FORAGING ECOLOGY OF AN AVIAN PREDATOR, THE HERRING GULL AND ITS COLONIAL EIDER DUCK PREY

by

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ABSTRACT

Behavioural studies of predator and prey are often made difficult by inability to quantify key parameters (e.g. prey densities) necessary for testing predictions derived from theoretical models. This is especially true of multi-species systems where trophic interactions are complex, and in habitats where observation of behaviour is hindered by complex habitat structure (e.g. dense vegetation, irregular terrain), limited accessibility (e.g. marine systems), low densities of species of interest, large-scale movement patterns, periods of darkness, and situations where foraging and reproduction are spatially segregated. Studies can also be compromised by disturbance (e.g. visits by researchers). Selection of a simple system in combination with different data gathering approaches can create opportunities for understanding behaviour, and sources of temporal and spatial variation.

I studied predator-prey interaction, focussing on the relationship between breeding herring gulls (*Larus argentatus*) and their common eider (*Somateria mollissima*) prey at the East Bay Migratory Bird Sanctuary in the eastern Canadian Arctic. At this location, herring gulls are distributed on a low-lying coastal plain and on a small treeless colony island with common eiders. Here, the relative simplicity of species assemblages, long daylight periods, lack of tall vegetation, quantifiable predator and prey densities, and behavioural, foraging and breeding parameters, make conditions ideal for gathering empirical data essential in exploring theoretical models of foraging behaviour.

I found that herring gulls modified their foraging activity in accordance with predictions derived from Optimal Foraging and Alternative Prey models. Specifically,
gulls searched more when net costs of foraging were reduced, and gull foraging intensity was highest in low lemming-abundance years. I also found that gull foraging decisions were modulated by risk of injury from aggressively defensive eider females. For example, gulls attempting to capture eider ducklings took more risks (i.e. were more likely to elicit aggressive defensive response from adult females) during years when lemming abundance was low. However, if environmental conditions were not conducive to lower-risk attack modes, likelihood of gull attack success was greatly reduced. Lastly, by way of a food supplementation experiment, I found that gull territorial attendance varied in relation to prey abundance within their respective territories, and that pair members allocated time within territorial boundaries in a way that increase defence of prey resources. This demonstrated that food resources within territories contributed to determining the proportion of time used toward extraterritorial forays.

I found that environmental conditions, risks of injury from reactive prey, differences in relative availability of prey arising from prey behaviour, the availability of alternative prey, and gull territorial behaviour, influenced gull foraging behaviour.
DEDICATION

The process that made this work possible was the result of a series of gracious, if not
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# TABLE OF CONTENTS

ABSTRACT ....................................................................................................................... ii
DEDICATION .................................................................................................................. iv
TABLE OF CONTENTS ................................................................................................. vi
LIST OF TABLES .......................................................................................................... vii
LIST OF FIGURES .......................................................................................................... x

CHAPTER 1 ...................................................................................................................... 1
General Introduction

CHAPTER 2 .................................................................................................................... 32
Foraging ecology of an avian predator, the herring gull: interactions between environmental conditions, prey behaviour, and functional prey availability

CHAPTER 3 .................................................................................................................... 84
Herring gulls depredating eider ducklings: interaction among environmental conditions, indirect trophic relationships, and risk

CHAPTER 4 .................................................................................................................. 142
Causes and consequences of variation in attendance of foraging territories by breeding herring gulls: An experimental study

CHAPTER 5 .................................................................................................................. 184
Conclusion

CURRICULUM VITAE
LIST OF TABLES

Table 2.1 Generalized linear models used to determine factors affecting gull counts (n=593) at the East Bay island colony, in 2000 and 2001 .................................................. 69

Table 2.2 Model-averaged parameter estimates and their 95% confidence intervals, from generalized linear models of gull counts (n=593) at the East Bay island colony, in 2000 and 2001 ........................................................................... 70

Table 2.3 Generalized linear models used to determine factors affecting overall and relative herring gull air search rates in eider nesting areas within 30 min periods (n=593) at the East Bay island colony, in 2000 and 2001 .............. 71

Table 2.4 Generalized linear models used to determine factors affecting overall and relative herring gull ground search rates in eider nesting areas within 30 min periods (n=593) at the East Bay island colony, in 2000 and 2001 ............................................. 72

Table 2.5 Exponentiated model-averaged parameter estimates representing Incident Rate Ratios (IRR) and their 95% confidence intervals, from generalized linear models of overall and relative herring gull search rates in eider nesting areas within 30 min periods (n=593) at the East Bay island colony, in 2000 and 2001 .............................................................. 73

Table 2.6 Generalized linear models used to determine factors affecting overall and relative herring gull search rates in eider nesting areas within 180 min periods (n=274) at the East Bay island colony, in 2000 and 2001 .............................................. 74

Table 2.7 Exponentiated model-averaged parameter estimates representing Incident Rate Ratios (IRR) and their 95% confidence intervals, from generalized linear models of overall and relative herring gull foraging activity rates in eider nesting areas within 180 min periods (n=274) at the East Bay island colony, in 2000 and 2001 .............................................................. 75

Table 2.8 Generalized linear models used to determine factors affecting overall and relative herring gull egg capture rates in eider nesting areas within 180 min periods (n=274) at the East Bay island colony, in 2000 and 2001; global model is shown in bold text .............................................................. 76

Table 3.1 Summary of lemming observations from the colony island and from a 2 X 2 kilometre study plot on the adjacent mainland coastal plain, by year .......... 122

Table 3.2 Summary of observations of focal broods (n=631) and herring gull search and duckling capture frequencies, by year ............................................. 123
Table 3.3 Generalized linear models used to determine factors affecting counts (n=90) of eider broods in transit undertaken in 2000 ................................................ 124

Table 3.4 Results of generalized linear models of counts of eider broods in transit obtained from scans (n=90) in 2000 ............................................................... 125

Table 3.5 Generalized linear models used to determine factors affecting herring gull total counts (n=102) obtained from scans of the colony from 2000 to 2002 inclusive ..........................................................................................................................126

Table 3.6 Results of generalized linear models of herring gull counts (n=102) obtained from scans of the colony from 2000 to 2002 inclusive ................................................ 127

Table 3.7 Generalized linear models used to determine factors affecting rates of air searches, of departing eider broods (n=631) by herring gulls from 1999 to 2003 inclusive ................................................................................................................128

Table 3.8 Generalized linear models used to determine factors affecting rates of ground searches of departing eider broods (n=631) by herring gulls from 1999 to 2003 inclusive ................................................................................................................129

Table 3.9 Results of negative binomial models of factors affecting search and duckling capture rates associated with departing eider broods (n=631) ....................130

Table 3.10 Generalized linear models used to determine factors affecting rates of duckling captures, from departing eider broods (n=631) by herring gulls from 1999 to 2002 inclusive ..................................................................................................131

Table 3.11 Pearson correlations among search, and search and duckling capture, frequencies per brood hour by year .......................................................... 132

Table 3.12 Summary of mean numbers of hens, ducklings, and hen to duckling ratios (SE) calculated upon commencement of individual focal brood observations, by year .............................................................. 133

Table 3.13 Frequencies of herring gull searches including total searches, total hen reaction, and occurrences of physical contact with eider hens ...................... 134

Table 4.1 Generalized linear models (generalized estimating equations) of components of daily male and female territorial attendance in relation to food (provided and self-procured), and day of year .......................................................... 172

Table 4.2 Generalized linear models (generalized estimating equations) of intrusion rate, intrusion duration, chase likelihood and likelihood of egg removal by intruders; for 2170 intrusions into six territories ................................................... 173
Table 4.3 Generalized linear models (generalized estimating equations) of duration, chase likelihood and likelihood of egg removal for 332 intrusions committed by known intruders (N=31) ...................................................... 174

Table 4.4 Generalized linear models (generalized estimating equations) of egg captures within six territories by their respective residents, and by intruders ........ 175
LIST OF FIGURES

Fig. 2.1a Year 1999 densities of incubated eider clutches (nests per hectare) and mean daily predation rates in relation to ice break-up and day of year .......................... 77

Fig. 2.1b Year 2000 densities of incubated eider clutches (nests per hectare) and mean daily predation rates in relation to ice break-up and day of year ...................... 78

Fig. 2.1c Year 2001 densities of incubated eider clutches (nests per hectare) and mean daily predation rates in relation to ice break-up and day of year ...................... 79

Fig. 2.2a Daily temperatures (°C) by year. The line within the box indicates the median, box limits represent 25th and 75th percentiles, whiskers represent 10th and 90th percentiles .............................................................................................. 80

Fig. 2.2b Daily wind speeds (km/h) by year. The line within the box indicates the median, box limits represent 25th and 75th percentiles, whiskers represent 10th and 90th percentiles .............................................................................................. 81

Fig. 2.3 Overall search and egg capture rates (per ha per 30 min) versus wind speed (km/h) calculated using all available data from years 2000 and 2001 pooled .................................................................................................................. 82

Fig. 2.4 Percentage of gull ground searches that elicited active defensive responses (all behavioural categories combined) from breeding eiders in relation to plot densities (nests/ha) in 1999, 2000 and 2001 combined ........................................ 83

Fig. 3.1 Number of common eider nests initiated per hectare by year on the island, calculated through summing counts from three nesting plots representing 1.13 of approximately 16 ha used for eider nesting .................................................... 135

Fig. 3.2 Wind speeds from first to last focal brood observation inclusively by year ......................................................................................................................... 136

Fig. 3.3 Temperatures measured every half-hour from first to last focal brood observation inclusively by year .................................................................................. 137

Fig. 3.4 Search and duckling capture rates (per brood per hour) in relation to day period for 631 eider broods observed from 1999 to 2003 ........................................ 138

Fig. 3.5 Annual variation in foraging activity (number of searches and duckling captures per h brood observed) by herring gulls within the eider colony from 1999 to 2003 ......................................................... 139
Fig. 3.6 Search and duckling capture rates (per brood per hour) in relation to wind speed (km/h) for 631 departing eider broods observed from 1999 to 2003 ... 140

Fig. 3.7 Search and duckling capture rates (per hour) in relation to different location type from 1999 to 2003 .......................................................................................... 141

Fig. 4.1 Relationship between territory size and number of active eider nests in 11 and 6 territories, in 2001 and 2002 respectively ....................................................... 176

Fig. 4.2 Relationship between territory area and active eider nest densities within 11 and 6 territories in 2001 and 2002 respectively ....................................................... 177

Fig. 4.3 Percentage of total time females from six territories spent in both incubation and non-incubation within their respective territories, and response to food intake (provided and self-procured) based on a combined total of 866.25 hours of observation during 18 days of incubation....................................................... 178

Fig. 4.4 Percentage of total time females from six territories spent in incubation within their respective territories, and response to food intake (provided and self-procured) based on a combined total of 866.25 hours of observation during 18 days of incubation....................................................... 179

Fig. 4.5 Percentage of total time females from six territories spent in non-incubation within their respective territories, and response to food intake (provided and self-procured) based on a combined total of 866.25 hours of observation during 18 days of incubation....................................................... 180

Fig. 4.6 Percentage of total time males from six territories spent in both incubation and non-incubation within their respective territories, and response to food intake (provided and self-procured) based on a combined total of 866.25 hours of observation during 18 days of incubation....................................................... 181

Fig. 4.7 Percentage of total time males from six territories spent in incubation within their respective territories, and response to food intake (provided and self-procured) based on a combined total of 866.25 hours of observation during 18 days of incubation....................................................... 182

Fig. 4.8 Percentage of total time males from six territories spent in non-incubation within their respective territories, and response to food intake (provided and self-procured) based on a combined total of 866.25 hours of observation during 18 days of incubation....................................................... 183
Chapter 1

General Introduction

Theoretical ecological models have enhanced greatly our understanding of ecological relationships. However, inability to accurately quantify key parameters necessary for testing predictions derived from theoretical models (e.g. prey densities in behavioural studies of predator and prey) can constitute a significant challenge. This is especially true of multi-species systems where trophic interactions are complex, and in habitats where observation of behaviour is hindered by complex habitat structure (e.g. dense vegetation, irregular terrain), limited accessibility (e.g. marine systems), low densities of species of interest, large-scale movement patterns, periods of darkness, and situations where foraging and reproduction are spatially segregated. Studies can also be compromised by disturbance (e.g. visits by researchers). Selection of a simple system in combination with different data gathering approaches can create valuable opportunities for understanding behaviour, and sources of temporal and spatial variation.

Theoretical perspectives on foraging behaviour

Optimal Foraging

While optimality theory initially generated the understanding that evolution leads to optimal solutions to problems faced by individuals, its application has shifted. More recently, it has been used as a means of testing our knowledge and understanding of
biological constraints that influence the results of evolution (Parker and Maynard-Smith 1990). Optimal Foraging Theory is based on the assumption that fitness is maximized through the optimization of food intake and that natural selection tends to favour individuals that forage optimally (Stephens and Krebs 1986). Avian predator-prey systems have been used successfully to test predictions of Optimal Foraging theory (Zach 1979, Gilchrist et al. 1998, Jetz et al. 2003, Sergio 2003). As individual foraging behaviour affects individual energy balance, Maurer (1996) presents the following general foraging model designed to help evaluate costs and benefits of foraging on rate of energy intake where E is the amount of energy obtained during the time T spent foraging:

\[ \frac{E}{T} = \frac{(E_t - E_f - E_p - E_i)}{(T_s + T_h + T_p + T_i)} \]

Where:

- \( E_t \) = total assimilable energy obtained during foraging
- \( E_f \) = energy spent searching, pursuing, and handling food
- \( E_p \) = energy spent in physiological processing of food
- \( E_i \) = energy spent in interactions with other organisms during foraging
- \( T_s \) = time spent searching for and pursuing food
- \( T_h \) = time spent handling food
- \( T_p \) = time spent during physiological processing of food
- \( T_i \) = time spent interacting with other organisms during foraging

Although other optimality models exist (Stephens and Krebs 1986), the Maurer model exemplifies the interplay of temporal and energetic foraging parameters. Following this model, avian predators are predicted to optimize the rate of energetic intake.
through use of tactics that, either singly or in combination, increase net energy gain. For example, this could be achieved by: 1) lowering time and/or energy spent searching through increased detection rates by foraging when visibility conditions are best, 2) lowering time and/or energy spent in physiological processing of food by ingesting only the digestible parts of prey, 3) lowering time and/or energy spent interacting with other organisms by foraging in unexploited patches, 4) lowering time and/or energy spent searching through increasing encounter rates with prey by foraging in areas of densely distributed prey, 5) lowering time and/or energy spent searching for prey by selecting energy-efficient foraging modes, or 6) combinations of these.

Lotka (1925) stated that the direction of evolution is largely a result of the ability of organisms to obtain and process energy rapidly and efficiently. Early foraging models were based on systems involving predators preying upon effectively non-reactive prey and under few constraints. Consequently, they were generally unsuitable for describing complex relationships between predators and prey occurring in the wild (Lima 2002). In reality, predators are often subjected to varied constraints that include environmental and biological factors, as well as the behaviour of defensive prey and competitors (conspecific or not) (Funston et al. 2001, Brown and Kotler 2004, Morris 2005). Now, Optimal Foraging theorists suggest animals should forage in ways that optimize behaviour, rather than simply maximizing of rates of energy intake (Stephens and Krebs 1986). Thus, animals can be expected to optimize foraging behaviour within changing constraints imposed by competition, risk of
predation, risk of injury, phylogenetic, environmental, and behavioural considerations, in ways that maximize fitness.

Critics of Optimal Foraging theory view models as useful in predicting only some, but not all, aspects of an animal's foraging behaviour. Pyke (1984) warned that a number of assumptions need to be considered before using predictions derived from Optimal Foraging models. First, the exact relationship between foraging traits constituting the foraging apparatus (see below) and fitness are often largely unknown. Foraging apparatus can be defined as the set of morphological, physiological and behavioural traits that individuals possess that influence their ability to forage and maintain a positive energy balance (Maurer 1996). These traits can include size and shape of external structures (e.g. wings, bill) required for foraging, digestive efficiency (Karasov 1990), and individual response to sensory stimulus when foraging. Second, Optimal Foraging models assume that traits of the 'foraging apparatus' are heritable, yet although heritability of morphological traits has been demonstrated, little is known of the heritability of physiological and behavioural traits. Third, potential problems arise when models assume that adaptations of the foraging apparatus result from conditions and characteristics of the current environment only (Gould and Lewontin 1979). Violation of these assumptions may lead to incorrect conclusions, or conclusions that may be correct but for unknown reasons (Maurer 1996). Despite these limitations Optimal Foraging models continue to offer a framework that is useful to investigators interested in behavioural tactics and trade-offs (Stephens and Krebs 1986).
Alternative Prey Theory and switching

The ability to shift behavioural foraging modes when faced with changes to the availability of resources of different quality can have important energetic consequences (Helfman 1990), and this flexibility may itself be selected as a foraging trait (Morse 1971). The measure of variability in a food resource has been defined as 'risk' (Stephens and Krebs 1986). The risk sensitivity hypothesis derived from the latter definition states that individuals that select patches with highly variable food supply are considered risk-prone while individuals that select patches with reliable food supply are risk-averse. By sampling (i.e. foraging in) and gaining information on variable and reliable food patches, individuals gain the option to switch from one patch to another. Stephens and Charnov (1982) presented a model that predicts individuals should spend more time sampling a variable patch than a reliable patch when the foraging value of the reliable patch drops below the average value of the variable patch.

Similarly, the Alternative Prey Hypothesis (Lack 1954, Angelstam et al. 1984) predicts that impacts of predation on alternative prey will vary with changing availability of focal prey, as the numerical and functional responses of predators fluctuate in relation to changing availability of focal prey. It further predicts that impacts on alternative prey will be greatest immediately following a marked decrease in the availability of focal prey (e.g. the year after the peak in small mammal abundance). Empirical evidence in support of the hypothesis is widespread (Abrams and Matsuda 1996, Wilson and Bromley 2001, Koch et al. 2005, Nyström et al. 2005). Although numerous studies have examined numerical and functional responses of
predators, few have examined how the latter responses are modulated by environmental conditions (Jetz et al. 2003, Sergio 2003, Quinn and Cresswell 2004). Although state-dependent risk-taking by predators has been assessed (Richards 1983, Houston 1993, Sherratt 2003), interplay among environmental conditions, fluctuation in focal prey availability and risk-taking by predators has not.

**Injury risk**

In contrast to the definition presented above, risk has also been defined more intuitively as a measure of probability of injury (or death) while foraging. Risk of injury (or death, typically via predation) constitutes a constraint to optimal foraging that can lead to less-than-maximal energy intake rates for foraging individuals. While most studies have focused on assessing risk of predation or injury for prey species as a foraging constraint (Quinn and Cresswell 2004), relatively few have examined the influence of risk of injury for the foraging predator (Gilchrist et al. 1998, Gilchrist 1999, Bèty et al. 2002, Sherratt 2003). It is reasonable to expect that any factor that potentially can compromise survival during foraging (e.g. exposure to predators, agonistic encounters with conspecifics, agonistic encounters with prey, etc.) can constitute additional constraints to foraging.

**Territoriality**

Better competitors are typically energetically more efficient and incur lower foraging costs (Sutherland 1996); and they may also be expected to occupy better patches, such that the quality of a given exploited patch is related to an individual’s foraging and/or competitive ability, as well as the density of competitors and/or prey.
Phenotypic differences between individuals that can include age, sex, size, social status, experience and competitive ability may also influence distribution of individuals and the establishment of a hierarchy (Funston et al. 1998). Hierarchy is defined by Wilson (1975) as “the dominance of one member of a group over another, as measured by superiority in aggressive encounters and order of access to food, mates, resting sites, and other objects promoting survivorship and reproductive fitness”. Theoretical models supported by empirical studies have demonstrated that dominant individuals that maintain territories within high quality patches (e.g. in areas of high prey densities) also enjoy higher reproductive success (Gross 1996). In contrast, subordinate individuals (e.g. typically young or immature non-breeders) will optimize foraging by exploiting different prey or by exploiting patches where and when there is low interference competition (e.g. typically patch margins or low quality patches) (Funston et al. 1998, Funston et al. 2001).

Most terrestrial birds defend territories (Lack 1968), and territory ownership and territory quality are likely to be important predictors of reproductive success and fitness, especially for species that defend combined breeding and foraging territories (Currie et al. 2000). However, competition for territories often leads to significant costs in terms of time and energy to maintain them (Goodburn 1991). Variation in breeding success within a species has been attributed to differences in territory quality, parental quality, parental experience and timing of breeding.

A territory has been defined as a fixed space from which an individual or group of mutually tolerant individuals actively excludes competitors from a specific resource or resources (Maher and Lott 1995). The resource in question must be physically

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defendable (Pianka 1978). In fact, territoriality may be more closely related to ease of
defence than strictly foraging considerations, especially in more heterogeneous
habitats (Eason 1992). Territoriality theory predicts territorial behaviour will develop
when fitness benefits outweigh costs of territory establishment and defence, provided
net fitness benefits of the territorial option exceed those of the non-territorial option
(Wilson 1975). The threshold model of territoriality predicts individuals should
defend territories when the resource of interest is at intermediate densities (Brown
1964, Davies 1980, Carpenter 1987, Maher and Lott 1995). In a review of ecological
determinants of territoriality among vertebrates, Maher and Lott (2000) suggest U-
shaped relationships between food and non-food resources, and territorial behaviour.
Cost-benefit analysis, analogous to the approach used in models of Optimal Foraging,
predicts that at high resource densities, costs of defence outweigh the benefits of
exclusivity over an abundant resource. Similarly, when resource densities are low,
benefits of defending a territory with little or no resources mean costs of territorial
defence outweigh meagre benefits provided through exclusivity. In both cases,
abandonment of territorial defence is predicted. For example, pied wagtails (Motacilla
alba) ceased defending territories at times of elevated resource abundance (Davies and
Houston 1983). Golden-winged Sunbirds (Drepanorhynchus reichenowi) and New
Zealand Bellbirds (Anthornis melanura) ceased defending territories or reduced
territories to a defendable size when intrusion rates exceeded an upper critical level
(Gill and Wolf 1975, Craig and Douglas 1986). Defence of territories also has been
shown to vary with changing environmental conditions (Breuner and Hahn 2003).
Predatory gulls can defend foraging territories within seabird colonies (Spear 1993,
Massaro et al. 2000), and territorial defence can vary with changing conditions (Grant Gilchrist, unpublished data). Predictors of territoriality other than prey density, such as prey quantity, predictability, distribution, quality, and ease of assessment, as well as non-food parameters such as space, predator population densities, habitat features (e.g. freshwater ponds), and weather also need to be quantified.

Game theory presents a number of alternative hypotheses as to why territoriality might be chosen as a tactic (Maynard-Smith 1982, Gross 1996). The two strategies hypothesis states that different strategies occur within the same species, and are heritable. By definition, both strategies must yield identical fitness payoffs or else the superior strategy would eventually replace the other (Dawkins 1980). The alternative conditional strategy hypothesis states individuals within a population can adopt different territorial tactics depending on condition or status which need not be heritable. The conditional strategy hypothesis predicts: 1) individuals have the ability to switch between tactics, 2) individuals using different tactics do not (but might for other reasons) achieve the same fitness benefits, and 3) individuals will select the option with highest fitness benefits, when choosing freely.

Game theory also suggests three separate hypotheses relating to dominance within territories. The arbitrary rule hypothesis suggests all competitors for territories adopt the ‘resident always wins’ rule, an evolutionarily stable strategy. A second hypothesis or “asymmetry” hypothesis predicts that territory owners ‘almost always win’ because they possess attributes that provide them a competitive edge during territorial disputes. For example, territorial residents should be larger or in better physiological condition than non-territory holders. The third (“payoff asymmetry”),
states that a territory holder has more to gain by winning a dispute than a non-territory holding intruder. Here, fitness benefits for a resident increase with time as severity of boundary disputes with neighbours decreases, whereas leaving a territory to establish a new one would signify a return to escalated disputes with new neighbours over ill-defined boundaries. In this case, residents possess a motivational edge over intruders and will be more willing than an intruder to enter into escalated conflict. Pianka (1978) states prior ownership provides territory holders with an advantage. Silverin (1998) examined the role of morphological characteristics, hormone levels (plasma testosterone, corticosterone) and behaviour of pied flycatchers (*Ficedula hypoleuca*) and concluded prior ownership to be crucial to maintaining territories from one year to the next. Moss and others (1994) found red grouse (*Lagopus lagopus*) males with experimentally increased testosterone levels were more aggressive and expanded the area of defended territories. Dominance can also occur outside territories. For example, immature gulls have been shown to be subordinate to adults at concentrated food sites such as refuse tips (Verbeek 1977, Monaghan 1980, Grieg et al. 1983, Monaghan et al. 1986).

Few studies have examined extraterritorial foray (ETF) effort during breeding or assessed potential trade-offs. Most studies have focused on extraterritorial activity in songbirds motivated by reproduction (Westneat 1988, Hanski 1992, Neudorf et al. 1997, Pitcher and Stutchbury 2000). Studies that have considered the potential contribution of foraging as a motivator of extraterritorial foray behaviour are rare (Neudorf et al. 1997), possibly due to the challenge of assessing prey availability within bird territories. Furthermore, difficulty in quantifying the frequency and
duration of extraterritorial forays in songbirds, on which most previous work has been
based, has limited the ability to examine the causes, consequences and sources of
variation in this behaviour particularly under changing environmental conditions.
Separation of extra-pair activity from foraging as motivators of extraterritorial forays
has been especially difficult, especially during breeding. To our knowledge, only one
study has examined experimentally the causes and consequences of extraterritorial
forays (Fedy and Stutchbury 2004).

The study system

The herring gull (Larus argentatus)

In Canada, the northernmost extent of the herring gull’s breeding range extends across
the northern Yukon and Northwest Territories mainland to Southampton Island, Foxe
Basin and the southern Baffin region (Harrison 1983, Gaston et al. 1986, Pierotti and
Good 1994). Only one subspecies is recognised in North America (Pierotti and Good
1994). Herring gulls are considered common throughout Southampton Island (Sutton
1932, Parker and Ross 1973). In Arctic regions, herring gulls nest on coastal islands,
both sympatrically with other species in colonies, and solitarily on boulders and small
islets situated in lakes and estuary systems (Cooch 1965, Pierotti and Good 1994,
Parker and Ross 1973). More recent surveys conducted by the Canadian Wildlife
Service in both Foxe Basin and Hudson Strait noted the occurrence of colonies
consisting of both herring gulls and common eiders (Somateria mollissima)
throughout those regions, and Inuit hunters consider the former common on
Southampton Island (Grant Gilchrist, unpublished data).
Several factors may influence food type and availability for gulls. These include weather, marine conditions, human discharge of waste (e.g. fish offal and open landfills), and inter- and intra-specific competition at concentrated food sources (Pierotti and Annett 1991, Spear 1993, Hebert et al. 1999, Massaro et al. 2000).

Research in the Bay of Fundy, the Gulf of Maine and elsewhere suggests that gull populations respond to changes in the marine environment, and that high gull populations reduce the reproductive success of other marine birds (Pierotti and Annett 1987, Spear 1993, Anderson and Devlin 1999, Gilchrist 1999, Massaro et al. 2000). Despite these issues, little is known about behavioural aspects of predator-prey interactions at eider colonies (but see Campbell 1975, Gerell 1985, Götmark and Åhlund 1988, Götmark 1989, Mehlum 1991, Swennen et al. 1993). This lack of information exists because eiders often nest on inaccessible islands, where behavioural observations are difficult (Munro and Bédard 1977). In addition, visits to colonies by researchers cause disturbance and artificially influence rates of gull predation (Milne and Reed 1974).

At East Bay, the herring gull population is divided into two groups distributed unequally within two areas. The island breeding gull population is situated within the large eider colony while the mainland gull population breeds in a low prey density environment on the surrounding mainland coastal plain. The ability to simultaneously quantify ecological and behavioural variables for both groups generates a unique opportunity to study spatial systems, habitat selection and behavioural tactics. Knowledge gained from the study will help researchers evaluate the potential impact of long-term changes in climate and the marine environment on herring gull predation.
within eider colonies in the Eastern Arctic. It will provide insight into behavioural mechanisms of avian predation, influences of intra and interspecific interactions on predation within mixed colonies, as well as provide the opportunity to compare the gull-eider relationship in northern Hudson Bay with other populations globally. Data generated will permit long-term investigation of predation at the site.

Both herring gulls and common eiders typically nest on islands; hence mortality due to mammalian predators is generally limited. Mammalian predators such as mink (*Mustela vison*), foxes (*Vulpes sp.*) and polar bears (*Ursus maritimus*) are known to take the eggs, young and adults of many seabird species (Folkestad 1982, Gerell 1985, Croll et al. 2005, Karel Allard pers. obs.). However, predation by birds (e.g. corvids and larids) at eider colonies is typical and widespread globally. Some researchers have concluded that nesting associations with large gulls benefit eider reproduction (Gerell 1985), while others have found the opposite effect (Götmark 1989). High predation rates have been estimated previously on common eiders nesting in the Saint Lawrence estuary, Canada (Munro and Bédard 1977), on Spitsbergen (Campbell 1975), and in northern Europe (Götmark and Åhlund 1988). Studies at certain colonies in the Bay of Fundy, Canada suggest that predation by great black-backed gulls (*Larus marinus*) can result in virtually complete reproductive failure (Mawhinney and Diamond 1999), while subsequent studies of common eider broods on the southern New Brunswick coastline and Grand Manan archipelago reported negligible loss of ducklings to predatory gulls (Blinn 2005).

Information regarding ecology of herring gulls at northern latitudes and their relationship with eider prey is sparse as few detailed studies exist despite the existence
of mixed colonies of gulls and eiders throughout the region (Cooch 1965, Reed and Erskine 1986, Gaston et al. 1986, Grant Gilchrist, unpublished data). Information stemming from a single study (Cooch 1965) of common eider ecology revealed the predatory nature of herring gulls within common eider colonies in the Arctic. However, Cooch destroyed all herring gull eggs at the site, limiting study of undisturbed gull-eider interaction.

Herring gulls are considered generalists and are known to consume a wide variety of prey. This study does not attempt to explore the whole diet of gulls at East Bay. Rather, it addresses questions pertaining to observed variability in the exploitation of known quantifiable prey types. It is therefore subject to additional unexplained variability arising from herring gull use of other unquantified (e.g. terrestrial invertebrates and marine organisms) and/or unknown prey.

Nonetheless, the herring gull-common eider system at East Bay is well suited to investigation of predator-prey relationships.

*Behavioural plasticity*

Responses to changing environmental conditions (e.g. weather), are contingent upon individual quality, and temporal and spatial considerations, and therefore may vary widely among individuals, locations or years. For example, glaucous gulls (*Larus hyperboreus*) are known to modify both foraging behaviour and intra-specific interaction with certain weather conditions as a means of maximizing returns on energy expenditure while minimizing risk of injury (Gilchrist and Gaston 1997, Gilchrist et al. 1998). Changing energetic demands for individuals are known to lead to changes in foraging behaviour in relation to breeding phenology (Blem 2000).
Herring Gull foraging behaviour may change in response to both breeding phenology and large-scale changes in the marine environment (e.g. food availability) (Massaro et al. 2000). Also, activities performed while foraging, such as flapping flight and active pursuit, are more energetically costly than others (e.g. soaring, “sit-and-wait” foraging) (Weathers and Sullivan 1989). Foraging American kestrels (Falco sparverius) expend more energy hovering than “sit-and-wait” hunting from a perch (Rudolph 1982); however, hovering provides superior foraging success. Wind-assisted hovering can reduce flight costs, making hovering advantageous in terms of optimizing energy intake rate. Hovering flight also enhances the ability of predators to pass slowly over nests and locate and depredate unattended nests more easily (Gilchrist et al. 1998). Kaspari (1990) suggests behavioural adjustments that lead to consumption of part of the food can be also be made in a way that increases net energetic gain (Robbins 1983) because processing parts of certain foods (e.g. egg shells) reduce processing efficiency by adding energetic costs and increasing physiological processing time.

**Prey behaviour**

Incubation behaviour in birds often influences nest success (Afton and Paulus 1992) and the need to maintain water balance during incubation by eiders is essential to survival. Water requirements can vary according to several factors including climate (Nagy and Peterson 1988) and condition (Aldrich and Raveling 1983, Bottittà 2001). Common eider hens periodically leave the nest to drink at fresh-water ponds (Swennen et al. 1993). Preliminary results indicate environmental factors partially determine common eider recess timing, frequency and duration, especially during
drying conditions of extreme intensity and/or duration (e.g. episodes of extreme
temperature or high temperature duration at which hens must pant for
thermoregulation) (Bottita 2001) resulting in a parent-offspring conflict. The main cost
of departure from the nest is increased risk to the unattended clutch. Remaining on the
nest may serve to protect the eggs but may also compromise survival of the hen
(Bottita 2001), while leaving the nest to drink at the wrong time may mitigate
dehydration but also result in additional risk for developing embryos. Events that force
hens to leave the nest even for short periods of time result in increased predator search
success (Gömark and Åhlund 1988, Swennen et al. 1993). Reduction of predation
risk through modification of incubation recess behaviour by eiders may constitute a
further constraint for gulls exploiting eider eggs. This may negatively affect predator
success through a reduction in opportunities for gulls. If incubating birds must trade­
off adult survival with current and/or future reproduction (Mallory and Weatherhead
1992), then individuals should respond adaptively through tactics that minimise risk
for both parent and offspring. For example, under normal conditions hens should
respond adaptively to increased predator foraging behaviour and delay recess timing
and/or reduce recess frequency and/or duration until predator foraging activity is lower
(i.e. when risk to eggs is lowest).

Study site
The study was conducted within the East Bay Migratory Bird Sanctuary (64°01N
81°47W) which covers 1,166 km² on Southampton Island, Nunavut, Canada from
1999 to 2003. The East Bay common eider colony (64°04N 81°40W) is located on a
small (36ha), treeless island. The island supports up to 4500 eider nests and 30 pairs

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of nesting herring gulls, while the surrounding coastal plain supports hundreds of additional pairs of breeding herring gulls. Other species also nest on the island and mainland within the sanctuary (Abraham and Ankney 1986, Allard and Gilchrist 2002). Gulls and eiders often leave their nests when disturbed by humans, leaving their eggs exposed and vulnerable to predation. To avoid this, the Canadian Wildlife Service constructs a network of blinds and canvas access tunnels prior to the annual arrival of the eiders. Blinds allow the observation of eider nesting plots of varying nesting density, and proximity to the ocean, freshwater ponds, and gull nests. Up to 250 eider nests can be observed from each blind. To date 62 (47 island, 15 mainland) adult herring gulls have been uniquely banded since 1996, permitting the study of individual behaviour. Commercial fishing and/or disposal of human or agricultural waste do not occur in the vicinity of the colony, conditions rarely met in studies of herring gulls elsewhere in the world.

OBJECTIVES

The main objective of the study was to examine foraging tactics and strategies of an avian predator exploiting locally-distributed prey under different scenarios; specifically, the combined effects of environmental and biological factors on foraging decisions of herring gulls nesting sympatrically with eiders. The study also aimed to assess the contribution of these factors to behaviour at both the local population and individual scales, complemented with experimental manipulation of prey abundance.

Chapters are presented in Articles format, such that each represents a stand-alone manuscript that will be or has been submitted to peer-reviewed journals for publication.
Chapter two explores the effects of environmental and biological factors on gull foraging activity during the eider incubation period over three years. Eider eggs are immobile and during incubation, nests are distributed at varying densities within the colony. I tested the following hypothesis and derived predictions: If gulls improve foraging efficiency through behavioural tactics that lower the energetic and/or temporal costs of foraging, then foraging rates should increase 1) with increasing density, so as to increase encounter rates with prey, 2) during daylight hours when light levels enhance detection of prey, 3) with higher wind speeds that allow a more energy-efficient hovering flight mode, 4) with lower temperatures as their metabolic expenditures increase, and 5) with higher tides as intertidal prey alternatives become less available. In addition, search and egg capture rates were assessed as both overall rates (events per hectare) and per capita rates (events per nest) to better evaluate allocation of foraging effort by gulls directed toward prey within the colony. Also, behavioural reaction of eider hens to searching gulls was quantified as a measure of risk of injury to gulls and potentially, as an additional constraint for the foraging predator. I further hypothesised that if eiders constituted a risk for foraging gulls then per capita foraging rates would be higher in lower density eider nesting areas.

In contrast with traditional multivariate methods that identify a single ‘final’ model from which all inferences are drawn, in this and the following chapter I used the AIC (Akaike’s Information Criterion) statistic as a model building tool to specify multiple models with varying explanatory strength given the data (Burnham and Anderson 2002). I did this principally due to high variability inherent in ecological data which often leads to more than one combination of variables contending for the
‘best’ model designation. To avoid introducing bias resulting from the selection of a single model, I averaged weighted estimates of each predictor across models having at least some explanatory strength. I drew inferences from these ‘unconditional’ estimates based on the frequency at which they appeared in ‘top’ models of the set, their magnitude, their precision and whether or not they bounded the ‘no effect’ value.

Chapter three assesses effects of environmental and biological factors on gull foraging activity during the eider duckling period over five years. In contrast with eggs, ducklings are mobile and depart the colony within 24 h of hatch and are typically accompanied by adult eider hens. Thus, different methods were used to explore hypotheses. I tested the hypothesis that gulls improve foraging efficiency through lowering energetic and temporal costs (or both) through the use of behavioural tactics. I predicted that foraging rates directed at individual broods would increase 1) during daylight hours when light levels enhance detection of prey, 2) with higher wind speeds that allow a more energy-efficient hovering flight mode, and 3) with low tides when broods must cross expansive tidal flats to reach the sea. Effects of large-scale fluctuation in small mammal abundance were also evaluated. I further predicted that gull foraging activity directed toward individual broods would increase with lower levels of small mammal abundance (alternative prey for the gulls). In addition, I measured the defensive behaviour of eider hens (departing the island with young) directed toward gulls as an index of risk of injury, and examined annual variation in the frequency and intensity of their response. Here, I predicted that gulls would take more risks (elicit a more intense response) in years of low small mammal abundance.
Chapter four explores the foraging activity of gulls and the attendance patterns of individual members of territorial pairs in relation to prey availability within their territories. I tested experimentally the general hypothesis that territorial birds face a trade-off between energetic gain and territorial defence, and that this trade-off is influenced by variation in food (in this case, eider eggs) abundance and accessibility within territories. I predicted that territorial residents should respond to increased food intake within their territory by 1) spending more time in their territory, 2) defending their territory from intruders more aggressively, and 3) that these responses should be most pronounced for individuals occupying territories containing limited resources. As sex can influence foraging ability and the outcome of interactions with competitors, especially in structurally dimorphic species (Pugesek 1983, Caldow and Furness 2000), I also predicted that change in behaviour would be most pronounced in females. I further hypothesised that costs incurred due to intrusion (e.g. prey depletion) would vary in relation to attendance patterns by residents. Specifically, I predicted that intrusion rate and duration, and likelihood of prey capture by intruders, would decrease with the presence and vary with the sex of the non-incubating member of the territorial pair, and increase with food provided experimentally.

In chapter five, I discuss the individual contributions of each of the three previous chapters and the ways in which together they demonstrate the importance of considering behaviour of both predator and prey when trying to understand relationships between them.
LITERATURE CITED


30

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Chapter 2

Title:
Foraging ecology of an avian predator, the herring gull: interactions between environmental conditions, prey behaviour, and functional prey availability

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ABSTRACT

From 1999 to 2001, we studied the foraging behaviour of herring gulls (*Larus argentatus*) within a common eider (*Somateria mollissima*) duck colony in Canada’s eastern Arctic. We quantified how rates of foraging activity and foraging success varied with wind, temperature, tide height, solar radiation, reproductive phenology of eiders, and eider nest densities. We found that gulls began consuming eider eggs as they became available, and ceased exploiting eggs upon onset of hatch of both gulls and eiders. Herring gulls did not force incubating hens off nests, but instead, took eggs only from unattended nests. Consequently, herring gulls within the colony foraged most intensively and were most successful during eider egg-laying when hen nest attendance was most sporadic. Also, eider hens aggressively defended their nests from gulls attempting to land or searching on foot. Other than at the lowest eider nesting densities, the proportion of gull ground searches that met with eider aggressive defence did not vary with eider nest densities. Rates of air and ground searches, and successful predation events, when calculated per hectare, increased with increasing eider nest densities. Although effect sizes were small, per capita air search rates decreased, while per capita ground search rates increased, with nest densities. Egg capture frequency did not vary with nest densities. Although gull numbers on the colony varied positively with tide height and negatively with light levels, these variables had little or no effect on gull search rates.

Our findings suggest: 1) prey (eider egg) availability is not accurately represented by prey abundance alone, and availability is quantified more accurately with the additional consideration of prey behaviour, 2) predator foraging behaviour is
modulated by changing environmental conditions; 3) numbers of predators at a site do not always directly reflect levels of prey exploitation; 4) eiders may gain little advantage in terms of reduced predation rates from nesting at high densities at this colony.

*Key words*: foraging, optimal foraging, model-averaging, prey availability, reactive prey, herring gull, *Larus argentatus*. 

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INTRODUCTION

Prey density is generally considered to be the primary determinant of both numerical and functional response of predators (Nicholson 1954, Krebs 1985). However, factors in addition to prey density can determine prey availability and influence predator foraging efficiency (Abrams 1993). Abiotic factors such as weather can influence the net value of foraging, thus modifying the magnitude of direct and indirect effects of predators on prey populations (Newton 1998). For example, weather conditions can act directly through modification of predator metabolic rates (Machmer and Ydenberg 1990), and indirectly by influencing foraging efficiency (Dunn 1974, Finney et al. 1999). Environmental conditions can also alter the ability of predators to detect and capture prey as well as modify behaviour and/or distribution of prey (Systad and Bustnes 2001, Jetz et al. 2003, Sergio 2003, Quinn and Cresswell 2004).

Foraging predators are expected to maximize the trade-off between energy gains and foraging costs (e.g. energy expenditures and injury risks) (Stein 1977, Zach 1979, Stephens and Krebs 1986, Jetz et al. 2003). Predators should therefore respond to changing conditions that modify this trade-off by adjusting their foraging effort (e.g. search rate), switching prey, and/or by changing foraging modes in ways that buffer effects of changing ecological constraints on intake (Jetz et al. 2003, Sergio 2003, Vlachos et al. 2003). For example, predators can increase their net energy gains by: 1) selecting energy-efficient foraging modes, 2) searching when prey are most easily encountered and detected, 3) minimizing interactions with competitors by foraging in unexploited patches, and 4) increasing encounter rates with prey by foraging in areas of highest prey density.
Although prey are known to modify their foraging behaviour according to predation risk (Quinn and Cresswell 2004), few studies have considered how predators are influenced by risk of injury while foraging. What is known suggests that injuries incurred through agonistic encounters with their own predators, conspecifics, and reactive prey, can influence predator decisions (Gilchrist et al. 1998, Gilchrist 1999, Béty et al. 2001, Sherratt 2003, Quinn and Cresswell 2004). However, there are few empirical studies demonstrating the contribution of environmental factors to the interplay between prey availability, prey vulnerability and injury risks faced by predators while foraging.

We studied herring gulls breeding within a common eider duck colony on Southampton Island, Nunavut, in the eastern Canadian Arctic, and predicted that herring gull foraging activity would be greatest: 1) in areas of highest eider nesting densities, 2) when herring gull numbers on the colony were highest, 3) when eider nest attendance levels were lowest (i.e. when eider eggs were exposed), 4) when moderate wind conditions permitted the most energy-efficient hover/glide search modes for gulls, 5) when increased daylight enhanced detection of prey, 6) when low ambient temperatures increased the metabolic rates of gulls and their chicks, and 7) when high tides limited access to alternate marine intertidal prey. We assessed predation rates as a function of area (eggs taken per hectare per hour), and also calculated per capita predation rates (eggs taken per eider nest per hour) as a measure of relative risk for prey. We evaluated this latter parameter because if low eider nesting densities contribute to weak nest defence by eiders, then those nests occurring at low densities should experience higher per capita search and egg capture rates by gulls.
METHODS

Study site

We conducted the study from 1999 to 2001 within the East Bay Migratory Bird Sanctuary (64°01N 81°47W) on Southampton Island, Nunavut, Canada. The East Bay common eider colony (64°04N 81°40W) is located on a small (36 ha), low-lying, treeless island which supports up to 4500 pairs of common eiders and 30 pairs of herring gulls annually, and limited numbers of other breeding bird species (Allard and Gilchrist 2002). As fewer than 50 pairs of king eiders (Somateria spectabilis) nest at the site, ‘eider’ unless otherwise stated, refers to common eider. Visits to the eider colony island by other gulls (Larus spp.) known to prey on eiders are rare, but parasitic jaegers (Stercorarius parasiticus) breed on adjacent coastal plains in low densities (Abraham and Ankney 1986) and visit the eider colony individually or in pairs almost daily. Commercial fishing does not occur in the region of the colony, and the nearest human community is 50 km to the west.

Mammalian predators include polar bears (Ursus maritimus), arctic foxes (Alopex lagopus) and Inuit hunters. Polar bear visits to the island are infrequent and typically short, although polar bears occasionally eat contents of eider and gull nests. Annual visits by foxes coincide with onset of egg-laying and result in depredation and caching of both eider and gull eggs; however, foxes are never observed after ice break-up in late June and early July, when the majority of eiders lay. Brief visits by Inuit hunters occur only prior to ice break-up.

Long daylight periods, lack of tall vegetation and high densities of both gulls and eiders make it possible to quantify the foraging behaviour of gulls in relation to
local environmental conditions, eider nesting densities, and reproductive timing, as well as behavioural interactions with prey and conspecifics.

**Weather, light and tides**

In 2000 and 2001, we recorded local weather data at 30-minute intervals using an automated weather station (Davis Instruments Corp. Hayward, CA). We positioned temperature, wind speed and solar radiation sensors 3 m above ground near the northern end of the colony. As the island is small (±400 m by ± 800 m), low-lying and flat, with no significant vegetation, we assumed temperature, wind, and light conditions experienced by gulls were similar in all parts of the colony.

The solar radiation sensor measured ambient light levels in mW·m⁻² for all wavelengths from 400 to 1100 nm. As this sensor’s output is affected by temperature, we corrected output data according to the manufacturer’s specifications.

We used tidal event timing data predicted by the Canadian Hydrographic Service for Coral Harbour, Nunavut (64°08N 83°10W) (approximately 40 km to the west), which we found to be within one half-hour of observed timing of tidal events at the study site.

**Study plots**

We selected four study plots based on eider nest densities that represented the range found within the colony. Plots were otherwise similar in overall disposition, terrain, and proximity to ocean and freshwater ponds. We established plot boundaries to maximize the number of common eider nests for which daily attendance could be determined with confidence by researchers from observation blinds. Plots were situated at least 50 m apart and varied in area between 1785 m² and 6063 m².
Collectively, the plots encompassed approximately 6% of the entire island (or roughly 15% of the colonised portion of the island). The maximum daily number of active eider nests per plot ranged from 12 to 109. To minimize disturbance we conducted all observations from blinds which were accessed through wood-framed canvas tunnels constructed prior to onset of egg-laying within the colony.

**Herring gull counts**

During observational watches we counted all gulls situated above the water line or flying within the airspace directly over the island, and also noted the proportion of the total count roosting at a common loafing area.

Gull breeding phenology was monitored through daily visits to herring gull nests on the island until lay dates of first eggs were recorded. Subsequently, nests were monitored from blinds or through opportunistic nest visits to determine hatch dates and breeding success.

**Herring gull foraging activity**

From observation blinds, we monitored herring gull foraging activity (frequency of air and ground searches, and egg captures) using a combination of daily continuous 3 h watches, distributed equally between AM and PM periods, and weekly continuous 24 h watches. 24 h watches took place at two of the four plots, while 3 h watches took place at all plots. To supplement these observations, additional 3 h watches were added to increase observational data relating gull foraging activity to environmental conditions (e.g. to increase the sample of 3 h periods occurring during windy conditions). We selected the minimum watch duration of 3 h to increase the
likelihood of observing rare egg captures (Altmann 1974). Gull search activity and egg captures were easily observed with the naked eye from blinds.

An ‘air search’ was defined as any gull flying over a study plot with its head tilted downward or to the side indicating active searching (Gilchrist et al. 1998). A ‘ground search’ was defined as any gull either walking across or landing within the boundaries of a study plot. An ‘egg capture’ was defined as any event during which a gull removed an eider egg from an eider nest within a study plot. We recorded time and location of all events and generated foraging activity rates by tallying these behavioural events per 30 minutes.

Common eider counts and behaviour

Counts of incubating common eiders within plots were conducted from blinds twice daily. For this study, egg-laying was defined as the period commencing with deposition of the first egg and ending when the maximum number of active nests was reached within a plot. Egg-laying was followed by incubation and subsequent exodus of hatchlings from the colony.

When laying eggs, eider females at this colony do not incubate or attend the nest site continuously, nor do they deposit down over the eggs. Thus, eggs essentially are left uncovered and unprotected from avian predators for 2-4 days following the laying of the first egg (i.e. typically 4 eggs are laid at this site). When clutches near completion, eider hens deposit down on the nest and over the eggs, and attend and incubate almost continuously until hatch (99.8% of the time) (Bottitta et al. 2003).

Intensity of eider response to gulls hunting was quantified from two blinds in 1999 and four blinds in 2000 and 2001. Response of common eider females to gull
ground and air searches was categorized according to increasing intensity. Common eider females either: 1) did not respond, 2) extended their necks and/or stood, 3) walked towards gull, 4) lunged towards, charged or chased gull, and 5) physically contacted gull (including biting and grasping with bill). Less intense behaviours always preceded or were included within more intense behaviours.

Statistical analyses
For most analyses, only years 2000 and 2001 were used, as data for several predictor variables were lacking for 1999 and only two observation blinds were available in that preliminary year. However, 1999 data are often discussed qualitatively or represented graphically. We analysed data for the period commencing with onset of eider egg-laying and ending with peak of eider egg hatch. In all years, this period covered most of the ±27 day herring gull incubation period, and included roughly the first 7 days of gull chick growth.

Factors influencing gull numbers, and search and egg capture rates, were analysed using generalized linear models (McCullagh and Nelder 1989). We used Poisson errors initially (typical for count data), but resulting deviance/degrees freedom ratios suggested poor fit, over-dispersion, or both (Burnham and Anderson 2002). However, desired fit was achieved using a negative binomial error structure which conformed visually to cumulative probability plots of our raw data (Byers et al. 2003). A log link function was used with foraging data (i.e. search rates, egg capture rates) while an identity link function was used for herring gull colony attendance data (PROC GENMOD; SAS Institute Inc. 2000). We compared variation in eider nest densities within and across years through examination of four eider nesting plots.
Support for models and predictor sets was determined using information-theoretic criteria (Burnham and Anderson 2002). Biologically relevant predictors and interactions between them were selected *a priori*, corresponding to hypotheses based on theory, similar previous studies, and our own knowledge of the system. Predictors were excluded from our initial selection only if they exhibited collinearity with other predictors beyond a threshold level (r $\geq 0.5$) (Green 1979). As our objective was to assess the contribution of predictors in the presence of others, some predictors were grouped according to hypotheses of interest (Jodice *et al.* 2002). Predictor groupings included: Annual effect (year), seasonal effect (date adjusted to eider breeding phenology), weather effects (wind speed, temperature), periodic effects (solar radiation, tide height), and encounter effects (number of gulls, eider nesting densities). Model sets contained all possible combinations of predictor groupings ensuring each individual predictor appeared an equal number of times (Burnham and Anderson 2002). Although subjective, we chose only first order interactions of interest related to our initial hypotheses that received intuitive support for inclusion into model sets; these and all other variables included in analyses are presented in individual tables of top model sets. Inclusion of additional variables and interactions, although potentially valuable, would constitute exploratory investigation that extends beyond the scope of the present study.

We used the AIC (Akaike's Information Criterion) statistic (with adjustment for small samples, AICc) for each model and ranked models according to their AICc values from lowest to highest (Burnham and Anderson 2002). Next, differences in AICc values ($\Delta$ AICc) between the most parsimonious model and all other models
considered were calculated. AICc weights (the probability that a given model is the best model tested, given the data) were determined for each model.

Model selection uncertainty occurs when many competing models have Δ AICc values of 4 or less (Burnham and Anderson 2002). In such cases, support for more than one model creates uncertainty as to which model is best. To avoid introducing bias by selecting a single model from which to draw inferences, we adopted a model-averaging strategy which involves averaging weighted estimates for each predictor across the model set. These "unconditional" estimates of coefficients and their standard errors were calculated for each predictor effect (Burnham and Anderson 2002).

Dependent count variables with a negative binomial distribution were 'linked' to independent variables with a log link function, such that the log of the mean of the dependent variable was linearly associated with associated independent variables. Hence, raw model-averaged parameter estimates were exponentiated to generate interpretable Incident Rate Ratios (IRR). An IRR represents a multiplier of the mean outcome and can be converted to a percent change by subtracting one and multiplying by 100. The result obtained should be interpreted as a percentage of growth or decline in the dependent variable due to a one-unit change in the independent variable, holding all else constant (Schweik 2000).

Behavioural data acquired through consecutive observations are typically autocorrelated (Zeger and Liang 1986). To minimize the consequences of temporal autocorrelation, we restricted data in accordance with results obtained from autocorrelation function plots of response variables derived from our 24 h watch data.
180 min observation periods were deemed statistically independent when separated by at least 6 h, while 30 min periods were found to be statistically independent when separated by at least 90 min, from watch end to beginning of next watch. Clearly, individual gulls were responsible for repeated searches and egg captures. However, not all individuals were marked, and marked individuals could not always be distinguished from one another when foraging (e.g. especially when searching from the air). Therefore, we assumed and treated individual searches as being independent from one another.

Search activity and egg capture rates were modelled separately. In contrast with search activity, egg capture events were found to occur several hours apart, while environmental predictors such as tide, temperature, and wind speed often varied significantly over shorter time periods. Hence, different temporal scales were required for different variables and questions of interest. For example, we modelled egg capture rates only against ecological predictors that do not vary over a 180 min period (e.g. year, density of nesting eiders, date, etc.). In contrast, due to higher event frequencies, we could model search activity rates against all predictors of interest (e.g. density of nesting eiders, number of gulls on the island, wind speed, tide height, temperature, etc.) at a higher resolution using 30 min sampling units.

It was important to evaluate how overall gull foraging activity, and the relative attention directed to individual eider nests by gulls, varied across the colony; specifically in relation to density of nesting eiders if closely grouped hens contribute to mutual nest defence. For this reason, rates of search and egg capture were calculated in two ways: 1) per hectare, defined hereafter as ‘overall rate’, and 2) per
capita (per active eider nest), defined hereafter as 'relative rate'. Both were used as separate but closely related response variables in our analyses.

We assumed that the individual response of eiders to gull ground searches would be consistent qualitatively between years; hence we pooled these data.

Day of year (DOY) represents the Julian date, where DOY 1 = 1 January and is corrected for year 2000, a leap year. Means are reported ±1 SE. Confidence intervals around parameter estimates were calculated using ±2 SE (Burnham and Anderson 2002).

RESULTS

Environmental conditions

Snow cover on the island receded to 10% by 13 June 1999, 20 June 2000, and 27 May 2001. Ice break-up at East Bay occurred on 6 July 1999, 9 July 2000 and 24 June 2001 (Figures 2.1a, 2.1b and 2.1c). Herring gulls were observed away from the island using open water leads and exposed intertidal flats as soon as these appeared following break-up. Of 1852 30 min weather observation periods in 2000, we recorded 78 periods with rain, 1774 without, and 68 with missing data. In 2001, 34 30 min periods experienced rain, 1454 did not, and 96 had missing data. Temperature ranges encountered were similar among years (Fig 2.2a). Because rare periods of high winds did not coincide with scheduled watches in 2001, we failed to gather behavioural data associated with wind speeds surpassing 30 km/h in that year. Wind speed data are presented in Figure 2.2b. We recorded solar radiation levels of 0 W/m² (range: zero to 868) during ±13 30 min periods daily in 2000, and an average of ±11.5 30 min periods
daily in 2001. This equates to approximately 6 hours per day of “night time” conditions during the study.

**Reproductive timing of gulls and eiders**

Herring gulls arrived at East Bay earlier in 2001 than in 1999 or 2000. Upon our arrival on 31 May 1999, 10 individuals were observed on the island. In 2000, first observations of herring gulls occurred on 24 May, two days after our arrival. In contrast, 20 gulls were observed on the colony upon our arrival on 23 May 2001. We noted gull stays early on were typically short and generally lasted less than one hour. In all years, initiation of herring gull clutches occurred prior to onset of common eider egg-laying. Onset of egg-laying by herring gulls and eiders always began after snow cover levels fell below 10%. In each year, this was prior to ice break-up. Median egg-laying for herring gulls occurred on 21 June 1999 (day 172: earliest=169, latest=174, n=15 nests), 25 June 2000 (day 176: earliest=174, latest=180, n=11 nests), and on 08 June 2001 (day 159: earliest=155, latest=163, n=21 nests). Gull eggs hatched 27±1 days later. The total number of gull pairs breeding on the colony (30) did not differ among the 3 years. Median egg-laying of eiders occurred on 3 July 1999 (day 184: n=207 nests), 3 July 2000 (day 185: n=244 nests), and on 26 June 2001 (day 177: n=378 nests). More eider hens established nests in 2001 than in 2000 ($\chi^2_{0.05,1}=6.72$, $P<0.01$) (Figs. 2.1b and 2.1c).

**Environmental factors and colony attendance by gulls**

Gull counts, which included both breeding and non-breeding individuals (range 8 to 78), were lower in 2000 than in 2001 and decreased with advancing date (Table 2.2 lines 1-3). The number of gulls counted on the island was highest with low light
levels (i.e. night). In contrast, counts increased with temperature, wind speed, and tide height. The interaction between wind speed and tide received little model support, was imprecise and bounded the no-effect value.

**Relationship between gull foraging activity and egg capture rates**

We gathered data during 234, 537.5 and 477 hours of observation from blinds in 1999, 2000 and 2001, respectively to maximize observation of rare events and allow us to control for autocorrelation (see Methods). Our models examine statistically independent subsets of data from 159 and 137.5 hours of observation taken from years 2000 and 2001 only. These subsets include 593 30 min observations and 274 180 minute observations for both years. Numbers of gull air and ground searches tallied per 180 minutes (n = 226) were strongly correlated with one another (2000: r=0.70, \( P<0.0001 \); 2001 r=0.67, \( P<0.0001 \)), as gulls often searched from the air before landing to search on foot for eggs. Search rates were correlated with egg capture rates, although ground search rates were more strongly correlated with egg captures (2000: \( r=0.35, P<0.0001 \); 2001: \( r=0.48, P<0.0001 \)) than were air search rates (2000: \( r=0.30, P=0.0009 \); 2001: \( r=0.21, P=0.03 \)).

**Factors affecting within-colony search activity by gulls**

*Encounter effects (number of gulls, eider nesting densities)*

Encounter effects appeared consistently in top models (Tables 2.3, 2.4). Specifically, estimates of the effect of number of gulls (island) on search activity, although lacking somewhat in precision, were positive, and did not bound the no-effect value across all models (Table 2.5 line 5). Results were similar for estimates of the effect of eider nesting densities (density), except in the case of the per capita air search rate model for
which the estimate was negative and reached the no-effect value (Table 2.5 line 4).

The effect of density on search rates at the 180 min temporal resolution were almost identical (Tables 2.5 and 2.7, line 4).

*Seasonal effect (Day of year adjusted to eider median laying date)*

The effect of day of year (phdate) on search rates appeared consistently in top models. Further, estimates of the effect across all models were important, precise, negative, and did not bound the no-effect value at either temporal scale (Tables 2.3, 2.4, 2.5 line 3, 2.6, 2.7 line 3).

*Weather effects (Temperature and wind speed)*

Weather effects appeared consistently in top models (Tables 2.3 and 2.4). Although precision was poor, estimates of the effect of temperature on gull ground search rates were negative, important and did not bound the no-effect value (i.e. gulls ground search rates were higher at low temperatures). Contrastingly, the effect of temperature on air search rates was less important, lacked precision and bounded widely the no-effect value (Table 2.5 line 7). Though precision was poor, the effect of wind speed on air and ground search rates was positive and important, across all models (Table 2.5 line 6, Fig 2.3).

*Periodic effects (Solar radiation and tide height)*

Periodic effects received little model support as predictors of air search activity (Table 2.3), and more support as predictors of ground search activity (Table 2.4). Specifically, the effect of solar radiation (solar) on air search rates was unimportant (Table 2.5 line 8), and though the effect on ground search rates was small, with a negative sign, its upper confidence interval reached the no-effect value (Table 2.5 line
Tide height data varied over nearly 3m in both 2000 (min=0.110 m, max=3.412 m) and 2001 (min=0.200 m, max=3.179 m). Though the tide effect appeared in top models for ground search rates only (Table 2.4) and was important, wide confidence intervals consistently bounded the no-effect value (Table 2.5 line 9), which compromised confident inference.

Factors affecting gull predation rates

Eider nesting densities

There was strong model support for the effect of eider nesting density (density) as a predictor of overall egg capture rates, and less so for per capita egg capture rates (Table 2.8 line 4). Though precision was lacking, the effect was important, positive, and did not bound the no-effect value (i.e. gulls made more egg captures per hectare in high density areas). Lack of strong model support and confidence intervals that bounded zero widely precluded confident inference on the effect of density on per capita egg capture rates.

Day of year adjusted to eider median laying date

Day of year appeared in all top models (Table 2.8). In models of overall and per capita egg capture rates, estimates of the predictor were negative and lacked some precision but did not bound the no-effect value, indicating egg capture rates declined as the season progressed (Table 2.7 line 3).

Effects of weather

We could not model effects of wind speed and temperature on egg capture rates directly (see methods). However, egg captures which occurred during periods used in our analyses were not more frequent in windy (wind speed>12.9 km/h (median wind
speed) than calm (wind speed < 12.9 km/h) periods ($\chi^2_{0.05,1}; P = 0.579$). Similarly, egg capture frequency on either side of the median temperature value (4.0 °C) did not differ ($\chi^2_{0.05,1}; P = 0.748$). Similarly, egg capture frequency did not differ between night time, morning, midday or evening periods ($\chi^2_{0.05,3}; P = 0.596$). Six of 24 30 minute periods, during which egg captures occurred, took place from 2100 to 0300.

In 2000, 4 of a total of 63 eggs depredated during all of our observations (including those not used in our analyses) were taken during rain. Of the 4, 3 were taken from the same unattended nest on the same day, while the remaining egg was taken from another nest during a period during which a trace rainfall amount (0.2 mm) was recorded. Similarly, none of a total of 50 eggs depredated was taken during a rainy period in 2001. As egg captures were sparse (especially during rain events), data were insufficient to conduct a formal test of the effect of rainfall on egg captures.

Factors affecting eider response to gull search activity

Eider hen response to flying gulls was infrequent, low in intensity (neck extension only), and occurred only when gulls hovered or passed slowly over nests at low altitudes.

During watches in 1999, 2000 and 2001 combined, we observed a total of 4192 ground searches by gulls in our study plots. Of these, 463 elicited a defensive reaction from eider hens (all intensities combined). Defensive hens were incubating, departing to or returning from a recess from incubation, or simply visiting the colony. We could not always reliably distinguish the reproductive status of eider females.

Frequency of eider reactions of all intensity categories elicited by gull ground searches differed with eider nest density when study plots were categorized as either
high density (>300 nests/ha) or low density (<300 nests/ha) ($\chi^2_{0.05,1}; P = 0.01$) (see figs. 2.1a, 2.1b and 2.1c). Further, we found a non-linear positive relationship between eider nesting density and eider response to gulls searching on foot (we perhaps inappropriately assumed eider response to individual ground searches would not differ among plots situated across the colony and among years, hence all response categories combined and years pooled) (Fig. 2.4). The effect was most apparent for low-level response categories (e.g. gull patrols were less likely to elicit low-level responses from eiders nesting solitarily).

**DISCUSSION**

Activity patterns of predators can be influenced by stochastic, instantaneous and/or cyclical variation in prey availability, prey vulnerability or risk to predators. For example, environmental change can lead to switching between foraging modes, patches, and prey sources (Irons *et al.* 1986, Massaro *et al.* 2000, Systad and Bustnes 2001, Béty *et al.* 2002). Also, diurnal patterns of solar radiation, temperature, and tide can lead to cyclical patterns of prey exploitation (Galusha and Amlaner 1978, Irons *et al.* 1986, Jetz *et al.* 2003). Predators can switch prey types in response to changes in density of focal prey, often resulting in modification of predation rates on alternative prey through indirect trophic interaction (Abrams and Matsuda 1996, Bety *et al.* 2001). Changing energetic demands, especially with regard to breeding phenology, are also known to lead to changes in foraging behaviour. However, behavioural plasticity of predators may vary widely among individuals, populations, and among years (Burger 1987, Blem 2000).
Gull attendance and reproductive timing

Herring gulls reach the floe edge at Southampton Island in late April and move inland to breed in mid-to-late May (Sutton 1932). Snow melt on the colony island varied between years, with 10% snow cover occurring more than three weeks earlier in 2001 than in 2000, and more than two weeks earlier than in 1999. Ice break-up timing was similar, with break-up in 2001 occurring over two weeks earlier than in 2000, and over a week earlier than in 1999. Gulls attended the colony earlier in 2001, and initiated clutches in early June of 2001, nearly two weeks earlier than in 2000 or 1999, likely a result of food availability related to early snow melt and ice break-up that year.

In each year, the first visits to the colony were brief (<1 h) and most gulls flew on an East-West axis to and from the colony, which suggested they were making foraging trips to the floe edge 23 km to the east (Sutton 1932).

Once gull clutches are initiated and eider egg-laying begins, some gulls nesting on the island may focus their foraging effort on the eider resource, a time when gull nesting territories are defended vigorously (Pierotti and Good 1994). The switch from marine food to eider prey coincident with gull clutch initiation, likely contributed to high egg predation levels at that time (Fig 2.1a-c; Bourget 1970). Although food resources near the nest site are important for female gulls during egg formation (Milne 1974, Ashcroft 1976), gulls at this colony consistently initiated their clutches one to two weeks prior to the onset of eider egg-laying. Thus, they did not rely on eider eggs as a resource for the formation of their own eggs. The number of gulls present on the colony was positively related to high wind speeds, high temperatures, low light levels,
and high tide conditions. The positive relationship between attendance and temperature suggests that gulls on the colony were away from the island more when their metabolic needs increased with lower ambient temperatures. Wind velocities (>30 km/h) might also modify the ability of gulls to locate prey at sea because waves caused by high winds have been shown to reduce foraging success of foraging seabirds (Dunn 1974, Finney et al. 1999). Poor foraging conditions away from the colony and/or the advantages of wind when searching for eggs within the colony may partially explain the observed positive relationship between wind speed and gull attendance.

**Factors affecting gull search activity**

Although relative darkness occurred for up to 6 h per day, evidence lacked suggesting low light conditions influenced air search activity by gulls, contrary to prediction. However, low light levels did markedly increase numbers of gulls on the colony (see below), and some of these would have been counted as ground patrols. Gulls may in part visit the colony in poor light to roost or because prey elsewhere become difficult to evaluate from the air. Although solar radiation appeared in top models of ground search activity, and the effect was non-negligible, confidence intervals that reached the no-effect value preclude confident inference.

The number of resident, breeding gulls on the island was stable across years, and even over the course of the breeding season. However, there were more non-breeding gulls present on the colony during high tides, at night, and during periods of high winds (Karel Allard, pers. obs.). Although we expected that most non-breeding gulls present on the island would hunt, this was generally not the case. These gulls
were typically inactive and rested together at the edge of the colony particularly at
night and during high tides, and similar roosting concentrations of gulls are commonly
observed elsewhere (Tinbergen 1953, Pierotti and Good 1994). Considering the
strong relationship between gull counts, and tide height and luminosity, we expected a
similar relationship between the latter predictors and search rates, with consequent
effects on egg capture rates. Search rates fluctuated with gull numbers but not with
tide height or luminosity. Considering the stable number (30) of gull nests on the
colony, and the high proportion of individuals banded on the island (Adults: 13/60 in
1999, 22/60 in 2000, 38/60 in 2001), we would have expected regular observations of
banded birds at the loafing area if any mixing occurred. This was not the case.
Instead, only non-breeders banded as chicks or juveniles, and failed breeders that year
occasionally were seen there. This evidence suggests individuals that attended the
loafing area were not actively breeding on the colony island. It is likely however that
some gulls from the common loafing area hunted. Alternatively, colony breeders that
were responsible for most of the search activity (chapter 3) perhaps came and went
from the colony following patterns similar to those of the loafing gulls.

Among avian predators, wind conditions can dramatically influence the
relative costs of different foraging techniques (Weathers and Sullivan 1989).
American kestrels expended more energy when hovering than when hunting from a
stationary perch, although foraging success was greatest when hovering (Rudolf
1982). Gliding into wind may lower energy expenditure, while simultaneously
enhancing the ability of avian predators to pass slowly over prey, and locate and
exploit vulnerable prey (Gilchrist et al. 1998). For herring gulls, energetic costs of
flapping flight are at least 5.6 times higher than the costs of wind-assisted soaring or gliding (Goldspink et al. 1978). At this site, herring gulls using gliding search modes passed more slowly over eider nests and this likely enhanced their ability to locate exposed eggs. As both air and ground search modes were correlated, the positive effect of wind on rates of both search modes was, as expected, consistent across models (Tables 2.3, 2.4 and 2.5). We also observed that gulls foraging under windy conditions attacked nests and retreated more quickly, which likely reduced their risks of injury when being attacked by defending eider hens (see below).

Air search rates increased with wind speed. Wind facilitated gliding flight, increased aerial manoeuvrability, and enhanced quick take-offs from standing positions. We suggest that at this site, wind contributed primarily to lowered energetic costs of search rather than to increased rates of egg capture, because eggs were not captured more frequently during windy conditions (see Results; Fig. 2.3). Thus, for herring gulls searching for exposed eider eggs, wind primarily lowered the energetic expenditure of searching. Wind also enhanced the ability of gulls to retreat with captured eggs before being attacked by defending eider hens, competing gulls, or kleptoparasites (Allard and Gilchrist 2002).

We expected wind conditions to affect which areas of the colony were searched by gulls. However, lack of support for the wind speed by density interaction for both air and ground search modes revealed that during calm conditions, gulls simply searched less. Nevertheless, there was some support for the suggestion that gulls in flight devoted greater attention to nests located in low density breeding areas, perhaps because capturing eider eggs initially detected from the air in low density
areas is less likely to result in interference from other gulls and defensive eider hens. Conversely, nests located in high density areas received more per-capita attention from gulls searching on foot. The bias we detected toward ground-searching in higher densities is most likely the result of likely consequence (i.e. mobbing by conspecifics) than cause (i.e. gull tactic). Conspecifics frequently mobbed gulls that captured eggs. In these cases we counted mobbing individuals as additional ground searches as they were well-positioned to take other eggs from the depredated nest or neighbouring unattended nests. Such mobbing occurred especially when gulls captured eggs in full view of competitors, which were more numerous in high density areas.

Environmental conditions apparently interacted primarily with search activity, and not with prey behaviour, to influence functional prey availability, specifically by influencing foraging efficiency through modification of the energetic costs of finding exposed eider eggs.

Factors affecting rates of egg capture

Egg captures were correlated to gull search activity (i.e. both air and ground searches). Ground search rates were more highly correlated than air search rates. We observed gulls begin searching for eider eggs in flight, then land when exposed eggs were detected. Hence, the air search mode likely represents the component of foraging directly influenced by environmental conditions, while the closely correlated ground search mode is more closely linked to egg capture opportunities, which are not as predictable. We used search rates as a proxy for egg capture rates to infer contribution of temperature, wind speed and solar radiation, tide height, and gull count predictors assessed at the 30 min resolution (see Methods). Although this inference is possibly...
justifiable, as effects of the latter predictors on egg capture rates could not be assessed directly, results suggest that increased wind speeds and/or lower temperatures likely did not lead directly to increased egg capture rates on the colony. Rather, the ability of gulls to search from the air cheaply over broader areas of the colony, especially during windy periods, likely increased their foraging efficiency.

Gull ground patrol rates increased with declining temperatures. This result lends further support to the segregation between the loafing and breeding gull components, as total gull numbers typically declined with low temperatures. Thus, low temperatures prompted gulls to search, but in different areas, based largely on whether or not they bred on the island.

Although we did not model rainfall events explicitly (because of their rarity), we found that egg captures were rare during rain, perhaps reflecting that eider eggs were not exposed under those conditions. Eider hens at this site spend less time away from their nests during wet weather, possibly to limit wetting of down and potential chilling of eggs (Bottitta et al. 2003).

As predicted, egg captures were more frequent overall in areas of high eider nest densities (Table 2.3). This makes intuitive sense as overall encounter rates with prey were typically higher than in areas of low prey densities. However, there was little or no support for nest density as a predictor of relative egg capture rates (egg captures per nest). Models of relative egg capture rates suggest that nests located in low density areas were not more likely to be depredated by gulls than nests in high density areas. Thus, individual eider nests occurring at low densities lost eggs to gulls at levels similar to those of nests occurring at high densities.
Both air and ground search rates, and overall and relative egg capture rates, declined as the season progressed in all 3 years. Eider nests initiated early clearly received disproportionate levels of per capita attention from foraging gulls, and suffered greater losses (Fig 2.1a-c). Mehlum (1991) similarly noted a downward trend in predation rates over the course of both eider egg-laying and incubation in a study of glaucous gull predation within an eider colony at Svalbard, Norway. We also found predation occurred only while females were away from the nest and that rates of predation were highest during initiation of eider clutches when eggs were left unattended.

A review of figures relating egg capture rates and nest densities to date suggests the decrease in foraging intensity was not triggered solely by the onset of ice break-up. Although gulls visited open water leads, egg capture rates at the colony were similar before and after ice break-up, at least until new eider nests were no longer being initiated. In all three years, the decrease in gull foraging activity coincided with the peak of the density curves calculated for each plot, suggesting that gulls focused on eider eggs, but only as long as some eider nests remained undefended during laying and exposed eggs were easily accessible.

Rates of gull egg captures within the eider colony were not simply a function of the number of eider nests present, but rather varied in accordance with nest attendance behaviour of eider hens. In other words eggs actively incubated by eider hens become functionally unavailable to foraging gulls with the sole exception of rare incubation recesses taken by eider hens. These findings emphasize the need to
examine predator foraging rates not only in terms of prey density but also in terms of factors that directly or indirectly influence functional prey availability.

**Factors affecting eider nest defence**

Agonistic interactions between predator and prey can have important consequences for egg capture success and risk of injury for the foraging gull. In a study of egg predation by glaucous gulls (*Larus hyperboreus*) within an eider colony, females attacked gulls in defending nest contents (Schamel 1977). Glaucous gulls pulled common eider females away from nests in order to capture eggs (Mehlum 1991), although this was never observed during the course of the present study of herring gulls. Instead, herring gulls took eider eggs opportunistically from unattended nests during egg-laying or when eider hens left the nest during recesses from incubation to drink. Gulls at the site attacked and retreated from the air more quickly during windy conditions, which likely reduced risks associated with exposure to defensive hens. Conversely, foraging from the air also may limit the foraging individual’s ability to investigate opportunities. Although lower encounter rates can be countered easily and cheaply by searching over wider areas when in the air, the same cannot be said as easily for searching low density areas from the ground.

Defensive response of eiders was weakest in eiders nesting at the lowest densities only (Fig 2.4). The effect was greatest at lower densities because proximity to incubating hens is more highly affected by density increases at such levels. The likelihood that gulls elicited a reaction from an incubating eider female increased sharply with increasing eider nest densities then stabilized at approximately 200 nests/ha. A positive relationship detected between increasing prey density and the
defensive response suggests that foraging by gulls at high densities carried greater risk of injury, as predicted. However, if choice of nesting density was driven solely by predation pressure, then hens would be expected to respond by always nesting at the highest densities possible to reduce susceptibility to predation. Instead, eiders nested at a range of densities within the colony and we did not detect an effect of eider nesting density on gull egg captures per nest. Additionally, gulls likely reduced risk associated with searching high density areas from the ground through behavioural tactics (e.g. increased awareness, carefully plotting trajectory, etc.), which buffer the expected increased defensive response of eiders, especially in the case of intense reactions. Ability to manage risk through behavioural tactics that reduce the likelihood of agonistic encounters with reactive prey may enable predators to exploit prey over a range of densities.

Eider nesting synchrony likely counters initially high levels of attention directed toward early laid eggs. In such conditions, it would be adaptive for eiders that initiate clutches the earliest to nest at the highest densities possible, which they did (Figs. 2.1a-c). With time and increasing total numbers of active nests on the colony, initiation of clutches later in low density areas would be less and less risky. Eventually, high numbers of active but not continuously incubated eider nests would saturate prey requirements of predators, further reducing risk for eider clutches.

Factors affecting prey availability

Our findings illustrate that it may not be sufficient to examine predator foraging efficiency in relation to prey densities alone without considering various trade-offs faced by the predator which determine prey accessibility. In some instances, energetic
considerations may modify expected rates of predation (i.e. optimal foraging). In
other instances, risks of injury for the predator may influence search modes and rates
of prey exploitation (Gilchrist et al. 1998). Instead, the results of this study emphasize
the need to examine factors that determine functional prey availability. This implies
the direct consideration of behaviour within predator-prey models, as studies that
neglect behavioural interactions within and between species are less apt to detect the
underlying processes that determine distribution of predator and prey, particularly if
they interact with weather, prey behaviour, etc. as they do in this study.

Methods of evaluating response rates also need to be examined carefully.
Calculation of per area rates, often used to characterise predation rates, were
inadequate for us to assess the relative attention and risk of predation directed to
individual prey items under different scenarios. Similarly, calculating per capita rates
alone also can lead to incomplete interpretation and inferences pertaining to the
distribution of a population of predators. Combinations can therefore be helpful in
helping researchers understand the nature of predator-prey interaction.

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Table 2.1. Generalized linear models used to determine factors affecting gull counts (n=593) at the East Bay island colony, in 2000 and 2001; global model is shown in bold text.

<table>
<thead>
<tr>
<th>Response model</th>
<th>K</th>
<th>ΔAICc</th>
<th>AICc weights</th>
<th>Sum of AICc weights</th>
</tr>
</thead>
<tbody>
<tr>
<td>Island gull count</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>year phdate wind temp solar tide</td>
<td>8</td>
<td>0.000</td>
<td>0.543</td>
<td>0.543</td>
</tr>
<tr>
<td>year phdate wind temp solar tide wind*tide</td>
<td>9</td>
<td>0.708</td>
<td>0.381</td>
<td>0.923</td>
</tr>
<tr>
<td>year wind temp solar tide</td>
<td>7</td>
<td>4.964</td>
<td>0.045</td>
<td>0.969</td>
</tr>
<tr>
<td>year wind temp solar tide wind*tide</td>
<td>8</td>
<td>5.712</td>
<td>0.031</td>
<td>1.000</td>
</tr>
</tbody>
</table>

K=number of estimable parameters in the model, year (annual effect), phdate (date adjusted to eider phenology), wind (wind speed), temp (temperature), solar (solar radiation), tide (tide height), wind*tide (wind speed and tide height interaction), plus intercept term and variance estimator.

Note: Models are ranked in order from most to least supported, given the data, but only models with Δ AIC ≤ 10 are presented.

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Table 2.2. Model-averaged parameter estimates and their 95% confidence intervals, from generalized linear models of gull counts (n=593) at the East Bay island colony, in 2000 and 2001.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Island gull count</th>
</tr>
</thead>
<tbody>
<tr>
<td>year 2001</td>
<td>0.000 (0.000, 0.000)</td>
</tr>
<tr>
<td>phdate</td>
<td>-0.100 (-0.192, -0.008)</td>
</tr>
<tr>
<td>wind</td>
<td>0.151 (0.001, 0.301)</td>
</tr>
<tr>
<td>temperature</td>
<td>0.283 (0.060, 0.507)</td>
</tr>
<tr>
<td>solar</td>
<td>-0.009 (-0.011, -0.006)</td>
</tr>
<tr>
<td>tide</td>
<td>3.183 (1.699, 4.667)</td>
</tr>
<tr>
<td>wind*tide</td>
<td>0.025 (-0.056, 0.106)</td>
</tr>
<tr>
<td>Intercept</td>
<td>46.255 (42.658, 49.852)</td>
</tr>
</tbody>
</table>

Note: Confidence intervals were estimated using ±2SE (Burnham and Anderson 2002). Parameters as in Table 2.1.
Table 2.3. Generalized linear models used to determine factors affecting overall and relative herring gull aerial search rates in eider nesting areas within 30 min periods (n=593) at the East Bay island colony, in 2000 and 2001; global model is shown in bold text.

<table>
<thead>
<tr>
<th>Response Model</th>
<th>K</th>
<th>Δ AICc</th>
<th>AICc weights</th>
<th>Sum of AICc weights</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Air search/ha/30 min</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>year phdate wind temp island density</td>
<td>8</td>
<td>0.000</td>
<td>0.349</td>
<td>0.349</td>
</tr>
<tr>
<td>year phdate wind temp solar tide island density</td>
<td>10</td>
<td>1.315</td>
<td>0.181</td>
<td>0.530</td>
</tr>
<tr>
<td>phdate wind temp island density</td>
<td>7</td>
<td>1.906</td>
<td>0.135</td>
<td>0.665</td>
</tr>
<tr>
<td>year phdate wind temp island density wind*density</td>
<td>9</td>
<td>2.047</td>
<td>0.125</td>
<td>0.790</td>
</tr>
<tr>
<td><strong>year phdate wind temp solar tide island density wind*density</strong></td>
<td>11</td>
<td>3.252</td>
<td>0.069</td>
<td>0.859</td>
</tr>
<tr>
<td>phdate wind temp solar tide island density</td>
<td>9</td>
<td>3.364</td>
<td>0.065</td>
<td>0.924</td>
</tr>
<tr>
<td>phdate wind temp island density wind*density</td>
<td>8</td>
<td>3.888</td>
<td>0.050</td>
<td>0.974</td>
</tr>
<tr>
<td>phdate wind temp solar tide island density wind*density</td>
<td>10</td>
<td>5.181</td>
<td>0.026</td>
<td>1.000</td>
</tr>
<tr>
<td><strong>Air search/nest/30 min</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>year phdate wind temp island density</td>
<td>8</td>
<td>0.000</td>
<td>0.261</td>
<td>0.261</td>
</tr>
<tr>
<td>phdate wind temp island density</td>
<td>7</td>
<td>0.101</td>
<td>0.248</td>
<td>0.509</td>
</tr>
<tr>
<td>phdate wind temp island density wind*density</td>
<td>8</td>
<td>1.797</td>
<td>0.106</td>
<td>0.616</td>
</tr>
<tr>
<td>year phdate wind temp island density wind*density</td>
<td>9</td>
<td>1.832</td>
<td>0.104</td>
<td>0.720</td>
</tr>
<tr>
<td>phdate wind temp solar tide island density</td>
<td>9</td>
<td>1.952</td>
<td>0.098</td>
<td>0.819</td>
</tr>
<tr>
<td>year phdate wind temp solar tide island density</td>
<td>10</td>
<td>2.107</td>
<td>0.091</td>
<td>0.910</td>
</tr>
<tr>
<td>phdate wind temp solar tide island density wind*density</td>
<td>10</td>
<td>3.357</td>
<td>0.049</td>
<td>0.958</td>
</tr>
<tr>
<td><strong>year phdate wind temp solar tide island density wind*density</strong></td>
<td>11</td>
<td>3.671</td>
<td>0.042</td>
<td>1.000</td>
</tr>
</tbody>
</table>

K=number of estimable parameters in the model, year (annual effect), phdate (date adjusted to eider phenology), wind (wind speed), temp (temperature), solar (solar radiation), tide (tide height), island (gull count), density (eider nests per ha), wind*density (wind speed and density interaction), plus intercept term and negative binomial dispersion parameter.

Note: Models are ranked in order from most to least supported, given the data, but only models with Δ AIC ≤ 10 are presented.
Table 2.4. Generalized linear models used to determine factors affecting overall and relative herring gull ground search rates in eider nesting areas within 30 min periods (n=593) at the East Bay island colony, in 2000 and 2001; global model is shown in bold text.

<table>
<thead>
<tr>
<th>Response Model</th>
<th>K</th>
<th>ΔAIC</th>
<th>AICc weights</th>
<th>Sum of AICc weights</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Ground search/ha/30 min</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>year phdate wind temp solar tide island density</td>
<td>10</td>
<td>0.000</td>
<td>0.535</td>
<td>0.535</td>
</tr>
<tr>
<td>year phdate wind temp solar tide island density wind*density</td>
<td>11</td>
<td>0.947</td>
<td>0.333</td>
<td>0.868</td>
</tr>
<tr>
<td>phdate wind temp solar tide island density</td>
<td>9</td>
<td>4.493</td>
<td>0.057</td>
<td>0.925</td>
</tr>
<tr>
<td>phdate wind temp solar tide island density wind*density</td>
<td>10</td>
<td>5.577</td>
<td>0.033</td>
<td>0.958</td>
</tr>
<tr>
<td>year phdate wind temp island density wind*density</td>
<td>9</td>
<td>6.179</td>
<td>0.024</td>
<td>0.982</td>
</tr>
<tr>
<td>year phdate wind temp island density</td>
<td>8</td>
<td>7.271</td>
<td>0.014</td>
<td>0.996</td>
</tr>
<tr>
<td><strong>Ground search/nest/30 min</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>year phdate wind temp solar tide island density wind*density</td>
<td>11</td>
<td>0.000</td>
<td>0.438</td>
<td>0.438</td>
</tr>
<tr>
<td>year phdate wind temp solar tide island density</td>
<td>10</td>
<td>0.738</td>
<td>0.303</td>
<td>0.742</td>
</tr>
<tr>
<td>phdate wind temp solar tide island density wind*density</td>
<td>10</td>
<td>2.446</td>
<td>0.129</td>
<td>0.871</td>
</tr>
<tr>
<td>phdate wind temp solar tide island density</td>
<td>9</td>
<td>3.059</td>
<td>0.095</td>
<td>0.966</td>
</tr>
<tr>
<td>year phdate wind temp island density wind*density</td>
<td>9</td>
<td>5.801</td>
<td>0.024</td>
<td>0.990</td>
</tr>
<tr>
<td>phdate wind temp island density wind*density</td>
<td>8</td>
<td>8.584</td>
<td>0.006</td>
<td>0.996</td>
</tr>
<tr>
<td>year phdate wind temp island density</td>
<td>8</td>
<td>9.703</td>
<td>0.003</td>
<td>0.999</td>
</tr>
</tbody>
</table>

K=number of estimable parameters in the model, year (annual effect), phdate (date adjusted to eider phenology), wind (wind speed), temp (temperature), solar (solar radiation), tide (tide height), island (gull count), density (eider nests per ha), wind*density (wind speed and density interaction), plus intercept term and negative binomial dispersion parameter.

Note: Models are ranked in order from most to least supported, given the data, but only models with Δ AIC ≤ 10 are presented.
Table 2.5. Exponentiated model-averaged parameter estimates representing Incident Rate Ratios (IRR) and their 95% confidence intervals, from generalized linear models of overall and relative herring gull search rates in eider nesting areas within 30 min periods (n=593) at the East Bay island colony, in 2000 and 2001.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Air search/ha/30 min</th>
<th>Air search/nest/30 min</th>
<th>Ground search/ha/30 min</th>
<th>Ground search/nest/30 min</th>
</tr>
</thead>
<tbody>
<tr>
<td>year 2000</td>
<td>1.131 (0.918, 1.393)</td>
<td>1.062 (0.902, 1.251)</td>
<td>1.412 (1.005, 1.985)</td>
<td>1.265 (0.886, 1.808)</td>
</tr>
<tr>
<td>year 2001</td>
<td>1.000 (1.000, 1.000)</td>
<td>1.000 (1.000, 1.000)</td>
<td>1.000 (1.000, 1.000)</td>
<td>1.000 (1.000, 1.000)</td>
</tr>
<tr>
<td>phdate</td>
<td>0.961 (0.953, 0.969)</td>
<td>0.955 (0.947, 0.963)</td>
<td>0.957 (0.943, 0.971)</td>
<td>0.954 (0.940, 0.968)</td>
</tr>
<tr>
<td>density</td>
<td>1.002 (1.002, 1.003)</td>
<td>0.999 (0.999, 1.000)</td>
<td>1.005 (1.003, 1.006)</td>
<td>1.002 (1.001, 1.004)</td>
</tr>
<tr>
<td>island</td>
<td>1.023 (1.014, 1.031)</td>
<td>1.022 (1.014, 1.030)</td>
<td>1.023 (1.007, 1.039)</td>
<td>1.022 (1.006, 1.038)</td>
</tr>
<tr>
<td>wind</td>
<td>1.029 (1.019, 1.039)</td>
<td>1.026 (1.016, 1.036)</td>
<td>1.039 (1.016, 1.062)</td>
<td>1.043 (1.017, 1.070)</td>
</tr>
<tr>
<td>temperature</td>
<td>0.982 (0.960, 1.006)</td>
<td>0.979 (0.957, 1.001)</td>
<td>0.957 (0.920, 0.996)</td>
<td>0.957 (0.920, 0.994)</td>
</tr>
<tr>
<td>solar</td>
<td>1.000 (1.000, 1.000)</td>
<td>1.000 (1.000, 1.000)</td>
<td>0.999 (0.999, 1.000)</td>
<td>0.999 (0.999, 1.000)</td>
</tr>
<tr>
<td>tide</td>
<td>1.010 (0.963, 1.059)</td>
<td>1.012 (0.964, 1.064)</td>
<td>0.904 (0.764, 1.070)</td>
<td>0.918 (0.779, 1.083)</td>
</tr>
<tr>
<td>wind*density</td>
<td>1.000 (1.000, 1.000)</td>
<td>1.000 (1.000, 1.000)</td>
<td>1.000 (1.000, 1.000)</td>
<td>1.000 (1.000, 1.000)</td>
</tr>
<tr>
<td>Dispersion</td>
<td>0.571 (0.479, 0.664)</td>
<td>0.543 (0.453, 0.634)</td>
<td>1.509 (1.208, 1.809)</td>
<td>1.355 (1.075, 1.635)</td>
</tr>
<tr>
<td>Intercept</td>
<td>-2.785 (-3.303, -2.267)</td>
<td>-0.010 (-0.485, 0.465)</td>
<td>-4.242 (-5.175, -3.310)</td>
<td>-1.683 (-2.638, -0.728)</td>
</tr>
</tbody>
</table>

*Negative binomial dispersion parameter.
Note: Confidence intervals were estimated using ±2SE (Burnham and Anderson 2002); dispersion parameter and intercept were not subjected to exponentiation. Parameters as in Table 2.3.
Table 2.6. Generalized linear models used to determine factors affecting overall and relative herring gull search rates in eider nesting areas within 180 min periods (n=274) at the East Bay island colony, in 2000 and 2001; global model is shown in bold text.

<table>
<thead>
<tr>
<th>Response model</th>
<th>K</th>
<th>ΔAICc</th>
<th>AICc weights</th>
<th>Sum of AICc weights</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Air searches/ha/180 min</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>year phdate density year*phdate</td>
<td>6</td>
<td>0.000</td>
<td>0.311</td>
<td>0.311</td>
</tr>
<tr>
<td>year phdate density year*density</td>
<td>7</td>
<td>0.518</td>
<td>0.240</td>
<td>0.552</td>
</tr>
<tr>
<td>phdate density</td>
<td>4</td>
<td>0.703</td>
<td>0.219</td>
<td>0.771</td>
</tr>
<tr>
<td>year phdate density year*density</td>
<td>6</td>
<td>1.468</td>
<td>0.149</td>
<td>0.920</td>
</tr>
<tr>
<td>year phdate density</td>
<td>5</td>
<td>2.723</td>
<td>0.080</td>
<td>1.000</td>
</tr>
<tr>
<td><strong>Air searches/nest/180 min</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>year phdate density year*phdate</td>
<td>6</td>
<td>0.000</td>
<td>0.321</td>
<td>0.321</td>
</tr>
<tr>
<td>phdate density</td>
<td>4</td>
<td>0.309</td>
<td>0.275</td>
<td>0.596</td>
</tr>
<tr>
<td>year phdate density year*density</td>
<td>7</td>
<td>1.117</td>
<td>0.184</td>
<td>0.780</td>
</tr>
<tr>
<td>year phdate density</td>
<td>5</td>
<td>1.764</td>
<td>0.133</td>
<td>0.913</td>
</tr>
<tr>
<td>year phdate density year*density</td>
<td>6</td>
<td>3.771</td>
<td>0.049</td>
<td>0.961</td>
</tr>
<tr>
<td>year phdate year*phdate</td>
<td>5</td>
<td>5.561</td>
<td>0.020</td>
<td>0.981</td>
</tr>
<tr>
<td>phdate</td>
<td>3</td>
<td>6.314</td>
<td>0.014</td>
<td>0.995</td>
</tr>
<tr>
<td>year phdate</td>
<td>4</td>
<td>8.355</td>
<td>0.005</td>
<td>1.000</td>
</tr>
<tr>
<td><strong>Ground searches/ha/180 min</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>year phdate density year*density</td>
<td>7</td>
<td>0.000</td>
<td>0.608</td>
<td>0.608</td>
</tr>
<tr>
<td>year phdate density year*density</td>
<td>6</td>
<td>1.805</td>
<td>0.246</td>
<td>0.854</td>
</tr>
<tr>
<td>year phdate density year*phdate</td>
<td>6</td>
<td>2.984</td>
<td>0.137</td>
<td>0.991</td>
</tr>
<tr>
<td>phdate density</td>
<td>4</td>
<td>9.576</td>
<td>0.005</td>
<td>0.996</td>
</tr>
<tr>
<td>year phdate density</td>
<td>5</td>
<td>9.933</td>
<td>0.004</td>
<td>1.000</td>
</tr>
<tr>
<td><strong>Ground searches/nest/180 min</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>year phdate density year*phdate</td>
<td>6</td>
<td>0.000</td>
<td>0.523</td>
<td>0.523</td>
</tr>
<tr>
<td>year phdate density year*density</td>
<td>7</td>
<td>0.995</td>
<td>0.318</td>
<td>0.841</td>
</tr>
<tr>
<td>year phdate density year*density</td>
<td>6</td>
<td>3.754</td>
<td>0.080</td>
<td>0.921</td>
</tr>
<tr>
<td>phdate density</td>
<td>4</td>
<td>4.685</td>
<td>0.050</td>
<td>0.971</td>
</tr>
<tr>
<td>year phdate density</td>
<td>5</td>
<td>6.112</td>
<td>0.025</td>
<td>0.995</td>
</tr>
</tbody>
</table>

K=number of estimable parameters in the model, year (annual effect), phdate (date adjusted to eider phenology), density (eider nests per ha), year*density (year and density interaction), year*phdate (year and date interaction), plus intercept term and negative binomial dispersion parameter.

Note: Models are ranked in order from most to least supported, given the data, but only models with ΔAIC ≤ 10 are presented.
Table 2.7. Exponentiated model-averaged parameter estimates representing Incident Rate Ratios (IRR) and their 95% confidence intervals, from generalized linear models of overall and relative herring gull foraging activity rates in eider nesting areas within 180 min periods (n=274) at the East Bay island colony, in 2000 and 2001.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Air search/ha/180 min</th>
<th>Air search/nest/180</th>
<th>Ground search/ha/180 min</th>
<th>Ground search/nest/180 min</th>
<th>Egg capture/ha/180 min</th>
<th>Egg capture/nest/180 min</th>
</tr>
</thead>
<tbody>
<tr>
<td>year 2000</td>
<td>0.742</td>
<td>0.789</td>
<td>0.507</td>
<td>0.557</td>
<td>0.892</td>
<td>0.999</td>
</tr>
<tr>
<td></td>
<td>(0.433, 1.269)</td>
<td>(0.472, 1.318)</td>
<td>(0.251, 1.024)</td>
<td>(0.275, 1.126)</td>
<td>(0.391, 2.035)</td>
<td>(0.655, 1.526)</td>
</tr>
<tr>
<td>year 2001</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
</tr>
<tr>
<td></td>
<td>(1.000, 1.000)</td>
<td>(1.000, 1.000)</td>
<td>(1.000, 1.000)</td>
<td>(1.000, 1.000)</td>
<td>(1.000, 1.000)</td>
<td>(1.000, 1.000)</td>
</tr>
<tr>
<td>phdate</td>
<td>0.952</td>
<td>0.946</td>
<td>0.933</td>
<td>0.923</td>
<td>0.911</td>
<td>0.914</td>
</tr>
<tr>
<td></td>
<td>(0.936, 0.969)</td>
<td>(0.930, 0.962)</td>
<td>(0.908, 0.958)</td>
<td>(0.899, 0.948)</td>
<td>(0.869, 0.956)</td>
<td>(0.877, 0.953)</td>
</tr>
<tr>
<td>density</td>
<td>1.002</td>
<td>0.999</td>
<td>1.004</td>
<td>1.001</td>
<td>1.004</td>
<td>1.001</td>
</tr>
<tr>
<td></td>
<td>(1.001, 1.003)</td>
<td>(0.999, 1.000)</td>
<td>(1.002, 1.005)</td>
<td>(1.000, 1.002)</td>
<td>(1.002, 1.005)</td>
<td>(0.999, 1.002)</td>
</tr>
<tr>
<td>density*</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
</tr>
<tr>
<td></td>
<td>(0.999, 1.001)</td>
<td>(0.999, 1.000)</td>
<td>(1.000, 1.005)</td>
<td>(0.999, 1.002)</td>
<td>(0.998, 1.003)</td>
<td>(1.000, 1.000)</td>
</tr>
<tr>
<td>year 2000</td>
<td>(0.999, 1.000)</td>
<td>(0.999, 1.000)</td>
<td>(1.000, 1.005)</td>
<td>(1.000, 1.002)</td>
<td>(1.000, 1.005)</td>
<td>(0.999, 1.002)</td>
</tr>
<tr>
<td>density*</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
</tr>
<tr>
<td></td>
<td>(1.000, 1.000)</td>
<td>(1.000, 1.000)</td>
<td>(1.000, 1.000)</td>
<td>(1.000, 1.000)</td>
<td>(1.000, 1.000)</td>
<td>(1.000, 1.000)</td>
</tr>
<tr>
<td>phdate*</td>
<td>1.011</td>
<td>1.010</td>
<td>1.023</td>
<td>1.031</td>
<td>1.009</td>
<td>1.004</td>
</tr>
<tr>
<td></td>
<td>(0.987, 1.035)</td>
<td>(0.987, 1.034)</td>
<td>(0.986, 1.062)</td>
<td>(0.995, 1.068)</td>
<td>(0.973, 1.046)</td>
<td>(0.985, 1.024)</td>
</tr>
<tr>
<td>phdate*</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
</tr>
<tr>
<td></td>
<td>(1.000, 1.000)</td>
<td>(1.000, 1.000)</td>
<td>(1.000, 1.000)</td>
<td>(1.000, 1.000)</td>
<td>(1.000, 1.000)</td>
<td>(1.000, 1.000)</td>
</tr>
<tr>
<td>Dispersion$^a$</td>
<td>0.471</td>
<td>0.459</td>
<td>1.074</td>
<td>1.031</td>
<td>0.635</td>
<td>0.651</td>
</tr>
<tr>
<td></td>
<td>(0.380, 0.563)</td>
<td>(0.369, 0.548)</td>
<td>(0.840, 1.309)</td>
<td>(0.803, 1.258)</td>
<td>(-0.164, 1.433)</td>
<td>(-0.152, 1.454)</td>
</tr>
<tr>
<td>Intercept</td>
<td>0.760</td>
<td>3.393</td>
<td>-0.620</td>
<td>1.974</td>
<td>-3.730</td>
<td>-1.184</td>
</tr>
<tr>
<td></td>
<td>(0.368, 1.151)</td>
<td>(3.016, 3.771)</td>
<td>(-1.135, -0.104)</td>
<td>(1.462, 2.487)</td>
<td>(-4.575, -2.886)</td>
<td>(-1.919, -0.449)</td>
</tr>
</tbody>
</table>

$^a$Negative binomial dispersion parameter.

Note: Confidence intervals were estimated using ±2SE (Burnham and Anderson 2002); dispersion parameter and intercept were not subjected to exponentiation. Parameters as in Table 2.3.
Table 2.8. Generalized linear models used to determine factors affecting overall and relative herring gull egg capture rates in eider nesting areas within 180 min periods (n=274) at the East Bay island colony, in 2000 and 2001; global model is shown in bold text.

<table>
<thead>
<tr>
<th>Response model</th>
<th>K</th>
<th>ΔAICc</th>
<th>AICc weights</th>
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K=number of estimable parameters in the model, year (annual effect), phdate (date adjusted to eider phenology), density (eider nests per ha), year*density (year and density interaction), year*phdate (year and date interaction), plus intercept term and negative binomial dispersion parameter.

Note: Models are ranked in order from most to least supported, given the data, but only models with Δ AIC ≤ 10 are presented.
Fig. 2.1a. Year 1999 densities of incubated eider clutches (nests per hectare) and mean daily predation rates in relation to ice break-up and day of year.

Ice break-up
6 July

Day (1 Jan = Day 1)
Fig. 2.1b. Year 2000 densities of incubated eider clutches (nests per hectare) and mean daily predation rates in relation to ice break-up and day of year.

Ice break-up
9 July

- A plot
- B plot
- C plot
- D plot

Day (1 Jan = Day 1)
Fig. 2.1c. Year 2001 densities of incubated eider clutches (nests per hectare) and mean daily predation rates in relation to ice break-up and day of year.

Ice break-up 24 June

Day (1 Jan = Day 1)
Fig. 2.2a. Daily temperatures (°C) by year. The line within the box indicates the median, box limits represent 25th and 75th percentiles, whiskers represent 10th and 90th percentiles, dots represent extreme observations.
Fig. 2.2b. Daily wind speeds (km/h) by year. The line within the box indicates the median, box limits represent 25th and 75th percentiles, whiskers represent 10th and 90th percentiles, dots represent extreme observations.
Fig. 2.3. Overall search and egg capture rates (per ha per 30 min) versus wind speed (km/h) calculated using all available data from years 2000 and 2001 pooled. Note: N<10 observations for certain wind speed categories at: A plot (45 to <50), B plot (25 to <50), C plot (35 to <50), and D plot (30 to <50).
Fig. 2.4. Percentage of gull ground searches that elicited active defensive responses (all behavioural categories combined) from breeding eiders in relation to plot densities (nests/ha) in 1999, 2000 and 2001 combined. $r^2_{\text{adj}} = 0.34; n = 10; P = 0.045$.

Equation $y = a(1-b^x)$, where $a$=maximum value of $y$, and $b=0.5$. 

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Chapter 3

Title:
Herring gulls depredating eider ducklings: interaction among environmental conditions, indirect trophic relationships, and risk

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ABSTRACT
From 1999 to 2003, we assessed sources of variation in vulnerability of common eider
(Somateria mollissima) ducklings to attacks by herring gulls (Larus argentatus) at
colony in Canada's eastern Arctic where both species breed. Each year, we monitored
the progress from the nest to the sea of randomly selected broods and examined
sources of annual variation, effects of year, day of year (adjusted to timing of
breeding), time of day, wind speed, tide and temperature, on air and ground search,
and duckling capture rates by gulls. Brood location type, gull attack mode, and eider
response to gull attacks were also considered.

We hypothesised that if defensive hens posed an important risk to foraging
gulls, then gulls would use tactics that lower risks of injury, balancing benefits of prey
capture with costs. Gull air searches were more frequent on windy days, when they
could hover over broods. Eiders defended aggressively, regularly entering into direct
physical contact with gulls, occasionally resulting in vigorous struggles. Duckling
capture rates at this site were low and highly variable among years, despite high
encounter rates with gulls. Years 2000 and 2001 were characterized with low search
and duckling capture rates. These years coincided with a peak in collared lemming
(Dicrostonyx groenlandicus) abundance at East Bay.

Our findings stress the importance of assessing the relative value of prey for
the predator in terms of costs, returns and risks, rather than inferring levels of prey
exploitation solely from numerical assessments of abundance.

Key words: foraging, behaviour, predation, risk, rate, alternative prey, lemming,
herring gull, common eider, duckling.
INTRODUCTION

Predation can influence population dynamics, community structure and prey behaviour (Taylor 1984), with predators responding both functionally and numerically to changes in prey availability (Nicholson 1954, Holling 1959, 1961). High predation rates can be expected where predator numbers, prey numbers and encounter rates between them are high (Nicholson 1954). However, generalist predators, by definition, have a broad food niche, and can "switch" among prey types to maximize their energetic gain (Begon et al. 1996). Predators may switch prey in response to changes in their relative abundance, particularly when focal prey become scarce, or when combined benefits outweigh costs and risks of exploiting alternative prey (Abrams and Matsuda 1996, Béty et al. 2002). Prey switching can modify the magnitude of prey exploitation by predators, and consequently their influence on prey populations (Helfman 1990, Massaro et al. 2000, Suryan et al. 2000).

The Alternative Prey Hypothesis (Angelstam et al. 1984) states that abundance of focal prey can alter impacts on alternative prey indirectly (Abrams and Matsuda 1996). For example, lemming populations exhibit demographic cycles that apparently "peak" every 3 to 4 years in the Canadian Arctic (Krebs 1993). Evidence suggests that high abundance of a focal prey species such as lemmings may lower levels of exploitation of alternative prey such as bird eggs and young by both mammalian and avian predators (Greenwood 1987, Krebs 1993). In the Arctic, lemming cycles may lead indirectly to important variability in predation rates of birds across years as their predators respond to changes in focal prey abundance (Summers and Underhill 1987, Wilson and Bromley 2001, Béty et al. 2002). Because collared lemmings
(Dicrostonyx groenlandicus) occur on Southampton Island, we expected the foraging activity of gulls within the eider colony and duckling departure to vary annually in relation to lemming abundance.

Foraging Theory predicts individuals will strive to maximize the trade-off between energy gains and foraging costs (Stein 1977, Stephens and Krebs 1986). Abundance of prey, effects of environmental conditions on foraging, and risks to the predator, may all be important and interact (Gilchrist et al. 1998, Béty et al. 2002). Abiotic factors can influence the net value of prey in several ways (Nicholson 1954). Predator search intensity and attack success may vary with environmental conditions (Stein 1977, Zach 1979, Stephens and Krebs 1986, Jetz et al. 2003). Further, prey can respond adaptively to changes in predation risk (Dawkins and Krebs 1979) through synchrony of breeding activities (e.g. dilution, selfish herd) (Hamilton 1971), and aggressive defence (Gilchrist et al. 1998). Aggressive defence can generate risk of injury for the foraging predator, thereby increasing the costs associated with certain foraging decisions.

Therefore, generalist predators can be expected to not only switch between prey types according to variation in prey abundance, but also modify their search and attack modes according to changing environmental conditions and prey behaviour (Lind et al. 1994, Gilchrist et al. 1998, Bety et al. 2002, Harcourt et al. 2002). Specifically, when focal prey is scarce, foraging predators should respond by exploiting alternative prey primarily to satisfy energetic requirements. In contrast, when preferred focal prey is widely available, alternative prey, depending primarily on its value, could continue to be exploited opportunistically, but the decision of when
and how to attack should be influenced by risk of injury, with attacks taking place to maximize likelihood of success while minimizing risk of injury.


High winds allow herring gulls to hover, and hovering has been shown to be energetically less costly than flapping flight in this species (Goldspink et al. 1978). Hovering flight also has been shown to enhance the ability of gulls to pass slowly over prey and attack and retreat quickly from the air (McAloney 1973, Gilchrist et al. 1998). In addition, high winds can create surf, making departure from the colony difficult for ducklings, stalling departing broods (McAloney 1973). Breaking waves caused by high winds can also separate ducklings from accompanying hens and lead to ducklings being washed ashore, facilitating depredation; (McAloney 1973) estimated 14.7% of duckling losses to gulls occurred during attempts to enter the water,
especially when seas were defined as 'rough', with abandonment of young by adult
eiders occurring only during such conditions.

Objectives

Here, we explore how environmental and ecological factors influence herring gull
foraging activity and attack success during departure of eider broods from a nesting
colony in arctic Canada. We predicted that rates of herring gull search and attack
activity directed towards eider ducklings would be greatest during: 1) daytime, when
the ability of gulls to detect ducklings is high, 2) during windy conditions, when costs
of flight are lowest and wind allows gulls to hover, attack and retreat from above, and
3) during low tide, when eider ducklings are exposed to gulls while crossing expansive
tidal flats to the sea. Further, inability to hover during calm wind conditions should
lead to gulls searching on foot, a situation where defensive potential of eider hens is
greatest; both of these factors should lower rates of duckling capture. Finally, we
hypothesised that if herring gulls relied on lemmings as an important food source, then
predation rates of ducklings would drop during years of high lemming-abundance and
vice-versa.

METHODS

Study area

The study took place at the East Bay common eider colony, located on a small (36 ha)
island, which lacks tall (> 5 cm) vegetation, within the East Bay Migratory Bird
Sanctuary on Southampton Island, Nunavut, Canada (from 1999 to 2003). The island
supports 30 pairs of herring gulls and up to 4500 pairs of common eiders, as well as
small numbers of other breeding birds including Canada geese (*Branta canadensis*), and brant (*Branta bernicla*) (Allard and Gilchrist 2002).

Parasitic jaegers (*Stercorarius parasiticus*) and long-tailed jaegers (*Stercorarius longicaudus*) breed and forage on the coastal plain within 5 km of the island, while snowy owls (*Nyctea scandiaca*), short-eared owls (*Asio flammeus*), rough-legged hawks (*Buteo lagopus*), peregrine falcons (*Falco peregrinus*), gyrfalcons (*F. rusticolus*), glaucous gulls (*Larus hyperboreus*), iceland gulls (*L. glaucoides*), and Thayer's gulls (*L. thayeri*) occur within the East Bay area (Abraham and Ankney 1986). However, of the latter, only herring gulls have been observed searching for and capturing eider ducklings at this site. Arctic foxes (*Alopex lagopus*) do not remain on the East Bay colony island after ice break-up, further limiting the diversity of predators that can exploit eider ducklings on the island.

Herring gulls are common throughout Southampton Island (Sutton 1932, Parker and Ross 1973) and breed at variable but low densities on the coastal plain adjacent to the East Bay island eider colony (Abraham and Ankney 1986, Allard, in prep.). Herring gulls are considered generalists and are known to feed on a wide variety of prey types, typically preferring marine prey (Pierotti and Good 1994). Large arctic-nesting congeneric gulls are also known to exploit terrestrial lemming prey throughout the Arctic (Wilson and Bromley 2001, Béty *et al.* 2002, Ebbing and Spaans 2002). Greenland collared lemmings occur both on the colony island and on the adjacent mainland coastal plain (Southampton Island). Adult collared lemmings weigh 40-100 g (Béty *et al.* 2002) while newly hatched eider ducklings weigh 50-70 g immediately after hatch (Devink *et al.* 2005).
Factors influencing vulnerability of eider ducklings to predation by gulls

*Time of day*

Eider groups leaving the colony were monitored throughout the day in the first two years (1999, 2000), and included attempted observations during night time hours. In subsequent years, observations began at first light (between 0200 and 0300) and ended in the late evening when light conditions deteriorated (between 2100 and 2200). For analyses, days were partitioned into four 6 h categories: 0300 to 0900, 0900 to 1500, 1500 to 2100, and 2100 to 0300 which correspond to morning, midday, evening, and night time periods respectively.

*Wind*

Weather was monitored at 30 minute time intervals using a Davis Instruments automated weather station located on the colony island. The wind speed sensor was placed 3 m above the ground on the NE part of the island and because the island is flat and small (< 800 m long), wind speeds measured are considered to be representative.

*Tide*

Tide data at 30 min intervals derived from predictions were available for the community of Coral Harbour, Nunavut (64°08N 83°10W), approximately 40 km west of the study site (Canadian Hydrographic Service).

*Lemming abundance*

Lemming abundance was quantified using an index based on visual encounters with lemmings by researchers conducting daily species surveys on foot, during searches for ground-nesting birds on both the colony island and within a 2 km² study plot on the adjacent mainland coastal plain ±5 km away (Stenhouse *et al.* 2001). Lack of
vegetation and flat terrain enhanced detection of lemmings. Daily sighting effort was comparable between sites and across years (Table 3.1 lines 2 and 5). Because abundance is likely the most important source of heterogeneity in detection probabilities (Royle and Nichols 2003), we used detection probabilities as an index of lemming abundance in the study area. Lemming observations were compiled into daily presence/absence data. The index was calculated by dividing the number of days lemmings were observed by the number of days observations were made, multiplied by 100 (Table 3.1 line 3).

**Behavioural observations of gulls and eiders**

*Gull foraging behaviour*

While we monitored departing eider broods, observations of foraging gulls were conducted using a combination of scan and focal sampling (Altmann 1974). Individual foraging gulls were difficult to follow for > 10 min at a time and regularly left our field of view. Consequently, we focused our observations on departing eider broods, and quantified the search and attack activity of gulls directed toward them.

We recorded rates of air and ground searches, and the number of ducklings captured (quantified as events per unit time that the brood was continuously observed). Specifically, air searches were counted whenever gulls flew into the airspace within a 3 m radius of any focal brood. Characteristics of individual air searches included time of search, and flight mode (hovering vs. flapping flight). To avoid counting flying birds in transit, only individuals with heads tilted forward or to the side were considered to be actively searching for prey (Gilchrist et al. 1998). A ground search included any gull standing or walking within a 3 m radius of a focal brood. For each
ground search, time of search, nearest distance between gull and duckling, and search duration were recorded.

In order to reduce variability in our assessment of rates and minimize variability due to changing environmental conditions, only broods observed continuously for 5 to 120 min were included in analyses.

**Eider brood departure activity**

In all years, general departure activity of broods from the eider colony was assessed twice daily by checking nest attendance of incubating common eider females at four study plots (Allard et al. in prep.). These nest attendance data were used to derive hatch dates and expected departure dates. With this information, a day of year index was derived based on median hatch date that allowed comparison of response variables across years. To assess departure rates in relation to time of day, the number of broods in transit in a designated area (which encompassed approximately 30% of the colony island) was counted every 30 min in 2000.

We considered that an “eider brood” consisted of “a grouping of any number of parentally related and/or unrelated eider females and young” (Öst and Bäck 2003). Note that this definition contrasts with Munro (1975), who defined a “crèche” as the grouping of any number of parentally unrelated female(s) and young, and a “brood” as a group consisting of parentally-related offspring and adults. Because we were unable to determine the relatedness of hens and ducklings at the time of observation, all discrete assemblages of ducklings and hens were treated as broods, regardless of relatedness, size or composition (Öst and Bäck 2003).
From observation blinds, departing broods were observed by the naked eye or with 20-60X telescopes. Prior to the beginning of each observation, the portion of the island visible from a given blind (typically a radius of 100 to 300 m), was scanned for all broods, regardless of whether they were moving or not. One of these broods was then selected for continuous observation. Efforts were made to avoid bias through use of strategies that ensured random rather than haphazard selection (i.e. die, lists of random numbers generated by computer, etc.). Observations continued until visual contact was compromised or lost, or in most cases, until the brood had departed the colony and had swum beyond 300 m of the island. For each departing brood, the following was recorded: time of day at the beginning of each observation, habitat location (land, shallow pond, intertidal zone, inshore < 50 m from shore, offshore > 50 m from shore), absolute number of ducklings in group, absolute number of hens in group. Broods were monitored continuously, and the timing of any changes in any of the above parameters was recorded.

**Gull numbers**

Gulls were counted on the island from blinds several times daily during departure of eider broods from the colony each year from 2000 to 2002, inclusively. As counts were infrequent relative to our continuous observations of departing broods, predation risk could not be modelled directly as a function of gull numbers. Instead, counts were analysed separately against the same suite of predictors used in analyses of brood vulnerability, based on four six-hour periods each day (those were: starting at 0300 and ending at 0900, starting at 0900 and ending at 1500, starting at 1500 and ending at 2100, and starting at 2100 and ending at 0300). Thus, we assessed how gull numbers...
fluctuated in relation to year, day period, wind speed, tide height, and date. No more than one count per day period (i.e. one count per six-hour day period) was included, and all counts of herring gulls analysed were separated by at least three hours to lessen the influence of temporal autocorrelation.

**Eider hen aggressive defence**

Response of common eider females within focal broods to gull ground and air searches was categorized according to increasing intensity. Common eider females either: 1) did not respond, 2) extended their necks and/or stood, 3) walked towards gull, 4) lunged towards, charged or chased gull, or 5) physically contacted gull (including biting and grasping with bill). Note that less intense behaviours always preceded or were included within more intense behaviours. We used only the highest level hen reaction elicited by each individual attack (gull air or ground search) in our analyses.

**Statistical analyses**

Factors influencing gull search and duckling capture rates were analysed using generalized linear models (McCullagh and Nelder 1989). We examined the number of air and ground searches, as well as successful duckling captures per brood per minute of brood observation. These were modelled against year, date (i.e. phenological date, or date adjusted to timing of breeding by correcting for deviation from the mean of the median laying date calculated in each year), time of day (categorical, 4 levels), tide height and wind speed. A negative binomial was selected over a Poisson error structure, commonly adopted in analyses of count data (Cameron and Trivedi 1990, Crawley 1993), as visual inspection of cumulative probability plots revealed a better fit with the former (following Cameron and Trivedi 1990, Crawley 1993, Byers et al...
Thus, a log link function was used with foraging data (i.e. search rates, egg capture rates) while an identity link function was used for herring gull colony attendance data only (SAS v. 8.2, PROC GENMOD, SAS Institute Inc. 2000). Rather than model rates directly, the log of the duration (time denominator) of each individual brood observation was included as an offset variable in analyses of rate responses. This offset variable ensures control of differences in the duration of individual brood observations in the modelling equation. We compared lemming abundance across years through daily presence/absence data derived from observation by researchers obtained from the island and the adjacent mainland coastal plain. Also, gull bolus contents were examined for lemming material during all but the last year of study to confirm that gulls at the colony consumed lemmings.

Support for models and predictor sets was determined using information-theoretic criteria (Burnham and Anderson 2002). Biologically relevant predictors and interactions between them were selected a priori, corresponding to hypotheses based on theory, previous studies, and our own knowledge of the system. Predictors were excluded from our initial selection only if they exhibited collinearity with other predictors beyond a threshold level (r≥0.5) (Green 1979). Model sets contained all possible combinations of biologically relevant predictors ensuring each individual predictor appeared an equal number of times (Burnham and Anderson 2002). The AIC (Akaike’s Information Criterion) statistic (with adjustment for small samples, AICc) was calculated for each model. Models were then ranked according to their AICc values from lowest to highest (Burnham and Anderson 2002). Next, differences in AICc values (Δ AICc) between the most parsimonious model and all other models
considered were generated. AICc weights (the probability that a given model is the best model tested, given the data) were determined for each model.

Model selection uncertainty arises with sparse data and when many competing models have Δ AICc values of 4 or less (Burnham and Anderson 2002). In such cases, support for more than one model creates uncertainty as to which model is best. To avoid introducing bias by selecting a single model from which to draw inferences, a model-averaging strategy was adopted which involves averaging weighted estimates for each predictor across the model set. These “unconditional” estimates of coefficients and their standard errors were calculated for each predictor effect (Burnham and Anderson 2002).

As count means were modelled under a log link assumption, exponentiation of parameter estimates generates Incident Rate Ratios (IRR). An IRR represents a multiplier of the mean outcome and can be converted to a percent change by subtracting one and multiplying by 100. The result obtained should be interpreted as a percentage of growth or decline in the dependent variable due to a one-unit change in the independent variable, holding all else constant (Schweik 2000).

All tests are two-tailed and means are reported ±1 SE. Confidence intervals around parameter estimates in tables were calculated using ±2 SE (Burnham and Anderson 2002).

RESULTS:

Gull foraging activity directed toward departing eider broods

Over the course of 5 years of study, 631 broods (which included 3320 ducklings) were followed for a total of 350.7 hours of continuous focal observations. Gulls performed
824 air searches, 261 ground searches, and captured 35 eider ducklings (Table 3.2). The number of breeding herring gull pairs remained stable at 30 on the colony island, but the number of eider nests varied among years (Fig. 3.1).

**Environmental factors**

Higher wind speeds were recorded in 1999 and 2002, during which wind speeds dropped below 17 km/h less than 25% of the time. In contrast, wind speeds in 2003 exceeded 17 km/h less than 25% of the time (Fig 3.2). 1999 and 2002 were cooler than other years in the study, with highs rarely reaching above 10 °C (Fig. 3.3). Temperature lows do not appear to differ markedly between years. Tide heights encountered between first and last focal observations of broods were similar across years (Fig. 3.4), although the range of tidal heights to which departing broods were exposed was lower in 2002, resulting from a shorter total sampling period.

**Factors affecting eider brood departure activity**

*Date*

Both the linear and quadratic date terms received model support (Table 3.3). The coefficient for the quadratic term was negative indicating numbers peaked at the midpoint of observations in that year. However, confidence intervals for the quadratic effect just reached the no-effect value (Table 3.4 lines 9, 12) precluding confident inference. However such a relationship between date and departure activity would be expected (see chapter two, Tables 2.1a-c, section 1).
**Time of day**

Fewer than 5% (18 of 432) of eider broods were monitored during night time in 1999 and 2000, as broods departed almost exclusively by day (Fig. 3.5). Numbers of ducklings counted on ponds in the scan area, where transiting broods gathered, staged or passed, were also lower during the night than all other day periods. Consequently, we focused our analysis on daytime periods (see Methods). Top models for year 2000 included the categorical day period variable (Table 3.3). Although the number of broods departing did not differ among the three six-hour daylight periods (0300 to 2100), their estimate values were clearly higher than the reference value for the night time period (Table 3.4 lines 1-4) and their confidence limits did not bound the no-effect value, lending support to our observation that broods departed by day.

**Wind speed and tide height**

Top models included the wind variable (Table 3.3), and confidence intervals around its raw estimate did not bound the no-effect value (1) (Table 3.4 line 10). This suggests numbers of eider broods counted on the colony increased with wind speed. The interaction between wind speed and day period received some support, appearing in top models, but the confidence intervals around raw estimates reached or bounded the no-effect value (1) (Tables 3.3, 3.4 lines 5-8).

Tide height received little model support and otherwise produced no evidence of influence on the departure activity of eider broods (Tables 3.3 and 3.4 line 11).
Factors affecting colony attendance by herring gulls

The year variable appeared in all top models (Table 3.5) suggesting total numbers of gulls present on the eider colony varied according to year. However, this appears to be true only for year 2000, which had a highly negative raw estimate value with confidence intervals that did not bound the no-effect value (0), indicating numbers of gulls counted on the colony were lower in that year (Table 3.6 line 1).

Tide height also appeared in all top models (Table 3.5). The estimate for the tide effect was positive and with wide confidence intervals that did not bound the no-effect value (Table 3.6 line 9). This evidence suggests strongly that gull attendance was positively associated with tide height, so that at high tides, more gulls were present on the island.

We were unable to detect an effect indicating a strong relationship between the number of gulls present on the eider colony and time of day, date, or wind speed. The time of day estimate generated little model support, and its confidence intervals bounded zero widely (Tables 3.5, 3.6 lines 4-7). Similarly, there was little model support for the date effect and confidence intervals bounded zero for raw estimates of both the linear and quadratic date terms (Tables 3.5, 3.6 lines 10 and 11). Wind speed also received little model support (Table 3.5), was unimportant, and confidence intervals around its estimate also widely bounded zero (Table 3.6 line 8).

Factors affecting gull air and ground search rates

Gull search rates varied by year (Tables 3.7 and 3.8). Air search rates were lower in 2000 and 2001 than in 2002 or 2003, but not 1999 (Table 3.9 lines 1-5, Fig. 3.5).
Ground search rates were lower in 1999, 2000 and 2001 than in 2003, but not 2002 (Table 3.9 lines 1-5, Fig. 3.5). The effect of wind speed on search rates received strong model support (Table 3.7). Although positive estimates for both air and ground search rates were somewhat imprecise, confidence intervals did not bound the no-effect value (Table 3.9 line 10). This evidence suggests gulls searched more in the air and on the ground as wind speeds increased (Fig. 3.6).

Neither the linear term for date adjusted to eider timing of breeding nor its quadratic received much model support as predictors of air search activity (Tables 3.7, 3.9 lines 12 and 13). In contrast, date received more model support as a predictor of ground search rate (Table 3.8). Specifically, the quadratic date term’s estimate for date was positive and its confidence intervals did not bound the no-effect value. This suggests ground search rates were higher initially, decreased to a minimum, then increased, with advancing date.

Time of day, and tide height received little model support in either models of air, or ground searches by gulls (Tables 3.7, 3.8 and 3.9 lines 6-9 and 11).

Factors affecting duckling capture rates

During 13.45 h of observation in 2003, no gulls were observed capturing ducklings from departing eider broods. Therefore, we analysed years 1999 through 2002 only to avoid problems of non-convergence of models of duckling capture rates. As expected, year appeared in all top models of the set (Table 3.10), reflecting annual variation in rates of duckling captures (number depredated per 100 ducklings observed calculated per 24 h: 1.08 (1999), 0.06 (2000), 0.08 (2001), 4.86 (2002), and 0 (2003) (Table 3.2). Confidence intervals around negative estimates for years 2000 and 2001 did not bound
zero, indicating capture rates were lower in those years than in 1999 and 2002 (Table 3.9 lines 1-5).

Both the linear and quadratic date terms appeared in top models, receiving much model support. Still, confidence limits around the raw estimate for the quadratic just reached the no-effect value. It remains possible and plausible that capture rates were higher at the beginning and end of the departure period (Table 3.9 line 13).

Duckling captures were never observed during night time. In fact, only in 1999 and 2000 were successful attacks recorded during the mid day period; all others occurred during morning and evening (Fig. 3.5). For this reason, we did not formally test the effect of day period on duckling capture rates due to sparseness of data.

Although wind appeared in the top model of the set (Table 3.10), it failed to gather much model support. Also, confidence intervals around its positive estimate bounded zero (Table 3.9 line 10). Similarly, very little evidence supported tide height as a predictor of duckling capture rates (Table 3.10 and 3.9 line 11). Raw data showing duckling captures by location (Fig. 3.8) suggest that ducklings were most vulnerable, in decreasing order, when located on the water within 50 m of the shoreline, within the intertidal zone and on land. However, lack of independence due to the fact broods passed from one landscape type to the next precludes formal testing and inference of an effect of location type on search and duckling capture rates.

**Relationship between gull searches and predation events**

With all years pooled, the number of ducklings taken per brood observed was positively correlated to both the number of air searches per brood \(N = 631, r = 0.47, P<0.0001\) and to the number of ground searches per brood \(N = 631, r = 0.39,\)
As expected, both search types were strongly correlated with each other (N = 631, r = 0.71, P<0.0001). Correlations by year are presented in Table 3.11.

**Factors affecting hen reaction towards gulls**

It was common for more than one eider female to accompany ducklings during departure. Consequently, gulls active near broods (within 3 m) would often elicit the reaction of several females, but generally not in unison. Rather than examine the frequency of inconsequential low-level behaviours we focused on recording the highest reaction level reached by hens during gull attacks. In particular, we examined the occurrence of physical encounters between hens and gulls. To clearly differentiate reactions by hens directed toward either air or ground-searching gulls, only searches that were purely aerial or purely ground-based were used in analyses (i.e. air searches that became ground searches were excluded).

*Response to ground and air searches*

We obtained many fewer reaction data for ground searches than air searches (211 vs. 629 respectively, all years combined). Of the ground searches, we detected no differences in the proportion that elicited a reaction (of any level) from hens when comparing years of high or low lemming-abundance (i.e. between 2000, 2001 pooled and 1999, 2002, 2003 pooled; Pearson $\chi^2$, P<0.069). Similarly, we found no evidence that proportion of strongly aggressive reactions to gulls on foot differed between low and high lemming years (Pearson $\chi^2$, P<0.427).

Brood composition data are summarized in Table 3.12. Although confidence intervals around means are wide, the number of hens per brood was highest, while
numbers of ducklings per brood and duckling/hen ratios were lowest in 2002, the year following the peak in lemming abundance.

The proportion of air searches that elicited a reaction of any level by eider hens was significantly higher in years of low lemming-abundance (Pearson $\chi^2$, $P<0.0001$), and the number of strongly aggressive reactions (in which contact was made between one or several defensive hens and the attacking gull) was also greater in years of low lemming-abundance (Pearson $\chi^2$, $P=0.010$) (Table 3.13). Among low lemming-abundance years only, the proportion of aggressive reactions involving contact between defensive eider hens and gulls was greater in 2002 than in 1999 and 2003 combined (Pearson $\chi^2$, $P=0.001$). We failed to detect the latter effect for strongly aggressive reactions to gull ground searches (Fisher’s exact test, $P=0.663$).

**Lemming abundance**

The frequency of lemming observations varied across years (Table 3.1, Fig. 3.6). Further, the indices of lemming abundance on the eider colony island and on the mainland of Southampton Island varied in unison (Fig. 3.6). Both the numbers of lemmings observed per day, and the frequency of lemming observations peaked in the consecutive years 2000 and 2001, at both sites (Fig. 3.6).

Gull boluses examined in the vicinity of gull nests at the site were typical of those observed elsewhere in the species’ range (pers. obs.). In contrast, several boluses examined in 2000 and 2001 were atypical in both colour and size, and did not appear to contain feathers. Three of seven and five of thirteen gull boluses collected near active nest sites of known gull individuals in 2000 and 2001 respectively, contained lemming bones and teeth. Three boluses contained evidence that up to four
individuals had been consumed (both upper and lower jaws) by single gulls. Remaining boluses examined were more typical in appearance and contained evidence of bird (feathers) and invertebrate prey (arthropod exoskeletons and mollusc shells).

**DISCUSSION**

**Numerical effects of Herring Gull predation**

Synchrony of breeding activities in colonial birds at high latitudes is widespread and may be particularly advantageous during vulnerable periods, (e.g. departure of young). Conversely, concentrations of prey in the form of large numbers of vulnerable young may serve to attract non-resident predators (reviewed by Wittenberger and Hunt 1985, Rodgers 1987). When large numbers of young depart a breeding area synchronously, they can numerically overwhelm local predator populations thereby lowering rates of predation (i.e. dilution) (Hamilton 1971).

Predation rates were derived from a combination of both near-shore and land observations, during the first 24h after nest exodus only, and are not meant to be projected further in time. Rates were calculated as the number of ducklings taken by herring gulls if 100 ducklings were observed continuously for 24h and are unadjusted for night time when little or no predation occurs (broods immobile or hidden under the wings of attending eider hens) (Mendenhall and Milne 1985, Åhlund and Göтmark 1989). If rates were adjusted for night time, estimates from this study would be somewhat (20-40%) lower. Åhlund and Götmark (1989) calculated rates adjusted for night time of zero (1981), eight (1982) for Salolfjorden and 12 (1982) for Byfjorden. Mendenhall and Milne (1985) found a rate of 11 (1974) on the Ythan estuary. Both of these teams focused on predation on the water in the vicinity of breeding islands and
not on the land. Åhlund and Götmark state "gulls hardly paid any attention to ducklings on land..." however wind conditions were not considered. At East Bay, although we observed more predation events on land, predation rates (ducklings captured per unit time) were highest in inshore and intertidal areas (Fig. 3.8) where during windy conditions broods stalled or encountered breaking waves. Ducklings were least vulnerable (predation rates were lowest) when moving over land, when on small shallow ponds within the colony or when offshore, possibly due to enhanced defensive ability of hens in those areas.

As encounter rates between herring gulls and eider ducklings at the colony were high, we predicted that predation rates would also be high. This was not the case. Instead, predation events observed during continuous monitoring of departure groups were rare (Table 3.2), and estimated adjusted rates of predation (following Mendenhall and Milne 1985; Åhlund and Götmark1989), were lower than rates reported at other eider colonies. Our highest rates were less than five ducklings taken per 100 ducklings observed per day in 2002 and slightly more than one in 1999. Our estimated lowest rates equalled zero in 2003 and neared zero in both 2000 and 2001.

The suggestion that rates of duckling predation at East Bay are lower than expected is also supported by estimates of energy requirements of the resident gull population (60 adults each year). Adult female herring gulls are estimated to require 200-260 kcal/day under thermal neutral conditions (removing all costs of chick feeding) (Norstrom et al. 1986). The energetic value of eider ducklings at the Bay of Fundy was estimated at 6.565±0.124 kcal/10 g (dry weight) (Gilliland, et al. 2004). Assuming an assimilation efficiency of 0.8 (Drent et al. 1992), a single 60 g duckling
with an approximate dry weight of ±20 g would have a conservative approximate value of ±10 kcal.

These estimates suggest adult gull intake rates of ducklings should amount to no fewer than 20 ducklings per day, based on gull daily energetic requirements. Excluding all other non-breeding gulls and the requirements of gull chicks (i.e. a deliberately conservative estimate of gull energy requirements on the colony), we estimated that if each of the 60 herring gulls breeding within the colony consumed 20 ducklings per day, then the resident gull population would consume approximately 1200 ducklings per day at an average of 50 ducklings per hour for the whole colony. Our monitoring efforts allowed us to quantify predation over a minimum of one third of the colony, and based upon these estimates, we should have observed an average capture rate of 17 ducklings per hour of observation. This was never the case. In fact, even during 2002, the year of highest duckling capture rates, rates of duckling predation averaged less than 0.5 captures per hour of continuous brood observations.

Collectively, our direct observations of duckling predation rates as well as estimates of herring gull energy requirements, suggest that herring gulls at East Bay do not rely on eider ducklings to meet their energetic demands.

Why then are herring gull predation rates so low at this site? We believe that there exists a dynamic relationship whereby the relative value of foraging on eider ducklings varies according to environmental and/or other factors at both short (daily) and long (annual) temporal scales. This suggests that gulls are constrained in one or several ways and/or alternative foraging opportunities exist for them elsewhere.
Factors affecting gull search and attack activity

Although tide was a strong predictor of herring gull numbers on the colony, tidal fluctuation did not affect search and capture frequencies.

Few eider broods departed at night, and as expected, we observed low gull search and capture rates during those periods (Fig. 3.5). Perhaps low light conditions make visual contact between hens and ducklings difficult, and they are reluctant to depart the colony under these conditions (Minot 1980). Also, during daylight hours, there was little influence of time period, with no pronounced peak of brood departure (Tables 3.3 and 3.4 lines 1-3) or gull search activity (Tables 3.7, 3.8 and 3.9 lines 6-9). However, when observation periods where wind exceeded 15 km/h were excluded from the analysis, departure activity was significantly greater in the morning and middle of the day and lowest in the evening and night.

Wind speed influenced gull attack mode. 25/35 ducklings were captured by gulls that attacked from the air using a “hover and drop” technique. In three of these cases, wind speeds during the attacks were above 10 km/h; in all other cases wind speeds exceeded 15 km/h. Alternatively, 10/35 ducklings were captured from the ground using a “run and grab” technique; in all but two of these cases, wind speeds were below 15 km/h. In one of the latter cases, a stray duckling, far from hens was taken by a ground-searching gull. In the other, a hovering gull dropped to the ground after having detected an opportunity, waited and then attacked from the ground.

The relationship between attack mode and wind speed exemplifies how variability in an environmental variable modifies the relative value of an attack and prey capture at a small temporal scale. When wind speeds exceeded 15 km/hr, gulls...
markedly increased air search activity and successful attack frequency also increased (Fig. 3.7). From the air, gulls could search greater areas, avoid interference from both kleptoparasites (Allard and Gilchrist 2002) and conspecific competitors on the ground, and defending eider females (Bustnes and Erikstad 1991). Most importantly, gulls could make repeated attacks from the air, presumably at little energetic expense. These repeated attacks from above agitated defending eider hens and exposed eider ducklings as hens left the group to lunge at gulls. Under windy conditions, gulls could easily retreat to safe altitudes with only slight wing adjustments while gliding over eider broods. Once a successful attack took place, a flying gull could quickly leave the site and escape harassment from eider hens and other gulls (McAloney 1973).

In summary, windy conditions (>15 km/hr) enhanced gull foraging intensity and success, especially at intermediate velocities (Fig. 3.7), perhaps because wind enhanced gulls’ ability to hover, harass broods from the air, attack exposed ducklings, and avoid defensive eider hens. The highest wind speeds might have reduced overall manoeuvrability and control, and hindered attack success. Brood vulnerability to attack by gulls likely increased during windy periods when broods were stalled for long periods or as they attempted to negotiate breaking waves at the shoreline.

**Lemming abundance and the Alternative Prey Hypothesis**

Even when controlling for time of day, wind speed, tide height, and eider egg-laying phenology, there remained strong annual effects in models of search and duckling capture rates. Numbers of herring gulls (breeding) remained constant while numbers of eiders varied, but not in unison with annual variation in gull search and duckling...
capture rates. Then, what is the factor that varies by year that is having such a
dramatic effect on duckling predation by gulls?

Gull search and duckling capture rates varied inversely with lemming
abundance, measured at two sites separated by 4 km of open salt water (Fig. 3.6). This
supports the Alternative Prey Hypothesis which predicts that abundance of focal prey
indirectly affects levels of predation on alternative prey. The marked drop in air and
ground search, as well as duckling capture rates, during years of high lemming-
abundance (2000 and 2001) demonstrates that gulls change their foraging habits in
relation to abundance of lemmings, particularly during years of peak lemming-
abundance.

We note that 2003 could be perceived as an aberration, as no duckling captures
took place during a year with low lemming-abundance. However, during that low
lemming year, gull search intensity was elevated and supported predictions. Here we
speculate that gulls searched the colony by wing even though calm wind conditions
were not conducive to the air search mode and the successful “hover and drop” attack
technique. This implies, that in a year of low lemming-abundance, and prevailing
calm wind conditions, gulls were required to use more costly flapping flight
(Goldspink et al. 1978) more often when searching from the air. Also, partly as a
consequence of low wind speeds, ground search rates were higher in 2003 than during
all other years of the study. Ground-based attacks, for which likelihood of injury is
conceivably greater, were not successful in 2003, despite increased frequency. This
suggests that success of a ground-based attack may be constrained by opportunity and
is not enhanced directly through increased effort by a foraging gull. It is also likely
that successful ground attacks in other years followed detection of vulnerable young 
(e.g. opportunities) made possible through hovering (i.e. more efficient aerial 
searching), which lower wind speeds did not allow in 2003.

Factors that interact to influence herring gull selection of duckling prey

Duckling captures at East Bay were less frequent than would have been expected, 
based on studies undertaken in analogous systems elsewhere. Nonetheless, gull 
searches and ensuing captures that did occur were influenced by environmental 
conditions, namely wind speed. This can be explained by the suggestion that 
environmental conditions modify the net gains derived from attacking eider broods. 
For example, during windy conditions, passage from land to sea can be limited by 
breaking waves which can separate ducklings from attending hens. Simultaneously, 
herring gulls gain the advantages of hovering and the aerial attack mode (harassing 
broods with less risk of injury from defending hens).

In addition to energetic expenditures, gulls should minimise risks through 
condition-dependent attack tactics, unless overall conditions force gulls to increase 
risk tolerance (e.g. during periods of food shortage). It is unlikely that observed 
increases in hen response to gull air searches were caused by increased hen vigilance 
during years of low lemming-abundance. Rather, it supports the prediction of the 
Alternative Prey Hypothesis that states predators are more likely to take risks during 
years of low lemming-abundance, and most of all in the crash year following a peak in 
abundance. This is supported by our finding that likelihood of physical contact 
between gull and eider was highest of all in the crash year that followed the peak, as 
predicted.
Together, these results suggest that there was interaction between lemming abundance, which in this system varied annually, and environmental conditions that varied over shorter time periods (i.e. often hours). The dynamics of these interactions apparently influenced search and capture rates and attack modes, as well as the level of aggressiveness of attacks by herring gulls (being greatest during years following peak lemming-abundance). Thus, the value of eider duckling prey to foraging herring gulls varied in relation to availability of lemmings, environmental conditions (namely wind speed) that influenced the net energetic cost of aerial and ground foraging modes, and risk which varied according to attack tactic and hunger, determined largely by the degree to which gulls have access to alternative prey.

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Table 3.1. Summary of lemming observations from the colony island and from a 2 X 2 kilometre study plot on the adjacent mainland coastal plain, by year.

<table>
<thead>
<tr>
<th>Location</th>
<th>1998</th>
<th>1999</th>
<th>2000</th>
<th>2001</th>
<th>2002</th>
<th>2003</th>
</tr>
</thead>
<tbody>
<tr>
<td>Days observed</td>
<td>3</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>20</td>
<td>10</td>
</tr>
<tr>
<td>Days possible</td>
<td>68</td>
<td>42</td>
<td>68</td>
<td>39</td>
<td>79</td>
<td>27</td>
</tr>
<tr>
<td>Days observed (%)</td>
<td>4</td>
<td>7</td>
<td>2</td>
<td>0</td>
<td>25</td>
<td>37</td>
</tr>
<tr>
<td>No. observed</td>
<td>5</td>
<td>*</td>
<td>2</td>
<td>0</td>
<td>22</td>
<td>15</td>
</tr>
<tr>
<td>Number observers</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>5</td>
<td>5</td>
</tr>
</tbody>
</table>

* Island, b Mainland

* Daily presence/absence only was recorded on the mainland in 1998.
Table 3.2. Summary of observations of focal broods (n=631) and herring gull search and duckling capture frequencies, by year.

<table>
<thead>
<tr>
<th></th>
<th>1999</th>
<th>2000</th>
<th>2001</th>
<th>2002</th>
<th>2003</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total broods</td>
<td>68</td>
<td>364</td>
<td>113</td>
<td>51</td>
<td>35</td>
</tr>
<tr>
<td>Total hours</td>
<td>36</td>
<td>215</td>
<td>52</td>
<td>35</td>
<td>14</td>
</tr>
<tr>
<td>Total ducklings</td>
<td>558</td>
<td>1832</td>
<td>552</td>
<td>211</td>
<td>167</td>
</tr>
<tr>
<td>Total air searches</td>
<td>227</td>
<td>173</td>
<td>98</td>
<td>283</td>
<td>44</td>
</tr>
<tr>
<td>Total ground searches</td>
<td>47</td>
<td>83</td>
<td>27</td>
<td>73</td>
<td>31</td>
</tr>
<tr>
<td>Total duckling captures</td>
<td>9</td>
<td>10</td>
<td>1</td>
<td>15</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 3.3. Generalized linear models used to determine factors affecting counts (n=90) of eider broods in transit undertaken in 2000. Models presented include only those with ΔAICc values<10; global model is shown in bold text.

<table>
<thead>
<tr>
<th>Response: Count of broods in transit model</th>
<th>K</th>
<th>ΔAICc</th>
<th>AICc weights</th>
<th>Sum of AICc weights</th>
</tr>
</thead>
<tbody>
<tr>
<td>phdate per4 wind phdate*phdate</td>
<td>11</td>
<td>0.000</td>
<td>0.560</td>
<td>0.560</td>
</tr>
<tr>
<td>phdate per4 wind tide phdate*phdate</td>
<td>12</td>
<td>2.449</td>
<td>0.165</td>
<td>0.724</td>
</tr>
<tr>
<td>phdate per4 wind per4*wind</td>
<td>9</td>
<td>3.675</td>
<td>0.089</td>
<td>0.814</td>
</tr>
<tr>
<td>phdate per4 phdate*phdate</td>
<td>7</td>
<td>5.059</td>
<td>0.045</td>
<td>0.858</td>
</tr>
<tr>
<td>phdate per4 wind phdate*phdate</td>
<td>8</td>
<td>6.018</td>
<td>0.028</td>
<td>0.886</td>
</tr>
<tr>
<td>per4 wind tide per4*wind</td>
<td>10</td>
<td>6.105</td>
<td>0.026</td>
<td>0.912</td>
</tr>
<tr>
<td>phdate per4 wind per4*wind</td>
<td>10</td>
<td>6.300</td>
<td>0.024</td>
<td>0.936</td>
</tr>
<tr>
<td>phdate per4 tide phdate*phdate</td>
<td>8</td>
<td>6.565</td>
<td>0.021</td>
<td>0.957</td>
</tr>
<tr>
<td>phdate per4 wind tide phdate*phdate</td>
<td>9</td>
<td>7.302</td>
<td>0.015</td>
<td>0.972</td>
</tr>
<tr>
<td>per4 wind</td>
<td>6</td>
<td>8.608</td>
<td>0.008</td>
<td>0.979</td>
</tr>
<tr>
<td>phdate per4 wind tide per4*wind</td>
<td>11</td>
<td>8.831</td>
<td>0.007</td>
<td>0.986</td>
</tr>
<tr>
<td>per4</td>
<td>5</td>
<td>9.586</td>
<td>0.005</td>
<td>0.991</td>
</tr>
</tbody>
</table>

K=number of estimable parameters in the model, phdate (date adjusted to eider phenology), per4 (period of the day), wind (wind speed (km/h)), tide (tide height (m)), phdate*phdate (quadratic date term), per4*wind (period of the day by wind speed interaction), plus intercept and negative binomial dispersion parameter.
Table 3.4. Results of generalized linear models of counts of eider broods in transit obtained from scans (n=90) in 2000. Incident rate ratios obtained through exponentiation of unconditional estimates and their 95% confidence intervals. Estimates of effects provided by model averaging across full model sets.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>LCI</th>
<th>UCI</th>
</tr>
</thead>
<tbody>
<tr>
<td>per4 (morning)</td>
<td>19.86</td>
<td>1.30</td>
<td>304.20</td>
</tr>
<tr>
<td>per4 (midday)</td>
<td>66.71</td>
<td>3.76</td>
<td>1184.06</td>
</tr>
<tr>
<td>per4 (evening)</td>
<td>30.17</td>
<td>1.95</td>
<td>466.98</td>
</tr>
<tr>
<td>per4 (night)</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>wind*per4 (morning)</td>
<td>0.88</td>
<td>0.77</td>
<td>1.01</td>
</tr>
<tr>
<td>wind*per4 (midday)</td>
<td>0.85</td>
<td>0.73</td>
<td>0.99</td>
</tr>
<tr>
<td>wind*per4 (evening)</td>
<td>0.88</td>
<td>0.77</td>
<td>1.00</td>
</tr>
<tr>
<td>wind*per4 (night)</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>phdate</td>
<td>1.27</td>
<td>0.98</td>
<td>1.66</td>
</tr>
<tr>
<td>wind</td>
<td>1.15</td>
<td>1.01</td>
<td>1.32</td>
</tr>
<tr>
<td>tide</td>
<td>1.02</td>
<td>0.93</td>
<td>1.11</td>
</tr>
<tr>
<td>phdate*phdate</td>
<td>0.99</td>
<td>0.98</td>
<td>1.00</td>
</tr>
<tr>
<td>Intercept</td>
<td>-4.26</td>
<td>-7.43</td>
<td>-1.09</td>
</tr>
<tr>
<td>Dispersion&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.01</td>
<td>-0.05</td>
<td>0.07</td>
</tr>
</tbody>
</table>

<sup>a</sup>Negative binomial dispersion parameter.

Note: Intercept and negative binomial dispersion parameter were not subjected to exponentiation. Parameters as in Table 3.3.
Table 3.5. Generalized linear models used to determine factors affecting herring gull total counts (n=102) obtained from scans of the colony from 2000 to 2002 inclusive. Models presented include only those with Δ AICc values<10; global model is shown in bold text.

<table>
<thead>
<tr>
<th>Response: Herring gull total count model</th>
<th>K</th>
<th>Δ AICc</th>
<th>AICc weights</th>
<th>Sum of AICc weights</th>
</tr>
</thead>
<tbody>
<tr>
<td>year tide</td>
<td>5</td>
<td>0.000</td>
<td>0.252</td>
<td>0.252</td>
</tr>
<tr>
<td>year per4 tide</td>
<td>8</td>
<td>0.721</td>
<td>0.176</td>
<td>0.428</td>
</tr>
<tr>
<td>year wind tide</td>
<td>6</td>
<td>0.848</td>
<td>0.165</td>
<td>0.593</td>
</tr>
<tr>
<td>year per4 wind tide</td>
<td>9</td>
<td>1.747</td>
<td>0.105</td>
<td>0.698</td>
</tr>
<tr>
<td>year phdate tide</td>
<td>6</td>
<td>2.232</td>
<td>0.083</td>
<td>0.781</td>
</tr>
<tr>
<td>year phdate wind tide</td>
<td>7</td>
<td>3.128</td>
<td>0.053</td>
<td>0.834</td>
</tr>
<tr>
<td>year phdate per4 tide</td>
<td>9</td>
<td>3.129</td>
<td>0.053</td>
<td>0.887</td>
</tr>
<tr>
<td>year phdate per4 wind tide</td>
<td>10</td>
<td>4.207</td>
<td>0.031</td>
<td>0.917</td>
</tr>
<tr>
<td>year phdate tide phdate*phdate</td>
<td>7</td>
<td>4.275</td>
<td>0.030</td>
<td>0.947</td>
</tr>
<tr>
<td>year phdate per4 tide phdate*phdate</td>
<td>10</td>
<td>4.946</td>
<td>0.021</td>
<td>0.968</td>
</tr>
<tr>
<td>year phdate wind tide phdate*phdate</td>
<td>8</td>
<td>5.170</td>
<td>0.019</td>
<td>0.987</td>
</tr>
<tr>
<td>year phdate per4 wind tide phdate*phdate</td>
<td>11</td>
<td>6.045</td>
<td>0.012</td>
<td>1.000</td>
</tr>
</tbody>
</table>

K=number of estimable parameters in the model, year (annual effect), phdate (date adjusted to eider phenology), per4 (period of the day), wind (wind speed (km/h)), tide (tide height (m)), phdate*phdate (quadratic date term), plus intercept and variance estimator.
Table 3.6. Results of generalized linear models of herring gull counts (n=102) obtained from scans of the colony from 2000 to 2002 inclusive. Estimates of effects provided by model averaging across full model sets.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>LCI</th>
<th>UCI</th>
</tr>
</thead>
<tbody>
<tr>
<td>year (2000)</td>
<td>-22.33</td>
<td>-29.03</td>
<td>-15.64</td>
</tr>
<tr>
<td>year (2001)</td>
<td>-4.81</td>
<td>-12.16</td>
<td>2.54</td>
</tr>
<tr>
<td>year (2002)</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>per4 (morning)</td>
<td>-1.65</td>
<td>-6.62</td>
<td>3.32</td>
</tr>
<tr>
<td>per4 (midday)</td>
<td>1.13</td>
<td>-2.60</td>
<td>4.86</td>
</tr>
<tr>
<td>per4 (evening)</td>
<td>-0.60</td>
<td>-3.89</td>
<td>2.69</td>
</tr>
<tr>
<td>per4 (night)</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>wind</td>
<td>0.05</td>
<td>-0.12</td>
<td>0.23</td>
</tr>
<tr>
<td>tide</td>
<td>5.44</td>
<td>2.95</td>
<td>7.94</td>
</tr>
<tr>
<td>phdate</td>
<td>-0.13</td>
<td>-0.83</td>
<td>0.58</td>
</tr>
<tr>
<td>phdate*phdate</td>
<td>0.00</td>
<td>-0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Intercept</td>
<td>55.63</td>
<td>36.24</td>
<td>75.03</td>
</tr>
</tbody>
</table>

Parameters as in Table 3.5.
Table 3.7. Generalized linear models used to determine factors affecting rates of air searches, of departing eider broods (n=631) by herring gulls from 1999 to 2003 inclusive. Models presented include only those with ΔAICc values<10; global model is shown in bold text.

<table>
<thead>
<tr>
<th>Response: Air searches/brood/min model</th>
<th>K</th>
<th>ΔAICc</th>
<th>AICc weights</th>
<th>Sum of AICc weights</th>
</tr>
</thead>
<tbody>
<tr>
<td>year wind</td>
<td>7</td>
<td>0.000</td>
<td>0.361</td>
<td>0.361</td>
</tr>
<tr>
<td>year phdate wind</td>
<td>8</td>
<td>1.956</td>
<td>0.136</td>
<td>0.496</td>
</tr>
<tr>
<td>year wind tide</td>
<td>8</td>
<td>2.049</td>
<td>0.129</td>
<td>0.625</td>
</tr>
<tr>
<td>year per4 wind</td>
<td>10</td>
<td>2.621</td>
<td>0.097</td>
<td>0.723</td>
</tr>
<tr>
<td>year phdate wind phdate*phdate</td>
<td>9</td>
<td>2.852</td>
<td>0.087</td>
<td>0.809</td>
</tr>
<tr>
<td>year phdate wind tide</td>
<td>9</td>
<td>4.013</td>
<td>0.048</td>
<td>0.858</td>
</tr>
<tr>
<td>year phdate per4 wind</td>
<td>11</td>
<td>4.653</td>
<td>0.035</td>
<td>0.893</td>
</tr>
<tr>
<td>year per4 wind tide</td>
<td>11</td>
<td>4.664</td>
<td>0.035</td>
<td>0.928</td>
</tr>
<tr>
<td>year phdate wind tide phdate*phdate</td>
<td>10</td>
<td>4.911</td>
<td>0.031</td>
<td>0.959</td>
</tr>
<tr>
<td>year phdate per4 wind phdate*phdate</td>
<td>12</td>
<td>5.692</td>
<td>0.021</td>
<td>0.980</td>
</tr>
<tr>
<td>year phdate per4 wind tide</td>
<td>12</td>
<td>6.699</td>
<td>0.013</td>
<td>0.993</td>
</tr>
<tr>
<td><strong>year phdate per4 wind tide phdate*phdate</strong></td>
<td>13</td>
<td>7.753</td>
<td>0.007</td>
<td>1.000</td>
</tr>
</tbody>
</table>

K=number of estimable parameters in the model, year (annual effect), phdate (date adjusted to eider phenology), per4 (period of the day), wind (wind speed (km/h)), tide (tide height (m)), phdate*phdate (quadratic date term), plus intercept and negative binomial dispersion parameter.
Table 3.8. Generalized linear models used to determine factors affecting rates of
ground searches of departing eider broods (n=631) by herring gulls from 1999 to 2003
inclusive. Models presented include only those with ΔAICc values<10; global model
is shown in bold text.

<table>
<thead>
<tr>
<th>Response: Ground searches/brood/min model</th>
<th>K</th>
<th>Δ AICc</th>
<th>Akaike Weight</th>
<th>Sum of Akaike weights</th>
</tr>
</thead>
<tbody>
<tr>
<td>year phdate wind tide phdate*phdate</td>
<td>10</td>
<td>0.000</td>
<td>0.624</td>
<td>0.624</td>
</tr>
<tr>
<td>year phdate wind phdate*phdate</td>
<td>9</td>
<td>1.730</td>
<td>0.263</td>
<td>0.887</td>
</tr>
<tr>
<td><strong>year phdate per4 wind tide phdate*phdate</strong></td>
<td>13</td>
<td>5.706</td>
<td>0.036</td>
<td>0.923</td>
</tr>
<tr>
<td>year phdate per4 wind phdate*phdate</td>
<td>12</td>
<td>6.702</td>
<td>0.022</td>
<td>0.945</td>
</tr>
<tr>
<td>year phdate phdate*phdate</td>
<td>8</td>
<td>8.346</td>
<td>0.010</td>
<td>0.955</td>
</tr>
<tr>
<td>year phdate tide phdate*phdate</td>
<td>9</td>
<td>8.382</td>
<td>0.009</td>
<td>0.964</td>
</tr>
<tr>
<td>year wind tide</td>
<td>8</td>
<td>8.483</td>
<td>0.009</td>
<td>0.973</td>
</tr>
<tr>
<td>year wind</td>
<td>7</td>
<td>9.420</td>
<td>0.006</td>
<td>0.979</td>
</tr>
<tr>
<td>year phdate wind tide</td>
<td>9</td>
<td>9.506</td>
<td>0.005</td>
<td>0.984</td>
</tr>
</tbody>
</table>

K=number of estimable parameters in the model, year (annual effect), phdate (date
adjusted to eider phenology), per4 (period of the day), wind (wind speed (km/h)), tide
(tide height (m)), phdate*phdate (quadratic date term), plus intercept and negative
binomial dispersion parameter.

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Table 3.9. Results of negative binomial models of factors affecting search and duckling capture rates associated with departing broods (n=631). Incident rate ratios obtained through exponentiation of unconditional estimates and their 95% confidence intervals. Estimates of effects provided by model averaging across full model sets.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Aerial searches/brood/min</th>
<th>Ground searches/brood/min</th>
<th>Duckling captures/brood/min</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimate</td>
<td>LCI</td>
<td>UCI</td>
</tr>
<tr>
<td>year (1999)</td>
<td>0.87</td>
<td>0.41</td>
<td>1.81</td>
</tr>
<tr>
<td>year (2000)</td>
<td>0.25</td>
<td>0.13</td>
<td>0.46</td>
</tr>
<tr>
<td>year (2001)</td>
<td>0.41</td>
<td>0.21</td>
<td>0.80</td>
</tr>
<tr>
<td>year (2002)</td>
<td>1.83</td>
<td>0.89</td>
<td>3.74</td>
</tr>
<tr>
<td>year (2003)</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>per4 (morning)</td>
<td>1.19</td>
<td>0.62</td>
<td>2.30</td>
</tr>
<tr>
<td>per4 (midday)</td>
<td>1.15</td>
<td>0.65</td>
<td>2.03</td>
</tr>
<tr>
<td>per4 (evening)</td>
<td>1.22</td>
<td>0.59</td>
<td>2.53</td>
</tr>
<tr>
<td>per4 (night)</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>wind</td>
<td>1.05</td>
<td>0.53</td>
<td>1.07</td>
</tr>
<tr>
<td>tide</td>
<td>1.00</td>
<td>0.95</td>
<td>1.05</td>
</tr>
<tr>
<td>phdate</td>
<td>0.99</td>
<td>0.92</td>
<td>1.06</td>
</tr>
<tr>
<td>phdate*phdate</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>Intercept</td>
<td>-1.61</td>
<td>-2.73</td>
<td>-0.49</td>
</tr>
<tr>
<td>Dispersion$^a$</td>
<td>1.79</td>
<td>1.34</td>
<td>2.23</td>
</tr>
</tbody>
</table>

$^a$ Negative binomial dispersion parameter.

Note: Intercept and negative binomial dispersion parameter were not subjected to exponentiation. Parameters as in Table 3.8.
Table 3.10. Generalized linear models used to determine factors affecting rates of duckling captures, from departing eider broods (n=631) by herring gulls from 1999 to 2002 inclusive (no duckling captures were observed in 2003). Models presented include only those with ΔAICc values<10; the time period variable was not analysed due to sparse data.

<table>
<thead>
<tr>
<th>Response: Duckling captures/brood/min</th>
<th>K</th>
<th>ΔAICc</th>
<th>Akaike Weight</th>
<th>Sum of Akaike weights</th>
</tr>
</thead>
<tbody>
<tr>
<td>year phdate wind phdate*phdate</td>
<td>8</td>
<td>0.000</td>
<td>0.555</td>
<td>0.555</td>
</tr>
<tr>
<td>year phdate phdate*phdate</td>
<td>7</td>
<td>1.854</td>
<td>0.220</td>
<td>0.775</td>
</tr>
<tr>
<td>year phdate tide phdate*phdate</td>
<td>8</td>
<td>3.132</td>
<td>0.116</td>
<td>0.891</td>
</tr>
<tr>
<td>year phdate</td>
<td>6</td>
<td>5.594</td>
<td>0.034</td>
<td>0.925</td>
</tr>
<tr>
<td>year phdate wind</td>
<td>7</td>
<td>5.893</td>
<td>0.029</td>
<td>0.954</td>
</tr>
<tr>
<td>year phdate tide</td>
<td>7</td>
<td>7.332</td>
<td>0.014</td>
<td>0.968</td>
</tr>
<tr>
<td>year phdate wind tide</td>
<td>8</td>
<td>7.765</td>
<td>0.011</td>
<td>0.980</td>
</tr>
<tr>
<td>year</td>
<td>5</td>
<td>8.071</td>
<td>0.010</td>
<td>0.989</td>
</tr>
<tr>
<td>year wind</td>
<td>6</td>
<td>8.848</td>
<td>0.007</td>
<td>0.996</td>
</tr>
</tbody>
</table>

K=number of estimable parameters in the model, year (annual effect), phdate (date adjusted to eider phenology), wind (wind speed (km/h)), tide (tide height (m)), phdate*phdate (quadratic date term), plus intercept and negative binomial dispersion parameter.
Table 3.11. Pearson correlations among search, and search and duckling capture, frequencies per brood hour by year.

<table>
<thead>
<tr>
<th>Year</th>
<th>Foraging events/ brood h&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Air searches</th>
<th>Ground searches</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999 (n=68)</td>
<td>Ground searches</td>
<td>0.36 ($P=0.0030$)</td>
<td>.</td>
</tr>
<tr>
<td></td>
<td>Duckling captures</td>
<td>0.61 ($P&gt;0.0001$)</td>
<td>0.08 ($P=0.4862$)</td>
</tr>
<tr>
<td>2000 (n=364)</td>
<td>Ground searches</td>
<td>0.57 ($P&gt;0.0001$)</td>
<td>.</td>
</tr>
<tr>
<td></td>
<td>Duckling captures</td>
<td>0.25 ($P&gt;0.0001$)</td>
<td>0.64 ($P&gt;0.0001$)</td>
</tr>
<tr>
<td>2001 (n=113)</td>
<td>Ground searches</td>
<td>0.22 ($P=0.0221$)</td>
<td>.</td>
</tr>
<tr>
<td></td>
<td>Duckling captures</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>2002 (n=51)</td>
<td>Ground searches</td>
<td>0.72 ($P&gt;0.0001$)</td>
<td>.</td>
</tr>
<tr>
<td></td>
<td>Duckling captures</td>
<td>0.43 ($P=0.0015$)</td>
<td>0.33 ($P=0.0189$)</td>
</tr>
<tr>
<td>2003 (n=35)</td>
<td>Ground searches</td>
<td>0.46 ($P=0.0050$)</td>
<td>.</td>
</tr>
<tr>
<td></td>
<td>Duckling captures</td>
<td>*</td>
<td>*</td>
</tr>
</tbody>
</table>

<sup>a</sup>brood h (brood hour) = number of continuous hours of observation per brood.
*Too few or no duckling captures to calculate correlation coefficients.
Table 3.12. Summary of mean numbers of hens, ducklings, and hen to duckling ratios (SE) calculated upon commencement of individual focal brood observations, by year.

<table>
<thead>
<tr>
<th></th>
<th>1999</th>
<th>2000</th>
<th>2001</th>
<th>2002</th>
<th>2003</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hens/brood</td>
<td>4.36 (0.42)</td>
<td>5.34 (0.27)</td>
<td>3.75 (0.31)</td>
<td>5.82 (0.58)</td>
<td>5.26 (0.54)</td>
</tr>
<tr>
<td>Ducklings/brood</td>
<td>8.11 (1.16)</td>
<td>5.02 (0.22)</td>
<td>4.84 (0.45)</td>
<td>4.02 (0.37)</td>
<td>5.09 (0.81)</td>
</tr>
<tr>
<td>Ducklings/hen</td>
<td>2.28 (0.25)</td>
<td>1.56 (0.07)</td>
<td>1.90 (0.14)</td>
<td>0.99 (0.11)</td>
<td>1.33 (0.26)</td>
</tr>
</tbody>
</table>
Table 3.13. Frequencies of herring gull searches including total searches, total hen reaction, and occurrences of physical contact with eider hens.

<table>
<thead>
<tr>
<th>Year</th>
<th>Total</th>
<th>Air searches</th>
<th>Ground searches</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Reaction</td>
<td>Contact</td>
</tr>
<tr>
<td>1999</td>
<td>193</td>
<td>185</td>
<td>20</td>
</tr>
<tr>
<td>2000</td>
<td>144</td>
<td>117</td>
<td>16</td>
</tr>
<tr>
<td>2001</td>
<td>78</td>
<td>52</td>
<td>2</td>
</tr>
<tr>
<td>2002</td>
<td>190</td>
<td>155</td>
<td>41</td>
</tr>
<tr>
<td>2003</td>
<td>24</td>
<td>24</td>
<td>1</td>
</tr>
</tbody>
</table>

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Figure 3.1. Number of common eider nests initiated per hectare by year on the island, calculated through summing counts from three nesting plots representing 1.13 of approximately 16 ha used for eider nesting.
Figure 3.2. Wind speeds from first to last focal brood observation inclusively by year. Bars within boxes indicate medians; box limits represent 75th and 25th percentiles, while whiskers represent 90th and 10th percentiles, respectively, dots represent extreme values.
Figure 3.3. Temperatures measured every half-hour from first to last focal brood observation inclusively by year. Bars within boxes indicate medians; box limits represent 75\textsuperscript{th} and 25\textsuperscript{th} percentiles, while whiskers represent 90\textsuperscript{th} and 10\textsuperscript{th} percentiles, respectively, dots represent extreme values.
Figure 3.4. Search and duckling capture rates (per brood per hour) in relation to day period for 631 eider broods observed from 1999 to 2003 (period 4 data are for 1999 and 2000 only). Numbers of broods observed by period are presented in parentheses.
Figure 3.5. Annual variation in foraging activity (number of searches and duckling captures per h brood observed) by herring gulls within the eider colony from 1999 to 2003 (mean±SE, N=631 broods). Lemming abundance indices for the island and the adjacent mainland coastal plain are presented below by corresponding year with the addition of 1998.
Figure 3.6. Search and duckling capture rates (per brood per hour) in relation to wind speed (km/h) for 631 departing eider broods observed from 1999 to 2003. Sample sizes by category are shown in parentheses.
Figure 3.7. Search and duckling capture rates (per hour) in relation to different location type from 1999 to 2003. Rates are calculated from totals.
Chapter 4

Title:
Causes and consequences of variation in attendance of foraging territories by breeding herring gulls: An experimental study

Authors:
KAREL A. ALLARD. Atlantic Co-operative Wildlife Ecology Research Network, Biology Department, University of New Brunswick, Canada
Role: Sampling design, data collection, data analysis, lead author, submission of MS
H. GRANT GILCHRIST. National Wildlife Research Centre, Carleton University, Canada
Role: Supervision, Logistical and financial support, study design and data analysis advice, data collection, writing advice and reviews of drafts
ANTONY W. DIAMOND. Atlantic Co-operative Wildlife Ecology Research Network, and Biology Department, University of New Brunswick, Canada
Role: Supervision, logistical and financial support, study design and data analysis advice, writing advice and reviews of drafts

Intended journal:
Behavioural Ecology
ABSTRACT

We studied herring gulls (Larus argentatus) occupying territories within a common eider (Somateria mollissima) colony in Canada’s Eastern Arctic. Gull breeding pairs took eggs from unattended eider nests located within variably-sized territories, all extending beyond what is typical for the species. In the second of a two-year study, we conducted a food supplementation experiment on six individually-marked territorial pairs during 18 days of incubation by placing eggs within territories. We hypothesised that if time allotted by territorial gulls to territorial attendance is related to prey abundance within territories, then experimentally increasing prey quantity should lead to increased attendance. Territories were mapped using locations of intra-specific agonistic encounters and landmarks, while territorial prey abundance was quantified through monitoring of nesting eiders and counts of eider nest cups after the breeding season. Territorial attendance by resident pairs was quantified through direct behavioural observation from blinds. Contribution to territorial defence by males and females within each pair, frequency and duration of territorial intrusions, likelihood of ensuing chase by territory residents, and rates of egg captures by residents and intruders were also assessed.

Females responded to food supplementation by increasing total time within their territory in both incubation and non-incubation. Males adjusted incubation time inversely from their mates and increased non-incubation attendance. Although males and females chased intruders, reducing intrusion duration and intruder egg-capture likelihood, non-incubating male residents were typically more
effective in defending the territory.

Gulls in this system compensated for shortcomings in abundance of prey within their territories by foraging extra-territorially. However, leaving territories attended only by the incubating individual also led to increased prey depletion through intruders taking eggs. Territorial pairs provided with supplemental food responded in a sex-specific manner, possibly to maximize defence of territory resources.

Key words: Herring gull, supplementary feeding, incubation, attendance, territoriality, territory, eider eggs, trade-off.
INTRODUCTION

Defence of a foraging territory (i.e. active exclusion of competitors from access to a resource) should enhance reliable access to food (Maher and Lott 1995, 2000, Adams 2001). Access to reliable food can be most valuable where food resources are scarce or highly variable, and the maintenance of feeding territories can increase lifetime fitness benefits (Maher and Lott 2000). However, limited access to predictable and defendable resources can result in fierce competition for foraging territories. Thus, while territorial individuals gain the benefits of reliability, they also incur additional costs associated with territorial defence (Maher and Lott 2000).

Although prey abundance is often a strong predictor of foraging territory size (reviewed by Adams 2001), the relationship can be expected to break down in the presence of alternative foraging tactics that determine prey capture rates within territories (Myers et al. 1979). For example, predators may switch foraging modes in response to changes in their energetic requirements, environmental conditions, or both (Mougeot et al. 1998). Furthermore, the ability of a predator to adjust territory size in response to changes in prey abundance can be severely limited when available habitat is saturated, and especially when territories are non-overlapping (Adams 2001, Mesterton-Gibbons and Adams 2003). When food supply within territories is not reliable and/or insufficient to meet requirements, territorial attendance patterns, rather than territory size, can be expected to vary as territorial residents forage elsewhere in search of prey (Myers et al. 1979, Palmer et al. 2001).
We studied the foraging ecology and territorial behaviour of herring gulls (*Larus argentatus*) breeding within a common eider (*Somateria mollissima borealis*) colony in the Canadian Arctic. We tested experimentally the general hypothesis that if territorial pairs are motivated to attend and defend their territories to achieve greater foraging efficiency, then territorial individuals should seek to obtain food resources and achieve satiation within their territories, a function of food availability (and intake) within the territory. Specifically, if territorial birds must balance energetic requirements with territorial attendance and defence, then this balance will be influenced by variation in food (i.e. eider eggs) availability (and consequent intake) within territories. We predicted that territorial residents should respond to increased food intake (provided or self-procured) within their territory by 1) spending more time in their territory, 2) defending their territory from intruders more aggressively, and 3) that these responses should be most pronounced for individuals occupying territories containing limited resources. As sex is known to be an important determinant of defensive and foraging ability, especially in structurally dimorphic species such as herring gulls (Pugseck 1983, Caldow and Furness 2000), we also predicted that these changes should be most pronounced in females.

As territorial residents must often exclude competitors from their territories, we further hypothesised that costs incurred due to intrusion (e.g. prey depletion) would vary in relation to attendance patterns by residents. Specifically, we predicted that intrusion rate and duration, and likelihood of prey capture by intruders, would decrease with the presence and vary with the sex of the non-
incubating member of the territorial pair, and increase with food provided experimentally.

METHODS

Study site

This study was conducted in 2001 and 2002 within a common eider duck colony (64°04N 81°40W), at East Bay, Southampton Island, in the northwest part of Hudson Bay, Nunavut, Canada. The colony is situated on a small (36ha) treeless island that supports up to 4500 pairs of common eiders, 50 pairs of king eiders (Somateria spectabilis), 400 pairs of black guillemots (Cepphus grylle), and 30 pairs of herring gulls. Smaller numbers of Canada geese (Branta canadensis), brant (B. bernicla), and snow buntings (Plectrophenax nivalis) also nest on the island.

Although most herring gulls at East Bay breed on the coastal plain of Southampton Island, we focused this study on the herring gulls nesting sympatrically with eiders on the colony island.

In Canada, the northernmost range limit for herring gull breeding extends across the northern Yukon, Northwest Territories and Nunavut. In Arctic regions, they nest on coastal islands (often with eiders and other species) as well as on boulders and small islands situated in lakes and estuaries (Cooch 1965, Pierotti and Good 1994). In Nunavut Territory in the eastern Canadian Arctic this northern limit extends from the mainland to Southampton Island, Foxe Basin and the southern region of Baffin Island (Pierotti and Good 1994). Herring gulls are commonly associated with ocean shorelines, lakes and large rivers.
Information regarding population dynamics and ecology of herring gulls at northern latitudes is uncertain as few detailed studies exist. Inuit hunters consider herring gulls common on Southampton Island (Grant Gilchrist, pers. obs.). In both Foxe Basin and Hudson Strait, herring gulls commonly nest in association with eiders (Cooch 1965). The herring gull is considered a generalist (Spaans 1971, Pierotti and Annett 1991) and is known to forage intertidally (Pierotti and Annett 1991), exploit food resources along shorelines (Massaro et al. 2000), and exploit avian prey (Pierotti and Good 1994), including eider duck eggs (Cooch 1965, Allard and Gilchrist 2002).

**Behavioural observations**

Large-scale changes in the environment, such as location and degree of ice cover, can greatly influence the distance animals must travel to reach prey resources in the Arctic (Gaston and Hipfner 1998). Also, changing energetic demands for individuals and their young while breeding can influence their foraging behaviour (Blem 2000, Massaro et al. 2000, Suryan et al. 2000). For these reasons, we chose to restrict our observations to the portion of the gull incubation period starting after ice break-up and ending when hatchlings of both gulls and eiders appeared within gull territories (±20 day period).

Although scan sampling methods that are used in many time-budget studies can provide measures of attendance, these were inadequate to assess rates of infrequent events in this system such as prey captures, territorial intrusions and chases (Altmann 1974). Hence in 2001, we used a stratified random approach to scheduling continuous daily behavioural watches (i.e. no shorter than 4 hours in
duration) and watched 13 territorial pairs. In 2002, we watched six territorial pairs more intensively; four of these had been studied the previous year. Based on the results obtained in 2001, we began observations at 0500 because at that time gull numbers on the colony were still high and conditions for behavioural observations and identification of marked individuals were best. Specifically, we undertook daily eight-hour continuous behavioural watches from two locations through 18 days of herring gull incubation.

We mapped the territories of uniquely marked (colour-banded) herring gulls by plotting locations of intra-specific agonistic encounters and boundary landmarks (Askenmo et al. 1994, Eason et al. 1999) on high-resolution air photos of the colony. We monitored territorial attendance by gulls, rates of eider egg capture and ingestion by gulls, and territorial defence behaviour of both males and females.

**Supplemental food experiment**

In 2002 only, we manipulated abundance of available prey by placing real eider eggs within focal herring gull territories according to a rotating schedule (chicken eggs were used with eider eggs when sufficient numbers of the latter could not be obtained). This schedule maximized the time between treatments, thereby limiting carryover effects from previous treatments. At this site eider females incubate almost continuously, with recesses of c. 17 min occurring once every two days (Bottita et al. 2003), suggesting that approximately one nest per 150 is left unattended at any given time. We placed four eggs at a time within treatment territories, as this exceeds the minimum daily energy requirement for two herring
gull adults (400 to 520 kJ/day; Norstrom et al. 1985). Eggs were placed under heavy, camouflaged canvas sheets (1 m X 1 m) similar in colour to the surrounding mossy vegetation approximately 16 h prior to commencement of watches. Canvas sheets were subsequently withdrawn by pulling ropes extended from observation blinds. Displacement of canvas sheets took place daily in all territories whether concealed eggs were present or not. We deployed eggs at three-day intervals in each of six territories, such that only two of six territories, always located in different parts of the colony (i.e. non-contiguous), received treatment each day.

In order to present pairs with a foraging option and prevent premature egg removal by intruders, deployment of supplemental food occurred only when both male and female members of the pair were present within the territory. To maximize likelihood of this being the case at the beginning of watches, and based on information gained the previous year, watches were initiated at 0500 each morning.

As our focus was the response of focal pairs to an increase in food availability within territories (i.e. supplemental food) the contribution of self-procured food intake before and during observations needed to be considered. Consequently, in analyses of attendance, it was assumed that territory residents would behave as if they had eaten supplemental food when: 1) they did not consume exposed supplemental eggs, presumably because they were otherwise satiated prior to deployment of eggs, and 2) they consumed naturally-occurring eggs acquired independently. Hence, a single binary treatment variable was
generated for each sex, named "food intake" which corresponded to consumption (or not) of eggs during the observation period (provided and self-procured, by each pair member). However, in analyses of intrusion, egg removal by intruders and territorial chases, which involved non-residents, we defined treatment as provision of supplemental food only. In instances where consumption of eggs did not occur during the observation period, remaining eggs were removed immediately at the end of the watch. This was done to further reduce potential lag or carryover effects that might compromise the validity of foraging observations the following day.

**Prey abundance**

Prey contained within territories consisted of eider eggs in eider nests. In 2001, prey abundance within territories was determined through counting nest cups within 20 m² cell samples located within territories. These random cell samples were obtained from a grid overlaid on a high resolution aerial photo of the colony. At the end of the season, using GPS coordinates and reference points from the air photo, selected cells were located within the colony and, with the help of a 20 m² rope quadrat laid on the ground, the number of active eider nests that they contained was counted. The latter counts were used to derive our estimates of territorial prey abundance (eider nests per ha). In 2002, instead of sampling randomly from within the colony, absolute total counts for all cells located within focal territories were obtained.
Statistical design

Correlated data are typical of many ecological studies (Diggle et al. 2002). Such data, arising through repeated measurement of individuals over time, are often unavoidable and may in many respects be desirable. Clearly, analysis of data generated from repeated observations of given subjects requires appropriate statistical tools. Controlling for within-subject variability through repeated measurements by using subjects as their own controls, can ultimately lead to more efficient estimates of regression coefficients and appropriate inferences (Diggle et al. 2002). More traditional statistical tests that do not account for repeated measurement are generally not robust against violation of assumptions pertaining to independence of errors (Diggle et al. 2002).

We analysed behaviours associated with both herring gull territoriality and experimentally manipulated territorial food availability, using Generalized Estimating Equations (GEE), an extension of Generalized Linear Models (PROC GENMOD using the statement REPEATED; SAS Institute Inc. 2000). GEEs, introduced by Liang and Zeger (1986), provide a method of analyzing correlated data that would be modeled inappropriately using traditional Generalized Linear Models. We analysed our suite of response variables using the logit, identity, and log link functions for binary, normal, Poisson and negative binomial error distributions, respectively. GEEs function as iterative processes using quasi-likelihood to estimate regression coefficients where correlation structures defined a priori account for within-subject correlation (Diggle et al. 2002). For all of our models we used an exchangeable structure to model the working correlation matrix.
(Diggle et al. 2002). GEEs (also known as marginal models) provide an average response for observations sharing the same covariates as a function of the covariates (Zeger et al. 1988). These models are particularly well suited to examine questions where population-level assessment of relationships between response and predictor variables is of interest (Diggle et al. 2002).

We considered "territory" as the repeated subject in models of attendance patterns, territorial intrusion rates, territorial intrusion duration, and likelihood of chase and egg capture as outcome of events is more likely to be similar within than among territories (Sutherland 1996). However, as repeated intrusions by a given individual cannot be considered independent, analyses of intrusion duration, and chase and egg capture likelihood were complemented by performing a second set of analyses. These analyses were conducted using data limited to records obtained exclusively for individuals of known identity (banded) using "individual" as the repeated subject (Bêty et al. 2002). However, it is recognized that this subset of 30 banded birds consists exclusively of individuals initially captured within the colony (most as breeders), and may be biased towards resident breeders rather than non-breeding gulls within the colony.

We concede that small sample size (i.e. six herring gull pairs) in this experiment could lead to low statistical power and that certain non-significant results consequently require cautious assessment. This may be especially true given the additional variation stemming from considering individuals having consumed provided eggs (i.e. treatment), with previously satiated individuals and individuals having consumed self-procured eggs during observations equally, in
analyses of attendance. Further, as the number of subjects observed in repetition (also known as “clusters”) was less than 20, inferences needed to be drawn from naïve model-based standard errors (Horton and Lipsitz 1999, Ballinger 2004) as under such conditions the latter have better statistical properties than empirical variance estimates. However, this less-desirable approach does not control for the nature of autocorrelation within clusters over time. In analyses with numbers of clusters of 20 or greater, empirical variance estimates with associated Wald statistics were used to assess significance of predictors (Horton and Lipsitz 1999, Ballinger 2004).

We did not conduct full factorial analyses (James and McCulloch 1990). Instead, variables included in the models were selected \textit{a priori} and correspond to hypotheses based on previous published studies and our prior knowledge of the system. Day of year was included in models to evaluate within-season changes in response patterns. Predictors were excluded from our initial selection only if they exhibited collinearity with other predictors beyond a threshold level ($r \geq 0.5$) (Green 1979). Except for the food supplement treatment factor which remained in, predictors were eliminated one at a time from models using a backwards stepwise approach. A tolerance level of 0.05 was used for main effects in final models. To achieve linearity (Zar 1999), the relationship between attendance and eider nest abundance within territories calculated for each year was examined in separate analyses, by sex, through regression of arcsine square-root transformed proportions of attendance measures against the log of the number of active eider nests located within each territory. Where appropriate, means are presented $\pm 1\text{SE}$.
RESULTS

Gull population size and timing of breeding

The number of herring gull territories within the East Bay colony has remained stable from 1999 to 2004 at 30 (±1) pairs. Territorial boundaries are established or re-established early in the season, remain fixed, and are defended through to departure of chicks from the nest. Combined breeding and foraging territories have not been reported previously in this species (Pierotti and Good 1994).

Ice break-up at East Bay occurred on 24 June 2001 and on 4 July 2002. In both years, herring gulls foraged within open water leads and exposed intertidal flats in East Bay within 1 km of the eider colony immediately following commencement of ice break-up. Median clutch initiation in herring gulls occurred on 8 June 2001 (28 of 35 eggs from 16 nests were depredated by a fox during egg-laying with replacements laid later), and 23 June 2002. Behavioural observations of gulls were made from 7 July to 20 July 2001 and from 8 July to 25 July 2002 inclusive. Hence, all behavioural data were collected after ice break-up and took place while gulls incubated clutches, ending with hatch of gull chicks. Median clutch initiation of common eiders occurred on 26 June 2001 and 3 July 2002.

Characteristics of territories

In all cases, the nests of herring gull pairs under study were located within territories used for foraging (N=13 in 2001, and N=6 in 2002). In 2001, 11 measured territories averaged 0.473 ha in size (range: 0.080 to 1.590), and contained a mean of 191 eider nests/territory (range: 7 to 557). Mean density of eider nests within focal territories was estimated to be 417 nests/ha (range: 75 to
In 2002, the mean size of 6 territories was 0.482 ha (range: 0.110 to 1.370) and a mean number of 175 eider nests/territory (range: 14 to 379). Mean density of eider nests within territories was 459 nests/ha (range: 127 to 979) (See fig. 4.1).

Territory size and the number of active eider nests within territories were positively correlated in 2001 ($r^2 = 0.814, P = 0.0001$), but not significantly so in 2002 ($r^2 = 0.393, P = 0.183$) (See fig. 4.1). In 2002, one of six territories exhibited atypically low nest densities for unknown reasons. The relationship became significant when this territory was omitted from the analysis ($P = 0.0383$). Contrary to prediction, we failed to detect a single clear relationship between territory size and prey density (nests/ha) in either year (Fig. 4.2).

**Intrusion and egg capture frequency in relation to eider nest density within territories**

In 2001, focal territories (N=11) were watched during 173.75 h of continuous observations under natural conditions, during which 16 eider eggs were captured from nests by territory residents. In 2002, focal territories (N=6) were observed for a combined total of 866.25 h (600.00 control, 266.25 treatment). We watched territorial gulls capture 111 eider eggs from within their respective territories (52 under natural conditions, 59 during supplemental food treatments). Under natural conditions, we failed to detect a relationship between egg captures by territory owners and eider nest abundance within their territories ($r^2 = 0.62, P = 0.064$).

In 2001, a total of 243 territorial intrusions were observed. Of these, 7 resulted in eggs being taken from territories by intruders. We observed a total of 2170 territorial intrusions (1377 during controls, 793 during treatment) in 2002. In
that year, we witnessed intruders take a total of 110 eider eggs from focal
territories (58 during controls, 52 during treatment). Under natural (control)
conditions both the number of territorial intrusions ($r^2 = 0.91, P = 0.003, N=6$), and
the number of eider eggs taken by intruders ($r^2 = 0.79, P = 0.019$) was positively
correlated with eider nest abundance within territories (nests/territory).

** Territory attendance in relation to the number of active eider nests per
territory**

Pairs never left their territories completely unattended during the study; at least
one bird was present at all times. Instances (in 2002) where herring gull eggs were
left uncovered (e.g. to chase intruders or during changeover of the incubating
individual) were extremely rare and lasted on average 35±31 seconds ($N=20$).

Transformed attendance measures for males and females in nine territories
in 2001 and six territories in 2002 were regressed against nest abundance (log
nests/territory) (see Methods). Overall, the proportion of total time that females
were present on territories (incubation and non-incubation behaviours combined)
was positively related to the number of active eider nests within their territories in
both years (Fig. 4.3) ($2001, r^2=0.49, P=0.037; 2002, r^2=0.90, P=0.004$). The
number of active eider nests was positively related to the proportion of time
females spent incubating in both years, but significantly so only in 2002 (Fig. 4.4)
($2001, r^2=0.39, P=0.075; 2002, r^2=0.78, P=0.020$). There was also a positive
relationship between the time females spent on their territories in activities other
than incubation and the number of active eider nests in 2002 (Fig. 4.5) ($r^2=0.92,
P=0.003$), but we failed to detect this in 2001 ($r^2=0.32, P=0.111$).
In contrast to females, we did not detect a significant relationship between the proportion of total time males were present on their territories and the number of active eider nests (nests/territory) in 2001 and 2002 (Fig. 4.6) (2001, $r^2 = 0.09$, $P = 0.422$; 2002, $r^2 = 0.52$, $P = 0.107$). Given that males and females do not incubate the nest simultaneously, the time males were incubating varied inversely with female nest attendance; hence, male incubation was negatively related to the number of active eider nests on their territories (Fig. 4.7). However, the proportion of time individual males spent on territories in other activities was positively related to the number of active eider nests located within territories in 2002 (Fig. 4.8) ($r^2 = 0.82$, $P = 0.014$) but we failed to detect this in 2001 ($r^2 = 0.193$, $P = 0.237$).

**Attendance patterns in relation to natural and supplemental food availability within territories**

Females increased the total time they were present within their territories in response to treatment (i.e. intake of provided or self-procured eggs) (Fig. 4.3, Table 4.1 section 1). Also, females responded to treatment by both incubating more (Fig. 4.4), and spending more time within territorial boundaries even when not incubating (Fig. 4.5). We did not detect an effect of date on these responses.

In contrast to females, we failed to detect a significant relationship between treatment and the total time males spent within their respective territories (Fig. 4.6; Table 4.1 section 2). As expected, the proportion of time males spent incubating varied negatively with treatment (Fig. 4.7). However, males increased their time spent within their territories not incubating with provided or self-procured egg
Factors influencing rates, and duration of territorial intrusion

We did not detect effects of treatment, attendance patterns of males or females or day of year on rates of intrusion within territories (n=2170, Table 4.2 section 1).

Similarly, we failed to detect an effect on the duration of intrusions into territories with intake of provided or self-procured eggs. However, the duration of intrusions into territories was lowest when both territorial residents were present (Table 4.2 section 2), and intrusion duration also decreased as the season progressed (n=2170). In analyses of 332 (of 2170) intrusions committed by 31 known individuals banded on the colony, the duration of individual intrusions was also lower when both territorial residents were present on their territory (Table 4.3 section 1). In contrast to the result obtained in analyses of all intrusions, we did not detect an effect of date on duration of intrusions committed by known individuals.

Intrusion duration was shortened by territorial chases by territory residents. Also, intrusions into territories by known non-breeding individuals lasted longer than those of their breeding counterparts. We did not detect an effect of neighbour status or sex of the intruder on the duration of intrusion.

We failed to detect an effect of treatment on the likelihood of an intruder being chased out of a territory by a resident (N=2170, Table 4.2 section 3), although a slight negative effect of treatment was detected in analyses of intrusions committed by known individuals (subset of 332 intrusions). Chases of intruders
occurred more often when both members of a territorial pair were present on the
territory. Males contributed significantly more to chases than females (N=2170,
Table 4.2 section 3). We failed to detect an effect of neighbour status (i.e. known
marked individuals from adjacent territories) or day of year on the likelihood of an
intruder being chased.

**Effects of attendance on egg removal rates by territory owners and intruders**

Under natural conditions, territorial residents removed singly 16/16 and 47/52 of
all eggs captured, in 2001 and 2002 respectively. We did not observe territorial
owners remove more than one egg from any eider nest in 2001, and observed this
on only two occasions in 2002. As expected, in 2002 the rate of egg captures by
resident gulls increased significantly when supplemental eggs were introduced into
their territories. Natural rates of egg removal by resident gulls were similar for
males and females (Table 4.4 section 1).

Under natural conditions intruders took eggs singly from eider nests within
gull territories 5/7 and 49/58 times in 2001 and 2002, respectively. Controlling for
resident presence, egg captures by intruders were significantly more likely to occur
when supplemental food was provided in territories (Tables 4.2 section 4 and 4.3
section 3). However, and as predicted, egg removal by intruders was less likely to
occur when both members of the territorial pair were present on the territory,
regardless of the sex of the non-incubating pair member (Table 4.2 section 4).
Likelihood of egg removal from territories by intruders declined with advancement
of date, but only in analyses of intrusions committed by known individuals (mostly
breeding adults from the colony). Analysis of data originating from observations
of these known individuals (which controlled for the repeated nature of visits committed by individual intruders) failed to detect significant relationships between rates of egg removal by intruders, and attendance status of the territorial pair, breeder status, neighbour status, or sex of the intruding individual (Table 4.3 section 3). These intriguing results suggest intensity of intrusion was maintained by banded individuals (mostly breeding adults from the colony), who held territories of their own, regardless of territory attendance patterns of the resident pair. This was not the case for the remainder of the gull population (i.e. non-breeders, young birds, breeders in transit).

**DISCUSSION**

Food resources for animals are often variable in nature particularly for those inhabiting environments at high latitudes. For example, availability of prey associated with open water in arctic environments can be severely affected by ice cover extent, which is known to vary annually (Gaston and Hipfner 1998, Salihoglu et al. 2001, Roth 2003, Arrigo and van Dijken 2004). In extreme cases, ice extent may determine the nature of prey for the predator (Pezzo et al. 2001). Similarly, cyclical fluctuation in lemming abundance is known to play an important role in determining reproductive success for many northern predatory species (Krebs 1993, Wilson and Bromley 2001, Béty et al. 2002). Generalist species can exploit a wide variety of prey types and can benefit from their ability to switch between them when their availability varies (Pierotti and Annett 1987, Pierotti and Good 1994, Massaro et al. 2000).

Large gulls often exhibit a variety of foraging tactics and a diverse diet which may include invertebrates, fish, and small mammals (Pierotti and Good 1994,
Gilliland et al. 2004). Predatory seabirds, including gulls, can also enhance their prey intake by defending foraging territories (Hamer et al. 1991, Spear 1993, Bukacinska et al. 1996, Catry and Furness 1999, Caldow and Furness 2000, Hahn and Peter 2003). For example, glaucous gulls breeding sympatrically with thick-billed murres (Uria lomvia) exploit murre eggs and defend foraging territories within large seabird colonies (Gilchrist et al. 1998). Gulls that adopt this territorial strategy hunt near their nests and largely avoid foraging at sea or over large expanses of terrestrial habitat, in contrast with glaucous gulls which are non-territorial (Gilchrist 2001). Similarly, great black-backed gulls (Larus marinus) also exploit seabird prey distributed within feeding territories (Massaro et al. 2000).

In our study, there was a clear relationship between the attendance patterns of territorial gulls and prey abundance within their territories. Females with territories that contained large numbers of naturally-occurring eider nests spent more time in their territories than those females whose territories contained fewer prey (Figures 4.3, 4.4 and 4.5).

Costs also were identified that arise from absence of the non-incubating member of the pair from territories; namely, longer intrusion duration, lower likelihood intruders are chased from territories, and increased likelihood of intruder success, all leading to increased egg-removal rates from territories by conspecific intruders. There may be other costs as well, including reduced nest defence (Morris 1987, Bukcinska et al. 1996, Calladine 1997) and mate guarding (Mougeot et al. 2002).
Further, experimental food additions within territories in 2002 demonstrated that food abundance largely determined the degree to which individuals attended their territories (Table 4.1 sections 1 and 2; Figures 4.3, 4.4, 4.5, 4.7 and 4.8). Territorial pairs responded to experimentally increased prey abundance by increasing their territory attendance, although this response varied by sex. Females spent more time within territories and devoted more time to incubation. This in turn allowed resident males to spend more time within the territory not incubating, and much of this time was spent defending the territory from intruding gulls (Table 4.1 section 2; Figure 4.8). Thus, resident gulls responded to increased prey availability in their territories by both incubating more (females), and by defending the territory from intruders more (males).

ACKNOWLEDGEMENTS

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Skebo, for their assistance and companionship. Joël Béty offered helpful input throughout the study, and Graham Forbes provided helpful advice at the design and early analysis stages.
LITERATURE CITED


Table 4.1. Generalized linear models (generalized estimating equations) of components (in parentheses) of daily male and female territorial attendance in relation to food (provided and self-procured), and day of year. ( Territory = repeated subject).

<table>
<thead>
<tr>
<th>Factors</th>
<th>Estimate</th>
<th>95% CI</th>
<th>P-value</th>
</tr>
</thead>
</table>
| **Response: Female attendance (h) per territory (N=6)**
| (Incubation + non-incubation) | Food for female: Yes | 0.2968 | 0.1466 | 0.4471 | **0.0001** |
| | Food for female: No | 0 | 0 | 0 | --- |
| (Incubation only) | Food for female: Yes | 0.2551 | 0.0865 | 0.4238 | **0.0030** |
| | Food for female: No | 0 | 0 | 0 | --- |
| (Non-incubation only) | Food for female: Yes | 0.5545 | 0.1563 | 0.9527 | **0.0063** |
| | Food for female: No | 0 | 0 | 0 | --- |
| **Response: Male attendance (h) per territory (N=6)**
| (Incubation + non-incubation) | Food for male: Yes | 0.0548 | -0.0171 | 0.1266 | 0.1351 |
| | Food for male: No | 0 | 0 | 0 | --- |
| (Incubation only) | Food for male: Yes | -0.2897 | -0.4708 | -0.1087 | **0.0017** |
| | Food for male: No | 0 | 0 | 0 | --- |
| (Non-incubation only) | Food for male: Yes | 0.4086 | 0.2182 | 0.5989 | **<0.0001** |
| | Food for male: No | 0 | 0 | 0 | --- |
| Day of year | 0.0247 | 0.0082 | 0.0411 | **0.0033** |

Explanatory variables (factors) entered into models were: supplemental food treatment, and day of year.

*Poisson errors with log link function; model based standard errors; offset=log(hours) (total hours of observation per day per territory).
Table 4.2. Generalized linear models (generalized estimating equations) of intrusion rate, intrusion duration, chase likelihood, and likelihood of egg removal by intruders; for 2170 intrusions into six territories. (Territory = repeated subject).

<table>
<thead>
<tr>
<th>Response Factors</th>
<th>Estimate</th>
<th>Lower</th>
<th>Upper</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Intrusion rate (N=6)</strong>&lt;sup&gt;a&lt;/sup&gt;</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Supplemental food: Yes</td>
<td>0.1773</td>
<td>-0.0335</td>
<td>0.3882</td>
<td>0.0993</td>
</tr>
<tr>
<td>Supplemental food: No</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
<td>---</td>
</tr>
<tr>
<td><strong>Intrusion duration (h) for all intrusions per territory (N=6)</strong>&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Supplemental food: Yes</td>
<td>0.0001</td>
<td>-0.0103</td>
<td>0.0101</td>
<td>0.9845</td>
</tr>
<tr>
<td>Supplemental food: No</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>---</td>
</tr>
<tr>
<td>Presence: Male free, female incub.</td>
<td>-0.0402</td>
<td>-0.0516</td>
<td>-0.0288</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Presence: Female free, male incub.</td>
<td>-0.0306</td>
<td>-0.0438</td>
<td>-0.0174</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Presence: Incubator only (ref.)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>---</td>
</tr>
<tr>
<td>Day of year</td>
<td>-0.0010</td>
<td>-0.0018</td>
<td>-0.0002</td>
<td>0.0197</td>
</tr>
<tr>
<td><strong>Chase likelihood for all intrusions per territory (N=6)</strong>&lt;sup&gt;c&lt;/sup&gt;</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Supplemental food: Yes</td>
<td>-0.1310</td>
<td>-0.3442</td>
<td>0.0823</td>
<td>0.2288</td>
</tr>
<tr>
<td>Supplemental food: No</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>---</td>
</tr>
<tr>
<td>Presence: Male free, female incub.</td>
<td>3.0357</td>
<td>2.7271</td>
<td>3.3443</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Presence: Female free, male incub.</td>
<td>1.9072</td>
<td>1.5751</td>
<td>2.2393</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Presence: Incubator only</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>---</td>
</tr>
<tr>
<td><strong>Likelihood of egg removal by intruders for all intrusions per territory (N=6)</strong>&lt;sup&gt;c&lt;/sup&gt;</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Supplemental food: Yes</td>
<td>0.4181</td>
<td>0.0077</td>
<td>0.8286</td>
<td>0.0459</td>
</tr>
<tr>
<td>Supplemental food: No</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>---</td>
</tr>
<tr>
<td>Presence: Male free, female incub.</td>
<td>-1.2950</td>
<td>-1.8396</td>
<td>-0.7504</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Presence: Female free, male incub.</td>
<td>-0.7626</td>
<td>-1.2961</td>
<td>-0.2292</td>
<td>0.0051</td>
</tr>
<tr>
<td>Presence: Incubator only</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>---</td>
</tr>
</tbody>
</table>

Explanatory variables (factors) entered into models were: supplemental food treatment, presence status (territory residents), and day of year.

<sup>a</sup>negative binomial errors with log link function; model-based standard errors; offset variable=loghours of period for which presence status was unchanged.

<sup>b</sup>normal errors with identity link function; model based standard errors.

<sup>c</sup>binomial errors; model based standard errors.
Table 4.3. Generalized linear models (generalized estimating equations) of duration, chase likelihood and likelihood of egg removal by intruders for 332 intrusions committed by known intruders (N=31). (Intruder=repeated subject).

<table>
<thead>
<tr>
<th>Response Factors</th>
<th>Estimate</th>
<th>Lower 95%CI</th>
<th>Upper 95%CI</th>
<th>P-value</th>
</tr>
</thead>
</table>
| **Intrusion duration (h) per intrusion committed by known individuals (N=31)**
| Supplemental food: Yes | 0.0116 | -0.0192 | 0.0423 | 0.4607 |
| Supplemental food: No | 0 | 0 | 0 | --- |
| Presence: Male free, female incub. | -0.0343 | -0.0539 | -0.0146 | 0.0006 |
| Presence: Female free, male incub. | -0.0228 | -0.0440 | -0.0016 | 0.0354 |
| Presence: Incubator only | 0 | 0 | 0 | --- |
| Chased by territory resident: Yes | -0.0316 | -0.0508 | -0.0124 | 0.0012 |
| Chased by territory resident: No | 0 | 0 | 0 | --- |
| Breeder intruder: Yes | -0.0524 | -0.0889 | -0.0159 | 0.0049 |
| Breeder intruder: No | 0 | 0 | 0 | --- |
| **Chase likelihood per intrusion committed by known individuals (N=31)**
| Supplemental food: Yes | -0.5788 | -1.1549 | 0.0026 | 0.0490 |
| Supplemental food: No | 0 | 0 | 0 | --- |
| Presence: Male free, female incub. | 2.9544 | 1.9145 | 3.9943 | <0.0001 |
| Presence: Female free, male incub. | 2.8586 | 1.9354 | 3.7818 | <0.0001 |
| Presence: Incubator only | 0 | 0 | 0 | --- |
| Sex intruder: male | -2.1714 | -3.2831 | -1.0598 | 0.0001 |
| Sex intruder: female | 0 | 0 | 0 | --- |
| **Likelihood of egg removal by intruders per intrusion committed by known individuals (N=31)**
| Supplemental food: Yes | 1.3176 | 0.5781 | 2.0572 | 0.0005 |
| Supplemental food: No | 0 | 0 | 0 | --- |
| Day of year | -0.0830 | -0.1477 | -0.0184 | 0.0118 |

Explanatory variables (factors) entered into models were: supplemental food treatment, presence status (territory resident), breeder status (intruder), sex (intruder), neighbour status (intruder), and day of year; chased by resident was added as a predictor to models of intrusion duration; intrusion duration was added as a predictor of probability of egg removal by intruders.

*Normal errors with identity link function; empirical standard errors.
*Binomial errors with logit link function; empirical standard errors.
Table 4.4. Generalized linear models (generalized estimating equations) of egg captures within six territories by their respective residents, and by intruders. (Territory=repeated subject).

<table>
<thead>
<tr>
<th>Factors</th>
<th>Estimate</th>
<th>Lower</th>
<th>Upper</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg captures by residents within their territories (eggs/h) (N=6)*</td>
<td>0.5817</td>
<td>0.1297</td>
<td>1.0354</td>
<td>0.0120</td>
</tr>
<tr>
<td>Supplemental food: Yes</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
<td>---</td>
</tr>
<tr>
<td>Egg captures by intruders (eggs/h) (N=6)*</td>
<td>0.5811</td>
<td>0.1630</td>
<td>0.9992</td>
<td>0.0064</td>
</tr>
<tr>
<td>Supplemental food: Yes</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
<td>---</td>
</tr>
<tr>
<td>Presence: Male free, female incub.</td>
<td>-1.3366</td>
<td>-1.8753</td>
<td>-0.7979</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Presence: Female free, male incub.</td>
<td>-0.7097</td>
<td>-1.2563</td>
<td>-0.1632</td>
<td>0.0109</td>
</tr>
<tr>
<td>Presence: Incubator only</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
<td>---</td>
</tr>
</tbody>
</table>

Explanatory variables (factors) entered into models were: supplemental food treatment, presence status (territory residents), and day of year.

*Negative binomial errors with log link function; offset variable=loghours of period for which presence status was stable.
Figure 4.1. Relationship between territory size and number of active eider nests in 11 and 6 territories, in 2001 and 2002 respectively.
Figure 4.2. Relationship between territory area and active eider nest densities within 11 and 6 territories in 2001 and 2002 respectively.
Figure 4.3. Percentage of total time females from six territories spent in both incubation and non-incubation within their respective territories, and response to food intake (provided and self-procured) based on a combined total of 866.25 hours of observation during 18 days of incubation.
Figure 4.4. Percentage of total time females from six territories spent in incubation within their respective territories, and response to food intake (provided and self-procured) based on a combined total of 866.25 hours of observation during 18 days of incubation.
Figure 4.5. Percentage of total time females from six territories spent in non-incubation within their respective territories, and response to food intake (provided and self-procured) based on a combined total of 866.25 hours of observation during 18 days of incubation.
Figure 4.6. Percentage of total time males from six territories spent in both incubation and non-incubation within their respective territories, and response to food intake (provided and self-procured) based on a combined total of 866.25 hours of observation during 18 days of incubation.
Figure 4.7. Percentage of total time males from six territories spent in incubation within their respective territories, and response to food intake (provided and self-procured) based on a combined total of 866.25 hours of observation during 18 days of incubation.

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Figure 4.8. Percentage of total time males from six territories spent in non-incubation within their respective territories, and response to food intake (provided and self-procured) based on a combined total of 866.25 hours of observation during 18 days of incubation.
Chapter 5

Conclusion

RATIONALE

A need exists to link empirical examples with theoretical foraging models. Further, identification of factors and knowledge of their influence on predator behavioural responses will lead to better understanding of the impacts of predation on prey (Miller et al. 2006).

FINDINGS

The main objective of the study was to examine the combined effects of how variable environmental and biological factors interact to influence foraging behaviour of herring gulls within a colony of nesting eiders. A second related objective was to examine how gulls varied in their behavioural responses to changing foraging constraints. Finally, to establish the relationship between foraging and territoriality at the site, I examined the contribution of prey intake (largely a function of availability) to territorial behaviour by experimentally adding available prey to territories. In so doing, I simultaneously tested predictions of Optimal Foraging (Stephens and Charnov 1982, Stephens and Krebs 1986) and Alternative Prey (Angelstam et al. 1984) theories. I also included predictions derived from previous work which examined how risk of injury during attack attempts influenced predator foraging decisions (Gilchrist et al. 1998, Béty et al. 2002).
Chapter two explored the effects of environmental and biological factors on gull foraging activity during the eider incubation period over three years. Gulls depredated eider eggs from unattended nests that were distributed at varying densities within the colony. Specifically, I tested hypotheses associated with potential effects of prey nest density, date in the breeding season, ambient light levels, wind speed, temperature, and tide height on gull foraging activity. In addition, search and egg capture rates were assessed as both overall rates (eggs taken per unit time per hectare) and per capita rates (eggs taken per unit time per nest) to better evaluate allocation of foraging effort by gulls directed towards eider nests within the colony. Also, the behavioural reaction of eider hens to searching gulls was quantified as an index of risk of injury that could alter choice among foraging alternatives (Houston 1993, Sherratt 2003). Gulls modified their search behaviour in relation to environmental and biological factors (chapter 2). This was especially the case for effects of wind speed on herring gull foraging activity. Also, gulls not only searched more, but were more successful when eider hens did not incubate continuously (i.e. when eggs were left unattended during the laying period). Gulls foraged more within high-density eider nesting areas where encounter rates were higher. Although there was some support that indicated gulls searching from the air directed more attention to individual nests in low density areas and the opposite for gulls searching from the ground, evidence did not support the suggestion that gulls were more successful in low or high density nesting areas. Further, aggressive defensive behaviour by eider hens nesting in close proximity to one another did not appear to deter foraging gulls. At the very least, I failed to detect a pronounced effect of nest density on foraging activity. Clearly, this
presents an interesting avenue for further study using a design better suited to generating confident inference in this area. Still, I speculate that it is likely that when searching from the ground, resident gulls, many of which had territories (see below), avoided aggressive defence by eider hens, buffering the expected increase of agonistic encounters with eiders in areas of high eider nest densities. This suggests that eiders might gain an advantage in nesting at high densities only early in the eider egg-laying period, when the effect of dilution is weakest and gulls are least likely to be satiated (Findlay and Cooke 1982).

Similarly, chapter three explores effects of environmental and biological factors on gull foraging activity during departure of eider ducklings from the colony over a five year period. I tested hypotheses related to the effect of wind speed, tide height, temperature and time of day, on foraging activity and rates of duckling capture by gulls. I also examined the contribution of annual lemming-abundance on rates of search and duckling capture on the colony. Here also, I measured the defensive behaviour of eider hens (departing the island with young) directed toward foraging gulls (behaviour that constituted risk of injury to the gull) and examined annual variation in the frequency and intensity of the response.

In contrast with eider eggs, eider ducklings are mobile prey, typically depart the colony within 24 h of hatch, and are often attended by more than one eider hen. The most striking and unexpected initial result was that, although levels of foraging activity directed toward eider ducklings were variable, they were consistently low when compared to other studies in analogous gull-eider systems elsewhere (Mendenhall and Milne 1985, Åhlund and Gömark 1989, Mawhinney and Diamond
1999). Also, effects of large-scale fluctuation in small mammal abundance on gull foraging behaviour were detected over five years. Specifically, I found that intensity of gull foraging activity directed toward eider ducklings departing the island varied inversely with lemming abundance in the vicinity of the eider colony, a result supported by examination of physical gull bolus evidence. I also found that the likelihood that gulls elicited a defensive response involving physical contact was highest in the crash year that followed peak lemming-abundance, suggesting that gulls in that year were more aggressive in their attack attempts, supporting theoretical predictions (Angelstam et al. 1984, Wilson and Bromley 2001). In addition, I found that environmental conditions, particularly wind speed, contributed to likelihood of gull searches directed at departing broods. I speculate that increased wind speed also likely contributed to increased attack success although we failed to support this statistically, likely due to sparseness of data (only 35 captures were observed in five years). Hence, not only was there strong evidence suggesting gull foraging activity varied in relation to lemming abundance, but foraging activity also varied with environmental factors that modified the net benefit of exploiting duckling prey in two ways. Firstly, foraging from the air was less energetically costly to gulls (Goldspink et al. 1978), and secondly, attacking from the air likely reduced the chances that gulls would suffer injury as a result of aggressive defensive behaviour.

In Chapter four I explored variation in foraging behaviour of individual herring gulls within the colony. Specifically, I examined foraging activity and attendance patterns of individuals in relation to prey availability and interference within their territories. Focus was directed at 1) contribution of food availability within territories
to determining territorial attendance patterns, and 2) costs in terms of eider egg removal by intruding gulls when territory owners were absent. A food supplementation experiment was used to test hypotheses. Gulls spent more time in their territories when their intake of prey increased naturally or experimentally within their territories. This finding was consistent both in territories that varied naturally with respect to eider nest abundance, and in experimental manipulation of prey abundance within a given territory. The positive response was strongest among territorial females. Females allocated more of their time spent within the territory to incubation of their own clutches. This allowed territorial males off the nest, and most remained within the territory increasing their defence of their territory.

Intrusions into territories lasted longer although we were unable to detect if they were more frequent when territory owners were absent. Territorial chases by owners decreased intrusion duration and likely reduced the likelihood of eggs being taken by intruders. Indeed, intruder success was highest when territory owners were absent from their territories.

For example, I speculate that a dominant gull that holds a territory can overcome disadvantageous foraging conditions through enhanced knowledge of eider prey behaviour and nest distribution. This knowledge can lead to reduced risk of injury, an advantage over competitors, and greater foraging efficiency. The implication here is that although individual gulls may adopt behavioural tactics in response to constraints imposed by the factors listed above, resident territorial gulls additionally may be able to partially circumvent some of these constraints through adoption of a territorial strategy.
As a whole, this study provides empirical support that the behavioural response of foraging predators may not be solely a function of prey abundance or density (Nicholson 1954, Abrams 1993). Although recent studies have examined how foraging behaviour can be influenced by environmental conditions (Gilchrist et al. 1998, Jetz et al. 2003, Sergio 2003, Quinn and Cresswell 2004), risk of injury (Funston et al. 2001, Lima 2002, Sherratt 2003, Brown and Kotler 2004, Morris 2005), and alternative prey (Wilson and Bromley 2001, Koch et al. 2005, Miller et al. 2006), I demonstrated how they interacted to influence the foraging behaviour of an avian predator: the herring gull. Additionally, stemming from observed differences in individual behaviour of gulls, I demonstrated through both observation and experimental manipulation that territorial ownership, sex, and attendance patterns of territory residents, also contributed to differences observed in behavioural responses among individual gulls foraging within the colony (chapter four).

This study exemplifies empirically that environmental conditions, risks of injury from reactive prey, differences in relative availability of prey arising from prey behaviour, the availability of alternative prey, and territorial behaviour, can interact and influence foraging behaviour.
LITERATURE CITED


Houston, A.I. The importance of state. In
Diet selection: an interdisciplinary approach to foraging behaviour. Edited by Hughes, R.N. Blackwell Scientific Publications.


Curriculum Vitae

KAREL ALLARD

Biology Department, University of New Brunswick,

EDUCATION

1999 – 2006:  Ph.D. Biology, University of New Brunswick

1991 – 1992:  Bachelor of Education (secondary) – Université de Moncton

1986 – 1989:  Bachelor of Science (honours) Biology – Université de Moncton

EMPLOYMENT

August 2005 – present:  Coordinator – Maritimes Breeding Bird Atlas
Bird Studies Canada

Environment Canada, Canadian Wildlife Service
Job description: Conducted research on seabirds to determine demographics, breeding behaviour, foraging behaviour, reproductive success, habitat use, movements and diet; publish in journals. Captured, marked and drew tissues samples from larid, alcid and anatid species. Examined use of prey by foraging gulls in relation to environmental conditions. Determined apparent survival for Arctic-breeding herring gulls. Examined prebasic moult phenology of large Arctic-breeding gulls. Examined growth rates of arctic breeding alcid and larid species. Examined use of polynyas by wintering eiders,
predators and competitors. Collaborated with other researchers examining marine birds and their habitats

April to May 2003:

**Academic program consultant**  
*Université Sainte-Anne, Church Point, NS*  
Job description: Created of a new multidisciplinary degree program (science, administration, education) in ecotourism

August to September 1996:

**Wildlife Technician**  
*Province of British Columbia, Forest Renewal B.C. Wildlife Habitat Inventory Program*  
Job description: Conducted species inventory of bat species in the Clayoquot Sound region of Vancouver Island

May to August 1989 – 1996:

**National Park Interpreter**  
*Canadian Heritage, Canadian Parks Service*  
*Mount Revelstoke, Glacier, Pacific Rim, and Fundy National Parks*  
Job description: Prepared and presented interpretive guided walks, talks, newspaper articles and special events. Conducted beached bird and Marbled Murrelet surveys (Pacific Rim) in collaboration with A. Burger (University of Victoria, Victoria, BC).

**ACHIEVEMENTS AND AWARDS**

2005:  
Graduate Bursary, University of New Brunswick

2004:  
Vaughan Graduate Fellowship in Marine Science

2004:  
Best student talk runner-up, Pacific Seabird Group conference, La Paz, Mexico (2004)

1999 – 2003:  
Northern Scientific Training Program Scholarships

2000:  
Vaughan Graduate Fellowship in Marine Science
PUBLICATIONS

Peer-reviewed journal articles


Non-refereed journal articles


Non-refereed contributions


