



Herring gulls target profitable Atlantic puffins during kleptoparasitic attack

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Kleptoparasitism is a foraging strategy where one individual steals a procured food item from another individual. Individual kleptoparasites can optimize their foraging strategy by targeting more profitable hosts or by modifying their behaviour to expend less energy than they would by foraging independently. Herring gulls, *Larus argentatus*, kleptoparasitize Atlantic puffins, *Fratercula arctica*, by intercepting adults as they return to their burrows with fish for their chicks. While this system has been studied extensively, much remains unknown, particularly from the herring gull's perspective. We tested predictors of herring gull host choice and the probability of success during kleptoparasitic attacks by conducting 73 30-minute focal samples of individual herring gulls at a breeding colony in Newfoundland, Canada. We recorded each puffin that approached the focal gull, categorizing them according to prey type carried, whether or not they landed, and whether or not they were attacked. For those puffins that were attacked, we also noted whether the gull succeeded in obtaining prey. Herring gulls did not attack puffins at random, but, rather, preferentially attacked puffins that carried larger prey, had already completed their landing, and landed closer to and/or in front of the gull. Gulls tended to be more successful at stealing a puffin's food when they attacked landed puffins and made physical contact with the puffin, but not when the puffin landed closer to them or when they were oriented towards the puffin. These findings suggest that herring gulls optimize their kleptoparasitic foraging strategy by targeting more profitable hosts.

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Optimal foraging theory predicts that animals will maximize their energy gain while minimizing their energy use and risk (MacArthur & Pianka, 1966; Schoener, 1971). For some species, stealing a procured food item from another individual of the same or a different species can be more profitable than foraging independently (Case & Gilpin, 1974; Iyengar, 2008; Rothschild & Clay, 1952). Known as kleptoparasitism, this stealing behaviour has been described in many species, including snails (Parries & Page, 2003), spiders (Henaut, 2000; Martišová, Bilde, & Pekár, 2009), mammals (Carbone, Du Toit, & Gordon, 1997) and birds (Brockmann & Barnard, 1979; Morand-Ferron, Sol, & Lefebvre, 2007). In general, kleptoparasitism tends to evolve in species that feed opportunistically, have high costs associated with self-foraging (e.g. because prey are scarce) and live in open environments where they can readily observe potential hosts following predictable patterns (Brockmann & Barnard, 1979; Paulson, 1985). As is the case

with any foraging strategy, the benefits of obtaining food through kleptoparasitism should outweigh the associated costs, including energy expenditure and the cost of injury (Case & Gilpin, 1974). Individual kleptoparasites may even optimize their foraging strategy by facultatively switching between kleptoparasitism and self-foraging, or by selectively attacking more profitable hosts. Some seabirds, for example, rely on kleptoparasitism during the chick-rearing period, when hosts carrying food to their offspring are abundant, but rely on self-foraging during the remainder of the year, when hosts carrying food are rare (Shealer, 2002). Other kleptoparasites optimize their foraging success by selectively attacking more profitable hosts. For example, in the kleptoparasitic spider, *Argyrodes globosus*, individuals optimize kleptoparasitism by preferentially attacking host species that do not aggressively defend their prey (Henaut, 2000).

More than one quarter of the species (23 of 88) within the family Laridae are documented kleptoparasites (Brockmann & Barnard, 1979). Gulls and terns are classic examples of kleptoparasitic foragers, exhibiting many of the life history characteristics associated with kleptoparasitism. Specifically, they often live in large multi-species colonies where potential hosts carry large and conspicuous

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prey along predictable foraging routes (Brockmann & Barnard, 1979; Iyengar, 2008). Studies of laughing gulls, *Larus atricilla* (Shealer, Floyd, & Burger, 1997), kelp gulls, *Larus dominicanus* (Steele & Hockey, 1995), black-headed gulls, *Larus ridibundus* (Ratcliffe et al., 1997), Arctic terns, *Sterna paradisaea* (Hopkins & Wiley, 1972), and common terns, *Sterna hirundo* (Hopkins & Wiley, 1972), show that some species optimize kleptoparasitic efficiency by preferentially attacking more profitable hosts. For example, black-headed gulls selectively attack Arctic terns, sandwich terns, *Sterna sandvicensis*, and common terns that are carrying larger and more numerous prey. The preference for larger prey may also increase the likelihood of obtaining the host's prey, as was observed during the kleptoparasitic attacks of Arctic and common terns on other Arctic and common terns (Hopkins & Wiley, 1972).

A model example of kleptoparasitism involving Laridae is the relationship between the herring gull, *Larus argentatus*, and Atlantic puffin, *Fratercula arctica*. Puffins nest in burrows in densely packed colonies on the slopes of oceanic islands, where herring gulls hold breeding territories (Finney, Wanless, Harris, & Monaghan, 2001; Pierotti, 1982). During the chick-rearing period, puffins follow predictable foraging patterns by often carrying large and conspicuous prey (e.g. adult capelin, *Mallotus villosus*, and adult sand lance, *Ammodytes* spp.) to their burrows to feed their chicks (Brockmann & Barnard, 1979; see Supplementary Video S1). Puffins also carry less conspicuous prey items to their burrows, including larval capelin, larval sand lance, cottids and blenniids (Baillie & Jones, 2003). Puffins are most susceptible to kleptoparasitism by gulls as they approach and land on the slope, especially during and after landing but before they enter the safety of their nesting burrow (Bond, 2016; Harris & Wanless, 2011; Supplementary Video S2). Research on the herring gull–puffin system has focused largely on the puffin's behavioural choices and potential consequences of being kleptoparasitized, with very few studies focusing on the factors associated with the herring gull's host choice and probability of success.

We tested the general hypothesis derived from foraging theory that herring gulls should optimize the efficiency of their kleptoparasitic attacks by targeting more profitable individuals. We tested this hypothesis by observing focal gulls as they interacted with Atlantic puffins during the concurrent chick-provisioning periods of both species. We predicted that gulls would preferentially attack puffins (1) carrying large prey versus small prey or no prey, (2) landing closer to versus farther from the gull and (3) landing in front of versus behind the gull. We predicted that gulls would be more successful during a kleptoparasitic attack when a puffin landed closer to the gull and in front of the gull, since both of these factors reduce the time available for the puffin to escape. We also predicted that gulls would be more successful when they physically grasped the puffin (Supplementary Video S2), as opposed to when they simply lunged towards it (Supplementary Video S3), since the gull's larger body size should afford greater control of the interaction.

METHODS

Field Methods

We conducted this study on Gull Island (47°15'32"N, 52°46'36"W), which is part of the Witless Bay Ecological Reserve, 35 km south of St John's, NL, Canada. The 1.6 × 0.8 km island is a breeding site for many seabirds, including Atlantic puffins (ca. 118 401 pairs when last surveyed in 2012; S. I. Wilhelm, Environment and Climate Change Canada - Canadian Wildlife Service, personal communication) and herring gulls (ca. 2698 pairs; Cotter et al., 2012). We selected nine sampling areas (range 7–28 m in width

and 10–30 m in slope length) on active puffin breeding slopes where herring gulls were also present, across the western and southern slopes of Gull Island in late June 2018. We avoided areas where other cliff-breeding species were present, where the slope ended in a cliff that dropped into the ocean, or where the vegetation was degraded, leaving the soil prone to erosion or collapse. The size of each sampling area was made as large as possible based on the surrounding topography, while still accommodating focal observations (see below).

Prior to conducting focal observations at each sampling area, we marked gulls by applying a dye paste (comprising 150 g of petroleum jelly, 10 ml of 70% isopropyl alcohol and 9 g of Procion MXDYE dye powder; Rupert, Gibbon & Spider, Inc. Healdsburg, CA, U.S.A.) on popular gull loafing sites following the methods outlined in Donehower and Bird (2005). We used a combination of red (040 Fuchsia), blue (068 Turquoise), yellow (004 Lemon Yellow) and black (150 Jet Black) dye powder. Gulls were passively and uniquely marked when their feathers contacted the dye directly or when they transferred the dye from their feet or bill to their feathers while preening. The dye remained visible for 1–2 weeks. We also established a grid of marking flags at approximately 4 m intervals at each sampling area, measuring the exact distance between each flag to provide a calibration scale for subsequent observations and measurements.

We conducted focal animal samples (Altmann, 1973) on individual herring gulls ($N = 73$) between 11 July and 12 August 2018, when puffins were provisioning their chicks. Schools of capelin were first confirmed in the surrounding Witless Bay 1 day before sampling began (i.e. 10 July 2018; www.eCapelin.ca; K. Busniuk, personal observations); more extensive data from an adjacent bay (Bellevue Beach) that historically had similar dates to Witless Bay further indicate that capelin spawning started on 7 July, peaked on 4 August and concluded on 8 August 2018 (H. Murphy, Fisheries and Oceans Canada, personal communication; DFO, 2019). Capelin were therefore likely present in Witless Bay during most of our focal samples. Sampling occurred between 0500 and 2100 hours, when visibility was at least 40 m and when there was little or no precipitation. The sampling window was restricted to 0500 to 2100 hours to ensure sufficient light for videorecording; this window should capture the majority of puffin provisioning attempts and kleptoparasitic attacks, as puffins are generally only active between dawn and dusk (K. Busniuk, personal observations; Harris & Wanless, 2011).

We chose focal gulls based on which gulls were passively dyed and which gulls were present at the sampling area during the sampling period. We used a given sampling area multiple times over multiple days until we had sampled all gulls that were opportunistically dyed at that area. We chose the order of the sampling areas in coordination with other research being conducted on the island and in consideration of slope stability, which was compromised at some locations due to the excess of rain at the beginning of the season. Occasionally, we also observed unmarked gulls in one of our sampling areas. If multiple unmarked gulls were sampled, we distinguished among them by ensuring that they were both visible throughout their focal sessions, or that they were separated from each other by at least 30 m. A buffer of 30 m was chosen because it exceeds the sum of an average gull's territory diameter (average diameter 1.5–7.6 m; Hunt & Hunt, 1976) and the error of the hand-held GPS (approximately 3 m; Garmin GPSMAP 78s, Garmin International, Inc., Olathe, KS, U.S.A.) that was used to mark gull locations.

We recorded each focal session with a high-definition video camera (Canon VIXIA HFR800, resolution 1920 × 1080 pixels, 60 frames/s progressive scan, MPEG-4 AVC/H.264; Mississauga, ON, Canada) positioned on a tripod inside a portable blind that we set

up below the study area at least 1 h before conducting the first focal sample at that area. Typically, the blind was left erected for multiple days, but sometimes environmental conditions forced us to collapse the blind between observations. We maintained an average distance (\pm SD) of 24.0 ± 7.8 m between the focal gull and the blind. We entered the blind at least 10 min before each observation period to reduce the risk that human disturbance would influence the birds. The gulls and puffins did not appear to be disturbed by our presence and always returned to the slope within 5 min of us entering the blind. We centred the focal gull within the camera's field of view and zoomed the camera to include an approximately 6 m radius around the focal gull, which captured the 4 m focal area around the gull (see Video Analysis below), the final stages of any puffin's approach to the gull's territory and the majority of gull attacks, which usually occur on the burrowing slope and rarely in the air (Finney et al., 2001; Hudson, 1985; Pierotti, 1983). The camera was panned to keep the gull in the centre of the field of view for the duration of the sample. Gulls were observed for 30 min or until the gull flew away and did not return. Trials that were shorter than 10 min were excluded ($N = 3$).

Although the video camera captured the overall interactions, it did not always have sufficient resolution or perspective to capture fine details, such as the presence and type of prey in a puffin's bill, or whether the gull successfully stole the prey. Therefore, we supplemented the video footage by observing interactions directly or through binoculars and by dictating observations onto the video recording's soundtrack using an external microphone (RadioShack 33–3013; RadioShack, Fort Worth, TX, U.S.A.).

For each puffin that entered the 4 m radius around the gull, we dictated the landing choice as completed (the puffin made contact with the slope and stopped flapping its wings) or aborted (the puffin did not contact the slope and continued flapping its wings, usually with either a sharp turn or with tail feathers splayed in a breaking configuration as it approached the slope), bill load as empty (no prey items protruding from the puffin's bill), full (prey items protruding from the puffin's bill) or unknown (the puffin's bill was not able to be observed either due to the speed of the approach or the orientation of the puffin) and prey size as small or large if items were present in the bill. Prey size was categorized based on the length of the prey item relative to the puffin's bill, where small prey were less than or equal to the depth of the bill and large prey were greater than the depth of the bill. We noted whether the puffin was attacked by the focal gull or by a neighbouring nonfocal gull and categorized the focal gull's host choice as either attack or no attack. Nonfocal gulls were defined as any gull other than the focal gull within the 4 m observation radius; this was most often the partner of the focal gull, but note that territory boundaries can be fluid and other gulls occasionally intruded upon the focal area during a focal session. An attack was defined as a rapid movement towards the puffin by either flying, running along the ground or lunging its neck towards the puffin (Supplementary Videos S2 and S3). We also noted the outcome of the kleptoparasitic attack as unsuccessful if the puffin retained all of its prey and as successful if the gull obtained some or all of the puffin's prey.

Video Analysis

We used the event recording software BORIS (v.6.2.3; Behavioral Observation Research Interactive Software, Torino, Italy; (Friard & Gamba, 2016)) to review and transcribe the video recordings. We used the calibration flags on the slope and a digital circle (Pixel-Stick, v.2.12.0, Plum Amazing Essential Software, Kailua-Kona, HI, U.S.A.) superimposed over the video to define the observation area (4 m radius) around the focal gull. For each puffin entering the focal sampling area, we recorded its landing choice, bill load, prey size,

and whether or not it was attacked using a combination of both video and audio recordings. While reviewing the video, we reanalysed any approaching puffins with unknown bill contents to categorize them into either small, large, unknown conspicuous or unknown. The category 'unknown conspicuous' was used for puffins that had visible prey, but for which the video lacked the resolution to categorize the contents into the small or large category. The category 'unknown' included puffins where a profile view of the bill was never observed or where the interaction occurred too quickly, resulting in a blurry video frame. In addition, we reanalysed all attacks made by focal and nonfocal gulls, noting whether or not the gull made physical contact with the puffin.

Whenever a puffin with prey landed within the focal area, we noted the orientation of the focal gull and the orientation of any nonfocal gull that attacked the puffin (facing the puffin if the longitudinal axis of the gull's body was pointed within 60° of the landed puffin; facing away from the puffin otherwise), the distance between the puffin and the focal gull and the distance between the puffin and any nonfocal gull that attacked the puffin. When measuring distance, we measured separately the horizontal and vertical distances between the centre of the puffin's head and the centre of the gull's head using a digital ruler (Ondesoft Screen Rulers v.1.13.1). To correct for slope, we calibrated the horizontal and vertical measurements separately using the horizontal and vertical calibration flags set out on the slope. We applied the Pythagorean theorem to the calibrated horizontal and vertical offsets to calculate the final distance between the gull and puffin.

After reviewing the videos, we excluded 10 of the remaining 70 focal samples from subsequent analyses due to camera perspective issues that may have resulted in inaccurate distance measurements (i.e. the calibration flags were difficult to see, or the camera was not in approximate perpendicular alignment with the slope). In total, we retained for analysis 60 focal sampling sessions (average length \pm SD: 24.4 ± 7.1 min), which corresponded to 24.4 h of observation. The data set included 1714 approaches by puffins to the focal area, including 1042 puffins with no visible prey, 201 with small prey, 277 with large prey, 77 with unknown conspicuous prey and 117 where the presence of prey could not be determined. Of these, 1415 puffins completed their landings near 60 focal gulls.

Statistical Analysis

Data were analysed in R (v.3.5.3; R Core Team, 2019) using Bayesian generalized linear mixed models (BGLMMs) implemented in the 'blme' package (v.1.0.4; Chung, Rabe-Hesketh, Dorie, Gelman, & Liu, 2013). The dependent variable was either focal gull host choice (i.e. whether or not an approaching puffin was attacked) or focal gull success (i.e. whether or not an attacking gull obtained some or all of the puffin's prey) and was always fitted using a binomial distribution and logit link. All models added a weak prior (multivariate normal distribution with standard deviation = 3) to the fixed-effect parameters and included gull identity as a random effect to account for possible dependencies among multiple data points derived from the same gull. Models did not include interactions among fixed factors because the models were derived from hypotheses that considered only main effects. Models with more than two predictor variables were checked for multicollinearity by calculating variance inflation factors (VIF) following the methods outlined in Zurr, Hilbe, and Ieno (2015); a value of 1 indicates no multicollinearity and values of 5 or greater indicate that the variables are influenced by multicollinearity. All VIFs were less than 1.1, and therefore, all variables were retained in each model. Results were considered statistically significant when $P \leq 0.05$, and to constitute a statistical trend when $0.05 < P \leq 0.1$.

Host Choice

We analysed focal gull host choice using three BGLMMs. All tests excluded interactions involving puffins with unknown bill contents, interactions where more than one gull attacked the puffin and attacks where a nonfocal gull attacked a puffin ($N = 141$). Nonfocal gulls were excluded because we did not systematically collect data from them during events where a puffin approached but was not attacked.

Our first model tested whether herring gulls were more likely to attack approaching puffins that had full versus empty bill loads ($N = 1597$ puffins and 60 gulls). Host choice (attack versus no attack) was included as the response variable and puffin bill load (full versus empty) was included as the explanatory variable. Puffins with empty bill loads and those categorized as 'unknown conspicuous' were then excluded from subsequent models, which included variables that described prey size. Our second model tested whether gulls were more likely to attack puffins that completed versus aborted their landing and that had large versus small prey ($N = 478$ puffins and 58 gulls). This model included host choice as the response variable and puffin landing choice (completed landing versus aborted landing) and prey size (large versus small) as explanatory variables. Our third analysis focused on the subset of puffins that completed their landings ($N = 202$ puffins and 48 gulls). This model tested whether gulls were more likely to attack puffins that landed in front of the gull, that landed closer to versus farther from the gull and that carried large versus small prey. Host choice was included as the response variable and prey size, distance between the landed puffin and the focal gull and gull orientation (towards versus away from the puffin) as the explanatory variables.

Gull Success

We analysed gull success using two BGLMMs. All tests excluded events where puffins approached with unknown bill contents, or where they were attacked by more than one gull ($N = 9$ events). Due to the rarity of kleptoparasitism, we included attacks by marked gulls (52 attacks attributed to 23 known individuals) and unmarked gulls. We assumed that all attacks by unmarked gulls within a given sampling area were committed by the same individual gull, which should provide a conservative estimate of the true number of gulls involved (22 attacks attributed to 6 gulls).

Our first model tested whether or not there was a relationship between the response variable, gull success (gull obtained some or all of the prey versus gull obtained no prey), and the explanatory variable, puffin landing choice (landed versus aborted; $N = 74$ attacks). Our second model focused on the subset of interactions in which the puffin completed its landing within a focal area ($N = 51$ attacks). We tested whether gulls were more likely to be successful when they made physical contact with the puffin, when the puffin landed in front of them and when the puffin landed closer to versus farther from them. This model included gull success as the response variable and attack type (physical versus no physical contact), distance between the landed puffin and the focal gull and gull orientation as explanatory variables.

Ethics Statement

We minimized disturbance to breeding birds by conducting all observations from a blind, by travelling to and from the blind along established pathways to reduce the risk of stepping on nests or burrows and by remaining inside a cabin when on the island but not conducting field research. The study required us to mark gulls so that we could identify them in field. Rather than capture and

colour-band gulls, we placed a dye paste at loafing sites so that the gulls would contact the paste and colour their own breast, belly and leg feathers in unique patterns. As in [Donehower and Bird \(2005\)](#), we detected no adverse effects of the dye on any aspect of gull behaviour. The dye faded from feathers within 1–2 weeks, and we removed the paste from loafing sites immediately after the gulls were dyed. Our research complied with the ASAB/ABS Guidelines for the use of animals in research and was approved by the Canadian Wildlife Service (Permit Number: SC2758), the Parks and Natural Areas Division of Newfoundland and Labrador's Department of Fisheries and Land Resources and the Institutional Animal Care Committee at Memorial University of Newfoundland (Permit Number: 17-03-DW).

RESULTS

We observed one or more kleptoparasitic attacks by approximately one-third of the focal gulls that had at least one opportunity for kleptoparasitism during their focal sample (20/59). Focal gulls had 555 opportunities for kleptoparasitism (i.e. provisioning puffins approaching the gull's focal area) and attacked 7.7% (43/555) of the time (10.4% of opportunities where a puffin completed a landing and 3.7% of opportunities where a puffin aborted a landing).

Host Choice

All kleptoparasitic attacks were directed at approaching puffins with conspicuous prey in their bill ([Table 1](#), Model 1; [Fig. 1](#)). Of the puffins that approached the focal area with either small or large prey items in their bill ([Table 1](#), Model 2), herring gulls were significantly more likely to attack those that carried large prey, as compared to small prey, and those that completed their landing, as compared to those that aborted. Of the puffins that landed within the focal area while carrying either small or large prey items ([Table 1](#), Model 3), herring gulls were significantly more likely to attack those that landed closer to them and those that landed in front of them. Gulls also tended to attack when landed puffins carried large prey items, as compared to small prey items, although this relationship was not statistically significant.

Gull Success

Focal and nonfocal gulls attacked 74 approaching puffins and successfully obtained some or all of the food from 15 of them. Gulls always failed when attacking a puffin that aborted its landing, but succeeded more than one-quarter of the time when attacking puffins that landed ([Fig. 2](#)), however, this relationship was not statistically significant ([Table 2](#), Model 4). Focal and nonfocal gulls attacked 51 puffins that landed within a focal area with food in their bill. When attacking puffins that landed within a focal area, herring gulls tended to be more likely to succeed when they made physical contact with the puffin ([Table 2](#), Model 5). Herring gull success was not related to the gull's distance or orientation to the landed puffin ([Table 2](#), Model 5).

DISCUSSION

Gulls were more likely to attack puffins that landed in front of them, that landed closer to them and that were carrying large conspicuous prey. Attacking gulls were never successful in stealing prey from a puffin that aborted its landing. However, gulls were successful in stealing some or all of a landed puffin's prey one-quarter of the time, which is similar to success rates reported in other studies (27%, [Corkhill, 1973](#); 32%, [Nettleship, 1972](#)). Gulls tended to be more

Table 1

Results of Bayesian generalized linear mixed models (binary response, logit link) predicting gull host choice (attack or no attack)

Model	Factor	Level	Estimate \pm SE	Z	P	Odds ratio (95% CI)
1 ^a	Bill load (empty)	Full	4.19 \pm 0.85	4.96	<0.001	66.0 (12.6–345.9)
2 ^b	Landing choice (aborted landing)	Completed landing	1.62 \pm 0.48	3.38	0.001	5.1 (2.0–13.0)
	Prey size (small)	Large	1.47 \pm 0.45	3.23	0.001	4.3 (1.8–10.6)
3 ^c	Distance to focal gull		-1.17 \pm 0.30	-3.95	<0.001	0.3 (0.2–0.5)
	Gull orientation (away)	Towards	1.85 \pm 0.62	2.97	0.003	6.2 (1.8–20.6)
	Prey size (small)	Large	1.26 \pm 0.66	1.91	0.056	3.5 (1.0–12.9)

In all models, focal gull identity was included as a random effect; puffins with unknown bill contents and those that were attacked by more than one gull were excluded. Reference categories for categorical predictor variables are included in parentheses below each variable.

^a Random effect of gull identity: variance = 1.40, SD = 1.18; N = 60 focal gulls and 1597 approaching puffins; excluded puffins approaching with unknown bill contents.

^b Random effect of gull identity: variance = 2.03, SD = 1.43; N = 58 focal gulls and 478 approaching puffins; excluded puffins approaching with bill loads other than small or large prey.

^c Random effect of gull identity: variance = 1.11, SD = 1.06; N = 48 focal gulls and 202 landed puffins; excluded puffins that did not land within 4 m of the focal gull and those with bill loads other than small or large prey.

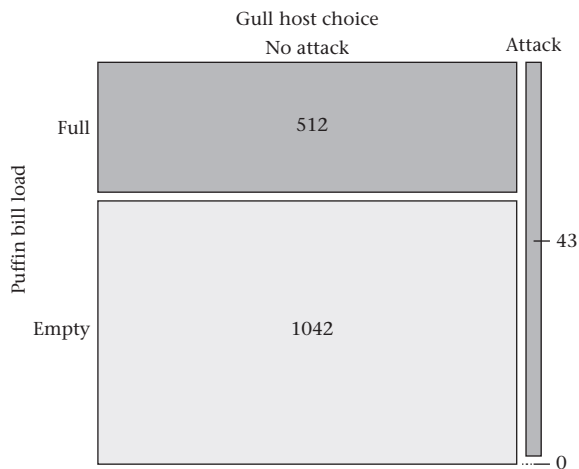


Figure 1. This mosaic plot shows the relationship between focal gull host choice (response variable) and the approaching puffin's bill load. Gulls only attacked puffins with conspicuous prey in their bill. Numbers indicate the count of events in each category.

successful at stealing a puffin's food when they made physical contact with the puffin, but not when the puffin landed closer to them or when they were oriented towards the puffin.

Gulls adjusted their behaviour in a manner consistent with them optimizing their foraging efficiency. Specifically, gulls preferentially attacked puffins with larger prey items, although it is unclear whether gulls targeted individual puffins based on the profitability or the conspicuousness of the puffin's prey, since larger prey are both more profitable (Wanless, Harris, Redman, & Speakman, 2005) and more conspicuous. Regardless, by targeting these individuals, the kleptoparasite increased the value of their potential reward. Host choice based on prey size has been documented in other studies (García, Favero, & Vassallo, 2010; Spencer, Russell, Dickens, & Dickens, 2017; Steele & Hockey, 1995), but most associate larger prey with longer handling times by the host, and, therefore, it is usually unclear whether the kleptoparasite is targeting hosts with larger prey or those that remain vulnerable to kleptoparasitism for longer. In puffins, chick provisioning (i.e. food handling) occurs inside the burrow and beyond the gull's reach, so the puffin's handling time probably does not influence the herring gull's choice. Instead, the gull is probably cueing into the size of the prey. Alternatively, it is possible that puffins carrying larger prey loads are encumbered and have a compromised reaction time, leaving them more vulnerable to attack by a kleptoparasite. Note, however, that these explanations are not mutually exclusive, as

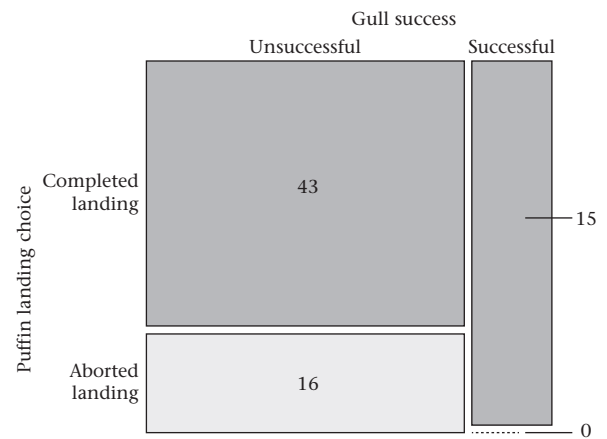


Figure 2. This mosaic plot illustrates the relationship between gull success (response variable, where success is defined as the gull obtaining some or all of the puffin's prey) and puffin landing choice. Gulls were never successful in obtaining prey from a puffin that aborted a landing attempt. Numbers indicate the count of events in each category.

gulls could target puffins carrying more profitable prey and those with slower reaction times.

In addition to targeting puffins with large bill loads, gulls preferentially attacked puffins that completed their landing, which further suggests that gulls are optimizing their foraging behaviour. Due to the puffin's adaptation to pursuit diving, their wings are shorter while maintaining the same aspect ratio (Pennycuik, 1987a). This adaptation reduces the puffin's manoeuvrability during landing and take-off, hampering its ability to glide at the low speeds necessary to land (Pennycuik, 1987b). Furthermore, due to the size and shape of the puffin's wings, once a puffin lands it is difficult for it to launch back into flight, which limits its options for escaping a gull (Nettleship, 1972). The herring gull is also presumably at a disadvantage if they attack a flying puffin because gulls first must launch themselves into the air, and puffins can sustain faster flying speeds (58–63 km/h; Harris & Wanless, 2011; Pennycuik, 1997) than herring gulls (37–54 km/h; Tucker & Schmidt-Koenig, 1971). Thus, herring gulls should be more successful when attacking puffins on the ground versus in the air. This study supports this supposition, by both a statistical trend and the observation that gulls never succeeded when attacking a puffin that aborted its landing.

Not all aspects of gull behaviour increased their likelihood of success. For example, in this study gulls were more likely to attack puffins that were closer to them, but this was not associated with increased success of stealing food. When puffins landed in closer

Table 2

Results of generalized linear models predicting gull success (gull obtained some or all of puffin's prey) during kleptoparasitic interactions

Model	Factor	Level	Estimate ± SE	Z	P	Odds ratio (95% CI)
4 ^a	Landing choice (aborted landing)	Completed landing	2.14±1.16	1.84	0.065	8.5 (0.9–83.4)
5 ^b	Distance to gull		-0.09±0.40	-0.23	0.820	0.9 (0.4–2.0)
	Gull orientation (away)	Towards	-0.90±0.84	-1.07	0.283	0.4 (0.1–2.1)
	Attack type (no physical contact)	Physical contact	1.64±0.85	1.92	0.054	5.1 (1.0–27.3)

Excludes puffins with unknown bill contents and puffins that did not land in a focal area, were not attacked or were attacked by multiple gulls. Reference categories for categorical predictor variables are included in parentheses below each variable.

^a Random effect of gull identity: minimum of 24 individual gulls were represented, variance = 0.49, SD = 0.70; N = 74 attacks.

^b Random effect of gull identity: minimum of 24 individual gulls were represented, variance = 0.80, SD = 0.89; N = 51 attacks.

proximity to the gull, the gull typically attacked by running along the slope instead of taking flight; when puffins landed farther from the gull, the gull typically jumped and flew towards the puffin (K. Busniuk, personal observation). Hudson (1985) described a similar pattern, where gulls would run towards and chase (termed 'run-chase') puffins that were close (an average of 2.9 m away), but fly and jump (termed 'fly-jump') towards puffins that were farther away (an average of 4.6 m away). Hudson (1985) noted that the success rates between the two strategies were similar, 17.8% and 16.3%, respectively, but that the fly-jump strategy was more energy intensive due to taking flight. Attacking closer puffins may, therefore, optimize a gull's foraging efficiency by using less time and energy. Additionally, adult gulls frequently kill, although rarely ingest, neighbouring chicks (Pierotti & Murphy, 1987). Preferentially attacking puffins that are closer to the gull and within the gull's core territory may therefore also allow the gull to protect its chick from neighbouring gulls (Hunt & Hunt, 1976).

During a kleptoparasitic attack, gulls tended to be more successful when they made physical contact with the puffin, obtaining the puffin's prey in 46.2% of attacks with physical contact, as compared to only 15.8% of attacks without physical contact. It is unclear, however, whether gulls were choosing between two distinct tactics, or whether an attack without contact is simply an incomplete attack that is nevertheless sometimes successful because the puffin drops its food. We often observed that when a gull did not make physical contact with the puffin, the puffin either aborted its landing, launched into flight or escaped into its burrow. The gull may avoid an aerial pursuit because it is unlikely to succeed due to differences in flying speed (Harris & Wanless, 2011; Pennycuik, 1997; Tucker & Schmidt-Koenig, 1971) or because the caloric benefit of the food item does not exceed the energetic demand of flight.

Approximately one-third of the focal gulls that had an opportunity to kleptoparasitize a provisioning puffin during their 30 min focal session attempted to do so, and those attempts were successful 7.7% of the time. Prey stolen from puffins is therefore an important food source to herring gulls rearing chicks on Gull Island. Although capelin kleptoparasitized from puffins tend to be smaller than those procured directly by independently foraging gulls (Pierotti, 1983), this prey provides an additional source of food for gulls that are confined to their territories and otherwise unable to procure food for themselves and their chicks. Indeed, when gulls have chicks, one or both parents remain on their territory for 80–93% of the day (Bukacińska, Bukaciński, & Spaans, 1996), which limits their ability to forage independently. Additionally, the frequency of kleptoparasitism may fluctuate with the availability of capelin. For example, kleptoparasitism may decline during capelin spawning, when gulls can capture the fish directly in shallow waters and on beaches (Penton, Davoren, Montevecchi, & Andrews, 2012). In contrast, kleptoparasitism may increase when capelin are less available or are in deeper water (i.e. deeper than the gull's body length), where puffins, but not gulls, can access

them (Brown & Nettleship, 1984). In our study, capelin were present and spawning in Witless Bay during most of our focal observations (www.eCapelin.ca; K. Busniuk, personal observation; H. Murphy, Fisheries and Oceans Canada, personal communication; DFO, 2019). Future research should monitor individual herring gulls for longer periods and throughout the breeding season to determine the prevalence of kleptoparasitic gulls within the population, seasonal variation in individual kleptoparasitic behaviour and the proportion of a gull's diet comprising stolen prey. Furthermore, future research should test whether an individual's propensity to kleptoparasitize is related to their age or sex, as it is in other species. In kelp gulls, for example, juveniles are more likely than adults to kleptoparasitize (Steele & Hockey, 1995), and, in roseate terns, *Sterna dougallii* (Shealer & Spindel, 2002), and magnificent frigatebirds, *Fregata magnificens* (Osorno, Torres, & Garcia, 1992), females are more likely than males to kleptoparasitize.

Despite the early interest in the effects of herring gull kleptoparasitism on the breeding success and behaviour of the puffin, little research has investigated this interaction from the herring gull's perspective. This study provides new insights into the split-second foraging decisions made by the herring gull and their consequences for foraging success during the chick-rearing period. We found that herring gulls do not attack puffins at random, but rather optimize their energy intake by targeting more profitable hosts.

Conflict of Interest

None.

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Supplementary Material

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