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Identifying Important Foraging Habitat for Colonial Waterbirds in an Urban Estuary: a Stable Isotope Approach

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Abstract.—Foraging habitat use by colonial waterbirds breeding in New York Harbor was examined to identify resources that were particularly important for the provisioning of young. Stable isotope values of carbon, nitrogen, and sulfur were measured in nestling waterbird feathers to determine the habitat type (ranging from marine to freshwater and anthropogenic) in which adults primarily foraged. Six species were investigated: Black-crowned Night-Herons (*Nycticorax nycticorax*), Great Egrets (*Ardea alba*), Glossy Ibises (*Plegadis falcinellus*), Double-crested Cormorants (*Phalacrocorax auritus*), Great Black-backed Gulls (*Larus marinus*), and Herring Gulls (*L. argentatus*). Waterbird populations exhibited both inter- and intra-specific variation in stable isotope values ($P < 0.001$), indicating variation in foraging habitat use among focal species across the estuary. Therefore, depending on the species- and region-specific conservation goal, management strategies would potentially need to target very different foraging habitats for protection and remediation. For instance, habitat use by Double-crested Cormorants closely reflected available habitat near nesting colonies, while Glossy Ibises used primarily freshwater resources at one colony and marine resources at another, despite the fact that both colonies were located in marine environments. Great Egrets and Double-crested Cormorants both showed significant regional variation in isotopic niche size, and both species of gulls (considered to be generalist scavengers) were found to have isotopic niche sizes reflecting a specialist diet. Stable isotope analysis of nestling feathers provided novel information about the foraging resources that were most important to waterbirds in regions across the harbor. Received 30 December 2013, accepted 11 August 2015.

Key words.—conservation, cormorant, diet, egret, gull, ibis, isotopic niche, New York Harbor, night-heron.

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The New York/New Jersey Harbor Estuary (hereafter the harbor) has an area of approximately 40,000 km² and provides a mosaic of urban habitat types for wildlife, including open water, freshwater and saltwater marsh, uplands, and the built environment. Small, abandoned islands in the harbor have become important breeding areas for many of New York State's waterbirds since their resurgence in the region in the 1970s (Harbor Herons Subcommittee 2010). Sixteen waterbird species have been known to reproduce on these islands and forage in the surrounding wetlands and waterways to feed themselves and provision their young (Craig 2012). Current knowledge and conservation efforts for these birds have generally focused on breeding population sizes and nesting phenology. However, the Harbor Heron Conservation Plan of the New York/New Jersey Harbor Estuary Program has recently called for research to expand our under-

standing to include the foraging behavior of waterbirds in this system (Harbor Herons Subcommittee 2010). To this end, we investigated foraging resource use through stable isotope analysis (SIA) of nestling waterbird feathers.

Stable isotope analysis of feathers reflects a bird's diet over the timescale of feather growth, and contains information about the relative importance of foraging resources during that period (Hobson and Clark 1992; Hobson 1999; Inger and Bearhop 2008; Bond and Jones 2009). Feathers from nestling birds in particular integrate the resources with which adult birds have provisioned their young, and are therefore most suitable for answering questions about local foraging behavior and diet on the breeding grounds (Cherel *et al.* 2000). Stable isotope values measured in a population (expressed in δ notation as parts per thousand; ‰) can be considered to describe an isotopic niche,

analogous to the n -dimensional hypervolume of the ecological niche (Hutchinson 1957). The isotopic niche is defined as an area in δ -space (‰) with isotopic values as coordinates (Newsome *et al.* 2007).

Isotopic values of carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$), and sulfur ($\delta^{34}\text{S}$) can be used to monitor diet, relative trophic position, and foraging habitat of birds (Bond and Jones 2009). $\delta^{13}\text{C}$ values indicate the extent of freshwater or marine resource use, with more negative (lower) values indicating more freshwater resource use, and less negative (higher) values indicating more marine resource use (Mizutani *et al.* 1990; Hobson and Clark 1992; Bearhop *et al.* 1999; Bond and Jones 2009). Higher $\delta^{13}\text{C}$ values can also result from inclusion of C_4 photosynthetic plant materials, such as foods containing corn or cane sugar, in the diet (Farquhar *et al.* 1989). In waterbirds, this indicates consumption of anthropogenic resources such as human food waste or intensive aquaculture (Hebert *et al.* 2009). When anthropogenic resource use is suspected, $\delta^{34}\text{S}$ can be added to the analysis, as this isotope provides a more straightforward measure of marine vs. freshwater resource use that is not influenced by anthropogenic foods (Lott *et al.* 2003). $\delta^{15}\text{N}$ values primarily indicate the relative trophic position at which a bird has foraged (Steele and Daniel 1978; Minagawa and Wada 1984; Hobson and Clark 1992; Bond and Jones 2009).

Six waterbird species were investigated in this study, including three species of long-legged wading birds: the Black-crowned Night-Heron (*Nycticorax nycticorax*), Great Egret (*Ardea alba*), and Glossy Ibis (*Plegadis falcinellus*); one species of diving bird: the Double-crested Cormorant (*Phalacrocorax auritus*); and two gull species: the Great Black-backed Gull (*Larus marinus*) and Herring Gull (*L. argentatus*). These six species were the most numerically abundant waterbirds nesting in the harbor during this study, and were selected to span the range in phylogeny, conservation status, and foraging strategy within the harbor's waterbird community (Craig 2012). In general, long-legged wading birds (ibises, egrets, and night-herons)

capture fish, crabs, amphibians, and aquatic invertebrates by wading into shallow waters and marshes (Davis and Kricher 2000; McCrimmon *et al.* 2001; Hothem *et al.* 2010); cormorants dive to capture live prey (primarily fish; Hatch and Weseloh 1999); and gulls scavenge for a variety of items ranging from fish to human garbage (Pierotti and Good 1994; Good 1998).

The objectives of this study were to examine foraging habitat use of a suite of waterbird species nesting within the harbor, and to identify the habitats that were particularly important among waterbird populations and across regions. We formulated three specific hypotheses: 1) that cormorants would have the highest correlation between nearby habitat availability and habitat use, as these birds can dive for prey in waters immediately surrounding their nesting habitats regardless of shoreline topography; 2) that long-legged wading birds would display broader resource use and larger isotopic niche size, particularly on islands that lacked shorelines with suitably shallow foraging habitat; and 3) that gulls would exhibit the largest isotopic niche size, as these birds are known to be primarily generalist scavengers.

METHODS

Study Area

This study was conducted across five islands in the harbor (Fig. 1): two in Lower Bay (Hoffman and Swinburne Islands), one in the East River (South Brother Island), and two in Jamaica Bay (Canarsie Pol and Elder's Point Marsh). These three focal regions (Lower Bay, the East River, and Jamaica Bay) were chosen because they contain the three largest and most diverse waterbird colonies in the harbor, and because they encompass a variety of aquatic habitat types ranging from brackish and freshwater tributaries to marine. Public access to all islands is restricted for the protection of waterbirds.

Hoffman and Swinburne Islands are manmade islands located off the east shore of Staten Island, New York (40° 34' 43.38" N, 74° 3' 13.51" W) in Lower Bay. Aquatic habitat in Lower Bay is primarily marine, as the bay opens onto the Atlantic Ocean. Canarsie Pol (40° 37' 16.03" N, 73° 52' 23.88" W) and Elder's Point Marsh (40° 38' 9.97" N, 73° 50' 55.50" W) are natural islands situated in the northwest region of Jamaica Bay. As in Lower Bay, aquatic habitat in Jamaica Bay is primarily marine, as the bay opens onto the Atlantic Ocean. South Brother Island (40° 47' 46.00" N, 73° 53' 53.02" W)



Figure 1. Map of the New York Harbor estuary indicating locations where feather samples were collected: Lower Bay (Hoffman and Swinburne Islands), East River (South Brother Island), and Jamaica Bay (Canarsie Pol and Elder's Point Marsh).

is a natural island situated between Riker's Island and the Bronx, New York. Aquatic habitat near South Brother Island ranges from brackish to freshwater.

Feather Collection

In June and July of 2009 through 2012, waterbird nestlings of each species were captured by hand at nesting colonies (Table 1). Between one and 10 contour feathers per individual were collected while the nestlings were handled for banding. In addition, between June and September of each year, contour feathers were collected from recently deceased waterbird nestlings of known species identity encountered on each island. All feather samples were stored in labeled paper envelopes and classified by species and location.

Stable Isotope Analysis

All feather samples were analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. A 1-mg sample (± 0.1 mg) of each feather was encapsulated in tin and analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using a Thermo Finnigan Delta V Advantage isotope ratio mass spectrometer interfaced to a NC2500 elemental analyz-

er. One internal laboratory standard of American mink (*Neovison vison*) tissue was analyzed for every 10 unknowns. A chemical methionine standard was used to measure instrumental accuracy across a gradient of amplitude intensities. Isotope corrections were performed using a two-point normalization (linear regression) of all raw $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data with two additional in-house standards: Cayuga Lake brown trout (*Salmo trutta*) and corn (*Zea mays*). Based on standard deviations of within-run replicate measurements of standards, analytical error was estimated to be $\pm 0.2\text{‰}$ for $\delta^{13}\text{C}$ and $\pm 0.3\text{‰}$ for $\delta^{15}\text{N}$.

A subset of Herring Gull samples ($n = 5$) was also analyzed for $\delta^{34}\text{S}$ to explore the potential for anthropogenic contributions to diet. For these individuals, a 1-mg sample (± 0.1 mg) of each feather was encapsulated in tin and analyzed for $\delta^{34}\text{S}$ using an isotope ratio mass spectrometer interfaced to an elemental analyzer. Internal laboratory standards were analyzed for every 10 unknowns. Based on standard deviations of within-run replicate measurements of standards, analytical error was estimated to be $\pm 0.3\text{‰}$ for $\delta^{34}\text{S}$. Results are relative to international standards of Pee Dee Belemnite for

Table 1. Regional comparisons of mean \pm SD $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of feathers sampled from colonial waterbird nestlings of six species in three regions of the New York Harbor estuary (June to September 2009-2012). Regions followed by different superscript letters signify significant intraspecific differences according to the Tukey-Kramer honest significant difference (HSD) test.

Species	Region	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	P-value
Black-crowned Night-Heron	Lower Bay	9	-18.9 ± 1.9	14.7 ± 2.1	> 0.05
	East River	6	-20.9 ± 3.4	14.3 ± 1.2	
Great Egret	Lower Bay ^a	25	-20.2 ± 2.2	14.4 ± 1.7	< 0.001
	East River ^a	29	-20.7 ± 2.9	14.8 ± 2.1	
	Jamaica Bay ^b	20	-15.4 ± 1.8	15.3 ± 0.8	
Glossy Ibis	Lower Bay ^a	19	-24.7 ± 2.1	8.0 ± 2.1	< 0.001
	Jamaica Bay ^b	4	-18.4 ± 2.5	10.5 ± 1.6	
Double-crested Cormorant	Lower Bay ^a	39	-16.5 ± 1.3	15.6 ± 1.0	< 0.001
	East River ^b	19	-20.5 ± 3.8	15.0 ± 1.7	
	Jamaica Bay ^c	16	-14.5 ± 0.3	15.6 ± 0.6	
Great Black-backed Gull	Lower Bay	37	-16.7 ± 0.5	15.9 ± 1.2	
Herring Gull	Lower Bay	32	-17.3 ± 0.7	12.8 ± 1.3	> 0.05
	Jamaica Bay	23	-17.1 ± 0.7	12.7 ± 1.3	

carbon, atmospheric air (N_2) for nitrogen, and Vienna Canyon Diablo Troilite for sulfur.

Statistical Analysis

Single-factor multivariate analysis of variance (MANOVA) and post-hoc analysis of variance (ANOVA) with the Tukey-Kramer honest significant difference (HSD) test were used to determine statistically significant variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values using a factor of nesting location or species depending on the analysis. A MANOVA of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was conducted using either mortality or year (by species) as the single factor to confirm that isotope values did not differ significantly between live and dead birds (Vasil *et al.* 2012) or across sampling years. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of feathers collected from live vs. dead nestlings and across multiple years were not found to differ significantly ($P > 0.05$); therefore, the data were analyzed regardless of mortality or collection year for all subsequent analyses. These statistical analyses were performed using JMP statistical software (SAS Institute, Inc. 2012).

When interpreting stable isotope results, we drew very conservative conclusions regarding relative trophic position from $\delta^{15}\text{N}$ values, as baseline $\delta^{15}\text{N}$ information was unknown in this system (Post 2002). Further caution was taken when comparing isotope values among multiple species, as the diet-tissue discrimination factors of many of these species are unknown (Bond and Diamond 2011). We only considered inter-specific isotopic differences greater than the standard deviation of discrimination factors of bird feathers (approximately 1.5‰ for carbon and 1.1‰ for nitrogen; Caut *et al.* 2009) to reflect differences in diet and foraging behavior among species.

Isotopic niche size (‰²) of each waterbird population was calculated with the Stable Isotope Analysis in R (SIAR) package (R Development Core Team 2014) us-

ing a Bayesian approach to estimate standard ellipse area (SEA_B) of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data (Jackson *et al.* 2011). This approach was chosen as it is well suited for small sample sizes, and it provides a measure of uncertainty around the estimated isotopic niche size allowing for statistical comparisons. The number of posterior draws in the model was set at 10^6 .

RESULTS

The waterbird community exhibited both inter- and intra-specific variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (whole MANOVA model: $F_{8,277} = 38.25$, $P < 0.001$). For each species discussed below, isotopic values are reported as mean \pm SD of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Table 1), and isotopic niche sizes are reported as the mode of the SEA_B posterior distribution (Fig. 2).

Of the three long-legged wading birds sampled in this study, only the Black-crowned Night-Heron exhibited no regional isotopic variation. Average $\delta^{15}\text{N}$ values for the Black-crowned Night-Heron were relatively high (14.7 ± 2.1 ‰ and 14.3 ± 1.2 ‰; Table 1) in both sampled regions, Lower Bay and the East River, respectively. Average $\delta^{13}\text{C}$ values were also regionally similar, and the range in $\delta^{13}\text{C}$ (from -25.8 ‰ to -14.8 ‰) suggested a broad mix of resource use from freshwater/brackish and marine habitats. This species foraged in a moderate sized isotopic niche

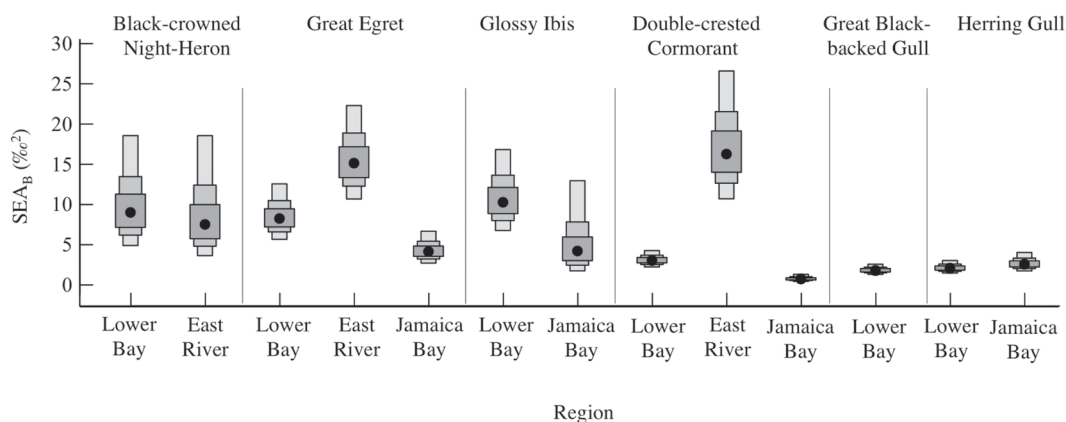


Figure 2. Density plot showing Bayesian estimated posterior distributions of isotopic niche size (SEA_B) with 50, 75 and 95% credible intervals in shaded boxes, and mode values of SEA_B indicated by black dots. Data for each species are divided into focal regions.

in comparison to other long-legged wading birds (9.3‰^2 in Lower Bay and 7.7‰^2 in the East River), and exhibited no significant regional variation in isotopic niche size (Fig. 2).

Great Egrets and Glossy Ibises both exhibited regional variation in isotope values ($P < 0.001$ for both species). Similar to Black-crowned Night-Herons, Great Egrets from Lower Bay and the East River had relatively high average $\delta^{15}\text{N}$ values ($14.4 \pm 1.7\text{‰}$ and $14.8 \pm 2.1\text{‰}$, respectively; Table 1), and a similar range of $\delta^{13}\text{C}$ values (from -25.3‰ to -13.7‰) with little regional variation. However, Great Egrets sampled from Jamaica Bay exhibited higher $\delta^{13}\text{C}$ values on average (Table 1), and ranged from -19.6‰ to -13.3‰ , indicating a greater proportion of marine resource use. Great Egrets also showed significant regional variation in isotopic niche size (Fig. 2), with a relatively large isotopic niche in the East River (15.4‰^2), an intermediate-sized isotopic niche in Lower Bay (8.6‰^2 , smaller than the East River; $P = 0.01$) and a small isotopic niche in Jamaica Bay (4.3‰^2 , smaller than Lower Bay; $P = 0.01$; Fig. 2).

Glossy Ibises were sampled in Lower Bay and Jamaica Bay (they did not nest in the East River during the sampling period), and exhibited isotopic variation between these regions ($P < 0.001$). This species had relatively low $\delta^{15}\text{N}$ values in both regions ($8.0 \pm 2.1\text{‰}$ in Lower Bay and $10.5 \pm 1.6\text{‰}$ in Jamaica Bay), and, in fact, exhibited the low-

est $\delta^{15}\text{N}$ values of the six species in this study. While ibises sampled from Jamaica Bay had $\delta^{13}\text{C}$ values within the range observed in other long-legged wading birds (from -20.9‰ to -16.1‰), the values observed in Lower Bay (ranging from -27.4‰ to -19.2‰) were significantly lower on average ($-24.7 \pm 2.1\text{‰}$; $P < 0.001$; Table 1), indicating a greater proportion of freshwater resource use. This species exhibited no regional variation in isotopic niche size, with a moderate-sized isotopic niche in Lower Bay (10.4‰^2) and in Jamaica Bay (4.4‰^2) (Fig. 2).

Double-crested Cormorants exhibited isotopic variation among all three focal regions ($P < 0.001$; Table 1). Relatively high $\delta^{13}\text{C}$ values were observed in birds from Jamaica Bay (from -15.1‰ to -14.2‰), indicative of a predominantly marine diet. Cormorants from Lower Bay had a broader $\delta^{13}\text{C}$ range (from -22.1‰ to -15.2‰) similar to that observed in Black-crowned Night-Herons and Great Egrets from this region. East River cormorants exhibited an even broader range (from -28.3‰ to -15.6‰) and lower average $\delta^{13}\text{C}$ value ($-20.5 \pm 3.8\text{‰}$; Table 1), suggesting a greater contribution of freshwater resources than observed in the other two regions. Average $\delta^{15}\text{N}$ values were relatively high (from $15.0 \pm 1.7\text{‰}$ to $15.6 \pm 1.0\text{‰}$; Table 1) and similar among regions. As observed in Great Egrets, the Double-crested Cormorants nesting in the East River had

a larger isotopic niche (16.7‰^2 ; $P < 0.001$) than those observed in the other two nesting regions (3.2‰^2 in Lower Bay and 0.8‰^2 in Jamaica Bay). The isotopic niche size in Lower Bay was in turn larger than that observed in Jamaica Bay ($P < 0.001$), although by a far narrower margin (Fig. 2).

The Great Black-backed Gull was only sampled in one location (Lower Bay), while the Herring Gull was sampled in Lower Bay and Jamaica Bay. Great Black-backed Gulls exhibited the highest average $\delta^{15}\text{N}$ value observed in this study ($15.9 \pm 1.2\text{‰}$; Table 1). The $\delta^{13}\text{C}$ values were also relatively high (ranging from -17.6‰ to -15.9‰), indicating a predominantly marine diet. Interestingly, despite its reputation as a generalist scavenger, this species exhibited a very small isotopic niche (1.9‰^2). The Herring Gull showed no regional isotopic variation. It had lower average $\delta^{15}\text{N}$ values than the Great Black-backed Gull ($12.7 \pm 1.3\text{‰}$ and $12.8 \pm 1.3\text{‰}$; Table 1), but similar $\delta^{13}\text{C}$ values (ranging from -19.1‰ to -15.8‰). Sulfur SIA was conducted on a subset of Herring Gull feathers from Jamaica Bay and Lower Bay to investigate potential anthropogenic resource use. SIA yielded an average $\delta^{34}\text{S}$ value of $10.0 \pm 2.1\text{‰}$, a lower value than would be expected in a marine-foraging bird (Lott *et al.* 2003). Interestingly, Herring Gulls also had a very small isotopic niche (2.2‰^2 in Lower Bay and 2.7‰^2 in Jamaica Bay), with no regional variation (Fig. 2).

DISCUSSION

The stable isotope approach used in this study allowed us to evaluate differences in foraging ecology among species nesting in three regions of the harbor, and identify the habitat types that were most important in the diet of individual populations within this urban estuary. Waterbird populations exhibited both inter- and intra-specific variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, indicating differences in foraging habitat use among regions and species. While it is not surprising to find differences in isotopic values among species with differing foraging ecologies (Inger and

Bearhop 2008), these findings suggest that, depending on the species- and region-specific conservation goal, management strategies would potentially need to target very different foraging habitats for protection and remediation.

Double-crested Cormorants from Lower Bay and Jamaica Bay had $\delta^{13}\text{C}$ values indicative of a predominantly marine diet, and suggested that birds likely foraged in the bays surrounding their respective nesting colonies as well as the coastal Atlantic Ocean. Cormorants from the East River exhibited a lower average $\delta^{13}\text{C}$ value, indicating a greater contribution of freshwater resources than observed in the other two regions. This is consistent with the brackish/freshwater environment surrounding the East River colony. Cormorants nesting in the East River also exhibited a larger isotopic niche than those observed in the other two nesting regions (five times the range observed in Lower Bay and 20 times that observed in Jamaica Bay), indicating that a wider range of foraging habitats and prey items contributed to the diet of these birds. This observation may reflect the diverse nature of foraging habitat availability in the East River and its freshwater tributaries. Alternatively, birds nesting at this location might have foraged at greater distances from the colony to meet their metabolic needs and those of their young, as the area surrounding this colony is highly developed and industrial. The resulting increased foraging distance would also explain the large range of $\delta^{13}\text{C}$ values (the largest range observed in this study).

As anticipated, Black-crowned Night-Herons exhibited a large range in $\delta^{13}\text{C}$ values and relatively large isotopic niches in both Lower Bay and the East River. As long-legged wading birds, their foraging strategy may have required them to forage at greater distances from their colony sites, exposing them to a large and overlapping range of foraging habitats.

In contrast to Black-crowned Night-Herons, Great Egrets had a significantly larger isotopic niche in the East River than in Lower Bay. The isotopic niche size was likely influenced by the same factors pro-

posed for cormorants. Egrets in Jamaica Bay exhibited very high $\delta^{13}\text{C}$ values suggesting a primarily marine diet. Together with a small isotopic niche, the data suggest that egrets nesting in Jamaica Bay likely also foraged in Jamaica Bay. This conclusion is supported by the presence of extensive suitable saltwater marsh and sandy beach habitat in this region.

Glossy Ibises exhibited a similar pattern in Jamaica Bay, with $\delta^{13}\text{C}$ values suggesting a primarily marine diet, and a relatively small isotopic niche, together indicating that these birds likely remained in Jamaica Bay to forage. Ibises in Lower Bay exhibited significantly lower $\delta^{13}\text{C}$ values suggesting that, despite the absence of freshwater resources surrounding their nesting colony, freshwater foraging habitats were the most important habitat type for this population during chick rearing. Their use of freshwater resources to feed their growing nestlings is consistent with studies conducted on White Ibis (*Eudocimus albus*) in Florida (Bildstein 1993). As with the other long-legged wading birds, it is not surprising that Glossy Ibises from Lower Bay would travel some distance from their nesting colony to forage, as the nesting islands in this region are manmade with steep stone shorelines unsuited for their foraging strategy. The observation that ibises from Lower Bay and Jamaica Bay used vastly different foraging habitat types and prey base is novel, and has not been suggested by observational methods. Ibises from both regions exhibited the lowest $\delta^{15}\text{N}$ values of the six focal species in this study. These low $\delta^{15}\text{N}$ values might have derived from a difference in source nitrogen in foraging habitats used by ibises, but most likely indicated that these birds generally relied on prey of a low relative trophic position. This is supported by the general foraging strategy of ibises, which, unlike egrets and night-herons, tend to forage by probing for invertebrates in shallow water, fields, and marshes (Davis and Kricher 2000).

Contrary to our expectation, gulls had among the smallest isotopic niches in this study. Interestingly, the Great Black-backed Gulls observed in Lower Bay exhibited $\delta^{13}\text{C}$

and $\delta^{15}\text{N}$ values very similar to those observed in cormorants in the same region (Table 1). The general understanding of the foraging strategies of cormorants (diving predators) and gulls (generalist scavengers) does not explain this similarity. Great Black-backed Gulls, however, have been known to exhibit predatory behavior (Good 1998), and were observed during this study consuming cormorant eggs and young when the cormorant colonies were disturbed. While it is possible that these species were eating different food sources with the same isotope value, we believe that the similarity was due to gulls consuming a combination of cormorant eggs and young, and scavenging for food scraps in the understory beneath the cormorant colony. Regardless of the specific scavenging or predatory behavior, our results suggest that cormorant-related diet items may be the most important food source for Great Black-backed Gulls nesting in Lower Bay. This specialized diet would explain the small isotopic niche observed in this species.

Herring Gulls sampled in both Lower Bay and Jamaica Bay exhibited relatively high $\delta^{13}\text{C}$ values (similar to those observed in the Great Black-backed Gull) but relatively low $\delta^{15}\text{N}$ values (Table 1). These $\delta^{15}\text{N}$ values might be explained by the scavenging of fish from lower trophic positions in a marine environment, although there is no simple mechanism for a generalist scavenger to specialize in lower trophic position carrion. This hypothesis was further undermined by sulfur SIA of a subset of Herring Gull feathers that yielded an average $\delta^{34}\text{S}$ value lower than would be expected in a marine-foraging bird (Lott *et al.* 2003). The most likely explanation for the isotopic values observed in Herring Gulls is anthropogenic resource use. Scavenging of human food waste could lead to the observed high $\delta^{13}\text{C}$ values through the consumption of C_4 photosynthetic plant materials such as corn- and cane sugar-based foods, as well as the relatively low $\delta^{34}\text{S}$ values due to the use of fresh water in agriculture. Such resource use could also lead to the lower observed $\delta^{15}\text{N}$ values due to the relatively low trophic position of these diet items. The distribution of

isotope values in Herring Gulls from Lower Bay and Jamaica Bay overlapped to an extent not observed in any other focal species suggesting that Herring Gulls exhibited little to no regional variation in foraging habitat use. With the additional evidence of small isotopic niche, suggesting limited variation in the diet, we conclude that anthropogenic foods were likely the primary resource used by Herring Gulls provisioning their young in both nesting regions sampled in this study.

Overall, SIA of nestling feathers provided novel information about the foraging resources that were most important to waterbirds in regions across the harbor, and should be used in the identification and prioritization of foraging habitats based on their importance to species of conservation concern. However, SIA alone cannot clearly distinguish among multiple foraging sites where similar foraging habitat types are available. Monitoring and tracking methods such as radio- and satellite-telemetry can provide information about physical locations frequented by individuals of a population, and can be used to compile the suite of sites for potential protection or remediation. Stable isotopes can then be used to prioritize foraging habitats based on the relative importance of the resources they provide, and also to modify and focus monitoring efforts on habitat types known to be of particular importance to a focal population. An integrative approach of observational methods and SIA will therefore facilitate both the identification of a suite of potential foraging sites, and the prioritization of those sites for waterbird conservation.

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LITERATURE CITED

- Bearhop, S., D. Thompson, S. Waldron, I. Russell, G. Alexander and R. W. Furness. 1999. Stable isotopes indicate the extent of freshwater feeding by cormorants *Phalacrocorax carbo* shot at inland fisheries in England. *Journal of Applied Ecology* 36: 75-84.
- Bildstein, K. L. 1993. White Ibis, wetland wanderer. Smithsonian Institution Press, Blue Ridge Summit, Pennsylvania.
- Bond, A. and I. Jones. 2009. A practical introduction to stable-isotope analysis for seabird biologists: approaches, cautions and caveats. *Marine Ornithology* 37: 183-188.
- Bond, A. L. and A. W. Diamond. 2011. Recent Bayesian stable-isotope mixing models are highly sensitive to variation in discrimination factors. *Ecological Applications* 21: 1017-1023.
- Caut, S., E. Angulo and F. Courchamp. 2009. Variation in discrimination factors ($\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$): the effect of diet isotopic values and applications for diet reconstruction. *Journal of Applied Ecology* 46: 443-453.
- Cherel, Y., K. A. Hobson and H. Weimerskirch. 2000. Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds. *Oecologia* 122: 155-162.
- Craig, E. C. 2012. New York City Audubon's Harbor Herons Project: 2012 nesting survey report. Unpublished report, New York City Audubon, New York, New York.
- Davis, W. E. and J. Kricher. 2000. Glossy Ibis (*Plegadis falcinellus*). No. 545 in *The Birds of North America* (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, Pennsylvania; American Ornithologists' Union, Washington, D.C.
- Farquhar, G. D., J. R. Ehleringer and K. T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* 40: 503-537.
- Good, T. P. 1998. Great Black-backed Gull (*Larus marinus*). No. 330 in *The Birds of North America* (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, Pennsylvania; American Ornithologists' Union, Washington, D.C.

- Harbor Herons Subcommittee. 2010. The Harbor Herons conservation plan - New York/New Jersey Harbor region (S. Elbin and N. Tsipoura, Eds.). New York-New Jersey Harbor Estuary Program, New York, New York.
- Hatch, J. J. and D. V. C. Weseloh. 1999. Double-crested Cormorant (*Phalacrocorax auritus*). No. 441 in *The Birds of North America* (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, Pennsylvania; American Ornithologists' Union, Washington, D.C.
- Hebert, C. E., D. V. C. Weseloh, A. Idrissi, M. T. Arts and E. Roseman. 2009. Diets of aquatic birds reflect changes in the Lake Huron ecosystem. *Aquatic Ecosystem Health & Management* 12: 37-44.
- Hobson, K. A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120: 314-326.
- Hobson, K. A. and R. G. Clark. 1992. Assessing avian diets using stable isotopes II: factors influencing diet-tissue fractionation. *Condor* 94: 189-197.
- Hothem, L. R., B. E. Brussee and W. E. Davis. 2010. Black-crowned Night-Heron (*Nycticorax nycticorax*). No. 74 in *The Birds of North America* (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, Pennsylvania; American Ornithologists' Union, Washington, D.C.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22: 415-427.
- Inger, R. and S. Bearhop. 2008. Applications of stable isotope analyses to avian ecology. *Ibis* 150: 447-461.
- Jackson, A. L., R. Inger, A. C. Parnell and S. Bearhop. 2011. Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology* 80: 595-602.
- Lott, C. A., T. Meehan and J. Heath. 2003. Estimating the latitudinal origins of migratory birds using hydrogen and sulfur stable isotopes in feathers: influence of marine prey base. *Oecologia* 134: 505-510.
- McCrimmon, D. A., Jr., J. C. Ogden and G. T. Bancroft. 2001. Great Egret (*Ardea alba*). No. 570 in *The Birds of North America* (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, Pennsylvania; American Ornithologists' Union, Washington, D.C.
- Minagawa, M. and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochimica et Cosmochimica Acta* 48: 1135-1140.
- Mizutani, H., M. Fukuda, Y. Kabaya and E. Wada. 1990. Carbon isotope ratio of feathers reveals feeding behavior of cormorants. *Auk* 107: 400-403.
- Newsome, S. D., C. Martínez del Río, S. Bearhop and D. L. Phillips. 2007. A niche for isotopic ecology. *Frontiers in Ecology and the Environment* 5: 429-436.
- Pierotti, R. and T. P. Good. 1994. Herring Gull (*Larus argentatus*). No. 124 in *The Birds of North America* (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, Pennsylvania; American Ornithologists' Union, Washington, D.C.
- Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83: 703-718.
- R Development Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>, accessed 10 September 2014.
- SAS Institute, Inc. 2012. JMP statistical discovery software v. 9. SAS Institute, Inc., Cary, North Carolina.
- Steele, K. W. and R. M. Daniel. 1978. Fractionation of nitrogen isotopes by animals: a further complication to the use of variations in the natural abundance of ^{15}N for tracer studies. *Journal of Agricultural Science* 90: 7-9.
- Vasil, C. A., M. J. Polito, W. P. Patterson and S. D. Emslie. 2012. Wanted: dead or alive? Isotopic analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of *Pygoscelis* penguin chick tissues supports opportunistic sampling. *Rapid Communications in Mass Spectrometry* 26: 487-493.