Competition between Herring Gulls and Great Black-backed Gulls over Natural and Anthropogenic Food Sources in the Gulf of Maine

Julia F. Cotton

Abstract. – Though Herring Gulls (*Larus argentatus*) and Great Black-backed Gulls (*L. marinus*) breed in mixed-species colonies from Maine to New York, in the last century the number of Great Black-backed Gulls has increased over that range while the number of Herring Gulls has decreased. Aggressive competition by Great Black-backed Gulls over nest sites, foraging habitat, and prey may be contributing to the Herring Gull's decline. Previous studies have examined the foraging habits of the two species in the rocky intertidal zone, but little work has examined how they interact with regards to anthropogenic food sources. In this study, I quantified the spatial and temporal use of the rocky intertidal zone by the two gull species on an offshore New England island during the breeding season. Additionally, to examine how the two species interact over lobster fisheries discard, I mimicked a lobster boat by experimentally discarding lobster bait (Atlantic herring, *Clupea harengus*) at offshore sites around the Isles of Shoals, ME. The density of gulls in the intertidal zone varied by species and with time during the breeding season, with peak density and foraging activity occurring most often in the mid- to late-July period, which is when chicks require the most nourishment. Great Black-backed Gulls were the most abundant species overall as well as the most abundant forager per kilometer, and they were densest along two specific regions of the coastline. The majority of gulls in the intertidal zone were loafers (resting, preening, etc.) rather than active foragers. In the fisheries discard experiment, Great Black-backed Gulls took more bait (26%) than did Herring Gulls (9%), though the amount of bait lost (65%) exceeded the amount of bait retrieved by either species of gull. It appears that as the proportion of Herring Gulls in a lobster boat-trailing flock increases, more pieces of bait go to Herring Gulls; in contrast, as the number of Great Black-backed Gulls in a flock increases, no greater amount of bait is taken by Great Black-backed Gulls, and the amount of bait taken by each individual may even decrease. This pattern may be related to inter- and intra-specific kleptoparasitism: though both species were observed engaging in kleptoparasitism, the majority of thefts (94%) were initiated by Great Black-backed Gulls and the most common form of theft was Great Black-backed Gull from Great Black-backed Gull (56%). This has implications for the foraging activities of each species and may in part explain observations that Herring Gulls attend vessels in large numbers whereas Great Black-backed gulls do not.

Introduction

The frequent coexistence of congeneric seabird species in the same breeding and foraging habitats (Rome and Ellis 2004, Fasola et al. 1989, Cody 1973) has attracted the attention of both ecologists and ornithologists, who have proposed various mechanisms to explain the persistence of seabird sympatry. Proposed explanations include behavioral, ecological, and physiological differences between the species such as asynchronous breeding (Cody 1973), differences in body size (Cody 1973), differences in prey size (Cody 1973), and partitioning of foraging habitat (Fasola et al. 1989, Cody 1973). All of these mechanisms promote coexistence and ecological isolation. Factors particularly relevant to selection include diet and prey acquisition, as diet has been linked to reproductive output (i.e. breeding success) in seabirds (Pierotti and Annett 1990). The foraging ecology of different seabird species has been pinpointed as a source of differences in reproductive traits (Lance and Roby 1998) and thus an understanding how seabirds partition their prey base may be crucial to elucidating their ecology and evolution.

While natural food sources can be partitioned among different seabird species by mechanisms such as prey size differences and foraging habitat zonation (Fasola et al. 1989, Cody 1973), many species of marine birds also supplement their diets with anthropogenic waste and fisheries discards (Yorio and Caille 1999, Belant et al. 1993, Pierotti and Annett 1990). For example, Yorio and Caille (1999) reported up to 23 different species of seabirds attending Patagonian trawl vessels. Among the birds feeding on the trawler discard, the most common attendee was the Kelp Gull (*Larus* *dominicanus*), which has been observed engaging in intraspecific kleptoparasitism (Bertellotti and Yorio 2001).

Some gull species (family Laridae) are known to be predatory while others are considered foragers and scavengers (Cody 1973), and many different species (such as the Kelp Gull) are known to feed on fisheries discards worldwide (e.g. Bartellotti and Yorio 2001, Yorio and Caille 1999, Oro and Ruiz 1997). In coastal New England, the large Great-black Backed Gull (*L. marinus*) (mass 1300-2000 g; Good 1998) and smaller Herring Gull (*L. argentatus*) (mass 800-1250 g; Pierotti and Good 1994) are both considered generalist predators that forage in the same habitats (Fig. 1.a, b) (Rome and Ellis 2004, Pierotti and Good 1994). Both also forage on fisheries discards in areas of Europe and North America (Camphuysen 1995, Furness et al. 1992).

Currently, Great Black-backed Gulls and Herring Gulls nest in mixed-species colonies along the New England coast from Maine to New York, including a large breeding colony in the Isles of Shoals off the coast of Maine (Ellis and Good 2006, Pierotti and Good 1994). Great Black-backed Gulls were not recorded breeding on the Isles of Shoals until 1930 (Jackson and Allen 1932), and prior to then, Herring Gulls were the most abundant breeding Larid species on the Isles of Shoals (Borror and Holmes 1990). By the early 1940s, Great Black-backed Gulls had expanded their breeding range southward to New York (Wilcox 1944). In recent years numbers of Great Black-backed Gulls on the Isles of Shoals have increased whereas numbers of Herring Gulls have decreased (J.C. Ellis, pers. comm.).

Great Black-backed Gulls appear to be displacing Herring Gulls for prime breeding territory (Ellis and Good 2006) and also may outcompete Herring Gulls for large crabs in the rocky intertidal (Rome and Ellis 2004). In Europe's North Sea the Great Black-backed Gull outcompetes Herring Gulls for fisheries discards in terms of number of fish swallowed per bird of each species present (Furness et al. 1992); few studies, however, have examined how Herring Gulls and Great Black-backed Gulls interact over New England lobster fisheries discard. It is known that Herring Gull chick diets in New England may be composed of up to 57% lobster bait (Goodale 2001), but the interspecific interactions between Herring Gulls and Great Black-backed Gulls foraging on lobster bait have not been thoroughly researched. While the interactions, distributions, and behaviors of Great-black Backed Gulls and Herring Gulls in the rocky intertidal have been examined (Rome and Ellis 2004), several years have passed since the last study quantifying gull numbers and behaviors in the intertidal zone was conducted. The numbers of gulls have continued to fluctuate over time, and this dynamic population change could effect how the two species interact over their natural food sources as well as anthropogenic food sources. In New England, the intertidal zone (natural habitat) and fisheries discards (anthropogenic) are two major sources of food for Herring Gull and Great Black-backed Gull (Goodale 2001, Good 1998, Pierotti and Good 1994), and a full picture of their feeding ecology can only emerge if both natural foraging behaviors and anthropogenically-driven foraging behaviors are studied.

I did an observational survey of gull density in the intertidal zone of the Isles of Shoals in order to examine how the density of gulls using the intertidal zone as a foraging habitat varies over the course of a single breeding season. I wanted to see 1) which species was the most abundant in the intertidal zone in terms of density and 2) how species abundance varied over time.

To see how the two gull species interact over anthropogenic food sources, I conducted a lobster fisheries discard (or "gull chumming") experiment. I wanted to determine 3) how the proportion of a given species in a flock affects the amount of bait taken by that species and 4) how the success of an individual member of a species is affected by flock composition.

Methods

Study Area

The intertidal distribution study was conducted at the Shoals Marine Laboratory on Appledore Island, Maine (42°58'N; 70°37'W), a 95-acre island in the Gulf of Maine located approximately 10 km off the coast of New Hampshire, USA. Appledore Island is part of a nine-island archipelago known as the Isles of Shoals. Its rocky shoreline is composed of metamorphic gneiss and schist and features cliffs and coves.

The fisheries discards/gull chumming study was conducted offshore from boats at several sites around the Isles of Shoals off the coasts of Appledore Island, Duck Island, Smuttynose Island, Cedar Island, and Lunging Island (Fig. 2). Several lobstermen set their pots in the coastal waters around the Isles of Shoals and flocks of gulls frequently attend vessels moving in and out of the waters around Portsmouth Harbor (J.F. Cotton, pers. obs.).

Intertidal Distribution of Foraging and Non-Foraging Gulls

I quantified gull distribution in the rocky intertidal zone of Appledore Island by scan sample on seven dates from late June through late July 2008. The intertidal zone is the area of shore exposed between the high tide mark and low tide mark. The rocky intertidal of the New England coast can be divided into three main zones based on the predominant sessile biota that characterize them: the barnacle zone (2.1-2.7 m above Mean Lower Low Water on Appledore Island (MLLW)), *Ascophyllum* zone (0.6-2.1 m above MLLW), and *Chondrus* zone (0.6 m above MLLW to the shallow subtidal zone) (Rome and Ellis 2004). All gulls located within this range were counted in the scan samples, as were any gulls in the area of water above the shallow subtidal adjacent to the shore (the "near shore" zone).

Gulls were recorded as foraging or non-foraging based on the schema presented in Rome and Ellis (2004). Foraging behaviors in the near shore included surface-plunging and surface-seizing, and foraging behaviors in the intertidal zone included consuming prey, picking the substrate, and searching (head pointed down at least 45 degrees to the substrate while walking or head pointed down while swimming). All other behaviors, including resting and preening, were counted as non-foraging.

Gulls in the intertidal were observed by binocular and by naked eye from an inflatable zodiac boat that remained approximately 15-20 meters from shore; this method did not disturb the gulls (i.e. they did not take flight or change their activities when the boat approached). The coast of the island was divided into twelve regions to facilitate quantification of gulls per kilometer and to help pinpoint areas of particularly high gull concentration (Fig. 3, adapted from Rome and Ellis 2004). On each scan sample day except for July 9 and July 10, the island was circled twice with the first circle beginning approximately 1 hr prior to low tide and the second approximately 30 minutes prior to low tide. This timing corresponded with maximum daily exposure of the entire intertidal zone. Due to inclement weather on July 9 and 10, only one scan sample circle of the island was completed on those days.

The abundance data for the two scan samples from each date were averaged to give a single abundance estimator for each date; for the two July days when only one circle of the island was completed, only the data from the first circle was used (thus abundance data from July 9 and July 10 represent only one scan sample of the intertidal rather than the average of two scan samples). The linear distance of the shoreline of each region was measured from a topographic map and gull counts were then converted to a density measure of gulls per kilometer.

The accuracy of gull counts during the scan samples was limited by the three-dimensional nature of the intertidal zone. In some areas where the intertidal zone extended horizontally as well as vertically, the topography allowed gulls to be out of view behind rocks. However, this was only an issue in a few regions and the number of gulls out of view was much less than the overall number of gulls per region.

Statistical Analysis of Intertidal Distribution

Two separate analyses were run, one on the total number of foraging and non-foraging gulls (i.e., all gulls in the intertidal) and one on foraging gulls only. Because the scan sample dates were clustered in time across late June and all of July, I pooled them into three groups by averaging gull densities: early (June 26, June 27, June 30), mid (July 9, July 10) and late (July 26, July 27). This allowed me to evaluate gull density as a function of time.

Each analysis was conducted using a repeated-measures analysis of variance (ANOVA) in SAS software (SAS ver. 9.1), with region treated as the subject measured during each time period and region, time, and species as fixed effects. Because each species was present within each region and time period, the design represents a split-plot with species as a small plot measured within the effect of region and time.

Gull Chumming

To examine the numbers, interactions, and bait-taking success of the two gull species, I mimicked a lobster boat by experimentally discarding bait fish around the Isles of Shoals a total of 14 times. Previous studies have used bycatch and non-commercial-sized fish as experimental bait discard to study gull kleptoparasitism behind trawlers (Bertellotti and Yorio 2001). Because I was interested in lobster fisheries discard rather than trawler discard, we obtained standard-sized buckets of lobster bait (Atlantic herring *Clupea harengus*) to manually throw overboard. For each gull chumming "run" (a run defined as a set of bait-tossing events at a single location), we used about half a bucket of bait, which amounted to around 8 bait tossing events at each location, though this number varied. Standard methodology for past fisheries discard experiments has been to discard bycatch, subsamples, and/or undersized fish from trawlers (Garthe and Scherp 2003, Walter and Becker 1997, Furness et al. 1992), which often already have attendant flocks of birds (e.g. Yorio and Caille 1999, Bartle 1974). In order to establish a flock behind our experimental vessel, pieces of bait were thrown off the back or side of the boat to attract gulls before the experiment began. The data recording commenced once we had a flock (more than one gull) attending the boat.

We ran our experiment from two different vessels. The first six runs, from late June to mid-July, were conducted from an inflatable zodiac. Since seabirds seem to be able to distinguish between fishing boats and other non-working vessels (Bartle 1974), we were concerned about the reliability of data collected from zodiacs and conducted the last eight runs from the J.B. Heiser, a 36-foot long research vessel owned by Shoals Marine Laboratory that more closely resembles a lobster boat in shape and size than a zodiac does. Post-hoc statistical tests (see Statistical Analysis of Gull Chumming Data section and Results - Gull Chumming) showed no significant difference between vessels.

At least three observers and I were present on every run. Each observer focused on one variable (or count) and gave their numbers to me to record. For every run I recorded the number of bait pieces tossed in each bait event, the number of each species of gulls in the active flock (defined as the flock visibly aiming for the bait), and the number of pieces of bait taken by each species ("taken" meaning carried off in the beak or swallowed). After the first few runs, we started recording whether any kleptoparasitism occurred (both intra- and inter-specific). Kleptoparasitism was recorded as Great Black-backed Gull from Great Black-backed Gull, Great Black-backed Gull from Herring Gull, Herring Gull from Herring Gull, or Herring Gull from Great Black-backed Gull.

When the J.B. Heiser was the experimental vessel, multiple runs were conducted sequentially on one day. However, each run can be considered independent because no birds followed the boat from one location to another. Though bait-tossing events at each site were not independent from each other due to the same birds often being present over the course of multiple tosses, site data was pooled (see Statistical Analysis of Gull

Chumming Data section) and lack of independence within each site was not a confounding issue.

Statistical Analysis of Gull Chumming Data

To find the total number of bait pieces taken by each species, the raw counts from each run and both vessels were added together.

For each run, the proportion of bait taken by each species was calculated by dividing the total number of bait pieces tossed by the number of bait pieces retrieved by each species. Finding the relative numbers of gulls in the attendant flocks presented a problem because the bait-tossing events at each site were not independent, meaning we had repeated measures on some of the birds (that is, we assumed that some of the same birds participated in more than one bait tossing event at a site). However, because my main interest was how the numbers of each species in the flock affected which species took bait, I averaged the proportion of gulls in the flock during each run by summing up the relative proportion present at each bait-tossing event. A similar success index has been used in comparing success of different species behind trawlers (Walter and Becker 1997).

A mixed-model ANOVA model was conducted in SAS software (SAS ver. 9.1) to evaluate the effect of species and vessel on the proportion of bait to the species and on the proportion of bait to individuals per species. Species and vessel were treated as fixed effects and the day of the experiment was treated as a random effect.

Results

Intertidal Distribution

1. Foraging and Non-Foraging Gulls (All Gulls)

I collected data over seven survey dates and observed about 1,401 Great Black-backed Gulls and 539 Herring Gulls in the intertidal zone (sum of the averages of both circles of the island on all dates).

Average density of all gulls of both species (foraging and non-foraging) across all survey dates ranged from 0.77 to 220.15 gulls/km, with peaks in regions 4 and 11 (Fig. 4). Great Black-backed Gull density ranged from 0.92 to 220.15 gulls/km; Herring Gull density ranged from 0.77 to 36.88 gulls/km.

Time had a significant effect ($p = 0.0195$) on the density of all gulls, with both species increasingly dense in the mid and late periods. Region also had a significant effect ($p < 0.0001$), specifically in regions 4 and 11 where gull densities were highest; and species had a significant effect ($p < 0.0001$). There was also a significant interaction between region and species ($p < 0.0001$) (Table 1).

Region had a significant effect on the density of Great Black-backed Gulls (*Num DF* = 11, *Den DF* = 22, F = 31.76, $p < 0.0001$) but not on the density of Herring Gulls (*Num DF* =11, *Den DF* = 22, $F = 1.33$, $p = 0.2745$).

The interaction between time period and species for both gull species and all time periods was significantly different from 0 except for Herring Gulls in the early period (Fig. 5). However, the time-species interaction was only significant for Great Black-backed Gulls (*Num DF* = 2, *Den DF* = 22, $F = 4.29$, $p = 0.0267$) and not for Herring Gulls (*Num DF* = 2, *Den DF* = 22, $F = 1.01$, $p = 0.3800$).

2. Foraging Gulls

Average density of foraging gulls per region across all survey dates ranged from 0 to 5.50 gulls/km (Fig. 6). Among foraging gulls in this study, Great Black-backed Gulls ranged in density from 0.44 to 5.50 gulls/km and were the most abundant species in regions 4, 11, and 12. Foraging Herring Gulls ranged in density from 0 to 0.85 gulls/km and were the most abundant species only in region 5.

Time had a significant effect ($p = 0.0308$) on the densities of both species, with the average densities of foragers increasing in the mid and late periods. Region also had a significant effect ($p = 0.0038$); when time and species are held constant, the density of gulls was significant in regions 4 ($p < 0.0001$), 5 ($p = 0.0002$), 11 ($p < 0.0001$), and 12 ($p = 0.0003$), all of which had high numbers of foragers, though not always of both species. Species also had a significant effect ($p < 0.0001$), and there was a significant interaction between region and species ($p = 0.0003$) (Table 2).

Region had a significant effect on the density of foraging Great Black-backed Gulls (*Num DF* = 11, *Den DF* = 22, $F = 7.76$, $p < 0.0001$) but not on the density of Herring Gulls (*Num DF* = 11, *Den DF* = 22, $F = 1.57$, $p = 0.1778$).

The interaction between time period and species for both gull species and all time periods was significantly different from 0 except for Herring Gulls in the early period (Fig. 7). However, the time-species interaction was not significant for Great Black-backed Gulls (*Num DF* = 2, *Den DF* = 22, $F = 2.94$, $p = 0.0739$) or Herring Gulls (*Num DF* = 2, *Den DF* = 22, $F = 2.94$, $p = 0.2677$).

Gull Chumming

1. Fates of all bait pieces

Out of all 855 bait pieces tossed, 26% (221 pieces) were taken by Great Black-backed Gulls, 9% (75 pieces) were taken by Herring Gulls, and 65% (559 pieces) were lost (Fig. 8).

2. Proportion of bait to each species

There was a positive relationship between the proportion of Herring Gulls in a flock and the proportion of bait to that species (R^2=0.42, $F_{1,11} = 7.99$, $p = 0.0165$) (Fig. 9). The relationship between the proportion of Great Black-backed Gulls in a flock and the proportion of bait to Great Black-back Gulls was not significant ($p = 0.8505$).

On average the proportion of bait taken by Great Black-backed Gulls was 0.2429 and the proportion of bait taken by Herring Gull was 0.06292 (Fig. 10). Species had a significant effect on the difference between the amounts of bait taken by each species ($p = 0.0006$). There was no significant effect of boat on proportion of bait taken by each species ($p = 0.8141$), so the data from the research vessel J.B. Heiser and the Zodiac runs have been combined (Table 3).

3. Proportion of bait to individuals of each species

There was an nearly-significant negative relationship between proportion of Great Black-backed Gulls in the flock and proportion of bait to each individual Great Black-backed Gull (R^2=0.2540, $F_{1,12} = 4.09$, $p = 0.0661$) (Fig. 11). The relationship between proportion of Herring Gulls in the flock and proportion of bait to each individual Herring Gull was not significant ($p = 0.6663$).

Species had a significant effect on the difference between the average amounts of bait taken by individuals of each species ($p < 0.0001$).There was no significant effect of boat on the proportion of bait taken per individual of each species ($p = 0.7779$), so the data from the research vessel J.B. Heiser and the Zodiac runs have been combined (Table 4).

4. Kleptoparasitism

There were 16 recorded kleptoparasitism events. 56% (9 events) were Great Black-backed Gull from Great Black-backed Gull; 38% (6 events) were Great Black-backed Gull from Herring Gull; 6% (1 event) were Herring Gull from Herring Gull; and there were no Herring Gull from Great Black-backed Gull events (Fig. 12). A Pearson Chi-Square Test indicates that these values are significantly different from the null ($p = 0.0025$).

Discussion

Intertidal Density and Distribution

Consistent with the findings of Rome and Ellis (2004), this study found that Great Black-backed Gulls dominated the intertidal zone in terms of abundance. A rough comparison between the summer 2001 data of Rome and Ellis (2004) and this study's summer 2008 data suggests that the average density of gulls of both species foraging in the intertidal may have decreased from 2001 to 2008. In the original Rome and Ellis

(2004) study, density of foraging gulls ranged from 1.65 to 9.46 gulls/km, whereas in this study we saw densities of only 0 to 5.5 foraging gulls/km. Additionally, within several regions where Herring Gulls had previously been the most abundant foragers in 2001, the density of foraging Herring Gulls decreased below the density of Great Black-backed Gulls, making the latter the more abundant of the two species in 2008. The density of all Great Black-backed Gulls in region 4, an area of known high gull abundance, was reported to be about 80 gulls/km in Rome and Ellis (2004), but was up to 134.29 gulls/km in 2008. These changes suggest that Great Black-back Gulls may be further displacing Herring Gulls from optimal foraging habitat, as speculated in Rome and Ellis (2004). However, the data are not directly comparable due to potential differences in survey methodology and care must be taken when drawing any conclusions from comparisons between the two studies.

One relationship demonstrated by this study and not entirely seen in Rome and Ellis (2004) is that time has a significant effect on gull abundance in the intertidal zone, and that species composition in the intertidal shifts over time. There was a general increase in overall gull densities in the intertidal over the course of July. Peak density of all Great Black-backed Gulls occurred in the mid and late periods, as did peak density of all Herring Gulls (refer to Fig. 5). Additionally, densities of foraging gulls of both species were highest in the late period (see Fig. 6). These mid-to-late-season peaks of density and foraging activity may be due to an increased need to provision growing chicks as the breeding season progresses, as the size of meals fed to chicks increases with the age of the chicks (Gilland et al. 2004).

Certain regions had higher densities of gulls than others. Of particular note are regions 4 and 11, known as Appledore Ledges and Larus Ledge (see Fig. 3). Densities of all Great Black-backed Gulls and of foraging Great Black-backed Gulls were highest in regions 4 and 11, and density of all Herring Gulls was also high in those same regions (refer to Figs. 4&6). The density of all Great Black-backed Gulls in regions 4 and 11 was about 6 to 10 times higher than in other regions, and for all Herring Gulls, density in those regions was up to 4 times as high. The results from this study coupled with previous studies (Rome and Ellis 2004) as well as personal observation indicate that regions 4 and 11 have a large effect on gull density. It is unclear exactly why Appledore Ledges and Larus Ledge attract so many gulls, but the vertical and horizontal relief of the areas may be part of the reason: both Appledore Ledges and Larus Ledge extend horizontally into the *Chondrus* zone, and the lower zones of the intertidal yield larger and more-preferential prey items such as crabs (Irons et al. 1986, Menge 1983).

Non-foraging gulls made up most of the gulls counted in regions 4 and 11 as well as in the other regions (Figs. 4&6). It seems that loafing (resting, preening, etc.) is the primary activity of most gulls in the intertidal zone (Irons et al. 1986). The intertidal zone may serve both as foraging habitat and like the "clubs" described by Tinbergen (1953), which he described as areas of neutral territory where gulls amass for social reasons (finding mates, surveying territories, etc.). Schreiber (1967) describes Herring Gull club activity as "preening, sleeping, or otherwise loafing", consistent with what I observed of loafing gulls in the intertidal. Thus the intertidal zone may have a dual function as a location for social behaviors and as a natural foraging habitat.

Foraging by the two gull species may be as much a passive activity as an active one. By loafing in the intertidal, especially in regions like 4 and 11 that have a large horizontal component at the lowest tidal level, gulls may opportunistically capture prey when it appears without moving far from their loafing location. Gulls could easily switch from loafing to actively foraging in the lower intertidal and near shore should they not encounter any prey by chance. Moreover, the intertidal zone is one of the closest available foraging habitats for gulls nesting on Appledore Island (Rome and Ellis 2004). Use of the intertidal, both for social reasons and for foraging, may give gulls a net energy gain by condensing feeding and social behaviors into an area of easy accessibility and prime prey abundance.

Gull Chumming

Great Black-backed Gulls dominated when foraging in mixed-species flocks for lobster bait discard, taking 26% of all bait pieces relative to the 9% taken by Herring Gulls. However, the majority of bait (65%) was lost, either sinking or ignored. In contrast, a study by Bertellotti and Yorio (2001) showed that Kelp Gulls handled over 76.5% of discarded bait fish. The discrepancy between their results and the 35% of bait handled by gulls in this study may be explained by a number of factors including familiarity with the vessel, different sample sizes, and different species. Observations by Bartle (1974) and my own personal observations indicate that gulls and other seabirds can recognize specific trawlers and lobster boats. The lack of familiarity with either of the two experimental vessels (the zodiac or the research vessel J.B. Heiser) may have resulted in hesitation on the part of the Herring Gulls and Great Black-backed Gulls, which could explain the sinking/lost bait. Bertellotti and Yorio (2001) also had a larger sample size and were studying a different species that is known to number in the hundreds when following trawlers (Bertellotti and Yorio 2001, Yorio and Caille 1999).

Furness et al. (1992) noted that "Herring Gulls and Lesser Black-backed Gulls tended to remain on the periphery of flocks at trawlers, apparently unable to compete with Great Black-backed Gulls, Gannets or Great Skuas, which took central positions close to where discards were dropped." Furness et al.'s (1992) observation is in line with my results that show Great Black-backed Gulls to be the superior discards scavengers over Herring Gulls. Additionally, Furness et al. (1992) reported that Herring Gull dropped 35% of the trawler discards they handled while Great Black-backed Gulls dropped only 5%, which may be another part of the reason why Great Black-backed Gulls outcompete Herring Gulls in obtaining bait.

Bait-taking success of Herring Gulls appears to depend on the proportion of Herring Gulls in the total flock. The positive linear relationship (see Fig. 9) suggests that the more Herring Gulls in the total flock, the more bait on average to Herring Gulls. However, there was no significant relationship between the proportion of bait taken by Herring Gulls and the proportion of bait to individual Herring Gulls.

In contrast, the bait-taking success of Great Black-backed Gulls appears to be independent of the proportion of Great Black-backed Gulls in the flock: there was no significant relationship between the proportion of Great Black-backed Gulls in the flock and the proportion of bait to Great Black-backed Gulls (i.e., the proportion of Great Black-backed Gulls in the flock did not affect the proportion of bait that was taken by Great Black-backed Gulls). There was a nearly-significant negative relationship between the proportion of Great Black-backed Gulls in the flock and proportion of bait to individual Great Black-backed Gulls, implying that more Great Black-backed Gulls in a flock may lead to decreased returns to each individual (Fig. 11).

In such a situation, Herring Gulls benefit from dominating a flock while Great Black-backed Gulls are penalized. The flocking behavior of Herring Gulls may have an effect similar to predator satiation. More Herring Gulls in a flock increases the odds of Herring Gulls getting bait while more Great Black-backed Gulls in a flock decreases the odds of any one Great Black-backed Gull getting bait. Le Corre and Jouventin (1997) observed a similar effect among Red-footed Boobies parasitized by Frigatebirds: single birds were chased more often than groups, and the chance of an individual bird being chased decreased as the size of the flock it was in increased. My observations on Herring Gull and Great Black-backed Gull kleptoparasitism further this comparison: the majority of kleptoparasitism events (94%) were initiated by Great Black-backed Gulls, and there were no cases of Herring Gull from Great Black-backed Gull kleptoparasitism. If Herring Gulls represent the majority of a flock, then Herring Gulls on a whole have a greater chance of getting bait because they effectively absorb (or satiate) kleptoparasitism by the Great Black-backed Gulls in the flock. If Great Black-backed Gulls represent the majority of a flock, the predominance of Great Black-backed Gull from Great Black-backed Gull kleptoparasitism could lead to lost bait (dropped and sunk) and a low probability of any individual getting bait.

This experiment examined bait-taking success as a function of a species' proportion in a boat-attending flock. It is possible that overall number of gulls rather than just proportion also influences which species gets bait, in the sense that there may be a threshold number of gulls of one species needed to overwhelm the other species. Unfortunately, flocks in this experiment rarely exceeded 13 birds. Elucidating details about possible threshold numbers would require a larger-scale study using vessels that are familiar to seabirds as sources of discards.

Fisheries discards are known to supplement seabird diets worldwide (Garthe and Scherp 2003, Pros 2002, Bartellotti and Yorio 2001, Yorio and Caille 1999, Oro and Ruiz 1997, Furness et al. 1992). The differential success of Herring Gulls and Great Black-backed Gulls foraging on lobster fisheries discards suggests that New England fisheries discards may have unequal impacts on different species of seabirds. It has been shown that Herring Gulls are being outcompeted in the intertidal for natural food sources (Rome and Ellis 2004), and it now appears that they also are suppressed when foraging on lobster fisheries discard. These observations support the theory that Herring Gulls are being further displaced by the larger and more-aggressive Great Black-backed Gull not only from their natural foraging habitats (Rome and Ellis 2003) but from anthropogenic food sources as well. In light of these observations, it remains to be seen whether the decline of Herring Gulls and population growth of Great Black-backed Gulls around the Isles of Shoals (J.C. Ellis, pers. comm.) will continue.

Acknowledgements

I am greatly indebted to J.C. Ellis for mentoring me in the field and guiding me through the protocols of seabird research; the Shoals Marine Laboratory Staff for their support; and the 2008 RIFS interns for their indispensable help collecting data. Thanks to K. Quinby, R. Nolan, B. Shattuck, L. Quevillon, D. Cohen, M. Driscoll, M. Searles, A.

Chaput, and T. Davis for all of their assistance in collecting gull chumming data. I am deeply grateful to J. Orrock for his indefatigable support and assistance in putting this manuscript together and analyzing data; without him this manuscript could not have been written. This project was supported by the Shoals Marine Laboratory Research in Field Science internship.

Literature Cited

Bartle, J.A. 1974. Seabirds of Eastern Cook Strait, New Zealand, in autumn. Notornis 21: 135–166.

Belant, J.L., T.W. Seamans, S.W. Gabrey, and S.K. Ickes. 1993. Importance of landfills to nesting herring gulls. The Condor 95: 817–830.

Bertellotti, M. and P. Yorio. 2001. Intraspecific host selection by kleptoparasitic Kelp Gulls in Patagonia. Waterbirds: The International Journal of Waterbird Biology 24: 182–187.

Borror, A.C. and D.W. Holmes. 1990. Breeding birds of the Isles of Shoals. 2nd Edition. Shoals Marine Laboratory, Ithaca, NY.

Brown, K. M., J. L. Tims, R. M. Erwin and M. E. Richmond. 2001. Changes in the nesting populations of colonial waterbirds in Jamaica Bay Wildlife Refuge, New York, 1974-1998. Northeastern Naturalist 8: 275–292.

Camphuysen, K. 1995. Herring Gull *Larus argentatus* and Lesser Black-backed Gull *L. fucus* feeding at fishing vessels in the breeding season: competitive scavenging versus efficient flying. Ardea 83: 365–380.

Cody, M.L. 1973. Coexistence, coevolution and convergent evolution in seabird communities. Ecology 54: 31–44.

Le Corre, M. and P. Jouventin. 1997. Kleptoparasitism in tropical seabirds: vulnerability and avoidance responses of a host species, the Red-footed Booby. The Condor 99: 162–168.

Fasola, M., G. Bogliani, N. Siano and L. Canova. 1989. Foraging feeding and time-activity niches of 8 species of breeding seabirds in the coastal wetlands of the Adriatic Sea. Bollettino-di-Zoologia 56: 61–72.

Furness, R.W., K. Ensor and A.V. Hudson. 1992. The use of fisheries waste by gull populations around the British Isles. Ardea 80: 105–113.

Garthe, S. and B. Scherp. 2003. Utilization of discards and offal from commercial fisheries by seabirds in the Baltic Sea. ICES Journal of Marine Science 60: 980–989.

Gilland, S.G., C.D. Ankney, and P.W. Hicklin. 2004. Foraging ecology of Great Black-backed Gulls during brood-rearing in the Bay of Fundy, New Brunswick. Canadian Journal of Zoology 82: 1416–1426.

Good, T. P. 1998. Great Black-backed Gull (*Larus marinus*). In The Birds of North

America, No. 330 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Goodale, W. 2001. Herring Gulls and lobster bait. <http://coa.edu/html/wgoodale.htm> accessed August 1, 2008.

Irons, D.B., R.G. Anthony, and J.A. Estes. 1986. Foraging strategies of Glaucous-winged Gulls in a rocky intertidal community. Ecology 67: 1460–1474.

Jackson, C.F. and P.F. Allen. 1932. Additional notes on the breeding of the Great Black-backed Gull in Maine. Auk 49: 349–350.

Lance, B.K. and D.D. Roby. 1998. Diet and postnatal growth in Red-Legged and Black-Legged Kittiwakes: an interspecies comparison. Colonial Waterbirds 21: 375–387.

Menge, B.A. 1983. Components of predation intensity in the low zone of the New England rocky intertidal region. Oecologia 58: 141–155.

Oro, D. and X. Ruiz. 1997. Exploitation of trawler discards by breeding seabirds in the north-western Mediterranean: differences between the Ebro Delta and the Balearic Islands Area. ICES Journal of Marine Science 54: 695–707.

Pierotti, R. and C.A. Annett. 1990. Diet and reproductive output in seabirds. BioScience 40: 568–574

Pierotti, R. J. and T. P. Good. 1994. Herring Gull (*Larus argentatus*). In The Birds of North America, No. 124 (A. Poole and F. Gill, eds.). The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

Pons, J.M. and P. Migot. 1995. Life-history strategy of the Herring Gull: changes in survival and fecundity in a population subjected to various feeding conditions. The Journal of Animal Ecology 64: 592–599.

Pros, J.M.A. 2002. Foraging ecology of seabirds at sea: significance of commercial fisheries in the NW Mediterranean. Ph.D. thesis, University of Barcelona.

Rome, M.S. and J.C. Ellis. 2004. Foraging ecology and interactions between Herring Gulls and Great Black-backed Gulls in New England. Waterbirds 27:200–210.

SAS. 2003. SAS for Windows, Version 9.1. SAS Institute Inc., Cary, NC, USA.

Schreiber, R.W. 1967. Roosting behavior of the Herring Gull in central Maine. The Wilson Bulletin 79: 421–431.

Tinbergen, N. 1953. The Herring Gull's World. Collins, London.

Walter, U. and Becker, P.H. 1997. Occurrence and consumption of seabirds scavenging on shrimp trawler discards in the Wadden Sea. ICES Journal of Marine Science 54: 684–694.

Wilcox, L. 1944. Great Black-backed Gull breeding in New York. Auk 61: 653–654.

Yorio, P. and G. Caille. 1999. Seabird interactions with coastal fisheries in northern Patagonia: use of discards and incidental captures in nets. Waterbirds 22: 207–216.

Tables

Table 1. Tests of fixed effects on both foraging and non-foraging gulls.

Effect	Num DF	Den DF	F Value	Pr>F
region	11	22	20.93	<.0001
time	2	22	4.73	0.0195
species	1	22	25.84	<.0001
region*species	11	22	12.16	<.0001
time*species	2	22	0.57	0.5740

Table 2. Tests of fixed effects on foraging gulls.

Effect	Num DF	Den DF	F Value	Pr>F
region	11	22	3.79	0.0038
time	2	22	4.09	0.0308
species	1	22	24.28	<.0001
region*species	11	22	5.53	0.0003
time*species	2	22	0.25	0.7841

Table 3. Tests of fixed effects on the proportion of species in the flock versus proportion of bait taken.

Effect	Num DF	Den DF	F Value	Pr>F
species	1	19	17.06	0.0006
boat	1	19	0.06	0.8141

Table 4. Tests of fixed effects on the proportion species in the flock versus proportion of bait to individuals of each species.

Effect	Num DF	Den DF	F Value	Pr>F
species	1	18	29.93	<.0001
boat	1	18	0.08	0.7779

Figures

Figure 1. A) Herring Gull (*L. argentatus*) B) Great Black-backed Gulls (*L. marinus*). Photos by J.F. Cotton.

A B

Figure 2. Locations of gull chumming sites around the Isles of Shoals. Each dot represents one chumming location except for the dot off of the northwest corner Appledore labeled *2*, where two chumming runs took place on separate days.

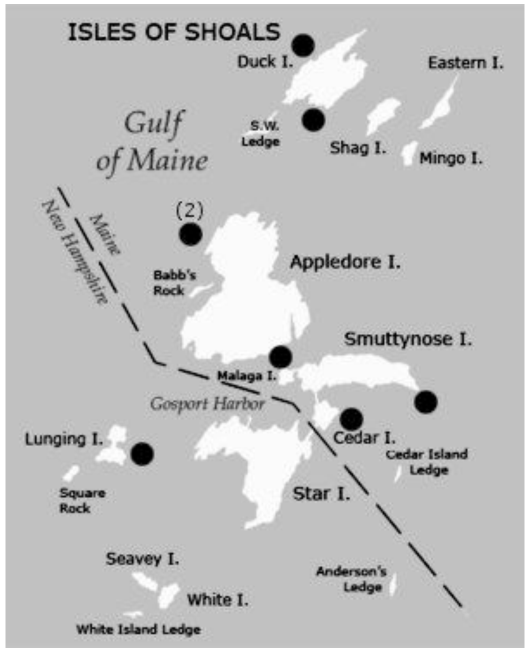

Figure 3. The black lines show divisions between regions used for quantifying gulls per km in the intertidal gull distribution surveys. Adapted from Rome and Ellis (2004).

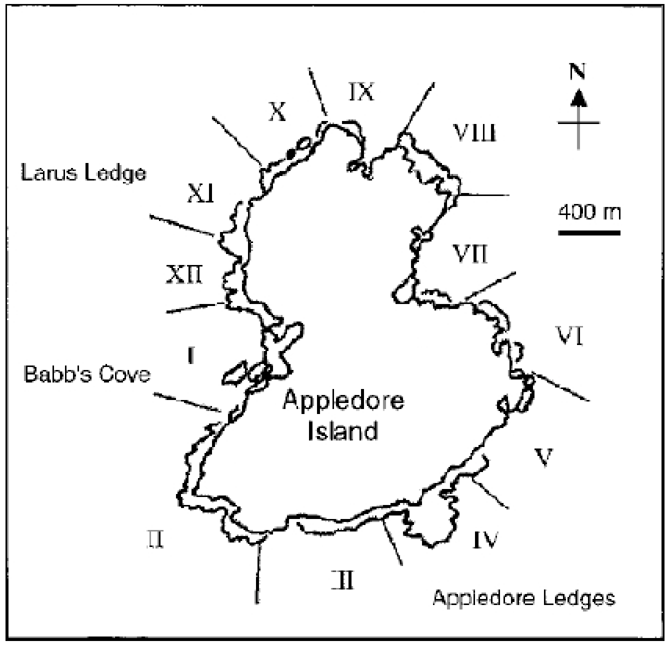

Figure 4. Distribution of all gulls (foraging and non-foraging) in the intertidal zone, with density averaged across all survey dates, ± SD.

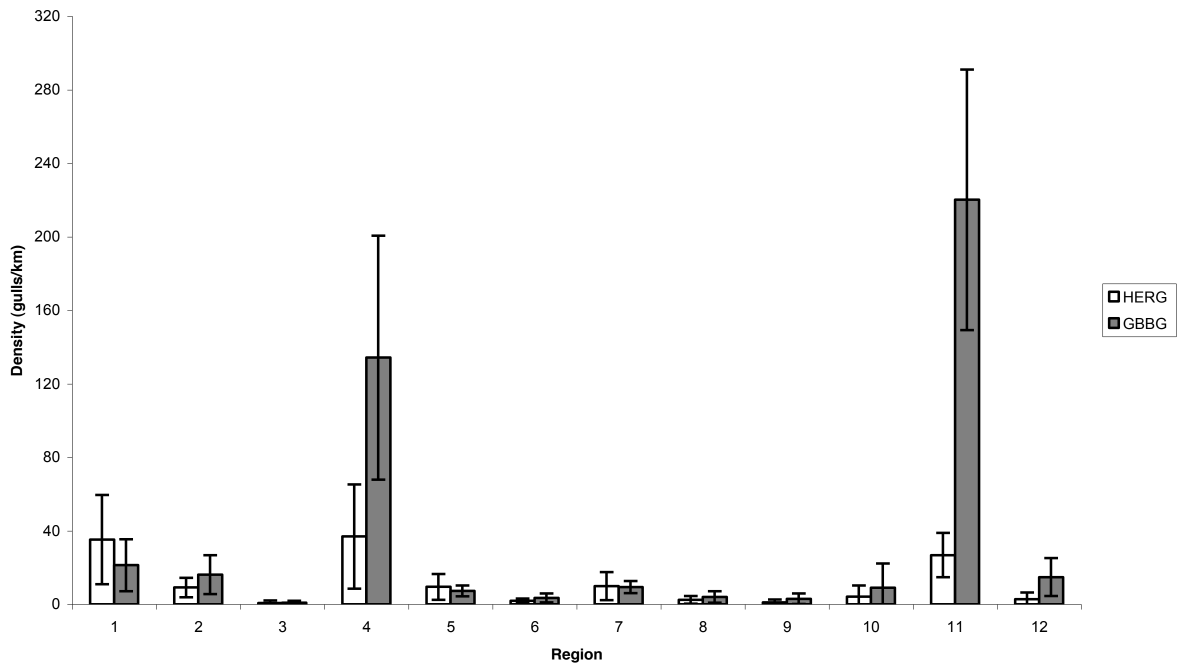

Figure 5. Density of foraging and non-foraging Great Black-backed Gulls and Herring Gulls over time ± SE.

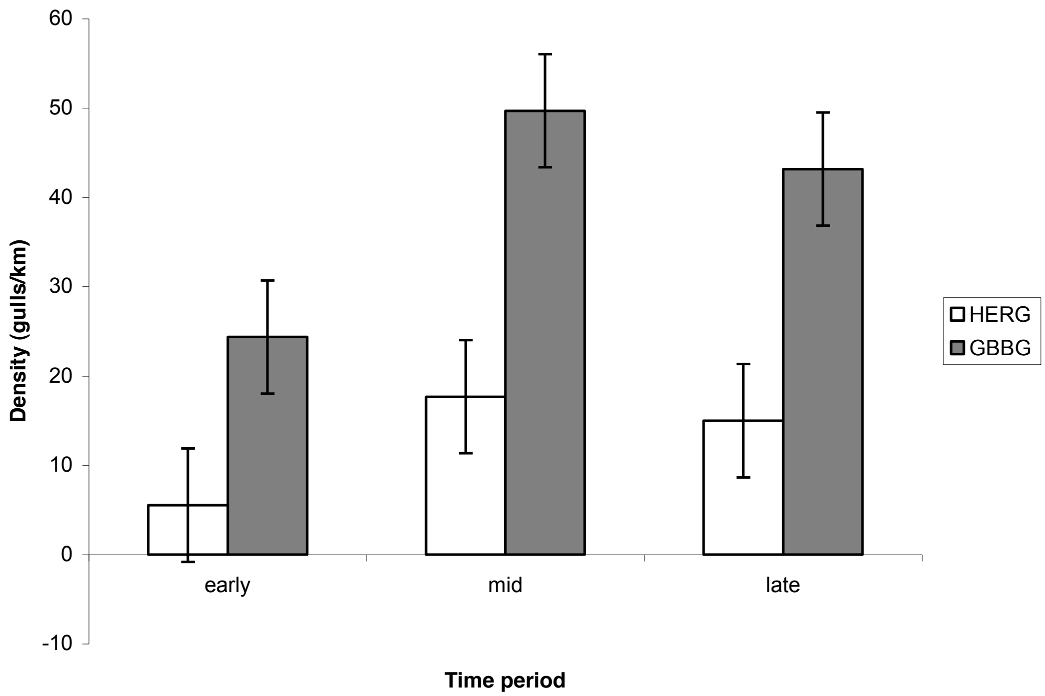

Figure 6. Distribution of foraging gulls of both species in the intertidal zone, density averaged across all survey dates ± SD.

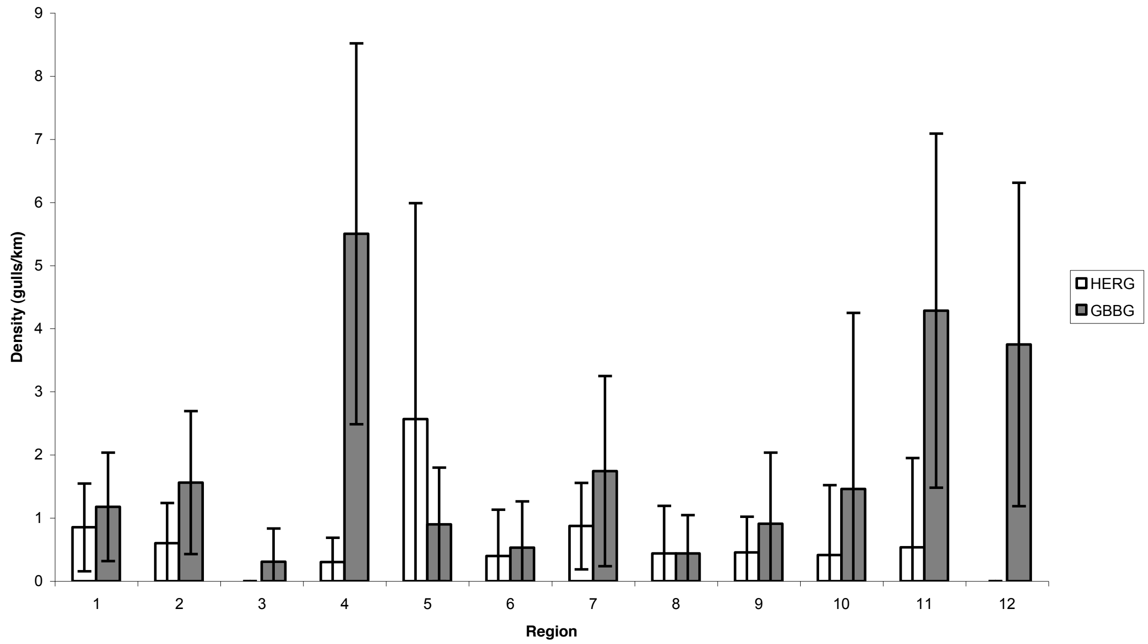

Figure 7. Density of foraging Great Black-backed Gulls and Herring Gulls over time ± SE.

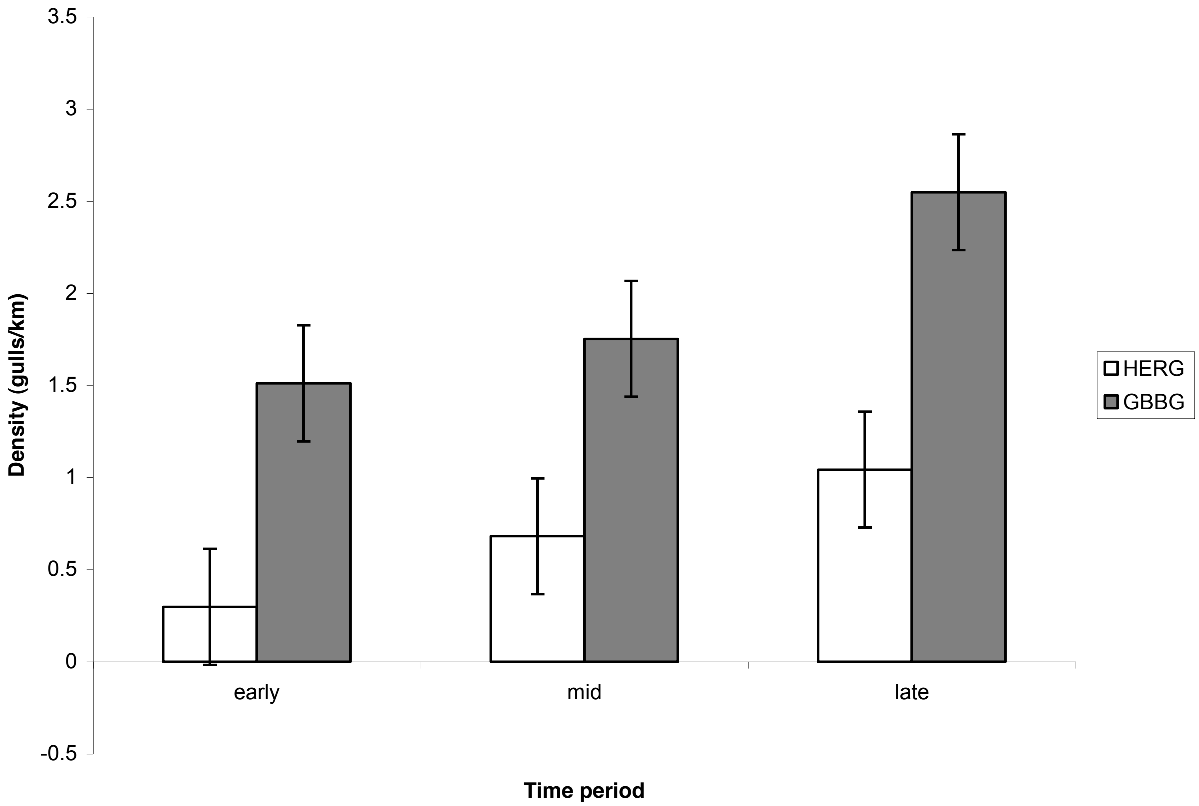

Figure 8. Fates of all bait pieces tossed in the gull chumming experiment.

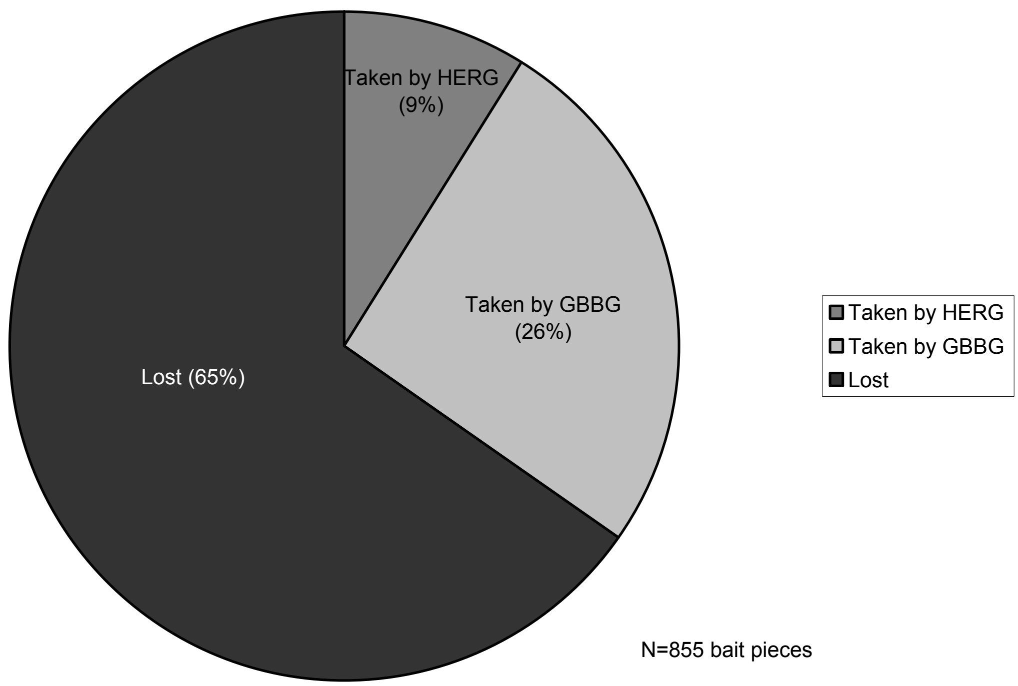

Figure 9. Flock composition by proportion of bait taken by each species.

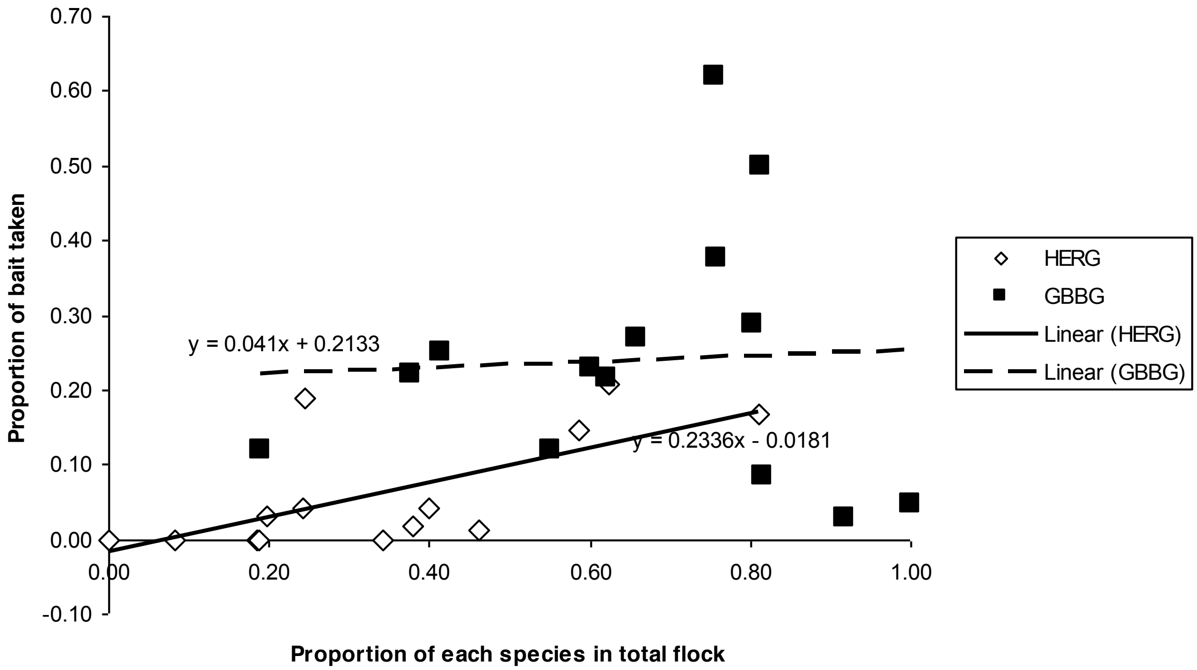

Figure 10. Average proportion of bait to each species.

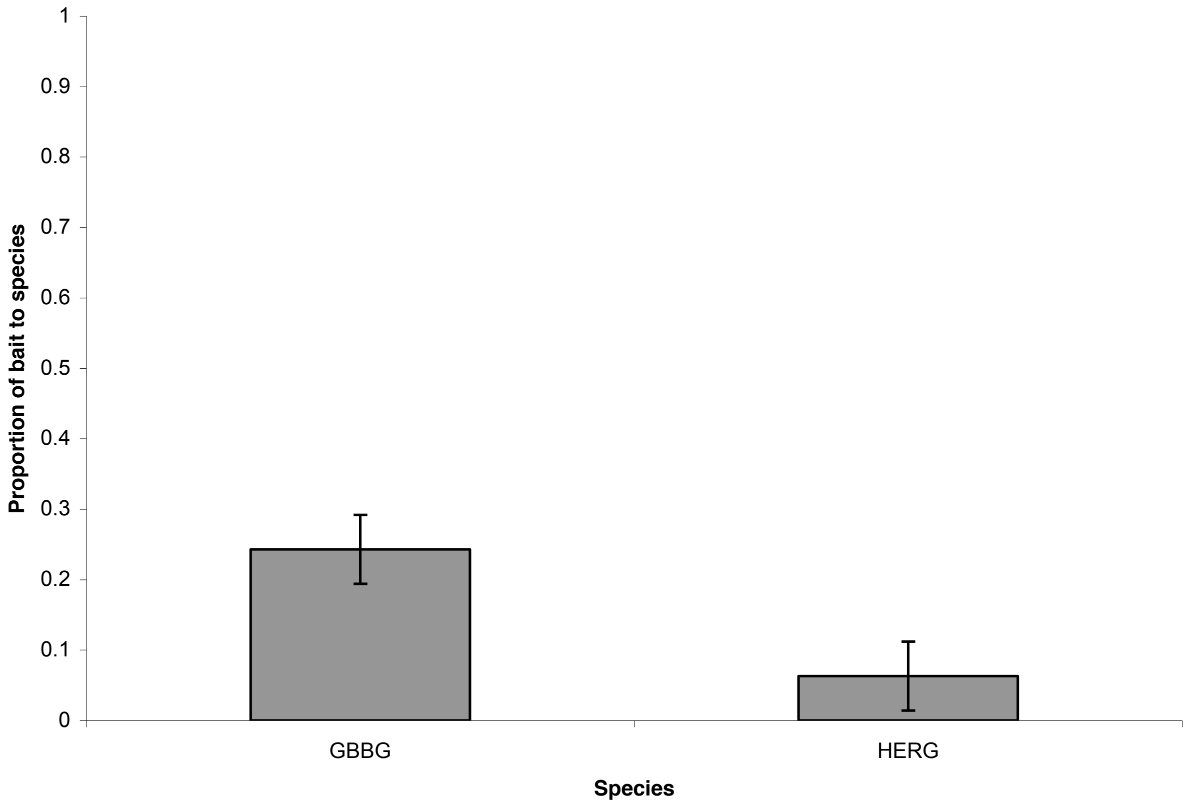

Figure 11. Proportion of each species in the flock by the average amount of bait taken by each individual.

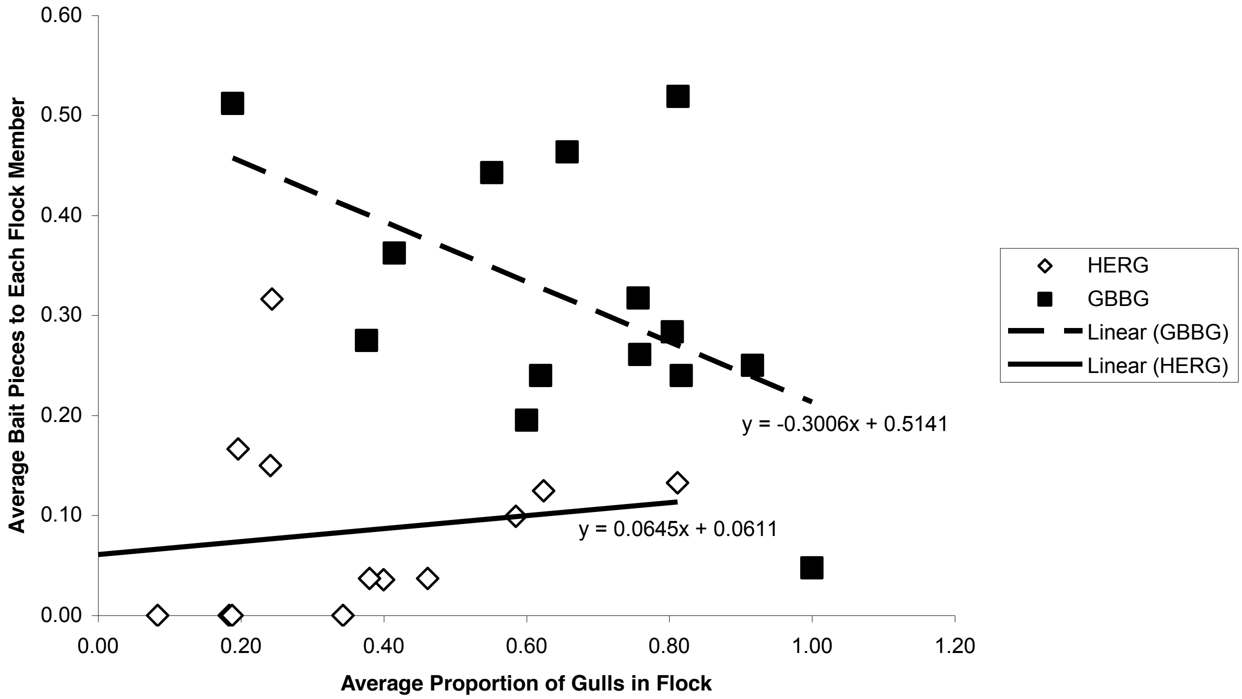

Figure 12. Kleptoparasitism by species.