

The Effects of Diet and Predation on Nesting
Herring Gulls (*Larus argentatus*) in Pukaskwa
National Park

by

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Abstract

Herring gulls (*Larus argentatus*) are used as ecological indicators of the coastal Lake Superior ecosystem in Pukaskwa National Park. Their populations have declined by 70% over the last 40 years, suggesting changes in the park ecosystem. Previous studies highlighted declining prey abundance as a possible contributing factor to population declines. Populations of avian predators that prey on herring gulls have simultaneously increased which could be a significant factor impacting gull population trends. Here, I assessed herring gull diets via stable isotope (nitrogen, carbon) and fatty acid indicators to investigate how diet may influence population trends through effects on physiological (stress-associated hormones), reproductive (egg size), and behavioural (nest attentiveness) endpoints. I additionally investigated the degree to which predation is affecting herring gull reproductive success by examining gull nest attentiveness during the day and night. Gulls utilizing anthropogenic food sources exhibited reduced levels of stress-associated hormones, increased egg size, and increased day-time nest attentiveness. Anthropogenic food sources are likely buffering the impacts of declines in aquatic food availability; however, gull populations are still declining. Use of camera traps to monitor herring gull nests revealed that gulls were significantly more attentive to their nests during the day compared to the night. Of the nine nests monitored with camera traps, five produced chicks. However, at three of these nests chicks were predated shortly after hatch. Nocturnal predation by great horned owls accounted for these predation events which were the most significant predation-related factor affecting herring gull nest success. Predation of chicks at night and of eggs during the day (by conspecifics and corvids) is likely contributing to declines in PNP herring gull populations. Understanding factors contributing to population trends in ecological indicator species is critical for species management and for identifying stressors that are likely

affecting the broader ecosystem. Herring gulls are archetypal examples of the “canary in a coalmine” indicator but in an ecosystem context. Changes in their diets and in variables associated with their physiology, reproduction, and behaviour point to significant changes occurring in the Lake Superior ecosystem. Integrated research across the Great Lakes is required to understand the extent of this change and its implications for the sustainability of wildlife populations.

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Chapter One General Introduction

Ecosystems have shown increasing change during recent decades with these changes largely due to anthropogenic disturbances (Vitousek et al., 1997). Concern regarding the impact of anthropogenic activities such as human-induced climate change on the environment, and biodiversity in particular, has gained the attention of the public and decision-makers (D'Andrea et al., 2009). Current rates of biodiversity loss have exceeded historical rates of extinction by roughly two to three orders of magnitude (Woodruff, 2001; Ehrlich & Pringle, 2008). The accelerated loss in biodiversity can alter and impair ecosystem function potentially causing detrimental consequences (Hooper et al., 2005). Freshwater species are considered to be one of the world's most threatened biological groups as freshwater biodiversity has experienced declines more than twice that of terrestrial biodiversity since the 1970s (Revenge et al., 2005; Loh et al., 2005; Tickner et al., 2020). Freshwater ecosystems are particularly vulnerable to change due to a wide variety of anthropogenic stressors that may affect ecosystem function (Dudgeon et al., 2006; Reid et al., 2019) with effects that can cascade throughout the food web (Vaughn, 2010).

The Laurentian Great Lakes and surrounding channels represent the largest surface freshwater ecosystem on Earth (Government of Canada and US Environmental Protection Agency, 1995). Over the last 50 years, the Laurentian Great Lakes have undergone major ecological changes (Johannsson et al., 2000; Madenjian et al., 2002; Mills et al., 2003; Dobiesz et al., 2005; Gorman, 2007; Bunnell et al., 2014; Paterson et al., 2014; Dai et al., 2019). Cudmore-Vokey and Crossman (2000) reported changes in compositional biodiversity through both the loss and introduction of species in the Great Lakes ecosystem. The rate at which these changes are occurring is far beyond historic norms due to human influences (Lodge, 1993; Lövei, 1997). Accordingly, there is an urgent need to focus conservation efforts on the biodiversity of the Laurentian Great Lakes (Sterner et al., 2017).

High trophic level bioindicator species can play an important role in assessing threats to freshwater ecosystems because they integrate changes that are occurring throughout the food web. High trophic level species often have a greater effect on ecosystems than would be expected, based upon their abundance alone (Dobson et al., 2006). When ecosystems change, high trophic level animals may be some of the first species to disappear (Dobson et al., 2006). By monitoring such species, we can recognize change and try to understand its underlying causes (Bibby, 1999). Colonial aquatic birds are useful indicator species in both marine and freshwater environments as they act as integrators of ecological processes (Furness and Camphuysen, 1997; Hebert et al., 1999a; Mallory et al., 2010). Their populations are relatively easy to assess during breeding, as is nest success/productivity. Much is also known regarding their ecology (Furness and Camphuysen, 1997). Past studies have shown that aquatic birds respond rapidly and sensitively when faced with changing environmental conditions (Furness and Camphuysen, 1997, Hebert et al., 2008, Paterson et al., 2014). In light of this, in 2008, the Parks Canada Agency (PCA) adopted colonial waterbird, i.e., herring gull (*Larus argentatus*) and great blue heron (*Ardea herodias*), population sizes as indicators of ecological integrity for Pukaskwa National Park (PNP) on Lake Superior (Drake et al., 2017). PNP is one of six national parks situated on the Great Lakes. The mandate of the Parks Canada Agency (PCA) is to conserve, maintain, and restore the ecological integrity of Canada's natural and cultural heritage (Parks Canada Agency, 2013). PCA defines ecological integrity as: "a condition that is determined to be characteristic of its natural region and likely to persist, including abiotic components and the composition and abundance of native species and biological communities, rates of change and supporting processes" (Parks Canada Agency, 2013). Management of protected areas such as PNP is challenging given the complex nature of ecosystems and colonial waterbird population trends have provided insights into ecosystem change

in the park (Laurich et al., 2019). For example, PNP's breeding herring gull population has decreased by 70% over the last 40 years possibly due to declines in aquatic food availability (Laurich et al., 2019). The declines observed in the breeding herring gull population appears to be serious for the species, however the interpretation of trends in this population must be placed into the context of the changing environment. The Lake Superior ecosystem has undergone significant changes throughout time due to anthropogenic activity, and these changes could have previously created favourable breeding conditions for the herring gulls. Breeding pairs that nest successfully present a high degree of nest site fidelity, however emigration to new areas is likely to occur when nesting locations become suboptimal. My research investigates how broad-scale changes occurring in the ecosystem may be creating unfavourable conditions leading to reduced herring gull success in PNP. A comprehensive analysis of data generated from the study of this indicator species may improve our understanding of the large-scale ecological changes that may be affecting the ecological integrity of PNP. Understanding the stressors affecting herring gulls is thus essential not only for the conservation of that species but is equally important for evaluating the state of PNP.

Lake Superior, the largest of the five Great Lakes, has undergone significant change through time with reductions in chlorophyll-*a* concentrations indicating decreases in primary productivity (Bunnell et al., 2014). Among other species, the rainbow smelt (*Osmerus mordax*) is an important prey fish in the Lake Superior ecosystem (Gorman, 2012). The rainbow smelt is a non-native species first found in the lake in 1930 (Van Oosten, 1937; MacKay, 1963; Becker, 1983). Their numbers peaked from the 1960s into the 1970s, making them one of the main prey fish in Lake Superior (Smith, 1968; Lawrie and Rahrer, 1972; Lawrie, 1978; Selgeby, 1982). Rainbow smelt populations in Lake Superior have since demonstrated steady declines over the

past 40 years (Figure 1.1) (Gorman, 2007; Bunnell et al., 2014) which could be an important factor contributing to declining trends in the PNP herring gull population.

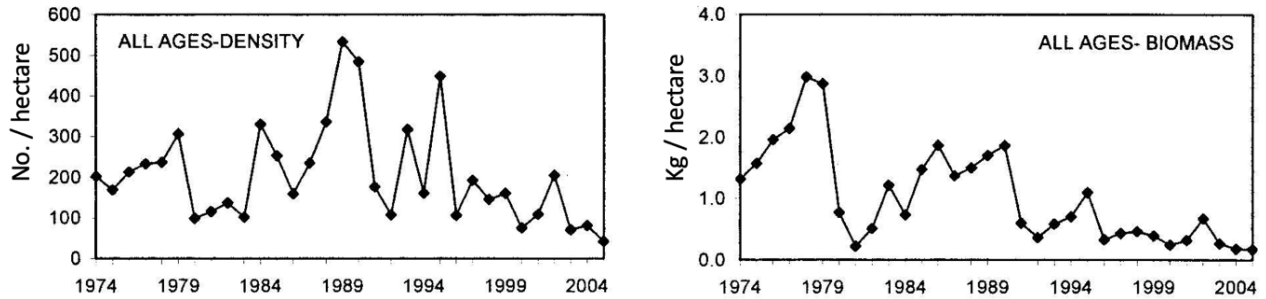


Figure 1.1 Annual estimates of mean density (number of fish/ha) and mean biomass (kg/ha) for Lake Superior rainbow smelt (*Osmerus mordax*) (all age classes) (reprinted from Gorman 2007).

The degree to which aquatic versus terrestrial food is being utilized by PNP herring gulls may be a critical factor influencing their breeding success (Laurich et al., 2019). Herring gull populations have suffered declines in both the northern and southern parts of the park, however declines appeared to be less severe in the northern population (Laurich et al., 2019). The northern population has access to landfills whereas the southern population rely to a much greater extent on dwindling aquatic food resources (Laurich et al., 2019). Considering this, anthropogenic food such as garbage may be buffering the effects of declining resources for the northern population, which is why my research focused on the northern gull population. The diet of the laying female can influence reproductive success through effects on the timing of breeding, egg size and quality, chick growth, and adult nest attentiveness during incubation and chick-rearing (Martin, 1987; Hebert et al., 2020). When highly nutritious foods such as fish are not readily available, other foods

may be consumed (e.g., songbirds, invertebrates, vegetation, small mammals, amphibians) (Macdonald and Mason, 1973; Fox et al., 1990; Ewins et al., 1994). Reductions in food availability and quality can cause elevated levels of stress within an individual (Wingfield and Kitaysky, 2002; Benowitz-Fredericks et al., 2008; Doody et al., 2008; Satterthwaite et al., 2012) and reduced resources available for reproduction (Hebert et al., 2020). Furthermore, gulls that do not have a reliable food source will travel farther distances to obtain required nutrients resulting in longer periods when their nests are unattended exposing them to higher predation risk.

Herring gulls are most vulnerable to predation during the breeding season (Weseloh et al., 2020). Breeding herring gulls are predated by many diurnal and nocturnal avian predators, such as the peregrine falcon (*Falco peregrinus*), bald eagle (*Haliaeetus leucocephalus*), and great horned owl (*Bubo virginianus*). During the 1960s-70s, bioaccumulation of organochlorine pesticides, such as DDT, caused detrimental effects on reproduction in avian species, particularly raptors (Noble et al., 1993). Such chemical contaminants resulted in reduced egg hatchability through eggshell thinning which led to drastic declines in North American raptor populations (Kirk and Hyslop, 1998; Noble et al., 1993) including populations in the Great Lakes ecosystem (Bowerman et al., 1993; Drake et al., 2017). Populations of many raptor species including bald eagles and peregrine falcons have since increased nationwide, coinciding with a ban on the use of organochlorine pesticides in the early 1970s (Kirk and Hyslop, 1998). According to the Canadian Peregrine Falcon Survey, peregrine falcons occupied 78 territories in Ontario in 2005, including 67 territorial pairs and 11 single individuals (Holroyd and Banasch, 2012). Of the 67 territorial pairs, 81% had confirmed nesting attempts with a total of 46 pairs successfully fledging young (Holyord and Banasch, 2012). Similarly, a survey conducted in 2010 reported an increase in peregrine falcon territories in Ontario to 119 (Figure 1.2) (Chikoski and Nyman, 2011). These data demonstrate

significant increases in Ontario populations compared to the 1970s when zero peregrine territories were reported (Holroyd and Banasch, 2012). Peregrines are known to scavenge adult herring gulls (Lockhart et al., 2020) and likely predate adults as well as young.

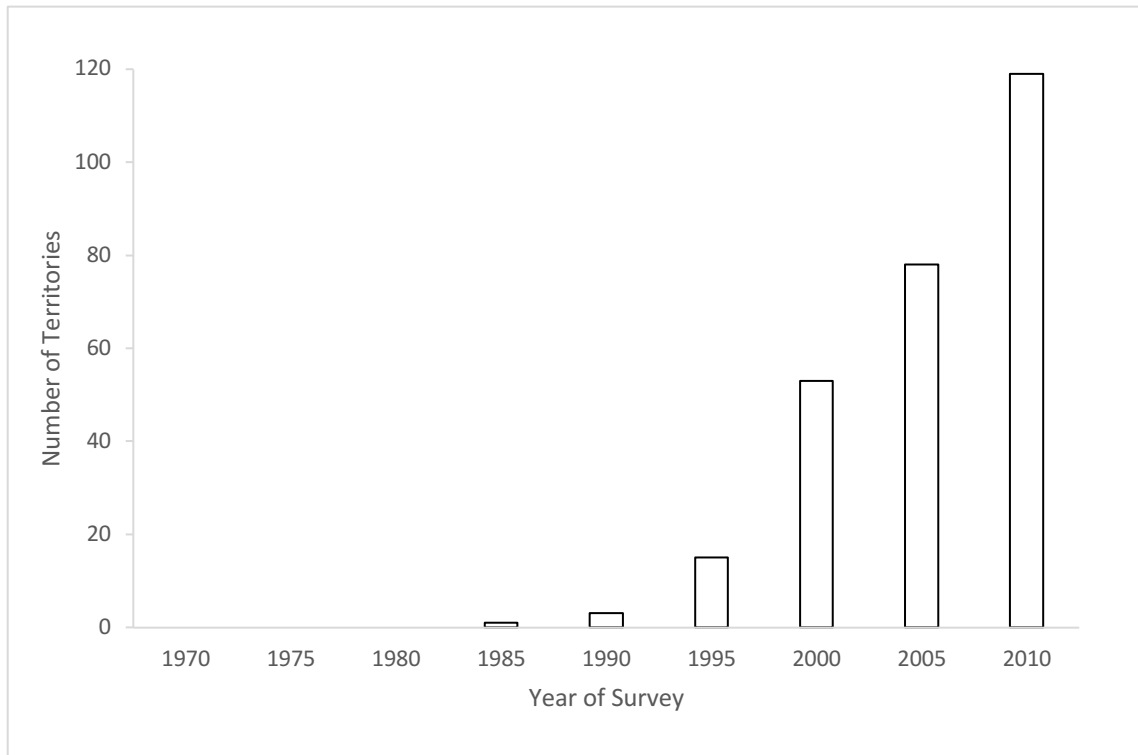


Figure 1.2 Trends in the number of peregrine falcon (*Falco peregrinus*) territories in Ontario based on quinquennial surveys (1970-2010) (reprinted from Chikoski and Nyman, 2011).

According to Christmas Bird Count (CBC) surveys, the number of bald eagles reported in Ontario was 14 in 1960, with less than 20 individuals counted each year until 1987 (National Audubon Society, 2020). Between the 1980s and early 2000s, eggshells of bald eagles from the Great Lakes region increased in thickness to levels comparable to those that occurred during the pre-DDT period (Best et al., 2010). Accordingly, from 1987 (CBC count = 33 eagles) onward,

bald eagle numbers in Ontario increased exponentially (National Audubon Society, 2020). The 2016 CBC survey reported 1307 individuals in Ontario (Figure 1.3) (National Audubon Society, 2020).

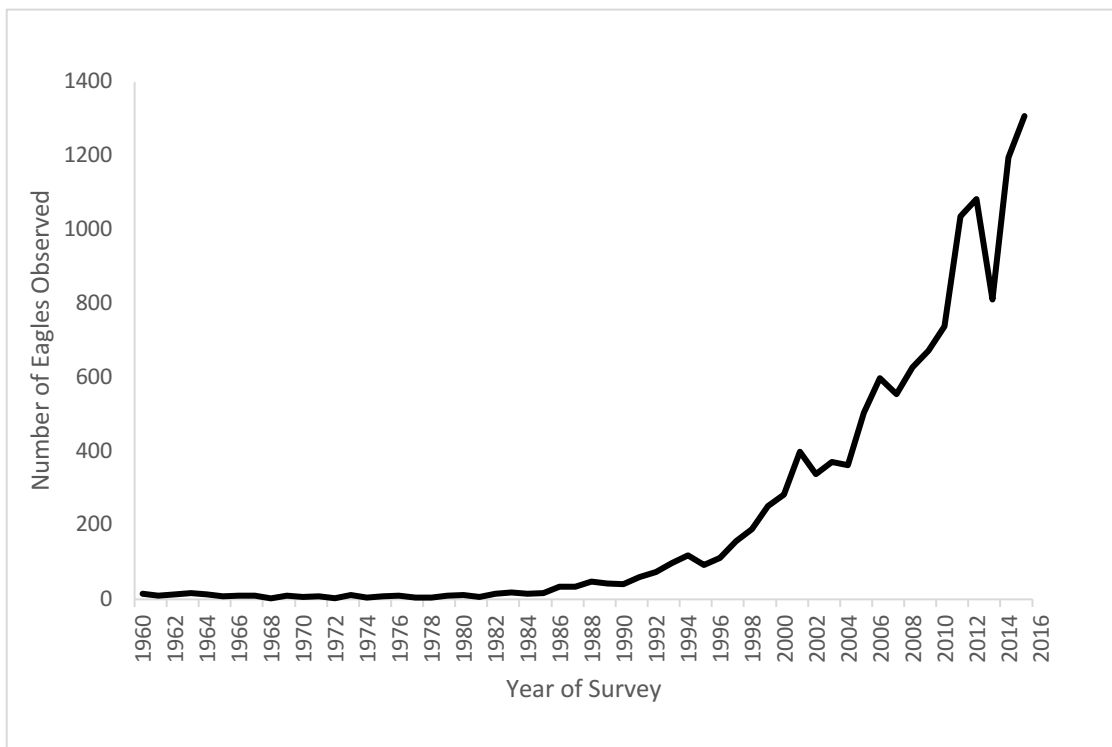


Figure 1.3 Trends in the total number of bald eagles (*Haliaeetus leucocephalus*) observed annually in Ontario during Christmas Bird Counts, 1960-2016 (National Audubon Society).

Contrary to the eagle and falcon species discussed above, great horned owls may have experienced minimal effects of organochlorine pesticides. That was likely due to the fact that great horned owls primarily eat small, low trophic level mammals that contain low levels of organochlorines (Blus, 1996). Individual owls consuming more contaminated prey, such as higher trophic level waterbird chicks, would have been exposed to much higher levels of organochlorines

and could have experienced negative effects. Unfortunately, few studies were conducted on great horned owls during the period of peak organochlorine pesticide use, i.e., 1950-1960s, but based upon the limited information available there is no evidence of organochlorine pesticide impacts on great horned owls (Blus, 1996). Limited information is available regarding trends in great horned owl populations in Canada and no information is available from the period of highest organochlorine pesticide use. Data from the Ontario Breeding Bird Atlas indicate that great horned owl populations showed a non-statistically significant increase from the first survey in 1981-85 to the latest survey in 2001-2005 (Cadman et al., 2007). More detailed, recent population surveys stemming from the Ontario Nocturnal Owl Survey show that great horned owl populations in northern Ontario remained relatively stable from 1995 to 2019 (Ontario Nocturnal Owl Survey, 2019). This limited information suggests that the predation risk posed by great horned owls to birds such as gulls has remained relatively stable over the last quarter-century in northern Ontario. Overall, however, the general population increases in important herring gull avian predator species suggest that predation on adult gulls, chicks, and eggs has likely increased in recent decades.

As integral components of PNP's biological community, declines in colonial waterbird populations, such as those observed in herring gulls, deserve attention. Given the documented declines in prey fish abundance and the increased populations of potential avian predators, my thesis research focused on examining how diet and predation may be influencing the PNP herring gull population. To accomplish this, I apply novel methods in Chapter 2 to define the herring gull diet and investigate relationships between diet and physiological, reproductive, and behavioural endpoints that could influence the fitness of individual gulls. In Chapter 3, I use remote imagery to document adult nest attentiveness and nest success of PNP herring gulls and I pay particular attention to the role of predation in explaining the observed patterns.

Chapter 2 - Defining the herring gull diet and relationships with life-history endpoints

I characterized herring gull diets by measuring biochemical dietary markers, i.e., carbon and nitrogen stable isotopes and fatty acids, in their eggs. I briefly discuss both groups of dietary markers below.

Stable Isotopes

Stable isotopes of nitrogen and carbon have been widely used in ecological studies to understand energy and nutrient transfer through food webs (for reviews see: Boecklen et al., 2011; Gannes et al., 1997; Glibert et al., 2019; Hobson, 1999; Kelly, 2000; Middelburg, 2014). Most studies have measured these light isotopes in bulk (i.e., whole tissue) samples as a means of improving our understanding of food web connections.

The utility of stable nitrogen isotopes ($^{15}\text{N}/^{14}\text{N}$, expressed as $\delta^{15}\text{N}$) for assessing organism trophic position has been recognized for decades (Minagawa and Wada, 1984) and they have been widely applied in ecological studies. $\delta^{15}\text{N}$ values generally increase 3-4‰ from one trophic level to the next; therefore, organisms occupying higher trophic positions have higher $\delta^{15}\text{N}$ values. Interpretation of $\delta^{15}\text{N}$ values in higher trophic level organisms needs to recognize the potential confounding effects of differences in $\delta^{15}\text{N}$ values associated with inorganic nitrogen entering the base of the food web. Baseline or source $\delta^{15}\text{N}$ values can vary spatially or temporally reflecting the origins of inorganic nitrogen (Kendall, 1998). In addition, nitrogen at the base of the food web may undergo chemical reactions, e.g. denitrification, that can greatly influence $\delta^{15}\text{N}$ values (Kendall, 1998). Baseline $\delta^{15}\text{N}$ values are reflected in $\delta^{15}\text{N}$ values of higher trophic level consumers (Anderson and Cabana, 2005; Hebert and Wassenaar, 2001). Hence, spatial differences

in isotopic baselines or changes in such baselines through time, e.g., seasonally, can limit the degree to which it is appropriate to compare bulk (i.e., whole tissue) $\delta^{15}\text{N}$ values in biota across space or time. However, in remote areas such as PNP that are mostly isolated from human influences, e.g., agriculture, industrialization, urbanization, bulk $\delta^{15}\text{N}$ values likely provide an accurate indication of organism trophic position.

Stable carbon isotopes ($^{13}\text{C}/^{12}\text{C}$, expressed as $\delta^{13}\text{C}$) provide insights into the origin of carbon utilized by consumers because $\delta^{13}\text{C}$ values change little ($\sim+0.4\text{‰}$ per trophic level) as they pass through food webs (Post, 2002). $\delta^{13}\text{C}$ values can be useful in identifying the origins of carbon entering food webs. For example, $\delta^{13}\text{C}$ values of primary producers in terrestrial, freshwater, and marine ecosystems are likely to differ. Phytoplankton in lakes generally exhibit lower $\delta^{13}\text{C}$ values (-32 to -46‰ ; France and Peters, 1997; Rau, 1980) but these values can increase greatly (up to -21‰ (France, 1995a)) under rapid growth conditions when cells experience carbon limitation. $\delta^{13}\text{C}$ values can differentiate sources of primary production in both freshwater (France, 1995a) and marine habitats (Miller et al., 2008) with production in nearshore/littoral habitats generally enriched in ^{13}C . Reduced water turbulence in such environments increases boundary layer effects resulting in less discrimination against ^{13}C during photosynthesis (France 1995a). Terrestrial C-3 (Calvin) foliage also exhibits low $\delta^{13}\text{C}$ values (-28‰ ; France, 1995b), while carbon from marine sources tends to have less negative $\delta^{13}\text{C}$ values (Hobson, 1987; McCarthy and Waldron, 2000). These general patterns can be complicated if consumers are utilizing terrestrial foods based on C4 (Hatch-Slack) plants as resulting $\delta^{13}\text{C}$ values in consumers will be greatly enriched in ^{13}C (DeNiro and Epstein, 1978). C4 plants, e.g., corn, can form important components of wildlife diets (i.e., consumption of garbage) particularly in human-dominated landscapes (Boggie et al., 2018) so their

unique $\delta^{13}\text{C}$ values may enhance the degree to which carbon isotopes can be used to discriminate consumer use of terrestrial versus freshwater resources (Hebert et al., 1999b; Hebert et al., 2008).

Fatty Acids

Lipids consist primarily of fatty acids and the latter are essential for normal growth and development in consumers. However, because consumers cannot synthesize many of the fatty acids that they need, they must acquire them through their diets (Arts et al., 2001). Hence, dietary fatty acid profiles in consumer tissues largely reflect what they have eaten (Iverson et al., 2004; Napolitano, 1999; Surai and Speake, 2008). Fatty acids are important in determining reproductive success. High-quality food containing adequate levels of essential amino and fatty acids is required to enable the synthesis of proteins essential for egg production (Murphy, 1996; Hebert et al., 2002). The fatty acid composition of the egg reflects the diet of the laying female (Farrell, 1998; Surai et al., 2001; Surai and Speake, 2008).

Specific fatty acids or groups of fatty acids are indicative of consumption of certain foods (Dalsgaard et al., 2003) that may also be reflective of the foraging habitats used by consumers. For example, long-chain, polyunsaturated, omega-3 (n-3) fatty acids (Figure 1.4) originate primarily in marine and, to a lesser extent, freshwater ecosystems. Hence, high proportions of these fatty acids in consumer tissues may indicate the use of aquatic food resources (Surai et al., 2001; Hixson et al., 2015). Alternatively, the presence of high levels of omega-6 (n-6) fatty acids (Figure 1.4) in consumer tissues may be indicative of the consumption of terrestrial foods (Olsen, 1999). Hence, the ratio of n-3/n-6 fatty acids may provide insights into the relative proportions of aquatic versus terrestrial foods in the diets of consumers (Hebert et al., 2006; Hebert et al., 2008; Hebert and Popp, 2018). Even though differences in fatty acid availability in foods originating from different habitat types are expected, little information is available integrating and comparing fatty acid

patterns in guilds of consumers occupying different habitat types, i.e., marine, freshwater, terrestrial. To address that, I examine fatty acid patterns in eggs from a variety of specialist bird species nesting in these three habitats across Canada and determine the degree to which egg fatty acid patterns distinguish species occupying these habitat guilds.

I use egg stable isotope values and fatty acid profiles to gain insights into the diets of PNP herring gulls. I then assess how gull diets are related to significant life-history endpoints that may influence the fitness of individual birds. Life-history endpoints are defined here as traits that influence an individual's fitness through effects on reproductive success and survival. I focus on three life-history-related endpoints associated with gull physiology (corticosterone), reproduction (egg size), and behaviour (nest attentiveness).

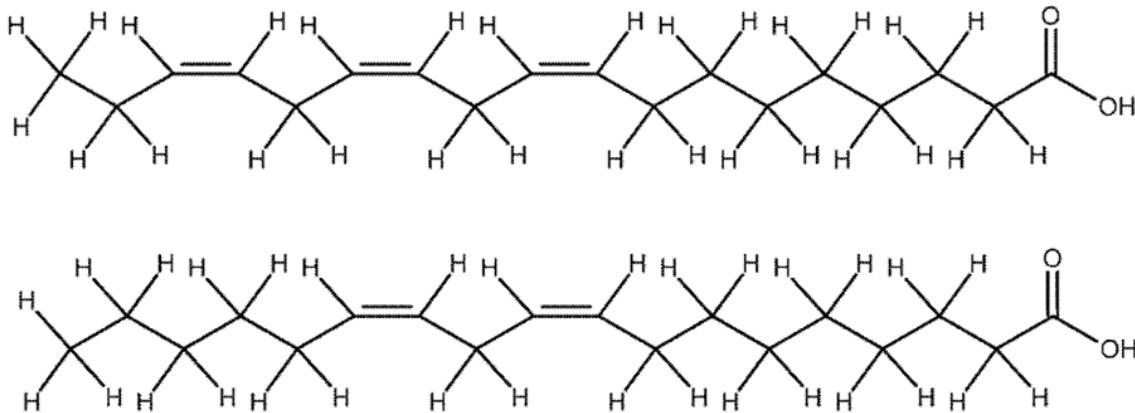


Figure 1.4 Chemical structures for representative n-3 fatty acid (top: α -linolenic acid) and n-6 fatty acid (bottom: linoleic acid). Relative to the methyl (-CH₃) end of the molecule, n-3 fatty acids have the first double bond on carbon 3 while n-6 fatty acids have the first double bond on carbon 6.

Gull Physiology - Corticosterone

Corticosterone is a naturally-occurring glucocorticoid hormone in birds, playing an important role in the regulation of energy use during all life history stages (Crespi et al., 2013; McEwen and Wingfield, 2003). Additionally, corticosterone can influence appetite and foraging behaviour, playing an important role in the acquisition of food (Sapolsky et al., 2000). In order to meet energy requirements, baseline corticosterone levels fluctuate according to seasonal activity patterns related to life-history events such as reproduction and migration (Sapolsky et al., 2000; McEwen and Wingfield, 2003). Stressful situations also activate the hypothalamic-pituitary-adrenal axis (Möstl and Palme, 2002; Busch and Hayward, 2009) which further stimulates the production of corticosterone (Aguilar et al., 2016). The production of corticosterone allows for the rapid mobilization of energy, which in turn coordinates the behavioural responses required for an individual to cope with adverse environmental conditions (Dallman et al., 2007; Sapolsky et al., 2000; Crespi et al., 2013). Under extremely stressful environmental conditions, corticosterone levels in females may surpass those associated with the normal regulation of energy metabolism, food acquisition etc. Such a situation has been characterized as an emergency life-history stage where a physiological or behavioural change occurs to enhance survival (Wingfield et al., 1998; Wingfield et al., 2003). In terms of reproduction, elevated corticosterone levels may contribute to changes in parental behaviour leading to nest abandonment or reduced parental attentiveness in order to ensure adult self-preservation (Wingfield et al., 1998).

Three hypotheses (CORT-Adaptation, CORT-Tradeoff, and CORT-Fitness) have been proposed for explaining relationships between corticosterone levels and reproductive investment or survival (Figure 1.5). The corticosterone-adaptation (CORT-adaptation) hypothesis predicts that individuals may upregulate corticosterone from baseline levels to meet the energetic demands

of reproduction with no implications for survival (Bonier et al., 2009; Crossin et al., 2012). The CORT-Tradeoff hypothesis predicts that as corticosterone levels increase, reproduction may be sacrificed to ensure survival (Patterson et al., 2014). The corticosterone-fitness (CORT-Fitness) hypothesis predicts that higher corticosterone levels simply lead to lower reproductive success and survival (Bonier et al., 2009). Despite their differences, all of these hypotheses predict negative relationships between very high levels of corticosterone and reproduction (Figure 1.5). At PNP, herring gull populations have shown very significant temporal declines suggesting that the PNP environment is a challenging one for breeding gulls. Under such a scenario, I interpret higher egg corticosterone concentrations in a negative light, that is, higher egg corticosterone concentrations may be an indicator that the females laying those eggs are experiencing the detrimental effects of increased environmental stress.

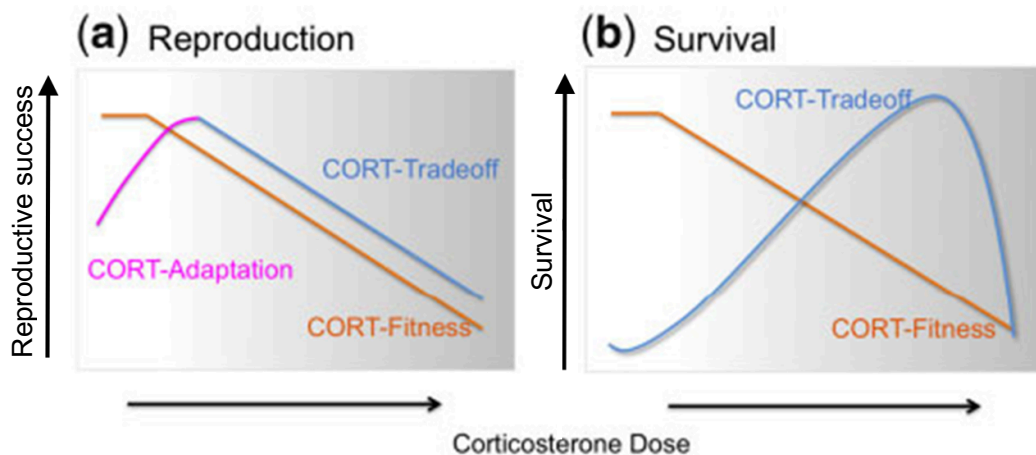


Figure 1.5 Three hypotheses (CORT- Adaptation, CORT-Tradeoff, CORT-Fitness) predicting how corticosterone (CORT) dose may affect the relationship between CORT, reproduction, and survival. (a) As CORT levels increase, reproductive investment may increase, until levels are high enough that reproduction is suppressed. All three hypotheses predict a decrease in reproduction at high levels of CORT (b) the CORT-Tradeoff hypothesis predicts that

increasing CORT may initially enhance survival but when CORT levels become too high the hypotheses predict a reduction in survival (modified from Breuner and Berk, 2019).

Corticosterone as a measure of stress can present a degree of intrinsic variability related to species specificity, daily and seasonal changes, as well as sex, reproductive status and age (Dantzer et al., 2014; Breuner et al., 2013; Royo et al., 2008). Under poor environmental conditions, females may adapt by depositing more corticosterone into their eggs (Love et al., 2005). Exposing embryos to higher levels of corticosterone may allow the female to manipulate the sex-ratio of her brood (Love et al., 2005). Increased corticosterone deposition into eggs can benefit a female experiencing poor or unpredictable conditions by skewing offspring sex to daughters rather than sons, with daughters being less energetically costly to rear (Trivers and Willard, 1973; Cameron and Linklater, 2002; Love et al., 2005). Individuals manipulating offspring sex ratios through corticosterone deposition to eggs could gain fitness benefits by reducing energy demands under adverse environmental conditions, hence it is possible that there could be a positive relationship between egg corticosterone levels and parental fitness (Bonier et al., 2009; Crossin et al., 2012). I briefly revisit this possibility in Chapter 4.

Another factor possibly complicating the interpretation of total corticosterone levels in biological tissues is the role of corticosteroid-binding globulin (CBG) protein (Breuner et al. 2013) in modulating the stress response in individuals (Malisch et al., 2010). Although the specific role of CBG has yet to be determined, it is possible that the measurement and examination of CBG is essential for the proper interpretation of corticosterone concentrations (Breuner et al., 2013). Even so, the vast majority of comparative research lacks the inclusion of CBG measurements in the analysis of stress in vertebrates (Breuner et al., 2013). Additionally, it remains debatable whether

the total amount or free amount of corticosterone in blood plasma is the biologically active component implicated in the stress response (Breuner et al., 2013). Despite these complications, corticosterone levels are considered to be useful indicators of stress (Sheriff et al., 2011).

In birds, corticosterone is commonly measured in blood and feathers (Royo et al., 2008). Eggs may be an alternative non-invasive matrix for evaluating stress associated with laying females (Royo et al., 2008). Maternal glucocorticoid concentrations during the reproductive period are reflected in egg corticosterone concentrations (Downing and Bryden, 2008) providing an integrated measure of stress over the period of egg production rather than an instantaneous response. The existence of archived eggs in frozen collections such as those in the National Wildlife Specimen Bank (Braune et al., 2010) may be an important resource for retrospective studies examining temporal changes and spatial differences in stress as inferred from egg corticosterone measurements. However, the value of eggs in this context must first be demonstrated. Considering that there is a limited amount of information available on the use of eggs for corticosterone analysis, I focus on that aspect here. In Chapter 2, I investigate relationships between dietary markers in eggs and egg corticosterone levels as a way to evaluate possible connections between diet and stress in breeding PNP herring gulls.

Gull Reproduction – Egg Size

The diet of an individual plays a crucial role in maintaining its fitness as it regulates the availability of resources necessary to successfully produce viable offspring (Hebert et al., 2009, Paterson et al., 2014). Small prey fish are rich in energy and nutrients making them a high-quality food resource for herring gulls on the Great Lakes (Fox et al., 1990; Ewins et al., 1994; Hebert et al., 1999b; Hebert et al., 2002). When fish availability declines, herring gulls will utilize other food

resources such as anthropogenic food waste (e.g. garbage). As a generalist forager, herring gulls can easily switch from high quality to less nutritious food; however, this can cause adverse effects to their fitness (Hebert et al., 2020). For example, herring gulls require a sufficient intake of lipid, proteins, and micronutrients for the proper formation of eggs (Hebert et al., 2020). Under conditions where the required dietary resources are restricted, egg quality may suffer as reflected in reduced egg size (i.e. volume) (Martin, 1987; Hiom et al., 1991; Bolton et al., 1992; Hebert et al., 2020). Chicks hatching from smaller eggs exhibit lower success (e.g., reduced hatching success, weakened immune system, slower growth, lower survival rate) in comparison to chicks hatching from larger eggs (Martin, 1987; Krist, 2011). Reduced food availability may additionally reduce the overall clutch size and negatively impact the number of chicks that fledge (Kilpi and Öst, 1998; Spaans et al., 1987). In Chapter 2, I investigate relationships between dietary markers in eggs and egg size as a way to evaluate possible connections between diet and resources available to breeding PNP herring gulls.

Gull Behaviour – Nest Attentiveness

Advances in still photography and video technology have broadened their application in behavioural studies (Cox et al., 2012). Remote photography methods, such as the use of camera traps, have enabled the collection of information that otherwise would be impractical to obtain through simple human observation (Cox et al., 2012). Additionally, digital technology has allowed data to be collected from locations that would be unreachable and unobservable from a human perspective, such as nests in burrows or in the forest canopy (Dyer and Hill, 1991; Proudfoot, 1996). Cameras provide researchers the opportunity to document rare and/or previously unknown behaviours such as egg and nestling cannibalism (Ben-Dov et al., 2006). Cameras also provide

researchers the opportunity to identify prey in bird diets (Hanula and Franzreb, 1995), identify predators (Thompson et al., 1999; Pietz and Granfors, 2000), study parental care (Grundel, 1987; Cartar and Monthomerie, 1987), as well as nesting behaviour (McRae et al., 1993; Nathan et al., 2001). Declines in food quality and/or food quantity can result in herring gulls spending more time foraging. In Chapter 2, I investigate relationships between dietary markers in eggs and nest attentiveness as a way to evaluate possible connections between diet and herring gull behaviour.

Chapter 3 - The role of predation in affecting gull nesting behaviour and success using remote imagery

Nest attentiveness is an important factor in determining nest success (Martin, 2002). Higher adult nest attentiveness provides increased protection of eggs and young from a variety of threats (Sullivan et al., 2020). Although factors such as adverse weather conditions tend to encourage adults to remain on the nest in order to provide optimal conditions for eggs and young (AlRashidi, 2016; Hart, 2016), factors such as food quality/quantity and predation have the opposite effect (Morris et al., 1976). Adults must balance their time between tending their nests and foraging for food (Martin, 1987). Declines in food quality and/or food quantity can result in herring gulls spending a greater time focused on foraging and less time spent on nest attentiveness (Laurich et al., 2019). Increased adult nest attentiveness leads to a shorter period until eggs hatch, which ultimately reduces the vulnerability of eggs to predation and other threats (Morris et al., 1976; Morris and Hunter, 1976; Vedder et al., 2017; Laurich et al., 2019).

Herring gulls are generally more vulnerable to predation during the breeding season (Weseloh et al., 2020). Similar to other colonial waterbirds, herring gulls have two main responses to predation: evading the predator by taking flight (Burger and Gocheffeld, 1991; Meehan and

Nisbet, 2002; Weseloh et al., 2020) and predator mobbing (Götmark and Anderson, 1984; Palestis, 2005; Mallory, 2016; Weseloh et al., 2020). When diurnal predators approach a nesting colony, gulls take flight and circle overhead while sounding alarm calls as they mob the predator (Weseloh et al., 2020). Flying predators such as raptors are pursued through the air while repeatedly being struck by multiple gulls, both with their bills and feet (Weseloh et al., 2020). Herring gulls will circle over and dive at terrestrial predators in order to strike them bodily or with excrement (Weseloh et al., 2020). This type of aggressive mobbing is a collective effort to drive the predator away from the colony (Weseloh et al., 2020). While mobbing is an effective counter-measure to deter predators during the day, this type of response does not seem to be used at night. In fact, little information is known about how gulls respond to nocturnal predators. Great horned owls, a primary nocturnal predator of herring gulls, feed not only on the eggs and chicks but on adult gulls as well (Southern et al., 1982). Considering this, adult gulls may be more vulnerable to nocturnal predation resulting in their leaving their nests to increase the likelihood of self-preservation (Southern et al., 1982; Sullivan et al., 2020). The length of time they are absent from their nests remains unclear. Other colonial waterbird species, such as common terns (*Sterna hirundo*), have been reported to desert their nests for up to eight hours in response to nocturnal predators (Nisbet and Welton, 1984). Similarly, California gulls (*Larus californicus*) have been observed to leave their nests for up to three hours in response to nocturnal predators (Jehl and Chase III, 1987). In Chapter 3 I investigate this, by determining the percentage of time that herring gulls spend attending their nests during the day and night. To further clarify differences in daytime and nighttime nest attentiveness, I classify absences according to duration and investigate similarities in adult nesting behaviour among nests. I expect that predators will have a more significant effect on nest attentiveness of PNP herring gulls during the night than during the day.

Chapter Two Lake Superior Herring Gulls Utilize Anthropogenic Food in a Prey-Impoverished Aquatic Environment

Introduction

Environmental changes observed in the Laurentian Great Lakes ecosystem are expected to have cascading impacts throughout the biotic community. Significant declines in top trophic level predator populations can be indicative of a shift in ecosystem state (Miller and Sydeman, 2004; Weimerskirch et al., 2003). Herring gulls have been used as environmental indicators on the Great Lakes for almost 50 years (Hebert et al., 1999a), as well as in other parts of Canada (Burgess et al., 2013; Dolgova et al., 2018) and Europe (Savinov et al., 2003; Thompson et al., 1993; Thorstensen et al., 2021). Pukaskwa National Park (PNP) is a large protected area (1877 km²) located along the northeastern shore of Lake Superior in northern Ontario, Canada. PNP's breeding herring gull population has experienced a 70% decline since the 1970s; however, population trends differ regionally with larger declines observed in the more isolated southern part of the park than in the north (Laurich et al., 2019). The differences observed between the northern and southern part of the park may be related to regional differences in food availability (Laurich et al., 2019).

As income breeders, herring gulls rely on the availability of resources near their breeding colonies during the reproductive period. In recent decades, the availability of small pelagic prey fish in Lake Superior near PNP has declined (Laurich et al., 2019). Gulls relying to a greater degree on this resource during breeding may be more food limited than conspecifics with more varied diets, particularly those with access to anthropogenic sources of terrestrial food, e.g., garbage. The degree to which food of anthropogenic origin is being utilized by PNP herring gulls may be a critical factor influencing their population trends. Traditional approaches for assessing diet composition in gulls include the analysis of pellets. Pellets are regurgitated by gulls and contain indigestible food remains. They are useful in evaluating diet composition but are biased because easier to digest food items, such as soft-bodied fish, are under-represented (Brown and Ewins,

1996). Past analysis of herring gull pellets from northern PNP suggests that anthropogenic foods along with fish are important components of the gull diet (Laurich et al., 2019). Other methods to assess diet composition provide an opportunity to either confirm or refute this finding.

The diet of individual herring gulls can also be assessed using intrinsic biochemical markers in eggs. Organism trophic position can be assessed using stable nitrogen isotopes ($^{15}\text{N}/^{14}\text{N}$, expressed as $\delta^{15}\text{N}$) (Minagawa and Wada, 1984) with higher trophic level consumers having greater $\delta^{15}\text{N}$ values. Eggs produced by gulls feeding on small prey fish generally have higher $\delta^{15}\text{N}$ values than birds feeding on terrestrial food (Hebert et al., 2008). Consumers associated with C4-based terrestrial food webs have $\delta^{13}\text{C}$ values enriched in ^{13}C (DeNiro and Epstein, 1978). Corn-based foods can be an important component of wildlife diets (e.g., consumption of garbage) in human-dominated landscapes (Boggie et al., 2018) so the unique $\delta^{13}\text{C}$ values associated with corn may enhance the degree to which carbon isotopes can be used to evaluate consumer use of anthropogenic sources of food (Hebert et al., 1999b, Hebert et al., 2008). Fatty acids are another group of biochemical tracers that are useful in evaluating gull diets as many essential fatty acids cannot be synthesized and thus must be acquired through provisioning (Arts et al., 2001). Some essential fatty acids are more prominent in aquatic versus terrestrial foods, and vice versa (Hixson et al., 2015; Olsen, 1999; Surai et al., 2001), and thus can be useful in understanding an individual's use of foraging environments. The fatty acid composition of bird eggs from species that are habitat specialists, i.e., terrestrial, freshwater, marine, are likely to differ. By measuring fatty acid profiles in a variety of habitat specialist species, I can elucidate a framework for interpreting fatty acid patterns in generalist species such as the herring gull. Such a framework may assist in determining the degree to which herring gulls from PNP are incorporating terrestrial versus freshwater foods in their diets.

Diets of laying females are reflected in the biochemical marker composition of their eggs (Farrell, 1998; Surai and Speake, 2008; Surai et al., 2001). Stable isotope and fatty acid tracers in herring gull eggs can indicate how diet may influence physiological, reproductive, and behavioural endpoints that ultimately affect population trends. For example, food availability and food quality can influence levels of stress-associated hormones in individual herring gulls (Benowitz-Fredericks et al., 2008; Doody et al., 2008; Satterthwaite et al., 2012; Wingfield and Kitaysky, 2002). If food is hard to find, birds may compensate by spending more time foraging and this may be related to elevated levels of stress-associated hormones (Crossin et al., 2012). In birds, activation of the hypothalamus-pituitary-adrenal axis occurs in response to stress leading to increased secretion of glucocorticoids (Cockrem, 2007). The stress-associated hormone, corticosterone, is a naturally occurring glucocorticoid in birds, with levels increasing in individuals experiencing unfavourable conditions (Wingfield, 2003). The production of glucocorticoids enables an individual to cope with a stressful environment by mobilizing energy stores (Dallman et al., 2007; Sapolsky et al., 2000). Ultimately, these coping mechanisms can lead to nest abandonment or reduce parental attentiveness in order to enhance the chances of adult survival (Wingfield et al., 1998). Egg corticosterone levels may, in part, reflect maternal stress experienced during the period of egg formation (Royo et al., 2008). However, there is some uncertainty regarding the mechanism behind the deposition of corticosterone in the egg, whether the female passively and/or actively regulates the maternal transfer of the hormone. Corticosterone concentrations in eggs can only be influenced by maternal stress during a relatively short period from albumen production until the initial phase of shell secretion. Because herring gulls are income breeders, restricted access to food during egg formation may invoke a stress response reflected in egg corticosterone levels. Reduced food availability may also be reflected in the quantity of

resources available for reproduction. One way of evaluating this is to examine egg size, i.e., egg volume. Reduced egg size may have adverse effects on early survival and growth of hatchlings (Williams, 1994), thereby reducing recruitment of young into the local gull population. Finally, reduced food availability may force gulls to compensate by spending more time foraging. During incubation, females need to replenish resources used for egg formation. This is especially important prior to the energetically demanding chick-rearing stage (Martin, 1987). Hence, birds may spend more time off their nests looking for food. This can be evaluated by measuring adult nest attentiveness. Gulls that do not have a reliable food source may travel farther and spend more time foraging in order to meet their nutritional requirements. The resulting absence of adults from their nests during incubation may increase the likelihood of egg or chick predation.

Here, I investigate how the diet of PNP herring gulls is related to significant life-history endpoints associated with gull physiology, reproduction, and behaviour. Based upon the analysis of PNP herring gull pellets, both terrestrial and aquatic foods are utilized by gulls in northern PNP (Laurich et al., 2019). Terrestrial food can be comprised of both natural prey, such as invertebrates, small mammals, and songbirds, as well as refuse of anthropogenic origin. Aquatic food is represented almost entirely by small prey fish that are rich in energy and nutrients, making them a high-quality food resource for Great Lakes herring gulls (Fox et al., 1990; Ewins et al., 1994; Hebert et al., 2002). Opportunities for gulls to scavenge discards from commercial fisheries in the area are very limited and have decreased from the 1970s to the present; reflecting declines in commercial fishery catch (<http://www.glf.org/great-lakes-databases.php>). Egg fatty acids and stable isotopes provide the means to assess how proportions of aquatic, terrestrial, and anthropogenic sources of food influence important life-history measures in PNP gulls. Given reported declines in abundance of small prey fish (Bunnell et al., 2014; Laurich et al., 2019), I

hypothesize that gulls benefit from relying more on terrestrial foods than aquatic prey. Egg dietary indicators are used to evaluate the use of terrestrial foods in general (assessed using fatty acids and stable nitrogen isotopes) and anthropogenic foods in particular (assessed using stable carbon isotopes) and effects of diet on life-history endpoints. I predict that birds utilizing aquatic food to a greater degree will have elevated levels of stress-associated hormones, will lay smaller eggs, and will spend less time attending their nests.

Methods

Egg samples

In May 2018, one egg was collected from 20 different herring gull nests from an island (Gull Rock; 48.59N, -86.31W) in the northern part of PNP (Figure 2.1).

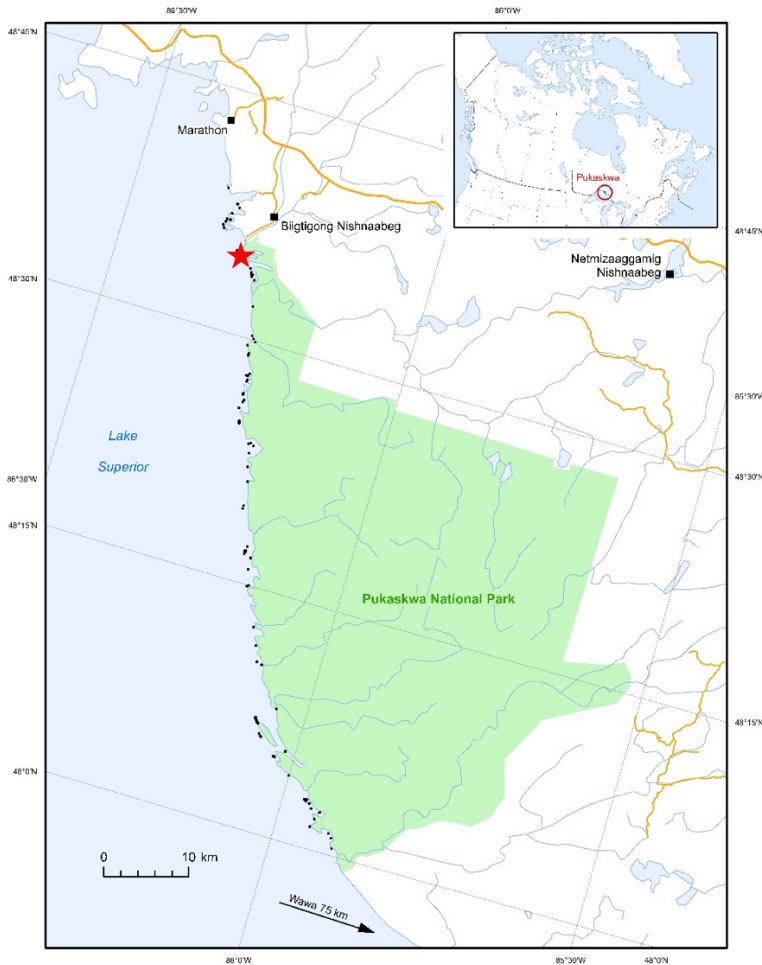


Figure 2.1 Location of Gull Rock study site (indicated by star) in Pukaskwa National Park, Lake Superior, Ontario, Canada. The black dots show herring gull nesting sites within the park.

At the time of collection, clutch sizes among sampled nests differed (1-egg clutches n=5, 2-egg clutches n=10, 3-egg clutches n=5). Clutch size may reflect the resources that the laying female has for egg formation. Alternatively, it may reflect laying date with less experienced, e.g. younger, birds laying later or nests that had been previously predated. Egg maximum length and breadth (mm) were measured in the field using digital calipers and the largest egg was collected from each nest to standardize for potential differences in egg quality through the laying sequence. Last-laid eggs in a 3-egg herring gull clutch are usually smaller than earlier laid eggs (Weseloh et al., 2020). Necessary permits for this work were obtained from Environment and Climate Change Canada (CA 0304 Amend 2) and the Parks Canada Agency (PUK-2018-27697).

Eggs were transported to the National Wildlife Research Centre in Ottawa where they were opened at their equator using a chemically-clean scalpel and egg contents, i.e., albumen and yolk, were homogenized together. Subsamples of these pools were stored frozen before analysis (-40°C for stable isotope analysis, -80°C for fatty acid analysis). Eggshells (with membranes removed) were dried at room temperature.

In addition to herring gulls, egg pools from species known to be habitat specialists were obtained from Environment and Climate Change Canada's National Wildlife Specimen Bank. These eggs were collected at locations across Canada in different years (Table 2.1). The specialists represented eight terrestrial, five marine, and four freshwater species (Table 2.1). Eggs from all species were processed using the same methods as described for herring gulls. Egg pools were created for 16 of the species by combining individual eggs on an equal-weight basis, the number of eggs per pool varied from three to 109 (Table 2.1). These pools were used to determine which fatty acids were most important in differentiating the fatty acid composition of eggs from bird species utilizing terrestrial, freshwater, and marine environments. Double-crested cormorant

(*Nannopterum auritum*) eggs were analyzed individually (n=13) and means were calculated to provide fatty acid data comparable to the pooled samples.

Habitat	Species	Scientific Name	Location	Collection year	Eggs in pool
Terrestrial	American Kestrel	<i>Falco sparverius</i>	St. Thomas, ON	1988	9
Terrestrial	American Robin	<i>Turdus migratorius</i>	Vancouver, BC	1997	9
Terrestrial	Blue Jay	<i>Cyanocitta cristata</i>	Chelsea, QC	2018	5
Terrestrial	Burrowing Owl	<i>Athene cunicularia</i>	Regina, SK	1993	8
Terrestrial	Eastern Bluebird	<i>Sialia salis</i>	Cambridge, ON	1995	7
Terrestrial	European Starling	<i>Sturnus vulgaris</i>	Graves Island Provincial Park, NS	2018	4
Terrestrial	European Starling	<i>Sturnus vulgaris</i>	Niagara Peninsula, ON	1987	109
Terrestrial	Loggerhead Strike	<i>Lanius ludovicianus</i>	Napanee, ON	2012	23
Terrestrial	Prairie Falcon	<i>Falco mexicanus</i>	Nanton, AB	1988	13
Marine	Atlantic Puffin	<i>Fratercula arctica</i>	Gull Island, NL	2000	5
Marine	Northern Fulmar	<i>Fularus glacialis</i>	Prince Leopold Island, NT	2008	5
Marine	Northern Gannet	<i>Morus bassamus</i>	Ile Bonaventure, QC	2009	5
Marine	Rhinoceros Auklet	<i>Cerorhinca monocerata</i>	Cleland Island, BC	2018	3
Marine	Rhinoceros Auklet	<i>Cerorhinca monocerata</i>	Pine Island, BC	1994	3
Marine	Thick-billed Murre	<i>Uria lomvia</i>	Prince Leopold Island, NT	2008	3
Freshwater	Caspian Tern	<i>Hydroprogne caspia</i>	Egg Island, Lake Athabasca, AB	2014	10
Freshwater	Caspian Tern	<i>Hydroprogne caspia</i>	Egg Island, Lake Athabasca, AB	2015	10
Freshwater	Common Tern	<i>Sterna hirundo</i>	Egg Island, Lake Athabasca, AB	2014	10
Freshwater	Common Tern	<i>Sterna hirundo</i>	Egg Island, Lake Athabasca, AB	2015	10
Freshwater	Common Tern	<i>Sterna hirundo</i>	Mamawi Lake, AB	2015	10
Freshwater	Forster's Tern	<i>Sterna forsteri</i>	Gordon Lake, AB	2015	4
Freshwater	Double-crested Cormorant	<i>Nannopterum auritum</i>	Flower Pot Is., Lake Superior, ON	2015	NA

Table 2.1 Egg samples from 17 habitat specialist bird species used for fatty acid analysis.

Eggs were collected from across Canada over a variety of years and were obtained from the National Wildlife Specimen Bank, Ottawa, Ontario.

Dietary markers in eggs

Fatty acid percent composition data for eggs of specialist bird species were used to identify the fatty acids that were most useful in distinguishing eggs of birds utilizing terrestrial, freshwater, and marine foraging habitats. Fatty acid analytical methods are described in Hebert et al. (2020). Fatty acid analysis was comprised of three steps: extraction of lipids using chloroform:methanol (modified from Folch et al., 1957), derivatization of their acyl chains to fatty acid methyl esters (FAMES), and gas chromatography (Agilent 6890N coupled with a flame ionization detector) of

the FAMES. Instrument configuration is described in Hebert et al. (2020). A 37-component FAME standard (Supelco; no. 47885-U) was used for FAME identification. Method blanks, in-house reference materials, and duplicate samples were used for quality control. Results were reported as percent contribution of individual fatty acids to total egg fatty acid concentrations. The ratio of n-3 to n-6 fatty acids was calculated and used as an index of aquatic versus terrestrial food in bird diets (Hebert et al., 2020). Higher n-3/n-6 ratios would be expected in eggs formed using more aquatic food (Hebert et al., 2020). Total omega-3 (n-3) fatty acid values were the sum of eicosapentaenoic acid (20:5n-3, EPA), docosahexaenoic acid (22:6n-3, DHA), α -linolenic acid (18:3n-3), eicosatrienoic acid (20:3n-3), and docosapentaenoic acid (22:5n-3). Linoleic acid (18:2n-6), γ -linolenic acid (18:3n-6), eicosadienoic acid (20:2n-6), dihomo- γ -linolenic acid (20:3n-6), and arachidonic acid (20:4n-6) were summed to estimate total omega-6 fatty acid values.

Intrinsic dietary markers (fatty acids and stable nitrogen and carbon isotopes) in egg contents were used to assess herring gull diets. Fatty acid analytical protocols were identical to those described for the specialist species but in addition to percent composition data, concentration data were also reported as milligrams of fatty acid per gram dry weight tissue. Protocols for stable isotope analyses were identical to those reported by Hebert and Popp (2018). Lipid-extracted egg contents resulting from the fatty acid method were freeze-dried and encapsulated in tin. Stable isotope analysis was completed using an Elementar Isotope Cube elemental analyzer with a DeltaPlus Advantage isotope ratio mass spectrometer (Thermo Scientific) with a ConFlo III. Stable isotope values were reported in delta (δ) notation as parts per thousand difference from a standard (Vienna Pee-Dee belemnite for carbon, atmospheric air for nitrogen). Stable isotope data were

normalized to internal reference materials as described in Hebert and Popp (2018). Quality control was done using sample duplicates and analytical precision was $\pm 0.2\%$.

Physiological, reproductive and behavioural endpoints

Egg corticosterone

Corticosterone from the laying female is present in the yolks of avian eggs (Henriksen et al., 2011). Qasimi et al. (2018) provided the first evidence of detectable amounts of corticosterone in eggshell. Here, corticosterone is measured in homogenized egg contents (yolk and albumen together) and in eggshell using a corticosterone enzyme immunoassay kit (ADI-900-097, Enzo Biochem Inc., Farmingdale, NY, USA). Extraction recoveries for pooled chicken egg homogenates spiked with 10 ng/ml and 1 ng/ml of corticosterone were 68% and 84%, respectively. Pools of chicken eggshell spiked with 1 ng/ml and 0.1 ng/ml of corticosterone showed recoveries of 76% and 87%, respectively. Quality control for corticosterone measurements in egg contents and eggshell involved the use of an Alpco rat control set, level #1, cat# 55-DEV99RC (Salem, NH, USA). Intra-assay variability was 9.5%; inter-assay variability 12.0%.

Egg contents processing and analysis

Prior to opening, the exterior of the eggs was cleaned with deionized water and dried. Eggs were opened at the equator using a scalpel and egg contents, yolk and albumen, were homogenized together (Polytron PT 2500 E, Kinematica, VWR 97057-700). 150 μ l of egg homogenate was placed in a 2.0 ml microcentrifuge tube; homogenized with 150 μ l of assay buffer for 10 seconds and left to equilibrate for 30 min. One ml of hexane/diethyl ether (50:50) was added; vortexed for

30 sec and then centrifuged for 5 minutes at 13K rpm (Eppendorf microcentrifuge model# 5417R, Eppendorf, Hamburg, Germany). The supernatant was transferred to a new microcentrifuge tube (without disturbing the pellet). The pellet was re-extracted with 1 ml 50:50 hexane/diethyl ether, vortexed for 30 seconds and centrifuged for 5 minutes at 13K rpm. The supernatant was transferred into the microcentrifuge tube containing the initial supernatant and evaporated on a concentrator (Eppendorf Vacufuge 5301, Eppendorf, Hamburg, Germany). Dried samples were reconstituted with assay buffer; vortexed well; sonicated for 15 min at 30°C and then filtered with a 0.45 um PTFE 13 mm filter and analyzed as per the kit instructions using a model DTX-880 multimode detector (Beckman-Coulter, Brea, CA, USA).

Eggshell processing and analysis

A 1.5 g eggshell sample was pulverised using a mortar/pestle such that remaining eggshell pieces fit into 4 x 1.8 ml flat-bottomed microcentrifuge tubes. A 7 mm stainless steel ball was added to each tube and the samples were further pulverized in a mixer mill (Retsch model# MM 301, Verder Scientific, Regus, PA, USA) for 4 min. at 20 cycles/sec. Resulting eggshell powder in the 4 tubes was combined and mixed to produce one homogeneous sample. One gram of eggshell (weighed to the nearest 0.01 g.) was placed in a 10 ml plastic centrifuge tube (with cap); 5 ml of methanol was added; vortexed briefly; sonicated (VWR Ultrasonic cleaner, cat# 97043-932, VWR, Radnor, PA, USA) for 30 min and shaken overnight (Fisher Temp Master Vortemp 56, Fisher Scientific, Portsmouth, NH, USA) at 50°C and 90 rpm. The centrifuge tube was then placed on another shaker (VWR W-150 Waver, VWR Scientific, Radnor, PA, USA) where it was laid flat and shaken at maximum pitch at speed 10 for 3 hr to ensure sample was well extracted. The tube was then centrifuged (Beckman model# J2-21ME, Beckman-Coulter, Brea, CA, USA)

at 5000 rpm for 10 min; the methanol fraction was removed to a glass culture tube (without disturbing the pellet). An additional 1 ml methanol was added to the original pellet; vortexed, centrifuged at 5000 rpm for 5 min; then the methanol fraction was removed and added to the first aliquot (without disturbing the pellet). The final methanol fraction was dried on a concentrator (Eppendorf Vacufuge model #5301, Hamburg, Germany) at 30°C. The dried sample was reconstituted in assay buffer; vortexed well; sonicated for 30 min.; vortexed again and left to sit overnight at room temperature, covered in Parafilm. The sample was filtered with a 0.45 um PTFE 13 mm filter and analyzed as per the kit instructions using a model DTX-880 multimode detector (Beckman-Coulter, Brea, CA, USA).

Quality control for corticosterone measurements in egg contents and eggshell involved the use of an Alpco rat control set, level #1, cat# 55-DEV99RC (Salem, NH, USA). Intra-assay variability was 9.5%; inter-assay variability 12.0%. The corticosterone enzyme immunoassay kit used to measure corticosterone in eggs was not specifically validated for herring gull egg corticosterone.

Corticosterone concentrations are reported as ng/g dry weight for eggshell and ng/g wet weight for egg contents. Measuring corticosterone in eggshell as well as in egg contents is advantageous when attempting to assess maternal stress. If eggs are at later stages of development, embryos will begin to generate corticosterone in response to stressful conditions, e.g., high temperature, so the corticosterone in egg contents may not reflect stress experienced by the laying female. Eggshell corticosterone, on the other hand, should not be influenced by stage of development as it is likely bound in the shell matrix. Here, I assess the relationship between corticosterone in these two matrices using freshly laid eggs.

Egg size

Length and breadth measurements (mm) taken prior to the opening of eggs (Figure 2.2) were used to calculate egg volume according to Ryder et al. (1975):

$$\text{Egg volume (cm}^3\text{)} = 0.489 \times (\text{length} \times \text{breadth}^2) / 1000$$



Figure 2.2 Measuring herring gull length and breadth on Gull Rock, Pukaskwa National Park, May 2022.

Incubation attentiveness

In 2018, nine of the 20 PNP nests from which eggs were sampled were monitored remotely using camera traps (Reconyx PC900 professional) (Figure 2.3). Clutch sizes differed among monitored nests: at the time of sampling three nests contained one egg, three nests two eggs, and three nests contained three eggs. The remote infrared cameras (no flash required) took one picture

per minute, 24 hours/day, throughout incubation (maximum ~ 1 month). Images were used to document gull behaviour and quantify nest attentiveness during the day (time = 0545 – 2144) and night (time = 2145 – 0544). The period of incubation varied among nests. When possible, nest attentiveness was assessed up until first hatch. The attentiveness of individual nesting pairs was assessed by calculating the percentage of time an adult bird was observed sitting on or was adjacent to, their nest. Gull presence/absence was determined for ~315,000 images in total over the nine nests. Intra- and interspecific predation of eggs and young (see Chapter 3), as well as scavenging of an adult carcass (see Lockhart et al., 2020), were also documented.

Male and female herring gulls share incubation duties with females spending somewhat more time on their nests (Weseloh et al., 2020). Seventy-six to 81% of herring gull pairs exhibit specialized feeding behaviours with mates foraging on similar foods (Pierotti and Annett, 1991). Evaluation of gull diet using eggs is expected to best reflect female feeding habits but because feeding behaviour between mates is usually similar, egg dietary markers are also expected to commonly reflect the diets of males. Hence, useful information should be obtained regarding relationships between diet and nest attentiveness using combined behavioural data from paired females and males.



Figure 2.3 Examples of remotely-obtained imagery for nesting herring gulls during the day and night on Gull Rock in Pukaskwa National Park, 2018.

Statistical analysis

Principal components analysis (PCA) using correlation matrices was conducted on the egg fatty acid percent composition data from specialist species. PCA was used to investigate the degree to which eggs from different specialist species (terrestrial, freshwater, marine) could be distinguished based on their fatty acid profiles. Fifteen fatty acids, present at $\geq 0.5\%$ of the total fatty acid content, were included in the PCA. Although PCA does not require data to be normally distributed, PCA results may be more reliable when that is the case. Therefore, when specific fatty acids did not meet normality assumptions they were \log_{10} -transformed before PCA (Table 2.2). PCA identified the fatty acids that were most useful in differentiating the fatty acid composition of eggs from the three habitats. Analysis of variance followed by Tukey's HSD test for unequal sample sizes assessed differences in principal component scores among eggs from the three habitat specialist groups. Residuals were used to check assumptions underlying the use of parametric statistics. Normality was assessed using P-P plots and Shapiro-Wilk tests; homogeneity of variance assumption was tested using Levene's test.

Analysis of variance was used to test for differences in dietary indicators ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, EPA concentration, %EPA, DHA concentration, %DHA) in PNP herring gull eggs collected from different sized clutches (1, 2, or 3-eggs).

Egg $\delta^{13}\text{C}$ values were used in an isotopic mixing model (Phillips and Gregg 2001) to estimate proportions of prey fish and anthropogenic foods in the diet of laying female gulls. The $\delta^{13}\text{C}$ end-member value for prey fish ($-26.20 \pm 0.70\text{‰}$) was based upon literature values (Harvey and Kitchell, 2000; Hebert et al., 1999b; Keough et al., 1996; Krüger et al., 2016) for Lake Superior rainbow smelt (*Osmerus mordax*) and lake cisco (*Coregonus artedii*), both important prey fish in that lake (Gorman, 2012). The $\delta^{13}\text{C}$ end-member value ($-18.99 \pm 2.40\text{‰}$) for anthropogenic food

was based upon the analysis of meat (pork, chicken, and beef) from commercial sources (Hebert et al., 1999b). Human refuse used by herring gulls was mostly composed of these three types of protein (Pierotti and Annett, 1991). End-member values were adjusted (+0.4‰) for possible fractionation of carbon isotopes during trophic transfer (Post, 2002).

PCA was used to summarize the herring gull dietary endpoints measured in each egg sample. Untransformed variables included in the PCA were: egg $\delta^{15}\text{N}$ values, estimates of anthropogenic food in the gull diet (from the $\delta^{13}\text{C}$ -based mixing model results), and the fatty acid endpoints that were most useful (i.e. %EPA, n-3/n-6, %DHA, %linoleic acid) in distinguishing fatty acid profiles among the specialist species.

Correlation analysis was used to examine the relationship between corticosterone concentrations in egg contents and eggshell. Linear regression analysis was used to examine relationships between PCA-derived diet indicators, i.e., principal component sample scores, and physiological (corticosterone), reproductive (egg volume), and behavioural (day and night nest attentiveness) endpoints. Again, residuals were used to check assumptions underlying the use of parametric statistics. All statistical tests were performed using Statistica 13.5 (StatSoft, 2018) with $\alpha = 0.05$. Alpha was not adjusted for multiple comparisons as this study was exploratory in nature with a primary goal of highlighting possible relationships for further study. Hence, the onus here is on the avoidance of committing Type II errors (Althouse, 2016; Feise, 2002; Perneger, 1998; Rothamn, 1990).

Results

Fatty acid profiles in specialist habitat bird species

Principal component 1 (PC1) accounted for 33.9% of the variability in the specialist bird species fatty acid data. Variable loadings are shown in Table 2.2. Fatty acids with the most negative loadings were the n-3 fatty acids: EPA (C20:5n-3) and DHA (C22:6n-3), along with the ratio of n-3/n-6 fatty acids. Linoleic acid (C18:2n-6) showed the highest positive loading on PC1. Mean PC1 scores of eggs from the three habitat specialist groups differed significantly (ANOVA $F_{2,19} = 468.2, p < .0001$, followed by Tukey's HSD test for unequal sample sizes) (Figure 2.4). Terrestrial bird species had the highest levels of linoleic acid while marine species had the highest levels of the n-3 fatty acids and the highest n-3/n-6 ratios. Freshwater species were intermediate.

Fatty Acid	Variable Loadings on PC1
C14:0	-0.29
C16:0	0.67
C16:1n7	0.16
C17:0	0.19
C18:0	-0.74
C18:1n9	-0.71
Log C18:2n6	0.94
Log C20:1n9	-0.57
Log C18:3n3	0.20
Log C20:2n6	0.27
Log C20:4n6	0.17
Log C20:5n3	-0.87
Log C22:5n3	0.10
C22:6n3	-0.79
Log n-3/n-6	-0.84

Table 2.2 Variable loadings on principal component 1 from the principal components analysis of percent fatty acid composition data in eggs of habitat specialist species. The most influential fatty acid endpoints are shown in bold

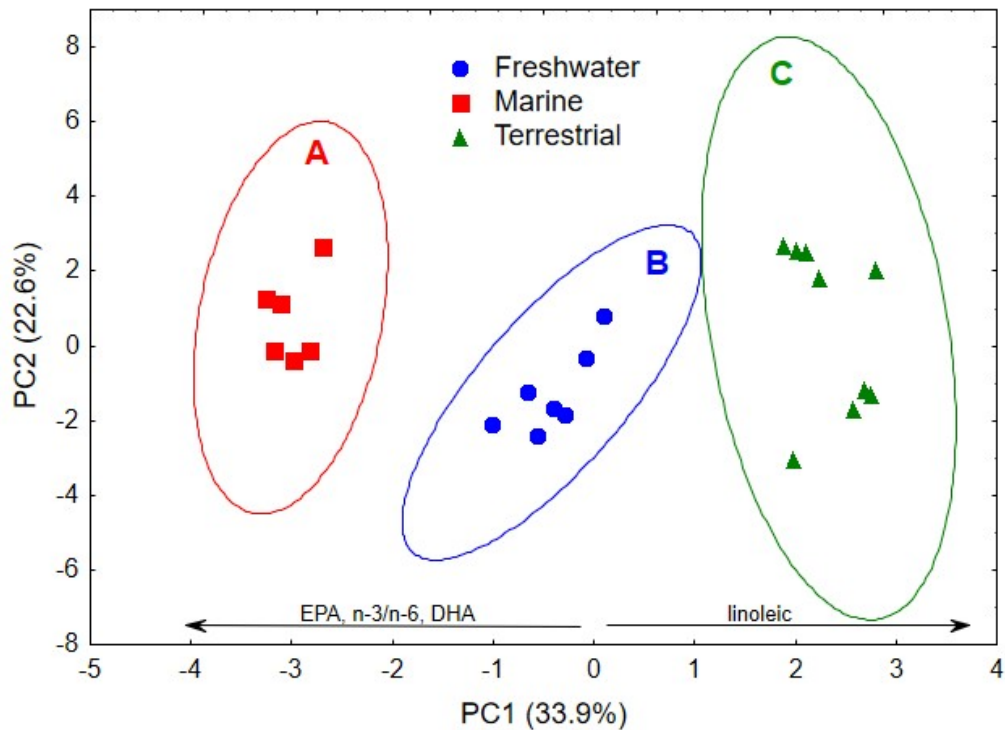


Figure 2.4 Principal component sample scores resulting from the principal components analysis of percent composition fatty acid data in eggs of bird species associated with specialized habitats (freshwater, marine, terrestrial). 95% confidence ellipses are shown for each habitat group, letters inside the ellipses indicate statistically significant differences among mean PC1 scores (ANOVA followed by Tukey’s HSD test for unequal sample sizes). Eggs with more negative PC1 scores had higher proportions of n-3 fatty acids (EPA, n-3/n-6, DHA) while eggs with more positive scores contained more n-6 fatty acids (linoleic acid).

PNP herring gull egg analyses

Fatty acid analysis of herring gull eggs focused on fatty acid endpoints that were most useful in differentiating the habitat specialist species. Stable isotope and fatty acid dietary markers did not differ in eggs collected from different sized clutches ($\delta^{13}\text{C}$ ANOVA $F_{2,17} = 3.31, p=.06$; $\delta^{15}\text{N}$ Welch's ANOVA $F_{2,5.7} = 0.33, p=.73$; EPA concentration ANOVA $F_{2,17} = 0.35, p=.71$; %EPA ANOVA $F_{2,17} = 0.51, p=.61$; DHA concentration ANOVA $F_{2,17} = 1.47, p=.26$; %DHA ANOVA $F_{2,17} = 2.97, p=.08$; linoleic acid concentration ANOVA $F_{2,17} = 1.58, p=.24$; %linoleic acid ANOVA $F_{2,17} = 0.92, p=.42$). In subsequent analyses, data from eggs collected from different sized clutches were combined. Dietary endpoints measured in this study (Table 2.3) exhibited considerable variability suggesting dietary differences among individual PNP herring gulls. Individual differences were also observed in the physiological, reproductive and behavioural endpoints measured (Table 2.3).

Measurement	Sample Size	Mean	Minimum	Maximum	Standard Deviation
$\delta^{13}\text{C}$ (‰)	20	-22.85	-23.82	-21.25	0.65
$\delta^{15}\text{N}$ (‰)	20	9.22	8.51	10.17	0.37
EPA (C20:5n-3) (mg/g)	20	0.42	0.15	0.78	0.18
DHA (C22:6n-3) (mg/g)	20	3.60	2.74	4.29	0.39
Linoleic Acid (C18:2n-6) (mg/g)	20	17.47	12.73	22.97	2.49
EPA (C20:5n-3) (%)	20	1.35	0.48	2.82	0.66
DHA (C22:6n-3) (%)	20	11.42	8.52	13.80	1.51
Linoleic Acid (C18:2n-6) (%)	20	5.53	3.58	6.94	0.82
n-3/n-6	20	0.46	0.32	0.59	0.08
Egg Content Corticosterone (ng/g)	20	2.08	0.75	3.84	0.77
Eggshell Corticosterone (ng/g)	20	0.36	0.13	0.58	0.13
Egg Volume (cm ³)	20	88.13	75.20	102.40	6.42
Day % Nest Attentiveness	9	95.32	80.80	99.70	7.16
Night % Nest Attentiveness	9	49.31	14.80	71.40	17.30

Table 2.3 Descriptive statistics for PNP herring gull (*Larus argentatus*) diet indicators

measured in eggs and physiological, reproductive, and behavioral endpoints.

Principal components 1 (PC1, 51.9%) and 2 (PC2, 19.9%) accounted for most of the variability in the diet indicator data. Egg n-3/n-6 ratios, % n-3 fatty acids and $\delta^{15}\text{N}$ were most important in contributing to variable loadings on PC1. These results indicated that PC1 was essentially a measure of the amount of aquatic versus terrestrial food in the gull diet. More positive PC1 scores were indicative of more aquatic food in the gull diet while more negative PC1 scores highlighted the use of terrestrial food. The percentage of anthropogenic food in the gull diet (as inferred from the isotopic mixing model using $\delta^{13}\text{C}$) had the highest variable loading on PC2 (Table 2.4).

Dietary Indicator	PC1 (51.9%)	PC2 (19.9%)
Egg $\delta^{15}\text{N}$	0.72	-0.48
%linoleic acid	-0.54	-0.42
%EPA	0.82	0.36
%DHA	0.80	-0.19
n-3/n-6	0.95	0.20
%anthropogenic	-0.28	0.77

Table 2.4 Variable loadings on principal components 1 and 2 from the principal components analysis of stable isotope and fatty acid composition data in eggs of PNP herring gulls. The most influential variables are shown in bold.

Corticosterone concentrations were correlated in egg contents and eggshell (Pearson $r = 0.69$ $p = .001$) (Figure 2.5). However, corticosterone concentrations were greater in egg contents versus shell (Table 2.3).

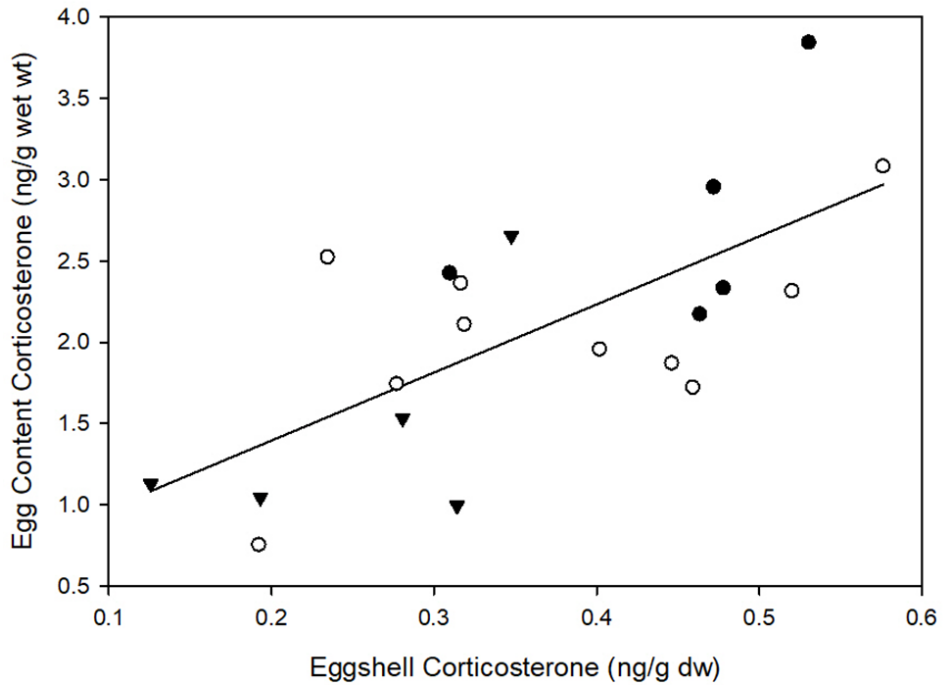


Figure 2.5 Positive relationship between eggshell corticosterone (ng/g dry wt) and egg content corticosterone (ng/g wet wt) in herring gull eggs from Gull Rock, Pukaskwa National Park, 2018. Clutch sizes at the time of egg collection are shown (one egg clutch = •, two egg clutch = ○, three egg clutch = ▼).

Results of the linear regression analyses revealed significant relationships between PCA-derived dietary indices and reproductive, physiological, and behavioural endpoints (Table 2.5). Pearson correlation coefficients are shown to indicate the direction (positive or negative) of the relationships. Percentage of time spent incubating during the day decreased with PC1 sample scores (Figure 2.6). Increased proportions of n-3 fatty acids and higher $\delta^{15}\text{N}$ values were measured in eggs from nests where adults were less attentive during daytime (Figure 2.6). PC1 scores were not related to other life-history endpoints (Table 2.5).

Variable	Life History Measure				
	Egg Volume	Egg Contents Cort	Eggshell Cort	%Day Attentive	%Night Attentive
N	20	20	20	9	9
PC1DietIndex	$r=-.24$ $p=.30$	$r=.04$ $p=.88$	$r=.29$ $p=.22$	$r=-.70$ $p=.035$	$r=-.33$ $p=.39$
PC2DietIndex	$r=.49$ $p=.027$	$r=-.63$ $p=.003$	$r=-.50$ $p=.025$	$r=.77$ $p=.015$	$r=.32$ $p=.40$

Table 2.5 Pearson correlation coefficients (r) and statistical significance of relationships between PCA-derived dietary endpoints in herring gulls and their life-history traits. Significant correlations are highlighted in bold. Cort is corticosterone measured in eggs, %Day Attentive and %Night Attentive refer to the percentage of time adult herring gulls attended their nests during the day and night.

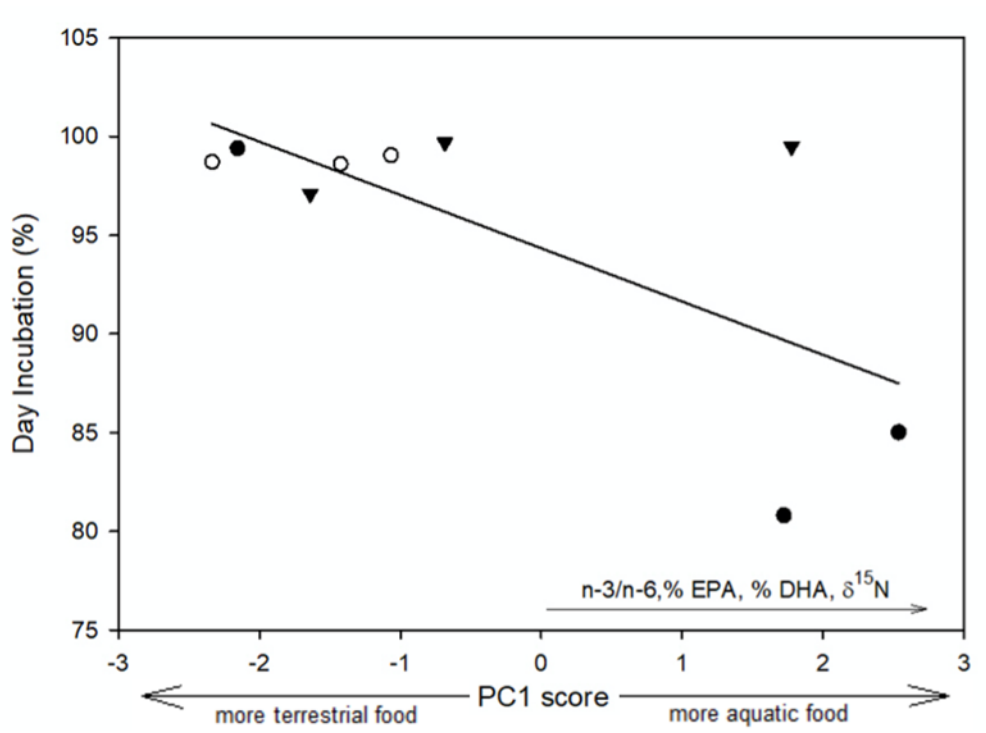


Figure 2.6 Negative relationship between egg PC1 score (increasing n-3 fatty acid content and egg $\delta^{15}\text{N}$ values) and percentage of time adult herring gulls attended their nests during daytime at Gull Rock, Pukaskwa National Park, 2018. Clutch sizes at the time of egg collection are shown (one egg clutch = ●, two egg clutch = ○, three egg clutch = ▼).

PC2 scores were primarily related to estimates of anthropogenic food in the gull diet (Table 2.4). For this reason and for ease of interpretation, we focus here on assessing relationships between estimates of anthropogenic food in the gull diet and life-history endpoints. Estimates of anthropogenic food in the gull diet were significantly correlated with corticosterone concentrations in eggshell ($r = -.60, p = .005$) (Figure 2.7A) and egg contents ($r = -.57, p = .009$) (Figure 2.7B). Corticosterone concentrations decreased as the percentage of anthropogenic food in the gull diet increased. The proportion of anthropogenic food in the gull diet was significantly correlated with

egg volume ($r = .47, p = .036$) (Figure 2.7C). As the amount of anthropogenic food increased, egg volume increased. The percentage of anthropogenic food in the gull diet was also significantly correlated with adult nest attentiveness. Adults associated with nests containing eggs with a more pronounced anthropogenic food signature spent a greater percentage of time attending their nests during the day ($r = .78, p = .01$) (Figure 2.7D) but not at night ($r = .30, p = .44$). Of the nine nests monitored with camera traps, three suffered chick loss that occurred exclusively during the night due to predation by great horned owls (*Bubo virginianus*) (see Chapter 3). Chicks were successfully reared from only three nests (nests #1, 5, 8), each producing one chick from three-egg clutches.

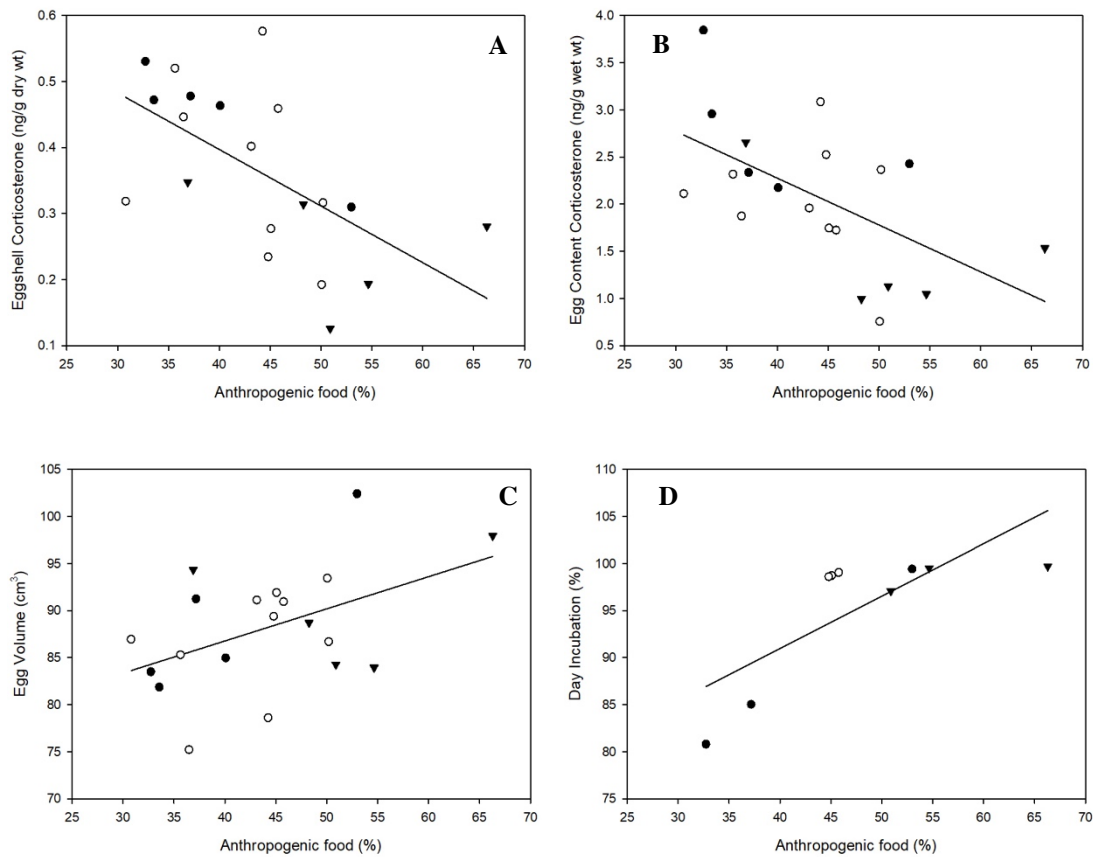


Figure 2.7 Relationships between estimates of the proportion of anthropogenic food in the diet of Gull Rock herring gulls and life-history endpoints. Negative relationship between estimates of the % of anthropogenic food in the gull diet and corticosterone concentrations (ng/g) in eggshell (panel A; $r = -0.60$, $p = 0.005$) and egg contents (panel B; $r = -0.57$, $p = 0.009$). Positive relationship between % anthropogenic food and egg volume (cm^3) (panel C; $r = 0.47$, $p = 0.036$). Positive relationship between % anthropogenic food and percentage of time adult herring gulls spent attending their nests during daytime (panel D; $r = 0.78$, $p = 0.01$). Clutch sizes at the time of egg collection are shown (one egg clutch = •, two egg clutch = ○, three egg clutch = ▼).

Discussion

Dietary markers measured in eggs were useful in evaluating the influence of diet on life-history endpoints in PNP herring gulls. Detrimental effects of feeding on natural aquatic prey were evident. Birds feeding on terrestrial foods benefited but consumption of anthropogenic food resources (as inferred from stable carbon isotope values in eggs) was the critical factor regulating the positive effects of consuming more terrestrial food. Increasing proportions of anthropogenic food in the gull diet had positive effects on important life-history attributes related to gull physiology (stress-associated hormone corticosterone), resources available for reproduction (egg size), and behaviour (incubation attentiveness during the day). In birds, corticosterone is commonly measured in blood and/or feathers (Royo et al., 2008). Lendvai et al.'s (2013) compilation of baseline and peak corticosterone concentrations in 119 avian species demonstrated great variability in concentrations. For example, baseline corticosterone concentrations ranged from 2.01 ng/ml to 29.55 ng/ml and peak corticosterone concentrations ranged from 12.30 ng/ml to 156.28 ng/ml (Lendvai et al., 2013). Literature values for corticosterone in eggs are lacking. Furthermore, no information is available regarding what constitutes normal levels of corticosterone in wild herring gulls. Hence, I cannot be certain that the higher corticosterone levels reported here had detrimental effects on adults or their progeny. Although previous studies have linked elevated corticosterone to negative effects in birds (see below), further research is required to understand the biological significance of elevated corticosterone concentrations in PNP herring gulls. However, the lower egg volumes reported here are consistent with those ($\sim <82 \text{ cm}^3$) associated with lower chick production in earlier studies on Lake Superior (Meathrel et al., 1987; Hebert, 1999). Hence, it is likely that the differences in egg size observed here were biologically significant in terms of possible effects on chick production. Given the high potential for diurnal

conspecific and interspecific predation of herring gull eggs and chicks (see Chapter 3), the absence of adult gulls from their nests during breeding would likely reduce reproductive success. Taken together, these results suggest that anthropogenic food subsidies are important for northern PNP gull populations. The utility of carbon isotopes reflected their greater specificity for discriminating between diets based upon natural aquatic versus anthropogenic foods. Because of the pervasive influence of corn in human foods, $\delta^{13}\text{C}$ values in those foods are very different from the natural foods of Great Lakes herring gulls. Hence, $\delta^{13}\text{C}$ values are especially useful in identifying the incorporation of anthropogenic foods into wildlife diets.

Fatty acid patterns in eggs of specialist species utilizing freshwater versus terrestrial habitats were very different. Eggs of freshwater species exhibited much higher proportions of the n-3 fatty acids, EPA and DHA, while the terrestrial specialists showed higher proportions of the n-6 fatty acid, linoleic acid. However, fatty acid measures were of limited utility in examining the impact of diet on gull life-history measures. PCA PC1 scores were largely driven by fatty acid measures but those scores showed only one significant correlation with a life-history measure, i.e., greater reliance on aquatic foods had a negative effect on daytime nest attentiveness. Unlike egg $\delta^{13}\text{C}$ values, fatty acid measures were not useful in identifying linkages between diet and gull physiology or reproductive success. This likely reflected the greater specificity of $\delta^{13}\text{C}$ to identify use of anthropogenic sources of food by gulls rather than just distinguishing between their use of aquatic versus terrestrial foods. Regardless of their relative utility, these two independent groups of dietary tracers, i.e. fatty acids and stable isotopes, provided consistent evidence that there were negative consequences for PNP birds feeding on natural, aquatic sources of food.

PNP herring gulls feeding to a greater extent on anthropogenic foods had lower levels of corticosterone in their eggs. This suggests that these birds may have profited from readily-available

anthropogenic foods, allowing for reductions in adult foraging effort. Food availability and food quality influence stress levels in individual breeding birds (Benowitz-Fredericks et al., 2008; Doody et al., 2008; Satterthwaite et al. 2012; Wingfield and Kitaysky, 2002). The reduced corticosterone levels in herring gull eggs observed here could have beneficial impacts on reproduction. Chick survival can be negatively affected by high maternal stress (Saino et al., 2005). Hayward & Wingfield (2004) found that higher plasma corticosterone in Japanese quail (*Coturnix coturnix japonica*) females negatively affected the growth rates of their offspring and caused higher activity in the hypothalamo-adrenal axis in offspring reaching adulthood. Similarly, barn swallow (*Hirundo rustica*) females with higher corticosterone levels produced eggs exhibiting lower hatchability as well as smaller chicks with slower plumage development (Saino et al., 2005). Rubolini et al. (2005) found that eggs of yellow-legged gulls (*Larus michahellis*) with higher levels of corticosterone took significantly longer to hatch, gave rise to chicks with reduced vocalizations for parental care, and exhibited reduced immune response. Hence, elevated egg corticosterone concentrations could contribute to declines in PNP herring gull populations through reductions in recruitment of young. A significant finding of this study was the positive correlation between corticosterone concentrations in egg contents and eggshell. Eggshell may be a useful, non-invasive, alternative matrix to assess levels of stress-associated hormones in birds. Assessing the utility of eggshell for corticosterone analysis is important because egg contents are not always available. From a conservation perspective, measuring corticosterone in eggshell is advantageous because it does not require collection of the whole egg thereby eliminating issues associated with destructive sampling. Furthermore, eggshells often remain in the nest after the breeding season ends providing opportunities for sample collection.

Food availability and quality prior to egg-laying may also alter reproductive success through impacts on egg size (Bolton et al., 1992) as well as other endpoints not examined here, e.g., chick growth, fledgling success (Kilpi & Öst, 1998; Spaans et al., 1987). Steigerwald et al. (2015) found that yellow-legged gulls utilizing anthropogenic food waste had increased body condition, egg volume, and clutch size compared to individuals that did not feed on refuse. Chicks hatching from larger eggs exhibit increased hatching success, stronger immune systems, faster growth rates, and higher rates of survival compared to chicks hatching from smaller eggs (Krist, 2011; Martin, 1987).

Adult attentiveness during incubation and chick-rearing is an important factor regulating reproductive success. Adults are faced with the trade-off of spending time on their nests incubating and guarding eggs versus time off the nest required for self-maintenance (Amininasab et al., 2016). In this study, the percentage of daylight hours herring gull attended their nests increased with terrestrial/anthropogenic food consumption. Gulls relying on terrestrial/anthropogenic food may have spent less time foraging allowing them to spend more time on their nests thereby deterring would-be predators and increasing nest success. Contrary to the high level of nest attentiveness displayed by gulls during the day, nighttime incubation attentiveness was much lower and was not related to diet indices. Given that gulls are primarily diurnal foragers, nighttime absences were not likely related to feeding activities. Instead, they were likely due to the presence of nocturnal predators (great horned owl) that posed a risk to both nest contents and incubating adults (see Chapter 3).

Fish may be the preferred food of herring gulls (Hebert et al., 2002) but the nutritional benefits associated with consuming them may be outweighed by the energetic cost of their capture in environments where fish are scarce (Hebert et al., 2008). Previous studies have shown that

declines in lake productivity and decreases in prey fish abundance have occurred across many of the Great Lakes (Bunnell et al., 2014; Hebert et al., 2008) including Lake Superior near PNP (Laurich et al., 2019). Low availability of aquatic prey in the PNP environment may be making a fish-based diet untenable for locally-breeding herring gulls. Instead, gulls may be relying more on landfills (see Figure 2.8) as a reliable source of frequently replenished, abundant food that reduces intraspecific competition (Oro et al., 2013). Results from this study indicated that there were positive effects in gulls utilizing anthropogenic foods, such birds had reductions in levels of stress-associated hormones, increases in egg size, and increases in daytime nest attentiveness. Over the past 40 years, the herring gull population in the north of PNP declined to a lesser extent (54% reduction in nest numbers) compared to the southern PNP population (78% reduction) (Laurich et al., 2019). Anthropogenic food subsidies are available exclusively in the north and may be buffering the effects of dietary stress; however, it is important to note that both populations have decreased through time.



Figure 2.8 Herring gulls foraging at the Marathon, Ontario landfill (48.75N, -86.32W) approximately 19 km due north of Gull Rock study site, May 24, 2022.

Although anthropogenic foods appear beneficial, birds feeding on such foods may experience detrimental effects through increased exposure to chemical contaminants (Gauthier et al., 2019; Tanaka et al., 2013), although this is not always the case (see Hebert et al., 2022). Use of anthropogenic foods may decrease availability of essential nutrients such as n-3 fatty acids (Hixson et al., 2015) while increasing exposure to pathogens (Collins and Kennedy, 1992; Hatch, 1996; Matejczyk et al., 2011). During my research, one adult herring gull died while incubating (see Lockhart et al., 2020). Although the cause of death could not be determined, symptoms exhibited by this bird were consistent with a disease etiology. Exposure to hazardous materials such as plastics (Plaza and Lambertucci, 2017) may also result from consumption of anthropogenic foods. Laurich et al. (2019) reported that 70% of herring gull pellets from the northern PNP herring gull population contained garbage. Ingestion of such material can be detrimental by obstructing gastrointestinal tracts, causing toxicity and/or increasing exposure to pathogens (Plaza and Lambertucci, 2017). Hatching and fledging success rates have been reported to be lower in some populations of herring gulls using landfills (Belant et al., 1998).

Herring gulls are generalist feeders that utilize a wide variety of other food sources when high-quality foods, such as fish, are not available (Hebert et al., 2002; 2020). Flexibility in feeding habits is advantageous for this species in its changing environment. However, many other Great Lakes bird species, e.g., Caspian tern, common tern, double-crested cormorant, are more specialized and rely solely on aquatic food resources. Tracking populations of these species will provide additional information regarding changes in Great Lakes ecosystems. However, if aquatic food availability declines precipitously, these species will abandon traditional nesting areas precluding monitoring activities. For this reason, continued monitoring of generalist species such as the herring gull is important.

Freshwater ecosystems are particularly vulnerable to change due to the wide variety of factors affecting them (Dudgeon et al., 2006; Reid et al., 2019). Over the last five decades the Laurentian Great Lakes have undergone major ecological changes (Bunnell et al., 2014). Declines in freshwater biodiversity have been underestimated (Dudgeon, 2010) due to assessments of global biodiversity loss focussing on terrestrial and marine ecosystems (Rockström et al., 2009). Pukaskwa National Park is one of six Canadian national parks situated on the Laurentian Great Lakes. Parks Canada's mandate highlights a commitment to conserving and maintaining or restoring the ecological integrity of Canada's national parks (Parks Canada Agency, 2013). Ongoing collection and analysis of ecological indicator data are essential for protected area management and such data need to be interpreted in a whole-system context that includes consideration of the state of the environment beyond park boundaries. Understanding the factors contributing to trends in colonial waterbird populations is important not only for the conservation of that group but is critical for understanding the factors influencing the ecological integrity of Pukaskwa National Park and, more broadly, the Lake Superior ecosystem. Species used as indicators of ecosystem state, such as herring gulls, respond to local-scale processes, e.g., availability of anthropogenic food sources, as well as larger-scale processes, e.g., lake-wide declines in aquatic food. They are archetypal examples of the "canary in a coalmine" indicator but in an ecosystem context. Changes in their diets and in variables associated with their physiology, reproduction, and behaviour point to very significant changes occurring in the ecosystems they inhabit. Integrated research across the Great Lakes is required to understand the extent of change and its implications for the sustainability of wildlife populations and other biota.

Chapter Three

Remote cameras reveal the importance of avian predation on Lake Superior herring gulls (*Larus argentatus*)

Introduction

Advances in camera technology have played an important role in ecological and behavioural studies by providing insights into events that would not otherwise be observable by humans. Accordingly, such technology has seen increasing use in wildlife studies to understand animal behaviour through the collection of data that would be difficult or impractical to collect due to constraints on logistics, funding, and time (Cox et al., 2012). Automatic photography units known as camera traps generate both still photographs and video. They can be programmed to capture images at regular intervals or through the activation of sensors that detect movement and/or body heat when an animal passes through the camera's field-of-view (O'Brien and Kinnaird, 2008). Camera trap technology has improved over the years, with smaller cameras capturing better resolution images. Increases in battery power, decreased power consumption, and improved storage capacity for images have greatly improved the operating life of camera traps in the field (O'Brien and Kinnaird, 2008). Because camera traps are inconspicuous and continually monitor their surroundings, they are very useful in capturing both daily behaviour and rare events that researchers would not otherwise be able to observe (O'Brien and Kinnaird, 2008). For example, camera traps can provide a better understanding of behaviour related to parental care and attentiveness (Grundel, 1987; Cartar and Montgomerie, 1987), nestling success (McRae et al., 1993; Nathan et al, 2001) and nest predation (Thompson et al., 1999; Pietz and Granfors, 2000). Additionally, camera traps can detect the behaviour of elusive nocturnal species that have previously evaded observation due to human vision limitations. Camera traps have been widely used in mammalian ecological and behavioural studies (O'Brien and Kinnaird, 2008) but they are also very useful for studying avian nesting ecology (Cox et al., 2012). For example, remotely obtained images have supplied researchers with new information regarding the role of predators

in determining nest success of a variety of species (Bolton et al., 2007). Considering that nest predation is one of the main causes of unsuccessful nesting (Ricklefs, 1969), identifying predators and studying their behaviour are essential components when attempting to understand factors contributing to declines in avian populations.

Since 1974, herring gulls (*Larus argentatus*) have been used in Environment and Climate Change Canada's Great Lakes Herring Gull Monitoring Program (Hebert et al., 1999). Waterbirds, such as herring gulls, are excellent bioindicators as they are sensitive to changes occurring in their environment, responding rapidly and conspicuously to changes in their habitat (Furness & Camphuysen, 1997; Hebert et al., 2008; Paterson et al., 2014; Rahman and Ismail, 2018). Over the last 50 years, the Laurentian Great Lakes have exhibited significant ecological changes (Johannsson et al., 2000; Madenjian et al., 2002; Mills et al., 2003; Dobiesz et al., 2005; Gorman, 2007; Bunnell et al., 2014; Paterson et al., 2014; Dai et al., 2019). These changes have affected herring gulls breeding on the Great Lakes (Hebert et al. 2008) and temporal declines in gull populations, particularly on the upper Great Lakes, highlight the utility of this species as an indicator of broad-scale changes occurring throughout the ecosystem. Considering this, herring gull population size was adopted by the Parks Canada Agency (PCA) as an indicator of ecological integrity for Pukaskwa National Park (PNP) located on Lake Superior (Drake et al., 2017). PNP's breeding herring gull population has decreased by 70% over the last 40 years. One factor contributing to this decline is a reduction in availability of aquatic food (Laurich et al., 2019) causing gulls to rely more on anthropogenic food sources (see Chapter 2). Declines in food quality and/or food quantity can result in herring gulls spending a greater amount of time focused on foraging and less time spent attending their nests (Chapter 2). Increased adult nest attentiveness leads to a shorter period until eggs hatch which reduces the vulnerability of eggs to predation and

other threats such as inclement weather (Morris et al., 1976; Morris and Hunter, 1976; Vedder et al., 2017; Laurich et al., 2019).

Another factor that may also contribute to the decline of PNP gull populations is predation. Herring gulls are prey to a variety of diurnal and nocturnal mammalian and avian predators. Mammal species such as raccoon (*Procyon lotor*), red fox (*Vulpes vulpes*), American mink (*Neovison vison*), and feral cat (*Felis catus*) can have negative effects on nesting colonial waterbirds (Southern et al., 1985; MacKinnon and Kennedy, 2014). One way that waterbirds try to avoid these predators is by nesting on offshore islands that are more difficult for mammals to access (Ellis et al., 2007). Avian species such as the peregrine falcon (*Falco peregrinus*), bald eagle (*Haliaeetus leucocephalus*), and great horned owl (*Bubo virginianus*) may also be important predators of gulls. Reproductive success of the peregrine falcon and bald eagle was detrimentally affected during the 1960s and 1970s by organochlorine pesticides such as DDT (Noble et al., 1993). Many raptor species exposed to higher concentrations of these chemicals experienced reduced egg hatchability because of eggshell thinning, which ultimately caused significant declines in raptor populations across North America (Kirk and Hyslop, 1998; Noble et al., 1993), including those surrounding the Great Lakes (Bowerman et al., 1993; Drake, 2017). In fact, peregrine falcons were extirpated from PNP in the 1970s (Nabigon and Patterson, 2021). Since the ban of many organochlorine pesticides in the 1970s, raptor populations have been recovering nationwide with numbers steadily increasing through time (Kirk and Hyslop, 1998). In Ontario, a significant increase in peregrine falcon numbers has been observed with a reported 119 peregrine territories in 2010 (Chikoski and Nyman, 2011) compared to zero territories in the 1970s (Holroyd and Banasch, 2012). Nesting in PNP was confirmed in 2000. In 2021, there were 10 known peregrine territories in the park, five of which were occupied and two had a breeding pair (Nabigon

and Patterson, 2021). Similarly, bald eagle populations in Ontario have increased exponentially with numbers rising from 33 individuals in 1987 to 1307 individuals in 2016 (National Audubon Society, 2020). Based on the limited information available on great horned owls, there is no evidence indicating that organochlorine pesticides negatively impacted their populations (Blus, 1996) but studies during the period of highest organochlorine use were very limited. Recent population surveys show that great horned owl populations in northern Ontario remained relatively stable from 1995 to 2019 (Ontario Nocturnal Owl Survey, 2019). However, increases in the populations of important avian predator species of herring gulls suggest that predation on adult gulls, chicks, and eggs has likely increased in recent decades which could be negatively affecting herring gull populations.

The vulnerability of herring gulls to predators increases during the breeding season, in large measure due to their ground-nesting behaviour that exposes them to both aerial and terrestrial predators (Weseloh et al., 2020). Herring gulls respond to diurnal predators with two main behaviours: evading the predator by taking flight (Burger and Gochefeld, 1991; Meehan and Nisbet, 2002; Weseloh et al., 2020) and predator mobbing (Götmark and Anderson, 1984; Palestis, 2005; Mallory, 2016; Weseloh et al., 2020). Predator mobbing is a collective effort by birds in a nesting colony to drive away predators by pursuing a predator through the air or repeatedly diving and striking the intruder with their bill and feet (Weseloh et al., 2020). This tactic is effective against diurnal predators but there is uncertainty regarding its usefulness in deterring nocturnal predators. To date, relatively little information is available regarding how herring gulls respond to nocturnal predators. Due to their limited vision in darkness, adult gulls may be more likely to leave their nest altogether for self-preservation when faced with nocturnal predators (Southern et al., 1982; Sullivan et al., 2020).

Nest attentiveness is an important factor determining nest success (Martin, 2002). Leaving the nest for long periods of time in response to predators (or other factors) could increase the likelihood of predation of chicks and eggs, ultimately resulting in decreased nest success. In Chapter 2, I identified qualitative differences in herring gull nest attentiveness during the day and night in PNP. Here, I quantitatively compare nest attentiveness during the day and night using still photographs obtained using camera traps. I then determine if there is evidence that predation or weather, i.e., precipitation, may be contributing to those nest attendance patterns. I predict that reduced nest attentiveness during the night may be related to the risk of nocturnal predation given that gulls have a limited ability to cope with nocturnal predators.

Methods

In 2018, camera traps (Reconyx PC900 professional, 3.1 megapixels, 40° lens angle, 40° detection angle) were installed adjacent to nine herring gull nests on Gull Rock in PNP (Figures 3.1, 3.2). One egg was collected from each nest for my research investigating gull diets (see Chapter 2). The remote infrared cameras (no flash required) took one picture per minute, 24 hours/day, throughout incubation (maximum ~ 1 month). Images were used to document gull behaviour and quantify nest attentiveness during the day (16-hour period; time = 0545 – 2144) and night (8-hour period; time = 2145 – 0544). The period of incubation varied among nests. When possible, nest attentiveness was assessed up until first hatch. Gull presence/absence was determined for ~315,000 images in total over the nine nests. Intra- and interspecific predation of eggs and young as well as scavenging of a dead adult (see Lockhart et al., 2020) were documented. Female and male herring gulls share incubation duties throughout the incubation period (Burger, 1987; Morris, 1987). Females may spend a greater amount of time incubating compared to males

(Pierotti, 1979) but the nest attentiveness estimates in this study are representative of the breeding pair.

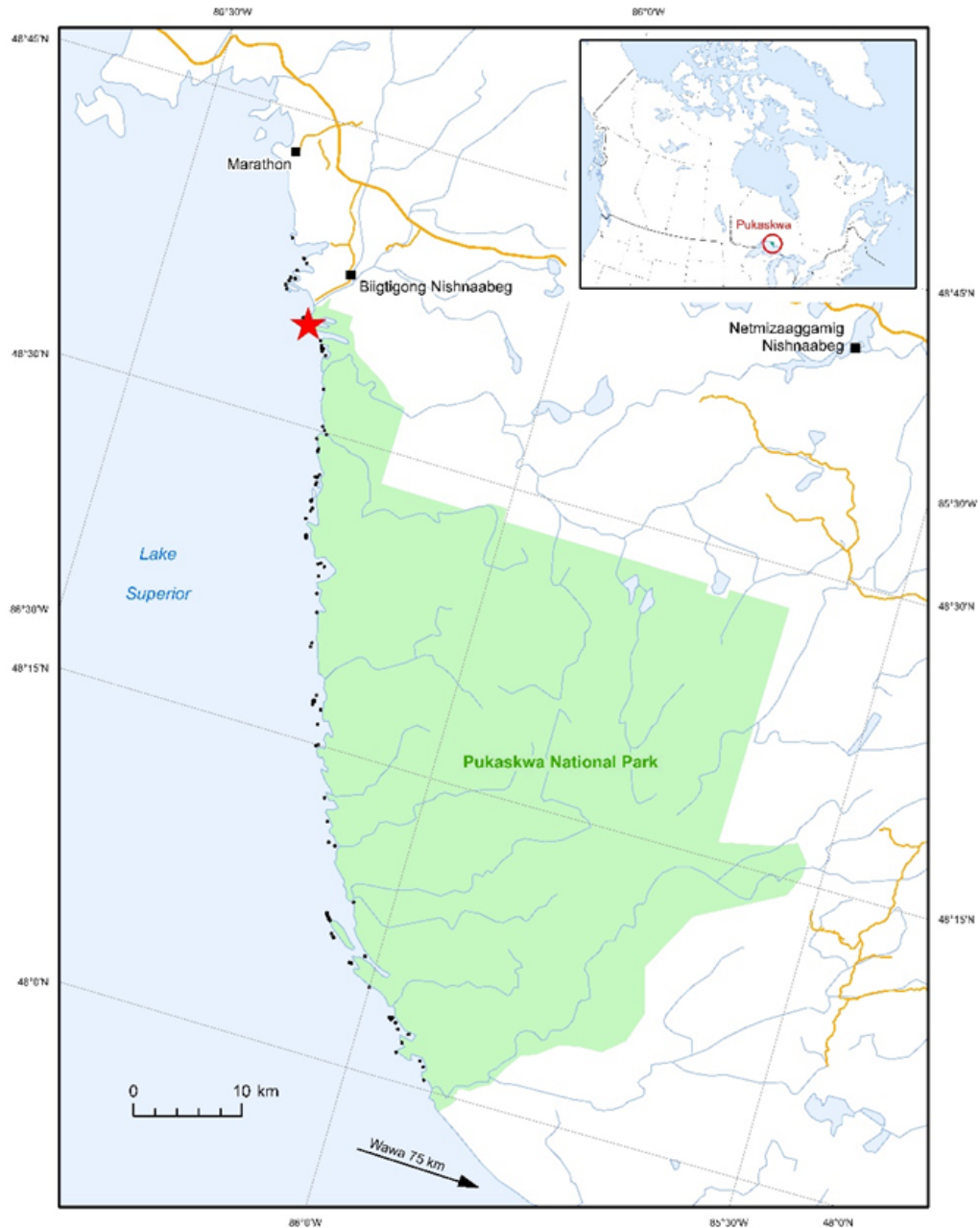


Figure 3.1 Location of Gull Rock study site (indicated by star) in Pukaskwa National Park, Lake Superior, Ontario, Canada. The black dots show herring gull nesting sites within the park.



Figure 3.2 Reconyx PC900 professional cameras set up to monitor herring gull nests in Pukaskwa National Park.

Nest attentiveness of mated pairs was assessed by calculating the percentage of time adult birds were observed sitting on, or were adjacent to, their nests. Daytime and nighttime attentiveness were assessed separately to allow comparisons between day and night periods. The number of adult nest absences were counted and categorized according to absence duration (seven absence duration categories: 1 minute, 2-5 minutes, 6-10 minutes, 11-20 minutes, 21-30 minutes, 31-60 minutes, 60+ minutes) for both daytime and nighttime. These data were expressed as the number of absences per hour to account for the difference in period length between day (16 hours) and night (8 hours). The number of adult nest absences was also compared between complete and incomplete nests. Complete nests were defined as having a complete clutch of three eggs while incomplete nests were defined as nests having less than three egg clutches. In general, modal clutch size of herring gulls is three eggs (Weseloh et al. 2020).

Detailed nest attentiveness data were examined over the same 10-day period for seven of the nine nests in order to visualize similarities or differences in behaviour among adults attending different nests. The influence of weather on gull behavior was also assessed using information,

i.e., evidence of precipitation, associated with each photo over the same 10-day period in order to capture gull behaviour patterns that might coincide with precipitation patterns. Evidence of precipitation was assessed on an hourly basis by visually looking for signs of precipitation in each of the photos. This included evidence of rain drops on nearby rocks or in puddles as well as water droplets on incubating gulls. Two of the nine nests (nests 3 and 5) were excluded from this analysis as nest attendance data for those nests did not coincide with the dates for the other seven nests.

Non-parametric (Mann-Whitney U) tests were used to determine whether there were differences between day and night in the total percentage of time adults attended their nests and in the number of hourly absences (discrete data) in each of the seven absence duration categories. Nest attendance data were also compared between nests containing complete (three-egg) and incomplete (< three-egg) clutches, these comparisons were done separately for night and day.

Results

Details regarding date and duration of monitoring, final clutch size, and nest success for each of the nine monitored nests are shown in Table 3.1. One egg was collected from each nest for dietary studies (see Chapter 2), therefore only the outcome of the remaining eggs (hatched, predated, etc.) in the nests were tracked.

Nest	Monitoring Start Date	Total Time Monitored (minutes)	Final Clutch Size	Number of Chicks Hatched	Number of Chicks Survived	Predation	Events
1	2018-05-17	52,703	3	1	1	N	Egg 1 collected Egg 2 hatch/survived Egg 3 did not hatch
2	2018-05-17	38,882	2	0	0	Y	Egg 1 collected Egg 2 HERG predation Nest abandoned
3	2018-05-17	6,082	3	0	0	Y	Egg 1 collected Adult died on nest - scavenged by PEFA Eggs 2 & 3 AMCR predation
4	2018-05-17	41,295	2	1	0	Y	Egg 1 collected Egg 2 hatch/GHOW predation
5	2018-06-08	10,388	3	2	1	Y	Egg 1 collected Egg 2 hatch/GHOW predation Egg 3 hatch/survived
6	2018-05-17	49,183	2	0	0	Y?	Egg 1 collected GHOW present Egg 2 unknown Nest abandoned
7	2018-05-17	31,746	2	0	0	Y	Egg 1 collected GHOW present Egg 2 AMCR predation
8	2018-05-17	47,253	3	2	1	N?	Egg 1 collected Egg 2 hatch/survived Egg 3 hatch/disappeared at night
9	2018-05-17	37,245	3	2	0	Y	Egg 1 collected Eggs 2 & 3 hatch/GHOW predation

Table 3.1 Information for individual herring gull nests regarding date of initiation and duration of monitoring, final clutch size, nest success and predation. Species codes are American crow (AMCR, *Corvus brachyrhynchos*), Great Horned Owl (GHOW), Herring Gull (HERG), Peregrine Falcon (PEFA). Question marks indicate some uncertainty in whether predation occurred or not as it was not directly captured on the camera.

Across all nine nests, it was evident that there were differences in the total percentage of time that nests were attended during the day and night (Figure 3.3).

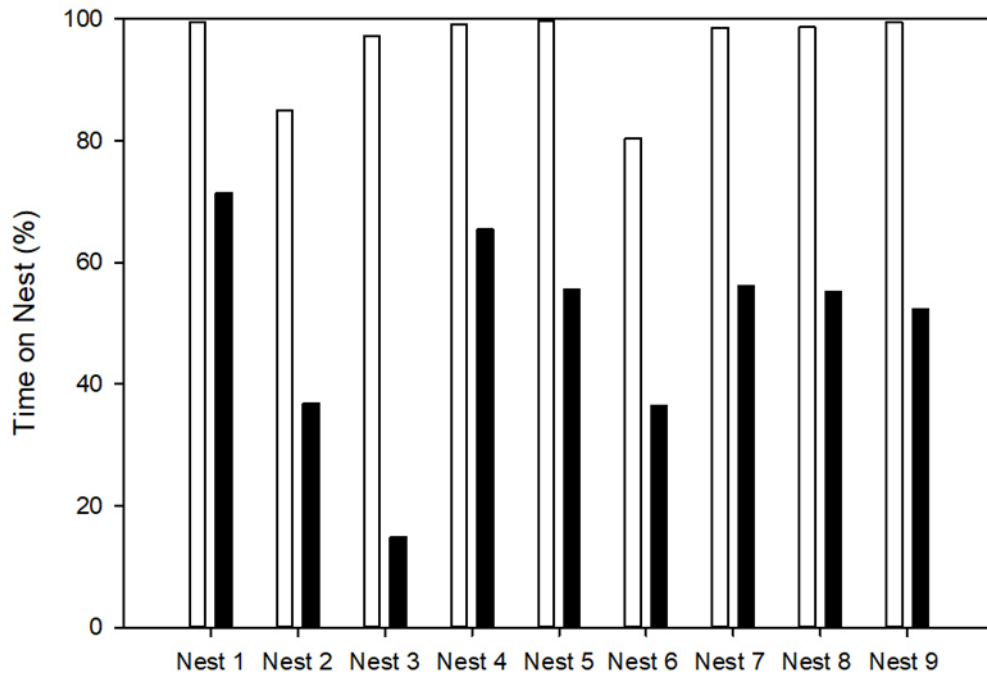


Figure 3.3 Proportion of total time adult herring gulls were present at their nests during daytime (white bars) and nighttime (black bars) through the nesting period (May-June, 2018) on Gull Rock in Pukaskwa National Park, 2018.

Gulls were significantly more attentive to their nests during the daytime (median percent nest attendance = 98.7%) compared to the night (median = 52.2%) (Table 3.2). The number of hourly absences during the night was significantly greater for the 2-5 minute absence category and for the 60+ minute absence category (Table 3.2, Figure 3.4). The number of absences for the other absence categories did not differ between day and night (Table 3.2)

Absence Duration	Median (Day / Night)		<i>U</i>	<i>p</i> -value	<i>z</i> -value/
1 minute	0.130	0.094	30.0	.38	0.88
2-5 minutes	0.026	0.082	7.5	.004	-2.87
6-10 minutes	0.002	0.008	39.5	.96	-0.04
11-20 minutes	0.002	0.006	39.5	.96	0.04
21-30 minutes	0	0.008	26.0	.22	-1.24
31-60 minutes	0	0.005	24.5	.17	-1.37
60+ minutes	0.002	0.096	0	<.001	-3.53
% of Time on Nest	98.7	55.2	0	<.001	3.53

Table 3.2 Statistical results comparing the number of nest absences per hour for PNP Herring Gulls attending their nests during the day (n=9) and night (n=9). Absences are categorized according to duration. Total percentage of time on the nest during day and night is also shown. Comparison of results for day and night were done by category using nonparametric Mann-Whitney U test.

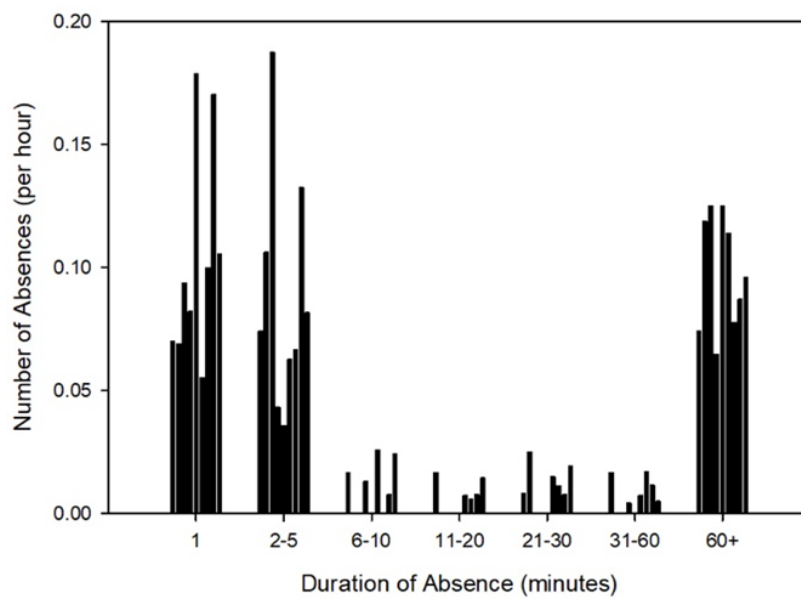
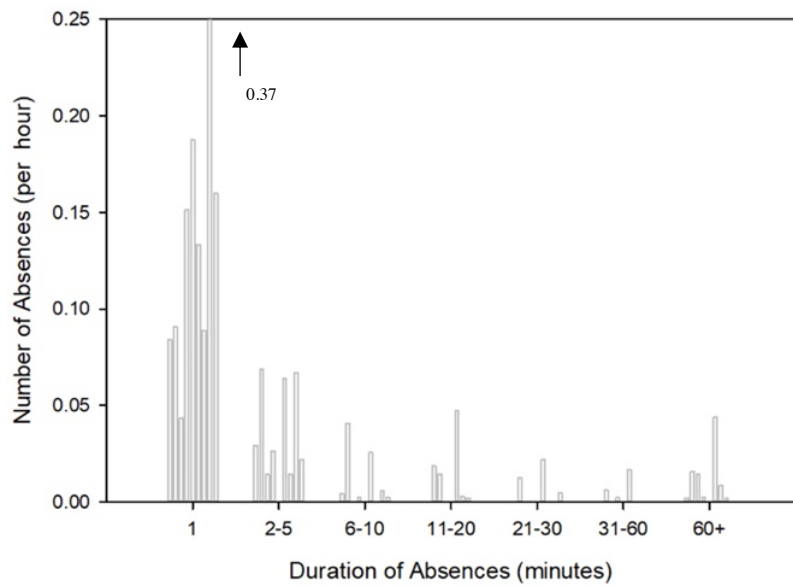


Figure 3.4 Number of adult herring gull absences from their nests per hour during daytime (top panel, white bars) and nighttime (bottom panel, black bars) for each of the nine monitored nests throughout the nesting period (May-June, 2018) on Gull Rock in Pukaskwa National Park. Within each duration category, each bar represents data for an individual herring gull nest and bars are arranged in order of ascending nest number (Nests 1-9).

No statistically significant differences were observed in the number of absences or in total nest attentiveness for complete versus incomplete clutches during the day or night (Table 3.3).

	Absence Duration	Median (Complete/Incomplete)		<i>U</i>	<i>p</i> -value	<i>z</i> -value/
Daytime	1 minute	0.160	0.111	8.0	.71	0.37
	2-5 minutes	0.022	0.045	6.5	.46	-0.73
	6-10 minutes	0.002	0.014	7.0	.54	-0.61
	11-20 minutes	0.000	0.011	4.5	.22	-1.22
	21-30 minutes	0.000	0.006	6.0	.39	-0.86
	31-60 minutes	0.000	0.004	2.5	.09	-1.71
	60+ minutes	0.002	0.012	2.0	.07	-1.84
	% of Time on Nest	99.40	91.8	3.0	.11	1.59
Nighttime	1 minute	0.110	0.076	3.0	.11	1.59
	2-5 minutes	0.130	0.065	2.0	.07	1.84
	6-10 minutes	0.008	0.007	10.0	.90	-0.12
	11-20 minutes	0.008	0.003	6.0	.39	0.86
	21-30 minutes	0.008	0.013	6.0	.39	-0.86
	31-60 minutes	0.005	0.006	9.0	0.90	-0.12
	60+ minutes	0.096	0.094	7.0	.54	0.61
	% of Time on Nest	55.20	46.40	10.0	1.0	0

Table 3.3 Statistical results comparing the number of nest absences per hour for Herring Gulls attending complete (clutch size = 3) (n=5) versus incomplete (clutch size < 3) (n=4) nests during the day and night. Absences are categorized according to duration. Total percentage of time on the nest during night and day for complete and incomplete nests is also shown. Comparisons of results for complete versus incomplete nests were done using nonparametric Mann-Whitney U test.

Detailed examination of nest attentiveness data indicated similar patterns of behaviour among individuals from different nests. Birds routinely left their nests around midnight and returned around 4 AM (Figure 3.5). There was no discernable pattern between precipitation and adult nest attentiveness suggesting other factors were more important in regulating adult behavior.

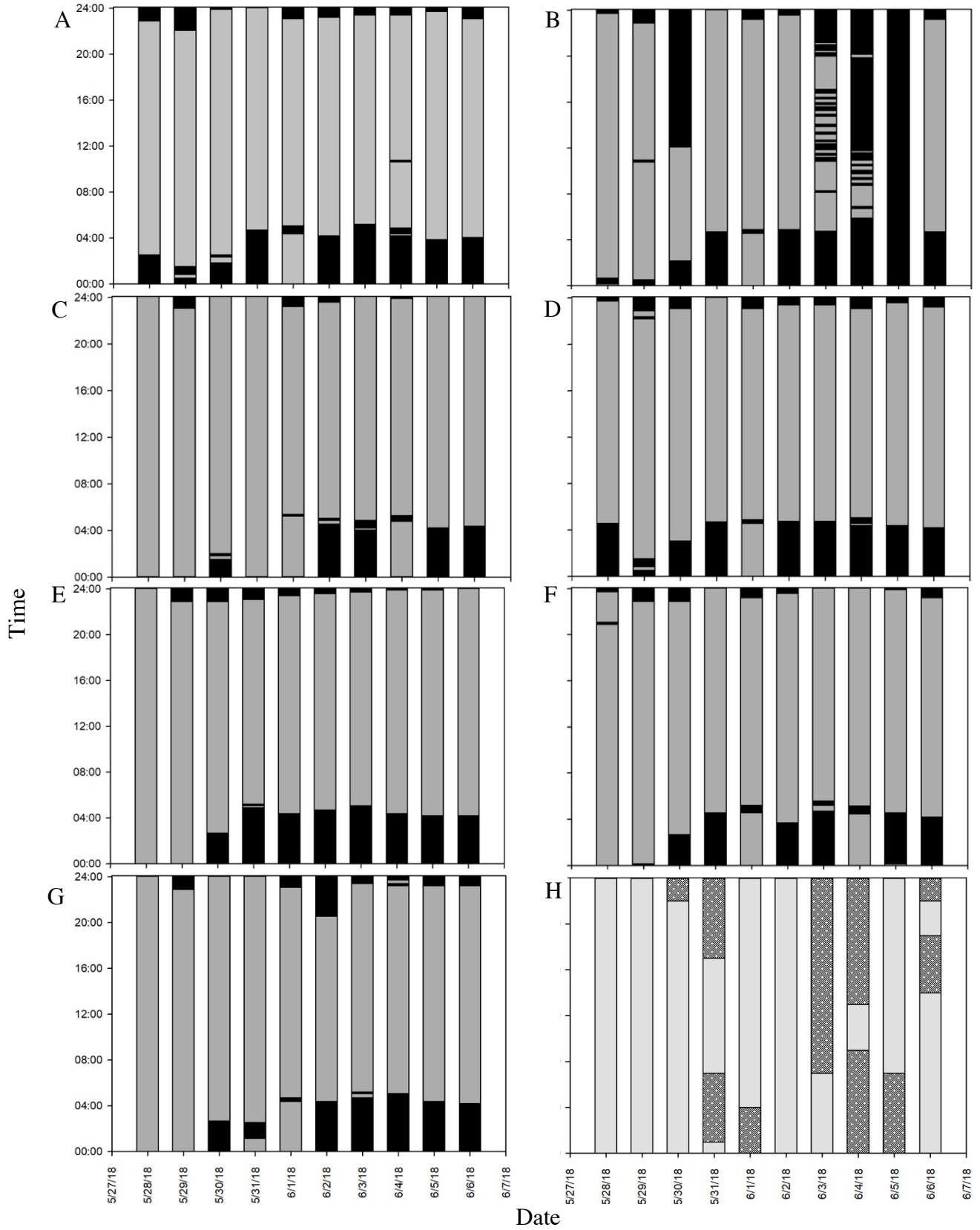


Figure 3.5 Hourly activity budgets of Gull Rock adult herring gulls (nests 1 (A), 2 (B), 4 (C), 6 (D), 7 (E), 8 (F), 9 (G)) and precipitation (H) pattern in Pukaskwa National Park over the same 10 consecutive days in 2018 (05-28-2018 to 06-06-2018). For A-G, grey-shaded area indicates the presence of an adult on the nest; black-shaded area indicates adult absence. For H, light grey-shaded area indicates no rain; dotted area indicates rain.

Of the nine nests monitored with camera traps, five nests produced eggs that hatched; however, chicks were reared successfully from only three nests (nests #1, 5, 8) (Table 3.1, Figure 3.6). Three nests with hatchlings suffered chick loss that occurred exclusively during the night due to predation by great horned owls (nests #4, 5, 9) (Table 3.1, Figure 3.7). Another nest (#6) visited by a great horned owl during the egg incubation period was later abandoned but there was no direct evidence of owl predation. Diurnal predation of gull eggs by herring gull (nest #2) (Table 3.1, Figure 3.8) and American crow (nest #7) (Table 3.1, Figure 3.9) was observed at two of the nine nests. The latter nest had earlier been visited by a great horned owl but the owl did not predate the egg. Great horned owl predation focused solely on newly hatched herring gull chicks. Scavenging of eggs by American crow occurred at the nest (#3) on which a peregrine falcon had earlier scavenged an adult herring gull that died during incubation (Figures 3.10 and 3.11).



Figure 3.6 Remote images of successful herring gull chick rearing from nest 1 (top) and nest 8 (bottom) on Gull Rock in Pukaskwa National Park in 2018



Figure 3.7 Remote images of nocturnal owl predation on newly-hatched herring gull chicks from nests 4 (top) and 5 (bottom) on Gull Rock in Pukaskwa National Park in 2018.



Figure 3.8 Remote image of intraspecific predation of herring gull egg from nest #2 on Gull Rock in Pukaskwa National Park in 2018.



Figure 3.9 Remote image of crow predated a herring gull egg from nest #7 on Gull Rock in Pukaskwa National Park in 2018.



Figure 3.10 Remote image of peregrine falcon scavenging an adult herring gull carcass on nest #3 on Gull Rock in Pukaskwa National Park in 2018.



Figure 3.11 Remote image of American crow scavenging herring gull eggs from abandoned nest #3 on Gull Rock in Pukaskwa National Park in 2018.

Discussion

Herring gulls spent almost all of their time during the day attending their nests and nest attentiveness was significantly greater during the day than the night. This could have reflected differences in risk posed by various types of predators as well as the varying ability of gulls to cope with daytime versus nighttime predators. Herring gulls are a long-lived species, living up to 30 years with an annual adult survival rate of 0.87 for Great Lakes populations (Gaston et al., 2013; Weseloh et al., 2020). Accordingly, herring gulls adjust their behaviour when faced with predators that threaten adult survival versus those that only affect the survival of eggs and young. Predators of adult gulls pose a risk to lifetime reproductive success while predators of eggs and young only influence annual reproductive success. Although predators were observed at the northern PNP breeding site during both day and night; the impact of nighttime predation on herring gull nest success was more evident.

Large diurnal avian predators, such as peregrine falcon and bald eagle, can pose a significant risk to the survival of adult herring gulls. However, in my study a large diurnal predator (i.e., peregrine falcon) was only recorded on a single occasion and it was observed scavenging an already dead herring gull. Diurnal predation events were restricted to egg predation by species of similar (conspecifics) or smaller (American crow) size relative to herring gulls and these species do not pose a lethal threat to adult herring gulls (Ewins, 1991). During the day, the relatively low risk of injury to adult herring gulls from large-bodied predators and the high risk to eggs and chicks from smaller predators may explain the very high daytime nest attentiveness exhibited by herring gulls. In colonial waterbird breeding colonies, many individuals of the same or different species utilize a common breeding space resulting in fierce competition and territorial behaviour. This can result in aggressive interactions that promote high nest attentiveness. In addition to the risk of egg

predation by the species mentioned above, ring-billed gulls (*Larus delawarensis*) were observed stealing nest materials from herring gull nests and, in some cases, attempted to take over nests if herring gulls were absent. Although ring-billed gulls were not observed predated herring gull nest contents, competition for nesting material could have been a factor encouraging high herring gull nest attentiveness during the day. Intra- and interspecific intruders into herring gull nesting territories are confronted in a charge or attack behaviour that usually causes the intruder to depart (Weseloh et al., 2020). This charging behaviour could explain the high number of short (1-minute duration) daytime absences compared to other absence categories.

A significant proportion of the monitored herring gull nests were predated during the night by great horned owls. As discussed above, large avian predators pose a risk to both adult herring gulls and to their eggs and young. During the day, mobbing large diurnal intruders such as falcons and eagles is an effective defense behaviour of herring gulls and other colonial waterbird species (Weseloh et al., 2020). However, at night there is no evidence that mobbing nocturnal predators occurs and the little evidence that does exist regarding herring gull defenses against such predators suggests that they resort to an escape behaviour (Patton and Southern, 1977; Southern and Southern, 1979). My results support this with herring gulls leaving their nests for extended periods during the night compared to the day. These absences did not coincide with precipitation events; instead, they may have reflected the apparent lack of defense mechanisms that herring gulls, and colonial waterbirds in general, have against nocturnal predators (Patton and Southern, 1977; Southern and Southern 1979).

Nocturnal predation can cause colonial waterbirds to leave their nests for extended periods of time (Morris and Hunter, 1976; Patton and Southern, 1977; Southern et al., 1982). For example, California gulls (*Larus californicus*) have been reported to leave their breeding colonies for periods

ranging from 30 minutes to three hours in response to nocturnal predation (Jehl and Chase III, 1987). Similarly, common terns (*Sterna hirundo*) desert their nests for up to eight hours in response to nocturnal predation by great horned owls (Nisbet and Welton, 1984; Arnold et al., 2006). The duration of nest abandonment can vary according to the apparent threat to the adult as determined by the proximity and activity of nocturnal predators (Arnold et al., 2006). I observed long nest absences, consistent with the possibility that herring gulls perceived significant danger during the night, preventing them from attending their nests often until dawn.

Great horned owls are a long-lived species with a lifespan that can exceed 20 years (Houston and Francis, 1995). They do not migrate and mated pairs are usually permanent residents exhibiting site fidelity, occupying their territory year-round and on a long-term basis (Artuso et al., 2020). Considering this, the great horned owl population in PNP is likely to remain abundant over the coming years and predation pressure by great horned owls could be an ongoing factor negatively affecting the local herring gull population. Herring gulls that nest in colonies that experience continuous predation for several years, whether it be on adults, eggs, or chicks, will sometimes move to another area (Weseloh et al., 2020). Great horned owl predation may have been responsible for herring gulls abandoning several of their nesting sites within one km of the mainland along the Atlantic coast (Weseloh et al., 2020). The nocturnal predation success exhibited by great horned owls during my study suggests that they will continue to take advantage of this prey resource into the future.

Although the herring gull population of PNP is declining, this is not necessarily an indication of negative change in the ecosystem. Herring gulls are used as an indicator of ecological integrity in PNP and, until recently, current-year nest abundance was compared to average nest abundance during the 1977-1981 period (Laurich et al., 2019; Parks Canada Agency, 2019).

During the 1970s, the dominant prey fish in Lake Superior was the rainbow smelt (*Osmerus mordax*), a non-native species of prey fish introduced to the area in the early 1930s (Gorman, 2007; Gorman and Hoff, 2009; Laurich et al., 2019). As a result, prey fish availability for herring gulls at that time may have been artificially high (Laurich et al., 2019). In addition, the presence of top trophic level avian predators was low due to the detrimental effects of chemical contaminants (Kirk and Hyslop, 1998). Unnaturally high prey abundance combined with decreased predation could have created an optimal nesting environment for herring gulls leading to higher reproductive success and larger breeding populations over time (Laurich et al., 2019).

Therefore, one interpretation of the current decrease in the PNP herring gull population is that the ecosystem may be returning to a state when anthropogenic influences on the ecosystem were less apparent. Interpretation of herring gull nest abundance as an indicator of ecological integrity in PNP is evolving to consider this possibility. Parks Canada now compares current-year nest abundance to that during the 1998-2017 period. This latter period better reflects current rainbow smelt biomass and trends in dietary markers measured in herring gulls (Laurich et al. 2019). This revised baseline period also better considers the current state of avian predator populations in PNP (Parks Canada Agency, 2019). Using this new comparative period, nest abundance of herring gulls in PNP is rated as being in stable, good condition (Laing and Patterson, 2020). Effective protected area management depends on an adaptive approach to the interpretation of ecological indicator data, based on current research.

Chapter Four General Summary

Herring gulls are the focal biomonitoring species in Environment and Climate Change Canada's Great Lakes Herring Gull Monitoring Program (GLHGMP) (Hebert et al. 1999a). In that context, they have been used since the 1970s to monitor the status of all five of the Great Lakes. The GLHGMP has identified declining populations of herring gulls at some sites over the last 40 years, particularly on the upper Great Lakes (C.E. Hebert, pers. comm.). However, the GLHGMP was not designed to provide detailed population data because research conducted as part of that program occurs prior to establishment of all nests within breeding colonies. Accurate census data are generated on a decadal frequency through surveys coordinated by ECCC in conjunction with other agencies (Environment and Climate Change Canada, 2022). More frequently collected data regarding gull population trends are uncommon but have been generated at specific locations. Here, my work centred around the detailed population trend information collected by the Parks Canada Agency at Pukaskwa National Park (PNP) on Lake Superior. At that location, herring gull populations declined by 70% over the last 40 years (Laurich et al. 2019).

On Lake Superior, there have been large declines in prey fish abundance and increases in populations of avian predators. Given those changes, my research objectives focused on evaluating how diet and predation were affecting the PNP herring gull population. This information is essential not only for the conservation of herring gulls but is equally important for evaluating the broader state of the PNP ecosystem. My research first focused on defining herring gull diets and investigated relationships between diet and physiological, reproductive, and behavioural endpoints that could influence the fitness of individual gulls. I then used images obtained from camera traps to document adult nest attentiveness and nest success, paying particular attention to the role of predation in explaining the observed patterns. Here, I discuss the key findings of my research as

well as their relevance for guiding possible future research avenues and implications for park management.

The diet of laying herring gulls plays a key role in determining the outcome of a breeding season as the availability of quality food is essential for reproductive success that, in turn, influences population trends through effects on recruitment of young. Reduced food quality and availability can invoke a stress response in gulls that can lead to higher levels of corticosterone in their eggs and lower quality eggs through reductions in egg size. Reduced food availability can result in adult gulls spending more time off their nests to forage which can ultimately increase the vulnerability of eggs and chicks to predation. By measuring stable isotopes and fatty acids in eggs I was able to identify the composition of herring gull diets and examine linkages between diet and egg corticosterone content, egg volume and adult nest attentiveness (**Chapter 2**).

As summarized in Chapter 2, the proportion of anthropogenic food in the gull diet had positive effects on gull physiology (stress-associated hormone corticosterone), resources available for reproduction (egg size), and behaviour (incubation attentiveness during the day). Gulls that used less terrestrial resources laid eggs with higher levels of corticosterone; however, no information is available regarding what constitutes normal levels of corticosterone in wild herring gulls. Hence, we cannot be certain that the higher corticosterone levels reported here had detrimental effects on adults or their progeny. Although previous studies have linked elevated corticosterone to negative effects in birds further research is required to understand the biological significance of elevated corticosterone concentrations in PNP herring gulls.

I found a significant positive relationship between corticosterone concentrations in egg contents and eggshell. To my knowledge, this is the first time that such a relationship has been documented. The positive relationship between corticosterone concentrations in egg contents and

eggshell is important as it points to the utility of eggshells for measuring stress-associated hormones in birds. The use of eggshell for measuring corticosterone may be advantageous in two ways. First, egg contents corticosterone levels measured in eggs during later stages of development, i.e., post mid-incubation, may not be reflective of stress experienced by the laying female. During later stages of development, embryos have the ability to generate corticosterone in response to stressful conditions, e.g., temperature fluctuations, and therefore corticosterone levels in egg contents may be more reflective of embryonic stress. Eggshell corticosterone, on the other hand, may not be influenced by embryonic development because eggshell corticosterone is deposited during the formation of the egg and is likely bound in the shell matrix. Testing this hypothesis through a controlled laboratory study would be an interesting avenue for future research. A further advantage of measuring corticosterone in eggshell versus egg contents is that measuring the latter requires destructive sampling. Eggshells, however, often remain in the nest once the nesting season is complete which make them available for opportunistic collection and later analysis. Use of eggshells in this way eliminates the need for destructive sampling that may not be possible for some species, e.g., species at risk, and it eliminates the need for whole egg collections that can disturb nesting birds. Human disturbance of birds during the breeding season can lead to nest abandonment and use of eggshells to measure corticosterone (and other endpoints) reduces that possibility. A worthwhile area for future research would be to further investigate corticosterone levels in eggshells as a means of assessing stress in wild birds.

Another important finding summarized in Chapter 2 was the identification of differences in the fatty acid composition of eggs from species that specialized in using different foraging environments. Egg fatty acid patterns were very useful in distinguishing birds feeding in terrestrial, marine and freshwater environments. For example, omega-6 (n-6) fatty acids, such as linoleic acid,

were useful in identifying terrestrial foragers, whereas n-3 fatty acids, such as eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), were useful in identifying birds feeding in marine and freshwater environments. Results from this analysis provided a novel, systematic assessment of the utility of fatty acids in distinguishing the diets of birds utilizing different foraging habitats. Results of my stable isotope analyses further improved our understanding of gull diets. In particular, stable carbon isotopes were very useful in distinguishing birds feeding specifically on anthropogenic food sources in terrestrial environments. These results were informative because they provided a better understanding of the importance of anthropogenic food sources to gulls nesting in PNP. I found that gulls utilizing terrestrial food sources, specifically increased proportions of anthropogenic food resources, had reduced levels of stress-associated hormones, increased egg size and increased nest attentiveness during the day. Gulls utilizing aquatic food sources showed opposite results, with increased levels of corticosterone, reduced egg size and reduced daytime nest attentiveness. One explanation for these results was that anthropogenic food resources were more plentiful than aquatic foods.

Higher concentrations of corticosterone in eggs, like those found in gulls utilizing aquatic food sources, may be indicative of negative effects of a scarce food supply. However, increased corticosterone levels in wildlife may not always be detrimental. It is possible that increased corticosterone can be an adaptation to environmental conditions in order to enhance the chances of successful reproduction. The corticosterone-adaptation (CORT-Adaptation) hypothesis predicts that individuals may upregulate corticosterone from baseline levels to meet the energetic demands of reproduction with beneficial effects on reproductive success (Bonier et al., 2009; Crossin et al., 2012). However, the three main hypotheses proposed to explain the relationship between corticosterone and reproduction (CORT-Adaptation, CORT-Tradeoff, CORT-Fitness) all predict

a decrease in reproductive success-related endpoints at high levels of stress (as reflected in tissue concentrations of the stress-associated hormone, corticosterone) (Breuner and Berk, 2019). In my research, I observed negative relationships between egg corticosterone concentrations and egg volume (Figure 4.1) as well as nest attentiveness (Figure 4.2). Increased levels of corticosterone in both egg contents and eggshell resulted in decreased nest attentiveness and decreased egg size. Both nest attentiveness and egg size are important factors contributing to overall reproductive success. This highlights the possibility that gulls breeding in PNP were experiencing stress levels that surpassed the ability of birds to adapt, leading to negative impacts on reproductive endpoints.

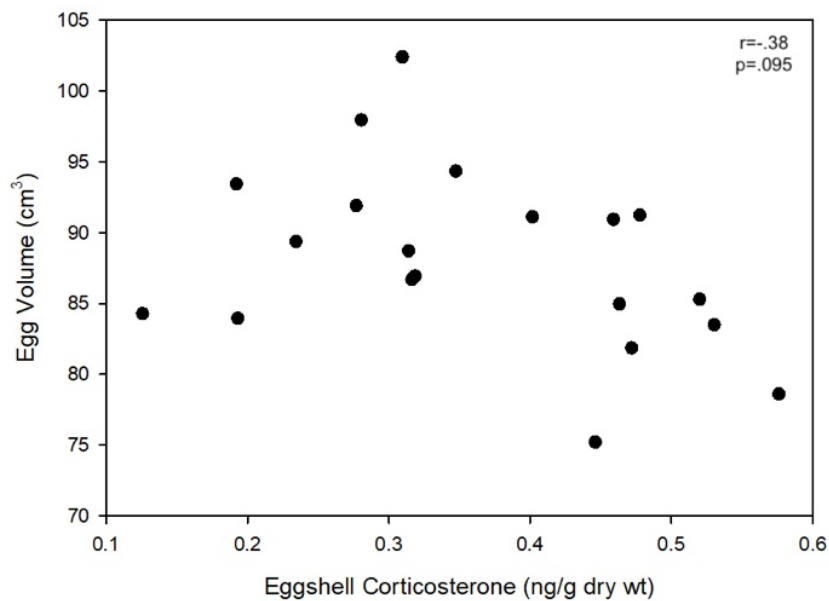
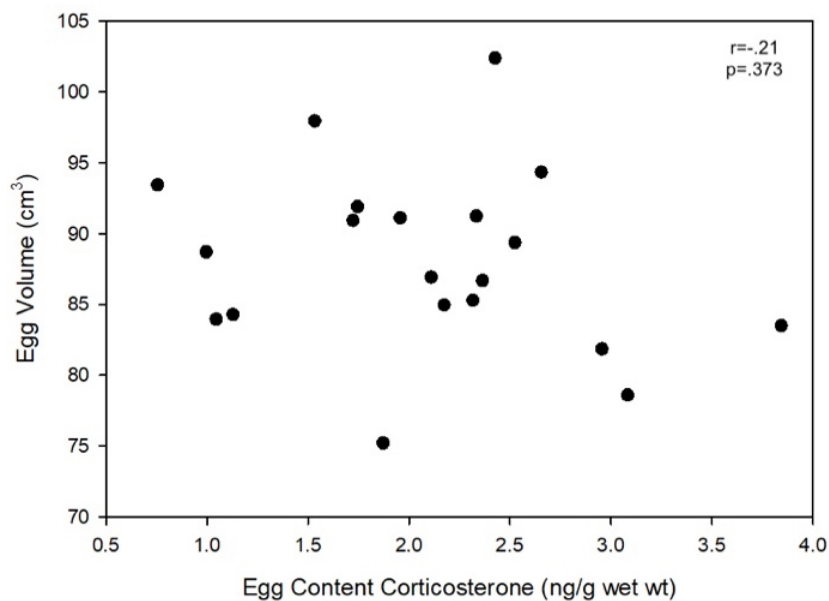


Figure 4.1 Non-significant negative relationships between egg content (top panel) and eggshell (bottom panel) corticosterone concentrations and egg volume. Eggs were collected from Gull Rock in Pukaskwa National Park in 2018.

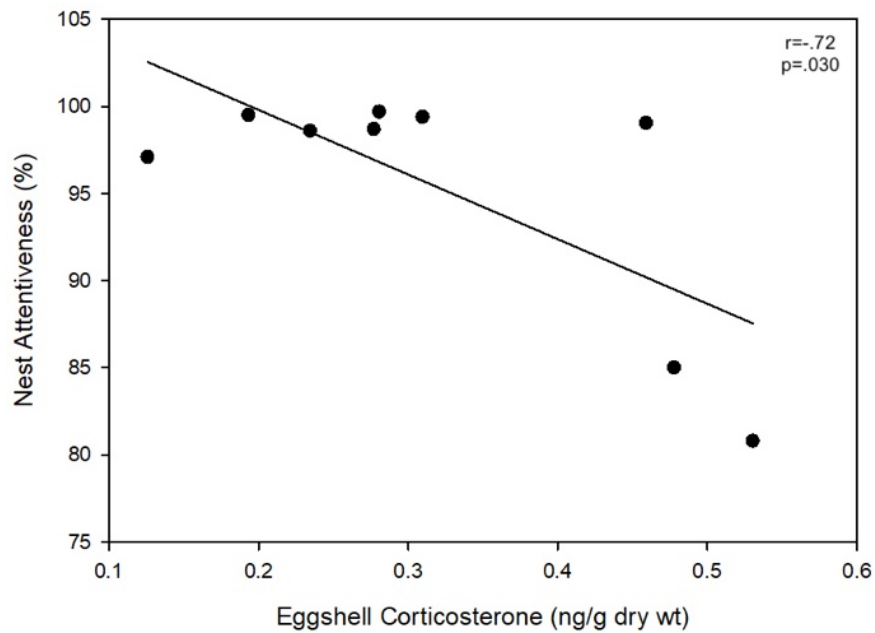
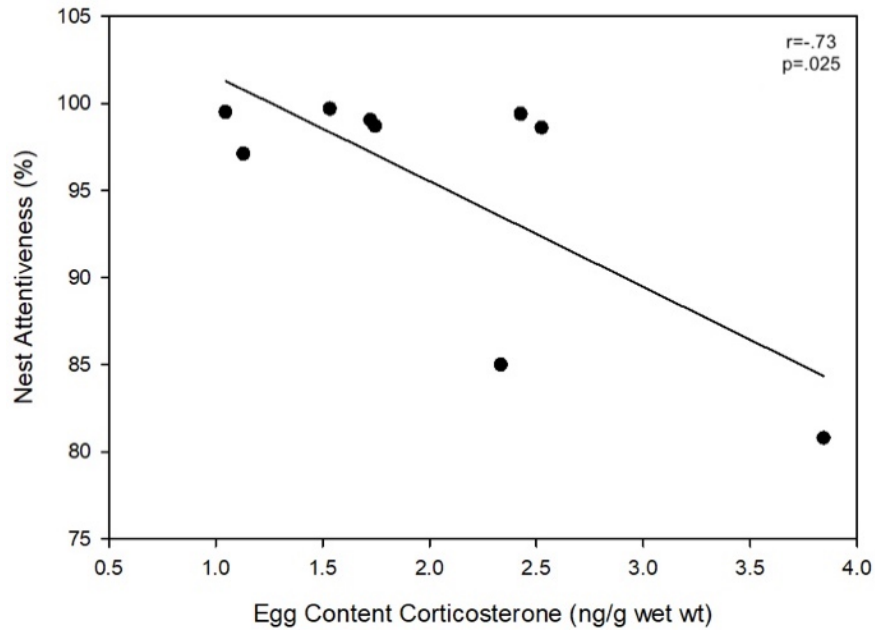


Figure 4.2 Significant negative relationships between herring gull egg content (top panel) and eggshell (bottom panel) corticosterone concentrations and herring gull nest attentiveness during the daytime on Gull Rock in Pukaskwa National Park in 2018.

In northern PNP, gulls exhibited positive effects from utilizing more terrestrial, anthropogenic foods in their diets. Although anthropogenic food resources can have negative effects on gull health through exposure to chemical contaminants (Tanaka et al., 2013; Gauthier et al., 2019), ingestion of plastics (Plaza and Lambertucci, 2017), and possible exposure to pathogens (Collins and Kennedy, 1992; Hatch, 1996; Matejczyk et al., 2011), my results point to these foods buffering the lack of aquatic food resources in the area. This is consistent with earlier research (Laurich et al. 2019) that compared herring gull populations in the northern and southern parts of PNP. The larger population decline in the southern population was thought to reflect the greater reliance of gulls from that area on aquatic food resources, whereas in northern PNP, the gull population experienced less drastic declines possibly because they exploited the local availability of anthropogenic foods. Considering the buffering effect anthropogenic foods may provide to gulls in the northern PNP population, their reliance on such foods is likely to continue, however this dependence could ultimately be an ecological trap for the gulls. Landfills provide a short-term solution to the lack of aquatic resources, yet may have detrimental effects with long-term use. Lower rates of successful hatching and fledging have been reported in some populations of herring gulls using food from landfills (Belant et al., 1998). Therefore, it is important that future studies investigate the negative side effects of utilizing anthropogenic food sources on the health of both young and adult gulls due to possible exposure to chemical contaminants, plastics, and pathogens. Overall, ongoing monitoring of herring gull populations should continue as that information will provide insights into the implications of declines in aquatic prey not only for herring gulls but also for other aquatic bird species.

Incubating gulls whose diets reflected increased use of anthropogenic food resources spent more time attending their nests during the day compared to those that utilized more aquatic food. However, this was not the case at night. Using remote camera traps, I was able to compare nest attentiveness during the day and night in PNP to determine if predation or weather could be contributing to differences in attendance patterns (**Chapter 3**). I found that gulls were significantly more attentive to their nests during the daytime compared to the nighttime, with greater numbers of 2-5 minute and 60+ minute absences at night. Birds routinely left their nests at midnight and returned around 4 AM. Out of the nine nests monitored using cameras, five hatched chicks; however, three of these nests suffered chick loss that occurred exclusively at night by great horned owls and two nests had great horned owl visitations before the chicks hatched. Considering that adult gulls largely lack defense mechanisms against nocturnal predators, my results suggest that gulls perceived great horned owls as a significant danger leading to nest abandonment for extended periods at night. This ultimately left their chicks exposed for a significant amount of time increasing the risk of predation by nocturnal predators. As a result, owls had a significant impact on the reproductive success of the nests I monitored in this population. Herring gulls that experience continuous predation in nesting areas will often move to another area. In this case, the high proportion of nests experiencing nocturnal predation suggests that predation is likely an important factor contributing to poor reproductive success at this northern PNP nest site. This could, in turn, be contributing to declines in PNP's herring gull population. Considering this, future research should aim to improve the availability of population data on nocturnal predators like the great-horned owl. Such improvements could provide a better understanding of the owl population in the area and their influence on herring gull population dynamics. Diminished sources of aquatic

food combined with significant predation may be acting together to negatively affect PNP herring gulls.

Future studies should equally consider looking further into the effects of higher corticosterone levels on embryonic development, specifically examining the utility of this hormone in determining the sex of embryos. Laying females experiencing poor and/or unpredictable conditions may deposit more corticosterone into their eggs to skew offspring sex from male to female as females are less energetically costly to raise (Trivers and Willard, 1973; Cameron and Linklater, 2002; Love et al., 2005). It would also be informative to investigate whether the deposition of corticosterone has resulted in a female-biased sex-ratio in the PNP herring gull population. Sex ratios can influence breeding behaviour with the ratio of females to males having impacts on population growth through reductions in the number of breeding pairs (Bessa-Gomes et al., 2004; Donald, 2007; Wedekind et al., 2013).

Although the changes occurring in the park ecosystem are having a negative impact on the herring gull population, other biotic and abiotic ecological indicators for PNP show that the ecological state of the park is good. Positive results for indicators such as water quality of rivers and streams, moose (*Alces alces*) population numbers, peregrine falcon (*Falco peregrinus*) territories, and grey wolf (*Canis lupus*) occupancy all indicate good ecological status for the park (Parks Canada Agency, 2022). Declines in herring gull populations may represent a return of the ecosystem to a state more similar to what prevailed in earlier decades prior to the many changes brought about by humans such as the introduction of alien species and release of toxic chemicals into the environment. Understanding factors affecting herring gull populations is critical information for park management as it reflects how the local ecosystem is responding to both small- and large-scale influences. The information gathered from bioindicator species ultimately

informs management decisions required for the maintenance of park ecological integrity. As large-scale influences, such as climate change, affect the Lake Superior ecosystem future change is inevitable. Ongoing study of herring gulls and other ecological indicators will continue to provide vital information for the management of protected areas and the larger ecosystem.

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