.885
		LA	0.19	0.19	1	1.01	0.314
		Effort	−0.10	0.09	1	1.32	0.250
		R^2	0.61[a]				
	Solved the	Intercept	44.05	17.19			
3	string-pull test	DHA	−0.86	0.35	1	10.14	0.001*
	(Yes/No)	$\delta^{13}C$	1.88	0.72	1	11.90	<0.001*
		Model 3 R^2	0.58[a]				

The responses were modeled using general linear models with a binomial distribution.
* Significant result ($p < 0.05$).
[a] Marginal R^2.

trophic niche on terrestrial and anthropogenic foods that were poor in n3-LCPUFAs. These differences existed despite all four colonies having free access to the marine environment. Nevertheless, important within population variation in the biochemical profiles of gulls existed, particularly among urban nesters, demonstrating that individuals from environments with similar degrees of urbanization had different foraging habits despite having access to similar foraging opportunities. In addition to large intra-colony variations, greater dietary variability existed between the urban colonies Long Pond and Spaniard's Bay than between the rural colonies Old Perlican and Salmonier. During their incubation period, gulls with less DHA and higher $\delta^{13}C$ in their red blood cells were more likely to solve the string-pull test, despite DHA and $\delta^{13}C$ being positively correlated. This combination of low DHA and high $\delta^{13}C$ indicates a mainly anthropogenic diet because anthropogenic food is deficient in n3-LCPUFAs and enriched in $\delta^{13}C$. Concentrations of other PUFAs important for cognition, such as EPA, ARA, and LA, did not predict whether gulls solved the string-pull test.

Gulls nesting at rural colonies with minimal access to anthropogenic food relied heavily on marine prey, as revealed by red blood cells with high levels of EPA and DHA and isotopic signatures matching those of marine organisms and marine consumers. This was predictable because nesting ring-billed gulls typically forage within a 20 km radius of their colony (Caron-Beaudoin et al., 2013; Patenaude-Monette et al., 2014). Since our rural colonies were located >50 km from any urban centre and had low degrees of urbanization, most rural nesters might have had more difficulties finding significant amounts of anthropogenic food. Although they also had access to freshwater lakes and a terrestrial environment comprising mainly boreal forest, the composition of their red blood cells nevertheless indicates that they foraged primarily in the marine

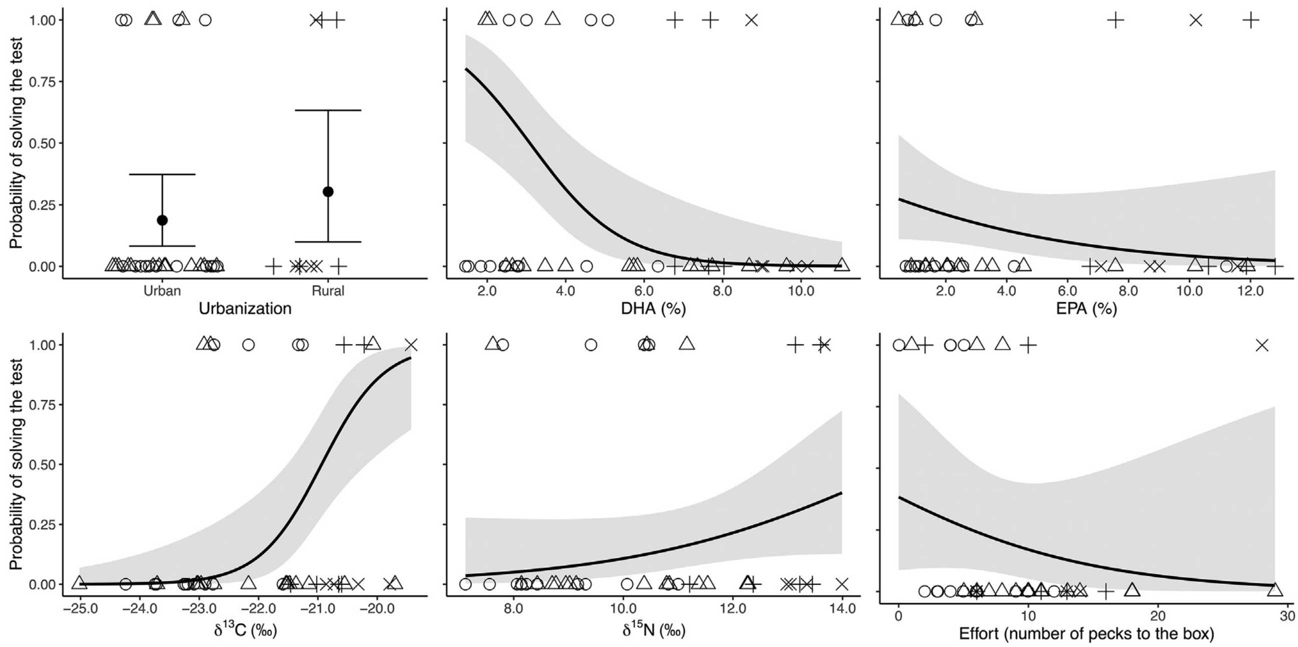

Fig. 4. Ring-billed gulls with less DHA and higher $\delta^{13}C$ in their red blood cells during incubation were more likely to solve the string-pull test during their first solving attempt. The concentrations of docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA) are expressed as relative concentrations (percentage of total identified fatty acids), the stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are expressed as parts per thousand (‰), and effort was measured as the number of times the bird pecked the box during their first solving attempt. Urbanization is a binary variable classifying Long Pond and Spaniard's Bay as urban and Old Perlican and Salmonier as rural colonies. Raw data indicate the solving performance of 43 banded gulls during their first solving attempt and are represented by the points, with shapes corresponding to colony (Long Pond = O, Spaniard's Bay = Δ, Old Perlican = +, Salmonier = x). The predicted relationships are represented by a black line with grey fill (95 % confidence interval).

environment. In contrast, urban gulls nesting at Long Pond and Spaniard's Bay relied more heavily on terrestrial and anthropogenic food sources, as evidenced by their overall low levels of EPA and DHA and high levels of ARA and LA in their red blood cells (Gladyshev and Sushchik, 2019; Mathieu-Resuge et al., 2021). Their isotopic signatures were also similar to those of terrestrial and anthropogenic food sources and to those of consumers of such foods, which further suggests a primarily terrestrial and anthropogenic diet (Davis et al., 2017; de Faria et al., 2021; Garthe et al., 2016).

Gulls from urban and rural colonies consumed different types of food on average, yet considerable variation also existed among the biochemical profiles of gulls nesting at the same type of colony, and even within the same colony. In particular, the broad trophic niche of urban nesters and their large range in n3-LCPUFA levels indicate important dietary variability at the individual level, despite urban gulls all having access to similar foraging opportunities. Differences in the choice of foraging habitats among ring-billed gulls nesting at the same colony have been reported previously (Caron-Beaudoin et al., 2013; Marteinson and Verreault, 2020), demonstrating that this species is not uniform in their dietary choices, at least during their incubation period. Even rural nesters showed individual variability in biochemical profiles, albeit to a lesser degree than urban gulls, despite having less anthropogenic food in their surrounding environment. Accordingly, we suggest that the urbanization of the gulls' colonies did not predict their performance at the string-pull test because it did not accurately represent the type of food consumed by individuals. As such, urban nesters that did not consume a lot of anthropogenic food might have underperformed at the string-pull test compared to other urban nesters that relied heavily on anthropogenic food, and vice versa for rural nesters, thereby blurring any potential effect of urbanization on problem-solving performance.

Isotopic signatures of urban nesters are consistent with a diet that includes some low trophic marine prey such as copepods and some freshwater fish and invertebrates. However, given that most urban gulls had low levels of n3-LCPUFAs in their red blood cells, such prey were likely limited. Despite having full access to a marine environment, urban nesters still seemed to prefer terrestrial and anthropogenic foods, which is consistent with previous studies of gulls nesting near coastal urban settlements (yellow-legged gull, *Larus michahellis*: Arizaga et al., 2013, de Faria et al., 2021; herring gull: Enners et al., 2018; black-headed gull, *Larus ridibundus*: Garthe et al., 2016). Several studies have even found that gulls forego nearby marine environments to forage at landfills or terrestrial food resources located farther away (Arizaga et al., 2014; de Faria et al., 2021; Spelt et al., 2019; Zorrozua et al., 2020). Anthropogenic food sources are often more reliable in terms of their presence, location, and the quantity of food they provide; their increased profitability may thus explain the success of opportunistic urban foragers (Belant et al., 1998; Oro et al., 2013; Shochat, 2004).

Although multiple gull species have experienced population increases in recent decades owing to an increased availability of anthropogenic food (Aponte et al., 2014; Auman et al., 2008; Duhem et al., 2008; Lenzi et al., 2019; Oro et al., 2013; Weiser and Powell, 2010), the fitness consequences for individuals of selecting anthropogenic foods with high energetic return versus more natural prey containing essential nutrients has not been resolved (Murray et al., 2018; Oro et al., 2013). Several studies show that consuming a mixture of terrestrial and marine foods may benefit a gull's fitness (Auman et al., 2008; Lenzi et al., 2019; Weiser and Powell, 2010), whereas consuming diets comprising only anthropogenic or terrestrial foods may impair fitness (O'Hanlon et al., 2017; Pierotti and Annett, 2001; Sotillo et al., 2019; Zorrozua et al., 2020). It also remains unclear how preferences to forage on anthropogenic foods arise in gulls. Future research should explore the consistency of individual ring-billed gulls' foraging niches throughout the year and among years to explore whether urban nesters compensate for poor n3-LCPUFA intake during incubation by consuming more marine organisms at other times of the year. In other species of gull, individuals nesting in urban centres forage more in the marine environment at other times of the year (kelp gull, *Larus dominicanus*: Burgues et al., 2020; yellow-legged gull: de Faria et al., 2021; California gull, *Larus californicus*: Peterson et al., 2017).

Gulls with less DHA in their red blood cells during incubation were more likely to solve the string-pull test. This was unexpected because, to

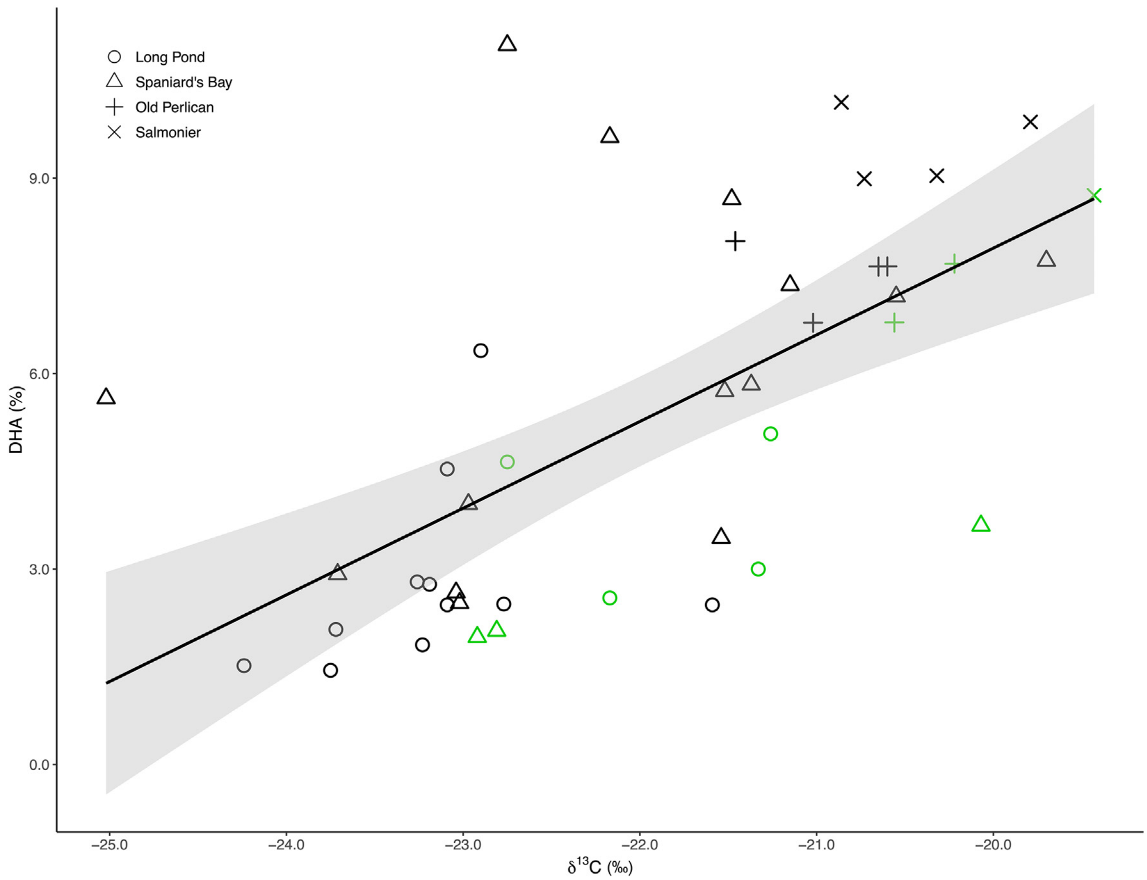

Fig. 5. Ring-billed gulls with less docosahexaenoic acid (DHA) and more carbon stable isotope ($\delta^{13}C$) in their red blood cells during incubation were more likely to solve the string-pull test during their first solving attempt. The relationship between the DHA and $\delta^{13}C$ is represented by the black line and fill (95 % confidence interval). DHA and $\delta^{13}C$ were measured in the red blood cells of 43 banded gulls (11 rural nesters and 32 urban nesters) that returned to their nest and interacted with the string-pull test box beyond eating the easily accessible sausage. DHA is expressed as relative concentration (percentage of total identified fatty acids) and $\delta^{13}C$ is expressed as parts per thousand (‰). Raw data are represented by the points, with shapes corresponding to colony and colour corresponding to their performance at the string-pull test (green = solved the test during their first attempt, black = failed to solve the test). The colonies in the legend are listed in order of decreasing urbanization gradient.

our knowledge, there is no evidence that enhanced tissue levels of DHA or increased consumption of n3-LCPUFAs impairs cognitive abilities. In contrast, our previous research suggests that increasing DHA in the tissues of ring-billed gull chicks might have improved their problem-solving skills, since chicks fed fish oil rich in DHA escaped a fence surrounding their nest and fledged at an earlier age than chicks fed a sugar water control (Lamarre et al., 2021). It is possible that birds that consumed large amounts of DHA also consumed inadequate amounts of ARA or of its precursor LA, since marine habitats rich in n3-LCPUFAs also tend to be relatively poor in n6-PUFAs (Gladyshev et al., 2016; Hixson et al., 2015; Twining et al., 2019). Although ARA is important for optimal neurological function (review by Hadley et al., 2016), we believe this explanation is unlikely because the concentration of ARA in the red blood cells did not predict whether gulls solved the string-pull test. We suggest instead that a gull's reliance on anthropogenic food determines both its probability of solving the string-pull test and its consumption of DHA, which is limited in anthropogenic food (Simopoulos, 2002). This explanation is supported by our finding that birds with higher $\delta^{13}C$ in their red blood cells were more likely to solve the string-pull test. $\delta^{13}C$ tends to be higher in marine ecosystems than in terrestrial ecosystems (Chisholm et al., 1982; Hobson, 1987; Hobson et al., 1994), but is also elevated in anthropogenic foods due to the abundance of sugarcane and corn in human products and in feeds given to livestock (Chesson et al., 2008; Schwarcz and Schoeninger, 1991; van der Merwe, 1982). Seabirds shifting their diets from marine organisms to refuse therefore tend to have reduced DHA and elevated $\delta^{13}C$ (Hebert et al., 2008, 1999), which is the combination that best predicted success in our string-pull test. We therefore suggest that reduced DHA and elevated $\delta^{13}C$ were not determinants of problem-solving ability, but, rather, consequences of exploiting anthropogenic food. In contrast to DHA and $\delta^{13}C$, urbanization, other fatty acids (EPA, LA, ARA), $\delta^{15}N$, and solving effort (number of pecks on the box) did not explain string-pull test performance, and their inclusion in our various statistical models did not change the relationships between string-pull test performance and $\delta^{13}C$ and DHA.

Among avian species and populations, brain size, innovation rate, and problem-solving ability are positively related to the ability to colonize new habitats and to thrive in urban settings (Audet et al., 2016; Griffin et al., 2017; Møller and Erritzøe, 2015; Sayol et al., 2020). As such, urban populations often outperform their rural counterparts during problem-solving tests (Audet et al., 2016; Biondi et al., 2021; Cook et al., 2017; Papp et al., 2015; Preiszner et al., 2017; Sol et al., 2011). Species and populations using a generalist foraging strategy, and those demonstrating high foraging flexibility, also tend to have larger relative forebrain size and higher innovation rates (Ducatez et al., 2015; Lefebvre et al., 1997; Overington et al., 2011). Our findings are partially consistent with these previous studies. Although urbanization did not predict the problem-solving abilities of the gulls in our study (we assume due to high within population variation in foraging habits), it was still the individuals with dietary signatures most associated with anthropogenic food (i.e., low DHA, high $\delta^{13}C$) that had better success at solving the string-pull test. Exploiting anthropogenic food is, in itself, considered to be an innovative behaviour (see innovation database in Lefebvre, 2021), which is associated with other proxies of cognition like residual brain size (Lefebvre et al., 2004; Overington et al., 2009), although some authors have argued that innovation can occur through non-cognitive means (see Lee and Thornton, 2021). Future studies should investigate whether anthropogenic foragers perform better at problem-solving tests because they have more experience obtaining foods from anthropogenic structures such as trash bins, and therefore may be more familiar with manipulating objects similar to those often used as problem-solving tests.

Paradoxically, our findings and previous studies demonstrate that birds foraging on anthropogenic food consume little n3-LCPUFAs (Andersson et al., 2015; Isaksson et al., 2017; Toledo et al., 2016), yet, n3-LCPUFAs are known to be important in animal cognition generally (Innis, 2008; Pilecky et al., 2021; Weiser et al., 2016). This raises an interesting question about whether aquatic birds and other avian species that are likely unable to convert ALA into EPA and DHA efficiently (Gladyshev et al., 2016; Twining et al., 2018) need to continue consuming n3-LCPUFAs throughout adulthood to preserve optimal brain structure and function, as is the case in mammals (Denis et al., 2013; Luchtman and Song, 2013; Pottala et al., 2014). Some studies suggest that the fatty acid profile of the avian brain becomes fixed by the end of embryonic development (Speake et al., 2003; Speake and Wood, 2005), but others show that ongoing consumption of n3-LCPUFAs can increase n3-LCPUFA content in the brain throughout the nestling stage (Lamarre et al., 2021; Price et al., 2018) and during adulthood (McCue et al., 2009). Therefore, the long-term effects of n3-LCPUFA deficiency on avian brain health and cognition remain unknown. As a first step in assessing whether ongoing n3-LCPUFA consumption continues to influence cognitive abilities beyond early development, the brains of adult birds feeding on different levels of EPA and DHA should be analyzed to determine whether reduced consumption of n3-LCPUFAs in adulthood leads to lower encephalic concentrations of these fatty acids. Future studies should also determine whether gulls mitigate a possible n3-LCPUFA deficiency during the breeding season by feeding on aquatic prey when they are not bound to their breeding colony. Finally, more research is needed to explore the homogeneity of cognitive abilities within urban and rural nesters to determine whether gulls nesting in urban environments tend to show more variations in cognitive traits, possibly because of greater differences in exposure to varying foraging opportunities or because of greater variations in consumption of key nutrients. Understanding potential links between the consumption of n3-LCPUFAs and cognition will provide critical insight into how declining n3-LCPUFAs will affect marine animals over the next several decades, when n3-LCPUFAs in the ocean are expected to all but disappear (Colombo et al., 2020; Hixson and Arts, 2016).

Data availability

The dataset used in this study is available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.4qrfj6qd3.

CRediT authorship contribution statement

Conceptualization: J.L.; Experimental Design: J.L., S.C., G.J.R., D.R.W.; Fieldwork: J.L., D.R.W.; Fatty Acid Analysis: J.L., S.C.; Video Coding: J.L.; Statistical Analysis: J.L., G.J.R., D.R.W.; Resources: S.C., G.J.R., D.R.W.; Writing - Original Draft: J.L.; Writing - Review & Editing: J.L., S.C., G.J.R., D.R.W.

Declaration of competing interest

The authors declare no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.157732.

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Foraging on anthropogenic food predicts problem-solving skills in a seabird

Supplementary material; Additional analyses

ADDITIONAL METHODS

As complementary analyses to our general linear models (GLMs) focusing on the gulls' performance at the string-pull test upon their first attempt at solving it, we also analyzed their performance upon repeated attempts using generalized linear mixed-models (GLMMs), since each subject could have attempted to solve the test over a maximum of three trials. Subject identity was included as a random factor to account for potential dependencies among multiple tests attempted by the same individual. Solving attempt (1, 2, or 3) was also included as a fixed effect in the models to control for a possible increase in success from repeated experience. Due to overparameterization issues, we could only apply this random effect and the fixed effect of attempt number to our most parsimonious models, as presented in the main text of the article (Table 2 model 2, Table 3 model 3). In addition to validating the GLMMs using diagnostic Q-Q plots and plots of residuals versus fitted values, as well as simulating the responses of all models in comparison with the raw data, we also checked that the random effect was normally distributed.

First, we used the entire sample of parents that showed an interest in solving the string-pull test during at least one trial (N=104, including N=47 banded parents and N=57 unbanded parents) to investigate the effect of urbanization (urban vs rural) on string-pull test performance. We also included in the model the number of pecks made to the box ahead of either solving the test or the test ending to test whether the gulls' effort influenced their probability of solving success. Using a GLMM with a binomial distribution, we included urbanization, effort, and attempt number as fixed effects, whether the subject solved the test as the dependent variable, and subject identity as a random effect.

Focusing on the subset of parents that we had captured and from which we obtained a blood sample (N=43), we then tested whether their levels of DHA and $\delta^{13}C$ predicted their success at the string-pull test. Once again, we restricted this analysis to trials in which the subject showed an interest in solving the string-pull test. Using a GLMM with a binomial distribution, we included DHA, $\delta^{13}C$, and attempt number as fixed effects, whether the subject solved the test as the dependent variable, and subject identity as a random effect.

ADDITIONAL RESULTS

Taking into account the gulls' repeated attempts at solving the test led to the same findings as described in the article's main text. The gulls' probability of success was not predicted by their effort at obtaining the food reward or by whether they were from an urban versus remote colony (Table S1 model 1). Less DHA and more $\delta^{13}C$ in the gulls' red blood cells continued to predict a higher likelihood of solving the test (Table S1 model 2). While including attempt number controlled for possible learning experience from repeated exposures to the test, this variable was never significant when included as a fixed effect in our models (Table S1).

Table S1. Ring-billed gulls consuming foods with less DHA and higher $\delta^{13}C$ had a greater probability of solving the string-pull test, whereas their colony's urbanization (urban versus rural) was not a significant predictor of solving performance. DHA is expressed as relative concentration (percentage of total identified fatty acids) and $\delta^{13}C$ is expressed as parts per thousand (‰). Solving effort was measured as the number of times the bird pecked the box during a solving attempt. Attempt number ranged from 1–3.

Model	**Response**	**Predictors**	**Estimates**	**Standard error**	**df**	**LR χ^2**	***p***
1[a]	Solved the string-pull test (Yes/No)	Intercept	-1.53	1.02			
		Urbanization (Urban)	0.16	0.72	1	0.05	0.824
		Effort	-0.12	0.16	1	0.71	0.401
		Attempt number	1.66	0.60	1	0.44	0.507

Model	Response	Predictors	Estimates	Standard error	df	LR χ^2	*p*
		Random effect	1.44[c]				
		Model 1 R^2	0.02[d]	0.40[e]			
2[b]	Solved the string-pull test (Yes/No)	Intercept	37.51	13.44			
		DHA	-0.79	0.28	1	7.88	0.005*
		$\delta^{13}C$	1.59	0.57	1	7.86	0.005*
		Attempt number	-0.12	0.60	1	0.04	0.846
		Random effect	<0.01[c]				
		Model 2 R^2	0.48[d]	0.33[e]			

The responses were modeled using generalized linear mixed-models with a binomial distribution. Subject identity was included as a random effect to account for the repeated attempts at solving the string-pull test.

* Significant result ($p < 0.05$)

[a] This model included all gulls (banded and unbanded) that attempted to solve the string-pull test; N=156 trials involving 104 gulls

[b] This model only included the gulls that attempted to solve the string-pull test and from which we obtained a blood sample; N=63 trials involving 43 gulls

[c] Standard deviation of the random effect

[d] Marginal R^2

[e] Conditional R^2

Foraging on anthropogenic food predicts problem-solving skills in a seabird

Supplementary material

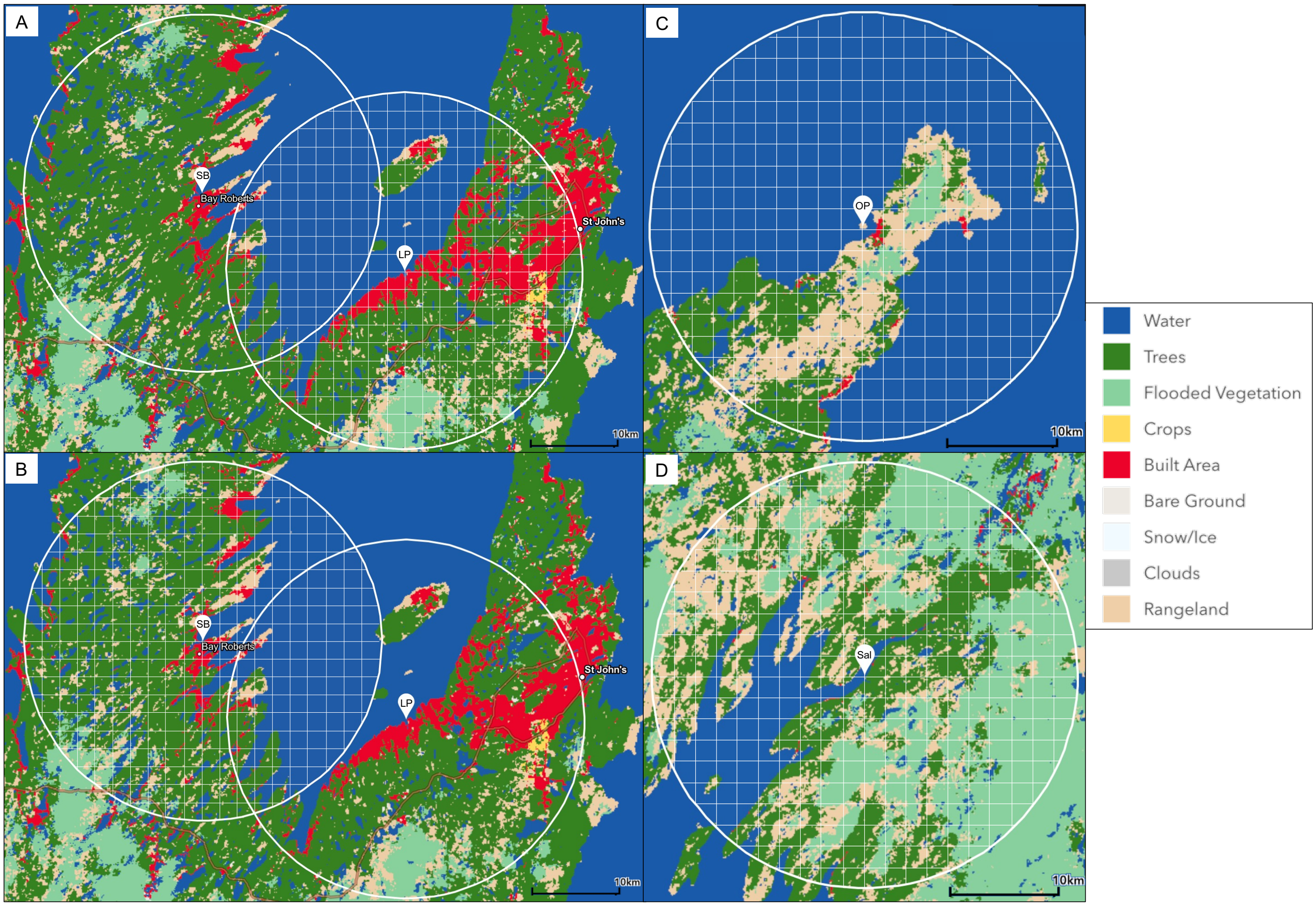

Figure S1. Each colony's urbanization gradient was measured using a land cover map produced by Karra et al. (2021), onto which a 2 x 2 km grid was superimposed (Suarez-Rubio and Krenn, 2018) over the foraging range of breeding ring-billed gulls (20 km radius from their nesting site: Caron-Beaudoin et al., 2013; Patenaude-Monette et al., 2014). The presence of built area (red) within a square was scored as comprising anthropogenic structures; the areas represented by these scored squares were summed and divided by the total area covered by the grid to obtain the percentage of the grid covered by anthropogenic structures. The degree of urbanization was A) 33.10% for the Long Pond colony (LP), B) 24.51% for the Spaniard's Bay colony (SB), C) 6.05% for the Old Perlican colony (OP), D) and 4.46% for the Salmonier colony (Sal).

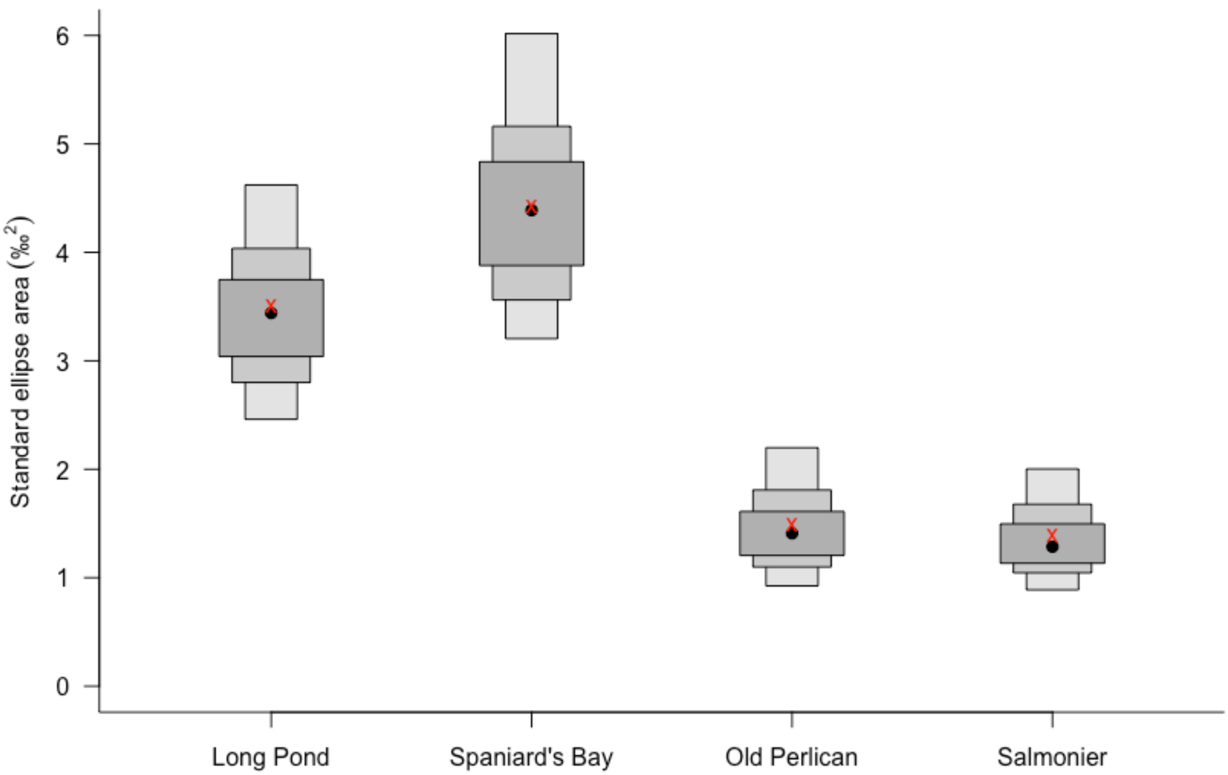

Figure S2. Density plot showing the credibility intervals of the Bayesian standard ellipse areas (SEA_b) by colony. The black dots correspond to the mode of the SEA_b for each colony, whereas the red x's correspond to the mean of the standard ellipse area corrected for small or unequal sample size (SEA_c). The light to dark grey boxed areas represent the 95, 75, and 50% credibility intervals around the SEA_b modes, respectively.

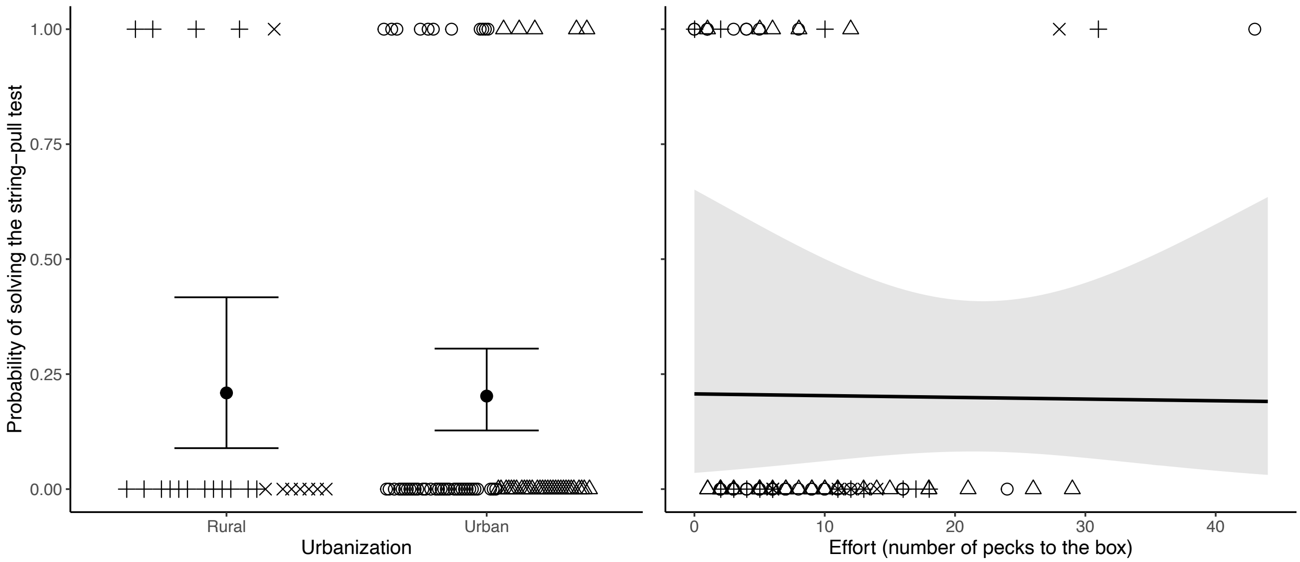

Figure S3. Urbanization (urban versus rural) did not predict ring-billed gulls' probability of solving the string-pull test during their first solving attempt. The effort put towards solving the test (measured as the number of times the bird pecked the box during their first solving attempt) was also not associated with the birds' likelihood of solving the test. Raw data are represented by the points, with shapes corresponding to colony (Long Pond = O, Spaniard's Bay = Δ, Old Perlican = +, Salmonier = x). The success probability estimates for urban and rural colonies are represented by the large black point with its 95% confidence interval. The predicted relationship between effort and solving success is represented by a black line with grey fill (95% confidence interval).

Species	Comparison	Foraging_hab	Location	Year	N	Mean_d13C	SD_d13C	Mean_d15N	SD_d15N	Figure	Reference
Amphipod	Potential_foc	Marine_inver	NFLD_Easter	2002	4	-20.9	1.7	9.7	1.72	3a	Sherwood, G.D., Rose, G.A., 2005. Stable isotope analysis of some representative fish and invertebrates of the Newfoundland and Labrador continental shelf food web. Estuar. Coast. Shelf Sci. 63, 537–549. https://doi.org/10.1016/j.ecss.2004.12.010
Aquatic Dipte	Potential_foc	Freshwater_i	SK_Saskatch	2013	27	-28.58	1.07	8.42	0.84	3a	Michelson, C.I., Clark, R.G., Morrissey, C.A., 2018. Agricultural land cover does not affect the diet of Tree Swallows in wetland-dominated habitats. The Condor 120, 751–764. https://doi.org/10.1650/CONDOR-18-16.1
Arctic char	Potential_foc	Freshwater_f	NFLD_Gande	2000_2001	16	-28.1	0.4	10.9	0.8	3a	Power, M., O’Connell, M.F., Dempson, J.B., 2005. Ecological segregation within and among Arctic char morphotypesin Gander Lake, Newfoundland. Environ. Biol. Fishes 73, 263–274. https://doi.org/10.1007/s10641-005-2137-4
Atlantic cod	Potential_foc	Marine_fish	NFLD_Northe	2013_2015	62	-19.47	0.54	14.82	0.72	3a	Krumsick, K., 2020. Trophic and size spectra modeling reveal key species interactions and quantify community recovery dynamics within Newfoundland and Labrador fisheries ecosystems. [Doctoral dissertation].[St. John's, Newfoundland]: Memorial University of Newfoundland.
Atlantic herri	Potential_foc	Marine_fish	NFLD_Northe	2018	15	-21.17	0.19	11.48	0.23	3a	Johnson, K.F., Davoren, G.K., 2021. Stable isotope analysis reveals that humpback whales (Megaptera novaeangliae) primarily consume capelin (Mallotus villosus) in coastal Newfoundland, Canada. Can. J. Zool. 99, 564–572. https://doi.org/10.1139/cjz-2020-0257
Atlantic macl	Potential_foc	Marine_fish	NB_KentIslar	2009	7	-19.3	0.5	12.7	0.3	3a	Steenweg, R.J., Ronconi, R.A., Leonard, M.L., 2011. Seasonal and age-dependent dietary partitioning between the great black-backed and herring gulls. The Condor 113, 795–805. https://doi.org/10.1525/cond.2011.110004
Atlantic salm	Potential_foc	Freshwater_f	NFLD_Twillic	2012	NA	-26.35	0.89	8.49	0.52	3a	Brush, J., 2016. Fish feeding variability over space and time in natural and regulated boreal rivers. [MSc thesis].[Waterloo, Ontario]: University of Waterloo.
Brook trout	Potential_foc	Freshwater_f	QC_Borealsh	2008	182	-28.7	1.02	5.93	0.48	3a	Glaz, P., Sirois, P., Nozais, C., 2012. Determination of food sources for benthic invertebrates and brook trout Salvelinus fontinalis in Canadian Boreal Shield lakes using stable isotope analysis. Aquat. Biol. 17, 107–117. https://doi.org/10.3354/ab00465
Capelin	Potential_foc	Marine_fish	NFLD_Northe	2017	15	-20.63	0.29	12.12	0.54	3a	Johnson, K.F., Davoren, G.K., 2021. Stable isotope analysis reveals that humpback whales (Megaptera novaeangliae) primarily consume capelin (Mallotus villosus) in coastal Newfoundland, Canada. Can. J. Zool. 99, 564–572. https://doi.org/10.1139/cjz-2020-0257
Copepod	Potential_foc	Marine_inver	NFLD_Northe	2017	20	-23.01	0.63	7.67	0.61	3a	Johnson, K.F., Davoren, G.K., 2021. Stable isotope analysis reveals that humpback whales (Megaptera novaeangliae) primarily consume capelin (Mallotus villosus) in coastal Newfoundland, Canada. Can. J. Zool. 99, 564–572. https://doi.org/10.1139/cjz-2020-0257
Earthworm, b	Potential_foc	Terrestrial_in	NB_BayofFur	2014_2015	NA	-27.9	2.5	5.5	1.7	3a	Shlepr, K.R., Ronconi, R.A., Hayden, B., Allard, K.A., Diamond, A.W., 2021. Estimating the relative use of anthropogenic resources by Herring Gull (Larus argentatus) in the Bay of Fundy, Canada. Avian Conserv. Ecol. 16, 2. https://doi.org/10.5751/ACE-01739-160102
Fast food bee	Potential_foc	Anthropogeni	USA	2007	162	-18	5.9	6.1	1.05	3a	Jahren, A.H., Kraft, R.A., 2008. Carbon and nitrogen stable isotopes in fast food: Signatures of corn and confinement. Proc. Natl. Acad. Sci. 105, 17855. https://doi.org/10.1073/pnas.0809870105
Fast food chi	Potential_foc	Anthropogeni	USA	2007	161	-17.5	1.35	2.3	0.65	3a	Jahren, A.H., Kraft, R.A., 2008. Carbon and nitrogen stable isotopes in fast food: Signatures of corn and confinement. Proc. Natl. Acad. Sci. 105, 17855. https://doi.org/10.1073/pnas.0809870105
Littoral crab	Potential_foc	Marine_inver	NS_BayofFun	2015	5	-15.9	1	10.6	0.6	3a	Shlepr, K.R., Ronconi, R.A., Hayden, B., Allard, K.A., Diamond, A.W., 2021. Estimating the relative use of anthropogenic resources by Herring Gull (Larus argentatus) in the Bay of Fundy, Canada. Avian Conserv. Ecol. 16, 2. https://doi.org/10.5751/ACE-01739-160102
Mink farm	Potential_foc	Anthropogeni	NS_BayofFun	2015	4	-21.5	1.7	8.9	1.9	3a	Shlepr, K.R., Ronconi, R.A., Hayden, B., Allard, K.A., Diamond, A.W., 2021. Estimating the relative use of anthropogenic resources by Herring Gull (Larus argentatus) in the Bay of Fundy, Canada. Avian Conserv. Ecol. 16, 2. https://doi.org/10.5751/ACE-01739-160102
Mussel	Potential_foc	Marine_inver	NS_BayofFun	2009	6	-17.9	0.2	6	0.2	3a	Steenweg, R.J., Ronconi, R.A., Leonard, M.L., 2011. Seasonal and age-dependent dietary partitioning between the great black-backed and herring gulls. The Condor 113, 795–805. https://doi.org/10.1525/cond.2011.110004
Polychaete	Potential_foc	Marine_inver	NFLD_Northe	2013_2015	8	-17.85	0.81	12.07	1.59	3a	Krumsick, K., 2020. Trophic and size spectra modeling reveal key species interactions and quantify community recovery dynamics within Newfoundland and Labrador fisheries ecosystems. [Doctoral dissertation].[St. John's, Newfoundland]: Memorial University of Newfoundland.
Redfish	Potential_foc	Marine_fish	NFLD_Northe	2013_2015	64	-20.27	0.58	12.21	0.81	3a	Krumsick, K., 2020. Trophic and size spectra modeling reveal key species interactions and quantify community recovery dynamics within Newfoundland and Labrador fisheries ecosystems. [Doctoral dissertation].[St. John's, Newfoundland]: Memorial University of Newfoundland.
Refuse	Potential_foc	Anthropogeni	USA_ButanoS	2012_2013	34	-20.7	4.9	3.6	1.8	3a	West, E.H., Henry, W.R., Goldenberg, W., Peery, M.Z., 2016. Influence of food subsidies on the foraging ecology of a synanthropic species in protected areas. Ecosphere 7, e01532. https://doi.org/10.1002/ecs2.1532
Sandlance	Potential_foc	Marine_fish	NFLD_Northe	2017	9	-21.19	0.18	10.11	0.1	3a	Johnson, K.F., Davoren, G.K., 2021. Stable isotope analysis reveals that humpback whales (Megaptera novaeangliae) primarily consume capelin (Mallotus villosus) in coastal Newfoundland, Canada. Can. J. Zool. 99, 564–572. https://doi.org/10.1139/cjz-2020-0257
Shrimp	Potential_foc	Marine_inver	NFLD_Northe	2013_2015	21	-19.5	0.37	10.77	0.46	3a	Krumsick, K., 2020. Trophic and size spectra modeling reveal key species interactions and quantify community recovery dynamics within Newfoundland and Labrador fisheries ecosystems. [Doctoral dissertation].[St. John's, Newfoundland]: Memorial University of Newfoundland.
Snow Crab	Potential_foc	Marine_inver	NFLD_Northe	2013_2015	25	-16.68	2.25	10.77	1.36	3a	Krumsick, K., 2020. Trophic and size spectra modeling reveal key species interactions and quantify community recovery dynamics within Newfoundland and Labrador fisheries ecosystems. [Doctoral dissertation].[St. John's, Newfoundland]: Memorial University of Newfoundland.
Squid	Potential_foc	Marine_inver	NFLD_Northe	2013_2015	8	-20.77	0.75	11.29	0.51	3a	Krumsick, K., 2020. Trophic and size spectra modeling reveal key species interactions and quantify community recovery dynamics within Newfoundland and Labrador fisheries ecosystems. [Doctoral dissertation].[St. John's, Newfoundland]: Memorial University of Newfoundland.
Terrestrial Di	Potential_foc	Terrestrial_in	SK_Saskatch	2013	25	-26.93	1.34	8.96	1.66	3a	Michelson, C.I., Clark, R.G., Morrissey, C.A., 2018. Agricultural land cover does not affect the diet of Tree Swallows in wetland-dominated habitats. The Condor 120, 751–764. https://doi.org/10.1650/CONDOR-18-16.1
American red	Comparable_	Terrestrial_bi	MB_DeltaMa	2003	7	-23.3	0.1	6.2	0.5	3b	Gagnon, C., Hobson, K.A., 2009. Using stable isotopes to track frugivory in migratory passerines. Can. J. Zool. 87, 981–992. https://doi.org/10.1139/Z09-086
American rob	Comparable_	Terrestrial_bi	MB_DeltaMa	2004	12	-22.8	0.2	10.1	0.4	3b	Gagnon, C., Hobson, K.A., 2009. Using stable isotopes to track frugivory in migratory passerines. Can. J. Zool. 87, 981–992. https://doi.org/10.1139/Z09-086
American wh	Comparable_	Freshwater_I	USA_SouthFl	2016	13	-18.16	0.77	6.38	0.23	3b	Murray, M.H., Kidd, A.D., Curry, S.E., Hepinstall-Cymerman, J., Yabsley, M.J., Adams, H.C., Ellison, T., Welch, C.N., Hernandez, S.M., 2018. From wetland specialist to hand-fed generalist: shifts in diet and condition with provisioning for a recently urbanized wading bird. Philos. Trans. R. Soc. B Biol. Sci. 373, 20170100. https://doi.org/10.1098/rstb.2017.0100
American wh	Comparable_	Freshwater_I	USA_SouthFl	2016	50	-21.01	1.95	6.71	1.01	3b	Murray, M.H., Kidd, A.D., Curry, S.E., Hepinstall-Cymerman, J., Yabsley, M.J., Adams, H.C., Ellison, T., Welch, C.N., Hernandez, S.M., 2018. From wetland specialist to hand-fed generalist: shifts in diet and condition with provisioning for a recently urbanized wading bird. Philos. Trans. R. Soc. B Biol. Sci. 373, 20170100. https://doi.org/10.1098/rstb.2017.0100
Atlantic puffi	Comparable_	Marine_bird	NFLD_Northe	2017	14	-19.7	0.22	12.21	0.27	3b	Jenkins, E.J., Davoren, G.K., 2021. Seabird species- and assemblage-level isotopic niche shifts associated with changing prey availability during breeding in coastal Newfoundland. Ibis 163, 183–196. https://doi.org/10.1111/ibi.12873
Black-legged	Comparable_	Marine_bird	QC_GulfStLa	2006_2007	21	-18.9	0.23	15.2	0.23	3b	Lavoie, R.A., Rail, J.-F., Lean, D.R.S., 2012. Diet Composition of Seabirds from Corossol Island, Canada, Using Direct Dietary and Stable Isotope Analyses. Waterbirds 35, 402–419. https://doi.org/10.1675/063.035.0305
California gul	Comparable_	Terrestrial_bi	USA_SanFran	2007_2008	19	-18.1	0.5	9	0.3	3b	Peterson, S.H., Ackerman, J.T., Eagles-Smith, C.A., 2017. Mercury contamination and stable isotopes reveal variability in foraging ecology of generalist California gulls. Ecol. Indic. 74, 205–215. https://doi.org/10.1016/j.ecolind.2016.11.025
California gul	Comparable_	Estuary_bird	USA_SanFran	2007_2008	7	-17.8	0.5	11.2	0.5	3b	Peterson, S.H., Ackerman, J.T., Eagles-Smith, C.A., 2017. Mercury contamination and stable isotopes reveal variability in foraging ecology of generalist California gulls. Ecol. Indic. 74, 205–215. https://doi.org/10.1016/j.ecolind.2016.11.025
Common mu	Comparable_	Marine_bird	NFLD_Northe	2017	27	-19.79	0.18	13.97	0.36	3b	Jenkins, E.J., Davoren, G.K., 2021. Seabird species- and assemblage-level isotopic niche shifts associated with changing prey availability during breeding in coastal Newfoundland. Ibis 163, 183–196. https://doi.org/10.1111/ibi.12873
Double-crest	Comparable_	Freshwater_I	ON_GreatLal	2009_2010	39	-22.6	0.5	15.6	0.5	3b	King, L.E., de Solla, S.R., Marentette, J.R., Lavoie, R.A., Kyser, T.K., Campbell, L.M., Arts, M.T., Quinn, J.S., 2017. Fatty acids, stable isotopes, and regurgitate reveal diet differences between Lake Ontario and Lake Erie double-crested cormorants (Phalacrocorax auritus). J. Gt. Lakes Res. 43, 132–140. https://doi.org/10.1016/j.jglr.2017.03.004
Glaucous-wi	Comparable_	Marine_bird	BC_Mandart	2010	15	-17.08	1.89	14.07	1.93	3b	Davis, M.L., Elliott, J.E., Williams, T.D., 2017. The glaucous-winged gull (Larus glaucescens) as an indicator of chemical contaminants in the Canadian Pacific marine environment: evidence from stable isotopes. Arch. Environ. Contam. Toxicol. 73, 247–255. https://doi.org/10.1007/s00244-017-0368-y
Glaucous-wi	Comparable_	Marine_bird	BC_ClelandI	2010	13	-16.82	0.7	15.3	0.3	3b	Davis, M.L., Elliott, J.E., Williams, T.D., 2017. The glaucous-winged gull (Larus glaucescens) as an indicator of chemical contaminants in the Canadian Pacific marine environment: evidence from stable isotopes. Arch. Environ. Contam. Toxicol. 73, 247–255. https://doi.org/10.1007/s00244-017-0368-y
Gray catbird	Comparable_	Terrestrial_bi	MB_DeltaMa	2005	10	-24.4	0.2	7	0.5	3b	Gagnon, C., Hobson, K.A., 2009. Using stable isotopes to track frugivory in migratory passerines. Can. J. Zool. 87, 981–992. https://doi.org/10.1139/Z09-086
Great black-l	Comparable_	Marine_bird	QC_GulfStLa	2006_2007	20	-19	0.89	12.8	1.79	3b	Lavoie, R.A., Rail, J.-F., Lean, D.R.S., 2012. Diet Composition of Seabirds from Corossol Island, Canada, Using Direct Dietary and Stable Isotope Analyses. Waterbirds 35, 402–419. https://doi.org/10.1675/063.035.0305
Herring gull (I	Comparable_	Marine_bird	QC_GulfStLa	2006_2007	20	-18.9	0.45	13	1.34	3b	Lavoie, R.A., Rail, J.-F., Lean, D.R.S., 2012. Diet Composition of Seabirds from Corossol Island, Canada, Using Direct Dietary and Stable Isotope Analyses. Waterbirds 35, 402–419. https://doi.org/10.1675/063.035.0305
Human (hair)	Comparable_	Anthropogeni	NFLD	2008_2012	16	-18.1	0.4	9.4	0.4	3b	Bataille, C.P., Chartrand, M.M.G., Raposo, F., St-Jean, G., 2020. Assessing geographic controls of hair isotopic variability in human populations: A case-study in Canada. PLoS One 15, e0237105. https://doi.org/10.1371/journal.pone.0237105
Least flycatcl	Comparable_	Terrestrial_bi	MB_DeltaMa	2006	15	-22.5	0.1	7.2	0.3	3b	Gagnon, C., Hobson, K.A., 2009. Using stable isotopes to track frugivory in migratory passerines. Can. J. Zool. 87, 981–992. https://doi.org/10.1139/Z09-086
Razorbill (RB	Comparable_	Marine_bird	NFLD_Northe	2017	20	-19.73	0.31	13.79	0.26	3b	Jenkins, E.J., Davoren, G.K., 2021. Seabird species- and assemblage-level isotopic niche shifts associated with changing prey availability during breeding in coastal Newfoundland. Ibis 163, 183–196. https://doi.org/10.1111/ibi.12873
Ring-billed g	Comparable_	Terrestrial_bi	QC_Deslauri	2010	63	-21.35	4.76	7.98	2.38	3b	Caron-Beaudoin, É., Gentes, M.-L., Patenaude-Monette, M., Hélie, J.-F., Giroux, J.-F., Verreault, J., 2013. Combined usage of stable isotopes and GPS-based telemetry to understand the feeding ecology of an omnivorous bird, the Ring-billed Gull (Larus delawarensis). Can. J. Zool. 91, 689–697. https://doi.org/10.1139/cjz-2013-0008
Ring-billed g	Comparable_	Freshwater_I	QC_Deslauri	2010	20	-20.8	2.24	8.8	1.34	3b	Caron-Beaudoin, É., Gentes, M.-L., Patenaude-Monette, M., Hélie, J.-F., Giroux, J.-F., Verreault, J., 2013. Combined usage of stable isotopes and GPS-based telemetry to understand the feeding ecology of an omnivorous bird, the Ring-billed Gull (Larus delawarensis). Can. J. Zool. 91, 689–697. https://doi.org/10.1139/cjz-2013-0008
Song sparrow	Comparable_	Terrestrial_bi	MB_DeltaMa	2007	10	-22.2	0.8	8.9	0.5	3b	Gagnon, C., Hobson, K.A., 2009. Using stable isotopes to track frugivory in migratory passerines. Can. J. Zool. 87, 981–992. https://doi.org/10.1139/Z09-086
Tree swallow	Comparable_	Terrestrial_bi	MB_DeltaMa	2008	10	-23.5	0.3	9.7	0.3	3b	Gagnon, C., Hobson, K.A., 2009. Using stable isotopes to track frugivory in migratory passerines. Can. J. Zool. 87, 981–992. https://doi.org/10.1139/Z09-086