Opportunistic predation of birds by breeding Herring Gulls (*Larus argentatus*)

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Abstract

Dietary specialization, exploiting a small fraction of available food resources, is commonly reported for gulls and skuas. Predation of birds by these species is usually considered a specialist strategy employed by the minority of the population but non-specialists also predate birds and may actually have a greater impact on the prey species. To date, most studies have focused on predatory bird-specialists, down-playing the possible importance of opportunistic predation by non-specialists. We addressed this by studying diet (regurgitated pellets and prey remains) and behavior of breeding Herring Gulls (*Larus argentatus*) over three summers at Gull Island, a mixed-species breeding colony in Lake Ontario. One-third of all pellets analyzed contained bird remains, primarily the most numerous breeding bird: Ring-billed Gull (*L. delawarensis*) chicks (51%) and adults (36%). Although all but one pair of Herring Gulls ate birds, all pairs maintained broad and mostly similar diets, with birds accounting for at most one-third of prey. Behavior also indicated that Herring Gulls at Gull Island were not predatory bird-specialists because predation was too infrequent to meet energetic requirements, was largely unsuccessful and was only ever observed when Ring-billed Gulls strayed into Herring Gull breeding territories. Instead, bird predation appeared mainly opportunistic, increasing with seasonal availability, access to shoreline, proximity to nesting Ring-billed Gulls and breeding territory size. Compared with predatory specialist Herring Gulls in the same region, individuals that predated birds at Gull Island did not display specialist behaviors and killed six times fewer birds (0.1–0.4 per day, on average) but were over 20 times more numerous (98% of the population versus 4%). Thus, our results indicate that opportunistic predation by non-specialists may have important consequences for prey species. Since opportunistic predation cannot be effectively managed using techniques widely advocated for specialist predators, it is essential to investigate cause of predation by large gulls prior to lethal management.

Introduction

Specialist predators have a narrow dietary niche, exploiting a small fraction of available resources, often more efficiently than generalists that utilize a wider range of prey [1].
has been growing interest in the causes and consequences of individual specialization, especially in diet studies [2–6]. Individual dietary specialization has been widely reported for seabirds, most commonly among Charadriiform species, of which large gulls Larus spp. or skuas Stercorarius spp., account for greater than 60% of records [7]. These two genera of birds often occupy similar upper trophic niches at mixed-species colonies, where they scavenge, feed on marine and terrestrial prey or predate other birds [8,9]. Predation of birds is commonly described as one specialist strategy employed by a small subset of individual large gulls and skuas, comprising from ~2–4% [10,11] to at most 14–20% [12–14] of individuals within the population. Non-specialists, however, may also predate birds and, because they comprise the majority of the breeding population, their overall impact on the prey species may be greater than that of specialist individuals [15].

Incorrect classification of specialists has important empirical repercussions because lethal control of large gulls is strongly advocated to control specialist individuals that predate conservation-important bird species [16,17]. Behavioral metrics that could be used concurrently to improve identification of predatory bird-specialists include: predation outside of a bird’s own breeding territory [18,19], use of specialized hunting behaviors [12,20,21], and elongation of breeding territories into feeding territories [12,22] or defense of separate feeding territories [10,14,15]. Lethal control methods may become ineffectual and ethically-questionable in cases where non-specialists are having a much greater overall impact. Thus, understanding the degree to which predation is opportunistic and the factors that promote predation of birds by non-specialists is of considerable importance.

To date, most studies of gulls and skuas have focused on predatory bird-specialists [10–12,14,17], as a consequence down-playing the importance of non-bird-specialists (throughout the paper we use the term “non-specialists” in reference to bird prey, acknowledging that these individuals may specialize on other prey). For most gulls and skuas, however, there likely exists a continuous gradient of exploitation of dietary items across the population [23], with individuals specializing to different degrees and also opportunistically exploiting other food resources. In most previous work, predatory bird-specialists are identified based on dietary threshold (e.g. birds comprising >75% of dietary items [13]). Such categorization may either ignore the impact of non-bird-specialists (e.g. [14]) or divide it among other dietary specialisms (e.g. [13]), unintentionally obscuring the large overall impact of non-specialists on prey populations.

Here, we investigate predation of birds by breeding Herring Gulls (Larus argentatus) within a large Ring-billed Gull (L. delawarensis) breeding colony in Lake Ontario. We focus at the within-colony scale because variation in diet between individuals and pairs within colonies [7,13] suggests that factors influencing diet act at this level. Previous studies in this region have concluded that the majority of predation by Herring Gulls at Ring-billed Gull colonies occurs through the action of predatory bird-specialists [11]. However, prior to our study, we observed extensive seasonal variation in the exploitation of Ring-billed Gulls as prey by Herring Gulls (as indicated by prey remains at breeding territories) which challenged this, suggesting instead that predation could be largely opportunistic. This motivated us to investigate the factors driving predation of birds by Herring Gulls at our colony to determine the degree to which opportunism can be an important component of bird predation by large gulls. Accordingly, we first quantified the level of Herring Gull dietary specialization through analyses of diet and behavior, and then examined factors associated with the frequency of bird predation by non-specialist individuals. If predation of birds is largely opportunistic, we predict that all study birds will predate birds and factors that increase opportunities for such predation (e.g. proximity to prey, availability of vulnerable chicks) will be most strongly associated with its prevalence.
Methods
Study site and field methods

We undertook a series of studies of Herring Gulls nesting at Gull Island, Presqu’ile Provincial Park, Ontario (43.98˚ N, 77.74˚ W) between May and July in 2009, 2015 and 2016. Gull Island is a 7.3 hectare, vegetated (but essentially treeless), low-lying, limestone island in Lake Ontario, ~300 m from the mainland. Approximately 100 pairs of Herring Gulls nested on the island in each year of the study. The majority of breeding territories were around the edge of the island and had lake access via a gravel beach but some also bred among other waterbirds in the vegetated island interior or on their own in a small colony (~30 nests) at the southeast end. As of 2016, this island also supported ~30,000 pairs of Ring-billed Gull, ~4,000 pairs of Double-crested Cormorant (*Phalacrocorax auritus*), ~600 pairs of Caspian Tern (*Hydroprogne caspia*), and ~100 pairs of Common Tern (*Sterna hirundo*).

All study activities were approved by Penn State University’s Institutional Animal Care and Use Committee (protocols #28103 and #45332) and permitted by the Canadian Wildlife Service Migratory Bird Conservation Act Scientific Permits CA 0242 and CA 0308 and banding permits 10431V, 10431W, and 10901 from Environment and Climate Change Canada.

In 2009, we studied 21 Herring Gull breeding territories, all located either on the edge of, or within, the Ring-billed Gull colony (categorized as “near to Ring-billed Gulls”) (Table 1). In 2015, we selected two different natural “treatment” groups: (i) Herring Gulls nesting on the edges of/within the Ring-billed Gull colony (“near to Ring-billed Gulls”: 17 nests) and (ii) Herring Gulls nesting within their own colony at the southeast end of the island (“away from Ring-billed Gulls”: 10 nests) (Table 1). We marked all study breeding territories with nest stakes for identification. We calculated territory size for each as the product of the lengths of the territory measured during incubation in two dimensions (along north-south and east-west axes). In each case, length was the sum of the two distances along the axis from the nest to where study birds ceased to dive at investigators and landed, and markers were placed at these distances and adjusted if this changed on subsequent visits during incubation. For a field-based metric of territory density, we measured “nearest neighbor distances”, defined as linear measurements between nest cups of the focal territory and nearest active gull nest cup.

In 2009 and 2015, we recorded diet throughout the season by searching each territory for regurgitated Herring Gull pellets and prey carcasses (including all eaten remains: carcasses, fresh bones, large feathered remains) (Table 1) for at least five minutes on either nine (2009) or six (2015) different occasions between 24 May and 14 July. In 2015, new study nests were added up until 29 June, so the number of times a territory was searched during the study varied from 2–6 per nest (mean = 4.1). At first visit, visibly-old pellets and bird remains were destroyed and not recorded; for subsequent visits, carcasses were identified to species and age (adult/chick), and contents of pellets were recorded. In-person and video observations were used in 2015 and 2016 to estimate frequencies of predatory attacks, territorial aggression (aggressive interactions to or from study adults), feeding, scavenging and chick-provisioning by the breeding Herring Gulls (Table 1). We distinguished predatory attacks from territorial aggression if one of the following criteria was fulfilled: prey was chased further in to the breeding territory; if prey temporarily escaped it was pursued; an attempt was made to drown prey; or an attempt was made to eat prey. In 2015, 37 Herring Gull territories (both study and neighboring territories) were observed in person for between 31 and 120 min (totaling 164 territory-hours of observation). Observations were made from a temporary blind at least 7 m from any study nest, or twice from a boat anchored 30 m offshore, using binoculars and a 20x spotting-scope between 29 June and 15 July: this encompassed the peak fledging period for Ring-billed Gulls. During the same period, 4–6 remote trail cameras (Bushnell Trophy Cam...
Aggressor 119774C, Bushnell Trophy Cam HD 119576 (Overland Park, KS) captured motion-triggered video of breeding Herring Gulls at 5 study territories during continuous periods (totaling 538 territory-hours of observation, range 40–222 h per territory). To supplement these data with observations encompassing the peak hatching period for Ring-billed Gulls (Table 1), 4–6 remote cameras (additional models: Browning Recon Force BTC-7FHD [Morgan, UT], Spypoint FORCE-11D [Swanton, VT]) were used in 2016 to record video at 8 study territories between 1 and 16 June during continuous 24–48 h periods (totaling 695 territory-hours of observation, range 29–238 h per territory).

In 2016, we also investigated the frequency with which gulls hunted outside their breeding territories (Table 1), a strategy used by predatory specialists [18,19]. Two infra-red trail cameras (Bushnell Trophy Cam HD) took combined motion-sensitive and time-lapse video (at least one 15 s video every 30 min) simultaneously either on the edge of the Ring-billed Gull colony next to (but not within) surrounding Herring Gull territories, or in the center of the Ring-billed Gull colony, at least 45 m from the nearest Herring Gull territory. Videos (87 and 68 observational-hours, respectively) were recorded on 6 d between 1 and 17 June (peak hatching period of Ring-billed Gulls) and examined for incidences of predation by Herring Gulls away from their breeding territories.

### Analyses

**Diet and evidence for predatory specialists.** In 2009, pellets were dissected and categorized as either fish, plant matter, terrestrial invertebrates, mammals, birds, or garbage; in 2015 only Ring-billed Gull remains (adult and chick) were quantified. Daily predatory impact was
calculated as the number of birds killed per study Herring Gull pair per day, using the number of Ring-billed Gull carcasses found in Herring Gull territories, since carcasses have greater longevity than pellets [24,25].

For each study pair in 2009, we recorded the number of prey categories utilized, the most common prey item eaten, and the proportion of pellets in which this item was recorded. To investigate evidence for predatory specialists, we calculated both dietary niche width and dietary niche overlap [26,27]. We used the number of different prey categories recorded as an index of dietary niche width for each breeding territory. We used Bolnick et al.’s [26] standardized modification of Petraitis’ [28] likelihood approach to estimate dietary niche overlap as the probability of each pair’s diet being drawn randomly from the population distribution. This generated a P-value in each case to test whether an individual’s diet differed significantly from that of the population [26]. Since different prey have different energy densities, prior to this test we rescaled each pair’s pellet data according to relative energetic contributions. For each category, this was done by first estimating the proportion of each pellet that contained this prey category and then summing all these proportions to give the number of pellets of only that prey category. For the bird prey category, this sum was divided by 1.7 to compensate for over-representation of bird remains in regurgitated pellets [24,25] and render each pellet equivalent to a single meal. For each category, we then multiplied the energy density of prey (kJ g⁻¹ [15,29–31]) by average meal size [32] to determine the energy provided. Finally, we scaled energy provided to make it relative to other categories (by dividing by the average energy provided by all six categories) and multiplied it by the number of pellets of that prey category.

For each study nest in 2009 and in 2015 with sufficient data (4+ searches), we used carcass data to calculate daily bird prey consumption on each visit: dividing the number of carcasses recorded by the days since last search. We estimated that >0.5 carcasses/d would provide for the daily energetic demands of the two members of a breeding pair (1460 kJ/d [13]), estimating 2834 kJ per carcass by assuming all predated chicks were near fledging weight (400 g [33]), had an energy density of 10.9 kJ/g and only 65% of the carcass was digestible [29].

Behavioral observations and evidence for specialist behavior. We report the frequency of predatory attacks and aggression by Herring Gulls in 2015 and 2016 and contrast these between birds breeding in territories near to Ring-billed Gulls and those breeding away from Ring-billed Gulls. We also report predatory attacks by Herring Gulls away from their breeding territories detected in videos recorded in the center and edge of the Ring-billed Gull colony in 2016.

To screen for any specialized predatory behavior, behaviors used by adult Herring Gulls during each observed predatory attack were compiled from all territorial video footage and watch observations. Since behaviors occurred at different stages of an attack we categorized them into one of four time categories based on when they occurred: 0 min (immediately), 0–1 min, 1–5 min, and >5 min since initial attack. Behaviors were then contrasted with those reported as territorial aggression in the literature [31].

Seasonality and factors associated with predatory diets. Pellet and carcass data from 2009 and 2015 were plotted to examine seasonal trends in the proportion of Ring-billed Gulls within Herring Gull diets. Pellet and carcass data were also analyzed separately within each year using generalized linear models (GLMs) with binomial errors to determine whether territory size [large vs. small: ≥ 73.5 m² (mean value) vs. < 73.5 m²], location [access to shoreline vs. no access to shoreline], and nearest neighbor distance affected the proportion of bird prey in dietary samples. In 2015, “treatment” (nesting near to Ring-billed Gulls vs. nesting in the small colony away from Ring-billed Gulls) and hatching date of the first egg from the focal Herring Gull nest (as a Julian date; “Hatching Date”) were additional predictors.
All GLM model selection was implemented in the R package MuMIn [34] to determine the most parsimonious model reduction [35] from the maximal model (main effects for all predictors). We tested GLMs for overdispersion (c-hat > 1) and corrected for this by ranking models by QAICc (instead of AICc) in the R package AICcmodavg [36]. Where competing models were within 2 QAICc of the top-ranked model, model averaging was used to determine the relative importance of each predictor across these competing models [35]. Number of model parameters (K), difference in ranking criteria from top model (ΔQAICc) and proportional likelihood of the model (QAICc weights: relative likelihood of the model divided by the likelihood sum of all models) are reported [35].

All means are reported with ± 1 SE and medians with [lower quartile, upper quartile], unless otherwise indicated.

Results

Diet and evidence for predatory specialists

Waterbird remains were found in 33% of all 265 pellets analyzed in 2009, garbage and other human foodstuffs in 24%, fish in 18%, plant material in 13%, mammal remains in 6.5% and insects in 2.6% (2.9% of items were unidentifiable). 51% of waterbird prey was Ring-billed Gull chick, 36% Ring-billed Gull adult, 2% Caspian Tern chick and 11% was unidentifiable. At any one territory, the most common prey item occurred at most in only 38 {30, 46} % of regurgitated pellets. Dietary niche width was broad: on average 4 {3, 5} of the 6 different prey categories were exploited by each study pair (range: 2–6 categories). Dietary niche overlap was common: only 25% (5/20) of pairs differed significantly in their use of prey categories (P<0.05) from the population average. Of those that differed, only 1 ate more birds and all still exploited prey from many different categories (niche width = 4–5 in all cases). Daily predatory impact (Ring-billed Gulls killed per Herring Gull pair per d) inferred from the number of Ring-billed Gull carcasses found in Herring Gull territories was 0.41 in 2009 and 0.10 in 2015.

Individual Herring Gulls varied widely in their predation of birds (Fig 1) and bird remains were found in all but one of the 48 study breeding territories (98%, Fig 1). For 27% (12/45) of study pairs the average predation rate across the season was >0.5 kills/d (sufficient to meet energetic demands) but no study pairs achieved this level during every sampling interval (see Seasonality and factors associated with predatory diets below).

Behavioral observations and evidence for specialist behavior

Twenty-two attacks of Herring Gulls on Ring-billed Gulls were observed during 164 territory-hours of in-person watches within the peak fledging period for Ring-billed Gulls (July 2015), and all took place within Herring Gull breeding territories (overall attack rate: 0.13 attacks/h/territory). However, only 36% of attacks resulted in a kill. These predatory attacks by breeding Herring Gulls were four-times more frequent at Herring Gull territories near to the Ring-billed Gull colony than those away from Ring-billed Gulls (0.24 vs 0.08 attacks/h/territory). This relationship followed that for territorial aggression (0.31 vs 0.07 aggressive interactions/h/territory, respectively). Attacks were less commonly observed on remote video recordings at Herring Gull territories: only 10 attacks were observed during 537 h of footage over the same period (July 2015). This is likely because of limitations in the field of view of cameras when vegetation and neighbors sometimes caused unexpected change to territory boundaries. No predatory attacks were ever observed in 695 h of remote video footage at Herring Gull territories during the peak hatching period for Ring-billed Gulls (May 2016). Also during this time period, no Herring Gulls were observed hunting outside their breeding territories, either
within the Ring-billed Gull colony or along its edge (155 h of time-lapse video recordings in 2016).

On average, attacks by Herring Gulls on Ring-billed Gulls lasted 3.9 ± 3.3 min (max = 22 min). During predation events, Herring Gulls engaged in the following behaviors: chasing; bill-, neck-, wing- and tail-grabbing; dragging; drowning; and pecking (of head or belly) (Fig 2). Although these events were clearly classified as attacks, these behaviors are not specialist behaviors as they are used by Herring Gulls during territorial disputes [31]. Within the first two minutes of an attack, Herring Gulls seized Ring-billed Gull chicks by their neck or bill (Fig 2) and, if within 1 m of the shoreline, attempted to drown them. Neck Grabs were by far the most common behavior in the first minute of an attack (Fig 2), and once a good neck hold was established the prey would be dragged further into the territory to be drowned or pecked. Wing and Tail Grabs were mainly the result of losing grip of the prey and attempting to recatch it after a brief chase (Fig 2). Pecking of the head and stomach occurred up to 5 min from initiation of the attack but was then replaced by active feeding (Fig 2).

Seasonality and factors associated with predatory diets

Pellet analyses indicated that more breeding Herring Gulls consumed Ring-billed Gull during peak hatching and peak fledging periods of Ring-billed Gulls (Fig 3). Carcass data, however, only indicated a marked increase during the peak fledging period (Fig 3).

In 2009, when all Herring Gull territories studied were close to Ring-billed Gull nests (i.e. there was no “treatment”), shoreline access and territory size were most important in determining the frequency with which both Ring-billed Gull remains were found in Herring Gull pellets and Ring-billed Gull carcasses were found in Herring Gull territories (Tables 2A and 3A and Fig 4A and 4B). In 2015, pellets containing Ring-billed Gull remains were slightly more common in Herring Gull territories located near to Ring-billed Gulls (0.44 ± 0.07) than in territories away from Ring-billed Gulls (0.35 ± 0.07) [“Treatment”]. However, this effect

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Fig 1. Variation in exploitation of Ring-billed Gulls as prey by Herring Gulls. Frequency of exploitation of Ring-billed Gull prey (RBGU) by individual Herring Gull pairs in (a) 2009 and (b) 2015, as indicated by either remains found in pellets or carcasses in territories. Data are only shown for pairs in which four or more days of dietary records were available.

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was secondary to having a territory with access to the shoreline (Table 2B, Relative Importances: 1.00 [Shoreline Access] vs 0.70 [Treatment]). These same relationships were stronger for the number of carcasses found in Herring Gull territories (0.67 ± 0.07 near to Ring-billed Gull colony vs. 0.51 ± 0.11 away from Ring-billed Gull colony; Table 3B, Relative Importances: 1.00 [Shoreline Access] vs 0.65 [Treatment]). Thus, overall consumption of Ring-billed Gulls by Herring Gulls was higher among territories with shoreline access (Fig 4C) close to the Ring-billed Gull colony (Fig 4D).

**Discussion**

Large gulls and skuas are well known for exhibiting individual dietary specialization [7] and predation of birds is widely reported as a specialist strategy employed by a minority of individuals in the population [14,15,17,32]. However, our analyses of diet and behavior revealed that predation of Ring-billed Gulls (the predominant bird prey) by Herring Gulls was opportunistic at Gull Island and not a specialist strategy. Dietary data indicated that Ring-billed Gulls, by far
the most numerous nesting waterbird in our study area, were widely exploited as prey, utilized by nearly all Herring Gulls in correspondence with their seasonal availability (Fig 3) and the proximity of both nests and roosts (Fig 4). Herring Gull pairs maintained broad dietary niches and limited any one prey type to a maximum of one-third of their diet. Only one pair exploited birds as prey significantly more than normal and even those individuals were not specialists as they also utilized many other prey types. Predation at individual Herring Gull territories occurred too infrequently to reliably meet all the energetic demands of a breeding pair throughout the season, was only observed within territories, and did not require specialized hunting behaviors (behaviors observed were those used during intraspecific territorial disputes, c.f. Fig 2 and [31]). The predatory attacks we did observe were also largely unsuccessful.
(only 36% of attacks observed resulted in death of the prey) and below success rates of specialist predatory gulls (50%-75%) [10,37] (but more successful than reported previously for opportunistic gulls (15%-22%) [38,39], probably because all chicks were attacked within herring gull breeding territories with no parent to defend them). Thus, although predating other birds comprised an important proportion of their diet (33% on average), Herring Gulls at Gull Island were non-specialists that opportunistically predated birds.

Our results contrast with the only other study in the region (Rogers City, western Lake Huron), where Herring Gulls bred within a colony of ~10,000 pairs of Ring-billed Gulls [11]. Of the ~30 Herring Gulls with territories on the perimeter of that Ring-billed Gull colony, only 25% fed on Ring-billed Gulls in one year of study but 71% predated gulls in the following year [11]. The authors attribute much of this variation to small sample sizes (n < 6) [11], but it is likely that opportunism is also occurring, with birds switching to predatory diets during food shortfall as in other studies [10,12]. However, many Herring Gulls at Rogers City did appear to be predatory-specialists, hunting outside their territories and having much larger territories (up to 120 m diameter [11]) than in our study (maximum of 30 m), consistent with the elongation of breeding territories into feeding territories by specialists that has been reported elsewhere (e.g. [22]). These birds also had a greater daily predatory impact (2.7 Ring-billed Gulls killed per pair per day) than in our study (0.41 in 2009, 0.10 in 2015). It should be noted that these perimeter-nesting specialists comprised only 3–4% of the Rogers City Herring Gull breeding colony. By contrast, at Gull Island practically all Herring Gulls consumed bird prey and thus predation by non-specialists is likely much more important. A similar but less

### Table 2. Highest-ranked GLM models predicting presence of bird remains in Herring Gull pellets.

| Parameters                  | K  | QAIC<sub>c</sub> | ΔQAIC<sub>c</sub> | QAIC<sub>c</sub> Weight | Parameters                  | K  | QAIC<sub>c</sub> | ΔQAIC<sub>c</sub> | QAIC<sub>c</sub> Weight |
|-----------------------------|----|------------------|-------------------|--------------------------|-----------------------------|----|------------------|-------------------|--------------------------|
| Shoreline Access            | 3  | 60.9             | 0.00              | 0.39                     | Shoreline Access            | 3  | 56.9             | 0.00              | 0.27                     |
| Shoreline Access, Territory Size | 4  | 62.3             | 1.40              | 0.20                     | Shoreline Access, Treatment | 4  | 57.4             | 1.56              | 0.21                     |
| Null Model                  | 2  | 62.8             | 1.89              | 0.15                     | Shoreline Access, Nearest Neighbor | 4  | 58.9             | 2.02              | 0.10                     |
| Shoreline Access, Nearest Neighbor | 4  | 63.8             | 2.97              | 0.09                     | Shoreline Access, Territory Size | 4  | 59.2             | 2.36              | 0.08                     |
| Territory Size              | 3  | 64.3             | 3.39              | 0.07                     | Shoreline Access, Hatching Date | 4  | 59.6             | 2.70              | 0.07                     |

Five highest-ranked GLMs from model selection of factors affecting whether Herring Gull pellets containing Ring-billed Gull remains in (a) 2009 and (b) 2015. Null Model—indicates intercept only for this parameter. Relative Importance of each predictor was (a): Shoreline Access = 1.00, Territory Size = 0.40; (b) Shoreline Access = 1.00, Treatment = 0.70.

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### Table 3. Highest-ranked GLM models predicting presence of bird carcasses in Herring Gull territories.

| Parameters                  | K  | QAIC<sub>c</sub> | ΔQAIC<sub>c</sub> | QAIC<sub>c</sub> Weight | Parameters                  | K  | QAIC<sub>c</sub> | ΔQAIC<sub>c</sub> | QAIC<sub>c</sub> Weight |
|-----------------------------|----|------------------|-------------------|--------------------------|-----------------------------|----|------------------|-------------------|--------------------------|
| Territory Size              | 3  | 46.3             | 0.00              | 0.59                     | Shoreline Access, Treatment | 4  | 50.8             | 0.00              | 0.22                     |
| Shoreline Access, Territory Size | 4  | 48.4             | 2.16              | 0.20                     | Shoreline Access            | 3  | 51.1             | 0.25              | 0.19                     |
| Territory Size, Nearest Neighbor | 4  | 48.8             | 2.56              | 0.16                     | Shoreline Access, Nearest Neighbor | 4  | 52.2             | 1.37              | 0.11                     |
| Shoreline Access, Territory Size, Nearest Neighbor | 5  | 51.1             | 4.84              | 0.05                     | Shoreline Access, Treatment, Hatching Date | 5  | 52.3             | 1.53              | 0.08                     |
| Shoreline Access, Nearest Neighbor, Hatching Date | 5  | 52.8             | 1.98              | 0.08                     |

Top-ranked GLMs from model selection of factors affecting whether Ring-billed Gull carcasses were found in Herring Gull territories in (a) 2009 and (b) 2015. For (b), the Relative Importance of each predictor was: Shoreline Access = 1.00, Treatment = 0.65, Hatching Date = 0.58, and Nearest Neighbor = 0.30.

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extreme situation to Gull Island has been reported for skuas: of all the birds predated by Great Skuas *Stercorarius skua* at a colony in Shetland, UK, > 70% were taken by non-specialists [15].

Exploitation of bird prey by our non-specialist Herring Gulls was associated with access to shoreline, proximity to nesting Ring-billed Gulls and, to a lesser extent, breeding territory size. These factors likely lead to increased frequency of Ring-billed Gull chicks (the most common bird prey exploited) straying into Herring Gull breeding territories. Having access to the shoreline within their territory likely increased encounters with fledgling Ring-billed Gull chicks that crèched on the beach in large numbers often without adults present (e.g. [40]), but also increased the chances of making a successful kill (drowning prey was a common predation tactic within the first minute of an attack). Although shoreline access was a strong predictor of

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**Fig 4. Factors associated with predatory diets of Herring Gulls.** Boxplot of most important factors predicting diet of Herring Gulls during the two years of intensive study: (a) territory size and (b) shoreline access in 2009, and (c) shoreline access and (d) treatment in 2015. Data are frequencies with which Ring-billed Gull chick (RBGU) carcasses or remains within pellets were found in Herring Gull territories. Note: all territories studied in 2009 were on the edge of/ or within the ring-billed colony and thus it was not possible to assess treatment effects in this year.

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predatory diets whether determined by pellets or carcasses, the two other factors were stronger predictors of the presence of eaten Ring-billed Gull carcasses than of bird remains in regurgitated Herring Gull pellets (compare Tables 2 and 3). This is presumably because carcasses are more conspicuous than pellets, which may quickly degrade [24,25]. These results suggest that non-specialist Herring Gulls exploit bird prey opportunistically and that easy access to vulnerable life-stages (such as undefended chicks) and situations that promote the success of attacks are critical factors promoting the exploitation of bird prey. Previous studies have reported that time constraints and predictability may be more important for gulls and skuas than energetic value of prey [13,23,41], with birds choosing diets that allow prolonged attendance at nests to defend against intruders [13]. Since predation of birds at Gull Island occurred exclusively within Herring Gull nesting territories, it is not surprising that nearly all study pairs opportunistically consumed birds and to a greater extent than at other colonies [11]. This opportunism agrees with interspecific and between-colony studies that show predation levels decline with limited access to bird prey [42] and greater availability of alternative prey [7].

Waterbirds often nest at high densities within large, mixed-species, breeding colonies [43]. For many waterbird species, such colonies generally support large proportions of their overall population [44,45]. Thus, even a low level of opportunistic predation by non-specialist gulls or skuas that also breed there could have a greater impact on these populations than that of a few specialist predatory individuals [42]. In our study of ~20% of the Herring Gulls breeding at Gull Island, as many as 292 Ring-billed Gulls were found killed inside Herring Gull territories during the chick-rearing stage (based on carcasses recovered in 2009). This equates to ~1,500 killed colony-wide on an annual basis and suggests that opportunistic predation by Herring Gulls affects ~5% of all 30,000 Ring-billed Gull nests. Although this level of predation may be low enough to be sustainable in this colony, our results indicate that where Herring Gulls numbers are proportionally higher, for example at smaller Ring-billed Gull colonies, this opportunistic predation could have major impacts on breeding success of prey species. Compared with predatory specialist Herring Gulls in the same region [11], individuals that predated birds opportunistically at Gull Island killed six times fewer birds (0.1–0.4 per day, on average) but were over 20 times more numerous (98% of the population versus 4%), implying a greater overall predation pressure. Thus, the potential impact of opportunistic predation by non-specialists should not be overlooked.

Although removing specialist gulls is strongly advocated as a cost-effective management strategy [16,17], opportunistic predation by large gulls cannot be effectively managed using the same techniques. This is because removed individuals would be quickly replaced by conspecifics that require no specialized behavior. Large-scale culling would be required which has been shown to be expensive, often ineffectual and socially undesirable [17,46–48]. It is therefore vital to confirm the presence of specialists before undertaking lethal control. Although presence of bird remains on breeding territories or in regurgitated pellets have been successfully used in the past to identify specialists (e.g. [17,46]), in our study these field signs were indicative of non-specialist gulls that ate birds opportunistically. Consequently, we advocate investigating both diet and behavior of potential specialists prior to implementing lethal management. Our results suggest that, if purely opportunistic, predation could be minimized through the creation of safe crèching or gathering areas for the waterbird species targeted by gulls, for example by use of exclusion-style fencing [49]. Such approaches would need to be tested and refined, but our study indicates that opportunistic predation occurs only within Herring Gull territories implying that physical barriers that prevent birds wandering into gull breeding territories could reduce the predatory impacts of large gulls at mixed-species breeding colonies.
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References

1. Schoener TW. Theory of feeding strategies. Annu Rev Ecol Syst. 1971; 2: 369–404. https://doi.org/10.1146/annurev.es.02.110171.002101

2. Szīgeti V, Kőrösi Á, Harnos A, Kis J. Lifelong foraging and individual specialisation are influenced by temporal changes of resource availability. Oikos. 2019; 128: 649–658.

3. Bolnick DI, Amarasekare P, Araújo MS, Burger R, Levine JM, Novak M, et al. Why intraspecific trait variation matters in community ecology. Trends Ecol Evol. 2011; 26: 183–192. https://doi.org/10.1016/j.tree.2011.01.009 PMID: 21367482

4. Araújo MS, Bolnick DI, Layman CA. The ecological causes of individual specialization. Ecol Lett. 2011; 14: 948–958. https://doi.org/10.1111/j.1461-0248.2011.01662.x PMID: 21790933

5. Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, et al. The ecology of individuals: incidence and implications of individual specialization. Am Nat. 2003; 161: 1–28. https://doi.org/10.1086/343878 PMID: 12650459

6. Dall SRX, Bell AM, Bolnick DI, Ratnieks FLW. An evolutionary ecology of individual differences. Ecol Lett. 2012; 15: 1189–1198. https://doi.org/10.1111/j.1461-0248.2012.01846.x PMID: 22897772

7. Ceia FR, Ramos JA. Individual specialization in the foraging and feeding strategies of seabirds: a review. Mar Biol. 2015; 162: 1923–1938. https://doi.org/10.1007/s00227-015-2735-4

8. Burger J, Gochfeld M. Family Laridae (Gulls). In: del Hoyo J, Elliot A, Sargatal J, editors. Handbook of the Birds of the World, Vol 3. Barcelona: Lynx Edicions; 1996. pp. 572–623.

9. Furness RW. Family Stercorariidae (Skuas). In: del Hoyo J, Elliot A, Sargatal J, editors. Handbook of the Birds of the World, Vol 3. Barcelona: Lynx Edicions; 1996. pp. 556–571.

10. Spear LB. Dynamics and effect of Western Gulls feeding in a colony of Guillemots and Brandt’s Cormorants. J Anim Ecol. 1993; 62: 399–414. https://doi.org/10.2307/5190
11. Southern WE, Southern MD. Herring Gulls specialize as Ring-billed Gull predators. Colon Waterbirds. 1984; 7: 105–110.

12. Votier S, Bearhop S, Ratcliffe N, Furness RW. Reproductive consequences for Great Skuas specializing as seabird predators. Condor. 2004; 106: 275–287.

13. Pierotti R, Annett CA. Diet choice in the Herring Gull: Constraints imposed by reproductive and ecological factors. Ecology. 1991; 72: 319–328.

14. Watanuki Y. Individual diet difference, parental care and reproductive success in Slaty-backed Gulls. Condor. 1992; 94: 159–171. https://doi.org/10.2307/1368805

15. Votier SC, Bearhop S, Ratcliffe N, Phillips RA, Furness RW. Predation by Great Skuas at a large Shetland seabird colony. J Appl Ecol. 2004; 41: 1117–1128. https://doi.org/10.1111/j.0021-8901.2004.00974.x

16. Scopel LC, Diamond AW. The case for lethal control of gulls on seabird colonies. J Wildl Manage. 2017; 81: 572–580. https://doi.org/10.1002/jwmg.21233

17. Sanz-Agualar A, Martínez-Abraín A, Tavecchia G, Mínguez E, Oro D. Evidence-based culling of a facultative predator: Efficacy and efficiency components. Biol Conserv. 2008; 142: 424–431. https://doi.org/10.1016/j.biocon.2008.11.004

18. Hatch JJ. Predation and piracy by gulls at a ternery in Maine. Auk. 1970; 87: 244–254.

19. Parsons J. Cannibalism in Herring Gulls. Br Birds. 1971; 64: 528–537.

20. Andersson M. Predation and kleptoparasitism by skuas in a Shetland seabird colony. Ibis (Lond 1859). 1976; 118: 208–217.

21. Votier SC, Crane JE, Bearhop S, de León A, McSorley CA, Mínguez E, et al. Nocturnal foraging by Great Skuas Stercorarius skua: Implications for conservation of storm-petrel populations. J Ornithol. 2006; 147: 405–413. https://doi.org/10.1007/s10336-005-0021-9

22. Pietz PJ. Feeding and nesting ecology of sympatric South Polar and Brown Skuas. Auk. 1987; 104: 617–627. https://doi.org/10.2307/4087271

23. van Donk S, Campbuysen KCJ, Shamoun-Baranes J, van der Meer J. The most common diet results in low reproduction in a generalist seabird. Ecol Evol. 2017; 7: 4620–4629. https://doi.org/10.1002/ece3.3018 PMID: 28690792

24. Votier SC, Bearhop S, MacCormick A, Ratcliffe N, Furness RW. Assessing the diet of Great Skuas, Catharacta skua, using five different techniques. Polar Biol. 2003; 26: 20–26. https://doi.org/10.1007/s00300-002-0446-z

25. Votier SC, Bearhop S, Ratcliffe N, Furness RW. Pellets as indicators of diet in Great Skuas Catharacta skua. Bird Study. 2001; 48: 373–376.

26. Bolnick DI, Yang LH, Fordyce JA, Davis JM, Svanbäck R. Measuring individual-level resource specialization. Ecology. 2002; 83: 2936–2941.

27. Sargeant BL. Individual foraging specialization: Niche width versus niche overlap. Oikos. 2007; 116: 1431–1437. https://doi.org/10.1111/j.0030-1299.2007.15833.x

28. Petraitis PS. Likelihood measures of niche breadth and overlap. Ecology. 1979; 60: 703–710.

29. Phillips RA, Thompson DR, Hamer KC. The impact of great skua predation on seabird populations at St Kilda: A bioenergetics model. J Appl Ecol. 1999; 36: 218–232. https://doi.org/10.1046/j.1365-2664.1999.00391.x

30. Hunt GL. Influence of food distribution and human disturbance on the reproductive success of Herring Gulls. Ecology. 1972; 53: 1051–1061. https://doi.org/10.2307/1935417

31. Nisbet ICT, Weseloh DV, Hebert CE, Mallory ML, Poole AF, Ellis JC, et al. Herring Gull Larus argentatus. In: Rodewald PG, editor. The Birds of North America Online. Ithaca, NY: Cornell Laboratory of Ornithology; 2017. Available: https://birdsona.org/Species-Account/bna/species/bergul

32. Pierotti R, Annett CA. Reproductive consequences of dietary specialization and switching in an ecological generalist. In: Kamil AC, editor. Foraging Behavior. Boston, MA: Plenum Press; 1987. pp. 417–442.

33. Oswald SA, Wails CN, Morey BE, Arnold JM. Caspian Terns (Hydroprogne caspia) fledge a Ring-billed Gull (Larus delawarensis) Chick: Successful waterbird adoption across taxonomic families. Waterbirds. 2013; 36: 385–388. https://doi.org/10.1675/063.036.0318

34. Barton K. MuMln: Multi-Model Inference. 1.15.6. R package. Vienna, Austria; 2016. Available: http://cran.r-project.org/package=MuMln

35. Burnham KP, Anderson DR. Model Selection and Multimodel Inference: A Practical Information Theoretic Approach. New York, NY: Springer-Verlag; 2002.
36. Mazerolle MJ. AICcmodavg. R package version 2.1–1. 2017. Available: https://cran.r-project.org/web/packages/AICcmodavg/index.html

37. Pichegru L. Increasing breeding success of an Endangered penguin: Artificial nests or culling predatory gulls? Bird Conserv Int. 2013; 23: 296–308. https://doi.org/10.1017/S0959270912000135

38. Velarde E. Predation of Heermann’s Gull (Larus heermanni) chicks by Yellow-Footed Gulls (Larus livens) in dense and scattered nesting sites. Colon Waterbirds. 1992; 15: 8–13.

39. Swennen C. Gull predation upon Eider Somateria mollissima ducklings: destruction or elimination of the unfit. Ardea. 1989; 77: 21–45.

40. Besnard A, Sadoul N, Lebreton J-D. First quantitative comparison of aggression between crèching and non-crèching larid species. Waterbirds. 2006; 29: 481–488. https://doi.org/10.1675/1524-4695(2006)29[481:FQCOAB]2.0.CO;2

41. Phillips RA, Catry P, Thompson DR, Hamer KC, Furness RW. Inter-colony variation in diet and reproductive performance of Great Skuas Catharacta skua. 1997; 152: 285–293.

42. Votier SC, Bearhop S, Crane JE, Manuel Arcos J, Furness RW. Seabird predation by great skuas Stercorarius skua–intra-specific competition for food? J Avian Biol. 2007; 38: 234–246. https://doi.org/10.1111/j.0908-8857.2007.03893.x

43. Parnell JF, Ainley DG, Blokpoel H, Cain B, Custer TW, Dusi JL, et al. Colonial waterbird management in North America. Colon Waterbirds. 1988; 11: 129. https://doi.org/10.2307/1520996

44. Jenkins CN, Van Houtan KS. Global and regional priorities for marine biodiversity protection. Biol Conserv. 2016; 204: 333–339. https://doi.org/10.1016/j.biocon.2016.10.005

45. Spatz DR, Newton KM, Heinz R, Tershy B, Holmes ND, Butchart SHM, et al. The biogeography of globally threatened seabirds and island conservation opportunities. Conserv Biol. 2014; 28: 1282–1290. https://doi.org/10.1111/cobi.12279 PMID: 24661307

46. Hario M. Reproductive performance of the nominate Lesser Black-backed Gull under the pressure of Herring Gull predation. Ornis Fenn. 1994; 71: 1–10.

47. Finney SK, Harris MP, Keller LF, Elston DA, Monaghan P, Wanless S. Reducing the density of breeding gulls influences the pattern of recruitment of immature Atlantic Puffins Fratercula arctica to a breeding colony. J Appl Ecol. 2003; 40: 545–552. https://doi.org/10.1046/j.1365-2664.2003.00810.x

48. Blodget BG, Henze L. Use of DRC-1339 to eliminate gulls and re-establish a tern nesting colony in Buzzards Bay, Massachusetts. Proc East Wildi Damage Control Conf. 1991; 5: 212–215.

49. Blokpoel H, Tessier GD, Andress RA. Successful restoration of the Ice Island Common Tern colony requires on-going control of Ring-billed Gulls. Colon Waterbirds. 1997; 20: 98–101.