

THE PILFERING OF PUFFINS: BEHAVIOURAL TACTICS OF HERRING GULLS  
AND ATLANTIC PUFFINS DURING KLEPTOPARASITIC COMPETITION

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A thesis submitted to the School of Graduate Studies in partial fulfilment of the  
requirements for the degree of

Master of Science, Cognitive and Behavioural Ecology, Faculty of Science  
Memorial University of Newfoundland

December 2019

St. John's, Newfoundland and Labrador

## Abstract

Kleptoparasitism is a foraging strategy whereby an individual steals a procured food item from another individual. Individuals can optimize their kleptoparasitic foraging strategy by modifying their behaviour to expend less energy than they would by foraging independently or by attacking more profitable hosts. Individuals vulnerable to becoming a host to a kleptoparasite can modify their behaviour to reduce the risk of losing prey to a kleptoparasite by using tactics such as handling food in areas inaccessible to the kleptoparasite or landing in groups. Observations of individual herring gulls (*Larus argentatus*) and approaches to the burrow slope by Atlantic puffins (*Fratercula arctica*) were conducted in summer 2018 on Gull Island, Newfoundland and Labrador. The findings of this study suggest that herring gulls optimize their kleptoparasitic foraging strategy by targeting more profitable hosts, and that puffins at risk of kleptoparasitism effectively mitigate their risk by engaging in evasive behaviour.

Keywords: Atlantic puffin, herring gull, kleptoparasitism, foraging, seabird, competition, behaviour

## Acknowledgments

I am grateful for the guidance, experience, and support provided by my supervisory committee (Drs David Wilson, Anne Storey, and Gregory Robertson) throughout my time as a MSc student. This thesis greatly benefits from the comments and suggestions provided by my committee.

Without the help of my field assistants (Scott Taylor, Victoria Mackey, Emma Lachance Linklater), I would not have been able to visit and remain at my field site for an extended period of time. An especially big thanks is owed to Emma, who stayed on Gull Island with me in 2018 for the entire research period, including an 18-day stint—braving a post-tropical depression, no showers, and angry territorial gulls. Additional thanks to the students from Queens University who periodically visited Gull Island in both 2017 and 2018 and provided endless laughs and card games through the field season. This thesis also benefits from contributions of David Fifield, Michelle Fitzsimmons, and Sabina Wilhelm, who helped with field work techniques, general advice, and company on Gull Island. Additionally, transportation provided by Environment and Climate Change Canada greatly reduced the cost of my field work and allowed for fresh food to be delivered to Gull Island, as well as for more frequent trips on and off that would not have been possible without their generous help.

I thank the members of David Wilson's Laboratory and the inhabitants of "The Zoo" for company and encouragement. I specifically thank Katrina, who started navigating Graduate school at the same point as me, for the frequent brainstorming

sessions, and company during video analysis and on our trip to the Animal Behaviour Conference in Chicago.

I thank the Natural Sciences and Engineering Research Council and the School of Graduate Studies for funding and scholarships received (Alexander Graham Bell CGS-MSc, Discovery Grant to D. Wilson, and the Commander Peter G. Chance Scholarship).

Finally, I thank those who provided necessary distractions through my time as a MSc Student. I am indebted to the Jellybean Row District (Girl Guides of Canada) and the 29th St. John's Guides for taking me in and allowing me to continue in the Sisterhood of Guiding while in Newfoundland. I thank my partner, Keegan Start (a fellow graduate student), for always being there to discuss new ideas and thoughts, as well as understanding when I needed to de-stress whether it be a trip for ice cream, a walk by the ocean to watch the seabirds, or a road trip across Newfoundland.

## Table of Contents

CHAPTER 1 A review of kleptoparasitism and the kleptoparasitic relationship between the herring gull and Atlantic puffin	1
1.1 Competition	1
1.2 Kleptoparasitism	1
1.2.1 Factors Affecting the Evolution of Kleptoparasitism in Birds	3
1.2.2 Studies of Kleptoparasitism	6
1.3 Study System	7
1.3.1 Study Site	9
1.3.2 Study Species: Atlantic Puffin – Herring Gull	9
1.4 Thesis Outline	12
1.5 Figures	14
1.6 Co-authorship Statement	15
1.7 Researcher Disturbance and Mitigation	16
1.8 References	17
CHAPTER 2 Behavioural tactics used by herring gulls during kleptoparasitic foraging	21
2.1 Abstract	21
2.2 Introduction	22
2.3 Methods	26
2.3.1 Field Methods	26
2.3.2 Video Analysis	30

2.3.3 Statistical Methods	31
2.3.3.1 Host Choice	32
2.3.3.2 Gull Success	33
2.4 Results	35
2.4.1 Host Choice	35
2.4.2 Gull Success	36
2.5 Discussion	37
2.6 Tables	41
2.7 Figures	43
2.8 References	49
CHAPTER 3 Behavioural responses of Atlantic puffins to the risk of kleptoparasitism by herring gulls	52
3.1 Abstract	52
3.2 Introduction	53
3.3. Methods	58
3.3.1 Field Methods	58
3.3.2 Behavioural Analysis	60
3.3.3 Statistical Analysis	63
3.4 Results	66
3.5 Discussion	68
3.6 Tables	72
3.7 Figures	73
3.8 References	76

CHAPTER 4 General discussion and conclusion	79
4.1 Introduction	79
4.2 Results Summary	80
4.3 Contributions to the Literature	82
4.4 Limitations	84
4.5 Future Work	85
4.6 General Conclusions	86
4.7 References	87
4.8 Supplementary Information	89

## List of Tables

Table 2.1	Results of generalised linear mixed models predicting gull host choice....	41
Table 2.2	Results of a generalised linear model predicting gull success during kleptoparasitic interactions.....	42
Table 3.1	Results of the pairwise comparisons of a generalised linear mixed model predicting puffin landing choice as a function of bill load.....	72



## List of Figures

Figure 1.1	A map of Canada showing the location of my study site at Gull Island, Newfoundland and Labrador.....	14
Figure 2.1	Photographic examples of a focal gull in its territory on a puffin breeding slope, a puffin that carried a large prey item moments before a focal gull made physical contact and stole its prey, and a puffin carrying a large prey item seemingly at risk of kleptoparasitism.....	43
Figure 2.2	A mosaic plot showing the relationship between focal gull host choice and the approaching puffin's bill load.....	44
Figure 2.3	Mosaic plots illustrating the relationship between focal gull host choice (response variable) and the puffin's A) prey size and B) landing choice.....	45
Figure 2.4	The relationship between focal gull host choice (response variable) and A) the distance between the landed puffin and the focal gull, B) the gull's body orientation relative to the landing puffin, and C) the puffin's prey size.....	46
Figure 2.5	A mosaic plot illustrating 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.....	47
Figure 2.6	The relationship between gull success (response variable, where success is defined as the gull obtaining some or all of the puffin's prey) and the attack type.....	48
Figure 3.1	Three puffins in flight showing A) empty bill with a yellow dashed line indicating the bill depth, B) small prey items, and C) a large prey item.....	73
Figure 3.2	A mosaic plot illustrating the relationship between the puffin's bill load (explanatory variable) and its landing choice.....	74
Figure 3.3	Box plots showing the distribution of the distance between the puffin and focal gull when landing with empty, large prey, and small prey bill loads.....	75

Figure 4.1	Diel variation of the mean rate of attack by focal gulls, the mean rate of provisioning puffins landing, and the mean proportion of provisioning puffins landing that are attacked.....	91
Figure 4.2	Seasonal variation of the mean rate of attack by focal gulls, the mean rate of provisioning puffins landing, and the mean proportion of provisioning puffins landing that are attacked.....	92

# **CHAPTER 1 A REVIEW OF KLEPTOPARASITISM AND THE KLEPTOPARASITIC RELATIONSHIP BETWEEN THE HERRING GULL AND ATLANTIC PUFFIN**

## **1.1 Competition**

Competition occurs when individuals vie for control of a shared resource, such as food. Competition can be described as exploitative or interference and can be either intraspecific (competitive interactions between two or more individuals of the same species) or interspecific (competitive interactions between two or more individuals of different species; Rothschild & Clay, 1952). Exploitative competition is when two or more individuals deplete a limited shared resource, but do not interact directly (Birch, 1957; Case & Gilpin, 1974; Park, 1957). For example, animals grazing in the same pasture deplete the vegetation available to both competitors. Interference competition occurs when two or more individuals engage in direct negative interactions, thereby interfering with the other's ability to obtain resources (Birch, 1957; Case & Gilpin, 1974; Park, 1957).

## **1.2 Kleptoparasitism**

Kleptoparasitism, also referred to as cleptoparasitism, piracy, pilfering, and food stealing (Brockmann & Barnard, 1979), is derived from the Greek word “kleptēs,” or thief, and “parasitos,” or “eating at another’s table”. It is considered a form of interference competition, where one individual or species engages in a direct interaction with another individual or species by stealing its procured food (Rothschild & Clay, 1952). While examples of individuals stealing food from food caches do occur, they are

generally not considered kleptoparasitism because there is no direct interaction between the parasite and the host. Iyengar (2008) amended the definition of kleptoparasitism by stating that the host must have expended energy to procure the food item and that the parasite must steal food that the host intends to eat or feed to its offspring; therefore, stealing food that is considered waste to the host is not considered kleptoparasitism. Kleptoparasitism relies on the concept that one individual benefits and one pays a cost; however, in studying natural systems, the kleptoparasite may also bear a cost, such as a loss of energy or injury during the attack (Case & Gilpin, 1974). It is therefore important to recognise the trade-offs made by the parasite when engaging in kleptoparasitism.

Kleptoparasitism is categorized as facultative or obligate. Facultative kleptoparasites have an alternative feeding mode, such as seabirds parasitizing their hosts during chick-rearing, but foraging independently for the remainder of the year (Brockmann & Barnard, 1979). Obligate refers to kleptoparasites that are completely dependent on their host for food, as they cannot forage independently. For example, lemon bees (*Lestrimelitta limao*) possess no structures for collecting pollen independently; therefore, their only way to procure food is to steal pollen and honey from other bee species (Wille, 1983).

Finally, kleptoparasites can be divided into specialists and opportunists. Specialist kleptoparasites are well-adapted to stealing food from their host (Furness, 1987). For example, great frigatebirds (*Fregata minor*) can discern which individual brown noddy (*Anous stolidus*) is carrying food in its crop (Gilardi, 1994). Opportunist kleptoparasites, such as gulls (*Larus* spp.), appear unable to determine whether their hosts have food in

their crop and, therefore, target hosts with conspicuous food, such as fish hanging out of the bill (Furness, 1987). It is important to note that, like many categories used to describe the natural world, the categories of kleptoparasitism are somewhat arbitrary and may exist in a continuum that varies among species, populations, and individuals.

### 1.2.1 Factors Affecting the Evolution of Kleptoparasitism in Birds

Brockmann and Barnard (1979) collated descriptions of facultative kleptoparasitism from the previous 40 years of ornithological literature. They outlined five conditions that are associated with an increased likelihood of a species being kleptoparasitic. First, species that live in intraspecific or interspecific groups may be more likely to develop kleptoparasitic tactics because unsuccessful foragers can use kleptoparasitic tactics to exploit successful foragers. Within interspecific groups, there may be a greater disparity in size and cognitive ability between individuals of different species (Morand-Ferron, Sol, & Lefebvre, 2007), leading to even greater opportunities for kleptoparasitism. This behaviour is exemplified by gadwalls (*Anas strepera*) pilfering macrophytes brought to the water surface by coots (*Fulica atra*; Amat & Soriguer, 1984). Second, predators pursuing prey that drop their food as a distraction are more likely to exploit the dropping behaviour and evolve a kleptoparasitic strategy. Predators targeting prey animals that drop their food during pursuit are more likely to be favoured by natural selection, since procuring food by parasitism requires less energy and involves less risk, as compared to predation (Grant, 1971). Third, individuals that scavenge leftover food are likely to evolve kleptoparasitism because scavenging involves many of the same behaviours as kleptoparasitism (Hatch, 1970). For example, Charadriiformes, particularly

gulls, are prone to scavenging dropped food, and, in many species, this behaviour has evolved into direct food thefts. Fourth, individuals that live with hosts that follow a predictable foraging pattern, such as transporting food back to the same location multiple times each day, or that possess visible food during transport or handling, increases the likelihood of the host being parasitized. Increases in prey size are associated with an increased risk of being kleptoparasitised, which is most likely due to the conspicuous nature of large prey and the increased handling time of the host to process larger prey (García, Favero, & Vassallo, 2010; Hopkins & Wiley, 1972; Spencer, Russell, Dickins, & Dickins, 2017; Steele & Hockey, 1995). Fifth, potential kleptoparasites living with species that control large quantities of high-quality food allows kleptoparasitism to become a reliable foraging strategy. Kleptoparasites may assess the size and quality of the food to determine if the payoff is high enough to risk potential injury associated with stealing from the host (Furness, 1987).

Morand-Ferron et al. (2007) used peer-reviewed scientific papers published between 1969 and 2002, in addition to the cases reported in Brockmann and Barnard's (1979) Appendix 1, to test the assertion by Brockmann and Barnard (1979) that kleptoparasitic behaviours are distributed non-randomly among avian assemblages. For example, Falconiformes and Charadriiformes compose 7% of the world's bird species, but disproportionately compose 60% of recorded kleptoparasites (Brockmann & Barnard, 1979). Using phylogenetic analyses, they determined that kleptoparasitic behaviours are distributed non-randomly among avian families, that kleptoparasitism has evolved

independently many times, and that the incidence of kleptoparasitism cannot be explained by phylogeny alone (Morand-Ferron et al., 2007).

Morand-Ferron et al. (2007) used a comparative approach to test five alternative hypotheses to explain the evolution of kleptoparasitism in avian families. First, the ‘brawn hypothesis’ states that a larger body mass of the kleptoparasite, as compared to the host, makes the host less likely to defend its catch. Larger body size also correlates with larger eyes and better visual acuity (Fernández-Juricic, Erichsen, & Kacelnik, 2004), possibly leading to more accurate kleptoparasitism attempts. Second, the ‘brain hypothesis’ suggests that kleptoparasites will have a larger brain in relation to their body size (residual brain size), as compared to the host. A larger brain may increase cognitive function, allowing for better decision making during attacks (Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005). The third hypothesis is that parasites consuming vertebrate prey may also have predatory traits, thereby pre-adapting the parasites for kleptoparasitism. The fourth hypothesis suggests that species that participate in multispecies foraging flocks are more likely to engage in kleptoparasitic interactions due to differential foraging success among species. The final hypothesis, first suggested by Paulson (1985), suggests that species living in open habitats have an increased probability of developing kleptoparasitic behaviours because hosts are more visible and easier to detect.

Using a phylogenetically controlled analysis, Morand-Ferron et al. (2007) found that families had a higher probability of evolving kleptoparasitism if they fed on vertebrate prey, lived in open habitats, and had larger residual brain size relative to their

host. These three hypotheses help explain the non-random distribution of kleptoparasitic behaviours within the class Aves (Morand-Ferron et al., 2007). They found no significant relationship with body size or participation in multi-species foraging flocks with the probability of a family evolving kleptoparasitism (Morand-Ferron et al., 2007).

### 1.2.2 Studies of Kleptoparasitism

Studies of kleptoparasitism often focus on optimal foraging theory, which predicts that animals will alter their behaviour to maximize their energy gain while minimizing their energy use and risk (Schoener, 1971). In some circumstances, engaging in kleptoparasitism can be more profitable than foraging independently, and individuals will often switch facultatively between kleptoparasitism and self-foraging as the costs and benefits shift.

Kleptoparasites can optimize their foraging strategy by selectively attacking more-profitable hosts. For example, hosts may be deemed more profitable by a kleptoparasite when they possess higher quality prey (García et al., 2010; Ratcliffe et al., 1997), do not aggressively defend their prey (Henaut, 2000), or have a reduced ability to handle prey efficiently (Ridley & Child, 2009). Several studies have also examined the host's evasion of kleptoparasitism by observing individuals engaging in different behavioural choices. For example, individuals may handle prey in areas inaccessible to the kleptoparasite (*i.e.*, underwater), selectively forage for small prey that require less handling (Steele & Hockey, 1995), engage in avoidance behaviours such as colony overflight (Blackburn, Hipfner, & Ydenberg, 2009) and delayed food transfer (Dies & Dies, 2005), or use a



swamping tactic which may function to overwhelm a kleptoparasite (Merkel, Nielsen, & Olsen, 1998; Rice, 1987).

### 1.3 Study System

Many gull species are prolific kleptoparasites and exhibit many characteristics associated with kleptoparasitism, such as living in open landscapes in dense colonies among many potential hosts carrying large conspicuous prey (Brockmann & Barnard, 1979; Hudson, 1985; Morand-Ferron et al., 2007). Studies have shown that some gulls can optimize their foraging strategy by attacking more profitable hosts (Ratcliffe et al., 1997; Shealer, Floyd, & Burger, 1997; Steele & Hockey, 1995).

A widely studied kleptoparasitic system is that of the herring gull (*Larus argentatus*) and Atlantic puffin (*Fratercula arctica*) in Europe and North America, where the gull intercepts the adult puffin's delivery of prey items to its chick within a burrow. Interest in this system began in the late 1960s when potentially damaging effects of kleptoparasitism were observed on puffin chicks. Nettleship (1972) first showed that 9.6% of all puffins returning with food were kleptoparasitised and that gulls were successful in 31.7% of all kleptoparasitism attempts. He suggested that kleptoparasitism is associated with reduced puffin chick survival and depressed breeding success (number of chicks estimated to have fledged plus those that survived to the last inspection). During the summer of 1969 in Newfoundland, Canada, puffin breeding success was 90.5% on Funk Island and Small Island, which had no gull interference (Nettleship, 1972), and only 37.1% on Great Island, which had gull interference (Nettleship, 1972). This study spurred research into the effect of kleptoparasitism on puffins; however, no subsequent study has

shown such severe consequences. Rice (1985) found no difference in puffin chick weight or fledging success among sites with differing gull pressures, despite finding evidence that puffins avoided gulls. Similarly, Finney et al. (2001) found no difference in puffin breeding success (% chicks fledged) between sites where gulls were experimentally removed ( $73 \pm 3\%$  puffin breeding success) and a control site where gulls were not removed ( $70 \pm 6\%$ ), despite statistically significant differences in kleptoparasitism risk (5% at the experimental site and 37% at the control site).

Owing to the seemingly urgent matter of low puffin breeding success, studies into the kleptoparasitic relationship have largely ignored the behavioural choices of the herring gull and possible tactics the gull may use to increase its success. A few studies have examined aspects of the puffin's behaviour in response to the risk of kleptoparasitism, including showing the potential of puffins to synchronize their landings while carrying prey (Merkel et al., 1998), to clump their landings in space when landing in areas of high gull density (Pierotti, 1983), and to rapidly enter their burrow during the chick rearing period (Rice, 1987). My study aims to examine the behavioural choices of herring gulls and Atlantic puffins as they engage in or avoid kleptoparasitism, respectively, as the majority of studies have focused only on one side of the kleptoparasitic relationship. Additionally, I aim to examine the consequences of the behavioural choices on the gull's success in obtaining prey and the puffin's success in retaining its prey. Through this thesis, I aim to bridge the information gap between the behaviour of the host and kleptoparasite by exploring how the behaviours are linked and how species respond to each other's behaviour and preferences.

### 1.3.1 Study Site

I conducted my study on Gull Island (47.3N 52.8W), a part of the Witless Bay Ecological Reserve, 35 km south of St. John's, NL, Canada (Figure 1.1). The 1.6 x 0.8 km island is a breeding site for many seabird species, including the Atlantic puffin (ca. 118,401 pairs when last surveyed in 2012; ECCC-CWS unpubl. data), herring gull (ca. 2,698 pairs; Cotter et al., 2012), common murre (*Uria aalge*; ca. 1,632 pairs; Robertson, Wilhelm, & Taylor, 2004), Leach's storm-petrel (*Hydrobates leucorhous*; ca. 179,743 pairs when last surveyed in 2012; ECCC-CWS unpubl. data) and black-legged kittiwake (*Rissa tridactyla*; ca. 5,351 pairs; Cotter et al., 2012). In general, the species breeding on the island are segregated according to breeding habitat; however, herring gulls nest in many habitats across the island, including among the puffin and storm-petrel burrows (Pierotti, 1982; Robertson, Fifield, Massaro, & Chardine, 2001).

### 1.3.2 Study Species: Atlantic Puffin – Herring Gull

The herring gull is a ubiquitous species with a range spanning North America (Pierotti, 1982). Gulls are mainly monogamous (Fitch, 1980) and, each year, the adults return to their breeding site in late-April, where they reconnect with their partner (Haycock & Threlfall, 1975). The pair builds their nest in a territory (1.8 to 46 m<sup>2</sup>) that they defend vigorously against other gulls (Hunt & Hunt, 1976). The female lays and shares incubation duties of one to four eggs (Haycock & Threlfall, 1975; Pierotti & Annett, 1991). After approximately 28 days, hatching begins and the chick-rearing period commences; during this period, both parents provision their offspring until they fledge 42 to 48 days later (Haycock & Threlfall, 1975).

The diet of herring gulls in Witless Bay tends to depend on nest location, with gulls nesting on rocky outcrops specializing on blue mussels, those in meadows specializing on adult Leach's storm-petrels, and those nesting amongst puffin burrows specializing on refuse (Pierotti & Annett, 1991). Historically, herring gulls in Witless Bay shifted their diet at the peak of hatching to consume capelin (*Mallotus villosus*; Haycock & Threlfall, 1975; Pierotti & Annett, 1991). However, compared to historical records, capelin abundance and timing of spawning has become more variable. Furthermore, common murrelets, which the gulls can exploit for eggs, have become more abundant (Bond, 2016). Therefore, the diet composition of herring gulls has shifted in recent years and become more variable and diverse. The herring gull can capture capelin directly when the capelin are near the surface or spawning on beaches, but the gull can also steal capelin from other species during periods where the capelin are otherwise inaccessible to gulls (Brown & Nettleship, 1984). The herring gull is a common facultative, kleptoparasite with many different hosts, including swans, loons, ducks, shorebirds, gulls and alcids (Harris & Wanless, 2011; Källander, 2006; Morand-Ferron et al., 2007). Studies examining gull (*Larus* spp.) kleptoparasitic behaviour have shown that some gulls adjust their behaviour to preferentially attack more profitable hosts (*i.e.*, those carrying larger prey loads; Ratcliffe et al., 1997; Shealer et al., 1997; Steele & Hockey, 1995).

The Atlantic puffin is a seabird found throughout the North Atlantic Ocean, from Europe to North America (Guilford et al., 2011; Harris & Wanless, 2011), and is a common host for the herring gull (Grant, 1971; Harris & Wanless, 2011; Rice, 1987). Puffins are monogamous – their estimated yearly divorce rate ranges from 3-13%, and

their estimated extra-pair paternity ranges from 0-7.6% (Anker-Nilssen, Kleven, Aarvak, & Lifjeld, 2008; Harris & Wanless, 2011). Each year, the adults return from the sea to their terrestrial breeding site in late-April and reconnect with their partner (Nettleship, 1972). They nest in burrows in the side of steep grass-covered slopes or between rock crevasses. In the burrow between mid-May and early June, the females lay a single egg that the pair incubates for 37-42 days (Guilford et al., 2011; Harris & Wanless, 2011; Nettleship, 1972).

Puffins display many characteristics that predispose them to be a host for a kleptoparasite (Brockmann & Barnard, 1979). For example, they nest in large, dense colonies, and commonly share the slope with nesting herring gulls (Harris & Wanless, 2011; Nettleship, 1972; Rice, 1987). Puffin chicks remain in their burrow until they fledge between the age of 38 and 44 days (Harris & Wanless, 2011). During this time, their parents provide the only source of nourishment (Harris & Wanless, 2011; Hudson, 1979), returning predictably to the same burrow multiple times per day, between late June and early September, with large quantities of conspicuous fish, including capelin, sandlance (*Ammodytes* spp.), cottids, and blenniids (Baillie & Jones, 2003), hanging visibly from their beaks (Nettleship, 1972; Rice, 1985, 1987). It is during this short provisioning period that they are potentially kleptoparasitised by gulls, which disrupts food delivery to the puffin chicks (Brockmann & Barnard, 1979; Harris & Wanless, 2011; Rice, 1987). This period ends between mid-August and the end of September when the chicks fledge and provisioning ceases (Nettleship, 1972).

#### 1.4 Thesis Outline

The main objectives of this study were to examine the kleptoparasitic relationship between the herring gull and Atlantic puffin and provide a balanced view of their kleptoparasitic behavioural interactions. The thesis comprises four chapters, and I intend to publish Chapters 2 and 3 as manuscripts.

This first chapter is the general introduction and provides the overarching theory and knowledge gaps that my studies addresses.

Chapter 2 investigates the kleptoparasitic interaction from the perspective of the herring gull. I examined extrinsic factors that contributed to the gull's host choice and success. Specifically, I examined the probability of a herring gull initiating a kleptoparasitic attack in relation to: (1) several aspects of the puffin's approach and landing (prey size, landing choice, and distance to the gull) and (2) the gull's orientation relative to the approaching puffin. Next, I examined the factors influencing the gull's kleptoparasitic success rate, including (1) several aspects of the puffin's approach and landing (landing choice and distance to gull), (2) the gull's orientation and (3) whether or not the gull physically contacted the puffin during the attack.

Chapter 3 investigates the behavioural tactics of the Atlantic puffin that allow it to avoid kleptoparasitism and retain its prey. Specifically, I examined the puffin's choice to land or abort its landing in relation to its bill load (presence or absence of prey and prey size). I examined the puffin's choice of landing location (distance to gull and location in relation to gull) based on its bill load (presence or absence of prey and prey size), as well

as examining the relationship between the puffin's chosen landing position and its risk of attack and subsequently losing prey to a herring gull.

Chapter 4 serves as a general discussion where I integrate the information gleaned in Chapters 2 and 3 with existing literature, and as a conclusion where I discuss future research directions. In addition, I included information about the diel and seasonal patterns in the rates of gull kleptoparasitism and puffin provisioning, as well as the proportion of puffins attacked, as supplementary information.

## 1.5 Figures

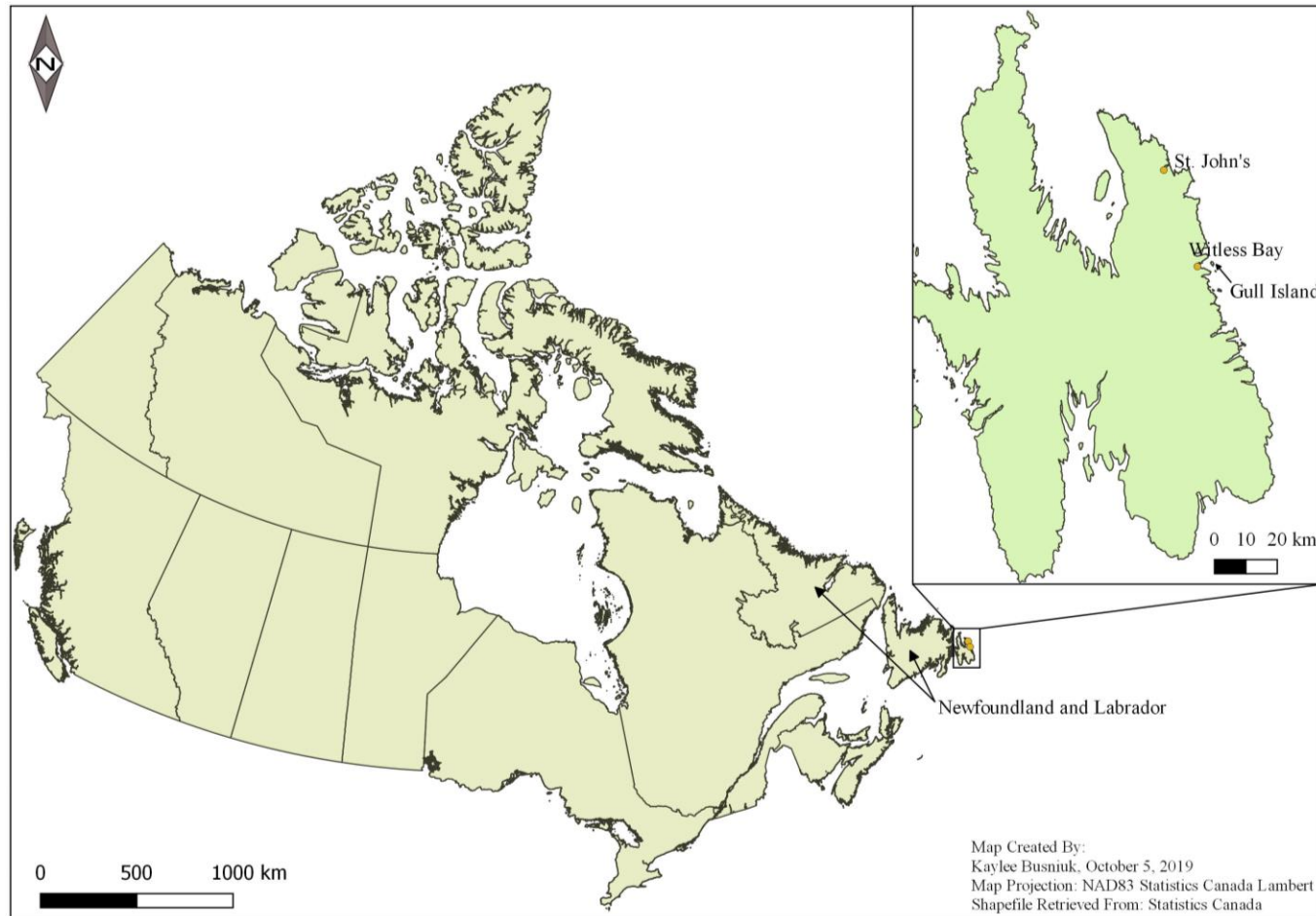


Figure 1.1 A map of Canada showing the location of my study site at Gull Island, Newfoundland and Labrador.



## 1.6 Co-authorship Statement

Manuscripts derived from Chapters 2 and 3 will include my supervisor, Dr. David Wilson, as a co-author. Under the supervision of David Wilson, and with input from my committee, Drs. Anne Storey and Gregory Robertson, I developed the research questions and design of the study used in this thesis. Data for this thesis were collected and analyzed by myself or under my direct supervision. With input from my supervisor and supervisory committee, I developed and conducted all statistical analyses. I wrote the chapters composing this thesis and made revisions based on the recommendations of David Wilson and my supervisory committee.

## 1.7 Researcher Disturbance and Mitigation

With any research project there will inevitably be some disturbance to the wildlife. It is our responsibility as researchers to mitigate the disturbance to an acceptable level. Care was taken to avoid disturbance to the birds, including avoiding work during peak provisioning periods and limiting the time spent on the breeding slope to allow for the parent puffins and gulls to return to their chicks, erecting the blind in a location not inhibiting the movement of gulls or puffins, and monitoring the birds for signs of stress while conducting work on the slope. We limited checks on the puffin's burrows, to on average, once every 1.5 days, and used a video scope to minimize contact with the puffins. Additionally, a pre-existing method for passively dyeing birds was used and tested first in a limited area to observe the effects on the gulls. To my knowledge, there did not appear to be any negative effects of the dye, and usually, only a small portion of the gull's feathers were dyed. Approval and permits for this project were sought and received from Animal Care Services of Memorial University of Newfoundland, the Government of Newfoundland and Labrador, and the Government of Canada.

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## CHAPTER 2 BEHAVIOURAL TACTICS USED BY HERRING GULLS DURING KLEPTOPARASITIC FORAGING

### 2.1 Abstract

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*) kleptoparasitise 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. To test predictors of herring gull host choice and the probability of success during kleptoparasitic attacks, I conducted 73 30-minute focal samples of individual herring gulls at a breeding colony in Newfoundland, Canada. I recorded each puffin that approached the focal gull, categorizing them according to prey type, whether or not they landed, and whether or not they were attacked. For those puffins that were attacked, I also noted whether the gull succeeded in obtaining the prey. Herring gulls did not attack puffins at random, but, rather, preferentially attacked puffins that carried larger prey, that completed their landing, that landed closer to the gull, and that landed in front of the gull. These findings suggest that herring gulls optimize their kleptoparasitic foraging strategy by targeting more profitable and vulnerable hosts.

## 2.2 Introduction

Optimal foraging theory predicts that animals will maximize their energy gain while minimizing their energy use and risk (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; Iyengar, 2008). In general, kleptoparasitism tends to evolve in species that feed opportunistically, that have high costs associated with self-foraging (e.g., because prey are scarce), and that 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).

In some kleptoparasitic species, individuals optimize their foraging strategy by facultatively switching between kleptoparasitism and self-foraging. 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. Other kleptoparasites optimize their foraging success by selectively attacking more-profitable hosts. For example, kleptoparasitic Arctic (*Sterna paradisaea*) and common terns (*Sterna hirundo*) preferentially attack other



Arctic and common terns carrying larger prey (usually herring, *Clupea harengus*), and are also more successful in obtaining the host's prey when the prey are large (Hopkins & Wiley, 1972). Similarly, in the kleptoparasitic spider, *Argyrodes globosus*, individuals optimize kleptoparasitism by preferentially attacking host species that do not aggressively defend their prey (Henaut, 2000).

Gulls are a classic example of kleptoparasitic foragers, exhibiting many of the life history characteristics associated with kleptoparasitism. Specifically, they often live in large multispecies colonies where potential hosts carry large and conspicuous prey along predictable foraging routes (Brockmann & Barnard, 1979; Iyengar, 2008). In the past, gull kleptoparasites were generally considered opportunistic, which implies that they do not discriminate among prospective hosts (Furness, 1987). However, studies of laughing gulls (*Larus atricilla*; Shealer et al., 1997), kelp gulls (*Larus dominicanus*; Steele & Hockey, 1995), and black-headed gulls (*Larus ridibundus*; Ratcliffe et al., 1997) have shown that some gulls 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 items. They also limit the number of successive attacks on an individual host, which reduces the host's ability to predict and evade surprise attacks (Ratcliffe et al., 1997). Kleptoparasitism is widespread amongst gulls; 27 of the 41 documented kleptoparasitic species within the Family Laridae are gulls (*Larus* spp.; Morand-Ferron et al., 2007).

The kleptoparasitic relationship between the herring gull (*Larus argentatus*) and Atlantic puffin (*Fratercula arctica*) is a model example of kleptoparasitism. Puffins nest in burrows on the slopes of oceanic islands in densely packed colonies, where herring gulls hold breeding territories (Finney et al., 2001; Pierotti, 1982). During the chick-rearing period, puffins follow predictable foraging patterns by carrying large and conspicuous prey (e.g., adult capelin, *Mallotus villosus*, and adult sandlance, *Ammodytes* spp.) to their burrows to feed their chicks (Brockmann & Barnard, 1979). Puffins also carry less conspicuous prey items to their burrows, including larval capelin, larval sandlance, cottids, and blenniids (Baillie & Jones, 2003). When puffins carry food to their burrows, herring gulls can act as both predators and kleptoparasites to puffins by opportunistically consuming their chicks and eggs, and stealing the prey items they provide to their chicks (Bond, 2016; Harris & Wanless, 2011). Research on the herring gull-puffin system has focused largely on the puffin's behavioural choices and potential consequences of being kleptoparasitised, with very few studies focusing on the factors associated with the herring gull's host choice and probability of success.

My objectives were to identify factors associated with host choice and success during kleptoparasitic attacks by herring gulls on Atlantic puffins. I achieved this by observing focal gulls as they interacted with Atlantic puffins during the concurrent chick-provisioning periods of both species. I focused on the interactions occurring at close proximity to or on the puffin burrowing slope, but it is important to acknowledge that kleptoparasitism by gulls can occur on the open water or while the puffin is flying over the ocean. I sampled a 4-m radius around each herring gull and characterized each puffin

that entered the focal area according to prey type, whether or not they landed, and whether or not they were attacked. For those puffins that were attacked, I also noted whether the gull succeeded in obtaining the prey and if the gull made physical contact with the puffin. I predicted that gulls would preferentially attack more profitable puffins, including (1) puffins carrying large prey versus small prey or no prey; (2) puffins landing closer to versus farther from the gull; and (3) puffins landing in front of versus behind the gull. I 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. I also predicted that gulls would be more successful when they physically grasped the puffin, as opposed to when they simply lunged towards it, since the gull's larger body size should afford greater control of the interaction.

## 2.3 Methods

### 2.3.1 Field Methods

I conducted my study on Gull Island (47.3N 52.8W), which is part of the Witless Bay Ecological Reserve, 35 km south of St. John's, NL, Canada. The 1.6 x 0.8-km island is a breeding site for many seabirds, including Atlantic puffins (ca. 118,401 pairs when last surveyed in 2012; ECCC-CWS unpubl. data) and herring gulls (ca 2,698 pairs; Cotter et al., 2012). I selected eleven sampling areas across the western and southern slopes of Gull Island in late-June 2018. The sampling areas ranged in size from 7–28 m in width and 10–30 m in slope length and were located on active puffin breeding slopes where herring gulls were also present.

Prior to conducting focal observations at each sampling area, I marked gulls by applying a dye paste (comprising Procion® MXDYE dye powder 9 g, petroleum jelly 150 g, and 70% isopropyl alcohol 10 mL) on popular gull loafing sites following the methods outlined in Donehower and Bird (2005). I 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. I also laid out a grid of marking flags at approximately 4-m intervals at each sampling area (Figure 2.1 A). I measured the exact distance between each flag to provide a calibration scale for subsequent observations.

Between 11 July and 12 August 2018, when puffins were provisioning their chicks, I conducted focal animal samples (Altmann, 1973), with individual herring gulls as the unit of replication (N=73). Sampling occurred between 0500 and 2100h, when visibility was at least 40 m, and when there was little or no precipitation. The sampling window was restricted to 0500 to 2100h to ensure sufficient light for video recording; this window should capture the majority of puffin provisioning attempts and kleptoparasitism, as puffins are generally only active between dawn and dusk (personal observations; Harris & Wanless, 2011).

I chose focal gulls based on which gulls were passively dyed and which gulls were present at the sampling area during the sampling period. I used a given sampling area multiple times over multiple days until I had sampled all gulls that were opportunistically dyed at that area. I arbitrarily chose the order of the sampling areas in consideration with other work being conducted on the island and slope stability due to the excess of rain at the beginning of the season. Occasionally, I also observed unmarked gulls in the same sampling area. If multiple unmarked animals were sampled, I 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 handheld GPS (approximately 3 m) that was used to mark gull locations. I recorded each focal session with a high-definition video camera (Canon VIXIA HFR800, resolution 1920x1080 pixels, 60 frames per second progressive scan, MPEG-4 AVC/H.264) positioned on a tripod inside a portable

blind that I set up below the study area at least 1 hour before conducting the first focal sample at that area. Typically, the blind was left erected for multiple days, but sometimes environmental conditions forced me to collapse the blind between observations. I maintained an average distance ( $\pm$  SD) of  $24.0 \pm 7.8$  m between the focal gull and the blind. I entered the blind at least 10 minutes 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 my presence and always returned to the slope within 5 minutes of me entering the blind. I 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, 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 (Figure 2.1 B) 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 minutes or until the gull flew away and did not return. Trials that were shorter than 10 minutes 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, I supplemented the video footage by observing interactions directly or through binoculars, and by dictating my observations onto the video recording's soundtrack using an external microphone (RadioShack 33-3013).

For each puffin that entered the 4-m radius around the gull, I 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 was less than or equal to the depth of the bill and large prey were greater than the depth of the bill. I noted whether the puffin was attacked by the focal gull or by a neighbouring non-focal gull and categorized the focal gull's host choice as either attack or no attack. Non-focal 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 it is important to 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. Attacks are not dependent on the outcome and, therefore, I 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.

### 2.3.2 Video Analysis

I used the event recording software BORIS (Behavioral Observation Research Interactive Software, version 6.2.3; Friard & Gamba, 2016) to review and transcribe the video recordings. I used the calibration flags on the slope and a digital circle (PixelStick, version 2.12.0, Plum Amazing Essential Software) superimposed over the video to define the observation area (4-m radius) around the focal gull. For each puffin entering the focal sampling area, I 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, I re-analyzed 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, I re-analysed all attacks made by focal and non-focal gulls, noting whether or not the gull made physical contact with the puffin.

Whenever a puffin with prey landed within the focal area (*i.e.*, Figure 2.1 C), I noted the orientation of the focal gull and the orientation of any non-focal 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 non-focal gull that attacked the puffin. When measuring distance, I 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 version 1.13.1).

To correct for slope, I calibrated the horizontal and vertical measurements separately using the horizontal and vertical calibration flags set out on the slope. I 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, I 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, I retained for analysis 60 focal sampling sessions (average length  $\pm$  SD:  $24.4 \pm 7.1$  minutes), which corresponded to 24.4 hours of observation.

### 2.3.3 Statistical Methods

Statistics were conducted in R (version 3.5.3; R Core Team, 2019), and generalised linear mixed models (GLMMs) were fitted using the "lme4" package (version 1.2-21; Bates, Maechler, Bolker, & Walker, 2015). Ideally all models would include a random variable accounting for focal gull identification, however, due to the rarity of kleptoparasitism there were not enough repeated samples for each individual for all models. Therefore, one model investigating host choice and all models investigating gull success resulted in quasi-complete separation causing the GLMMs to fail to converge. Subsequently, these models excluded the random effect. Dropping the random effect of

gull identity meant that some gulls contributed multiple data points to the analyses (attacks per gull ranged between zero and six). However, I reran each GLMM that did not converge as a generalised linear model (GLM) and found that the results were consistent with respect to statistical significance. Therefore, I used GLMMs with gull ID as a random effect when models would converge, and GLMs or a chi-square when they would not converge.

Models with more than two predictor variables (models 1-3) were checked for multicollinearity by calculating variance inflation factors (VIF) following the methods outlined in Zurr, Hilbe, and Ieno (2015); a value of one indicates no multicollinearity and values of 5 or greater indicate that the variables are influenced by multicollinearity. All VIFs calculated were less than 1.12, 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  $0.05 < p \leq 0.1$ .

#### 2.3.3.1 Host Choice

I analyzed focal gull host choice (*i.e.*, whether or not an approaching puffin was attacked) using a chi-square test, and two GLMMs with binomial error structure (logit link) and gull identity as a random variable to account for repeated interactions with the same individual. All tests excluded interactions with puffins with unknown bill contents, interactions where more than one gull attacked the puffin, and attacks where a non-focal gull attacked a puffin (N = 141). Non-focal gulls were excluded because I did not systematically collect data from them during events where a puffin approached but was not attacked.

I first tested whether herring gulls were more likely to attack approaching puffins that had full versus empty bill loads (N = 1597 puffins and 60 gulls). I used a chi-square test without the Yates Continuity Correction because all expected values were greater than 10. Puffins with empty bill loads and those categorized as "unknown conspicuous" were then excluded from subsequent GLMMs, which included variables that described prey size. Second, I used a GLMM to test 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). My third analysis focused on puffins that completed their landing (N = 202 puffins and 48 gulls), and used a GLMM to test 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.

#### 2.3.3.2 Gull Success

To investigate gull success (defined as the gull obtaining some or all of the puffin's prey), I included data from attacks by both focal and non-focal gulls, with at least 24 individual gulls represented in the data. These results do not control for individual variation and should be interpreted with caution. All tests excluded events where puffins approached with unknown bill contents, or where they were attacked by more than one gull (N = 9 events).

First, I used a chi-square test (rather than a generalised linear model, which is unable to execute when the data displays quasi-complete separation) to determine whether or not there was a relationship between gull success and puffin landing choice (N = 74 attacks). The expected frequencies were less than 5 and, therefore, to avoid

violating the rules of the chi-square test, I applied the "N-1" chi-square test (Campbell, 2007). My second analysis focused on the subset of interactions in which the puffin completed its landing within a focal area (N = 51 attacks). Using a generalised linear model (binomial error structure with a logit link), I 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.

## 2.4 Results

### 2.4.1 Host Choice

I observed one or more kleptoparasitic attacks by approximately one third (20/59) of the focal gulls that had at least one opportunity for kleptoparasitism during their focal sample. Focal gulls had 555 opportunities for kleptoparasitism (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). All kleptoparasitic attacks occurred when an approaching puffin was carrying conspicuous prey in its bill (Chi-square test  $\chi^2_{1,1597} = 82.97$ ,  $p = <0.001$ , Figure 2.2).

Of the puffins that approached the focal area with either small or large prey items in their bill (Table 2.1, Model 1), herring gulls were significantly more likely to attack those that carried large prey (as compared to small prey; Figure 2.3 A) and those that completed their landing (as compared to those that aborted; Figure 2.3 B).

Of the puffins that landed within the focal area while carrying either small or large prey items (Table 2.1, Model 2), herring gulls were significantly more likely to attack those that landed closer to them (Figure 2.4 A) and those that landed in front of them (Figure 2.4 B). Gulls also tended to attack when landed puffins carried large prey items (as compared to small prey items; Figure 2.4 C), though this relationship was not statistically significant.

#### 2.4.2 Gull Success

Focal and non-focal gulls attacked 74 approaching puffins and successfully obtained some or all of the food from 15 of them. There was a significant relationship between gull success and puffin landing choice ( $\chi^2_{1,74} = 5.19, p = 0.022$ ). Specifically, 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 (Figure 2.5).

Focal and non-focal 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 were significantly more likely to succeed when they made physical contact with the puffin (Table 2.2, Model 3, Figure 2.6). Herring gull success was not related to its distance or orientation to the landed puffin (Table 2.2; Model 3).

## 2.5 Discussion

I observed herring gulls kleptoparasitising Atlantic puffins that were returning to their burrows with food for their chicks. For each approaching puffin, I noted its bill contents (presence or absence of prey and prey size), landing choice, whether or not it was attacked, and, if it was attacked, whether or not the attack was successful. For those puffins that completed their landing with prey in their bill, I also measured the focal gull's distance and orientation in relation to the landed puffin. Additionally, I measured the distance and orientation of attacking non-focal gulls in relation to the landed puffin. Gulls were more likely to attack puffins that landed in front of them, puffins that landed closer to them, and puffins 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 were more 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 a way that is consistent with them optimizing their foraging efficiency. Specifically, gulls preferentially attacked puffins with larger prey items, though it is unclear whether gulls targeted individuals based on the profitability or the conspicuousness of the host'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 (e.g., García et al., 2010; Spencer et al., 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 (food handling) occurs inside the burrow and beyond the gull's reach, so the host'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. It is important to note that these explanations are not mutually exclusive, as gulls could target those which carry 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 have become shorter while maintaining the same aspect ratio (Pennycuick, 1987a). This adaptation disadvantages the puffin by reducing the puffin's maneuverability during landing and take-off, hampering its ability to glide at the low speeds necessary to land (Pennycuick, 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 (58-63kph; Harris & Wanless, 2011; Pennycuick, 1997) than herring gulls (37-54kph; 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, since gulls were never observed to be successful 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. However, attacking closer puffins may nonetheless optimize their foraging efficiency, since shorter attacks presumably require less time and energy. Furthermore, gulls may need to remain within their core territory to protect their chicks from being killed by neighbouring gulls (Hunt & Hunt, 1976).

During a kleptoparasitic attack, gulls were 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. However, it is unclear whether gulls are choosing between two distinct tactics, or whether an attack without contact is simply an incomplete attack that is nonetheless sometimes successful because the puffin drops its food. I often observed that when a gull does 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 they are unlikely to succeed due to differences in flying speed or because the calorific benefit of the food item does not exceed the energetic demand of flight.

Kleptoparasitism appears to be widespread among the herring gull population on Gull Island, Newfoundland, indicating that prey stolen from puffins may be an important food source to the gulls during chick rearing. Although capelin kleptoparasitised 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% to 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 (*i.e.*, Brown & Nettleship, 1984).

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. I found that herring gulls do not attack puffins at random, but rather optimize their energy intake by targeting more profitable hosts.

## 2.6 Tables

Table 2.1 Results of generalised linear mixed models (binary response, logit link) predicting gull host choice (attack or no attack). Reference categories for categorical predictor variables are included in parentheses below each variable.

Model	Factor	Level	Estimate $\pm$ SE	Z	p	Odds Ratio (95% CI)
1 <sup>a</sup>	Landing Choice (Aborted Landing)	Completed Landing	1.78 $\pm$ 0.52	3.45	0.001	6.0 (2.2 – 16.6)
	Prey Category (Small)	Large	1.61 $\pm$ 0.48	3.32	0.001	5.0 (1.9 – 13.0)
2 <sup>b</sup>	Distance to Focal Gull		-1.10 $\pm$ 0.28	-3.88	<0.001	0.3 (0.2- 0.6)
	Gull Orientation (Away)	Towards	1.98 $\pm$ 0.63	3.14	0.002	7.3 (2.1 – 25.1)
	Prey Category (Small)	Large	1.23 $\pm$ 0.67	1.82	0.069	3.4 (0.9 – 12.8)

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.

SE = standard error, CI = confidence interval, SD = standard deviation. Significant p-values are in bold ( $p \leq 0.05$ ) and trends are italicised ( $0.05 < p \leq 0.10$ )

<sup>a</sup> Random effect of gull identity: variance = 1.90, SD = 1.38, N =58 focal gulls and 478 approaching puffins; excluded puffins approaching with bill loads other than small or large prey

<sup>b</sup> Random effect of gull identity: variance = 0.43, SD = 0.65, N =48 focal gulls and 202 landed puffins; excluded puffins that did not land within 4m of the focal gull and those with bill loads other than small or large prey

Table 2.2 Results of a generalised linear model predicting gull success (gull obtained some or all of puffin's prey) during kleptoparasitic interactions. Reference categories for categorical predictor variables are included in parentheses below each variable.

Model	Factor	Level	Estimate $\pm$ SE	Z	p	Odds Ratio (95% CI)
3 <sup>a</sup>	Distance to Gull		-0.07 $\pm$ 0.37	-0.18	0.858	0.9 (0.4 – 1.9)
	Gull Orientation (Away)	Towards	-0.86 $\pm$ 0.79	-1.09	0.278	0.4 (0.1 – 2.1)
	Attack Type (No Physical Contact)	Physical Contact	1.63 $\pm$ 0.74	2.20	0.039	5.2 (1.1 – 26.9)

Puffins with unknown bill contents, those that did not land in a focal area, those that were not attacked and those attacked by multiple gulls were excluded.

SE = standard error, CI = confidence interval. Significant p-values are in bold ( $p \leq 0.05$ ) and trends are italicised ( $0.05 < p \leq 0.10$ )

<sup>a</sup> N=51 attacks, a minimum of 24 individual herring gulls were included in this analysis

## 2.7 Figures



Figure 2.1 These photographs show examples of A) a focal gull in its territory on a puffin breeding slope surrounded by marking flags, B) a puffin that carried a large prey item moments before a focal gull made physical contact and stole its prey, and C) a puffin carrying a large prey item seemingly at risk of kleptoparasitism by the herring gull.

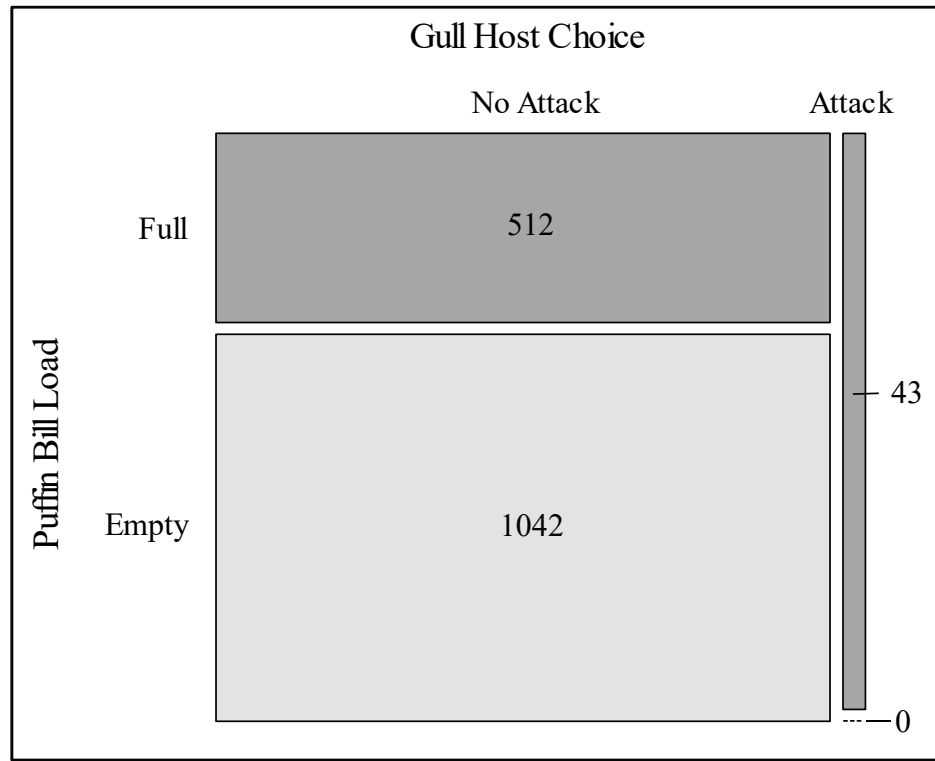


Figure 2.2 This mosaic plot shows the relationship between focal gull host choice (response variable) and the approaching puffin's bill load. Gulls only attacked puffins that possessed conspicuous prey in their bill. Numbers indicate the count of events in each category.

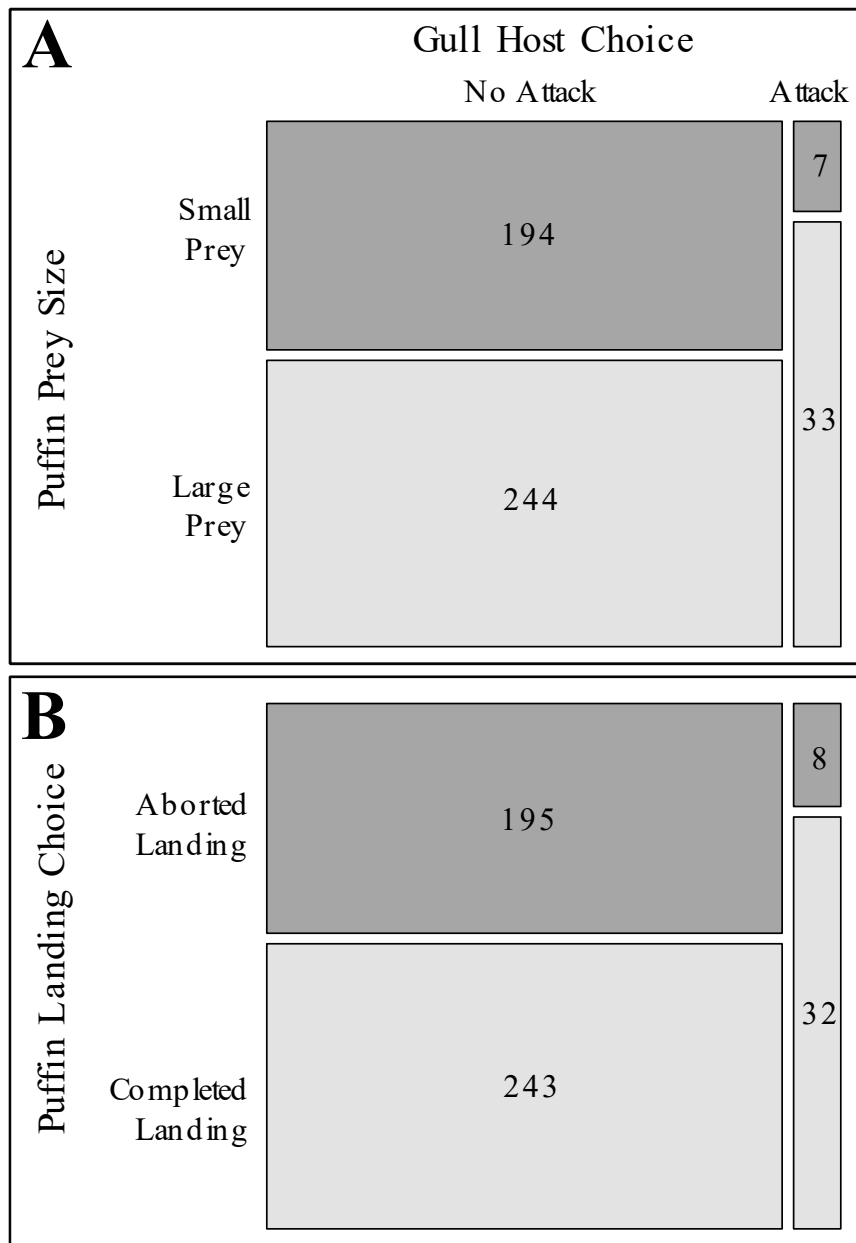


Figure 2.3 These mosaic plots illustrate the relationship between focal gull host choice (response variable) and the puffin's A) prey size and B) landing choice. Gulls were more likely to attack approaching puffins with large prey and those that ultimately completed a landing on the slope. Numbers indicate the count of events in each category.

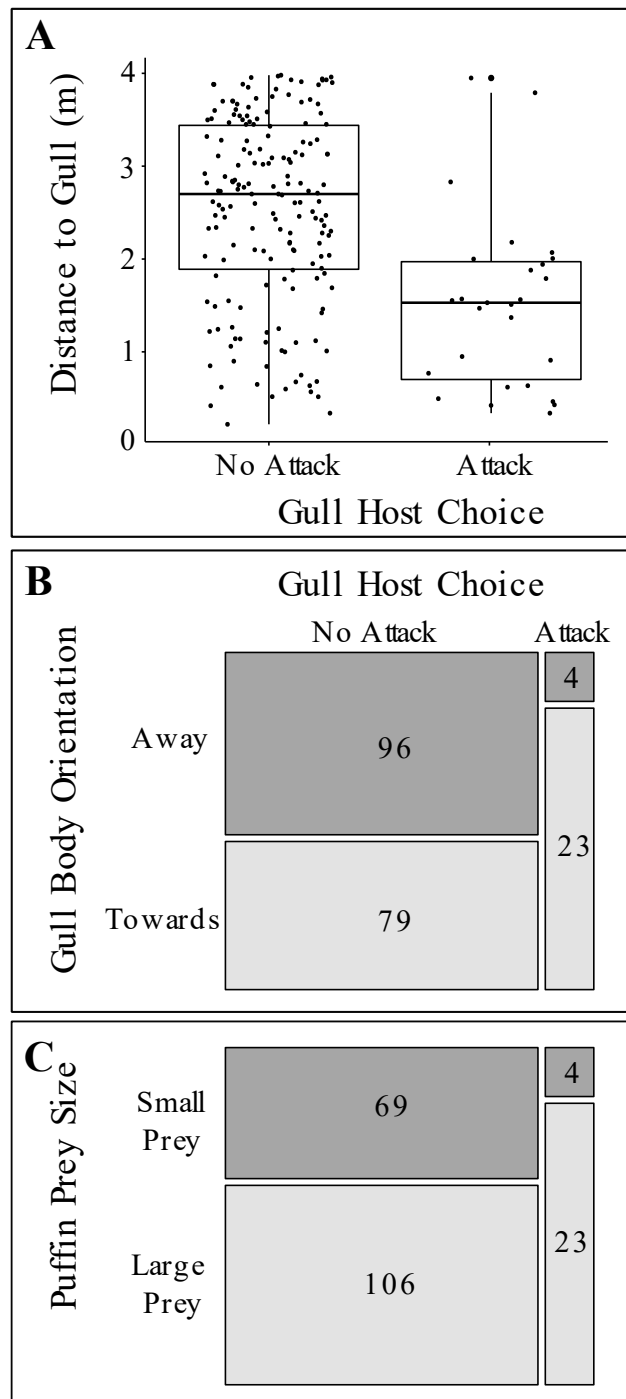


Figure 2.4 The relationship between focal gull host choice (response variable) and A) the distance between the landed puffin and the focal gull, B) the gull's body orientation relative to the landing puffin, and C) the puffin's prey size. Gulls were more likely to attack puffins in close proximity, those they were oriented towards, and those that carried large prey. Numbers indicate the count of events in each category and each dot represents one completed puffin landing.



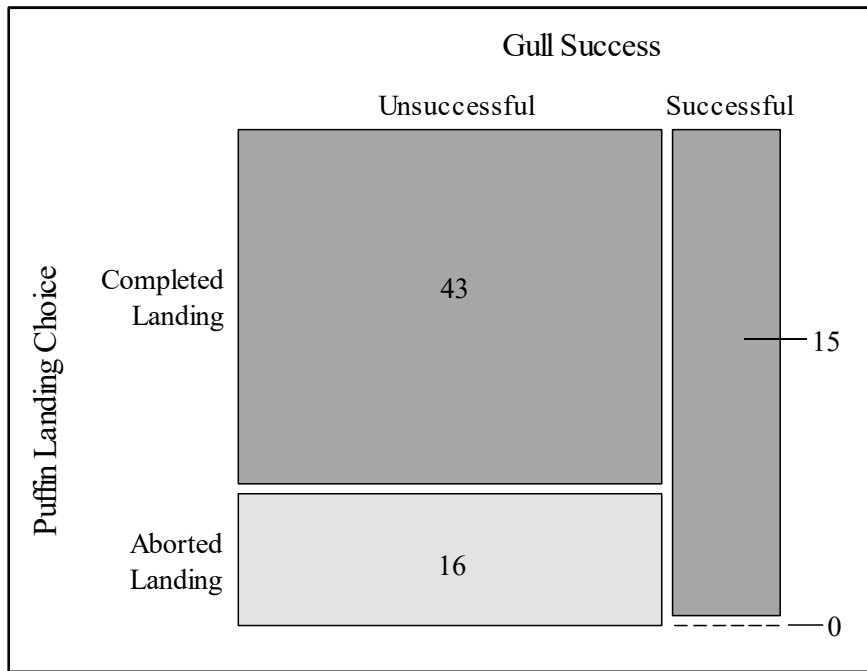


Figure 2.5 This mosaic plot illustrates the relationship between gull success (response variable, where success is defined as the gull obtaining some or all of the puffin's prey) and puffin landing choice. Gulls were never successful in obtaining prey from a puffin that aborted a landing attempt. Numbers indicate the count of events in each category.

		Gull Success	
		Unsuccessful	Successful
Attack Type	No Physical Contact	32	6
	Physical Contact	7	6

Figure 2.6 The relationship between gull success (response variable, where success is defined as the gull obtaining some or all of the puffin's prey) and attack type. Gulls were more successful when they made physical contact with a puffin during a kleptoparasitic encounter. Numbers indicate the count of events in each category.

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## CHAPTER 3 BEHAVIOURAL RESPONSES OF ATLANTIC PUFFINS TO THE RISK OF KLEPTOPARASITISM BY HERRING GULLS

### 3.1 Abstract

Kleptoparasitism is a foraging strategy where one individual steals procured food from another individual. Avian hosts to kleptoparasites often display behavioural tactics that reduce the risk of losing prey, including handling food underwater, landing in groups, and foraging at night. Atlantic puffins (*Fratercula arctica*) are a common host for herring gulls (*Larus argentatus*), which kleptoparasitise puffins returning to their burrows with fish for their chick. This system has been studied for over 60 years, yet information about if and how the puffin mitigates its risk is lacking. In my previous chapter, gulls preferentially attacked puffins that completed their landing, that landed nearby, and that possessed large prey; they also always failed to obtain the puffin's prey when they attacked a puffin that aborted its landing. In this study, I tested the hypothesis that puffins mitigate risk by altering their landing behaviour. I recorded each puffin that approached the focal gull and categorized them according to prey type, landing choice, landing location, and whether or not they were attacked. For puffins that were attacked, I also noted whether the puffin retained its prey. Results show that puffins at risk of kleptoparasitism effectively mitigate their risk by engaging in evasive behaviour and aborting their landing. However, they did not respond to the increased risk associated with carrying large versus small prey. Therefore, gulls and puffins may value prey differently. Every catch may be equally valuable to a puffin providing the sole nourishment for its chick, however, prey derived by kleptoparasitism compose only part of the gull's overall diet allowing the gull to selectively target hosts carrying larger prey.

### 3.2 Introduction

Many animals optimize their survival and reproduction by balancing investments in conflicting activities (Ghalambor & Martin, 2001; Stearns, 1989). For example, animals often balance time spent being vigilant with time foraging (Houston, McNamara, & Hutchinson, 1993; Lima, Valone, & Caraco, 1985), thereby allowing them to optimize both safety and energy gain. Other animals mitigate predation risk by foraging in safer but less-profitable patches, or by foraging in the safety of a group in which resources must be shared (Houston et al., 1993).

Kleptoparasitism is a form of interference competition in which one individual steals a procured food item from another individual (Birch, 1957; Case & Gilpin, 1974; Rothschild & Clay, 1952). Like predation, kleptoparasitism involves the procurement of food resources; however, the cost to the host is not death, but the loss of food resources, time, and energy (Broom, Luther, & Ruxton, 2004). Kleptoparasitism has been described in many taxa and can occur during the capture (Henaut, 2000), handling (Wood, Stillman, & Goss-Custard, 2015), transport, or consumption of prey (Carbone et al., 1997; Hatch, 1970). It is most conspicuous among birds, especially seabirds that transport prey items from the ocean to their chicks on land. Some bird species act as kleptoparasites, others as hosts, and some as both (Morand-Ferron et al., 2007). Species are more likely to be hosts if they live in open habitats where kleptoparasites can easily detect them, live in large dense colonies, follow predictable foraging patterns, and transport large quantities of conspicuous prey, as these characteristics are conducive to a stable, reliable, and

profitable food source for the kleptoparasite (Brockmann & Barnard, 1979; Morand-Ferron et al., 2007).

Just as prey species have evolved behavioural tactics that balance predation risk and foraging efficiency, many kleptoparasitic host species have evolved tactics that balance foraging efficiency with the risk of being kleptoparasitised. For example, individuals may avoid kleptoparasitism by handling food underwater (Amat & Aguilera, 1989), landing in groups that overwhelm and confuse kleptoparasites (Le Corre & Jouventin, 1997; Merkel et al., 1998; Rice, 1987), delaying their landing when a kleptoparasite is nearby (Blackburn et al., 2009), and provisioning at night (Hailman, 1964; Le Corre & Jouventin, 1997; Watanuki, 1990). As with many antipredator strategies, the tactics for avoiding kleptoparasitism can be costly. Coordinating grouped landings and delayed landings (Blackburn et al., 2009) adds flight distance, time, energy, and stress to a provisioning trip, and handling food underwater and provisioning at night (Watanuki, 1990) impairs the host's ability to see, leaving it more vulnerable to collisions and predation.

The Atlantic puffin (*Fratercula arctica*) is an ideal host for a kleptoparasite. It breeds in large dense colonies on the exposed slopes of oceanic islands, and, during the approximately 40-day chick-rearing period, provides the sole source of nourishment to its chick by repeatedly and predictably transporting large amounts of conspicuous fish (*i.e.*, capelin, *Mallotus villosus*; sandlance, *Ammodytes* spp.; sprat, *Sprattus sprattus*; Figure 3.1) in its bill to its nesting burrow (Brockmann & Barnard, 1979; Harris, 1980; Harris & Wanless, 2011; Hudson, 1979; Nettleship, 1972). During provisioning, adult puffins can



be kleptoparasitised by many species, including razorbills (*Alca torda*), corvids (*Corvus modedula*, *C. corvax*, *C. corone*), gulls (*Larus fuscus*, *L. glaucescens*, *L. marinus*, *L. argentatus*, *Rissa tridactyla*), skuas (*Catharacta skua* and *Stercorarius parasiticus*), and frigatebirds (*Fregata magnificens*) (Morand-Ferron et al., 2007). They can be kleptoparasitised in flight (Grant, 1971) or while at sea, but are especially vulnerable after landing on the slope and before entering the safety of their nesting burrow (Hudson, 1985; Nettleship, 1972; Rice, 1987). Puffin wing morphology is adapted to pursue prey underwater (Pennycuik, 1987), but that morphology also impairs the puffin's maneuverability during landing and take-off. Consequently, puffins often miss their burrow entrances during landing and expose themselves to the risk of kleptoparasitism by walking to their burrows along the slope. Furthermore, once a puffin lands, it often struggles to launch back into flight, which hampers its ability to escape a kleptoparasite that intercepts it on its way to its burrow (Nettleship, 1972). Since puffin chicks rely on their parents for food, the parents must eventually land on the slope and attempt to enter their burrow.

Being kleptoparasitised may be costly because the puffin must return to the ocean to catch more fish, thereby increasing its flight time, energy expenditure, and the time until its chick is fed (Baillie & Jones, 2003; Øyan & Anker-Nilssen, 1996). Nettleship (1972) suggested that these costs reduce fledging success (number of chicks estimated to have fledged plus those that survived to the last inspection), which was 90.5% on islands without kleptoparasitic gulls and only 37.1% on islands with gull kleptoparasitism. No

subsequent study, however, has shown such severe reproductive consequences (Finney et al., 2001; Rice, 1985).

There is some evidence that puffins exhibit behaviour that mitigate their risk of being kleptoparasitised. For example, puffins carrying fish synchronize their landings (Merkel et al., 1998; Rice, 1987), are more likely to clump their landings in space in areas of high herring gull density (Pierotti, 1983), and are more likely to take flight immediately after landing if a gull attack is imminent (Nettleship, 1972). Adult puffins also enter their burrows more rapidly during the chick provisioning period, when they frequently carry food to their burrows, than during the preceding incubation period, when they do not carry food to their burrows (Rice, 1987). However, previous studies did not examine the behavioural differences between puffins experiencing different levels of risk (*i.e.*, those carrying and those not carrying prey) during the same timeframe.

In the current study, I test the hypothesis that puffins mitigate their risk of kleptoparasitism during chick provisioning by altering their landing behaviour in response to immediate risk factors. Specifically, I observed approaching puffins whose burrows were within the territory of a herring gull (*L. argentatus*), which is a common kleptoparasite of Atlantic puffins in Europe and North America (Corkhill, 1973; Hudson, 1985; Nettleship, 1972; Rice, 1987). I focused my observations on puffins that landed, or attempted to land, within 4 m of a gull, since herring gulls preferentially attack puffins that land, or attempt to land, within this distance (Chapter 2; Hudson, 1985).

I made two predictions based on my hypothesis and knowledge of gull behaviour. Gulls never attack puffins that have an empty bill, prefer to attack puffins carrying large versus small prey, and always fail when attempting to steal prey from a puffin that aborts its landing (Chapter 2). If puffins actively mitigate risk, then I predicted that they would be more likely to abort their landings when approaching with large prey versus no prey, and that their likelihood of aborting would be intermediate when approaching with small prey. An attack is more likely to occur when the distance between the gull and the landing puffin is shorter (Chapter 2). Moving upslope also requires more time and energy for a gull than moving downslope (Birn-Jeffery & Higham, 2014; Nudds & Codd, 2012; Schmidt-Nelsen, 1972), which may select for gulls attacking from upslope. If puffins actively mitigate risk, then I predicted that they would be more likely to land upslope and farther away from the gull when landing with large prey versus no prey, and that these effects would be intermediate when landing with small prey. This study investigates whether Atlantic puffins are sensitive to their kleptoparasitism risk by explicitly testing the relationship between bill contents (empty, small, and large prey) and pre- and post-landing behaviour. It also investigates the potential implications of changes in a puffin's behaviour on the risk of being attacked and losing its prey to a herring gull.

### 3.3 Methods

#### 3.3.1 Field Methods

My study site was located on Gull Island in the Witless Bay Ecological Reserve, 35 km south of St. John's, NL, Canada. The island is a breeding site for many seabirds, including Atlantic puffins (ca. 118401 pairs, 0.73 occupied burrows per m<sup>2</sup> when last surveyed in 2012; ECCC-CWS unpubl. data) and herring gulls (ca. 2,698 pairs; Cotter et al., 2012).

In June 2018, before puffin chicks hatched, I selected eleven sampling areas distributed across the western and southern slopes of the island. The sampling areas ranged in size from 7–28 m in width and 10–30 m in slope length and were located on active puffin breeding slopes where herring gulls were present. At each area, I laid out a grid of marking flags at 4-m intervals to provide a calibration scale for subsequent distance measurements.

Between 11 July and 12 August 2018, when puffins and gulls were provisioning their chicks, I conducted 73, 30-min observation sessions in which I observed all puffins landing, or attempting to land, within 4 m of a focal gull. Each session focused on a single gull, and different sessions always involved different gulls, which I selected opportunistically and without replacement. The majority of gulls were distinguished by unique dye patterns on their plumage (details in Chapter 2). Those that were not marked were separated from each other by a minimum of 30 m, which exceeds the diameter of

their territories (range: 1.5–7.6 m; Hunt & Hunt, 1976) and reduces the likelihood of resampling the same gull.

Although a few puffins on the island had been marked with coloured leg bands in the context of previous studies, the vast majority had not. Even when a puffin was banded, it usually was not possible to see its leg bands in flight or as it moved rapidly through the tall grass to its burrow. However, individual puffins were unlikely to visit their burrow more than once during a single 30-min observation session because puffin chicks only receive an average of  $4.67 \pm 0.59$  (mean  $\pm$  SE; N=10) visits per day from both parents (Rector, 2011). In some cases, I sampled what I believed to be members of a breeding gull pair (N=11 pairs) based on observed behaviours such as interaction with the same chick and territory defence. As a result of the gulls sharing a territory, it is possible that I observed some of the same individual puffins during two sampling sessions. However, given the short sampling sessions, low visitation rates, and the inability to distinguish individual puffins, I treated all approaching puffins as though they were different individuals.

Observation sessions were conducted between 0500 and 2100h, when visibility was at least 40 m and there was little or no precipitation. I recorded each observation session with a high-definition video camera (Canon VIXIA HFR800, resolution 1920x1080 pixels, 60 frames per second progressive scan, MPEG-4 AVC/H.264) positioned on a tripod inside a portable blind that I set up below the study area at least 1 h before conducting the first observation session at that area (average distance  $\pm$  SD

between the blind and each gull being observed was  $24.0 \pm 7.8$  m). I entered the blind at least 10 minutes before each observation session began to reduce human disturbance. I zoomed the camera to include an approximately 6-m radius around the focal gull, which captured the 4-m focal area around the gull, plus the final stages of any puffin's approach to the focal area. Throughout the 30-min session, I panned the camera to keep the focal gull in the centre of the field of view. Because the video camera did not always have adequate resolution or perspective to capture the fine details of an event (e.g., presence and type of prey in a puffin's bill), I augmented the recording by observing the target area directly or through binoculars and dictating my observations onto the camera's audio track using an external microphone (RadioShack 33-3013). Three of the 73 observation sessions were excluded from subsequent analyses because the gull flew away within the first 10 min of the session.

### 3.3.2 Behavioural Analysis

Following the field season, I used the event recording software BORIS (Behavioural Observation Research Interactive Software; version 6.2.3; Friard & Gamba, 2016) to review the videos and transcribe all events where a puffin entered the 4-m focal area surrounding the gull. For each event, I used a combination of video and my recorded dictation to score five categorical variables, including the puffin's landing choice, landing position, bill load, whether or not it was attacked, and the outcome of any attack. Landing choice was scored as 'completed' if the puffin contacted the slope and stopped flapping its wings, and as 'aborted' if 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. I observed some puffins aborting a landing only a few centimetres from touching the slope, therefore, puffins appear to be capable of aborting a landing during its entire approach to the slope. For those puffins that completed their landings, landing position was scored in relation to the focal gull and to any non-focal gull that attempted to kleptoparasitise the puffin. Landing positions included ‘upslope’ if the puffin's feet were above the gull's body, and ‘not upslope’ in all other cases. Bill load was scored as ‘empty’ if no prey items protruded from the bill, ‘small’ if the prey protruding from the bill were shorter than or equal in length to the depth of the puffin’s bill, ‘large’ if the prey were longer than the depth of the bill, and ‘unknown’ if the puffin’s speed of approach or orientation prevented me from accurately scoring bill load (Figure 3.1). Finally, I noted whether or not the puffin was attacked by the focal gull or by a neighbouring non-focal gull; an attack was defined as a rapid movement towards the puffin by flying, running along the ground, or lunging the neck towards the puffin. Attacks are not dependent on their outcome and, therefore, I also noted the outcome of the kleptoparasitic attack as ‘retained’ if the puffin retained all of its prey, and ‘lost’ if the puffin lost some or all of its prey.

In addition to the five categorical variables, I used the video to measure the distances between the landed puffin and the closest gull, focal gull, and any non-focal gull that attempted to kleptoparasitise the landing puffin; distance measures were taken when the puffin first contacted the slope. To measure distance, I measured the horizontal and vertical offsets, in pixels, between the puffin and gull, and then converted them into real distances by comparing them to the known horizontal and vertical offsets between the

calibration flags that were visible in the video (see Chapter 2 for complete details). I measured distances for each puffin that landed with prey, but due to the large number of puffins approaching without prey (1030 of 1484 total known events), and the time needed to diligently measure each one, it was not feasible to measure the distance for every puffin landing without prey. Instead, I measured a subsample of up to 20 randomly selected puffins that landed without prey during each focal session (some sessions contained fewer than 20 puffins landing with an empty bill load). Ideally this study would also include a measurement of the distance between an individual puffin's landing location and its burrow, however, since puffins were not individually identifiable and many puffins did not enter their burrow within the observation period it was impossible to quantify this distance for many observations, particularly for puffins that landed with no conspicuous prey.

While analysing the videos, I noticed that many gulls that ultimately attempted to kleptoparasitise an approaching puffin would move towards the puffin's landing location moments before the puffin landed on the slope. Consequently, my measurement of the distance between the landing puffin and the gull, as well as the puffin's landing position, might not have been controlled entirely by the puffin. I therefore noted whether or not the gull was moving as the puffin landed so that I could exclude these events from analyses of puffin landing location (*i.e.*, position and distance to gull).

I excluded 10 of the 70 remaining observation sessions from subsequent statistical analyses due to camera perspective issues that may have obscured the distance measurements. I also excluded all events from within a session in which the puffin's bill



load was scored as ‘unknown’ (187 events), or where more than one gull attacked an individual puffin (9 events); this necessitated the removal of two additional observation sessions. The final dataset included 1484 events in which a puffin landed or attempted to land within 4 m of a focal gull, distributed among 58 observation sessions (average session length  $\pm$  SD: 24.4  $\pm$  7.1 minutes) totalling 24.4 hours of observation.

### 3.3.3 Statistical Analysis

My first prediction was that approaching puffins would be more likely to abort their landings if they had conspicuous prey in their bill, since gulls do not attack puffins with empty bills and preferentially attack puffins with large versus small prey (Chapter 2). I expected that puffins carrying large prey would be most likely to abort their landing, followed by those holding small prey and then those with empty bills. Using a generalised linear mixed model (GLMM; binomial error and logit link, observation session as a random effect), I tested whether the response variable, landing choice (completed, aborted), was associated with the explanatory variable, bill load (empty, small prey, large prey). Data for this analysis included 1484 approaches by puffins.

My second prediction was that puffins should land farther away from the gull and be more likely to land upslope from the gull when carrying large prey versus small prey or no prey. Data for these analyses excluded aborted landings (258 events), landings where the focal gull was not the closest gull to the landing puffin (168 events), and landings where the gull changed its position as the puffin was landing (30 events). I used a GLMM (binomial error structure, logit link, observation session as a random effect) to

test for a relationship between the response variable, landing position (upslope, not upslope), and the explanatory variable, bill load (empty, small prey, large prey). I used a GLMM (gamma error structure, log link, observation session as a random effect) to test the relationship between distance to the focal gull at the time of landing and bill load.

In addition to my two predictions about how puffins might adjust their landing behaviour in response to risk, I investigated the consequences of puffin landing location by testing whether it was associated with the probability of being attacked, and, for those puffins that were attacked, whether it was associated with their probability of retaining prey. Using a GLMM (binomial error structure, logit link, observation session as a random factor), I tested for a relationship between whether or not a landed puffin was attacked (response variable) and the explanatory variable, landing position (upslope, not upslope). Data for this analysis excluded aborted landings (258 events), landings where the focal gull was not the closest gull to the landing puffin (168 events), and puffins with empty bill loads (385 events); however, the data did include events where the gull moved immediately before the puffin landed because most attacks began with the gull making preparatory movements towards the projected landing location of the puffin. Using a generalised linear model and events where a landed puffin was attacked, I then tested for a relationship between the response variable, outcome (retained, lost), and the explanatory variable, landing position in relation to the attacking gull (upslope, not upslope). Given the small number of attacks by focal gulls, I included in this analysis attacks by both focal (N=34) and non-focal gulls (N=17) that occurred within the focal area. Unlike in the previous analyses, observation session was not included as a random effect to control for

potential dependencies among data because the model otherwise failed to converge due to the small number (range: 1-3) of observations for each session. The results of this model should therefore be interpreted with caution.

All statistics were conducted in R (version 3.5.3; R Core Team, 2019). Linear and generalised linear mixed models were fitted using the "lme4" package (version 1.2-21; Bates et al., 2015), and the overall models tested for statistical significance using the "car" package (version 2.1-5; Fox & Weisberg, 2019). Multiple pairwise comparisons were conducted using the "multcomp" package (version 1.4-8; Hothorn, Bretz, & Westfall, 2008). Results were considered statistically significant when  $p \leq 0.05$ , and to constitute a statistical trend when  $0.05 < p \leq 0.1$ . Where an overall model involving a multi-level predictor variable was significant, multiple pairwise comparisons among the levels of that factor were conducted using a Bonferroni adjustment to control Type I error.

### 3.4 Results

I observed the approach of 1484 puffins with identifiable bill contents, including 267 (18.0%) with large prey items, 187 (12.6%) with small prey items, and 1030 (69.4%) with no prey.

Consistent with my first prediction, there was a significant difference in the likelihood that a puffin would land based on its bill contents (Analysis of Deviance Type II Wald Chi-square:  $\chi^2_{2,1484}=146.30$ ,  $p < 0.001$ ; Figure 3.2). Specifically, puffins carrying large and small prey were significantly more likely than puffins not carrying prey to abort their landings near gulls (Table 3.1). Only 5.9% (61/1030) of puffins approaching without prey aborted their landings, as compared to 39.3% (105/267) of puffins carrying large fish and 49.2% (92/187) of puffins carrying small fish. Puffins with large prey were not significantly more likely than puffins with small prey to abort their landing (Table 3.1).

My second prediction was that puffins landing with large prey should be more likely than puffins with small prey to land upslope and farther from the gull, and that puffins with large or small prey should both be more likely than puffins without prey to land upslope and farther from the gull. Contrary to this prediction, I found no significant difference in landing position (upslope versus not upslope) based on bill load (Analysis of Deviance Type II Wald Chi-square:  $\chi^2_{2,469}=3.36$ ,  $p = 0.187$ ), and no evidence that the distance between the landing puffin and the focal gull varied as a function of the puffin's bill load (Analysis of Deviance Type II Wald Chi-square:  $\chi^2_{2,469}=0.53$ ,  $p = 0.768$ ; Figure 3.3).

Among puffins that landed while carrying large or small prey, landing position (upslope or not upslope) was not significantly associated with the likelihood of being attacked (Analysis of Deviance Type II Wald Chi-square:  $\chi^2_{1,115}=0.85$ ,  $p = 0.355$ ) or with whether or not the puffin retained its prey (Analysis of Deviance Type II:  $\chi^2_{1,51}=2.14$ ,  $p = 0.143$ ). Most puffins that were attacked (76.4%, 39/51) retained their prey, though several of these individuals (23.1%, 9/39) failed to enter their burrows because they took flight during the attack.

### 3.5 Discussion

I observed Atlantic puffins returning from sea to their burrows on Gull Island, NL, Canada. By focusing on approaches where a potentially kleptoparasitic gull was present on the slope near the puffin's burrow, I tested the behavioural reactions of Atlantic puffins to their risk of kleptoparasitism, as defined in Chapter 2 (*i.e.*, risk of attack and loss of prey as a function of bill load and landing behaviour). I predicted that puffins would be most likely to abort their landing whenever they approached with large prey, less likely to abort when they approached with small prey, and least likely to abort when their bill was empty. Consistent with my prediction, approaching puffins were more likely to abort their landings when approaching with food in their bills, though puffins carrying large prey were not more likely than those with small prey to abort. I also predicted that puffins with large prey would be more likely than puffins with small prey to land upslope and farther from the gull, and that puffins with any prey would be more likely than puffins without prey to land upslope and farther from the gull. Contrary to my prediction, I found no evidence that puffins alter the distance between their landing location and the focal gull or alter their landing position (upslope versus not upslope from the focal gull) based on their bill contents. Finally, I assessed the consequences of a puffin's landing position and found that landing upslope did not reduce the likelihood of being attacked or the likelihood of retaining their prey when they were attacked.

Puffins carrying prey were more likely than puffins without prey to abort their landing near a potentially kleptoparasitic gull. One possible explanation for this is that the gull altered its behaviour in response to a puffin approaching with food, and that the

puffin responded to these extrinsic cues by aborting its landing. A second possible explanation is that aborting a landing is a state-dependent behaviour that depends on whether or not the puffin is carrying food. My study design cannot distinguish between these two possibilities, and, to the best of my knowledge, no other study in the literature has distinguished between these two mechanisms either. In sandwich terns (*Sterna sandvicensis*), for example, individuals carrying larger prey spend more time flying around the colony than individuals carrying small prey, suggesting that the altered behaviour reduces the risk of being attacked by kleptoparasitic gulls (Dies & Dies, 2005). Yet it is also unclear whether sandwich terns are altering their behaviour in response to the food they are carrying (*i.e.*, state-dependent) or in response to differential cues provided by gulls targeting terns with large versus small prey. Future work should continue to focus on comparing the behaviour of puffins that are and are not at risk of kleptoparasitism by examining the landing choice of puffins with and without prey in areas where gulls are and are not present. This would shed light on how the puffin's behaviour changes in response to intrinsic and extrinsic cues of risk.

Regardless of the underlying mechanism, aborting a landing requires additional time and energy for the puffin and delays its chick being provisioned. However, because gulls only target puffins approaching with food (Chapter 2), and always fail to obtain food from a puffin that aborts its landing, the time and energy costs of aborting may be offset by the reduced risk of being kleptoparasitised. I note, however, that puffins carrying large prey were not more likely than puffins carrying small prey to abort their landing, despite the herring gull's preference to attack puffins with large versus small prey

(odds of attack were almost 400% higher for puffins approaching with large versus small prey; Chapter 2). Therefore, puffins adjust their behaviour in response to kleptoparasitic risk, but not in response to different degrees of risk. This result suggests that gulls and puffins value prey differently. Adult puffins provide the sole source of food to their chicks, so every catch may be equally valuable. Gulls, however, can afford to selectively target puffins carrying large prey because prey derived by kleptoparasitism compose only part of their overall diet. An alternative explanation that future studies may be able to shed light upon is that the puffin may perceive the increased risk, but its reaction speed is compromised by carrying a large load, and therefore, it is unable to adjust its behaviour.

Although gulls preferentially attack puffins that land closer to them while carrying prey (Chapter 2), puffins carrying prey were not more likely than puffins without prey to land farther from the gull. This is possibly a result of constraints on the landing locations of adult puffins. Adult puffins have a poor walking ability on land and, therefore, may have a particular location in which to land to efficiently deliver prey to their chick and to minimize the distance they must walk on land before entering the burrow. For example, the approaching puffin may disregard the gull's position and instead land in the location that facilitates the easiest or fastest burrow entry. Alternatively, the puffin may consider the location of the gull relative to its burrow rather than to itself. For instance, if a gull was located to the left of the puffin's burrow entrance, then the puffin could increase the distance between them by landing to the right of its burrow, as opposed to landing above, below, or to the left of its burrow. This study was unable to test these possibilities. Future studies could test this by determining whether puffins with food land closer to their



burrow entrance than puffins without food, or whether they land on the side of their burrow opposite a gull.

Previous studies investigating how puffins respond to kleptoparasitism risk were limited by technology and the lack of research on herring gull host choice, and, consequently did not or could not directly compare the behaviour of puffins with and without prey. With this study, I built upon this previous literature by explicitly testing for the first time the relationship between a puffin's bill contents (empty, small, or large prey) and its behaviour pre- and post landing. This study shows that puffins approaching burrows in close proximity to gulls actively mitigate their risk of being kleptoparasitised by adjusting their landing behaviour according to whether or not they have prey in their possession. Specifically, puffins approaching a burrow near a gull are more likely to abort their landing if they have prey in their bill.

### 3.6 Tables

Table 3.1 Results of the pairwise comparisons of a generalised linear mixed model (binary response, logit link, observation session as a random effect) predicting puffin landing choice (aborted or completed landing) as a function of bill load (large prey, small prey, or empty).

Pairwise Comparison	Estimate $\pm$ SE	Z	P
Large - Empty	2.36 $\pm$ 0.22	10.48	<0.001
Small - Empty	2.53 $\pm$ 0.24	10.43	<0.001
Small - Large	0.18 $\pm$ 0.24	0.72	>0.999

Puffins with unknown bill contents were excluded. Estimate =  $\beta$  regression coefficient  
SE = standard error

Significant p-values are in bold ( $p \leq 0.05$ ). Estimate and SE reported on a log-odds scale.  
N = 58 observation sessions and 1484 approaching puffins.

### 3.7 Figures

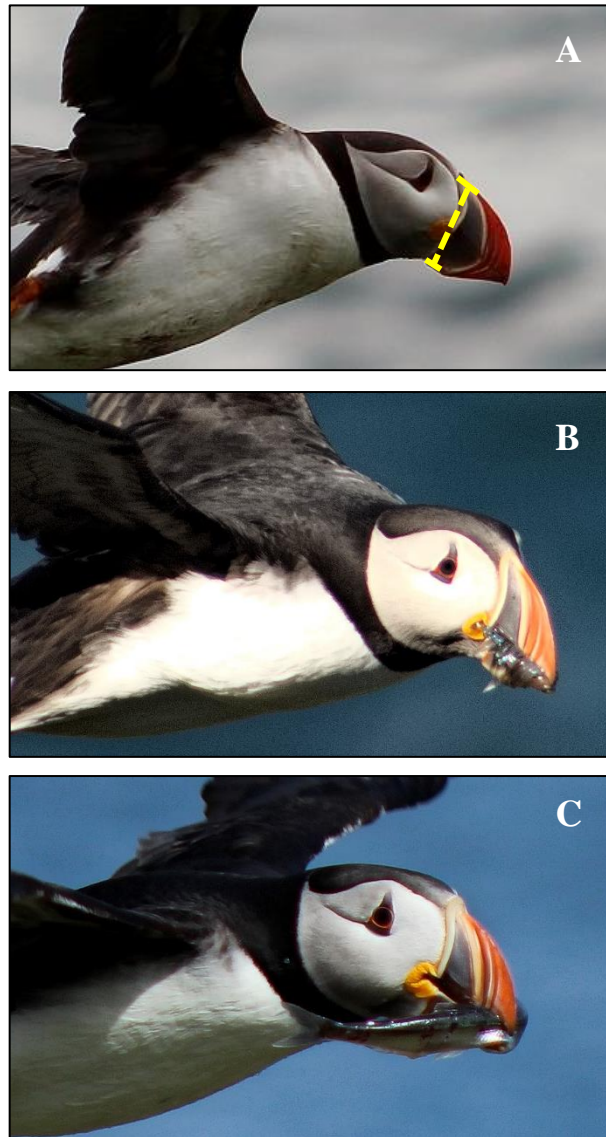


Figure 3.1 Three puffins in flight showing A) empty bill with a yellow dashed line indicating the bill depth B) small prey items, and C) a large prey item. Original figure in colour.

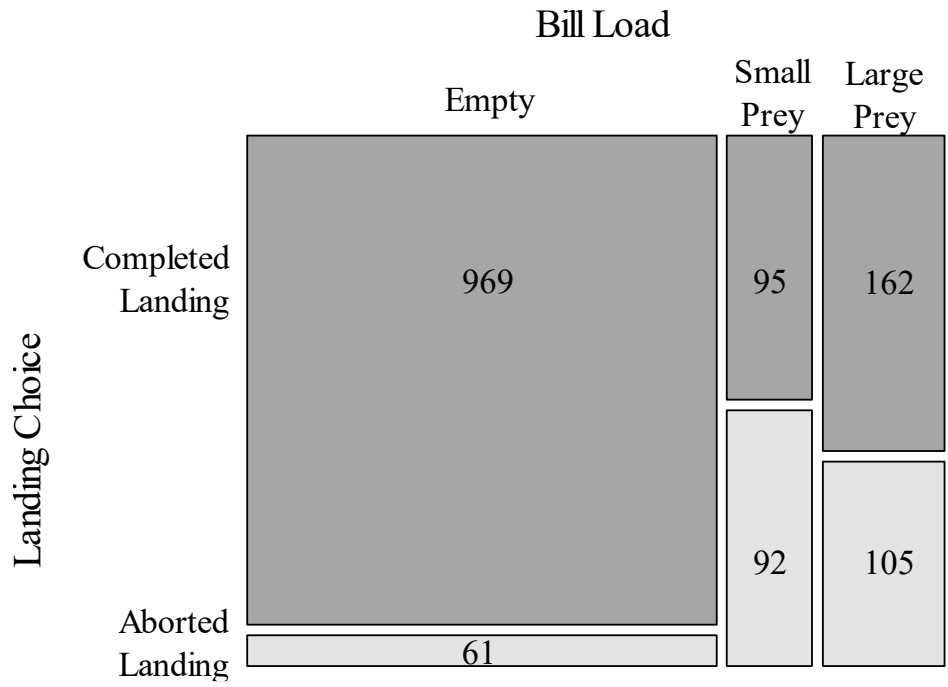


Figure 3.2 This mosaic plot illustrates the relationship between the puffin's bill load (explanatory variable) and its landing choice. Puffins were more likely to abort a landing when they carried small and large prey as compared to when they did not carry prey. There was no difference in the likelihood of aborting a landing when carrying small versus large prey.

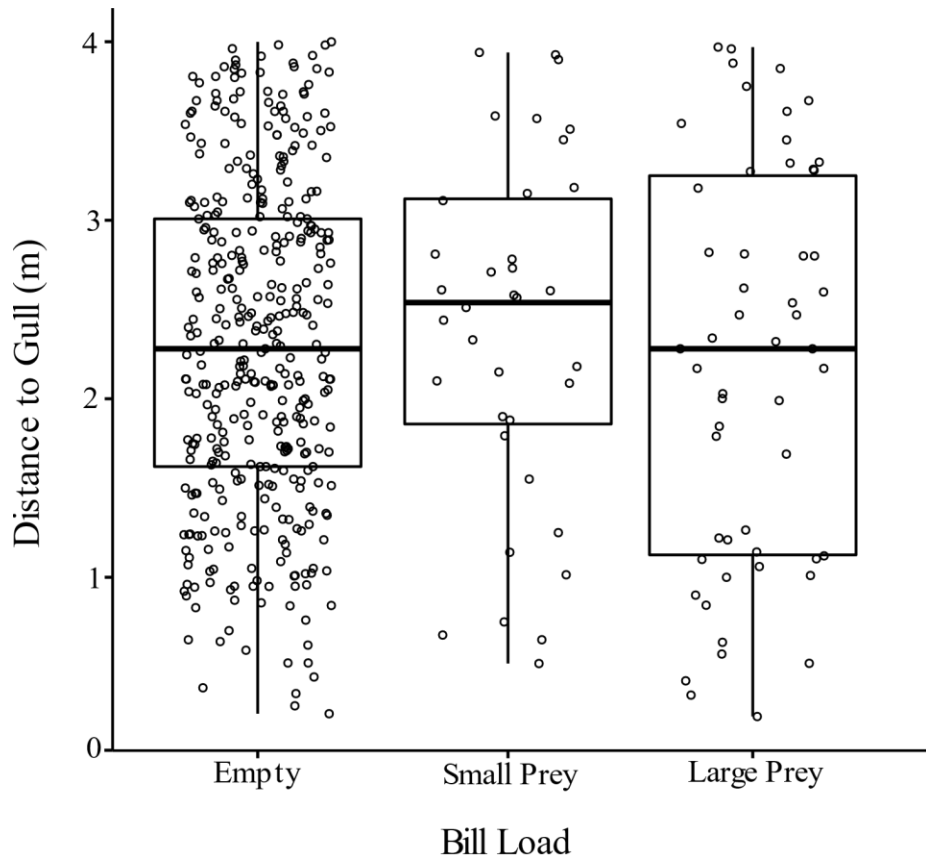


Figure 3.3 Box plots showing the distribution of the distance between the puffin and focal gull when landing with an empty bill, small prey, and large prey. The puffin's bill load did not influence the distance between the puffin and focal gull upon landing within the focal area.

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## **CHAPTER 4 GENERAL DISCUSSION AND CONCLUSION**

### **4.1 Introduction**

Kleptoparasitism is a form of interference competition where one individual engages in a direct interaction with another individual by stealing its procured food (Brockmann & Barnard, 1979; Rothschild & Clay, 1952). Kleptoparasitism can be a more profitable foraging strategy than self-foraging if the benefits of obtaining food through kleptoparasitism outweigh the associated costs, which include energy expenditure and the potential for injury (Case & Gilpin, 1974). In some species, individuals can optimize their foraging strategy by facultatively switching between kleptoparasitism and self-foraging (Tasker, Jones, Blake, & Dixon, 1985) and by selectively attacking more profitable hosts (Hopkins & Wiley, 1972). For example, hosts with more valuable and conspicuous prey are more likely to be kleptoparasitised; often this occurs when the host carries large prey items, which are often associated with a longer handling time (Lima et al., 1985) and more time for kleptoparasitism to occur (Amat & Aguilera, 1990; Dies & Dies, 2005; Hopkins & Wiley, 1972; Spencer et al., 2017). Many host species use behavioural tactics that can reduce the risk of being kleptoparasitised. For example, individuals may avoid kleptoparasitism by handling food underwater (Amat & Aguilera, 1989) or by delaying their landing when a kleptoparasite is nearby (Blackburn et al., 2009). Tactics for avoiding kleptoparasitism can be costly because they can impair the host's ability to see or add flight distance, time, and energy to a provisioning trip.

The relationship between the herring gull (*Larus argentatus*) and Atlantic puffin (*Fratercula arctica*) is a model example of kleptoparasitism. Gulls often establish territories and nests on top of the puffin burrowing slopes, in densely packed puffin colonies (Finney et al., 2001; Pierotti, 1982). When puffins and gulls are rearing their chicks, adult puffins follow predictable foraging patterns by carrying conspicuous prey items to their burrows to feed their chicks (Brockmann & Barnard, 1979; Harris & Wanless, 2011). Herring gulls can intercept the returning puffins by lunging towards them and grabbing onto them, sometimes causing the puffins to drop their prey (Hudson, 1985; Pierotti, 1983; Rice, 1987). My objectives for this thesis were to identify factors associated with gull host choice and to explore how puffins mitigated their risk of being attacked. I also investigated how the behavioural choices of the gull and puffin influenced the outcome of a kleptoparasitic attack.

#### 4.2 Results Summary

In Chapter 2, I showed that herring gulls preferentially attack puffins that land in front of them, that are carrying larger prey items, that complete their landings, and that land in closer proximity to the gull. Some of these choices suggest that gulls are targeting hosts to optimize the gull's energy gain by either increasing the likelihood of success, decreasing the gull's energy use, or targeting individuals with more profitable prey. Puffins adjusted their decision to abort based on their bill contents, where those carrying large or small prey aborted more often than those that did not possess prey. This decision suggests that puffins are also optimizing their behaviour, based on either their state (prey or no prey) or by subtle cues exhibited by gulls in response to a puffin approaching with

prey (e.g., crouching or moving towards the puffin's probable landing location). Puffins used landing choice as an effective tactic for avoiding kleptoparasitism. By aborting their landings, puffins were less likely to be attacked, and, of those that were attacked during an aborted landing, none lost their prey. Puffins did not always behave as expected, however, as they did not show a tendency to abort their landings more often when carrying large prey versus small prey, despite a gull's preference to attack puffins with large versus small prey. Similarly, puffins did not alter the distance between their landing location and the gull when landing with prey, despite the gull's preference to attack puffins landing in closer proximity.

While conducting the current study, I also collected data describing diel and seasonal variation in the rates of puffin provisioning and associated kleptoparasitism. As this information has yet to be reported in the literature, I have included it as supplementary information in this thesis. I determined that gulls attempt to kleptoparasitise puffins throughout the daylight hours (0500 to 2100h) and throughout the entire season when puffins are provisioning their chicks. Puffins provisioned most actively in the morning, whereas gulls kleptoparasitised most actively in the afternoon, suggesting that the odds of a puffin losing its prey to a gull are highest in the afternoon. A possible explanation for why gulls engage in kleptoparasitism most often during the period of low puffin provisioning is that the gulls may be better able to target approaching puffins that have prey when fewer puffins are landing at once. Puffin provisioning also peaked seasonally between 14 and 21 days after their median hatch date, which corresponds to when all viable eggs had hatched. Gull hatching was not monitored

systematically, but I observed chicks hatching in late-June to early-July. Therefore, gull chicks ranged from being the same age as puffin chicks to approximately three weeks older. The seasonal pattern mirrors that described for puffins in European colonies (Cook & Hamer, 1997). There were no apparent patterns in seasonal kleptoparasitic pressure; instead, puffins were at risk throughout the entire chick-rearing period.

#### 4.3 Contributions to the Literature

Research on kleptoparasitism has contributed valuable insight into how animals optimize their foraging strategies by making rapid decisions and adjustments to their behaviour. Specifically, many studies have compared the host's prey size with its likelihood of being kleptoparasitised, and showed that kleptoparasites seem sensitive to prey size during these often rapid interactions (Hopkins & Wiley, 1972; Ratcliffe et al., 1997; Spencer et al., 2017). However, as many studies have indicated, prey size is often positively correlated with the host's handling time, so it is often unclear whether kleptoparasites target hosts with larger prey because of the increased reward or because of the increased time and opportunity for attack.

The herring gull – Atlantic puffin system provides an avenue to explore prey size without the confound of handling time because the majority of handling occurs within a burrow inaccessible to the gull. However, puffins are still vulnerable to kleptoparasitism when they land on the slope with prey before entering their burrow. In this study, prey-carrying puffins that ultimately entered their burrow spent a median of  $1.0 \text{ s} \pm 15.3 \text{ SE}$  (N=97) on the slope. I suspect that the duration of time a puffin spends on the slope will not be associated with their likelihood of being attacked, since gulls appear to choose

their host while the puffins are still flying towards the slope (personal observation; Harris & Wanless, 2011). During kleptoparasitic attacks, I often observed gulls making anticipatory movements towards the puffin's landing location in the seconds before the puffin landed. Gulls, therefore, appear to choose their hosts based on prey size, as opposed to the increased handling time that is commonly associated with larger prey in other systems; however, a study is still needed to statistically rule out the association between time spent on the slope and vulnerability to kleptoparasitism. At this point, it remains unclear whether gulls assess prey size per se, or whether targeting is based on the increased conspicuousness or caloric value associated with larger prey, or alternatively, if puffins carrying large loads have a slower reaction time leaving them more vulnerable to kleptoparasitic attack. Nevertheless, this study provides valuable insight into decision making by kleptoparasites by beginning to separate characteristics of the prey from the host's prey handling time and the associated opportunities for the kleptoparasite to attack.

I showed that Atlantic puffins do adjust their behaviour in a way that minimizes their risk of prey loss. Puffins may use external cues to decide whether or not to land while carrying conspicuous prey or may rely purely on their state (prey or no prey). A likely external cue is the herring gull subtly changing its behaviour as it observes an incoming puffin with prey. For example, from observations during fieldwork and video analysis, I observed some herring gulls seemingly tracking incoming puffins carrying prey by panning their head as the puffin flew in, as well as some gulls seemingly crouching lower to the ground as the puffin flew above them. It is possible that the puffin is responding to these cues displayed by the gull when assessing its risk of

kleptoparasitism. It is also possible that puffins recognize their risk of kleptoparasitism when carrying versus not carrying prey and adjust their landing choice accordingly. As with many aspects of behavioural ecology, these two mechanisms may not be mutually exclusive, and puffins may consider both their state and the gull's behaviour when choosing whether or not to land.

#### 4.4 Limitations

There are three main limitations that should be considered when assessing the conclusions of this study. First, this study could not account for puffin identity, so it is possible that the same individual was observed during multiple focal observation sessions or during multiple visits within a session. However, the low burrow visitation rates of puffins (4.67 visits per day  $\pm$  0.59, mean  $\pm$  SE; Rector, 2011), combined with the short focal sampling sessions (30 min) over various colony locations, suggests that most observations were based on different individuals. Nevertheless, future research involving identifiable puffins would remove this concern by allowing puffin identification to be included as a random effect in the statistical models. Second, I could not include gull identity in some of my statistical models examining the outcome (success) of kleptoparasitic attacks because the small number of attacks would cause the models to fail to converge. Future research could address this limitation by sampling individual gulls for a longer period of time to ensure a sufficient number of observed attacks per gull. Third, the results of this thesis were based on one year of data collected on Gull Island. It is possible that seasonal changes to prey abundance, specifically capelin, or changes to the weather (*i.e.*, unseasonably cold, or wet weather) may change the costs and benefits of

engaging in kleptoparasitism or avoidance behaviour. Anecdotally, during the 2017 field season gulls also appeared to preferentially target puffins in closer proximity and those carrying larger prey, but, unfortunately, those data could not be included in this thesis due to changes in methodology.

#### 4.5 Future Work

There are several avenues for extending this research. First, research involving identifiable puffins could test whether different puffins experience different levels of kleptoparasitic risk, and whether they employ different tactics for avoiding kleptoparasitism. Second, understanding factors such as prey availability and how the gulls use prey stolen from puffins would help explain the behavioural choices by both the gull and puffin. For example, it is possible that the gulls and puffins may be more motivated to steal or protect their prey at different stages of chick development, or during periods of prey scarcity. This research could fully account for the costs and benefits experienced by both puffins and gulls, as suggested by Rice (1987). Third, future research should develop models that test whether the puffins and gulls are behaving in ways that optimize their foraging strategies and ability to fledge chicks. On many occasions, I observed that the prey stolen from puffins was fed to the herring gull's chick, and I suspect that the additional calories it provided would have been advantageous to the herring gull's reproductive success. Finally, future work should aim to understand how both puffins and gulls interact with their environment by building on the work conducted by Nettleship (1972). Nettleship (1972) found that puffins nesting on level habitat were more likely to be attacked as compared to those nesting on sloped habitat. It is possible

that puffins and gulls that nest in different habitats use different tactics to commit or avoid kleptoparasitism. This work was conducted solely on grassy marine slopes and, therefore, there is potential to study puffins nesting in rock crevasses and those on plateaus.

#### 4.6 General Conclusions

This study built upon decades of research into avian kleptoparasitic research by investigating herring gull host choice and Atlantic puffin avoidance behaviours, as well as the consequences of the behaviours. To my knowledge, this is the first study of behavioural choices in a kleptoparasitic system that considers the perspective of both the kleptoparasite and the host, particularly within the herring gull – Atlantic puffin system. In addition, this study showed that herring gulls do not attack puffins at random and have clear preferences of host choice, many of which increase their foraging efficiency. Finally, to my knowledge this is the first study to consider behavioural differences between avian hosts that are and are not at risk of kleptoparasitism by testing the avoidance behaviour of individual Atlantic puffins.



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#### 4.8 Supplementary Information

This supplementary information includes data incidentally collected during field work for Chapters 2 and 3 which was useful for describing diel and seasonal variation in the rates of puffin provisioning and associated kleptoparasitism. To my knowledge these patterns have not been reported in the literature but may be useful to researchers designing efficient experiments.

From 27 June to 21 July 2018, I monitored 39 individually identified puffin burrows (burrows containing either an egg or an adult bird) using a burrow scope (Peep-a-Roo video probe, Sandpiper Technologies, Manteca, CA) and manual checks (gently feeling the inside of the burrow, a technique known as grubbing) to determine hatch date (accuracy:  $\pm 1.5$  days). Known hatch dates allowed the seasonal trends to be interpreted within the context of the puffin's breeding cycle. The contents of each burrow were recorded with the following options in different combinations: adult, egg (warm, cool, cold, hatching or pipped), chick (wet or fluffy), or empty.

Using the same dataset used in Chapters 2 and 3, I used 57 independent focal samples of individual herring gulls (average length  $\pm$  SD:  $24.2 \pm 7.2$  min; total 23.0 h) to estimate the rate of puffin provisioning and kleptoparasitism within a standard area of  $50 \text{ m}^2$  (*i.e.*, an area with a 4-m radius around the focal gull). I excluded a total of 16 focal samples for this analysis due to the camera perspective potentially leading to inaccurate distance measurements and observations which occurred in the same video as a previous sample that would have led to counting some individual puffins more than once. I

excluded all events where a puffin did not complete a landing within the focal area or had unknown bill contents.

Using each focal gull as the unit of replication, I determined the rate at which puffins landed with full bill loads ( $\text{h}^{-1}$ ; “rate of puffin provisioning”), the rate at which puffins landing with full bill loads were attacked ( $\text{h}^{-1}$ ; “rate of focal gull attack”), and the proportion of provisioning puffins that were attacked in relation to the total number of provisioning puffins. If no provisioning puffins landed within 4 m of a focal gull ( $N = 8$  focal gulls), the rate of focal gull attack and the proportion of provisioning puffins attacked were excluded, as the gull did not have an opportunity to kleptoparasitise. I sorted each focal session into 2-h time bins (starting at 0500h and ending at 2100h) and 8-day seasonal bins (beginning six days after the median hatch date of 39 monitored puffin burrows and ending 37 days later). I then calculated the average rate ( $\pm$  SE) of puffin provisioning ( $\text{h}^{-1}$ ), the average rate ( $\pm$  SE) of focal gull attack ( $\text{h}^{-1}$ ), and the average proportion ( $\pm$  SE) of provisioning puffins that were attacked for each hourly (Figure 4.1) and seasonal (Figure 4.2) bin.

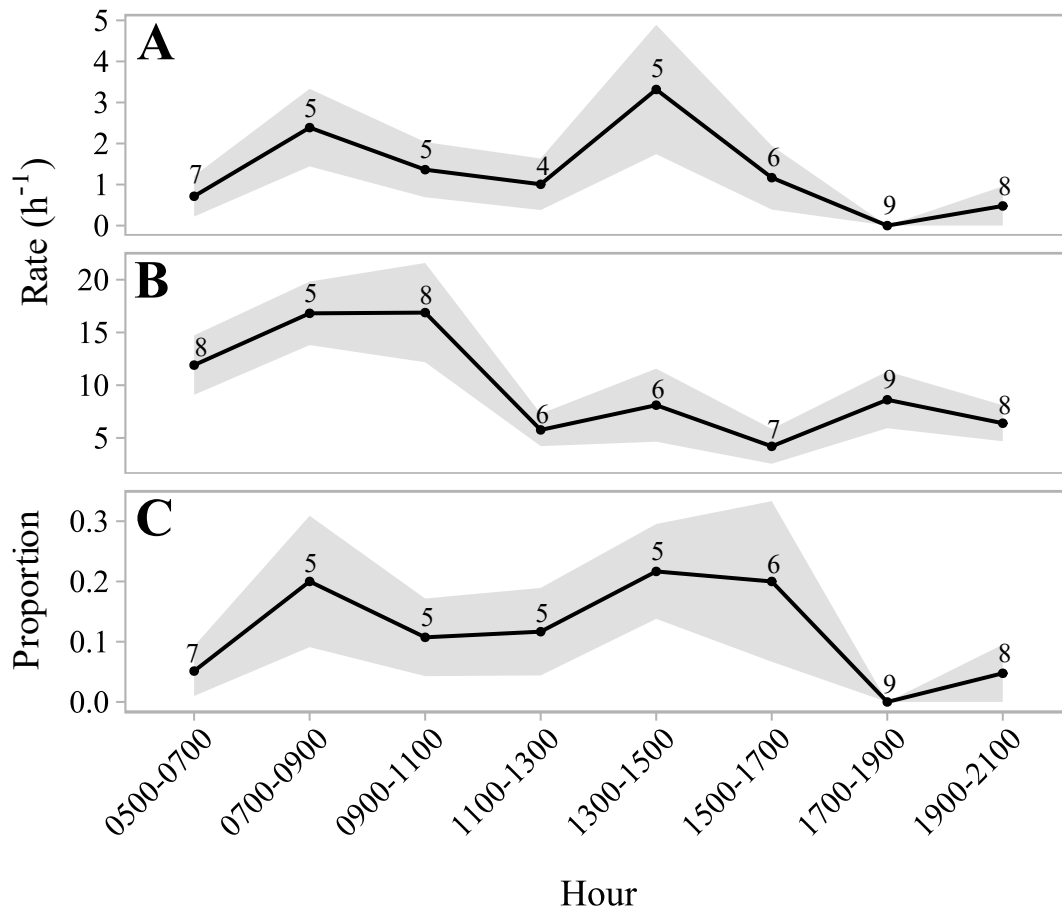


Figure 4.1 Diel variation, displayed in two-hour bins, of A) the mean rate of attack by focal gulls (number of attacks per hour  $\pm$  SE), B) the mean rate of provisioning puffins landing within 4 m of a focal gull (number of puffins landing with prey per hour  $\pm$  SE) and C) the mean proportion of provisioning puffins landing within 4 m of a focal gull that are attacked ( $\pm$  SE). Replicates were based on 30-minute focal sessions, which were each based on a different gull and the 4-m radius around it. The numbers above the line indicate the number of focal sessions included for each bin. Gulls were excluded from the calculation of kleptoparasitism rate and proportion if no puffins landed within 4 m of them during their focal session (N = 8).

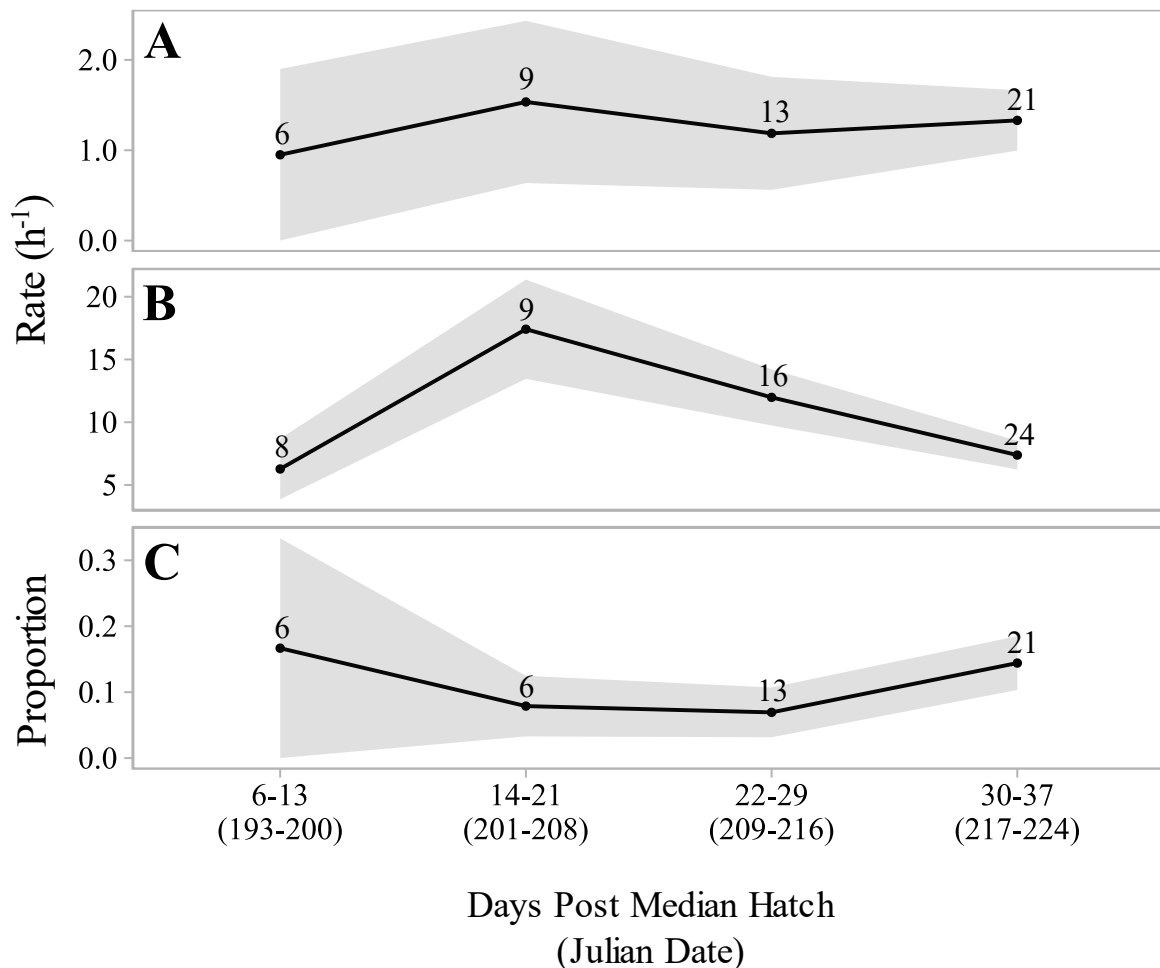


Figure 4.2 Seasonal variation, displayed in eight-day bins, of A) the mean rate of attack by focal gulls (number of attacks per hour  $\pm$  SE), B) the mean rate of provisioning puffins landing within 4 m of a focal gull (number of puffins with prey landing per hour  $\pm$  SE), and C) the mean proportion of provisioning puffins landing within 4 m of a focal gull that are attacked ( $\pm$  SE). Replicates were based on 30-minute focal sessions, which were each based on a different gull and the 4-m radius around it. The numbers above the line indicate the number of focal sessions included for each bin. Gulls were excluded from the calculation of kleptoparasitism rate and proportion if no puffins landed within 4 m of them during their focal session (N = 8).