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Foraging Ecology and Interactions between Herring Gulls and Great Black-backed Gulls in New England

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Abstract.—Numbers of Great Black-backed Gulls (*Larus marinus*) and Herring Gulls (*L. argentatus*) along coastal New England have changed dramatically during the last century. In recent years, Great Black-backed Gulls have displaced Herring Gulls from optimal breeding sites, thus potentially contributing to the recent decline of the Herring Gull. Although the quality of foraging habitat is also a strong determinate of reproductive success, potential for competition and interactions between these two species in natural foraging habitats have been largely ignored. In this study, the diet and prey preference of the two species were compared. In addition, the spatial and temporal patterns in foraging activities were examined and interspecific interactions in the rocky intertidal zones were also described. Diet and prey preference of the two species greatly overlapped, with both species consuming a large percentage of marine invertebrates (30-60%), especially crabs. Foraging differed, and the Great Black-backed Gull consumed more crabs from the shallow subtidal zone than the Herring Gull. In regions where numbers of gulls were relatively high, Great Black-backed Gulls initiated all aggressive interspecific interactions. In September, when some Great Black-backed Gulls had moved from breeding to overwintering grounds, 1) the size of Jonah Crab (*Cancer borealis*) carapaces increased in Herring Gull prey, and 2) the numbers of Herring Gulls consuming crabs increased. These findings suggest that during the breeding season, aggression by the Great Black-backed Gull, especially in areas of high numbers, may suppress the ability of the Herring Gull to forage and obtain larger crabs from the shallow subtidal zone at our study site. *Received 27 October 2003, accepted 20 February 2004.*

Key words.—*Larus argentatus*, Herring Gull, *Larus marinus*, Great Black-backed Gull, foraging, seabird, avian diet, rocky intertidal, *Cancer borealis*.

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In seabird communities, species from the same family often coexist (Cody 1973; Fasola *et al.* 1989; Arcos *et al.* 2001). Ecological isolating mechanisms promoting coexistence include differential body size (Cody 1973; Fasola *et al.* 1989), asynchronous breeding seasons (Cody 1973), partitioning of foraging habitats (Cody 1973; Hunt and Hunt 1973; Mudge and Ferns 1982) and prey type (Garthe *et al.* 1999; Arcos *et al.* 2001). Partitioning of foraging habitats and prey during the breeding season can have important fitness consequences since the quality of diet during the breeding season is a strong determinant of reproductive success in seabirds (Pierotti and Annett 1990, 1991; Annett and Pierotti 1999).

In the family Laridae, two or more species commonly co-occur in coastal areas. During the past century along the east coast of North America, dramatic increases in the Herring Gull (*Larus argentatus*) and Great Black-backed Gull (*L. marinus*) numbers have led to greater overlap in ranges of the two species (Drury 1973; Ewins *et al.* 1992; Good 1998). As a result, both species currently breed sympatrically on offshore islands throughout New England, although in the first half of the twentieth century Herring Gulls were by far the most abundant species breeding on these islands (Drury 1973; Borror and Holmes 1990). After reaching a peak in the 1970s and 80s, however, Herring Gull numbers declined at several sites along the east coast of North America (Cavanagh 1992; Brown *et al.* 2001; Robertson *et al.* 2001), whereas the Great Black-backed Gull continued to increase (Borror and Holmes 1995; Brown *et al.* 2001). In North America, the Great Black-backed Gull is the largest and heaviest gull, approximately 500-1000 g heavier than the Herring Gull (Pierotti and Good 1994; Good 1998). In fact, the male adult Herring Gull (wing length 429 ± 10.3 mm [$x \pm$ SD]; Evans *et al.* 1995) are rarely as large as female adult Great Black-backed Gulls (wing length 478 ± 9.3 mm [$x \pm$ SD]; Megyesi 1996) in North America. McGill-Harelstad (1985) suggests that the larger-bodied Great Black-backed

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Gull displaced Herring Gulls from optimal breeding sites, thus contributing to the latter's recent decline.

Little is known about the interactions between these two gull species in natural foraging habitats, despite the potential impact on reproductive success. Both gull species are considered generalist predators and forage in various habitats including the low intertidal and shallow subtidal zones, offshore, mudflats, landfills, and within seabird colonies (Belopol'skii 1957; Pierotti and Good 1994; Good 1998). While both species are considered kleptoparasites, the Great Black-backed Gull steals prey from the Herring Gull at landfills and in intertidal habitats (Verbeek 1979; Good 1992a). Moreover, in coastal areas of Europe and North America, both species forage on discarded fisheries products (Camphuysen 1995; Walter and Becker 1997; Hüppop and Wurm 2000), but the Great Black-backed Gull out-compete the Herring Gull for this resource (Furness *et al.* 1992). In New England, both species forage at landfills and dumps (Pierotti and Good 1994; Good 1998), but Herring Gulls tend to rely more heavily on this resource (Wells 1994). Improved sanitation practices and the closing of landfills are suggested as having contributed to the decline of the Herring Gull (Buckley and Buckley 1984), and may have increased reliance by both species on natural foraging habitats, such as intertidal and subtidal habitats, mudflats, or offshore feeding grounds (Good 1992, 1998; Pierotti and Good 1994). As a consequence, interspecific interactions may be increasing in these habitats.

In this study, foraging behavior and interspecific interactions between Great Black-backed Gulls and Herring Gulls in intertidal and subtidal habitats are quantified on Appledore Island, Maine, the site of one of the largest breeding colonies of both species (Borror and Holmes 1990; Good 1998). Specifically, this study addresses the following questions: 1) What are the diets and prey preferences of the Great Black-backed Gull and the Herring Gull during the breeding season? 2) What are the spatial and temporal patterns in foraging activities of the two species? 3) What are the frequencies of interspecific interactions in intertidal and subtidal habitats? and 4) How does the Herring Gull's foraging activities and diet change in the late summer, after the majority of Great Black-backed Gulls have left the breeding grounds?

METHODS

Study Area

This study was conducted at the Shoals Marine Laboratory, Appledore Island, in the Gulf of Maine (42°58'N; 70°37'W; Fig. 1). Appledore Island is part of a nine-island archipelago located approximately 10 km off the coast of New Hampshire, USA. The shoreline is composed of exposed rocky headlands and boulder coves.

Great Black-backed Gulls began breeding on the Isles of Shoals in the first quarter of the twentieth century (Jackson and Allen 1932), the time when appreciable numbers of Herring Gulls were already breeding there (Borror and Holmes 1990). Since 1975, the number of Herring Gulls has declined by half, while Great Black-backed Gulls have more than doubled. The most recent published breeding census, conducted in 1989, estimated that 1,083 Herring Gull and 841 Great Black-backed Gull pairs nested on Appledore Island (Borror and Holmes 1995).

During the breeding season, both gull species inhabit off-shore islands from March through September (McGill-Harlestad 1985). However, the exact timing is slightly offset: the Great Black-backed Gull initiates nesting approximately two weeks earlier than the Herring Gull (Erwin 1971) and moves off to the mainland two to four weeks before the Herring Gull (J. C. Ellis, pers. obs.).

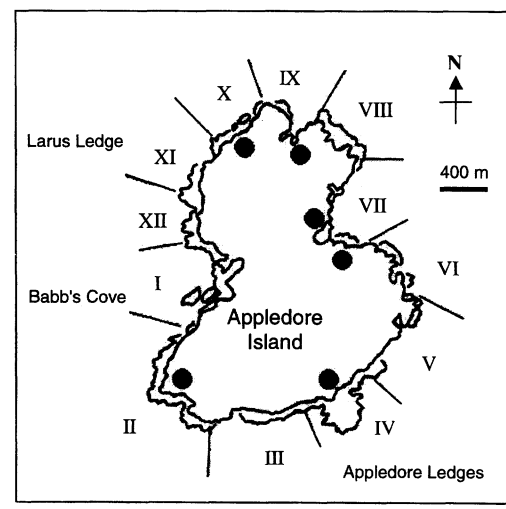

Figure 1. Distribution of study sites on Appledore Island, Maine, USA (42°58'N; 70°37'W) in the Gulf of Maine, 10 km off the coast of New Hampshire. Black dots indicate sites of prey remains collections. Black lines indicate a division among regions for island surveys of gull foraging behavior and distributions; regions are labeled I through XII.

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The rocky intertidal and shallow subtidal zones, where gulls forage, can be divided into three distinct zones characterized by the predominant sessile species: the barnacle zone (2.1-2.7 m above Mean Lower Low Water (MLLW)), *Ascophyllum* zone (0.6-2.1 m above MLLW), and *Chondrus* zone (0.6 m above MLLW to the shallow subtidal zone). Gulls also forage in the "near shore" zone, which is the shallow subtidal zone adjacent to the shore. These zonation heights were determined using data from an ongoing intertidal monitoring study on Appledore Island (M. N. Dethier, pers. comm.).

Diet

Gull diets were described from collections of pellets and whole prey remains collected from nesting territories. Previous studies comparing pellets, stomach contents, chick and mate feeding, and regurgitations indicated that pellets and prey remains closely reflected dietary composition (Spaans 1971; Pierotti and Annett 1987, 1990). Prey remains were collected from 15-20 haphazardly chosen nests within six sub-colonies of each gull species on Appledore Island (Fig. 1). Remains were collected approximately every two weeks from June through September 2001. Therefore, remains represent the gull's diet only during the mid to late breeding season.

Prey remains were sorted and assigned to the following categories: fish, human refuse, terrestrial vertebrates, crab, and other marine prey items. All remains were cleared from territories at the end of each collection period. The first collection (9 June 2001) was not included in the analysis because it was impossible to determine how long these prey items had accumulated.

Previous studies and preliminary observations indicated that crabs were the most abundant marine prey item (Good 1992b; J. C. Ellis, unpubl. data). Therefore, species and sizes of crabs found in prey remains were compared. All carapaces were identified to species, and the maximum carapace width was measured for Jonah Crab (*Cancer borealis*), the most abundant crab species in remains. Occasionally, crab chelae were found without an associated carapace. To estimate size using chelae, the regression from Novak (2000) [$CW = (0.379\ CL - 0.00476\ CL^2 + 3.5)^2$] was applied to calculate maximum carapace width (CW) from chelae length (CL).

Gull Prey Preference

To compare preferences of the two gull species with respect to crab prey, two tethering experiments were conducted that offered choices between different crab species or different crab sizes. In both experiments, crabs were tethered during low tide to the shallow subtidal zone, where gulls regularly capture crabs. Two sites for tethering were used: Babb's Cove, which was dominated by Herring Gulls, and Larus Ledge, which was dominated by Great Black-backed Gulls (Fig. 1).

Live crabs were tethered by fastening a small plastic loop to the posterior portion of the carapace with a marine epoxy (A-788 Splash Zone Compound, Kop Coat), coated with a maroon or black nail polish to closely match carapace color. To restrict crab mobility, carapace tethers were attached to exposed *Chondrus* plants with a dark, tarred nylon cord, approximately 20 cm long. Tethered crabs were placed far enough apart to prevent them from interacting with one another.

In the first experiment, a trial consisted of three tethered crabs, one crab from each of the following species that was of similar size: Jonah Crab, Rock Crab (*C. irroratus*), and Green Crab (*Carcinus maenas*). Preliminary analyses indicated that the Jonah Crab was preferred (see Results), and therefore a second tethering experiment was conducted to examine the preference for either small (50-65 mm carapace width), medium (70-85 mm), or large (90-105 mm) Jonah Crab. In both experiments, tethered crabs were observed from a distance, using binoculars if necessary, to avoid disturbing foraging gulls. The first crab handled or eaten was recorded.

Distribution and Foraging Behavior

Spatial patterns of foraging gulls were investigated by comparing numbers of gulls per km: (a) around the entire island and (b) among foraging microhabitats. Surveys of gull numbers and foraging behavior were conducted on nine dates between mid-June and mid-September. During each survey, gulls were observed from a boat 15-20 m from shore that circled the island twice; this method did not disturb gulls (i.e., cause flight or cessation of feeding). The first circle began approximately 1 h prior to low tide and the second at 30 min prior to low tide. The perimeter of the island was divided into twelve geographic regions (Fig. 1), and gulls were counted in each region in order to determine 1) the distributional patterns of gulls and 2) to determine if certain areas had particularly high concentrations of foraging gulls, since these areas can be indicative of habitats with high abundance, availability and quality of prey items (Schoener 1971). On a topographic map, the linear distance of shoreline was measured within each of these regions, and then abundance data was converted to number of gulls per km of shoreline for both surveys on each date.

During each survey, the species and behavior of each individual gull in intertidal and shallow subtidal zones was recorded. Gull behavior was scored as non-foraging, foraging in the intertidal, or foraging in the water. Non-foraging behavior included resting, preening and all other activities not associated with foraging. Gulls captured prey from the shallow subtidal zone, by swimming and surface-plunging or surface-seizing (Ashmole 1971). Gulls captured prey from exposed intertidal zones by walking and picking prey off emergent substrates (Dumas 1990). Foraging behavior was divided into the following three categories: 1) consuming prey, primarily large (>30 mm carapace width) crabs, 2) picking prey off the emergent substrates, or 3) searching (head pointed down at least 45° toward the substrate while walking or head extended and looking down while swimming). The zone in which each behavior took place was also recorded (see Study Area section for explanation of zones).

Interspecific Aggressive Interactions

The number of Herring Gulls and Great Black-backed Gulls per zone and the frequency of interspecific aggression were quantified at three sites with relatively high numbers of foraging gulls per km (as determined from island surveys): Larus Ledge, Appledore Ledges, and Babb's Cove (Fig. 1). Instantaneous scan samples (Altmann 1974) were used to quantify gull behavior at each site once every month (June-August 2001). Scans began 4 h prior to low tide and continued until 30 min after low tide. An instantaneous scan sample was conducted every 15 min. In each scan, the frequencies and

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identities of adults engaged in aggressive behavior were recorded. The following types of aggressive behavior were recorded: upright aggressive (Moynihan 1958), jab (Moynihan 1958), and charge (lunge or running approach by an adult with wings generally extended; charging bird terminates behavior before making contact with target bird [Butler and Janes-Butler 1982]).

Statistical Analyses

To determine how diet varied between the Herring Gull and Great Black-backed Gull, prey remains were pooled from all nests of each species within each colony for each sampling date. The frequency of occurrence was calculated by dividing the number of remains in each prey category by the total number of remains found on that sampling date. Similarly, the frequency of occurrence of each crab species was calculated by dividing the number of crab carapaces for each crab species by the total number of crab carapaces found in remains on a single sampling date. The average carapace width was calculated in each colony collection for each collection date. Prey composition, crab species, and crab size were compared for both species by sample date and were transformed (arcsin-square root) to satisfy requirements for normality and homogeneity of variances. One-way repeated measures ANOVAs were used to determine whether the two species differed in: 1) the percentage of each prey category (i.e., crab, refuse, etc.), 2) the percentage of each crab species, and 3) the size of Jonah Crab remains through the breeding season. Chi-square tests were used to determine the preference of the gull species for crab species and size, as determined by tethering experiments.

To analyze gull foraging behavior, gull numbers per km from the two surveys on each date were averaged, and then values among all dates within each region, or replicate, were averaged. A two-way ANOVA was performed to test for the effects of gull species and zone on numbers of foraging gulls per km. Transformation of the abundance data did not correct for heterogeneous variances; therefore, the alpha value was set to a more conservative level (0.01) in order to reduce the probability of making a Type I error and analyses were run on untransformed data (Underwood 1997). Preliminary analyses indicated that numbers of foraging gulls per km were highest in the *Ascophyllum* and *Chondrus* zones (see Results); therefore, a second two-way ANOVA examining the effects of foraging behavior and gull species was performed for gulls foraging in only *Chondrus* and *Ascophyllum* zones.

To determine how aggressive interactions varied spatially, two separate one-way ANOVAs were preformed. The first examined how the number of aggressive interactions per number of gulls varied from the high intertidal to the shallow subtidal, and the second examined how the number of aggressive interactions per number of gulls varied from June through late August.

RESULTS

Diet

Prey remains collected from colonies included: garbage (especially chicken), fish [caught directly from the ocean, from fisheries offal and bait from lobster boats (Goodale 2000)], terrestrial vertebrates [including Muskrats (*Ondatra zibethica*), juvenile Herring Gulls, and unidentified rodents], and intertidal and shallow subtidal prey [including Blue Mussels (*Mytilus edulis*), Green Sea Urchins (*Strongylocentrotus droebachiensis*), American Lobsters (*Homarus americanus*), and crabs (Jonah Crab, Rock Crab and Green Crab); Fig. 2a, b]. Marine sources (intertidal and subtidal zones) provided nearly half of the prey remains, with a substantial percentage of the total prey consisting of crabs (30-60%). Garbage, another abundant category, comprised over one-third of prey remains for both species (Fig. 2a, b).

The percentage of crab in prey remains of the Herring Gull was significantly greater than that of the Great Black-backed Gull, whereas the percentage of fish and terrestrial prey were greater in prey remains of the Great Black-backed Gull (Table 1; Fig. 2a, b). In the diet of both species, the percentage of fish decreased significantly from June to September 2001 (Table 1; Fig. 2a, b).

The most abundant crab species was Jonah Crab in both Great Black-backed Gull and Herring Gull prey remains, although the percentage of this species relative to other crabs was higher in Great Black-backed Gull remains (Table 1; Fig. 2c, d). Jonah Crab in prey remains of the Great Black-backed Gull were significantly larger than in those of Herring Gull remains (repeated measures ANOVA, gull species $F_{1,10} = 26.7$, $P < 0.001$). The size of crab carapaces found in remains increased with time (repeated measures ANOVA, time $F_{5,6} = 6.12$, $P = 0.05$; Fig. 3).

Prey Preferences

In the crab species preference experiments, Herring Gulls chose Jonah Crab significantly more often than Rock Crab or Green Crab (67% [14/21] vs 24% [5/21] vs 10% [2/21], respectively; $\chi^2_2 = 12.4$, $P < 0.01$). Similarly, Great Black-backed Gulls chose Jonah Crab significantly more often than Rock Crab or Green Crab (71% [15/21] vs 19% [4/21] vs 10% [2/21], respectively; $\chi^2_2 = 17.5$, $P < 0.001$). In crab size preference

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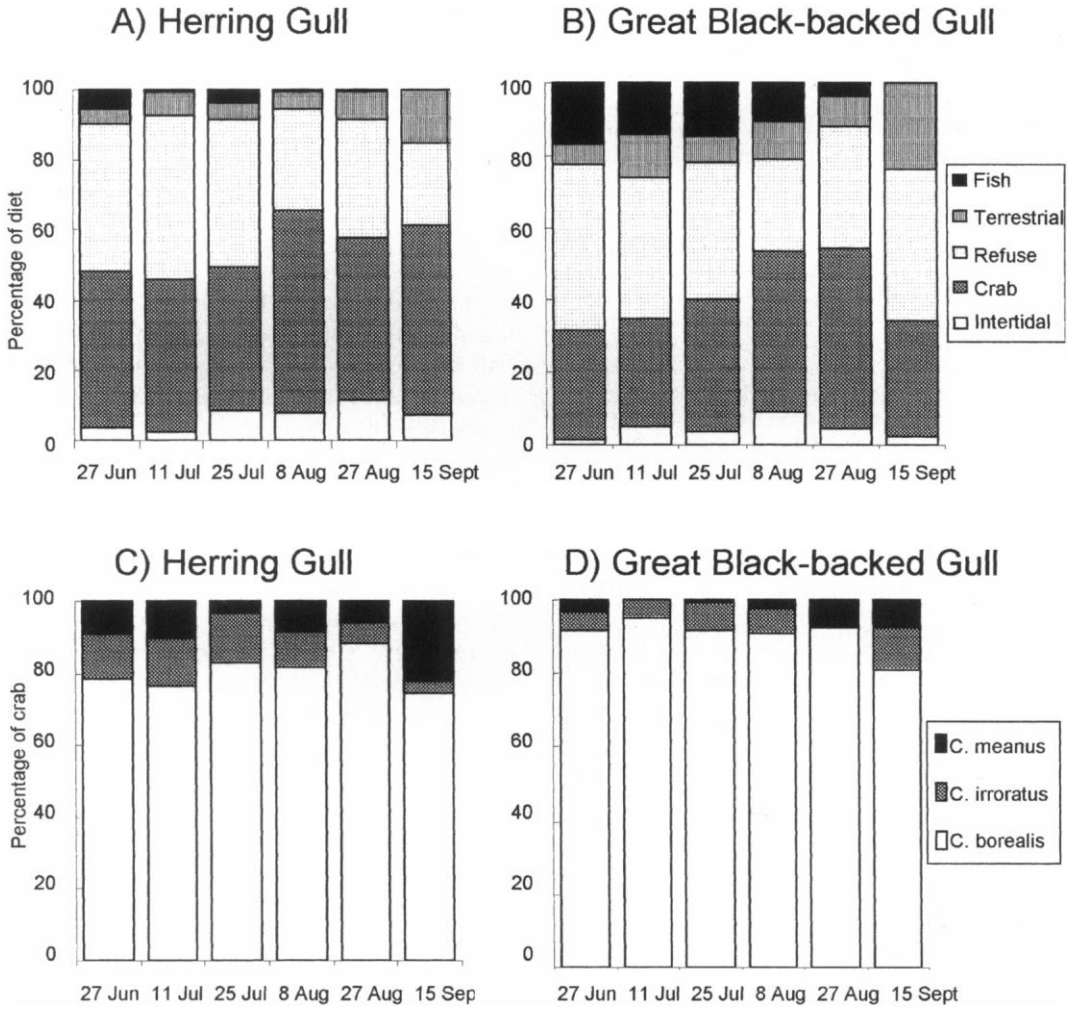

Figure 2. Prey remains collected from (A) Herring Gull and (B) Great Black-backed Gull sub-colonies on Appledore Island, ME from June-September 2001. N = 1,245 total prey remains in Herring Gull collections and N = 1,521 total prey remains in Great Black-backed Gull collections. Percentage of each of three crab species represented in crab carapaces collected from (C) Herring Gull and (D) Great Black-backed Gull sub-colonies on Appledore Island, ME from June-September 2001. N = 718 total crab carapaces in Herring Gull collections and N = 539 total crab carapaces in Great Black-backed Gull collections. Error bars represent ± 1 SE. See Table 1 for results of statistical analyses.

experiments, Herring Gulls chose medium sized crabs most often (67% [16/24]; χ^2_2 = 14.6, P < 0.01), whereas Great Black-backed Gulls chose the largest crabs most often (54% [13/24]; χ^2_2 = 8.87, P < 0.05).

Distribution and Foraging Behavior

Numbers of foraging gulls ranged from 1.65 to 9.46 gulls per km among geographic regions of the Appledore Island shoreline (Fig. 4a). Two areas with relatively high numbers of both foraging and non-foraging Great Black-backed Gulls occurred on the island (regions 4 and 11), whereas Herring Gulls where generally more evenly distributed among the regions (Fig. 4a, b). Within the two areas with large numbers of foraging gulls per km (regions 4 and 11), the ratio of Herring Gulls to Great Black-backed Gulls increased in August (Fig. 4c).

Numbers of foraging Herring Gulls and Great Black-backed Gulls per km were significantly higher in the *Chondrus* zone compared to the *Ascophyllum* and near shore zones (two-way ANOVA: zone $F_{2,66}$ = 62.5, P < 0.001; Fig.

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Table 1. Results from repeated measures ANOVAs testing for the effect of gull species over time. For each gull species, two separate percentages were calculated. In the first percentage, the frequency of occurrence was calculated by dividing the number of remains in each prey category by the total number of remains found on a single sampling date. Percentages were calculated separately for Herring Gulls and Great Black-backed Gulls (N = 1,245 total prey remains for Herring Gull; N = 1,521 total prey remains for Great Black-backed Gull). In the second percentage, the frequency of occurrence was calculated by dividing the number of crab carapaces for each crab species by the total number of crab carapaces found in remains on a single sampling date. Percentages were calculated separately for the Herring Gull and Great Black-backed Gull (N = 718 total crab carapaces for Herring Gull; N = 539 total crab carapaces for Great Black-backed Gull). To avoid overestimation, claws and pellets were not included in counts if other remains of the same prey category were collected at the same nest. Separate tests were run for each prey remains category and crab species. Percentages (x ± SE) are averaged over all sampling dates, although time is considered a separate factor in the analysis.

				Percentage	
Prey remains	F value	df	P	Great Black-backed Gull	Herring Gull
Fish					
Gull species	21.9	1, 10	<0.001	10.0 ± 2.7	1.8 ± 0.9
Time	17.7	5, 6	<0.01		
Refuse					
Gull species	0.112	1, 10	n.s.	37.7 ± 2.9	36.3 ± 3.7
Time	8.48	5, 6	<0.02		
Terrestrial					
Gull species	11.9	1, 10	<0.01	11.3 ± 2.5	7.1 ± 1.7
Time	1.65	5, 6	n.s.		
Crab (all species)					
Gull species	5.20	1, 10	<0.05	37.2 ± 3.4	47.9 ± 2.6
Time	4.24	5, 6	n.s.		
Other intertidal species					
Gull species	0.238	1, 10	n.s.	4.3 ± 1.1	6.8 ± 1.3
Time	1.91	5, 6	n.s.		
Crab species					
Jonah Crab					
Gull species	12.1	1, 10	<0.01	90.5 ± 2.0	80.3 ± 2.1
Time	0.895	5, 6	n.s.		
Rock Crab					
Gull species	12.8	1, 10	<0.01	5.8 ± 1.5	9.8 ± 1.7
Time	2.92	5, 6	n.s.		
Green Crab					
Gull species	2.42	1, 10	n.s.	3.7 ± 1.3	9.8 ± 2.7
Time	0.724	5, 6	n.s.		

5a). Within the near shore zone, numbers of Great Black-backed Gulls were higher than Herring Gulls (0.504 ± 0.144 gull/km vs. 0.144 ± 0.048 gull/km, respectively; x ± SE), although these patterns were only considered a trend due to the conservative alpha acceptance level used (two-way ANOVA, gull species × zone $F_{2,66} = 3.19$, $P < 0.05$; Fig. 5a).

There were significant differences between the two species in the frequencies of types of behavior exhibited by foraging individuals in the *Chondrus* and *Ascophyllum* zones (two-way ANOVA, effects: activity $F_{2,66} = 27.0$, $P < 0.001$; gull species × activity $F_{2,66} = 9.38$, $P < 0.001$, Fig. 5b). On average, more Herring Gulls were picking (1.44 ± 0.181 gull/km) and searching (2.92 ± 0.355 gull/km) than Great Black-backed Gulls (0.29 ± 0.131 gull/km; 1.84 ± 0.470 gull/km, respectively), although more Great Black-backed Gulls were eating (1.29 ± 0.252 gull/km) than Herring Gulls (0.272 ± 0.055 gull/km; Fig. 5b). The average proportion of Herring Gulls eating crabs tended to increase later in the breeding season (Fig. 6).

Interspecific Aggressive Interactions

Of 27 interspecific aggressive interactions observed during foraging observations,

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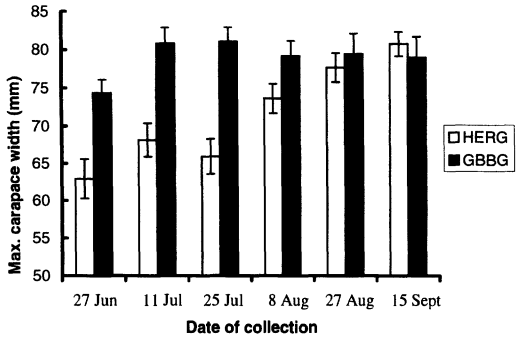

Figure 3. The maximum carapace width for all Jonah Crab carapaces in prey remains June- September 2001. N = 980 carapaces. Error bars represent ± 1 SE. □ HERG = Herring Gull, ■ GBBG = Great Black-backed Gull; See Table 1 for results of statistical analyses.

all were initiated by Great Black-backed Gulls. In general, the number of interspecific aggressive interactions per gull increased leading up to and peaked at low tide (Fig. 7a); the period of maximum amount of foraging gulls.

DISCUSSION

This study demonstrated that: 1) the Great Black-backed Gull and Herring Gulls had similar diets and preference for crab species from summer-early autumn, indicating an overlap in resource utilization and a high potential for competition between the two species in the intertidal during the breeding season, 2) the Great Black-backed Gull consumed more crabs in the intertidal than Herring Gulls and dominated, numerically and behaviorally, all foraging habitats with relatively high numbers of foraging gulls, and 3) the Great Black-backed Gull won all aggressive interactions with Herring Gulls. A natural "removal" experiment occurred when Great Black-backed Gulls began to emigrate from Appledore Island to the mainland approximately one month prior to Herring Gulls. At lower Great Black-backed Gull numbers per km: 1) the mean size of Jonah Crabs found in Herring Gull remains increased, 2) numbers of Herring Gulls consuming crabs in the intertidal increased and 3) there was a trend of decreasing interspecific aggressive interactions.

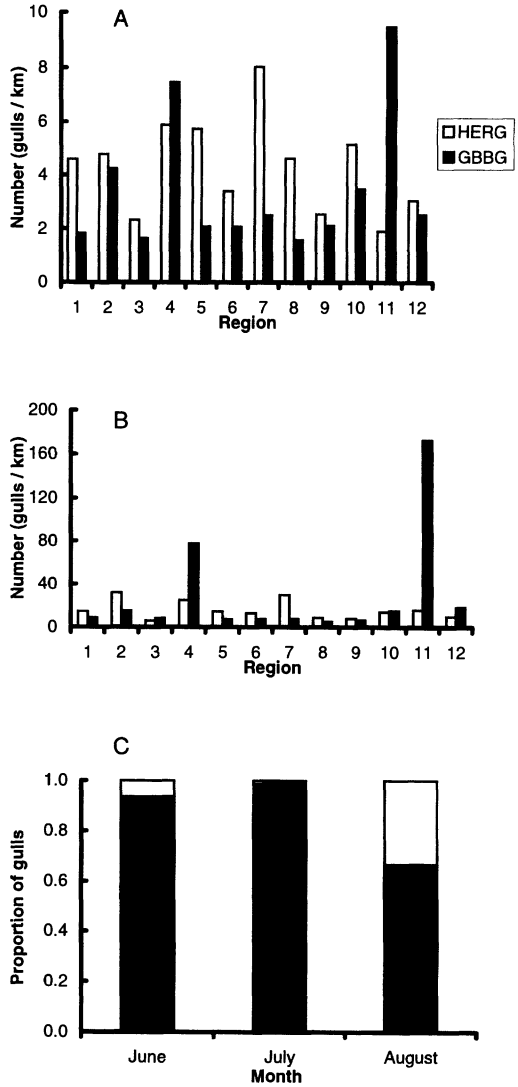

Figure 4. A) Distribution of foraging Herring Gulls and Great Black-backed Gulls among the twelve regions at Appledore Island (see Fig. 1) B) Distribution of foraging and non-foraging Herring Gulls and Great Black-backed Gulls among the twelve regions. Note the two high gull abundance regions (regions 4 and 11). C) In regions 4 and 11, the proportion of Herring Gulls to Great Black-backed Gulls increased from June - late August 2001. Error bars represent ± 1 SE. □ HERG = Herring Gull, ■ GBBG = Great Black-backed Gull; See text for results of statistical analyses.

These findings suggest that aggressive Great Black-backed Gulls may suppress foraging by Herring Gulls and inhibit their ability to obtain larger crabs from the intertidal on Appledore Island during the breeding season.

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Diet and Prey Preferences

The Great Black-backed Gull and Herring Gull showed a great degree of similarity in diet and prey preference, indicating an overlap in resource utilization and a high potential for competition. This is similar to the findings of other studies of the two species (Belopol'skii 1957; Hunt and Hunt 1973; Greig *et al.* 1986; Pierotti and Good 1994; Garthe and Hüppop 1996; Good 1998; Hüppop and Wurm 2000). Although diets were similar, the Great Black-backed Gull tended to have a larger percentage of the most preferred prey items (Jonah Crab, larger crabs). These results suggest that the Great Black-backed Gull has a competitive advantage in foraging, as found in other comparative studies of the two species (Verbeek 1979; Greig *et al.* 1986; Hunt and Hunt 1973; Hudson and Furness 1988; Furness *et al.* 1992).

On Appledore Island, the intertidal zone is an important foraging ground for both gull species during the breeding season as prey items from this habitat comprised nearly half of all prey remains. Results from prey and surveys of gulls foraging on Appledore Island suggest that gulls are utilizing other foraging habitats as well, such as the intertidal zone on the mainland or on other offshore islands, landfills, or offshore foraging areas. Although gulls can forage up to 40 km from breeding sites (Kubetzki and Garthe 2003), locality can be important since travel time directly reduces time spent attending

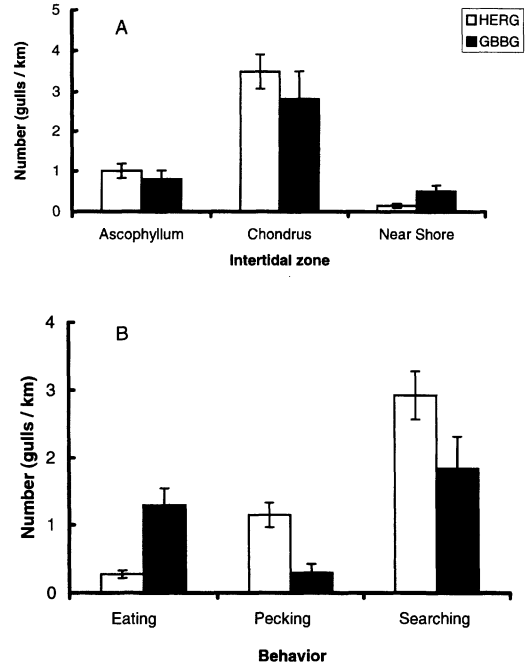

Figure 5. A) Numbers of foraging gulls per km (x ± SE) in three intertidal zones, ranging from the high intertidal zone (*Ascophyllum*) to the shallow subtidal (near shore). B) Numbers of foraging gulls per km (x ± SE) engaged in each of the three foraging activities: eating, picking and searching. Numbers were averaged over all regions. □ HERG = Herring Gull, ■ GBBG = Great Black-backed Gull; See text for results of statistical analyses.

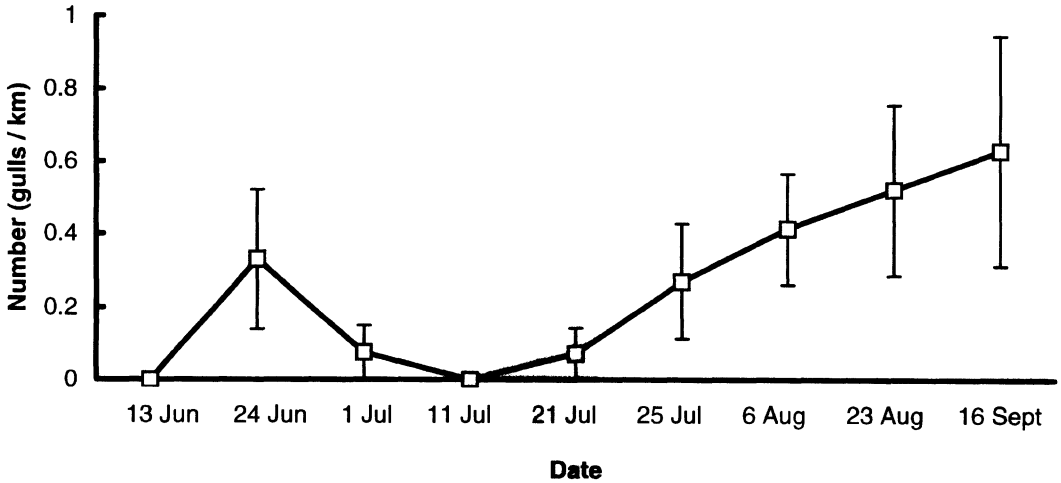

Figure 6. Numbers of Herring Gulls consuming crab (eating) per km in the intertidal from June-September 2001. Error bars represent ± 1 SE.

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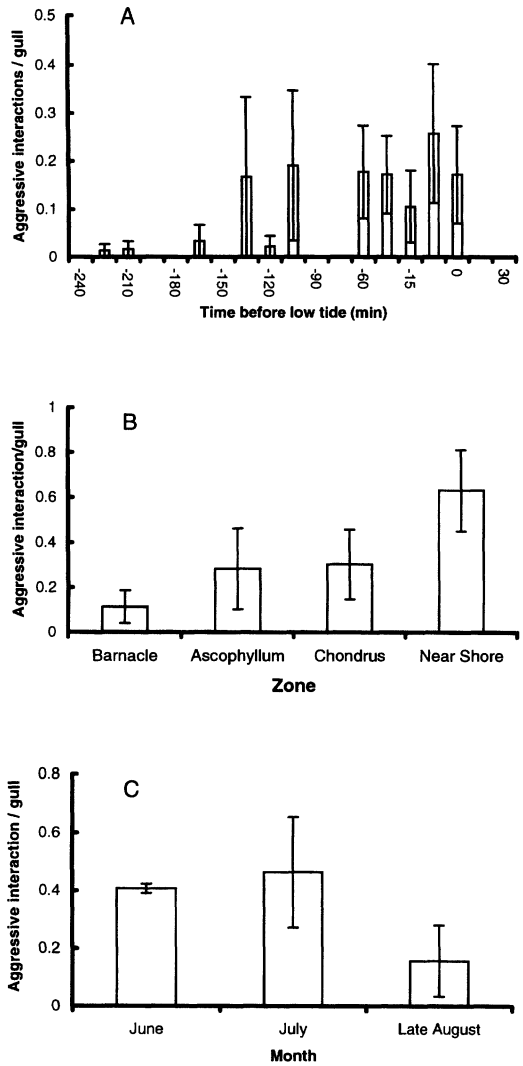

Figure 7. The number of aggressive interactions/gull (A) during a falling tide, (B) from the high intertidal (barnacle zone) to the low intertidal/shallow subtidal (near shore), (C) from June-August 2001. All aggressive interactions were won by Great Black-backed Gulls. Observations were conducted at Larus Ledge, Appledore Ledges, and Babb's Cove (Fig. 1). Error bars represent ± 1 SE.

territories, and lower nest attendance is correlated with a higher frequency of territory intrusion and predation on chicks (Pierotti 1982, 1987; Morris and Black 1980). When gulls are inhabiting Appledore Island during the breeding season, the intertidal zone is one of the closest foraging habitats, compared to open landfills (e.g., Somersworth Municipal Landfill, NH; 29 km), or offshore foraging grounds. Gulls also obtain discarded bait (fish) from lobster boats both offshore and near the island.

Crab was a greater percentage of the diet for the Herring Gull than for the Great Black-backed Gull (Fig. 2a, b), although intertidal behavioral observations indicated that the Great Black-backed Gull foraged for crabs more often than the Herring Gull (Fig. 5b). This apparent paradox may be explained in part by the fact that crabs are either eaten in the intertidal or brought back to the colonies, where prey remains were collected, to be eaten or fed to mates and young. Herring Gulls may travel from the intertidal to colonies to consume crabs more often in order to avoid interference from Great Black-backed Gulls that often steal prey from Herring Gulls in the intertidal area (Verbeek 1979; M. S. Rome, pers obs).

In the crab size preference experiments, the Herring Gull preferred medium-sized crab whereas the Great Black-backed Gull, a much larger species, preferred the largest crabs. Prey remains indicate that the Great Black-backed Gull, on average, consumed medium sized crabs. The Herring Gull did not consume medium sized crabs until late August-September, when the numbers of Herring Gulls eating crab in the intertidal increased. At Nahant, Massachusetts, foraging Herring Gulls greatly outnumbered Great Black-backed Gulls in the intertidal zone. At this site, Herring Gulls consumed the largest available Jonah Crabs (Dumas 1990), further suggesting that the Great Black-backed Gull affected the ability of the Herring Gull to forage on the largest crabs at Appledore Island.

Intertidal Foraging Distribution and Behavior

While both gull species utilize the intertidal zone on Appledore Island as an important foraging ground during the breeding season, foraging behavior and distribution of the two species differed. The Great Black-backed Gull generally obtained large crabs from the lowest foraging zones, whereas the Herring Gull picked smaller organisms, such as small crabs (<50 cm carapace width) or mussels, from higher intertidal zones (Fig.

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5a, b). Lower intertidal zones typically contain greater densities of larger prey (invertebrates) than higher zones (Irons *et al.* 1986; Menge 1983). Although upper zones have smaller organisms, there is the potential for shorter prey handling and searching times in these zones (Irons *et al.* 1986). Herring Gulls may be less abundant in the more profitable, low intertidal zone if: 1) aggressive interactions from Great Black-backed Gulls directly drove them out, 2) Herring Gulls prefer to forage in less profitable areas that provide spatial refuges from Great Black-backed Gull interference, or 3) Herring Gulls are unable to capture crabs from the shallow subtidal. Interference from the Great Black-backed Gull may have a large influence on the distribution and foraging behavior of the Herring Gull. Likewise, in patchy foraging habitats in Europe, smaller gulls tended to forage in less productive areas when in the presence of larger gulls (Hunt and Hunt 1973). Foraging on less productive prey can negatively impact breeding success for gulls (Noordhuis and Spaans 1992; Annett and Pierotti 1999).

Currently, it is unclear whether the Great Black-backed Gull will continue to increase at the expense of the Herring Gull, leading to competitive exclusion, or whether growth trends of both species will stabilize. Past trends in gull numbers have been heavily influenced by human activity (Kadlec and Drury 1968; Drury 1973), and the Great Black-backed Gull and Herring Gull are currently controlled throughout New England. Our results suggest that change in Great Black-backed Gull numbers may have important effects on Herring Gull foraging ability during the breeding season.

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