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FORAGING ECOLOGY OF FOUR GULL SPECIES AT A COASTAL–URBAN INTERFACE

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Abstract. Coastal urban environments provide a potentially diverse source of food for gulls, including items of marine, terrestrial, and anthropogenic origin. Our objective was to examine variation in the diet and use of feeding habitat of four species of gulls, the Laughing (*Leucophaeus atricilla*), Herring (*Larus argentatus*), Great Black-backed (*L. marinus*), and Ring-billed (*L. delawarensis*), at a coastal–urban interface. We necropsied, identified the sex and age class, and quantified the stomach contents of 1053 Laughing, 249 Herring, 67 Great Black-backed, and 31 Ring-billed Gulls collected near the New York City metropolitan area in 2003 and 2004. Great Black-backed Gulls specialized on marine foods, whereas Ring-billed Gulls were generalists. Laughing Gulls and Herring Gulls favored marine foods and foraged in marine habitats but also used terrestrial and anthropogenic food sources. We found evidence that demographics influenced the gulls' choice of diet and use of feeding habitat. Laughing Gulls and Herring Gulls switched their use of feeding habitats at various stages of breeding, exploiting terrestrial prey and feeding habitats most during chick rearing. Interspecific and intraspecific differences in the four species' diet and use of feeding habitat apparently allow for their coexistence at this coastal–urban interface.

Key words: *Charadriiformes, dietary analysis, foraging, gulls, Larus, urban.*

Ecología de Forrajeo de Cuatro Especies de Gaviota en una Interface Costera-Urbana

Resumen. Los ambientes urbanos costeros pueden potencialmente brindar una fuente variada de alimentos a las gaviotas, incluyendo elementos de origen marino, terrestre o antrópico. Nuestro objetivo fue examinar la variación en la dieta y en el uso del hábitat de forrajeo de cuatro especies de gaviotas, *Leucophaeus atricilla*, *Larus argentatus*, *Larus marinus* y *Larus delawarensis*, en una interface costera-urbana. Realizamos la necropsia, identificamos el sexo y la clase de edad, y cuantificamos el contenido estomacal de 1053 individuos de *L. atricilla*, 249 de *L. argentatus*, 67 de *L. marinus* y 31 de *L. delawarensis* colectados cerca del área metropolitana de la ciudad de Nueva York en 2003 y 2004. *L. marinus* se especializó en alimentos marinos, mientras que *L. delawarensis* fue generalista. *L. atricilla* y *L. argentatus* prefirieron los alimentos marinos y forrajearon en hábitats marinos pero también usaron fuentes de alimento terrestres y antrópicas. Encontramos evidencia de que la demografía influyó la selección de la dieta y el uso del hábitat de forrajeo de las gaviotas. *L. atricilla* y *L. argentatus* intercambiaron sus usos de los hábitats de forrajeo en varias de las fases de cría, explotando principalmente presas y hábitats de forrajeo terrestres durante la cría de los polluelos. Las diferencias inter e intra específicas en la dieta y en el uso del hábitat de alimentación de las cuatro especies aparentemente permite su coexistencia en esta interface costera-urbana.

INTRODUCTION

As human populations grow exponentially worldwide, increasing urbanization may affect avian populations in a variety of ways (Vitousek et al. 1997, Marzluff et al. 2001). Although for many species of birds the effect of urbanization is negative (McKinney 2002, Lim and Sodhi 2004), others, such as the Canada Goose (*Branta canadensis*), have adapted to urbanized areas and consequently expanded in population size. Gulls (Laridae) are one

such group that has adapted to human-dominated environments and activities (Belant 1997, Rock 2005).

The ranges and abundance of gulls around the world increased substantially during the latter half of the 20th century (Blokpoel and Spaans 1991, Aumen et al. 2008, Coulson and Coulson 2009). In North America gull populations (of several species) have increased considerably, at least in part because of the availability of human-derived food sources such as waste-management facilities (e.g., landfills), discards from

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fishing enterprises, agriculture, and cities where gulls can scavenge (Belant and Dolbeer 1993, Ryder 1993, Good 1998). Gulls have generalist diets and use a variety of aquatic and terrestrial habitats, food types, and foraging strategies (Burger 1988, Annett and Pierotti 1989, Kubetzki and Garthe 2003, Aumen et al. 2008). Urban environments in coastal areas (freshwater and marine) provide a potentially diverse source of food and foraging opportunities for gulls, including prey of aquatic, terrestrial, and anthropogenic origin. Their opportunistic and generalized feeding behavior may allow gulls to shift their diet and feeding habitat use to forage in a variety of aquatic and terrestrial habitats. This flexibility may be particularly important in situations where several species occur together, resulting in competition for available food resources (Burger and Gochfeld 1983, Arcos et al. 2001, Rome and Ellis 2004, Steenweg et al. 2011).

In urban areas, particularly coastal ones, gulls' foraging ecology is little studied (Rock 2005, Kubetzki and Garthe 2007). A better understanding of the food habits and the temporal patterns of food selection of gulls occurring sympatrically within coastal urban environments is needed to allow for more effective resolution of human–gull conflicts. We had an opportunity

to study the summer diets of four sympatric gull species and determine how these species use foods from a variety of aquatic and terrestrial sources.

In this study, we examined the diet and feeding-habitat use of four species of gulls that occur sympatrically in the coastal–urban interface near Jamaica Bay, New York. Our objectives were to (1) assess interspecific variation of the four species' diets, (2) determine if these diets varied by sex and age class, and (3) examine temporal variation in the diets of the Herring Gull (*Larus argentatus*) and Laughing Gull (*Leucophaeus atricilla*) and at various stages of the breeding cycle.

METHODS

STUDY AREA AND SPECIES

In our study, we addressed four species, the Laughing Gull, Herring Gull, Great Black-backed Gull (*Larus marinus*), and Ring-billed Gull (*L. delawarensis*). We obtained birds collected at John F. Kennedy International Airport (40° 38' N, 73° 47' W), located on the southwestern end of Long Island, New York (Fig. 1). Many of the Laughing Gulls, Herring

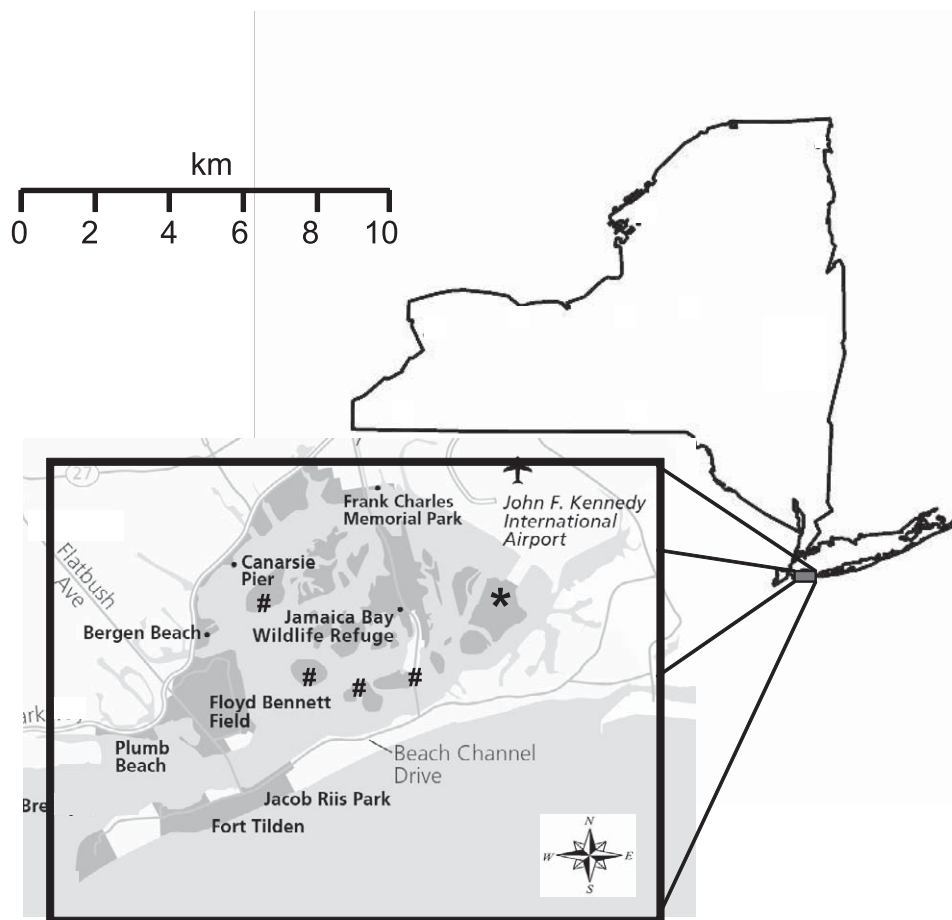


FIGURE 1. Location of the John F. Kennedy International Airport (i.e., gull collection sites) in relation to a Laughing Gull colony in the Joco Marsh island complex, represented by an asterisk (*), and Herring Gull and Great Black-backed Gull colonies, represented by pound signs (#), within the Gateway National Recreation Area, represented by the gray shading.

Gulls, and Great Black-backed Gulls were likely associated with nesting colonies in the Jamaica Bay Unit of Gateway National Recreation Area, which is adjacent to the airport (Fig. 1; Dolbeer et al. 1997, Brown et al. 2001, Sommers et al. 2001). In 2003 and 2004, the Laughing Gull colony in the Joco Marsh island complex had an estimated 2199 and 2083 nests, respectively (Washburn et al. 2004); this is the only colony of the Laughing Gull known in New York State (Washburn et al. 2012). Several colonies of the Herring Gull and Great Black-backed Gull are located on islands within Gateway National Recreation Area (Sommers et al. 2001). Ring-billed Gulls do not breed on Long Island, the nearest known colonies being in upstate New York (Ryder 1993). Although all age classes of the Ring-billed Gull (including adults) commonly winter along Long Island, subadults constitute the vast majority of the population during the summer.

Marine and terrestrial habitats that might provide opportunities for gulls' foraging at this coastal–urban interface include salt marshes, tidal bays and mudflats, residential lawns and gardens, parks and other areas of mowed turfgrass, and the airfield. The airfield covers 1995 ha, vegetated with large areas of cool-season turfgrasses, sparse weedy vegetation, and some small trees and shrubs. Gulls also have access to anthropogenic foods (e.g., human refuse) in the surrounding urban and suburban areas.

GULL COLLECTION

From 19 May to 4 September of 2003, we salvaged 470 Laughing Gulls as a random sample from those shot under the program to reduce gull–aircraft collisions at the airport (Dolbeer et al. 1993; Washburn et al. 2005). From 18 May to 16 September 2004, we salvaged all four species, totaling 583 Laughing Gulls, 249 Herring Gulls, 67 Great Black-backed Gulls, and 31 Ring-billed Gulls. The digestive system of each bird was injected with 70% ethyl alcohol at the time of collection (Rosenberg and Cooper 1990). Each specimen was labeled, placed in a plastic bag, and frozen within 6 hr of collection. Frozen gulls were shipped to the U.S. Department of Agriculture, Wildlife Services, National Wildlife Research Center, Ohio Field Station, located in Sandusky, Ohio, for necropsy. On the basis of previous studies of time of retention in the gut of fishes consumed by Herring Gulls (Hilton et al. 1998) and of seeds consumed by Yellow-legged Gulls (*L. michahellis*; Nogales et al. 2001), we believe the stomach contents of each gull likely represent the prey items that bird had consumed very recently, during the previous 6 to 12 hr.

NECROPSY AND DIETARY ANALYSES

We thawed and necropsied all gulls salvaged for this study. We categorized Laughing Gulls by plumage as age 0 (hatched that year), age 1 (1 yr old), age 2 (2 yr old), or age ≥ 3 (≥ 3 yr old) (Grant 1986, Belant and Dolbeer 1996). Herring Gulls, Great Black-backed Gulls, and Ring-billed Gulls we aged by plumage (Grant 1986) as hatched that year, subadult (1, 2, or 3 yr old), or adult (≥ 4 yr old). All gulls were sexed by examination of internal anatomy.

We removed and examined the contents of the stomach, proventriculus, and esophagus (referring to this entire complex as the stomach) of each gull. Using a 10 \times binocular microscope, we identified organisms to the lowest taxonomic level possible by standard taxonomic methods. We categorized each food item by its most likely source (marine, terrestrial, or anthropogenic). For each individual bird, we visually estimated the (volumetric) aggregate percentage (totaling to 100%) of all prey items of marine origin (e.g., crabs, fish), terrestrial origin (e.g., insects, vegetation), and anthropogenic origin (e.g., livestock bones, French fries) (Hyslop 1980, Rosenberg and Cooper 1990).

Thirty-seven gulls had completely empty stomachs, and 289 gulls had only nonfood items (e.g., grit, plastic) in their stomachs. Although we believe these data are interesting, the nonfood items (primarily grit) do not provide information regarding specific locations where gulls were feeding, and interpretation of this information is complicated because this material can remain in the digestive tract for an extended/unknown amount of time. Consequently, we removed these individuals from datasets prior to summary and statistical analyses.

STATISTICAL ANALYSES

We calculated the percent frequency of occurrence (FO%) of major food items (i.e., >10 occurrences) and food-origin types as the number of stomachs that contained that item or type, expressed as a percentage of the total number of stomachs examined (Duffy and Jackson 1986, Granadeiro et al. 2002, Catry et al. 2006). We calculated the mean aggregate percentage (MAP) of food-origin types by averaging the aggregate percentage of each type (marine, terrestrial, or anthropogenic) within all stomach samples of a given species, sex, age class, or stage of breeding (Swanson et al. 1974, Duffy and Jackson 1986, Gilliland et al. 2004, Anderson et al. 2008).

For the Laughing Gull, we found no differences in diet between 2003 and 2004 when we compared the FO% of each food-origin type (all $P > 0.20$) with G -tests for independence (Zar 1996) and compared MAP by food-origin type and year (all $P > 0.35$) with a two-way analysis of variance (ANOVA). Consequently, we pooled the 2003 and 2004 data for that species in all further analyses.

We compared the FO% of each food-origin type by species with G -tests for independence. The MAP data were normalized by arcsin transformations. We used two-way ANOVA and Fisher's protected LSD tests (Zar 1996) to determine if MAP varied by food-origin type (indicative of feeding habitat use) and species. We used SAS (SAS Institute 1999) for all statistical analyses and considered test results significant if $P \leq 0.05$.

On the basis of previous studies (Burger 1996, Dolbeer and Bernhardt 2003) and local information (including necropsy data from this study), we defined the stages of the Laughing Gull's breeding cycle as egg-laying (15 May–25 May), incubation (5 June–15 June), chick rearing (25 June–1 August),

and post-breeding (15 August–1 October). For the Herring Gull we defined these stages as incubation (15 May–25 May), chick-rearing (1 June–15 July), and post-fledging care of young (1 August–1 September; Pierotti and Good 1994, Tims 1999). We assumed most of the breeding gulls were at these stages during these periods; we excluded gulls collected outside these dates from the analyses by stage of breeding.

We compared the FO% of each food-origin type by sex and age class for all four species and by stage of breeding for the Laughing Gull and Herring Gull with *G*-tests for independence. We used three-way ANOVA and Fisher's protected LSD tests to determine for each species if MAP varied by food-origin type, sex, and age class. In addition, we used two-way ANOVA and Fisher's protected LSD tests to determine if for adult Laughing Gulls and Herring Gulls MAP varied by food-origin types and stage of breeding.

RESULTS

INTERSPECIFIC VARIATION IN DIET

All four gull species fed upon a wide variety of prey items presumably obtained from marine, terrestrial, and anthropogenic sources (Table 1). Laughing Gulls, Herring Gulls, Great

Black-backed Gulls, and Ring-billed Gulls consumed a total of 59, 45, 13, and 24 different prey items, respectively.

Eggs of the horseshoe crab (*Limulus polyphemus*) were the item most frequently consumed by Laughing Gulls (Table 1). Laughing Gulls also preyed upon small crabs such as European green crabs (*Carcinus maenas*), terrestrial insects such as beetles and ants, and small fish such as northern pipefish (*Syngnathus fuscus*) and bay anchovy (*Anchoa mitchilli*). Herring Gulls consumed crabs such as Atlantic rock crabs (*Cancer irroratus*), Jonah crabs (*C. borealis*), and blue crabs (*Callinectes sapidus*) with the highest frequency but human refuse such as chicken, fruits, vegetables frequently as well (Table 1). Fishes such as blueback herring (*Alosa aestivalis*) and Atlantic menhaden (*Brevoortia tyrannus*) were the most common prey of Great Black-backed Gulls, which also frequently consumed horseshoe crab eggs and large crabs (Table 1). Ring-billed Gulls fed on human refuse more frequently than on other foods, such as marine crustaceans (e.g., *Gammarus* spp.) and terrestrial invertebrates (Table 1).

All four gulls foraged, at least to some degree, in marine habitats (e.g., intertidal and shallow subtidal areas), terrestrial

TABLE 1. Frequency of occurrence (%FO) of foods of marine, terrestrial, and anthropogenic origin consumed by four species of gulls collected at John F. Kennedy International Airport, May–September 2003 and 2004.

	Laughing Gull ^a	Herring Gull ^b	Great Black-backed Gull ^c	Ring-billed Gull ^d
<i>n</i> ^e	817	191	43	23
Marine origin	70	64	84	39
Fish	10	7	44	0
<i>Limulus</i> eggs and larvae	29	9	21	9
Crabs	16	30	16	4
Shrimp	5	1	0	4
Bivalves	3	9	0	0
Unidentified crustaceans	2	6	14	9
Terrestrial origin	34	14	9	57
Birds	1	2	5	0
Earthworms	3	3	0	4
Cockroaches	1	0	0	4
Coleoptera (beetles)	12	5	2	4
Formicidae (ants)	6	2	0	4
Orthoptera (grasshoppers)	2	1	0	0
Mulberries	4	1	0	0
Plant material	7	4	2	9
Anthropogenic origin	17	33	12	35
Chicken	7	12	5	0
Bread	4	5	0	22
Fruits and vegetables	5	16	9	30

^aLaughing Gulls with empty stomachs (*n* = 19) and with only nonfood items (*n* = 217) were excluded prior to analyses.

^bHerring Gulls with empty stomachs (*n* = 8) and those with only nonfood items (*n* = 50) were excluded prior to analyses.

^cGreat Black-backed Gulls with empty stomachs (*n* = 10) and those with only nonfood items (*n* = 14) were excluded prior to analyses.

^dRing-billed Gulls with only nonfood items (*n* = 8) were excluded prior to analyses.

^eNumber of stomachs examined that contained one or more food items.

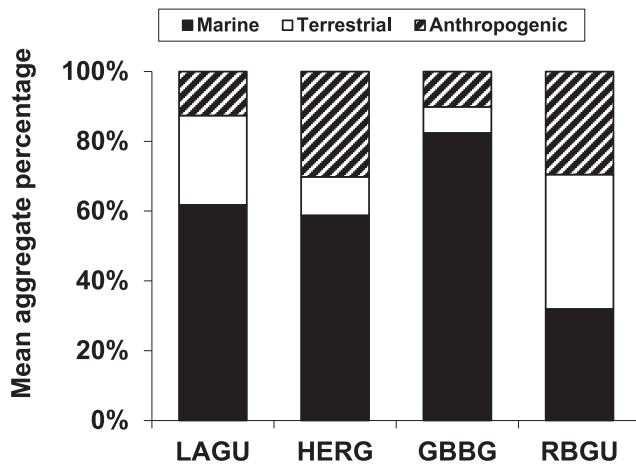


FIGURE 2. Mean aggregate percentage of foods of marine, terrestrial, and anthropogenic origin consumed by four species of gulls collected at the John F. Kennedy International Airport, May–September 2003 and 2004. LAGU, Laughing Gull; HERG, Herring Gull; GBBG, Great Black-backed Gull; RBGU, Ring-billed Gull.

habitats (e.g., grassland and turfgrass), and anthropogenic habitats (e.g., refuse containers). Among the four species, the frequency of occurrence of foods of marine ($G_3 = 16.3$, $P = 0.001$), terrestrial ($G_3 = 50.3$, $P < 0.001$), and anthropogenic ($G_3 = 27.3$, $P < 0.001$) origin differed (Table 1). The mean aggregate percentage among food-origin types (indicative of feeding habitat use) also varied (ANOVA, food-origin type \times gull species interaction: $F_{6,3221} = 15.23$, $P < 0.001$; Fig. 2).

Great Black-backed Gulls foraged predominantly in marine habitats; this species consumed prey of marine origin with the greatest frequency and had MAP of marine foods higher than that of the other gulls (Table 1, Fig. 2). From the FO% and MAP of terrestrial food items, it appears Ring-billed Gulls and Laughing Gulls foraged in terrestrial habitats more than did Herring Gulls and Great Black-backed Gulls (Table 1, Fig. 2). Herring Gulls and Ring-billed Gulls used anthropogenic food sources more than did Laughing Gulls and Great Black-backed Gulls (Table 1, Fig. 2).

DEMOGRAPHIC INFLUENCES

The influence of demographics on the four species' diet and use of feeding habitats varied, but were found no significant interactions of sex with age class (ANOVA; all $P > 0.30$). In neither the Laughing Gull nor Great Black-backed Gull did sex influence diet choice (G -tests; all $P > 0.25$) or use of feeding habitat (ANOVA; all $P > 0.15$) (Table 2). In the Herring Gull, by contrast, males consumed prey items of marine origin with a frequency greater than did females ($G_1 = 4.9$, $P = 0.03$). In the Herring Gull, sex influenced the MAP by food-origin type (ANOVA, food-origin type \times sex class interaction: $F_{3,480} = 14.3$, $P < 0.001$). Male Herring Gulls used marine feeding habitats more than did females, whereas their use of terrestrial and anthropogenic food sources was similar (Table 2). Female Ring-billed Gulls consumed marine foods more frequently ($G_1 = 4.8$, $P = 0.03$) than did males. Among food-origin types, MAP of male and female

TABLE 2. Frequency of occurrence (%FO) and mean aggregate percentage (MAP) \pm SE of foods of marine, terrestrial, and anthropogenic origin consumed by male and female Laughing Gulls^a, Herring Gulls^b, Great Black-backed Gulls^c, and Ring-billed Gulls^d collected at John F. Kennedy International Airport, May–September 2003 and 2004.

	Marine		Terrestrial		Anthropogenic	
	%FO	MAP	%FO	MAP	%FO	MAP
Laughing Gull						
Male ($n = 429$)	67	59.3 \pm 2.2	34	25.0 \pm 1.9	21	15.7 \pm 1.6
Female ($n = 353$)	72	63.6 \pm 2.4	35	27.3 \pm 2.2	14	9.1 \pm 1.4
Herring Gull						
Male ($n = 95$)	72	66.3 \pm 4.6	13	9.0 \pm 2.7	27	24.7 \pm 4.3
Female ($n = 96$)	56	51.4 \pm 4.9	16	12.9 \pm 3.3	39	35.7 \pm 4.8
Great Black-backed Gull						
Male ($n = 21$)	86	84.0 \pm 7.8	10	9.5 \pm 6.6	10	6.4 \pm 5.0
Female ($n = 22$)	82	80.9 \pm 8.4	9	5.5 \pm 4.6	14	13.6 \pm 7.5
Ring-billed Gull						
Male ($n = 14$)	21	13.3 \pm 8.2	64	47.4 \pm 12.3	43	39.3 \pm 12.8
Female ($n = 9$)	67	61.1 \pm 16.2	44	24.6 \pm 14.3	22	14.3 \pm 10.3

^aLaughing Gulls with empty stomachs ($n = 19$), with only nonfood items ($n = 217$), of unknown sex ($n = 5$), or of unknown age ($n = 30$) were excluded prior to analyses.

^bHerring Gulls with empty stomachs ($n = 8$) and those with only nonfood items ($n = 50$) were excluded prior to analyses.

^cGreat Black-backed Gulls with empty stomachs ($n = 10$) and those with only nonfood items ($n = 14$) were excluded prior to analyses.

^dRing-billed Gulls with only nonfood items ($n = 8$) were excluded prior to analyses.

TABLE 3. Frequency of occurrence (%FO) and mean aggregate percentage (MAP) \pm SE of foods of marine, terrestrial, and anthropogenic origin consumed by Laughing Gulls^a, Herring Gulls^b, and Great Black-backed Gulls^c of various age classes collected at John F. Kennedy International Airport, May–September 2003 and 2004.

Age (in years or class)	Marine		Terrestrial		Anthropogenic	
	%FO	MAP	%FO	MAP	%FO	MAP
Laughing Gull						
Hatching-year ($n = 30$)	80	70.5 \pm 7.7	23	14.5 \pm 5.8	17	15.0 \pm 6.3
1 ($n = 41$)	83	77.1 \pm 6.0	24	16.8 \pm 5.3	7	6.1 \pm 3.6
2 ($n = 223$)	71	66.9 \pm 3.0	29	23.2 \pm 2.7	13	9.9 \pm 1.9
≥ 3 ($n = 488$)	67	56.8 \pm 2.1	39	28.7 \pm 1.9	20	14.4 \pm 1.4
Herring Gull						
Hatching-year ($n = 25$)	48	56.8 \pm 9.6	16	12.0 \pm 6.6	48	31.2 \pm 8.9
Subadult ($n = 89$)	73	70.4 \pm 4.7	11	9.9 \pm 3.0	25	19.7 \pm 4.1
Adult ($n = 77$)	58	46.1 \pm 5.5	17	11.9 \pm 3.4	38	42.0 \pm 5.6
Great Black-backed Gull						
Hatching-year ($n = 6$)	67	63.3 \pm 20.3	50	36.7 \pm 20.3	0	0.0 \pm 0.0
Subadult ($n = 11$)	82	78.6 \pm 12.1	0	0.0 \pm 0.0	27	21.4 \pm 12.1
Adult ($n = 26$)	89	88.5 \pm 6.4	4	3.8 \pm 3.8	8	7.7 \pm 5.3

^aLaughing Gulls with empty stomachs ($n = 19$), with only nonfood items ($n = 217$), of unknown sex ($n = 5$), or of unknown age ($n = 30$) were excluded prior to analyses.

^bHerring Gulls with empty stomachs ($n = 8$) and those with only nonfood items ($n = 50$) were excluded prior to analyses.

^cGreat Black-backed Gulls with empty stomachs ($n = 10$) and those with only nonfood items ($n = 14$) were excluded prior to analyses.

Ring-billed Gulls differed (ANOVA, food-origin type \times sex class interaction: $F_{4,480} = 5.34$, $P = 0.01$). Female Ring-billed Gulls foraged in marine habitats more than did males, whereas males used anthropogenic sources more than did females (Table 2).

In the Laughing Gull, the FO% of food-origin types varied (marine: $G_3 = 7.8$, $P = 0.04$; terrestrial: $G = 10.0$, $P = 0.02$; anthropogenic: $G_3 = 9.2$, $P = 0.02$) by age class (Table 3), as did MAP (ANOVA, food-origin type \times age class interaction: $F_{6,2345} = 5.18$, $P < 0.001$). Overall, older (i.e., ≥ 3 years old) Laughing Gulls consumed more terrestrial and anthropogenic foods and less marine foods than did subadults (Table 3). Adult Herring Gulls consumed marine prey less frequently ($G_2 = 7.0$, $P = 0.03$) and anthropogenic foods more frequently ($G_2 = 6.1$, $P = 0.04$) than did subadults (Table 3). Among food-origin types, MAP varied (ANOVA, food-origin type \times age class interaction: $F_{4,480} = 6.42$, $P < 0.001$) across age classes in Herring Gulls. Subadult Herring Gull use of marine and anthropogenic feeding habitats was more and less, respectively, than that of adult and hatching-year conspecifics (Table 3). Hatching-year Great Black-backed Gulls consumed terrestrial foods much more frequently ($G_2 = 9.8$, $P = 0.008$). Age class influenced the MAP among food-origin types in Great Black-backed Gulls (ANOVA, food-origin type \times age class interaction: $F_{4,480} = 3.24$, $P = 0.02$). Hatching-year Great Black-backed Gulls used terrestrial feeding habitats considerably more than subadults and adults (Table 3). Only subadult (i.e., 1-yr-old and 2-yr-old) Ring-billed Gulls were

collected; thus, no age-related comparisons were made for this species.

VARIATION AMONG BREEDING STAGES

Frequency of occurrence of prey items of marine ($G_3 = 31.9$, $P < 0.001$) and terrestrial origin ($G_3 = 49.2$, $P < 0.001$) varied among the breeding stages for adult Laughing Gulls, whereas anthropogenic foods were present with equal frequency ($G_3 = 2.2$, $P = 0.53$) throughout the breeding season (Fig. 3). Breeding stage influenced the MAP among food-origin types in Laughing Gulls (ANOVA, food-origin type \times breeding stage interaction: $F_{6,1448} = 18.0$, $P < 0.001$). Adult Laughing Gulls switched the importance of feeding habitats during the chick-rearing period, apparently obtaining more food in terrestrial feeding habitats and less in marine feeding habitats than during the egg-laying, incubation, and post-breeding periods (Fig. 3).

Interestingly, adult Herring Gulls displayed a pattern of diet and feeding habitat switching during the breeding season similar to Laughing Gulls. Adult Herring Gulls consumed terrestrial prey items more frequently ($G_2 = 9.9$, $P = 0.001$) during the chick-rearing stage than during the incubation and post-fledging care stages (Fig. 4). Among food-origin types, MAP varied across breeding stages in Herring Gulls (ANOVA, food-origin type \times breeding stage interaction: $F_{4,182} = 2.98$, $P = 0.02$). Adult Herring Gulls used terrestrial feeding habitats more and marine feeding habitats less during the chick-rearing stage than during the incubation and post-fledging care periods (Fig. 4).

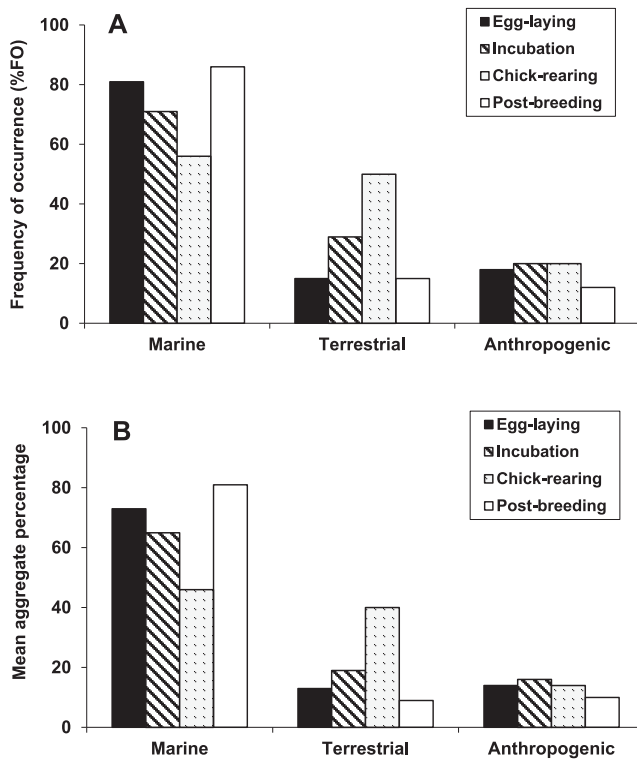


FIGURE 3. Frequency of occurrence (A) and mean aggregate percentage (B) of foods of marine, terrestrial, and anthropogenic origin consumed by adult Laughing Gulls collected at various stages of the breeding cycle, May–September 2003 and 2004.

DISCUSSION

We found that at coastal–urban interfaces gulls are opportunistic and forage on a diversity of prey items and use a variety of aquatic (e.g., intertidal zones, mud flats) and terrestrial feeding habitats (e.g., parks, lawns, refuse containers). Not unexpectedly, diet choice and feeding-habitat use varied among the four species we studied. The Great Black-backed Gull was primarily a marine specialist, focusing predominantly on the marine environment. In contrast, the Ring-billed Gull had the most generalized and opportunistic feeding strategy, using the whole mosaic of the coastal–urban interface. The Laughing Gull and Herring Gull were intermediate in their feeding strategies between the other two gulls. Overall, the patterns of gull foraging we observed are consistent with other studies and information regarding the feeding habits of the Laughing Gull (Burger 1988, 1996), Herring Gull (Götmark 1984, Pierotti and Good 1994, Rome and Ellis 2004), Great Black-backed Gull (Götmark 1984, Good 1998, Gilliland et al. 2004, Rome and Ellis 2004), and Ring-billed Gull (Jarvis and Southern 1976, Ryder 1993).

Sex- and age-related differences in feeding behavior and foraging efficiency have been observed in other gulls and terns

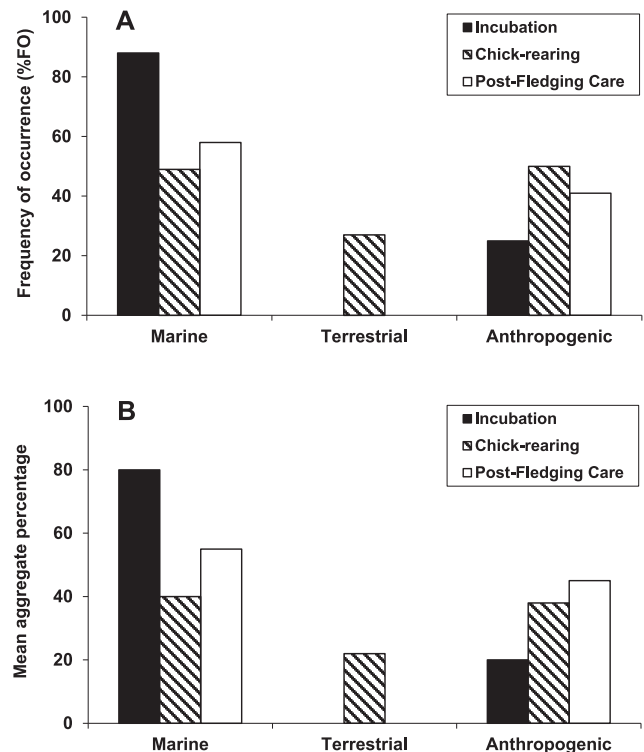


FIGURE 4. Frequency of occurrence (A) and mean aggregate percentage (B) of foods of marine, terrestrial, and anthropogenic origin consumed by adult Herring Gulls collected at various stages of the breeding cycle, May–September 2004.

(Burger and Gochfeld 1983, Burger 1987, 1988, Pons 1994). In this study, we found evidence of variation in prey selection and use of feeding habitats by sex and age group. Sex-based differences in gulls' prey selection and use of feeding habitat could be associated with differences between the sexes in nutritional requirements (Bukacińska et al. 1996, Pierotti and Annett 1991), parental roles during breeding (Pierotti 1981), or foraging efficiency by habitat (Sibly and McCleery 1983, Pons 1994, Duhem et al. 2005). Age-specific variation in food choice and use of feeding habitat might reflect patterns of food abundance and availability, a difference between adult and subadult gulls in nutritional needs (Pierotti and Annett 1991), differences in foraging and feeding ability by age group (i.e., subadults might be less efficient or lack knowledge; Burger and Gochfeld 1983, Greig et al. 1983, Burger 1987), or other factors. Interestingly, our findings suggest hatching-year gulls have the foraging skills necessary to effectively exploit a variety of food resources from several habitats.

Although the results of our study reflect diet choice and habitat use by gulls feeding themselves (Ydenberg 1994), breeding Laughing Gulls, Herring Gulls, and Great Black-backed Gulls are also provisioning nestlings during June and July (Pierotti and Good 1994, Burger 1996, Good 1998,

Washburn et al. 2004). When provisioning nestlings, gulls travel considerable distances (up to 40 km) and forage inland, away from breeding colonies (Gorke and Brandl 1986, Cavanagh 1992, Dosch 2003, Duhem et al. 2005). Consequently, diets of nestling gulls contain large amounts of terrestrial prey such as insects and of anthropogenic foods such as refuse (Kirkham and Morris 1979, Dosch 1997, Schmutz and Hobson 1998, Knoff et al. 2002). Terrestrial prey might be selected if it is of a size or consistency appropriate for young chicks to handle and consume (Annett and Pierotti 1989, Gilliland et al. 2004) and/or meets the specific nutritional needs (e.g., protein) of growing chicks (Kirkham and Morris 1979, Pierotti and Annett 1990, Bukacińska et al. 1996, Schmutz and Hobson 1998). Terrestrial prey (e.g., insects), in particular those in seasonally high abundance and presumably available to foraging Laughing Gulls and Herring Gulls during the nestling period, are likely both an important food for adult gulls feeding themselves and nutritionally important for gull chicks (Ydenberg 1994, Dosch 1997, Davoren and Burger 1999, Bernhardt et al. 2010).

Switching feeding habitats at various stages of the breeding cycle appears to be an important part of these species' feeding strategy. Gulls that switch feeding habitats might do so because of changes in prey abundance and availability (Murphy et al. 1984, Pierotti and Annett 1990, Steenweg et al. 2011), changes in the nutritional requirements of adult gulls (Pierotti and Annett 1991, Pons 1994), or aspects of their breeding biology (e.g., rearing chicks; Annett and Pierotti 1989, Schwemmer and Garthe 2008). Although feeding-habitat switching might be a common strategy in gulls, the specific habitats used appears to vary by species and breeding location. Breeding Glaucous Gulls (*L. hyperboreus*) in Alaska (Schmutz and Hobson 1998) and breeding Yellow-legged Gulls in France (Duhem et al. 2005) consume more prey of terrestrial origin after the hatching of their chicks. In contrast, while rearing chicks Black-headed Gulls (*L. ridibundus*) decrease their use of terrestrial feeding habitats and increase their use of marine habitats (Schwemmer and Garthe 2008).

Like all methods of dietary analysis, examination of gastrointestinal contents has inherent biases (Duffy and Jackson 1986, Rosenberg and Cooper 1990). Differential digestibility of consumed food items (e.g., aquatic and terrestrial invertebrates, plant material) and associated potential biases has been documented in dietary studies of a variety of avian species, including blackbirds (Williams and Jackson 1981), crows (Berrow et al. 1992), songbirds (Dillery 1965, Custer and Pitelka 1975), and waterfowl (Briggs et al. 1985, Bourget et al. 2007, Anderson et al. 2008). We suspect that some quickly digested foods were under-represented and relatively indigestible items were likely over-represented in our dietary analyses.

In conclusion, we found that the four gull species that occur sympatrically at this coastal–urban interface consume a

diversity of foods and forage in numerous aquatic and terrestrial habitats. We found evidence that demographics (i.e., sex, age) influenced gulls' diet choice and feeding-habitat use. Laughing Gulls and Herring Gulls switched their use of feeding habitats at various stages of breeding; feeding more on terrestrial prey and in terrestrial habitats during the chick-rearing stage. Interspecific and intraspecific differences in feeding strategies within and among the four gull species, either through niche segregation, spatial segregation of foraging locations, or a combination thereof, apparently allows for their coexistence at this coastal–urban interface. Future research is needed to elucidate other aspects of the foraging, movement, and reproductive ecology of gulls associated with major urban areas adjacent to freshwater and marine coastal environments.

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