THE IDENTIFICATION OF ECTOPARASITES, THEIR EFFECTS, AND OTHER SELECTED POTENTIAL PATHOGENIC ORGANISMS ASSOCIATED WITH A BREEDING SEABIRD COLONY ON MIDDLETON ISLAND, ALASKA

by

BRIANNA MARIE WILLIAMS

(Under the Direction of Michael J. Yabsley)

ABSTRACT

The biological importance of Middleton Island, Alaska, to nesting seabird populations has been recognized for decades (Ramey and Hatch, 2005). Several species of pelagic seabirds breed on the island, including the Pelagic Cormorant (*Phalacrocorax pelagicus*), the Glaucous-winged Gull (*Larus glaucescens*), the Black-legged Kittiwake (*Rissa tridactyla*), the Common Murre (*Uria aalge*), the Rhinoceros Auklet (*Cerorhinca monocerata*), and the Tufted Puffin (*Fratercula cirrata*). Long-term studies of these colonies indicate population fluctuations with some species (e.g., Pelagic Cormorants, Black-legged Kittiwakes, Tufted Puffins, and Common Murres) exhibiting an overall decline. This study was designed to assess if selected potential pathogenic organisms affect seabirds at this location. In the first chapter, I identified ectoparasites from breeding seabirds; two species of ticks *Ixodes signatus* and *Ixodes uriae*, three species of fleas, *Ceratophyllus vagabundus vagabundus*, *Mioctenopsylla artica hadweni*, and *Mioctenopsylla traubi traubi*, and seven species of lice *Autromenopon transversum*, *Eidmaniella pellucida*, *Pectinopygus insularis*, *Quadraceps obliquus*, *Quadraceps ornatus*, *Saemundssonia calva*, and *Saemundssonia lari*. From ticks and fleas, we found evidence of two *Rickettsia*

species. In the second chapter, I experimentally evaluated the effects of parasitism on Black-legged Kittiwake chicks. I found relatively high burdens of ticks (mean 2.19, range 0-42), and that ectoparasites reduced fledging rate and nestling skeletal growth. In the third and fourth chapters, respectively, we surveyed the six species for vector-borne infectious agents (*Babesia*, *Borrelia*, *Haemoproteus*, *Plasmodium*, and *Leucocytozoon*) and influenza A virus (IAV). We did not find evidence vector-borne agents or IAV were circulating on Middleton Island. However, we noted high prevalence of antibodies to IAV in adults, and low prevalence in chicks. Antibody positive samples tested by hemagglutination inhibition (HI) against five hemagglutinin (HA) subtypes (H1, H4, H5, H13, and H16), revealed previous exposure to all subtypes tested, with H16 and H5 antibodies as the most predominate. Seabirds are an important group of avian fauna of conservation concern, and declines have become pronounced over recent decades. Little research has been conducted to determine if pathogenic organisms could be playing a role. Our study highlights the need to monitor vulnerable seabird populations, such as those on Middleton Island, for potential pathogens and effects thereof.

INDEX WORDS: Middleton Island, seabirds, ectoparasites, ticks, fleas, lice, *Ixodes*, avian influenza

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BSFR, University of Georgia, 2012

A Dissertation Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

DOCTOR OF PHILOSOPHY

ATHENS, GEORGIA

2022

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DEDICATION

I would like to dedicate this dissertation to my endlessly patient husband, Philip M. Berger, without whose unwavering support and love, these adventures and this product would have been impossible. In addition, this dissertation is dedicated to my son, Owen M. Berger. May you always be inquisitive about the natural world and demonstrate love for all that live in it.

ACKNOWLEDGEMENTS

First, I would like to thank my major professor, Michael J. Yabsley. It was his teaching and guidance in my formative education that sparked my interest in the vast world of wildlife disease ecology. It was also his patience and support that guided me through the often-painful process of completing this body of work. While I never envisioned myself falling in love with birds, it was easy for me to trust you when you sent me to the "ends of the Earth." It has been my privilege to be challenged under your tutelage.

To my committee members Drs. Dave Stallknecht, Andrew Ramey, and Richard Chandler for guiding me through the various portions of my graduate schooling. Dr. Stallknecht expanded my passion for wildlife into the world of virology and cell culture. I am grateful for the hours we spent sharing a lab bench and the hours spent sharing your vast knowledge and advice. Dr. Chandler gave me the first opportunity to expand my learning not simply to the field of wildlife biology, but also to the field of teaching. I attribute the many visits to your office hours, fumbling through Program R, to finding my passion for teaching others. And Dr. Ramey pushed me to be a better scientist and writer. Thank you for your attention to detail and persistence to making this final product the best possible.

To those members of The Southeastern Cooperative Wildlife Disease Study. During my time spent here, I have seen many students, faculty, and staff come and go and then return to study again at this place. Few institutions garner this much loyalty, and fewer deserve it in the way SCWDS does. I am eternally grateful for the friendships and professional connections I have made through being a part of SCWDS. Dr. Kishana Taylor, thank you for being my friend

and confidant through these many years. There are many more to thank including Kayla Garrett, Jojo Crum, Sarah Peltier, Alec Thompson, Barbara Shock, Sarah Sapp, Rebecca Poulson, Chris Cleveland, Matthew Walter, for sharing knowledge, coffee, or a laugh.

To those that helped with field assistance including my amazing technicians, Morgan Walker and Mason Stothart, who were literally stranded on a (mostly) deserted island with me for months working in extreme conditions with temperamental subjects. And to "The Canadians," Josh Cunningham, Shirel Khane-Rapport, Elsa Kern-Lovick, and Angelike Aleksieva for field assistance, and becoming my Middleton Island family. To the other temporary residents of Middleton Island, Scott and Martha Hatch, your wisdom and experience with the colonies there is awe-inspiring, and I hope only to have a fraction of your love for the natural world. And to Annie, thank you for the pets.

To those who helped fund this project, including the U.S. Geological Survey through the Wildlife Program of the Ecosystems Mission Area and the Georgia Ornithological Society. Support was also provided by the Southeastern Cooperative Wildlife Disease Study member states through the Federal Aid to Wildlife Restoration Act (50 Stat. 917), by a US Department of the Interior Cooperative Agreement with SCWDS, and the Daniel B. Warnell School of Forestry and Natural Resources.

I have eternal gratitude to my family for their support through this journey. It is not easy to love someone who is working on a dissertation, but you all managed to shower me. Thank you to my parents, Lee and June Williams, for teaching me I can do whatever I set my mind to. Thank you to my Mother-in-law, Mary Berger, for chasing a baby out of my office time and time again while I wrote. Thank you to my son, Owen, for being an inspiration and driving force to finish, I hope you are proud of Mama. And, finally, to my husband, Philip Berger, there are no

words to adequately express my gratitude for you being by my side for these many years while this project has always taken part of me away. Thank you for always encouraging me and helping me to shine in pursuit of my dreams.

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CHAPTER 1

INTRODUCTION

This study was designed to determine if selected potential pathogenic organisms affect health and survival of seabirds breeding on Middleton Island, Alaska (59°44’ N, 146°33’ W). The biological importance of this location to nesting seabird populations has been recognized for decades (Ramey and Hatch, 2005). At least seven species of pelagic seabirds breed on the island, including Pelagic Cormorant (*Phalacrocorax pelagicus*), Glaucous-winged Gull (*Larus glaucescens*), Black-legged Kittiwake (*Rissa tridactyla*), Thick-billed Murre (*Uria lomvia*), Common Murre (*Uria aalge*), Rhinoceros Auklet (*Cerorhinca monocerata*), and Tufted Puffin (*Fratercula cirrata*) (Rausch, 1958). Long-term studies of these colonies indicate that they undergo fluctuations in reproductive success, with cohorts experiencing significant mortality or complete failure in some years. Although food availability is believed to influence reproductive success and resulting population changes, other factors are likely involved.

Multiple studies have examined growth parameters and nesting success of bird species on Middleton Island. However, minimal research has been conducted on disease ecology and its effects on breeding birds at this site. Colonial nesting, characteristic of the seabirds of interest, provides survival advantages; however, cohabitation in close proximity also increases the risk of disease (Alexander, 1974; Møller, 1993). Pathogen transmission may increase with increased interspecific contact and behaviors such as nesting site fidelity, characteristics common in pelagic seabirds (Brown and Brown, 1986; Hatch et al., 2011). High burdens of ectoparasites

also can change hosts' behavior and physiology and reduce reproduction and survival of young (Aeschlimann, 1991; Duffy, 1983).

In addition to behavioral changes associated with high parasite burdens, population-level effects, such as lower nest success and greater chick mortality, are significant concerns (Anderson and Ma, 1978; Gauthier-Clerc et al., 1998). In England, high tick (*Ixodes uriae*) burdens were correlated with population reductions of Black-legged Kittiwakes; however, the study did not investigate the effects of ticks on individual birds (Boulinier and Danchin, 1990). Additionally, an observational study in Peru reported that high nest ectoparasite burdens caused Guanay Cormorants (*Leucocarbo bougainvillii*), Peruvian Booby (*Sula variegata*), and Peruvian Brown Pelican (*Pelecanus thagus*) to abandon nests (Duffy, 1983). A study of Cliff Swallows (*Hirundo Pyrrhonota*) in the United States reported that high ectoparasite loads cause reduced body mass and early fledging (Brown and Brown, 1986; Lehman, 1993).

Ticks are distributed worldwide and are second only to mosquitoes in terms of their potential as pathogen vectors (Jongejan and Uilenberg, 2004). Ticks can also negatively affect their hosts (e.g., exsanguination, predisposition to secondary infections, direct skin damage, etc.) (Sonenshine and Roe, 2014). However, knowledge about seabird ticks, while increasing, is still limited. Seabird colonies provide suitable habitat for shelter-seeking ticks to complete various portions of their lifecycle (Diethrich et al., 2011). The most common ticks reported from seabird colonies in the palearctic and North Pacific region are *Ixodes signatus, Ixodes uriae, Carios capensis,* and *Carios maritimus,* all of which have been associated with pathogen transmission (Banks, 1908; Zumpft, 1952; Choe and Kim, 1987a; Choe and Kim, 1987b). Other ectoparasites of interest to seabird health include fleas, mites, and lice. Health issues, such as anemia, lowered reproductive success, and nest abandonment have been documented with high levels of tick, flea,

and mite infestations (Clayton, 1990; DeVaney, 1976; Booth et al., 1993; Lehmann, 1993). In addition, female Blue Tits (*Cyanistes caeruleus*) infested with nest ectoparasites had higher levels of heat shock proteins, indicating increased stress compared to females utilizing treated nests (Martinez-de la Puente et al., 2011). Because some species of lice and mites have coevolved with their host species, they are considered nonpathogenic; however, controlled studies are needed to investigate possible pathogenic effects of these ectoparasites (Barker, 1996; Page et al., 1996).

Ectoparasites are known to occur on Middleton Island seabirds and could contribute to observed population declines at this site. In addition, it is important to investigate possible pathogen transmission. Seabirds can be hosts to numerous potentially pathogenic vector-borne organisms, such as *Haemoproteus*, *Plasmodium*, *Leucocytozoon*, *Babesia*, and *Borrelia* (Wobeser, 1997; Evans and Otter, 1998; Hublak, 2004; Atkinson, 2008; Yabsley et al., 2009; Lobato et al., 2011; Yabsley et al., 2012; Palinauskas et al., 2013). Several species of these vector-borne organisms can cause morbidity and mortality of seabirds (Nuttal, 1984; Yabsley et al., 2009; Argilla et al., 2013). In addition, some of these organisms may be zoonotic and can be moved long distances through bird migration (Cooper, 1990; Takano et al., 2009; Lobato et al., 2011). Few studies have been conducted on the ectoparasite fauna of seabirds in Alaska, although we know that birds on Middleton Island are heavily infested by ectoparasites (Ramey, unpublished data). To date, no surveillance for potentially pathogenic vector-borne organisms has been conducted on seabirds nesting on Middleton Island, Alaska.

The role of wild birds in the circulation of influenza A viruses (IAV) has been widely studied; however, recent evidence suggests the ecological role seabirds have in the transmission of AIV may differ from that of waterfowl. While movements of pelagic seabirds outside of

breeding are understudied, many seabirds are known to be long-distance migrants. Intraspecific and interspecific mixing of seabirds during migration, at breeding sites or wintering areas could facilitate cross-species transmission of IAV and long-distance spreading of virus (Garamszegi and Moller, 2007; Hall et al., 2013; Lebarbenchon et al., 2009; Pereda et al., 2008; Van Borm et al., 2001; Winker & Gibson, 2010; Ramey et al., 2016; Ramey et al., 2017; Reeves et al., 2018). For example, viruses that reassort with Eurasian lineages of IAV have been found in North American gulls (Wallensten et al., 2005; Krauss et al., 2007; Ramey et al., 2010; Wille et al., 2011). Alaska has been suggested as an important mixing ground for Eurasian and North American viral lineages as inferred from viruses identified in Anseriformes and Charadriiformes birds, which may be unsurprising given this location is geographically situated within flyways used by birds inhabiting Asia and North America (Koehler et al., 2008; Pearce et al. 2009; Pearce et al. 2010; Ramey et al., 2010; Hill et al., 2017; Ramey et al., 2018). Furthermore, as early as 2006, Alaska was identified as a likely point of introduction for Asian H5 highly pathogenic avian influenza viruses (HPAIV) into North America by wild birds (Interagency Working Group, 2006; Winker et al., 2007; Koehler et al., 2008; Winker & Gibson, 2010; Harris et al., 2016; Ramey et al., 2022).

The importance of Middleton Island as a potential mixing ground for IAVs is relatively unknown. Only one survey, conducted in 2010, examined the prevalence of IAV in seabirds on Middleton Island, Alaska (USFWS/USGS, 2011). This study was conducted on a small number (n=100) of Glaucous-winged Gulls, and all pools were negative; however, avian influenza has been previously reported in various gull species in Alaska, so additional sampling is warranted (Ramey et al., 2010; Wille et al., 2011). Understanding baseline prevalence of IAVs associated

with the avifauna inhabiting Middleton Island and the role birds play in the transmission of avian influenza may be important for informing wild bird IAV surveillance.

Spatial isolation on island communities can represent a barrier to the introduction and transmission of pathogens; this could potentially result in locally naïve populations. Naïve wildlife populations are of specific interest to pathogen transmission and maintenance in the context of a rapidly changing climate. Climate change predictions suggest changes of vertebrate host behavior and distribution for vector species (McCarty, 2001; Walther et al., 2002; Ogden et al., 2006; Eisen et al., 2008; Ogden et al., 2008; Hongo et al., 2012). It has been predicted that shifts in vectors and hosts will alter the distribution of pathogen ranges (Süss et al., 2008; van Hemert et al., 2014; Dantas-Torres, 2015; Eisen et al., 2016). Understanding the baseline prevalence of pathogens in seabird populations, such as those utilizing Middleton Island, may prove important for understanding the distribution of potential pathogenic organisms and may be useful for identifying potential populations at risk for disease emergence. Furthermore, this study would provide a foundation for long-term monitoring for early detection of infection in naïve hosts in the arctic.

The objectives of this project were to:

(1) Assess the prevalence and diversity of ectoparasites on breeding birds on Middleton Island and selected microorganisms including *Rickettsia* and *Babesia* within ticks and fleas,

(2) Conduct a survey of six species of breeding seabirds on Middleton Island for potentially pathogenic vector-borne organisms including *Babesia*, *Borrelia*, *Haemoproteus*, *Plasmodium*, and *Leucocytozoon*,

(3) Experimentally evaluate whether treatment of Black-legged Kittiwake nest sites with mild insecticide will reduce average tick burdens and characterize the differences in morphometric measurements (i.e. weight, wing chord, culmen, tarsus-metatarsus, and tail length) at discrete time periods, growth rate (i.e. the average change in individual morphometric measurements), health parameters (i.e. hematocrit and heterophil:lymphocyte ratio), and fledge success between those nestlings in treated nests compared to those in control nests,

(4) Determine prevalence of avian influenza infection and antibodies and attempt to identify the hemagglutinin subtypes associated with seabirds inhabiting Middleton Island.

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CHAPTER 2

LITERATURE REVIEW

Middleton Island

Middleton Island, Alaska (59°44' N, 146°33' W) is approximately 13km^2 in area and located about 115 km off the mainland in the Gulf of Alaska (Figure 1) (Miller, 1953). It emerged from the sea approximately 4,300 years ago during a period of tectonic shifting (Plafker and Rubin, 1997). The last major tectonic event, which occurred in 1964, created a large shelf under previously existing cliffs, increasing the number of shorebird nesting sites (Plafker and Rubin, 1997). The biological importance of Middleton Island to nesting seabird populations has been recognized for decades (Ramey and Hatch, 2005). At least seven species of pelagic seabirds breed on the island including, Pelagic Cormorant (*Phalacrocorax pelagicus*), Glaucous-winged Gull (*Larus glaucescens*), Black-legged Kittiwake (*Rissa tridactyla*), Thick-billed Murre (*Uria lomvia*), Common Murre (*Uria aalge*), Rhinoceros Auklet (*Cerorhinca monocerata*), and Tufted Puffin (*Fratercula cirrata*) (Rausch, 1958).

Previously used for six years during the cold war as a United States Air Force installation, associated structures on the island were decommissioned in the early 1960s. Nesting Black-legged Kittiwakes and Pelagic Cormorants began using these structures as nest sites, including the main communications radar tower. The tower was subsequently modified by a cooperation of the United States Geological Survey-Biological Resources Division (USGS-BRD) and U.S. Fish and Wildlife Service to allow access to nesting adults and chicks via window panels (Figure 2). Seabirds also use the cliffs surrounding the island for nesting.

Average temperature for the warm season (June to September) ranges from approximately 9-15°C and, in the cold season (November to April), from 1-6°C (Adapted from Weather Spark). There is variation in precipitation throughout the year, with the majority being rainfall. The wet season occurs between August and March, where 40% of days have over a millimeter of precipitation. Average total precipitation for Middleton Island is 136 cm. While wind speed varies throughout the year, the average wind speed 10 meters above ground ranges from 4.7 to 8.7 meters/second. The longest day of the year occurs in June and includes 18 hours and 40 minutes of daylight, and the shortest occurs in December and is 6 hours and 3 minutes.

Seabird Natural History

Seabirds are found on every continent and have diverse life histories. Generally, seabirds are long-lived iteroparous breeders. Age at first breed is highly varied, ranging from two years to over seven years old and is correlated to body size as in most species, with those that have larger bodies breeding later (Stearns, 1980). However, there is evidence that seabird breeding is determined by adult survival; those long-lived species breed later than those that have reduced survival (Gaston, 2004).

Though many seabirds are wide-ranging, long-distance migrants, they often return to their natal sites for breeding, where they form large mixed-species colonies (Harrison et al., 2018; Davies et al., 2021a; Fauchald et al., 2021a). Colonial breeding has many advantages, including protecting of an individual from predation by aggregation to avoid detection of any one individual (Alexander, 1974; Irvine et al., 2021). Furthermore, the best breeding sites on island communities are far from most terrestrial predators, but this habitat is limited. so aggregation is necessary. Conversely, some species, like large predatory gulls, may be drawn to other breeding colonies for the abundant prey. Colonies may also act as “information centers,” where individual

birds receive information about the location of food sources and birds feed in flocks within these prime locations, although there is considerable debate about this hypothesis (Ward & Zahavi, 1973; Bayer, 1982).

Members of the Families Laridae, Phalacrocoricidae, and Alcidae are generally ground breeders. However, many seabirds choose ground nesting sites with some protection, such as building on the surfaces of cliffs, burrowing underground, or other means of concealment to protect nestlings. Clutch size, as with other long-lived birds, is generally small, except for members of Phalocrocaracidae, which may lay more than five eggs (Ashmole, 1963; Lack, 1966; Goodman, 1974, Ydenberg & Bertram, 1989). Procellariiformes and terns that spend time feeding pelagically almost exclusively lay a single egg (Sotherland and Rahn, 1987). The time of incubation is highly correlated with the length of the developmental period (Lack, 1968).

Most seabirds are monogamous during a single breeding season (Hudson, 1985). The need for parental involvement in foraging and chick rearing makes a monogamous partnership ideal for seabirds as one parent can spend extended time foraging while the other can incubate eggs or, after hatch, protect the flightless chicks. Seabirds generally share parental duties between the sexes. Either one will constantly remain on the nestling while it is flightless and work in shifts to relieve each other. However, this behavior may make parents more susceptible to predators or parasites found around the nesting site. Diurnal visits to some species' nest sites may help avoid adult predation s and conceal nests (McNeil et al., 1993). This behavior of shared parental duties also reduces the overall time that parents can forage. Compensation is made through selection of nest sites near foraging areas.

In many species of seabirds, nestlings will grow to adult size or larger than the parents. Chick obesity is a beneficial life strategy as foraging trips for the parents may be long, and

overweight chicks are more likely to survive through times of low provisioning (Hamer et al., 2000). Furthermore, larger chicks allow the parents to be away from the nest longer for their own forage. This absence requires a large amount of food be carried from the forage areas to the nest. Most seabirds, thus, have evolved to carry food loads within the body that can be regurgitated to the young and, in some cases, the ability to preserve foods in the body. Young generally are fed at the nest or nearby until near adult size is reached, being either precocial (in the case of the Auks) or semi-precocial (Gulls) according to the classifications determined by Nice (1962).

Reproductive success over a seabird's lifespan is highly variable, depending on species and populations. In general, lifetime reproductive success is lower in birds than in other terrestrial species, but it is theorized that, because of small clutch size, it is far lower in seabirds (Blueweiss et al., 1978). However, it should be noted that, because seabirds may live well over 20 years, it is difficult to determine the total reproductive success of an individual. Reproductive success, generally, increases with age as individuals gain breeding experience (Reid, 1988; de Forest and Gaston, 1996).

Once they reach adulthood, survivorship is relatively high in seabirds, as most species have a 90% or better chance of surviving until the next year (Gaston, 2004). However, because of their pelagic nature, studies are challenging and can generally only be conducted at single sites (Harrison et al., 2018; Davies et al., 2021a). Larger seabirds and those that feed offshore likely have increased lifespans, but this can vary between species, populations, and even years at the same site (Lack, 1968). There is some evidence of senescence, or that survival probability is reduced in very old seabirds. There is also evidence that survival may also be low among young birds. (Coulson and Wooller, 1979; Crespin et al., 2006; Reed, 2008).

Black-legged Kittiwakes

Black-legged Kittiwakes (Family: Laridae) are considered one of the most widely distributed and numerous gull species with a worldwide population size of 3,460,000-4,410,000 associated with the North Pacific and North Atlantic on all continents in the Northern Hemisphere (Birdlife International, 2019). However, population numbers are believed to bedeclining, and they are considered a vulnerable species worldwide (Descamps et al., 2017; BirdLife International, 2019). There are two genetically distinct subspecies; the Pacific subspecies, *Rissa tridactyla pollicaris*, and the Atlantic subspecies, *Rissa tridactyla tridactyla;* however, there is significant overlap in their range (Patirana, 2000; McCoy et al., 2005; Trevail et al., 2021). The Atlantic subspecies is more productive than their Pacific counterparts but are smaller and have shorter lifespans (Hatch et al., 2009).

Black-legged Kittiwakes are one of the smaller gulls (365-400 grams) and exhibit size sexual dimorphism, with females being slightly smaller than males. Head-bill length is used for sex differentiation (Helfenstein et al., 2004). As their name would imply, they have black feet and legs with a vestigial hind toe (Grant, 1986). Adult kittiwakes have a white head and body, dusky gray rounded wings with black outer wing tips, black rectrices, a slightly forked tail, and a yellow bill. Immature kittiwakes have a black "nuchal collar," a black stripe on the outer primaries, and a black bill (Dwight, 1925; Figure 3a).

Black-legged Kittiwakes are pelagic and rarely found inland in Alaska outside the breeding season. Breeding season in the northern Pacific occurs from mid to late March to late August. Black-legged Kittiwakes are primarily monogamous during the breeding season, and older birds that arrive at the breeding site are often already paired (Biderman et al., 1978; Nysewander, 1983; Mercier et al., 2021). Generally, they are thought to practice natal philopatry

(Hatch, 2009). However, several studies have noted that nest fidelity may not be as high in seabirds as previously thought, including the kittiwake (Coulson and Neve de Mevergnies, 1992; Coulson, 2016). In some colonies, natal philopatry was only between 11- 33% (Porter and Coulson, 1987; Coulson and Coulson, 2007). Movements between colonies may represent individuals leaving their natal sites in favor of better-quality habitat (Suryan et al., 2001; Acker et al., 2022).

Black-legged Kittiwakes are colonial nesters and may create nesting colonies of many thousands (del Hoyo et al. 1996). They nest on the edges of coastal cliffs in close proximity, and mixed species breeding grounds are common throughout their range. Nest material is comprises grasses, twigs, mud, and other natural materials, which can create habitat for nidicolous ectoparasites (Cullen, 1957; Maunder & Threlfall, 1972).

Black-legged Kittiwakes practice asynchronous egg-laying, with 1-3 eggs laid approximately 2-3 days apart (Gill and Hatch, 2002; Maunder and Threllfall, 1972). Both parents incubate eggs in approximate even time periods, relieving each other for foraging expeditions (Coulson and Wooler, 1984). Chicks are semi-precocial at hatch, with open eyes and downy feathers, weighing 30-44g (Maunder and Threllfall, 1972). They grow rapidly, gaining approximately 400 g at approximately day 30, then reducing weight before fledging. During the nesting period, parental attendance is relatively even between the sexes and depends on chick age, with lessened involvement as the chick ages and lowered food availability (Roberts and Hatch, 1993; Kahane-Rapport et al., 2022). Food, generally fish or marine invertebrates found close to the water surface, is delivered directly to the chick from the crop (Cullen, 1957; Coulson and Macdonald, 1962). Siblicide is common, and generally, the first hatched chick will kill the

subsequent hatches by pushing the other out of the nest or pecking the scalp until death (Braun and Hunt, 1983).

Chicks, when flighted, leave the nest on first excursions between days 32-50 (Nysewander, 1983). Full fledge occurs between days 34- 58, but chicks will return to the nest to beg parents for food (Maunder and Threlfall, 1972). Immature kittiwakes are pelagic for the first 2-3 years of their lives and return to natal sites after this time (Cramp and Simmons, 1983). The average age of first breed occurs between 3-5 years but depends on location. While life expectancy is unknown, it is generally considered to be approximately 13 years (Hatch et al., 1993).

Common Murre

Of the seabirds that nest on Middleton Island, the Common Murre (Family: Alcidae) is arguably the most studied worldwide. They have a circumpolar distribution, and numbers are estimated to be over 18,000,000 (del Hoyo et al., 1996). There are five recognized subspecies of the Common Murre. Two occur in the North Pacific south to California (*U. a. inornata* (Salomonsen, 1932), and *U. a. californica* (Bryant, 1861), and three occur from the North American Atlantic into Europe (*U. a. aalge* (Pontoppidan, 1763), *U. a. albionis* (Witherby, 1923), and *U. a. hyperborean)* (Salomonsen 1932). The Atlantic and Pacific subspecies are genetically distinct (Friesen et al., 1996). While uncommon, hybridization with Thick-billed Murres (*Uria lomvia*) in overlapping breeding grounds can occur (Friesen et al., 1993; Friesen et al., 1999).

Common Murres are large seabirds averaging 800-1,125 grams (Ainley et al., 2002). They are black to brown on their heads, wings, and back, with a white venter that extends onto the neck in an inverse “U” shape (Figure 3b). They have black, pointed bills and gray feet with

extensive webbing. Similar in appearance to their close relatives, the Thick-billed Murre, the two species can be distinguished by the thickness of the bill and by the extension of the white venter onto the neck; the bill of the Thick-billed Murre is much more pointed.

Considered to be one of the most social seabirds, outside of the breeding season murres will form large rafts and may attend breeding colonies outside of the breeding season (Dunn et al., 2020). Furthermore, murres nest within very close proximity to each other and commonly occur in mixed colonies. They are highly attracted to sites with established colonies (Parker et al., 2001). Murres are monogamous and may stay paired for many years (Hudson, 1985; Harris et al., 1996; Harris et al., 1997). However, female murres will copulate with nearby non-mate neighbors within the colonies as an assurance for possible infertility in their chosen mate (Walsh, 2001). They lay a single egg on bare rock with no nest formation (Tuck, 1961). Within the colony, there is very high synchronicity with egg laying; 90% of eggs are laid within 15 days of each other (Hatch and Hatch, 1990).

Both parents develop an incubation patch on their underbelly (Birkhead, 1993). They incubate eggs standing up for approximately 32 days after lay (Boekelheide et al., 1990). Chicks are semi-precocial when hatched with downy gray feathers and large tarsus, approximately 45% of the adult size (Mahoney and Threlfall, 1981). Both parents are active in feeding, although rarely are chicks left alone at the nest site, although during this occurrence, they may be adopted by failed breeders within the colony (Birkhead and Nettleship, 1984). Chicks are primarily fed fish, and, in the Northern Pacific, they are preferentially fed capelin (Piatt, 1987).

While timing varies throughout their range, chicks leave the nest site after 20 days while still flightless (Sealy, 1973; Ainley et al., 2002). Departure time is highly synchronous within colonies, more so than egg laying (Tuck, 1961). Approximately 48 hours before nest departure,

after sunset, males begin to coax the chick away from the nest and towards water through a specialized departure call. Chicks may jump off of steep cliffs followed closely by either parent, or they may follow the waiting parent into the water by following the calls below. Once in the water, the chick and male parent will duet call until reunited. The male parent will lead the flightless chick to nearby foraging areas, where it will remain for protection and feeding for approximately 1-2 months (Harris and Birkhead, 1985).

Because of this breeding strategy, murres are highly susceptible to predators, especially those with anthropomorphic introduction (Jones and Byrd, 1979; Birkhead and Nettleship, 1995). In Alaska, foxes, humans have introduced for fur production, were responsible for the loss of up to 250,000 Common Murre eggs in a breeding colony on Shaiak Island in 1976 (Peterson, 1982). Natural predators of chicks and eggs include other large gulls, ravens, and crows (Schauer and Murphy, 1996; Ainley et al., 2002).

Survival at sea is largely unknown, but the age of first return to natal breeding sites varies between 2-7 years depending on locality. Age of first breed is highly variable but generally occurs between ages 3-9. In areas with abundant food and habitat availability, Common Murres will breed annually; however, in years where the habitat is poor, poor habitat events or because of the loss of a mate, breeding adults may not breed every year (Harris and Wanless, 1995). Survivorship is challenging to estimate, but the oldest known wild Common Murre was 26 years and five months (Clapp et al., 1982).

Glaucous-winged Gull

The Glaucous-winged Gull (Family: Laridae) is found year-round down the western coast of North America and as far south as Baja California, often associated with urban habitats (Hayward and Verbeek, 2008). There are poor estimates of total population sizes; the North

American Breeding Bird Survey indicates approximately 380,000 breeding individuals (Sauer et al., 2017). While it is debated and poorly studied, there is some indication that this species may be declining in parts of its range while population numbers may be increasing in other parts. Glaucous-winged Gulls hybridize with several species, including the Western Gull (*L. occidentalis*), Herring Gulls (*L. argentatus*), and Glaucous Gulls (*L. hyperboreus*).

These gulls are considered one of the largest in North America, weighing 890-1360 grams, with the females being slightly smaller than the males. They are primarily white across the head, tail, dorsal, and ventral sides. They have light gray wingtips, pink legs, and a yellow bill with a red spot on the lower mandible. Juveniles have brown, mottled streaking across the head and breast (Figure 3c). Glaucous-winged Gulls in the Aleutians are larger than others across their range (Bell, 1996).

Glaucous-winged Gulls are highly gregarious, and non-breeding and breeding distributions overlap significantly. They generally occur alone or in pairs outside the breeding season but in large colonies during the breeding season. After arrival on the colony for breeding, partners may choose multiple nest sites but only complete one. Selection is favorable to those at low elevation (0-90m above sea level) on bare ground, under rocky cover, or in low herbaceous cover (Campbell et al., 1990; Vermeer and Devito, 1987). Nests are created by scraping the earth and piling loose material around the bare site (Patten and Weisbrod, 1974).

Clutch size is typically 1-4 eggs laid approximately two days apart (Hayward and Verbeek, 2008; Atkins et al., 2021; Nurhan and Henson, 2021). Parents develop three incubation patches each, and both sexes spend equal time incubating the nest (Schultz, 1951; Vermeer, 1963). Hatch occurs approximately 27 days after lay. Chicks are hatched with mottled gray and black downy feathers and are semi-precocial; they are mobile and able to leave the nest but still

rely on their parents for feeding. Glaucous-winged Gulls are highly omnivorous, and parents will feed chicks fish, invertebrates, scavenged carcasses, and non-organic material (Ward, 1973). Chicks are flighted by approximately day 43 but will remain at the colony until approximately day 57 (Vermeer, 1963).

While survivorship is generally unknown, it is theorized that most mortality occurs in the first two years (Butler et al., 1980). Age at first breed is between years 4-7, and most will return to their natal colonies (Reid, 1988). Most birds do not disperse more than 200 km from their natal sight, but a few have been documented to move long distances (Butler et al., 1980). Because of their propensity towards omnivory, they are highly associated with urban areas and are often associated with landfills or fishing waste (Schmidt, 1986). The life expectancy is 9.5 years; however, a banded bird was 32 years old (Campbell et al., 1990).

Pelagic Cormorant

The Pelagic Cormorant (Family: Phalacrocoracidae) may be the least studied species that utilizes Middleton Island. This species can be found as year-round residents of the Northern Pacific into Asia and as far south as Baja California. There is no global estimate for population size, but North American populations are estimated to be approximately 130,000, with an overall decreasing trend (Delany & Scott, 2006; Hobson, 2013). Unlike their name implies, Pelagic Cormorants do not spend the non-breeding season at sea but prefer areas close to shore where they occur in small groups or singularly.

These birds are the smallest cormorant species, with the females weighing less than males (1.5-1.7 and 1.75-2 kilograms, respectively; Palmer, 1962). Across the body, feathers are dark iridescent with purple-hued necks and green hues across the head and back (Figure 3d). Wings and underparts may present as a buffy bronze, and the head and neck may be adorned with white

filoplumes. Legs and feet are black or dark gray with extensive webbing. Breeding adults develop a bright yellow-green iris, often a distinct white patch on the rump, a reddish-brown patch on the lower mandible, and a bright red gular patch. Their bills are otherwise dark and have a distinct hook on the tip.

Nest sites are similar to Black-legged Kittiwakes, though Pelagic Cormorants tend to be more gregarious in their selection. They often nest on the side of cliffs or in sea caves in close proximity, but they may also nest in cavities on the ground or man-made structures (Hatch et al., 1979). Colonies often switch roost sites between years (Siegel-Causey and Hunt, 1986). Both sexes are responsible for nest building, although trial nests may be constructed several times before a final nest is created. Nest material comprises twigs, sticks, grasses, other materials, and excrement and is added throughout the season until chicks are completely fledged (Van Tets, 1959).

While there is no evidence of a clutch size gradient along latitudinal lines, there is geographic variation within clutch laying where those nesting in more secluded habitats lay more eggs (Hobson, 2013). Across their range, clutch size can range from 2-7 eggs (Baird et al., 1983; Cannon, 1990; Robertson, 1971). Egg laying is asynchronous, andboth parents share incubation duties for approximately 29 days (Boekelheide et al., 1990). Chicks are naked and altricial when hatched, weighing 30-40 grams, but quickly develop sparse gray downy feathers (van Tets, 1959).

Both parents attend to chicks in the nest. Parents provide shade for chicks until feather development, which generally occurs 42- 49 days post-hatch (Cannon, 1990). Brooding duties are switched for forage. Cormorants forage by diving, and dives may be over 100m, although typically are shorter (Dow, 1964; Kotzerka et al., 2011). Diet primarily consists of non-schooling

fish and benthic invertebrates (Ainley et al., 1981). Chicks beg by head waving while parents attend to one chick at a time. To feed, chicks insert their heads into the mouth of the parent, and meals are regurgitated (Robertson, 1971). However, breeding can be heavily influenced by climate and food, which can cause adults to abandon nests, thus increasing nest predation (Carter et al., 1984; Sydeman et al., 2001).

Age of fledging is relatively unknown, but chicks leave the nest at approximately day 40-50 for exploratory flights (Drent and Guiguet, 1964). First flights generally occur when chicks chase the parents to beg for more food. Juveniles do not return to the nesting site until approximately two years (Hatch et al., 2011a). While they may reach sexual maturity by year two, average age of first breed is three years (van Tets, 1959). Adult survivorship is unknown, but a bird from British Columbia was recorded as 17 years and ten months (Clapp et al., 1982).

Rhinoceros Auklet

The Rhinoceros Auklet (Family: Alcidae) has the most southerly distribution of the seabirds in this study. Outside of the breeding season, they reside in the North Pacific from Canada south to Baja California (Gaston and Dechesne, 1996). They breed as far north as the Aleutians and the Gulf of Alaska but do not generally go into the Bering Sea. In the western Pacific, they range from Korea to Japan. Because they breed in burrows, accurate population estimates are challenging, but it is estimated that there are 1.5 million breeding birds and 2-3 million total birds (Byrd et al., 1993).

Rhinoceros Auklets are medium seabirds weighing 389-616 grams, with females weighing slightly less than their male counterparts within the same area (Vermeer, 1979). The wings, back, and head are dark brown, while the throat and underwings are a lighter gradient (Figure 3e). The underside is a dirty white to light gray that extends onto the lining of the wing.

White plumes, three to seven cm long, extending from the top of the eye and behind the lower mandible. The legs, feet, and bill are brownish-orange outside of the breeding season. During breeding, the bill becomes bright orange, and both sexes develop their namesake: a yellow horn, one to three centimeters high on the top of the bill. This horn may remain vestigial after the breeding season.

Throughout their range, auklets are one of the first visitors to a breeding colony where pair bonding is developed. Nest construction begins early in the season. Like all members of the puffin family, they create extensive burrows. Site selection is generally for areas ten meters above sea level within densely forested areas or areas with dense vegetative coverage intermixed with sloping cutouts for easy flight take-off and landing (Wilson, 1977). Both parents use large claws to excavate nest sites within burrows which may be 1-5 meters long and lined with grasses and leaves (Leschner, 1976). The nesting site is generally lower than the entrance of the burrow.

Only one egg is laid per clutch; however, in the event of mortality, they have been known to lay a replacement clutch (Summers and Drent, 1979). Both parents seemingly care for the egg, as both have brood patches on the venter; however, time away from the nest may be extended for several days without detrimental effects on the hatch. Chicks weigh 46-64 grams at hatch and have dark gray downy feathers and a preeminent horn (Bertram, 1988).

While the role of parents is unknown for this species, both parents return to the nest at night with bill loads, indicating that, like in most seabirds, parental duties are relatively even (Wilson, 1977). Rhinoceros Auklet diet is generalist, but they prefer to forage in small schooling fish communities (Wilson and Manuwal, 1986; Cunningham et al., 2018). Younger chicks do not leave the burrow but may approach the entrance at night, while Older chicks may leave at night to move around the entrance. Time of departure is correlated with food availability, growth rate,

and predation pressure (Harfenist, 1991). Chicks are not fully flighted at nest departure but may flutter to the water at day 38-56 (Summers and Drent, 1979).

Little is known about the development of chicks once they leave the nest site. Much of what is known about auklet biology is presumed from research on closely related puffins. Age at first breed is thought to be approximately three years, and they breed annually. While there is some evidence that Rhinoceros Auklets return to their natal sites to breed, nest fidelity rates are unknown (Wilson, 1977).

Tufted Puffin

It is difficult to disagree with the assessment of Tufted Puffins (Family: Alcidae) written by Piatt and Kitaysky (2002) when they open their review with the statement, "Tufted Puffins are cool." Considered to be the most pelagic of the Family Alcidae, they are gregarious throughout the Northern Pacific, where they can be found along coastlines in the summer breeding season or over deep waters in their winter range. They range from as far north as the Chuchki Sea in the southern Artic Ocean and south down to California. While population estimates are conservative because in-nest burrow census is challenging to perform, current numbers are thought to be over 3.5 million across the Northern Pacific and declining (del Hoyo et al., 1996).

While not as highly decorated as the Atlantic Puffin (*Fratercula arctica*), Tufted Puffins are noticeable by their bright orange feet and bills, white faces, and long yellow feather tufts that occur in the breeding season (Figure 3f). Bills possess a variable number of grooves and rictal rosettes during this time. Outside of the breeding season, they are significantly more subdued in their plumage, being a dark brown with lighter brown or gray to white streaks behind the eyes instead of their signature tufts. During this time, grooves on the bill are lost, but it remains orange at the tip and darker near the nares. They are very stocky with short wings but are

powerful flyers while airborne. Males are generally larger than females, although geographic variation also plays a role in size (Shiomi and Ogi, 1991; Gaston and Jones, 1998). Overall size ranges from 520-1,000 grams.

Throughout their range, breeding biology can be variable, but they are generally colonial nesters that nest on small islands in mixed colonies (Wehl, 1980). Pair formation occurs close to the nesting colony on the water (Mikhtaryantz, 1977). Courtship includes males chasing chosen females and opening and closing their mouths to present the bright linings of their mouths. If allowed, the male will approach the female, and they will bill, or rub their bills together, before copulation. The tufted puffin spends much of its time at breeding sites on social displays (Vodolazova and Klenova, 2021). Nest sites are generally selected on steep cliffs where puffins create large extensive burrows. Like the Rhinoceros Auklet, they use their claws to excavate tunnels up to five meters long and line the nesting area with nearby twigs and grasses. Many burrows contain multiple passages and can be used for multiple years (Baird and Jones, 1983).

One egg is laid per clutch, but if lost it can be replaced 10-21 days after loss (Wehle, 1980). Both parents incubate the eggs and have two brood patches, each on the lateral side of the venter. Eggs may be left for several hours to a day without detrimental effects. Eggs hatch after 41-54 days, and chicks are semiprecocial with dark gray downy feathers and have a prominent white egg tooth (Baird and Jones, 1983; Amaral, 1977). They are 61.4-70.3 grams at hatch but grow relatively linearly, depending on food availability (Baird and Jones, 1983; Kitaysky, 1996). Both parents trade off continuously brooding between days one and four but then leave the chicks unattended intermittently throughout the day. Parents feed the chick a wide variety of prey items in the burrow twice daily. Prey selection is driven by diving habitats, over 100 meters, when puffins will search the bottom for benthic fish and invertebrates as well as schooling fish

(Ainley and Boekelheide, 1990; Burger, 1991; Hatch and Sanger, 1992; Piatt and Anderson, 1996; Piatt and Kitasky, 2002).

Chicks are ready to fledge at days 38-59 (Wehle, 1980). They generally depart the nest at night by flight or walking to open water. During this time, adults are not present, and they provide no care to the juveniles on the water (Piatt and Kitasky, 2002). There are few data about the juvenile life history of the Tufted Puffin, but they are believed to stay pelagic until breeding. Age of first breed is unknown but presumed to be similar to that of the Atlantic Puffin that breeds between years 3-5 (Harris, 1984). Total life span is unknown, but, as in other seabirds, it is thought to be over 20 years.

Seabirds in Decline

Seabird species have been extensively studied as they are indicators for long-term and large-scale marine ecosystem health (Piatt et al., 2007; Einoder, 2009; Ramos and Furness, 2022; Paiva, 2022). It has been theorized that, overall, seabirds are the most threatened group of avian fauna and that declines have become more pronounced over the last several decades (Croxall et Al., 2012; Paleczny et al., 2015). Furthermore, those seabirds with pelagic life history traits are more threatened than those that frequently utilize coastal habitats because they tend to have smaller clutch sizes, so it is more difficult to recover from detrimental losses. Some theorized reasons for the global decline of seabirds include habitat degradation of shore and breeding sites, lack of food or changing ranges of food, and competition with novel invasive species.

Anthropomorphic pollution is arguably the top contributor to marine and coastal habitat degradation (Ryan et al., 1987; Thompson et al., 2009a; Thompson et al., 2009b; Elliott and Elliot, 2013). Plastic pollution, which can cause entanglement or ingestion, has been estimated to be a risk for 90% of the world's seabirds (Derraik, 2002; van Franeker et al., 2011; Wilcox et al.,

2015; Ryan, 2018; Linneberg et al., 2021; Baak et al., 2020; Kühn and van Franeker 2020). Seabirds will ingest large amounts of plastic debris, which can cause the impairment of digestive efficiency, damage to the gastrointestinal tract, and leaching of chemicals from the plastic (Day et al., 1985; Ryan, 1987; Auman et al., 2019; Laist, 1997; Tanaka et al., 2013; Lu et al., 2019). Reduced digestive efficiency can lead to poor body condition and lowered fledge success (Lavers et al., 2014). While many of these studies have been conducted in the southern hemisphere, Middleton Island is known for debris pollution associated with the 2011 tsunami impacting the Northern Pacific Ocean (Opfer et al., 2012; Murray et al., 2018). Furthermore, studies provide evidence that plastic is an increasing problem in remote Arctic areas, especially as human activity increases (Mallory et al. 2006; Provencher et al. 2009; Provencher et al. 2010; Smith and Stephenson 2013).

Furthermore, mercury contamination from anthropogenic sources such as fossil fuel consumption, mining, and chemical production has become a significant concern for the arctic (Braune et al., 2015; Dietz et al., 2009; AMAP, 2021). Seabirds, which are at the top of the food chain in marine environments, have shown bioaccumulation of the toxic form of methylmercury (Provencher et al., 2014; Peck et al., 2016; Albert et al., 2019; Chastel et al., 2022). Even in low exposure, methylmercury can lead to adverse effects on avian reproduction and lowered immune function (Wolfe et al., 1998; Scheuhammer et al., 2007; Brasso and Cristol, 2008, Hawley et al., 2009, Hallinger and Cristol, 2011; Jackson et al., 2011). Research in seabirds, while gaining interest, is limited. However, studies show that mercury accumulation may reduce fat reserves (an essential factor in reproduction and survival for marine birds), increase parasitic infections, reduce immune function, and cause neurological changes (Thompson et al., 1992; Wayland et al., 2001; Wayland et al., 2002; Scheuhammer et al., 2008; Bond and Diamond, 2009; Bond et

al., 2015; Ackerman et al., 2016; Dietz et al., 2021; Pollet et al., 2022). Furthermore, high levels of mercury may reduce egg hatchability, fledge success, nest attendance, and forage time, and cause deformities in avian embryos in breeding seabirds which may lead to overall population declines (Evers et al., 2004; Heinz et al., 2009; Braune et al., 2012). The Arctic, including Alaska, has been pinpointed as a sink to atmospheric mercury (AMAP, 2021).

Large-scale reduction and movement of large and small fauna in marine ecosystems has been well noted (Lotze et al., 2006; McCauley et al., 2015; Ford et al., 2021; Fauchald et al., 2021b). In particular, the decline of fisheries because of human impacts has been the most notable defaunation of any taxonomic group (Jackson et al., 2001; Mueter, 2022). In conjunction with increasing anthropomorphic fisheries demands, these declines leave seabirds potentially with what remains, which may be less preferable prey. Lowered food quality (e.g., low lipid content) may reduce overall fitness in species with limited ability to carry rations, energetically expensive foraging behaviors, and those whose digestive efficiency is lowered with lipid quality (Österblom et al., 2008). Furthermore, the movement of fisheries may cause range shifts and migration differences in pelagic seabirds (Patterson et al., 2021). Warm winters and lowered sandeel fishery recruitment adversely affect Black-legged Kittiwake populations in the North Sea (Frederiksen et al., 2004).

Discard from large commercial operations has become a critical non-foraging supplemental food source for some seabird species (Voteir et al., 2013). However, industrial fisheries may have large-scale impacts directly on seabird species as they can be accidental by-catch (Furness, 2002; Dasnon et al., 2022). A range of 160,000 – 320,000 seabirds are estimated to be killed each year globally as a result of long-line fisheries by-catch; however, large gaps in reporting and research make this a conservative estimate (Anderson et al., 2011; Pott and

Widenfield, 2017; Jannot et al., 2021). Certain species may be more or less vulnerable to by-catch, including those that forage closer to the surface (Lewison et al., 2014).

There is increasing research on the population impacts of climate change on marine species, especially concerning species in the northernmost ranges (Walther et al., 2002; Markon et al., 2018; Previdi et al., 2021). Oscillations in climate have caused population fluctuations in seabird colonies related to food availability (Irons et al., 2008). Climate modeling has resoundingly predicted that global ocean temperature will continue to rise (Abraham et al., 2013; Pershing et al., 2018). Specifically, in the North Pacific, it is theorized that a significant regime shift moving from warm to cool conditions occurred in 2008 (Hatch, 2013). This shift to cool water is associated with higher capelin numbers, the Black-legged Kittiwake's preferred diet, and thus higher numbers of fledged young. Conversely, a large mass of warm water, colloquially known as "The Blob," has appeared intermittently off the coast of Alaska since 2013 and has had a significant impact on food sources. This water mass has increased surface temperature by as much as six °C (Bond et al., 2015; Cavole et al., 2016; Peterson et al., 2016; Gentemann, 2017; Jones et al., 2018; Amaya et al., 2020; Piatt et al., 2020). Increased surface water has been correlated with mass die-off events of forage fish species and seabirds during this time (Walsh et al., 2018; von Biela et al., 2019; Jones et al., 2018; Piatt et al., 2020).

Furthermore, rising sea levels may contribute to the loss of seabird breeding habitat (Reynolds et al., 2015). One study modeled the effects of habitat loss from anthropomorphic factors in relation to the winter migration of seabirds and found that only the most flexible species would sustain minimal population losses and the least flexible faced possibilities of extinction (dolman and Sutherland, 1995). Loss of breeding grounds, even in colonial nesting species, may contribute to density-dependent mortality and nest failures during the breeding

season (Kokko et al., 2004). Climate change has been theorized to be responsible for pushing back the timing of the breeding in polar seabirds, which may reduce brooding time and have consequences for over-winter survival (Gaston and Hipfner, 1998; Gaston et al., 2005; Barbraud and Weimerskirch, 2006; Gaston et al., 2009). Rapid warming in the northern ranges of the world has raised issues about how disease will also change in the near future (van Hemert et al., 2014; Ma et al., 2021). Many vectors depend on warmer temperatures for life history and, thus traditionally have not been found in the extreme north. However, with increasing temperatures because of climate change, range expansion of ectoparasites has been predicted. With the presence of ectoparasites, the assumption of pathogen transmission is an important research consideration.

Introduction of novel non-native species such as squirrels, rats, and mice to areas inhabited by breeding seabirds is considered to contribute to the decline of seabirds (Atkinson, 1985; Courchamp et al., 2003; Towns et al., 2006; Wanless et al., 2007; Jones et al., 2008; Ruffino et al., 2008; Ruffino et al., 2009; Kürle et al., 2021; Oliveira et al., 2022). Invasive predators, such as red foxes and cats, have contributed to significant declines in individual populations (Peterson, 1982). In Alaska specifically, foxes have had widespread impacts on ground-nesting birds, including geese, ptarmigan, waterfowl, seabirds, and shorebirds (Bailey, 1993). Rats may extirpate ground-nesting species such as Tufted Puffins and Cassin's Auklets (Ebbert and Byrd, 2002). Arctic ground squirrels have been introduced through mainland Alaska and islands near the coast and have been known to prey on ground nesting birds, although the actual impacts are unknown (Geist, 1933). However, there has recently been considerable debate about the true long-term effects of introduced species on native populations (Gurevitch and Padilla, 2004).

Seabird Health

Group living and colonial nesting, common among seabirds, provide many survival advantages; however, close proximity linked with this cohabitation also increases the risk of pathogen transmission and exposure (Alexander, 1974; Møller, 1993). The risk of transmission increases with a high level of interspecific contact and high nesting site fidelity, characteristics common in species of seabirds such as those of interest in this study (Brown and Brown, 1986; Hatch et al., 2011a). Conversely, spatial isolation can represent a major barrier to the introduction and transmission of pathogens on island communities. However, migration over long distances may provide a key mechanism for pathogen transmission and introduction.

Migratory birds can play a prominent role in the ecology and circulation of microorganisms (Cooper, 1990; Wobeser, 1997). Because of their large home range sizes and long lifespan, seabirds may have a greater exposure risk to pathogenic organisms. These may include zoonotic pathogens or organisms that may have impacts on other wildlife species. Some of the documented potentially pathogenic microorganisms associated with migratory birds include arboviruses (such as eastern and western equine encephalitis, Sindbis alphaviruses, West Nile and St. Louis encephalitis), avian influenza virus, Newcastle disease virus, anatid herpesvirus-1, *Chlamydophila psittaci*, *Anaplasma phagocytophilum*, *Borrelia burgdorferi*, *Campylobacter jejuni*, *Salmonella enterica*, *Pasteurella multocida*, Bisgaard Taxon 40, *Mycobacterium avium*, *Candida*, *Aspergillus fumigatus*, *Eimeria*, *Sarcocystis* and blood parasites (Leighton & Gajadhar, 1986; Gajadhar & Leighton, 1988; Monroe et al. 1994; Enstipp & Gremillet, 2002; Yabsley et al., 2002; Hubalek, 2004; Yablsey & Gibbs, 2006; Atkinson, 2008; Knowles et al., 2019; Khan et al., 2019). While many of these organisms may or may not cause clinical disease among infected individuals, many can have sublethal effects or can cause clinical

disease in immunocompromised individuals such as those in rehabilitative situations or during periods of chronic stress. Specific organisms of interest in this study include avian haemosporidians, *Babesia*, *Borrelia burgdorferi*, *Rickettsia*, and avian influenza virus.

Avian Haemosporidians

Avian haemosporidians refers to a large, diverse group of organisms, including the genera *Plasmodium* (responsible for Avian Malaria), *Leucocytozoon*, and *Haemoproteus*, which is further broken into two subgenera, *Haemoproteus* and *Parahaemoproteus* (Valkiūnas, 2005). They have been noted to infect over 23 orders of avian taxa. There is debate about the taxonomy of these parasites, as species delineations have been historically delineated by morphological characteristics as well as hosts. However, recent molecular studies have shown that many previously reported species are actually species complexes, and some different species from different hosts are conspecific and just exhibit morphological differences (Garnham 1966; Valkiūnas, 1997; Bensch et al., 2000; Bensch et al., 2004; Bensch et al., 2009; Hellgren et al., 2013; Dimitrov et al., 2014; Field et al., 2018; Barrow et al., 2018; Ellis et al., 2019; Huang et al., 2019). While the vectors for many species are unknown, it is believed that the former three are vectored by haematophagos dipteran insects as follows: *Plasmodium* is transmitted by mosquitoes in the Culicidae, *Leucocytozoon* is transmitted by black flies in the family Simuliidae, *Haemoproteus* is transmitted by hippoboscid flies in the family Hippoboscidae, and *Parahaemoproteus* by biting midges in the family Ceratopogonidae (Desser and Bennett, 1993; Atkinson & van Riper III et al., 1991; Quillfeldt et al., 2011). These insects are the definitive host of the parasite where both sexual and asexual reproduction occurs, while vertebrates act as intermediate hosts where asexual occurs.

Plasmodium, *Leucocytozoon*, and *Haemoproteus* are all vector-borne and undergo a complex development in their vertebrate hosts (Valkiūnus, 2005). Generally, for all three genera, the life cycle begins in the invertebrate midgut, where sexual reproduction occurs and a zygote forms. This zygote embeds and forms an oocyst in the wall of the midgut of the invertebrate host and produces sporozoites until this oocyst ruptures into the body cavity. The sporozoites travel through the body to the salivary glands, where they are released into the vertebrate host upon the invertebrate host feeding. When the insect feeds, saliva containing anti-coagulant enzymes and the sporozoites are injected into the bloodstream. From the bloodstream, the sporozoites invade into tissue cells, developing into cryptozoites and then merozoites outside the blood cell. These merozoites develop into sexual maturity in the erythrocytes of the avian host, where a new invertebrate host can subsequently take them. Parasites can remain in the bloodstream for years.

Because avian haemosporidians are maintained in dipteran vectors, suitable environmental conditions are necessary for development, including temperature, precipitation, wind speed, and freshwater breeding habitat (Eide and Fallis, 1972; van Riper III et al., 2002; LaPointe et al., 2010). Furthermore, it is likely that mosquitoes and biting flies may follow the 10° C annual isotherm and cannot survive larval development during freeze, or under -1° C. High wind speeds with a lack of vegetative refugia have been noted to reduce the dipteran vectors in tundra environments (Service, 1980; Bennett et al., 1992; Ramey et al., 2012). Low ambient temperatures at high altitudes and extreme latitudes may limit the ability of avian haemosporidians to reproduce within the host (Warner, 1968; LaPointe et al., 2010; Loiseau et al., 2012). However, there is much variability of haemosporidians to tolerate temperature fluctuations and still replicate, with time frames of exposure ranging from 15 minutes to 23 days (Ball and Chao, 1961; Santiago-Alarcon et al., 2012).

The severe effects of avian malaria have most notably been studied in bird species in Hawaii, where introduced vectors allow for transmission to native birds, and the parasite was responsible for the extinction or threatened status of over 50 endemic species (Warner, 1968; van Riper III et al., 1986; Atkinson et al., 1995). There are few other reports of mortality in free-ranging adult birds, but haemosporidian mortality has been noted in penguins in Australia (Cannell et al., 2013). Most notably, wild bird mortalities are associated with juvenile birds, as has been noted with *Leucocytozoon* with the yellow-eyed penguin (*Megadyptes antipodes*), Canada Goose (*Branta Canadensis*) and Pink Pigeon (*Columba mayeri*), and *Plasmodium* in American Robins (*Turdus migratorius*) (Herman et al., 1975; Beier et al., 1981; Peirce et al., 1997; Dawson and Bortolotti, 2000).

This juvenile mortality effect of parasitism is further demonstrated by experimental studies such as that conducted by Sol et al. (2003), which demonstrated the "selection hypothesis," or the idea that juveniles that are parasitized are more likely to die than adults, by infecting Pigeons (*Columba livia*) with *Plasmodium*. Additionally, studies have demonstrated mortality in waterfowl infected with *Leucocytozoon* and Eurasian Siskins (*Carduelis spinus*), Common Crossbills (*Loxia curvirostra*), and Common Starlings (*Sturnus vulgaris*) exposed to *Plasmodium* (Fallis and Bennett, 1966; Palinauskas et al., 2015; Ilgūnas et al., 2016). Furthermore, avian haemosporidia has been indicated to have a variety of potentially severe effects on captive and rehabilitated animals, including lethargy, leukocytosis, lymphocytosis, anemia, myocarditis, nephritic disease, fluid in the coelomic cavities, hepatic disease, and mortality (Fix et al., 1988; Cranfield et al., 1990; Cranfield et al., 1994; Graczyk et al., 1995; de Macchi et al. 2013; Cannell et al. 2013).

Aside from the acute effects of avian haematozoans on free-ranging hosts, sublethal effects have also been documented. Wild birds often develop long-term infections. It has been theorized that sublethal effects may be more widespread than reported, but these effects are difficult to study and document (Valkiūnas, 2005). Predation risk by Eurasian Goshawk (*Accipiter gentilis*) and the European Sparrowhawk (*Accipiter nisus*) was demonstrated to be 16-25 times higher for prey individuals infected with haemosporidians (Møller and Nielsen, 2007). *Haemoproteus* infections have been associated with lower immune function in Passerines (Ots and Hõrak, 1998; Dunn et al., 2013). Asghar et al. (2015) noted reduced telomere length in Great Red Warblers (*Acrocephalus arundinaceus*) infected with *Plasmodium*, which has been correlated with reduced life expectancy. Hemoglobin was noted to be higher in breeding Great Tits (*Parus major*) treated with a mild insecticide (Krams et al., 2013).

Conversely, there is evidence that haemosporidian infections may have negligible impacts among infected hosts. Multiple studies have found that infections with haemosporidia do not affect survival probability (van Oers et al., 2010; Hammer et al., 2016; Podmokła et al., 2017; Ellis et al., 2020). Specifically, passerines that have co-evolved with these parasites are likely to experience deleterious effects (Palinauskas et al., 2008). Furthermore, in one study in Great Tits, researchers noted that infections with heamosporidia reduced survival probability but increased reproduction, providing support that reproductive effort can offset individual fitness (Pigeault et al., 2018). However, it is important to note that host-parasite interactions are complex, and parasites often differ in their effects on the different hosts (Kulma et al., 2013).

Breeding biology of the avian host may play a major role in the epidemiology of haemosporidia. Highest levels of parasitemia were noted in Gray Catbirds (*Dumetella carolinensis*) during the breeding season, which was theorized to be due to hormonal fluctuations

(Garvin et al., 2003). Seasonality was simulated with corticosterone treatment in House Sparrows (*Passer domesticus*), and higher parasitemia was noted during the spring and early summer surrounding breeding (Gibson, 2010). Furthermore, it has been theorized that mate selection through the brightness of breeding plumage is parasite-mediated (Hamilton and Zuk, 1982). Body condition of American Kestrels (*Falco sparverius*) was lower after egg laying in the presence of *Haemoproteus* parasites (Dawson and Bortolotti, 2000). Parental involvement has been shown to increase with treatment of Blue Tits (*Cyanistes caeruleus*) with an anti-malarial drug, resulting in higher fledge success and lower inequalities within individual broods (Merino et al., 2000; Knowles et al., 2010). In a colony of breeding Purple Martins (*Progne subis*), females infected with hematozoa had similar clutch sizes but lower breeding success; however, infected Pied Flycatchers (*Ficedula hypoleuca*) laid fewer eggs than their uninfected counterparts (Davidar and Morton 1993; Sanz et al., 2001). In a study of House Martins (*Delichon urbicum*), treatment with primaquine, an anti-malarial drug, increased clutch size, hatch success, and fledge (Marzal et al., 2004).

Most seabirds that have been studied have lacked haemosporidian infections (Earlé and Underhill, 1992; Bennett et al., 1992; Engström et al., 2000; Quillfgelt et al., 2011). The few reports of blood parasites in seabirds are generally centered in tropical or temperate climates. Most reports in seabirds are described from penguins (Family: Spheniscidae), and most of these are *Plasmodium relictum* and *Leucocytozoon tawaki* or other unspecified *Leucocytozoon* species (Fantham and Porter, 1944; Laird, 1950; Fallis et al., 1976; Graczyk et al., 1995; Levin et al., 2009; Hill et al., 2010). In frigate birds, *Haemoproteus iwa* and other undescribed *Haemoproteus* species have been reported (Clark and Swinehart, 1969; Lowery, 1971; Work and Rameyer,

1997; Madsen et al., 2007; Quillfgelt et al., 2010; Levin and Parker, 2012). *Haemoproteus skuae* has been described from family Stercorariidae.

Several species of *Haemoproteus* and *Plasmodium* have been reported from Family Laridae, including *Haemoproteus larae* and *Haemoproteus passeris* from gulls (Genus *Larus*), and undescribed *Plasmodium* species from terns (genus *Sterna*) (Coatney, 1938; Pierce, 1981a; Pierce, 1981b; Ruiz et al., 1995; Bosch et al., 1997; Martínez-Abraín et al., 2002; Padilla et al., 2006; Quillfedlt et al., 2010). Several undescribed *Plasmodium* species have been described from family Procellariidae, and only one undescribed *Haemoproteus* from a Red-footed Booby (*Sula sula*) (Warner, 1968; Padilla et al., 2006). Recently, *Haemoproteus jenniae* from the Swallow-tailed Gull (*Creagrus furcatus*) has been described as morphologically and genetically distinct from *Haemoproteus larae* (Levin et al., 2012). *Leucocytozoon ugwidi* is the only species that has been reported from family Phalacrocoracidae in the Cape Cormorant (*Phalacrocorax capensis*) and Little Pied Cormorant (*Phalacrocorax melanoleucos*) in South Africa (Mackerras and Mackerras, 1960; Parsons et al., 2010).

Few studies examine the prevalence and diversity of haemosporidians in Alaska but they have been increasing in recent years. Those reports primarily originate on the mainland and are not associated with island communities. In a study conducted on 32 different Passerine species, *Plasmodium* was determined to be able to be transmitted at higher latitudes but not above 64°N (Loiseau et al., 2012). More specifically, passerine species in the southern interior of Alaska have been reported to have infections with *P. vaughani* as well as *L. dubreuili*, *L. fringillinarum*, *H. fallisi*, *H. paruli,* and *H.fringillae* with varying prevalence dependent on host species (Deviche et al., 2001; Deviche et al., 2010). Regarding *Leucocytozoon* and *Haemoproteus* in Alaska, infections have been reported in Rusty Blackbirds (*Euphagus carolinus*), Northwestern

Crows (*Corvus caurinus*), and Swainson's Thrushes (*Cathuarus ustulatus*) and prevalences tend to be higher than *Plasmodium* (Barnard et al., 2010; Dodge et al., 2013; van Hemert et al., 2019). Conversely, one study of Black-capped Chickadees (*Poecile atricapillus*) in the southwest interior of Alaska found *Plasmodium* in higher prevalence than *Heamoproteus*. However, they did not test for *Leucocytozoon* (Wilkonson et al., 2016).

In the most comprehensive study, Oakgrove et al. (2014) sampled 98 species of migratory and resident bird species throughout the interior of Alaska. They found 48 species infected with one or more haemosporidians which were only identified to genus level. While negative species were not reported, positive species were in the Orders Passeriformes, Columbiformes, and Galliformes. Notably, all three parasitic genera have been identified in Ruffed Grouse (*Bonasa umbellus*), Spruce Grouse (*Falcipennis canadensis*), Sharp-tailed Grouse (*Tympanuchus phasianellus*), Sooty Grouse (*Dendrogapus fuligninosus*), and *Leucocytozoon* and *Haemoproteus* were detected in Rock Ptarmigan (*Lagopus muta*), Willow Ptarmigan (*Lagopus lagopus*), and White-tailed Ptarmigan (*Lagopus leucura*) (Stabler et al., 1967a; Stabler et al., 1967b; Smith et al., 2016).

In aquatic birds, Oakgrove et al., also found three species positive in order Charadriformes: the Semipalmated plover (*Charadrius semipalmatus*), the Solitary sandpiper (*Tringa solitaria*), and the Spotted sandpiper (*Actitis macularius*) (2014). Several studies have detected *Leucocytozoon simondi* as well as other unspecified *Leucocytozoon, Haemoproteus,* and *Plasmodium* in waterfowl, including Green-winged Teal (*Anas crecca*), American Wigeon (*Anas americana*), Mallard (*Anas platyrhinchos*), Northern Pintail (*Anas acuta*), Lesser Scaup (*Aythya affinis*), Tundra Swan (*Cygnus columbianus*) (Meixell et a., 2016; Ramey et al., 2012; Reeves et al. 2015). Furthermore, Spectacled Eiders (*Somateria fischeri*), a sea duck (Family: Anatidae)

were surveyed for hematazoa in the Yukon-Kuskokwim Delta and Artic Coastal Plain, and only *Leucocytozoon simondi* was detected (Reed et al., 2018). Emperor Geese (*Anser canagicus*) and Cackling Geese (*Branta hutchinsii minima*) in Alaska have been found to be infected with *Leucocytozoon, Haemoproteus*, and *Plasmodium* (Hollmén et al., 1998; Ramey et al., 2014; Buchheit et al., 2021; Ramey et al., 2021). To our knowledge, no studies have evaluated the baseline prevalence of hematazoa in wild seabird species breeding in Alaska.

Avian Piroplasms

Other blood parasites of birds include the piroplasms, named for their pear-shape within the host blood cells. There are currently three genera in this group, including *Theileria*, *Cytauxzoon*, and *Babesia*, although only the latter has been reported from birds. *Babesia* spp. are a protozoan parasite in the order Apicomplexa. Worldwide, this group of parasites is important pathogens of domestic animals, humans, and some wildlife species. There are currently over 100 recognized species of *Babesia* divided into two general groupings of small (1.0 to 2.5 μm) and large (2.5 to 5.0 μm) *Babesia* (Homer et al., 2000). However, as descriptions are primarily based on morphology, which can be very similar between parasite species and can also vary drastically within hosts, true speciation is the subject of great debate among parasitologists (Persing and Conrad, 1995; Schnittger et al., 2012). Molecular work is now often used to break these parasites into five groups: *Babesia* sensu stricto, *Cytauxzoon*, *Theileria*, *Babesia microti*-like, and the western piroplasms. It is considered one of the most common vertebrate parasites worldwide and has significant veterinary and human health impacts. There are over 100 known definitive hosts across various of taxa (Telford et al., 1993). Molecular evidence demonstrates for the polyphyletic origin of avian *Babesia* species from mammalian species and is thought to originate from host-switching of avian ticks to their mammalian counterparts (Muñoz-Leal and González-

Acuña, 2013; Muñoz-Leal and González-Acuña, 2015; Yabsley et al., 2017). The vectors of avian *Babesia* are unknown, but it is thought to be a tick (Yabsley and Shock, 2013).

The life cycle of *Babesia* has coevolved to coincide with that of the life cycle of the postulated tick vector, and the adult stage takes place only after transmission to the host (Homer et al., 2000). While not completely understood for all species, the life cycle is generally composed of three parts: (1) gamogony, or fusion of gametes in the invertebrate gut, (2) sporogony, or the asexual reproduction in the salivary glands of the invertebrate vector, and (3) merogony, the asexual reproduction in the vertebrate host (Kakoma and Mehlhorn, 1993). The life cycle begins when the tick vector takes a blood meal from an infected host, and the gametes release and begin to fuse. These formed zygotes travel through the invertebrate body until they reach the salivary glands. Sporogony is divided into two parts; where development of a sporoblast first begins after the movement to the salivary glands from the midgut and completes development after a tick takes a subsequent blood meal where sporozoites develop and then are secreted into the host epidermis surrounding the feeding site. Once in the host, the sporozoites attach to the host erythrocytes and develop into trophozoites which divide asexually throughout the bloodstream.

Little is known about the effects of *Babesia* infections on avian species. The only known species to cause clinical disease in birds is *Babesia shortii* (Peirce, 2000). In raptors and other birds of prey, *B. shortii* can cause clinical disease, including anemia and acute mortality (Croft and Kingston, 1975; Samour and Pierce, 1996; Samour et al., 2005; Willette et al., 2009). Specifically, in seabirds, *Babesia* infections have been associated with anemia, leukocytosis, and reduced hepatic function in African penguins (Vanstreels et al., 2015; Parsons et al., 2016). Also, reduced survival and acute mortality have been observed in Common Murres from California,

USA, and Cape Cormorants and King Penguins (*Aptenodytes patagonicus*) from South Africa, which were admitted to rehabilitation centers (often for other reasons such as oiling) (Yabsley et al., 2009; Parsons et al., 2016; Parsons et al., 2018). Treatment of seabirds with primaquine has been noted to reduce parasitemia and clinical signs of babesiosis in African penguins and Cape Cormorants; however, removal of vectors is believed to be more effective for the overall management of *Babesia* (Vanstreels et al., 2019).

There are currently 16 known species of *Babesia* that infect birds, which fall into three distinct phylogenetic groups, but several uncharacterized species have been identified morphologically or genetically (Peirce, 2000; Beaufrere et al., 2007; Savage et al., 2009; Paparini et al., 2014; Martínez et al., 2015; Vanstreels et al., 2015; Montero et al., 2016; Yabsley et al., 2017). Of those that have been characterized, there are multiple species of *Babesia* that infect seabirds, including *Babesia poelea* from Brown boobies (*Sulsa leucogaster*), *Babesia peircei* from African Penguins and Little Penguins (*Eduyptula minor*), *Babesia bennetti* from Yellow-legged Gulls (*Larus cachinnans*), *Babesia ungwidiensis* in Great Cormorants (*Phalacrocorax carbo*) and Cape Cormorants, and *Babesia uriae* from Common Murres (*Uria aalge*) (Peirce and Feare, 1978; Earlé et al., 1993; Work and Rameyer, 1997; Merino, 1998; Peirce, 2000; Esparaza et al., 2004; Yabsley et al., 2006; Yabsley et al., 2009; Peirce and Parsons, 2012). Recently a new *Babesia* sp., referred to as Babesia sp. YLG, was described from Yellow-legged Gulls (*Larus michahellis*) in France (Bonsergent et al., 2022). Several unnamed Babesia species also infect seabirds, including gannets, gulls, and terns in New Zealand and penguins in Australia (Paparini et al., 2014; Vanstreels et al., 2015; Yabsley et al., 2017).

In Alaska, only one species of *Babesia* has been reported; *Babesia microti* in rodents (i.e., voles, shrews, and mice) (Fay and Rausch, 1969; Goethert et al., 2006). Although some strains of

B. microti are zoonotic, this strain in Alaska has not been associated with human infections. Regarding birds and this parasite, a study conducted in New York that tested larval ticks from wild birds found that four species of wild birds were resistant to *B. microti* infections (Hildebrandt et al., 2010; Hersh et al., 2012; Hersh et al., 2014). To our knowledge, no studies surveyed avian species for piroplasms within this geographic region.

Borrelia burgorferi

Borreliosis is the most common vector-borne zoonosis in temperate regions of the Northern hemisphere and is caused by spirochetes in the *Borrelia burgdorferi* sensu lato group (Stanek and Strle, 2003; Kurtenbach et al., 2006). It was first described in 1977 in Old Lyme, Connecticut, the namesake for the disease caused in humans in the United States (Steere et Al., 1977). It is a member of the Order Spirochaetes, characterized by its spiral morphology and flagellum used for bacterial motility. There are 12 species currently included in the *B. burgdorferi* sensu lato group, but the most significant three include those pathogenic to humans: *B. burgdorferi, B. garinii, and B. afzelii* (Baranton et al., 1992; Canica et al., 1993; Kurtenbach et al., 2002). The *Borrelia* spirochete is transmitted by a diverse group of ixodid ticks (Burgdorfer et al., 1982). The primary tick vectors associated with North American transmission are *Ixodes scapularis* and *Ixodes pacificus*; however, the seabird tick, *Ixodes uriae*, is a competent vector (Olsen et al., 1993; Nadelman and Wormser, 1998; Gray, 1998). Numerous vertebrate hosts, primarily small mammals such as mice in the genus *Peromyscus* in North America, are reservoirs that maintain the bacteria in nature (Levine et al., 1985; Donahue et al., 1987; Mather et al., 1989; Wolcott et al., 2021).

Like the previously discussed piroplasms, spirochete development is closely related to the biology of the tick vector. Ixodid ticks undergo three developmental stages (larva, nymph, and

adult), where they feed on a vertebrate host for varying amounts of time (Gray, 1998). Larval ticks feed on an infected vertebrate host, and the blood meal travels to the midgut where, in the case of seabird ticks, it will overwinter (Burgdorfer et al., 1989). Survival in the invertebrate midgut is regulated by changes in gene expression in the bacteria which adapts for better survival in the basic and nutrient-poor environment (Yang et al., 2000; Tilly et al., 2008). During this overwinter, the tick vector molts from the larval to the nymphal stage. During this stage, when a nymph takes a blood meal, bacteria replicate in the midgut and travel to the salivary gland (Korenberg, 1994; Leuba-Garcia et al., 1994; Gray, 1998). The bacteria are then transmitted into the skin of the host. Bacteria again change gene expression for survival in the vertebrate reservoir, which is warmer and has a neutral pH (Barbour et al., 1983; Barbour et al., 1986; Yang et al., 2000). There is little known about the pathogenicity factors for *Borrelia* within the host. Some research has indicated that virulence may be associated with the flagellum, which is tucked alongside the bacteria's surface or surface protein (Ge et al., 1996; Yang et al., 2000; Stewart et al., 2006; Cabello et al., 2007). This placement might allow the bacteria to evade the immune response of the host. While rare, *Borrelia* may also be transmitted transovarially within the tick (Burgdorfer and Keirans, 1983; Burgdorfer et al., 1988; Burgdorfer et al., 1989).

Many wildlife species have been identified as reservoirs for *Borrelia* worldwide, with rodents and hares being the primary species implicated in the transmission. However, no comprehensive review of the potential reservoirs has been conducted, and large gaps in knowledge still exist in understanding the role different wildlife may play in the maintenance of the bacteria. While large mammals are not considered to play a major role in the maintenance of *Borrelia* as spirochetes are not maintained passed clinical phases (Sala and De Faveri, 2016). Instead, the main reservoirs are small mammals, including the most competent reservoir, the

white-footed mouse (*Peromyscus leucopus*). Birds can also serve as a reservoir, but most studies have focused on the Order Passeriformes (Humair, 1998; Humair, 2002; Comstedt et al., 2006). Several studies have attempted to experimentally infect birds with *Borrelia* to determine immune response and pathological changes but have found no clinical disease (Burgess, 1989; Bishop et al., 1994).

It has been suggested that seabirds may play a much more significant role in the transmission of spirochetes than previously thought because of the wide range of *Ixodes uriae* and the migratory nature of seabirds (Olsen et al., 1993; Olsen et al., 1995). There is no evidence of the *Borrelia* complex being pathogenic to seabird hosts. The first report of *Borrelia* in *I. uriae* was on Bonden Island, Sweden, where it was noted that ticks parasitizing Razorbills (*Alca torda),* Common Murres, Black Guillemots (*Cepphus grylle*), and Herring Gulls had very low infections with *Borrelia* by phase-contrast microscopy, PCR, and culture (Olsen et al., 1993). However, ticks from the northern and southern hemispheres are genetically distinct with little to no evidence of the exchange of genetic material; thus, movement of *Borrelia* by the tick vector would be limited (Gylfe et al., 2001). Furthermore, regional movement of ticks is also likely limited because of their short attachment rates during the breeding season when host movement is also limited. Evidence for transhemispheric exchange stems from the genetic similarity of *Borrelia* in the northern and southern hemispheres; thus, it is assumed that the pathogen is being maintained and moved within a seabird host. This concept is further supported by the fact that migration can cause the reactivation of *Borrelia* in a non-seabird host (Gylfe et al., 2000).

Several orders of seabirds have been identified as *Borrelia* reservoirs, including those in orders Charadriiformes, Procellariiformes, and Sphenisciformes (Khan et al., 2019). Prevalence of antibodies in Black-legged Kittiwakes to *Borrelia* in several colonies over the North Atlantic

was estimated to be 18.6% (Staszewski et al. 2008). Specifically, studies have primarily focused on Northern Atlantic populations for the seabirds most closely related to those investigated in this study. Chambert et al. (2012) noted that even though there is the potential for Black-legged Kittiwakes to be exposed to *B. garinii,* there appears to be no effect on the survival of adults through multiple breeding seasons. Furthermore, antibodies can be maternally transferred in colonies where the bacterial agent is present in the tick vector, and those chicks that receive maternal antibodies mount a higher immune response when challenged in natural systems (Gaspirini et al., 2006). While most studies have looked at antibody response, *Borrelia garinii* was isolated in low numbers in Atlantic Puffins on the Faeroe Islands (Gylfe et al., 1999). Another study that isolated *Borrelia* noted that strains from seabird ticks in Northern Europe associated with the Baltic Sea had a molecular polymorphism on the outer surface proteins, which may indicate a novel seabird tick *Borrelia* in the area (Bunikis et al., 1996). They also noted a wide distribution of the same strain of *B. garinii* across the north Atlantic into Sweden and Russia.

Limited studies have investigated *Borrelia* infections in birds and their tick vectors in the northern Pacific Ocean. Comstedt et al. (2009) found that approximately 33% of *I. uriae* in the North Pacific, specifically the Commander Islands of Russia, were positive by qPCR for *Borrelia garinii* spirochetes; however, they did not detect this bacteria from the blood of Tufted Puffins. The authors theorize that the lack of skin testing might account for the lack of *B. garinii* in the birds. Because the birds were not under any stress, such as migration, reactivation of the bacteria was not present. They did find a large diversity (20 strains) of *B. garinii* within the tick populations associated with the seabird colonies, giving more evidence that *B. garinii* is one of the most heterogeneous strains of the sensu lato group. In the most comprehensive study through

the Northern Pacific, Lobato et al. (2011) studied the prevalence of anti-*Borrelia* antibodies for seabirds on three western Alaska islands and four islands in the western Pacific. Of the species tested, including the Black-legged Kittiwake, the Common Murre, the Crested Auklet (*Aethia cristatella*), the Horned Puffin (*Fratercula corniculate*), the Least Auklet (*Aethia pusilla*), the Parakeet Auklet (*Aethia psittacula*), the Red-legged Kittiwake (*Rissa brevirostris*), and the Thick-billed Murre, only a very low prevalence was found and only in both species of murres and the Tufted Puffin. Olsen et al. (1995) tested low numbers of ticks associated with Tufted Puffins in Egg and St. Lazaria Islands, Alaska, but found no *Borrelia* infections. Because previous studies have been conducted on relatively few islands in Alaska, it is important to broaden study areas to understand the role seabirds may play in the global transmission of the *B. burgdorferi* sensu lato group.

Influenza A Virus

Influenza A Virus (IAV) is an enveloped, negative-sense, single-stranded, segmented RNA virus in the family Orthomyxoviridae (Webster et al., 1992; Horimoto & Kawaoka; 2005). There are four genera in this family: Influenza A, which can infect humans, birds, pigs, and horses, Influenza B, which can infect humans and seals, Influenza C, which can infect humans, pigs, and dogs, and Influenza D, which infects pigs and cattle. Influenza A viruses are comprised of eight protein segments: PB2, PB1, PA, hemagglutinin (HA) gene, nucleoprotein (NP) gene, neuraminidase (NA)gene, matrix (M) gene, nonstructural proteins (NS). IAVs are divided into antigenic subtypes based on the HA and NA. Subtype specificity is delineated numerically by the hemagglutinin type (H1-H18) and neuraminidase type (N1-N11) which are important targets for the immune system (Earn et al., 2002, Olsen et al., 2006, Webster et al., 1992). IAV can evolve or change using two mechanisms. As with any pathogen, IAVs are susceptible to random

mutations, leading to antigenic drift. Because of the segmented nature of the IAV genome, they can also undergo genetic reassortment with other IAVs, dramatically changing the genomic composition of resulting viruses.

Avian influenza was first reported in 1878 as “fowl plague.” As early as 1901, a virus was the suspected causative agent. The first isolation of IAV, subtype H5, occurred in South Africa from a Common Tern (*Sterna hirundo*) in 1961 (Becker, 1966). In addition to being classified based on HA and NP subtypes, IAVs from birds are broken into two general categories based on their pathogenicity: Highly Pathogenic Avian Influenza (HPAI) and Low Pathogenic Avian Influenza (LPAI) (Alexander, 2000). Two subtypes (H5 and H7) are the dominant groups responsible for HPAI outbreaks. At least six subtypes of avian influenza are known to infect humans: H5N1, H5N6, H7N3, H7N7, H7N9, and H9N2.

Most IAVs isolated from seabirds have been from the Family Laridae (Stallknecht and Brown, 2007). The most common hemagglutinin subtypes found in gulls are H13 and H16, and some gull strains show limited ability to replicate in non-gull hosts (Fouchier et al., 2005; Hinshaw et al., 1982; Brown et al., 2012). Some evidence suggeststhat these subtypes diverged from other AIVs relatively recently (Webster et al., 1992; Wille et al., 2011). Only a single gull strain, H13,, has caused an epizootic in domestic birds; however, some H13 isolates can infect domestic birds experimentally (Sivanandan et al., 1991; Brown et al., 2012). Although H13 and H16 are the most common, all other subtypes have also been detected in Laridae except for H17 and H18, which seem to be specific to bats (Arnal et al., 2015).

It is also important to note that seabirds have very diverse life history traits that vary based on abiotic, temporal, and anthropogenic factors which impact IAV transmission (Arnal et al., 2015; Hicks et al., 2022). Because of their propensity to practice high nest site fidelity,

seabird breeding populations tend to be highly structured, and this structure may restrict viral transmission within and between communities (Friesen et al., 2007). However, in the case of Middleton Island, it has been noted that adults are potentially foraging in the same areas as adults from other nearby island communities (Roberts and Hatch, 1993; Kotzerka et al., 2010). We also know that newly fledged kittiwake chicks are visiting other areas on Middleton Island and potentially other nearby island communities (Roberts and Hatch, 1994).

Intraspecific and interspecific mixing of seabirds during migration, at breeding sites or wintering grounds could facilitate cross-species transmission of avian influenza and long-distance intercontinental spreading of virus (Garamszegi and Møller, 2007; Pereda et al., 2008; Lebarbenchon et al., 2009; Winker and Gibson, 2010; van Borm et al., 2012; Hall et al., 2013; Blagodatski et al., 2021; Hill et al., 2022). Migration is a well-known factor in pathogen transmission (Altizer et al., 2011). North American lineages of IAVs from gulls have been known to reassort with Eurasian lineages of IAV. One report from the Northern Atlantic (Newfoundland) found a herring gull that had all eight segments from a Eurasian clade (Huang et al., 2014).

Alaska may be a mixing ground for North American and Eurasian lineages as evidenced in both waterfowl and gulls (Winker et al., 2007; Koehler et al., 2008; Winker et al., 2010; Ramey et al., 2010). The interhemispheric dispersal of IAV by migratory birds has been proposed to exhibit “dilution by distance,” as you sample further from overlapping migratory flyways (Pearce et al., 2009). This dilution effect can be further reinforced by the phylogenetic analyses of LPAI viruses from northern pintails, wild ducks, seabirds, and H3N2 virus from humans (Hatchette et al., 2004; Liu et al., 2004; Nelson et al., 2007; Pearce et al., 2009; Ramey et al., 2010; Ramey et al., 2010; Pearce et al., 2011). There is weak evidence to suggest a species

effect on the clustering of influenza lineages, but instead, it seems strain circulation is driven by spatial and temporal factors (Chen and Holmes, 2009). This spatial and temporal aspect lends credence to the idea that strains will infect multiple species of birds sharing breeding and foraging areas, characteristics demonstrated by sampling birds on St. Lawrence Island, Alaska (Ramey et al., 2010). Furthermore, within the general seabird group, most reassorted Eurasian/North American IAV strains across intercontinental lineages have been reported from members of Laridae (Lebarbenchon et al., 2009; Ramey et al., 2010; Wille et al., 2011; van Borm et al., 2012; Huang et al., 2014; Arnal et al., 2015).

Transmission of IAV in waterfowl is mainly fecal-oral, especially in Anatidae, where water contaminated with fecal material is often ingested during foraging behaviors. However, fecal-oral transmission may play less of a role in the transmission dynamics of family Laridae as oral transmission may be more important because higher amounts of virus are shed via the oropharynx (Bahl & Pomeroy, 1977; Brown et al., 2012; Costa et al., 2011). Receptor sites within the different subtypes might cause this differential shedding. In gulls, α2, 3-linked sialic acids (SA) are strongly expressed in the ciliated epithelium of the upper respiratory tract (Franca et al., 2013). However, the direct mechanism these receptors' role is unknown.

Furthermore, the diet of gulls is more generalist (fish and other vertebrates) compared to waterfowl which tend to be strongly herbivorous. The propensity of some species to forage on carcasses of other bird species (e.g., Glaucous-winged Gulls) may lend to greater direct transmission (Brown et al., 2008). Conversely, species with an exclusively pelagic feeding pattern may avoid environmental exposure to surface water where IAV may persist (Hinshaw et al., 1980; Halvorson et al., 1980; Ito et al., 1995). Furthermore, fecal-oral transmission in this environment may not be as likely for seabird colonies as salinity has been known to reduce

persistence (Brown et al., 2009; Stallknecht et al., 1990). Pelagic environments with high salinity and strong currents are unlikely to maintain the concentration of influenza needed to infect new hosts (Swayne and Slemons, 2008).

There is general seasonality for IAV in waterfowl species, where peak infection tends to occur from late summer to early fall in the Northern Hemisphere. However, in members of Laridae, circulation of viruses demonstrates a split seasonality, where seabird infections have been found associated with travel to the breeding sites and fall migration. For example, peak prevalence of influenza in Black-headed Gulls (*Chroicocephalus ridibundus*) in the Netherlands occurred right after the breeding season (Verhagen et al., 2014). Low population turnover, as gulls are long-lived species may account for the lack of strong seasonality as they have much longer to develop immunity, while waterfowl, especially hunted waterfowl, have much higher population turnover. Even though exposure rate at discrete time periods, such as the breeding season, may be low, repeated exposures over the life span of the bird may result in high antibody prevalence (Wilson et al., 2013).

Higher levels of host immunity can lower active infection rates as a smaller portion of the population is susceptible to future infections, and those with previous exposure demonstrate less viral shedding (Webster et al., 1992; Costa et al., 2010; Jourdain et al., 2010). This high host immunity in seabird populations might relate to herd immunity, as well as in some studies, breeding seabirds had nearly 90% seroprevalence for IAV antibodies (Lang et al., 2016). Antibody response to IAVs in seabirds may be more robust than that of waterfowl because of their lifespan, as stronger immune response is needed for longer antibody persistence. (Lee, 2006; Arnal et al., 2015). Antibodies may also not have to be as diverse as in gull species as two predominating subtypes are circulating in gulls: H13 and H16. Little is known about the potential

for transferring maternal antibodies against IAV to Laridae chicks. However, in a study conducted on maternal antibody transfer of anti-*Borrelia*-specific antibodies, it was assumed that after two weeks, the IgY is catabolized in Black-legged Kittiwakes (Staszewtski et al., 2007a; Staszewski et al., 2007b).

In general, there are few reports of influenza A viruses from pelagic birds, and there is little indication of population-level impacts in these birds (Wallensten et al., 2005; Melville and Shortridge, 2006; Granter et al., 2010; Tøennessen et al., 2011). Of the seabird species that nest on Middleton Island that have been surveyed for IAV, Common Murres are the most common to be infected (Table 1). Common Murres have been infected with subtypes H1, H5, H9, H10, H11, and H12 (Ramey et al., 2010; Huang et al., 2014). All fully sequenced viruses from Common Murres in Newfoundland were H1N2, but they showed reassortment with Eurasian lineage viruses and high gene diversity (Huang et al., 2014). Furthermore, despite spatial differences with no overlapping foraging areas, the same strain was isolated from two different segregated breeding colonies that share overwintering and staging areas. This overlap indicates that IAV was circulating in these populations in the wintering area well before initial detection.

Although studies have investigated IAV infections in Glaucous-winged Gulls worldwide, few studies have involved large-scale surveillance efforts, and data suggest generally low prevalence (Table 1). Of the species nesting on Middleton Island, this species has been reported to harbor the most diverse IAVs subtypes. In 2006, an Alaska Interagency Influenza Working Group ranked Glaucous-winged Gulls as a high priority for influenza surveillance. However, IAV surveillance on Glaucous-winged Gulls conducted in 2010 found a very low virus isolation prevalence (34%, or 1/295) (USFWS/USGS, 2011). Conversely, surveillance conducted from 2011-2015 at the Izembek National Wildlife Refuge in Alaska found that prevalence ranged

from 2-14% (Reeves et al., 2018). This latter study also found that 47 of 153 (30.7%) isolates were Asian/mixed origin clades of AIVs. Worldwide, numerous subtypes have been reported in Glaucous-winged Gulls, including H1, H3, H4, H5, H11, H13, and H16 (Winker et al., 2008; Wille et al., 2011; Ramey et al., 2016; Reeves et al., 2018).

Despite Black-legged Kittiwakes being one of the most numerous gull species worldwide, little research has been conducted on influenza in this species. In Norway, IAVs have been isolated in a low prevalence (5%) of chicks and up to 15% of adults. High seroprevalence (71.3%) was also reported (Tøennessen et al., 2011). Other studies have not isolated IAVs from Black-legged Kittiwakes and have found relatively low antibody seroprevalence (0%-28%) (Munster et al., 2007; Walghren et al., 2008; Ip et al., 2008; Germundsson et al., 2010). Black-legged kittiwakes have been previously reported to be infected with subtypes H4, H13, and H16 (Obenauer et al., 2006; Tøennessen et al., 2011; Hall et al., 2013). Interestingly, a retrospective study on influenza subtypes demonstrated that a Black-legged Kittiwake was infected with the H16 subtype in 1975, long before the initial detection of this subtype in the Black-headed Gull in 2005 (Fouchier et al., 2005; Obenauer et al., 2006). Among the isolations from Black-legged Kittiwakes in Eastern Canada, mixed Eurasian and North American gene segments have been reported (Hall et al., 2013).

Previously, there have only been two small studies on IAV in Pelagic Cormorants, and no viruses were detected (Wahlgren et al., 2008; Ip et al., 2008). According to the Influenza Research Database (IRD), a single fecal swab from a Pelagic Cormorant was submitted to the University of California during a 2007 surveillance effort; however, it was not tested (Zhang et al., 2017). In Suliformes in general, Lebarbenchon et al. (2015) found only a 2% antibody prevalence. Otherstudies have failed to find any antibody-positive birds (Laver and Webster,

1972; Artois et al., 2002; Albini et al., 2014). Most research on influenza in *Phalacrocorax* comes from diagnostic laboratories where carcasses were submitted in the case of mortality events. Similarly, little research outside of mortalities submitted to diagnostic laboratories has been conducted on Rhinoceros Auklets or Tufted Puffins, and, of the studies that have examined these species, no viruses have been detected (Jessup et al., 2009; Siembieda et al., 2010; Yoshino et al., 2015; Zhang et al., 2017; Jones et al., 2019; Knowles et al., 2019).

Alaska has been repeatedly documented as an important mixing ground for Eurasian and North American lineage IAVs, resulting in the extensive detection of interhemispheric reassortants Anseriformes and Charadriiformes birds (Koehler et al., 2008; Pearce et al., 2009; Pearce et al. 2010; Ramey et al., 2010). The significance of an IAV exchange from Eurasia to North America through Alaska was highlighted by the introduction of the A/Goose/Guangdong/1/96 (Gs/Gd) Gs/GD to North America in 2014 (Ip et al., 2015; Lee et al., 2015; Pasick et al., 2015; Torchetti et al., 2015; Lee et al., 2016 Ramey et al., 2016; Zhou, 2016; Lee et al., 2017; Hill et al., 2017). The outbreak resulting from this introduction was the largest in the history of the United States and led to a loss of an estimated 50 million domestic poultry (Ramos et al., 2017). There is evidence of ongoing intercontinental exchange of avian influenza viruses, including those causing HPAI, such that risks to the population health of both wild and domestic birds from similar introductions are enduring (Jeong et al., 2019; Ramey et al., 2018; Lycett et al., 2020; Caliendo et al., 2022; Ramey et al., 2022; Gerlach, 2022).

The importance of Middleton Island and the seabirds that breed on the island to the global transmission of influenza is unknown. Only one study has surveyed for viruses on Middleton, and that study only included 100 Glaucous-winged Gulls (USFWS/USGS, 2011). No viruses were isolated during that study, but no serological assays were conducted to look at

possible previous exposure. Because transmission in seabirds has been linked with the breeding season, this site provides a unique opportunity to sample six different seabirds. Table 1 includes a review of IAV studies that have been conducted on the six seabird species included in our studies.

Ectoparasites and seabirds

In addition to pathogen transmission, high levels of ectoparasites (e.g., ticks and fleas) can change the host's behavior which may reduce reproduction and survival of young (Aeschlimann, 1991; Duffy, 1983; Merino and Potti, 1995). In addition to individual mortalities and behavioral changes associated with hyperparasitism, larger population effects, such as lower nest success and increased chick mortality, are of concern (Anderson and May, 1978; Brown and Brown, 1992; Richner and Heeb, 1995; Gauthier-clerc et al., 1998). High parasite loads, such as *Ixodes* and *Ornithodorus* ticks, have been correlated with reductions in populations of black-legged kittiwakes (Boulinier and Danchin, 1996). These detrimental effects of ectoparasitism can be increased during adverse environmental conditions are present (de Lope et al., 1993).

Indirect effects associated with the presence of ectoparasites include accumulation and lowered resistance of toxins as well as pathogen transmission, which could result in clinical disease (Gothe et al., 1979; Nuttal, 1984). Severe clinical disease has been shown to cause massive breeding failures in seabird populations and abnormal development of chicks (Feare, 1976). Nest site abandonment in cormorants has been proposed as a method of escape from large ectoparasite infestations. Furthermore, some of these birds travel large distances during migration, so they could play a more significant role in the ecology and epidemiology of many pathogens, by maintaining infection cycles and dispersal (Cooper, 1990; Hatch et al., 2011; Wobeser, 1997).

Ectoparasites of interest in this study include ticks, fleas, and lice. To date, fleas and lice have never been documented in the literature at Middleton Island. Some issues, such as anemia, lowered reproductive ability, and nest abandonment found with high levels of tick parasitemia, have also been documented with high flea and lice infestations (Clayton, 1990; DeVaney, 1976; Booth et. al, 1993). However, there is also evidence that lice and fleas coevolved with species, and some level of normal infestation could be established (Barker, 1996; Page et. al, 1996). Research on seabirds fleas and lice focuses mainly on the arthropod ecosystem and co-evolutionary relationships between parasite and host rather than on the effects of infestations (Khan et al., 2019).

Fleas

Fleas (Order: Siphonaptera) are small, blood-feeding parasites that occur worldwide. While research has remained historically limited outside of a few species, over 2,500 species of fleas have been identified from a wide variety of avian and mammalian taxa (Coulson et al., 2009). Most fleas (approximately 95%) parasitize mammals, while the rest feed on avian species. Fleas are divided into 16 different families, but all of the avian-infesting fleas are in five families, including the Ceratophyllidae, Leptopsyllidae, Pulicidae, Pygiopsyllidae, and Rhopalopsyllidae (Whiting et al., 2008). Four flea genera have been reported from seabird species: *Ceratophyllus* from members of *Aethia*, *Larus*, *Pagophila*, and *Phalocrocorax; Glaciopsyllus* on Antarctic seabirds of *Fulmarus* and *Pagophila; Mioctenopsylla* from members of *Rissa*, *Larus*, and *Phalacrocorax*; *Parapsyllus* from *Pterodroma*, *Pachyptila*, *Puffinis*, *Procellaria*, *Pelagodroma*, and *Pelecanoides*; and *Xenopsylla* from *Calonectris*, *Larus*, and *Puffinus* (Vermeil, 1955; Traub et al., 1983; Murray et al., 1990; Steele et al., 1997; Gomez-Diaz et al., 2008; Mifsud et al., 2008; Stefan et al., 2015; Khan et al., 2019).

Based on phylogenetic analyses, it is believed that the Siphonaptera have adapted secondarily to avian hosts (Smit, 1962; Holland, 1985; Lewis and Galloway, 2001). Fleas most likely adapted to avian species through contact with traditional rodent hosts (Traub et al., 1983; Winkler and Sheldon, 1993). Seabird fleas are theorized to have evolved after host switching events on island communities where rodents and birds coexisted in close quarters (Tripet et al., 2002). These host-switching events on island communities have led to parasite specialization and speciation of seabird fleas. However, aggregation of nests within a mixed seabird colony may lead to generalist fleas within the overall metacommunity, where one flea species will parasitize any bird species present.

While most fleas demonstrate marginal host specificity, life history and host preferences in avian species are further determined by the environmental requirements of the larvae. Temperature, humidity, and refugia largely determine the living requirements of the flea. However, many species have developed a tolerance to harsh conditions, and some may be able to tolerate a wide range of environmental pressures. It is generally thought that species with a more gregarious host preference also have a broad environmental tolerance (e.g., temperature, humidity, etc.). However, host specificity in parasites is also largely dependent on host behavior and the host's dispersal patterns, which can constrain intermixing of parasite subpopulations (Tripet et al., 2002).

There are four stages in the holometabolous life cycle of a flea: the egg, larval and pupal stages, and adult. However, parasitism of birds by fleas is most commonly quantified through the surrounding environment, as only the adult stage requires a blood meal from the host. New generations cocoon and stay dormant between periods of time when the host is not present at the nest site (Humphries, 1967; Du Feu, 1987; Tripet et al., 2002). Because of these opposing

adaptations to mammalian fleas that remain on or near the host for the entirety of their life cycles, bird fleas have developed specific morphologic characteristics to become more ambulatory, thus engaging in host-seeking behavior. These fleas have greater abilities to jump and climb via an enlarged pleural arch with higher levels of resilin to store energy (Bennet-Claark and Lucey, 1967; Rothschild et al., 1973; Burrows, 2009). They also have enlarged eyes and darker cuticles to prevent dehydration during times when hosts are away from the nests.

Morphology of adults is heavily relied upon for the identification of fleas. Adult fleas are small, generally 1-10mm in length. Their bodies are sclerotinized, bilaterally compressed, with strong hind legs, and are made of three distinct thoracic segments. Adult fleas use this flexible body and hind strong legs to jump large distances up to 150 times their body size (Bitam et al., 2010). They are characterized by sensory organs and specialized setae, which allow them to seek out and maneuver through the host body. Sensory organs include large, well-developed eyes to seek out hosts with short antennae for sensing and copulation. On the posterior end of the body, fleas uniquely possess a sensillum, or sensory organ, which can aid in detecting air movement, vibrations, and temperature differences for host-seeking and predator evasion. Many species have a ctenidium, or comb made of stout spines, on the head and/or the prothorax, along with other setae across the body, which assists in resisting dislodging of the flea from the host (Humphries, 1967).

Few studies have determined the effects of flea infestations on wild birds, and even fewer studies on seabirds. Although most studies have focused on domestic poultry, there have been several studies on passerines, and some studies noted adverse effects (Richner and Heeb, 1995; Fitze et al., 2004; Fair et. al, 2007). The introduced sticktight flea (*Echidnophaga gallinacea*) of domestic poultry causes reduced mass, lowered hematocrit, higher heterophil: lymphocyte ratios,

and mortality in the endangered Florida scrub Jay (*Aphelocoma coerulescens*) (Boughton et al., 2006). This flea can cause many detrimental effects in a variety of wild and zoo birds, including the Victoria crowned pigeon (*Goura victoria*), the Crested Pigeon (*Ocyphaps lophotes*), the Noisy Miner (*Myzantha melanocephala*), the Black-backed Magpie (*Gymnorhina ribicen*), the Grey-crowned Babbler (*Pomatostomus temporalis*), and the Galah (*Eolophus roseicapilla*) (Mactier, 1970; Gyimesi et al., 2007). Experimental studies on Great Tits (*Parus major*) have demonstrated that *Ceratophyllus* fleas affect nest site selection, can cause delayed lay dates, higher rates of nest desertion, and lower rates of hatch success and brood size (Richner et al., 1993; Oppliger et al., 1994; Christe et al., 1994; Christe et al., 1996a, Christe et al., 1996b). Another experimental study on European Starlings noted an association between anemia and fleas in the nests (Gwinner et al., 2000).

For seabirds specifically, Kristjánsson et al. (2016) documented adult agitation in Common Eiders (*Somateria mollissima*) infested with fleas, leading to less incubation time and more nest attendance by other females within the colony. Furthermore, there is a correlation between higher rates of bloodied eggs with higher ectoparasite loads. Adult *Ceratophyllus* fleas deposit blood by to provide nutrition to larvae, thus indicating high loads may increase blood loss in adults and nestlings (Harriman et al., 2008; Harriman and Alisauskas, 2010; Kristjánsson et al., 2016). In areas of higher mammalian predator activity, Cory Shearwaters (*Calonectris diomedea borealis*) have higher ectoparasite loads which may result in lower body condition and breeding failures likely because increased stress from ectoparasites may impair immune function making individuals more susceptible (Hervías et al., 2013). Experimentally, European Storm-petrels (*Hydrobates pelagicus*) were treated with a fumigant to remove all ectoparasites from nestlings on Benidorm Island, and it was found that the decreased fleas and lice burdens resulted

in higher growth rates (Merino et al., 1999). It should be noted that several taxa of ectoparasites were present within the nest sites, although the authors presumed the fleas to have the most detrimental effects on fledglings.

Because, in their adult stage, adult fleas take blood meals from the host, they can transmit certain pathogens. Fleas have been implicated in the transmission of several pathogens, including bacterial pathogens such as *Yersinia pestis, Rickettsia*, *Francisella tularensis*, *Listeria*, *Salmonella*, and *Bartonella*, as well as parasitic organisms such as *Trypanosoma* spp. and *Acanthocheilonema*, a cause of canine filariasis (Bitam et al., 2010; Sekeyová et al., 2012;). There has been little evidence that fleas play a major role in the maintenance or transmission of viruses in avian species; however, they can transmit viruses such as feline leukemia virus (FeLV), myxoma virus, calicivirus, and, experimentally, Omsk Hemorrhagic Fever (Sapegina and Kharitonova, 1969; Mead-Briggs and Vaughan, 1975; Shepherd and Edmonds, 1977; Vobis et al., 2003; Vobis et al., 2005; Mencke et. al, 2009). Fleas transmit pathogens either through taking a blood meal by the vector or through ingestion of the vector's feces by the vertebrate host. Furthermore, the life cycle of certain parasites may be completed when a host digests the entire flea species while grooming.

Ceratophyllus vagabundus is the most common and widespread flea for seabirds in the Northern Pacific. This flea is found primarily in the Northern hemisphere and is common in colonial nesting habitats (Haddow et al., 1983; Lewis and Galloway, 2001). However, because of the broad host range, the historical taxonomic classification of this species is complicated. Multiple investigators have described this species from multiple bird species in different geographic areas. Currently, there are three accepted subspecies of *Ceratophyllus vagabundus*: *C. v. vagabundus*, *C. v. insularis*, and *C. v. alpestris*. The latter subspecies is found only in the

Alps. Host associations can vary geographically as *C. v. vagabundus* in Alaska has been reported to parasitize *Larus* gulls, eiders, and birds of prey; however, in the Northern Atlantic region, *C. v. vagabundus* has only been reported from geese and gulls. However, widespread surveillance data on avian fleas is generally lacking.

The flea genus *Mioctenopyslla* is most commonly associated with members of *Rissa* and *Phalacrocorax*. This genus can be distinguished from other members of Ceratophyllidae by their long protonums, followed by short, broad, and pale pronatal ctenidium, or combs. There are two species within this genus, and each includes two subspecies. *Mioctenopyslla artica* was first described on Novaya Zemlya, an island in northern Russia (Rothschild 1921). The subspecies *Mioctenopyslla artica hadweni* has been reported from kittiwakes in Alaska, while *Mioctenopyslla artica artica* is found in boreal areas of northern Europe (Holland, 1985; Haddow et al., 1983). *Mioctenopyslla traubi* was first described by Holland and Jellison in 1952 in western Canada. The European species found throughout Siberia and Russia is *Mioctenopyslla traubi kurilensis*, whereas *Mioctenopyslla traub*i *traubi* is found throughout western Canada and south on Alaska Islands. The preferred hosts are members of Phalacrocoracidae but can be found on other seabirds, especially those closely associated with cormorants. Between these two species found in the area of interest, they can be distinguished by the number of spines on the ctenidium; *Mioctenopyslla artica hadweni* have approximately 13, while *Mioctenopyslla traub*i *traubi* have approximately 16 (Holland, 1985). The flea species associated with the seabird species that breed on Middleton Island are reviewed in Table 2.

Lice

Lice (order: Phthiraptera) are wingless obligate parasites divided into sucking lice (suborder Anoplura) and chewing lice/Mallophaga (suborders Ischocera, Amblycera, and

Rhynchophthirina). Chewing lice spend their entire life cycle on the host (Nelson and Murray, 1971). All species are hemimetabolous, or lack a pupal stage, and the life cycle includes an egg stage, three instar-nymphal stages, and an adult stage. The egg, or nit, takes 4-10 days (depending on the species and external conditions) to hatch. Development of the instar phases typically takes 3-12 days each, and nymphs can be morphologically distinct or similar to the adult stage, although all nymphs lack reproductive organs. The adults are dorsoventrally depressed, allowing them to lay against host feathers, hair, or body. The typical life span of an adult louse is approximately 30 days, and mature females typically lay one egg per day.

Chewing lice possess chewing mouthparts which differentiate them from the Anoplura. However, the mandibles of each chewing lice suborder differ in structure and purpose. The Rhynchophthirinia, which consists of the monophyletic family Haematomyzidae, parasitize mammalian species, and have elongated snouts terminating in the mandibles. The Amblycera possess maxillary palps, a less evolved chemoreceptive anatomy, and vertical mouthparts which can be adapted to sucking blood (Clay, 1970; Marshall, 2003). Because of these adaptations, Amblycera are more mobile, so they can avoid detection and may leave the host in search of others, especially following a mortality event. In contrast, Ischnocera possess horizontal mouthparts and generally spend the entirety of their life cycle on a single host, and generally live in refugia to avoid detection. Avian chewing lice typically have two claws per leg as opposed to mammalian species, which possess a single claw per leg.

There are approximately 4,464 valid species of Mallophaga; however, the exact number of species is not fully understood because many new host associations have been published under new epithets, so new morphologic and/or molecular work is needed on this group (Price et al., 2003). Chewing lice are most commonly associated with avian species, with some 3,910 valid

species reported from birds. As an example, there are 332 louse species associated with 306 species in the order Charadriiformes. However, many reports of lice from the general seabird group are from general biology studies on the birds or opportunistic reports in conjunction with concurrent projects or submissions to rehabilitation or diagnostic centers. Thus, to fully understand host association and lice diversity, large-scale surveillance studies are needed. Lice associated with the seabirds of interest in this study are listed in Table 3.

Seabird lice are believed to have closely evolved alongside their host species following Fahrenholz's Rule, with heavy support for cospeciation with minimal host-switching (Eichler, 1941; Page, 1996; Page et al., 2004; Johnson et al., 2004; Banks et al., 2006). However, there is debate about this theory as several studies that failed to show a correlation between the phylogenetic relationships of louse species with that of their hosts (Hopkins, 1942; Clay, 1950; Page, 1991; Page, 1994; Page et al., 1998; Mey, 1999). This lack of consensus implies that host specificity in lice may be more complicated than previously thought. Furthermore, when the host-to-louse associations were calculated by host taxon, most associations averaged more than one, which implies that lice are not strictly host-specific. Instead, there are multiple mechanisms proposed by several authors which can explain the lack of consensus. As explained by Johnson and Clayton (2003), "these include 1) host-switching, 2) sorting events (extinction and "missing the boat"), 3) duplication (speciation of the parasite in the absence of host speciation), and 4) failure of the parasite to speciate in response to host speciation."

The effects of chewing lice on bird species have been extensively studied in domestic poultry (Johnson and Clayton, 2003). Irritation and increased grooming rates can result in reduced body size and egg production (Brown, 1974; Nelson et al., 1977; Arends, 1997; Price and Graham, 1997). In wild birds, feather loss and breakage have been associated with louse

infestations (Njila and Godson-Ibeji, 2021). In Barn Swallows (*Hirundo rustica*) and Rock Ptarmigan, it was noted that chewing lice create holes in the tail feathers, causing breakage, which may reduce aerodynamic efficiency and mating potential due to parasite-mediated sexual selection (Clayton. 1991; Kose et al., 1999; Bosner, 2001; Stenkewitz et al., 2017). This facilitated selection has also been seen in Rock Doves (*Columbia livia*), where increased preening can increase metabolic rate, which causes trade-offs such as courtship displays and overwinter survival rates (Clayton, 1990; Booth et al., 1993). Increased mass of the bursa of Fabricius, the organ responsible for B cell development, in juvenile Rock Ptarmigan was noted for birds with high chewing lice loads (Stenkewitz et al., 2015). Further research has shown louse ectoparasitism negatively correlates with these birds' fecundity (Stenkewitz et al., 2016). Only one study has examined the effects of lice on seabirds but found no correlation between load size and growth of individual chicks (Daunt et al., 2001). However, load size positively correlates with seabird density (Rivera- Parra et al., 2014). Furthermore, while lice tend to exhibit aggregation like other macroparasites, it has been noted to be reduced in colonial nesting birds, which is likely because lice are more likely to be transmitted between individuals horizontally (Rózsa et al., 1996).

While typically not considered a significant source in wild populations, there is some evidence that avian lice species may transmit pathogens to their hosts. However, there are a many reports of lice transmitting avian filarial worms. An important example is the transmission of *Sarconema eurycerca*, a heartworm of swans and geese, by *Trinoton anserinum* (Seegar et al., 1976; Cohen et al., 1991). Several generalist louse species have been implicated as vectors for the filaroid *Eulimdana* of Charadriiformes (Bartlett and Anderson, 1990; Bartlett, 1993). Other examples include transmission of *Pelecitus fulicaeatrae*, a nematode of coots, by

Pseudomenopon lice (Bartlett and Anderson, 1987; Bartlett and Anderson, 1989) and transmission of *Filaria cypseli*, a filaroid parasite of African Swifts (*Cypsellus affinis*) in Kenya by *Heterodoxus spiniger* (Dutton, 1905). In addition, *Pasturella multocida*, the causative agent of avian cholera, has been detected in the midgut of chewing lice feeding on infected hens; however, no transmission studies have been conducted to determine vectoral capacity (Derylo, 1970).

Ticks

Ticks (Order Parasitiformes) are highly diverse obligate blood-feeding parasitic arachnids in Suborder Ixodida. Tick species are divided into three families: Ixodidae (hard-bodied ticks), Argasidae (soft-bodied ticks), and Nuttallielliae (a monophyletic family one species *Nuttalliella namaqua*) (Gugliemone et al., 2010). Currently, there are 193 and 702 recognized species in the Argasidae and Ixodidae, respectively, but several new species of ticks are described annually. The presence, or lack thereof, of a scutum covering all or a portion of the dorsal side can distinguish members of these two families. Additionally, the mouth parts differ, with the Ixodidae having terminal mouthparts that extend out and the Argaside having ventrally located mouthparts. The general life cycles differ as well. For soft ticks, the life cycle contains a larval stage, two or more nymphal instar stages, and a reproductively mature adult stage. Hard ticks have the same three life stages: larvae, nymph, and adult, but there is only one nymphal stage. Duration of feeding is also different for the families as soft ticks take short, repeated blood meals at each stage of their instar development, whereas hard-bodied ticks attach to the host for much longer depending on the life stage.

Of the approximately 900 species of ticks, 29 species have been reported to infest seabirds. Seabird colonies provide suitable restricted habitat for shelter-seeking ticks to complete

various portions of their lifecycle (Dietrich et al., 2011). Because seabird hosts are only present at nest sites, where parasites are, for a few months of the year (i.e., during breeding season), completion of the lifecycle for these ticks can take up to four years (Eveleigh & Threlfall, 1974; Steele et al, 1990). The most common tick species infesting colonies in the Palearctic and North Pacific region are the hard ticks *Ixodes signatus* and *Ixodes uriae* and the soft ticks *Carios capensis* and *Carios maritimus* (Choe and Kim, 1987a; Choe and Kim, 1987b; Dietrich et al., 2011; Khan et al., 2019). A review of the ticks associated with the breeding seabirds found on Middleton Island can be found in Table 4. Of note, previous studies on Middleton Island have only reported *Ixodes uriae* and *Ixodes signatus*; thus this review will focus on life-history traits associated with these two species (Dietrich et al., 2014; Hahn et al., 2020).

Although similar in many ways in their life history traits and often lumped together in discussions of seabird parasites, it is important to note that *I. signatus* and *I. uriae* are distinct species. While *I. uriae* are considered a gregarious species in terms of host specificity, *I. signatus* is strongly associated with members of Phalacrocoracidae or species nesting nearby (Guglielmone et al, 2014). Choe and Kim (1987) suggested that they would have different microniches on the avian host to avoid competition where both tick species are found. Furthermore, *I. signatus* has been demonstrated to be less likely to transmit certain pathogens, such as members of Bunyviridae, than *I. uriae* (Lvov et al., 1972). They can easily be distinguished morphologically by the spurs on Coxa I-III: *I. uriae* lacks spurs altogether, while *I. signatus* has only external spurs (Horak et al., 2003).

Most research on Ixodid ticks of seabird colonies has been conducted on *Ixodes uriae*, although it is believed that *Ixodes signatus* shares life-history traits. These ticks parasitize more than 60 bird species, including auks and gulls in the Northern Hemisphere and penguins and

albatrosses in the Southern Hemisphere (Dietrich et al., 2011). It is a nidicolous nest inhabiting tick of seabirds. Muzaffar & Jones (2007) suggest that *I. uriae* uses a combination of passive waiting and active questing from hosts cues to find a host (Sonenshine, 1991). Feeding lasts 3-12 days with each feeding period and increases with each life stage (Dietrich, 2011). To avoid being removed from the host by grooming during this critical stage, ticks have evolved to counter the hosts' inflammatory and hemostatic responses to ensure feeding success. To do this, they use a multitude of biomolecules released in the tick saliva (Ribeiro et al., 1985; Ribeiro, 1987; Ribeiro, 1989; Šimo et al., 2017). There is also evidence that these immunomodulatory activities facilitate the transmission of tick-borne pathogens (Jones et al., 1989; Labuda et al., 1993; Nuttall and Labuda, 2004; Macháčková et al., 2006).

After feeding, ticks return to refugia, where they either molt or lay eggs and die. It takes 55-145 days for engorged nymphs and 50-105 for engorged larvae to molt, respectively (Eveleigh & Threlfall 1974). During this time, ticks remain aggregated in direct contact with each other in sheltered areas such as nests, rocks, or other debris (Eveleigh and Threlfall, 1974). Adult females can mate with multiple males, producing highly genetically diverse offspring (McCoy & Tirard, 2002). A clutch can contain 200-600 eggs (Eveleigh and Threlfall, 1974). Male adult ticks do not feed but wait for opportunities to mate with females before dying (Zumpt 1952). However, if a tick fails to find a host, it can delay feeding and extend its life span by one year (Barton et al. 1996).

While off the host, the thermal tolerance of *Ixodes uriae* ranges from -20° to 40° C except during feeding when they are intolerant of extreme temperatures (Lee and Baust, 1982; Lee and Baust, 1987). Interestingly, respiration rates seem unaffected in freezing temperatures (Lee and Baust, 1982). Engorgement rates of *I. uriae* in Palmer, Alaska, were higher with sustained high

temperatures (Benoit et al., 2009). However, despite research that suggests a wide thermal tolerance should be correlated with a high tolerance for dehydration, *I. uriae* experiences high water loss rates (Danks, 2000; Benoit et al., 2007; Davies et al., 2021b). Because these ticks do not drink to replenish moisture, cool and hydrating atmospheres, as seen in coastal environments in off-host refugia, is an important habitat component for these species.

Thus, unsurprisingly, *I. uriae* does not have known hosts closer to the equator than 48 degrees latitude (either north or south). *Ixodes uriae*, like other Ixodid tick species parasitizing seabirds, probably originated in the southern hemisphere and have been introduced to the northern hemisphere via transhemispheric movement of seabirds (Zumpt 1952; Dobson and Barker 1999). This evolutionary history divides *Ixodes uriae* into fairly distinct clades in respect to geographic region. It has been theorized that dispersal of ticks occurs at the end of the breeding season when newly fledged individuals visit other sites and other colonies. However, Gylfe et al., (2001) contest that there may be transhemispheric movement of *I. uriea* by seabirds as those ticks in the northern hemisphere are largely monophyletic, and thus are genetically distinct from those found in the southern hemisphere. Though it is unlikely that disease moves between the poles (Petterson et al., 2020).

Ticks are distributed worldwide and are second only to mosquitoes in terms of arthropod transmission of pathogens (Jongejan and Uilenberg, 2004). Most research associated with ixodid ticks and seabirds has been focused on the causative agent of Lyme disease, the *Borrelia burgdorferi* senso lato group. Of these, *Borrelia garinii* has been reported in *Ixodes uriae* associated with Black-legged Kittiwakes, Common Murres, and Tufted Puffins (Hoberg and Wehle, 1982; Olsen et al., 1995; Staszewski, et al., 2008; Lobato et al., 2011; Chambert et al., 2012). While *Ixodes scapularis* is considered to be the main vector of the *Borrelia burgdorferi*

senso stricto group, *Ixodes uriae* is theorized to also be a competent vector, although experimental studies are lacking (Olsen et al., 1993; Gylfe et al. 1999; Gylfe et al., 2001; Smith et al., 2006).

Ticks can also have direct negative effects on their hosts (e.g., exsanguination, predispose to secondary infections, direct skin damage, etc.). Direct impacts of *I. uriae* infestation on its seabird hosts, include reduction of hematocrit, behavioural changes, and the energetic cost of mounting an immune response (Boulinier & Danchin 1996; Sheldon & Verhulst 1996; Wanless et al., 1997; Mangin et al. 2003). Furthermore, experimental studies, primarily conducted on passerines, where ectoparasites were removed from nesting sites, showed that high ectoparasite loads can cause reduced body mass, early fledging, lowered hematocrit, and higher polychromasia (Brown and Brown, 1986; Lehman, 1993; McKilligan, 1996; Alves, 1997; Szép and Møller, 1999; Szép and Møller, 2000). However, only one study has experimentally evaluated the impacts of ectoparasites (including fleas, mites, and ticks) on nesting seabirds. In that study, the growth rate and hematocrit of nesting Storm Petrels (*Hydorbates pelagicus*) was negatively correlated with ectoparasite numbers (Merino et al., 1999). Indirect effects associated with presence of ectoparasites include accumulation and lowered resistance to toxins through impairment of nerves, as well as pathogen transmission which could result in clinical disease (Gothe et. al., 1979; Nuttal, 1984).

Along with individual mortalities and behavioral changes associated with hyperparasitism, greater population effects, such as lower nest success, reduced growth rates of nesting chicks, and greater chick mortality, may be of concern (Anderson and May, 1978; Morbey, 1996; Gauthier-clerc et.al., 1998; Bergström et al., 1999; Bosch et al., 1997; Bosch and Figuerola, 1999; Ramos et al., 2001; Mangin et al., 2003). In England, high loads of *Ixodes uriae*

ticks were correlated with reduction in populations of Black-legged Kittiwakes; however, the study did not investigate the effects of ticks on individual birds (Boulinier and Danchin, 1990). An observational study in Peru suggested that high nest ectoparasite burdens caused cormorants, boobies, pelicans to abandon nests (Duffy, 1983). Severe clinical disease from ectoparasite infestation can cause massive breeding failures in seabird populations as well as abnormal development of chicks (Feare, 1976).

Cyclical dynamics of tick infestations and their seabird hosts are an important aspect of the parasite-host dynamics in breeding colonies. One study found that, during the first 30 years of a seabird colony being established, tick abundance increases with colony size and then remains relatively stable (Danchin, 1992). However, as tick abundance increases, effects on the seabird hosts increase, which could potentially impact population numbers (Boulinier and Danchin, 1996; Ramos and Drummond, 2017). In subsequent years to a failure or abandonment, lower tick density has been noted (Danchin, 1992; Dietrich et al., 2011). The active tick density at any point in a colony can be estimated by counting the number of ticks on a chick in the nest, and further research is needed to determine if this metric may be able to help predict changes in populations (Ramos and Drummond, 2017).

Climate change is having widespread effects on wildlife throughout the world and is an important consideration for parasite-host dynamics of seabird colonies and their ticks. The effect of climate change on vectors and vector-borne pathogens is a growing concern, especially in the northern-most latitudes where effects are likely to be amplified because new vectors and their pathogens may be able to establish (Süss et al., 2008; van Hemert et al., 2014; Dantas-Torres, 2015; Eisen et al., 2016). Depending on the region, climate change likely will increase the range and abundance of certain tick species (Estrada-Pena, 2009; Léger et al., 2013). In one study, an

increase of 1°C increase in winter temperature increased the prevalence of ticks on Thick-billed Murres the following summer by 5% (Descamps, 2013). Furthermore, climate change is predicted to increase atmospheric humidity, cause rising sea levels, erode coastlines, increase oceanic acidity, and shift plant and animal community distributions (Walther et al., 2002; Markon et al., 2018). These changes are particularly worrisome for seabird communities as anthropogenic changes can reduce food availability, interrupt the timing of breeding, create loss of breeding grounds, and push non-endemic species into competition with natives (Gaston and Hipfner, 1998; Kokko et al., 2004; Gaston et al., 2005; Barbraud and Weimerskirch, 2006; Gaston et al., 2009; Reynolds et al., 2015). Effects such as these may compound the negative effects ectoparasitism and pathogen transmission may have on individuals and overall population of seabirds. Thus, it is increasingly important to monitor vulnerable seabird populations, such as those on Middleton Island, for long-term changes in ectoparasitism and potential effects.

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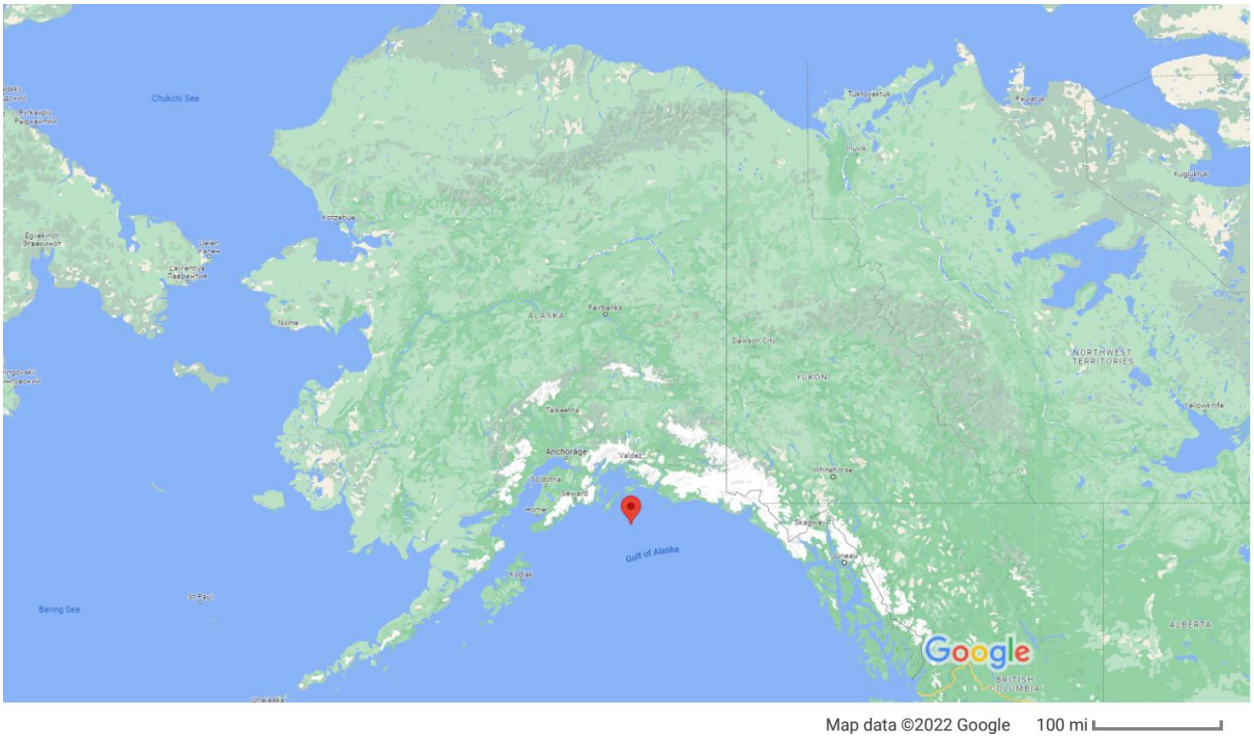

Figure 2.1. Location of Middleton Island, Alaska (59°44’ N, 146°33’ W) indicated by red arrow (Data from Google Maps © 2020).

Figure 2.2. Tower and interior of tower used by nesting Black-legged Kittiwakes (*Rissa tridactyla*) and Pelagic Cormorants (*Phalacrocorax pelagicus*) on Middleton Island, Alaska.

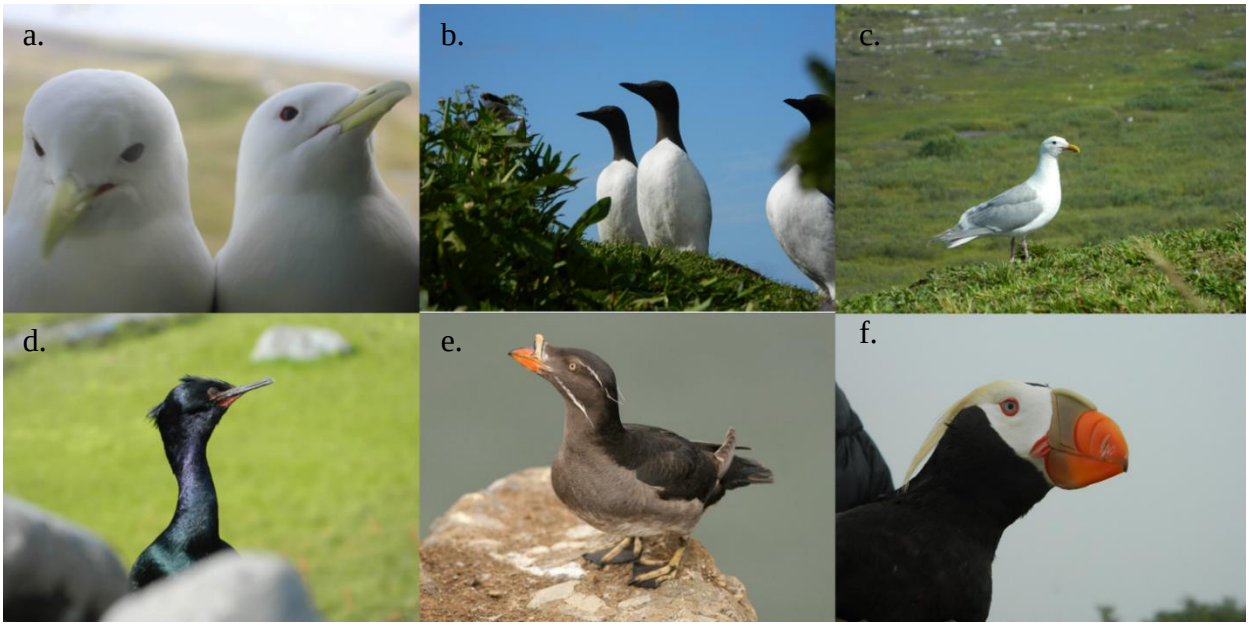

Figure 2.3. Seabirds (a. Black-Legged Kittiwake (*Rissa tridactyla*), b. Common Murre (*Uria aalge*), c. Glaucous-winged Gull (*Larus glaucescens*), d. Pelagic Cormorant (*Phalacrocorax pelagicus*), e. Rhinoceros Auklet (*Cerorhinca monocerata*), and f. Tufted Puffin (*Fratercula cirrata*)) using Middleton Island, Alaska for breeding

Table 2.1. Review of screening for avian influenza viruses, or exposure thereto, in six species of seabirds using Middleton Island, Alaska. Screening Methods are as follows real-time reverse transcriptase PCR detection of the matrix gene (rRT-PCR), virus isolation in embryonated chicken eggs (VI) and enzyme-linked immunosorbant assay (ELISA), virus neutralization of sera (HI/NI), and rapid diagnostic testing for influenza (RIDT). (*Indicates fecal samples only)

Species	Location	Positives	Tested	Prevalence	Screening Method	Viral Subtypes	Reference
Black-legged Kittiwake (*Rissa tridactyla*)	Europe	0	58	0	rRT-PCR		Munster et al., 2007
	Alaska, USA	0	2	0	VI, rRT-PCR		Ip et al., 2008
	Norway	0	2	0	rRT-PCR		Germundsson et al., 2010
	Hornøya, Norway	20	200	0.10	rRT-PCR	H4	Toennessen et al., 2011
	Hornøya, Norway	57	98	0.58	ELISA, HI/NI	H13, H16	Toennessen et al., 2011
	Canada	1			rRT-PCR	H13N6	Hall et al., 2013
	Newfoundland and Labrador, Canada	0	109	0	rRT-PCR		Wille et al., 2014
	Svalbard, Norway	4	17	0.24	ELISA		Lundgren, 2018 (Master's Thesis)
	Svalbard, Norway	9	53	0.17	ELISA		Lee et al., 2020
Common Murre (*Uria aalge*)	Sakhalin Island, Russia	1	100	0.01	VI	H3N2	Sazonov et al., 1977
	Sakhalin Island, Russia	32	142	0.23	HI/NI		Sazonov et al., 1977
	Bonden island, Sweden	3	26	0.13	VI	H6N2	Wallensten et al., 2005

	Krimpen and Lekkerkerk, Netherlands	0	6	0	rRT-PCR		Munster et al., 2007
	Öland, Sweden	3	623	<0.01	rRT-PCR		Munster et al., 2007
	Norway	0	88	0	rRT-PCR		Munster et al., 2007
	Alaska, USA	1	76	0.01	VI		Ip et al., 2008
	Alaska, USA	2	76	0.03	rRT-PCR		Ip et al., 2008
	Newfoundland and Labrador, Canada	71	1317	0.05	rRT-PCR		Wille et al., 2014
	Newfoundland, Canada	51	115	0.44	ELISA		Wille et al., 2014
	Newfoundland and Labrador, Canada	14	32	0.44	VI	H4, H1N2	Wille et al., 2014
Glaucous-winged Gull (*Larus glaucescens*)	Alaska, USA	1	770	<0.01	rRT-PCR	H16N?	Winker et al., 2008
	Alaska, USA	0	8	0	rRT-PCR		Ebbert et al., 2010
	California, USA	0		0	rRT-PCR		Siembieda et al, 2010
	Alaska, USA	69	1256*	0.06	rRT-PCR		Ramey et al., 2015; Reeves et al., 2018
	Alaska, USA	20	1256*	0.02	VI	H1N1, H3N8, H4N6, H5N2, H11N2 H13N2, H16N3	Ramey et al., 2015; Reeves et al., 2018
Pelagic Cormorant (*Phalacrocorax pelagicus*)		0	11	0	VI		Wallgren et al., 2008.
	Alaska, USA	0	3	0	VI, rRT-PCR		Ip et al., 2008

Rhinoceros Auklet (*Cerorhinca monocerata*)	California, USA	0	2	0		Jessup et al., 2009
	California, USA	0		0	rRT-PCR	Siembieda et al, 2010
	Hokkaido, Japan	0	1	0	RIDT	Yoshino et al., 2015
	Washington, USA	0	7	0	rRT-PCR	Knowles et al., 2019
Tufted Puffin (*Fratercula cirrata*)	Alaska, USA	0	4	0	VI, rRT-PCR	Ip et al., 2008
	California, USA	0		0	rRT-PCR	Siembieda et al, 2010
	Alaska, USA	0	8	0	rRT-PCR	Jones et al., 2019

Table 2.2. Review of flea species (Order: Siphonaptera) associated with six species of seabirds using Middleton Island, Alaska.

Host Species	Flea Species	Location	Flea Collected	Positive Hosts	Hosts Sampled	Prevalence	Reference
Black-legged Kittiwake (*Rissa tridactyla*)	*Ceratophyllus vagabundus vagabundus*	Alaska, USA	1		1*		Harriman, et al., 2011
		Svalbard, Norway	1		3*		Mehl, 1992
		Nordland, Norway	310		14*		Mehl, 1992
		Finmark, Norway	50		8*		Mehl, 1992
		Romsdale, Norway	401		17*		Mehl, 1992
	Ceratophyllus vagabundus insularus	California, USA	93		8		Trolle and Jensen, 2001
	Ceratophyllus garei	Romsdal, Norway	7		17		Mehl, 1992
	Mioctenopsylla artica artica	Svalbard, Norway	757		3*		Mehl, 1992
			157		13*		Coulson et al, 2009
			118		23*	0.2-0.9	Pilskog et al., 2014
		Finmark, Norway	28		8*		Mehl, 1992
	Mioctenopsylla artica hadweni	Novaya Zemlya, Russia	1		1*		Rothschild, 1922
		Alaska, USA	6	2	22	0.09	Choe and Kim, 1988

Common Murre (*Uria aalge*)	*Ceratophyllus pelecani*	California, USA	1		“many”		Marshall and Nelson, 1967
Glaucous-winged Gull (*Larus glaucescens*)	*Ceratophyllus niger*						James-Veitch and Booth, 1954
Pelagic Cormorant (*Phalacrocorax pelagicus*)	*Ceratophyllus pelecani*	California, USA	“many”		“many”		Marshall and Nelson, 1967
	Mioctenopsylla traubi			7	7	1	Ballard and Ring, 1979
Rhinoceros Auklet (*Cerorhinca monocerata*)							
Tufted Puffin (*Fratercula cirrata*)	*Actinopsylla suavis*	Oregon, USA	2	2	3*		Clifford et al., 1970
	Ceratophyllus lari or *pelecani*	Oregon, USA	1	2	2*		Clifford et al., 1970

* Indicates specimen were pulled from individuals and/or nest sites

Table 2.3. Review of chewing louse species (Order: Mallophaga) associated with six species of seabirds using Middleton Island, Alaska.

Host Species	Louse Species	Location	Lice Collected	Positive Hosts	Hosts Sampled	Prevalence	Reference
Black-legged Kittiwake (*Rissa tridactyla*)	*Saemundssonia lari*	Höfn, Iceland	20	1	1		Timmerman, 1949
		Maine, USA	1	1			Kierans, 1966
		Alaska, USA	81	11	22	0.5	Choe and Kim, 1987a
		Newfoundland, Canada		8	29	0.27	Threllfall and Fitzpatrick, 1977
	Quadraceps ornatus	Höfn, Iceland	1	1	1		Timmerman, 1949
		Alaska, USA	205	15	22	0.68	Choe and Kim, 1987a
		Newfoundland, Canada		8	29	0.27	Threllfall and Fitzpatrick, 1977
	Austromenopon transversum	Alaska, USA	5	3	22	0.14	Choe and Kim, 1987a
Common Murre (*Uria aalge*)	*Saemundssonia calva*	California, USA	1	1	1		Kellog, 1896
		Reykjavík, Iceland	1	1	1		Timmerman, 1949
		Alaska, USA	184	21	29	0.72	Choe and Kim, 1987a
		Oregon, USA	13	7	10	0.7	Clifford et al., 1970
		Newfoundland, Canada		16	34	0.47	Eveleigh & Threlfall, 1976

				9	25	0.36	Ballard and Ring, 1979
			11	9	41	0.21	Muzaffar, 2000
	Quadraceps obliquus	Alaska, USA	1122	29	29	1	Choe and Kim, 1987a
		Oregon, USA	82	7	10	0.7	Clifford et al., 1970
		Newfoundland, Canada		29	34	0.85	Eveleigh & Threlfall, 1976;
				25	25	1	Ballard and Ring, 1979
			79	10	41	0.24	Muzaffar, 2000
	Austromenopon uriae	Alaska, USA	159	21	29	0.72	Choe and Kim, 1987a;
		Oregon, USA	40	7	10		Clifford et al., 1970
		Great Britain, United Kingdom	83				Timmerman, 1954
				29	34	0.85	Eveleigh & Threlfall, 1976
			158	3	41	0.07	Muzaffar, 2000
				23	25	0.92	Ballard and Ring, 1979
	Austromenopon sp.	Newfoundland, Canada					Wheeler and Threlfall, 1989
Glaucous-winged Gull (*Larus glaucescens*)	*Actornithophilus funebris*						Hopkins and Clay, 1952
	Austromenopon transversum						Hopkins and Clay, 1952
	Saemundssonia sp.		1	1	22	0.05	Ballard and Ring, 1979

Pelagic Cormorant (*Phalacrocorax pelagicus*)	*Pectinopygus insularis*	Alaska, USA	38	4			Choe and Kim, 1987b
	Eidmaniella pellucida	Alaska, USA	2	4			Choe and Kim, 1987b
	Eidmaniella kuwani	California, USA	2			“many”	Marshall and Nelson, 1967
Rhinoceros Auklet (*Cerorhinca monocerata*)	*Quadraceps ambestrix*	Oregon, USA	1	1	1		Timmerman, 1974
	Saemundssonia acutipecta	California, USA	1	1	1		Kellog, 1896
Tufted Puffin (*Fratercula cirrata*)	*Saemundssonia* sp.	Alaska, USA	3	1	1		Hoberg and Whele, 1982
	Menacanthus chrysophaeus	Oregon, USA	4	1	1	1	Clifford et al., 1970

Table 2.4. Review of tick species (Order: Ixodida) associated with six species of seabirds using Middleton Island, Alaska.

Host Species	Tick Species	Location	Ticks Collected	Positive Hosts	Hosts Sampled	Prevalence	Reference
Black-legged Kittiwake (*Rissa tridactyla*)	*Ixodes uriae*	Newfoundland, Canada	1	1	29	0.03	Fitzpatrick and Threllfall, 1977
			908		230	0.68	McCoy et al., 1999
		Alaska, USA	5	2			Hoberg and Whele, 1982
			2582	20	22	0.91	Choe and Kim, 1987a
			30	30	40	0.75	McCoy et al., 2005
			78	57			Dietrich et al., 2012
		Great Britain, United Kingdom	209	133	747	0.18	Danchin, 1992
			1580	513	1132	0.45	Boulinier and Danchin, 1996
			24		48	0.5	Wanless et al., 1997
			144	60	135	0.44	McCoy et al., 2005
			106		37		Nunn et al., 2005
		Cap Sizun, France	25	15	66	0.23	McCoy et al., 2005
		Nordland, Norway	18*	3	20	0.15	Mehl and Traavik, 1983
			24	14	20	0.7	McCoy et al., 2005
		Finmark, Norway	6	1	1	1	Mehl and Traavik, 1983

			75	75	88	0.64	McCoy et al., 2005
			29	21			Duneau et al., 2008
			29	12			Dietrich et al., 2012
		Kamtchatka, Russia	142	66			Dietrich et al., 2012
		Akureyri, Iceland	30	24			Duneau et al., 2008
			30	24			Dietrich et al., 2012
		Mýrasýsla, Iceland	28	17			Duneau et al., 2008
			28	17			Dietrich et al., 2012
		Vestfirőir, Iceland	20	1			Duneau et al., 2008
	Ixodes signatus	Alaska, USA	29	6	22	0.27	Choe and Kim, 1987a
Common Murre (*Uria aalge*)	*Ixodes uriae*	Newfoundland, Canada		15	28	0.54	Eveleigh and Threllfall, 1975
			6		16	0.31	McCoy et al., 1999
		British Columbia, Canada	180	1	25	0.04	Ballard and Ring, 1979
		Great Britian, United Kingdom		48	166	0.29	Wanless et al., 1997
			37		23		Nunn et al., 2005
			128	34			Dietrich et al., 2012
		Maine, USA	23				Smith et al., 2006

		Kamtchatka, Russia	109	83			Dietrich et al., 2012
		Alaska, USA	2	2			Hoberg and Whele, 1982
			2777	28	29	0.97	Choe and Kim, 1987a
			71	40			Dietrich et al., 2012
		Akureyri, Iceland	28	39			Duneau et al., 2008
			30	22			Dietrich et al., 2012
		Vestfirőir, Iceland	12	7			Duneau et al., 2008
		Mýrasýsla, Iceland	19	31			Duneau et al., 2008
			29	24			Dietrich et al., 2012
		Finmark, Norway	30	29			Duneau et al., 2008
			29	12			Dietrich et al., 2012
		Norland, Norway	63	4	7	0.57	Mehl and Traavik, 1983
	Ixodes signatus	Alaska, USA	70	8	29	0.28	Choe and Kim, 1987a
Glaucous-winged Gull (*Larus glaucescens*)	*Ixodes uriae*	British Columbia, Canada	1	1	22	0.05	Ballard and Ring, 1979
Pelagic Cormorant (*Phalacrocorax pelagicus*)	*Ixodes uriae*	Alaska, USA	244	4			Choe and Kim, 1987b
	Ixodes signatus	Alaska, USA	115	4			Choe and Kim, 1987b

		British Columbia, Canada	24	1		Hearle, 1938
			408	2		Spencer, 1960
Rhinoceros Auklet (*Cerorhinca monocerata*)	*Ixodes uriae*	British Columbia, Canada	28	28		Dietrich et al., 2012
			14			Duran et al., 2014
		Alaska, USA	13	1		Hoberg and Whele, 1982
Tufted Puffin (*Fratercula cirrata*)	*Ixodes uriae*	Alaska, USA	49	9		Hoberg and Whele, 1982
			8			Olsen et al., 1995
			32	>2		Dietrich et al., 2012
			20			Duran et al., 2014
		Kamtchatka, Russia	30	23		Dietrich et al., 2012
	Ixodes signatus	Alaska, USA	1	1		Hoberg and Whele, 1982
	Ixodes auritulus	Oregon, USA	4	1	1	Clifford, 1970

CHAPTER 3

ECTOPARASITES AND ASSOCIATED PATHOGENS ON A BREEDING SEABIRD COLONY ON MIDDLETON ISLAND, ALASKA[1]

[1] Williams, B.M., A.M. Ramey, S.A. Hatch, and M.J. Yabsley. To be submitted to *Veterinary Parasitology: Regional Studies and Reports.*

Abstract

Seabird colonies provide habitat for shelter-seeking ticks and other hematophagous insects, such as fleas, lice, and mites, to complete various portions of their lifecycle. In turn, blood-feeding insects may serve as vectors for bacterial and parasitic agents with the potential to adversely affect avian health. We sampled six species of seabirds, including the Black-legged Kittiwake (*Rissa tridactyla*), Pelagic Cormorant (*Phalacrocorax pelagicus*), Common Murre (*Uria aalge*), Glaucous-winged Gull (*Larus glaucescnens*), Tufted Puffin (*Fratercula cirrhata*), and Rhinoceros auklet (*Cerorhinca monocerata*) nesting on Middleton Island, Alaska in 2014 and 2015 for ectoparasites. We also tested ectoparasites for several bacterial and parasitic agents, specifically: *Borrelia*, *Babesia*, and *Rickettsia*. We identified two species of ticks, *Ixodes uriae* and *Ixodes signatus*, three species of fleas, *Ceratophyllus vagabundus vagabundus*, *Mioctenopyslla artica hadweni*, and *Mioctenopyslla traubi traubi*, and six species of chewing lice, *Austromenopon transversum, Eidmaniella pellucida, Pectinopygus insularis, Quadraceps obliquus, Quadraceps ornatus, Saemundssonia calva*, and *Saemundssonia lari*. We did not detect *Borrelia* or *Babesia* in sampled ticks; however, *Rickettsia* was detected in 37/85 *I. uriae* and 6/22 *I. signatus*. Sequences from 21 *I. uriae* and four *I. signatus* were all *Rickettsia amblyommatis*. *Rickettsia* was detected in 8 of 119 fleas of all three species; sequences from four fleas (two *C. vagabundus vagabundus* and one each of *M. artica hadweni* and *M. traubi traubi*) were *Rickettsia felis*. Based upon our finding of *Rickettsia* in previously unreported species, it is likely that this pathogen is found in a broad range of ticks and fleas with a larger distribution than currently recognized. While our study is consistent with previous reports of ectoparasites in that we found ectoparasites previously identified on these species or on similar seabirds, it also

provides new data on abundance and infestation rates of ectoparasites for the various host species breeding on Middleton Island.

Introduction

Middleton Island, Alaska, is a small island of approximately 16 km^2 located south of Prince William Sound in the Gulf of Alaska that has been recognized as providing important colonial nesting seabird habitat since at least 1956 (Rausch, 1958) (Figure 1a). Numerous species of seabirds breed on the island including Black-legged Kittiwake (*Rissa tridactyla*), Pelagic Cormorant (*Phalocrocorax pelagicus*), Common Murre (*Uria aalge*), Glaucous-winged Gull (*Larus glaucescnens*), Tufted Puffin (*Fratercula cirrhata*), and Rhinoceros auklet (*Cerorhinca monocerata*). This island was a United States Air Force installation from 1958-1964, and associated structures were decommissioned in 1964. Soon after the base decommission, Black-legged Kittiwakes and Pelagic Cormorants began using these structures as nesting habitat. To facilitate research, one radar tower (Figure 1b) was modified by the United States Geological Survey-Biological Resources Division (USGS-BRD) and U.S. Fish and Wildlife Service to allow access to nesting adults and chicks via window panels (Figure 1c). Pelagic seabirds also nest on natural cliffs (Black-legged Kittiwake, Pelagic Cormorant, Common Murre), the ground (Glaucous-winged Gull), and in burrows (Tufted Puffin and Rhinoceros Auklet) throughout the Island.

Seabird colonies, such as those on Middleton Island, provide suitable habitat for shelter-seeking ticks and other hemataphagous ectoparasites such as fleas, lice, and mites, to complete various portions of their lifecycle (Dietrich et al., 2011). Health issues, such as anemia, lowered reproductive success, and nest abandonment, have been documented in seabirds with high levels of tick, flea, and mite infestations (Clayton, 1990; DeVaney, 1976; Booth et al., 1993; Lehmann,

1993; Kristjánsson et al., 2016). The most common ticks reported from seabird colonies in the Palearctic and North Pacific region are *Ixodes signatus, Ixodes uriae, Carios capensis,* and *Carios maritimus*, all of which have been associated with transmission of pathogens (Banks, 1908; Zumpft, 1952; Choe and Kim, 1987a; Choe and Kim, 1987b; Khan et al., 2019; Hahn et al., 2020). In addition, seabirds are hosts for tick-borne pathogens such as *Babesia* and *Borrelia* spp. (Wobeser, 1997; Hublak, 2004; Atkinson, 2008; Yabsley et al., 2009; Lobato et al., 2011; Chambert et al., 2012; Yabsley et al., 2012). Most research on ixodid ticks and seabirds has been focused on the causative agent of Lyme disease, the *Borrelia burgdorferi* senso lato group. For example, *Borrelia garinii* has been reported in Black-legged Kittiwakes, Common Murres, and Tufted Puffins from Europe and eastern North America that were reported to be parasitized by *Ixodes uriae* (Staszewski et al., 2008; Lobato et al., 2011; Chambert et al., 2012).

Fleas commonly associated with seabirds include *Ceratophyllus*, *Mioctenopsylla, Parapsyllus*, and *Xenopsylla* spp. (Coulson et al., 2009; Khan et al., 2019). Few studies have determined the effects of fleas on seabird species; however, at least one study examined the effects on one species of sea duck. Specifically, Kristjannson et al. (2016) noted adult agitation associated with flea infestations in nesting Common Eiders (*Someteria mollissima*) as well as the occurrence of blood on the surface of eggs which could indicate blood loss from flea bites. Fleas have also been implicated in the transmission of pathogens such as *Rickettsia* and *Bartonella* in wildlife and domestic animals and can be mechanical vectors of avipoxviruses (Bitam et al., 2010; Sekeyová et al., 2012; Kane et al., 2012).

Avian lice are extremely diverse (>3,000 species) but are generally understudied in seabirds. Seabird lice are considered to have closely evolved alongside their host species with minimal host-switching following the Fahrenholz Rule, which states, “In groups of permanent

parasites, the classification of the parasites usually corresponds directly [to] the natural relationships of the hosts" (Eichler, 1941; Page, 1996; Page et al., 2004; Johnson et al., 2004; Banks et al., 2006). Typically, avian lice are not a significant source of transmission of pathogens, but it is unclear which chewing lice are common on North Pacific seabirds and whether or not they may cause adverse health impacts to their avian hosts.

Although ectoparasites have been reported on Middleton Island seabirds, both anecdotally and from broad surveys, prior studies were limited in scope with low sample sizes (McCoy et al., 2005; Hahn et al., 2020). In this study, we aimed to sample the ectoparasite fauna more systematically and characterize the prevalence and diversity of ticks and fleas affecting six species of breeding seabirds on Middleton Island, Alaska. Furthermore, we assessed if ticks and fleas harbored potential pathogens capable of conferring adverse impacts to host species. This information may be used to establish baseline prevalence of ectoparasites and their associated pathogens in a breeding seabird colony.

Methods

We sampled six species of breeding seabirds inhabiting Middleton Island during May-August in 2014 and 2015: Black-legged Kittiwake, Pelagic Cormorant, Common Murre, Glaucous-winged Gull, Tufted Puffin, and Rhinoceros Auklet. Collection method varied by species and included capturing birds with a wire hook inserted through a hole below window panels (Figure 3.1c) (Black-legged Kittiwake and Pelagic Cormorant adults), a noose pool (Common Murres), by hand net (Rhinoceros Auklet adults), by excavating a hole in nesting burrows (Rhinoceros Auklet chicks and Tufted Puffins), or by hand (Black-legged Kittiwake, Pelagic Cormorant, and Glaucous-winged Gull chicks). Captured birds were manually restrained and examined for ectoparasites by visual examination of the head, breast, belly, wings, tail, and

feet. The number of ticks was recorded, and representative samples of ticks and opportunistic samples of fleas and lice, when observed, were collected from birds and preserved in 100% ethanol. Nest material from Black-legged Kittiwakes and Pelagic Cormorants using the tower was also collected from nest sites post-fledge and searched for ectoparasites. Ectoparasites found in nesting material were preserved in 100% ethanol. Parasites collected were identified using appropriate dichotomous keys (Traub et al., 1983; Holland, 1985; Horak et al., 2002; Price et al., 2003; Galloway, 2019). All capture and sample procedures were reviewed and approved by the University of Georgia's IACUC committee (A2014 01-006).

To determine differences in prevalence of ectoparasites (ticks and fleas) between years, species, and age groups, we performed a Chi^2 analysis with a Yates correction or by Fisher's Exact test for those with sample size below ten. A one-way analysis of variance (ANOVA) was used to determine if there were differences in the abundance of total ticks collected between the two *Ixodes* species, between collection years by species, and between tick life stages by species. We also used ANOVA to determine if there were differences in the burdens of ticks on the different bird species by year and by age. Pairwise comparisons to determine which groups were significant were conducted by conducting a Tukey's honestly significant difference (HSD) test. For all statistical testing, $p < 0.05$ was considered significant. Genomic DNA from a subsample of fleas and ticks was extracted using the Qiagen DNA Purification Kit (Germantown, MD) following the manufacturer's protocol for tissue or a slightly modified protocol (for ticks) that included parasite bisection and an overnight incubation at 56°C in lysis buffer and proteinase K as described by Ammazzalorso et al. (2015). Tick DNA samples were screened by nested polymerase chain reaction (PCR) assays that targeted partial *Borrelia* flagellin, *Babesia* 18S rRNA, and *Rickettsia* 17kDa genes using previously described protocols (Yabsley et al., 2012;

Shock et al., 2014) (Supplemental Table 1). Flea DNA was screened for *Rickettsia* using primers targeting the 17kDa gene (Azad et al., 1992). Amplicons were visualized on 0.8% agarose gels stained with Gel Red Nucleic Acid Gel Stain 10,000X in DMSO (Biotium, Hayward, CA). Appropriately sized amplicons were bi-directionally sequenced at the University of Georgia Genomics Facility (Athens, Georgia). Chromatograms were analyzed using Geneious Prime 2021.2.2, and consensus sequences were generated. Sequences were compared with related sequences using the nucleotide BLAST function available through the National Center for Biotechnology Information (NCBI). A sample was considered positive if a band was visualized at the expected target size in comparison to a known control. For *Rickettsia* species assignment, the species was considered to be determined if the amplified product shared $\geq$90% identity and coverage with genetic information previously reported for a *Rickettsia* species.

Results

A total of 833 and 954 ticks in 2014 and 2015, respectively, were collected and identified. Ticks were identified from Black-legged Kittiwake, Pelagic Cormorant, Tufted Puffin, and Rhinoceros Auklet, but not Common Murres and Glaucous-winged Gulls. Two species of ticks were identified on seabirds inhabiting Middleton Island: *Ixodes uriae* (n= 768 and 910 in 2014 and 2015, respectively) and *Ixodes signatus* (n=43 and 37). Our data indicate that there were significantly higher burdens and prevalence of *Ixodes uriae* on Black-Legged Kittiwake and Pelagic Cormorant chicks compared with their adult counterparts ($p< 0.0001$ and $p< 0.0001$, respectively) as well as compared with Glaucous-winged Gull ($p< 0.0001$ and $p< 0.0001$) and Tufted Puffin ($p=0.001$ and $p=0.005$) chicks (Table 1; Supplementary Figure 1). Black-legged Kittiwake chicks also had significantly higher burdens and prevalence than Tufted Puffin Chicks. When comparing adults between species sampled, there were no significant differences in

prevalence or abundance of *I. uriae*, except Common Murre adults had a significantly lower prevalence than Black-legged Kittiwake and Pelagic Cormorant adults.

Ixodes signatus was only detected on cormorants and in low numbers (mean 1, range 0-9). All *I. signatus* identified were adult ticks. Prevalence of *I. signatus* among cormorant adults was 10/41 (24.4%) and 9/28 (32.1%) in 2014 and 2015, respectively. Prevalence of *I. signatus* among cormorant chicks was 15/56 (26.8%) was 12/29 (41.4%) in 2014 and 2015, respectively. There were no significant differences between prevalence or abundance between adults and chicks or by year.

A total of 1,240 adult females, 215 adult males, and 203 nymphs of *Ixodes uriae* from birds and eight adult females, three adult males, and nine nymphs from the surrounding environment were identified. For *Ixodes signatus*, 27 adult females, 28 adult males, and one nymph were collected. Significantly more I. uriae were collected than I. signatus ($p < 0.00001$). All life stages of both ticks were found on seabirds inhabiting Middleton Island; however, adult ticks were more commonly observed than nymphs for *I. uriae* species ($p < 0.00001$). We also collected 29 larval ticks from both years but did not identify these to species.

A total of 73 and 165 fleas (Order: Siphonaptera) from 2014 and 2015, respectively, were collected from Pelagic Cormorants, Black-legged Kittiwakes, and Common Murres. Three species were identified as *Ceratophyllus vagabundus vagabundus* (n=41, 63), *Mioctenopsylla artica hadweni* (n=24, 77), and *Mioctenopsylla traubi traubi* (n=8, 24) (Table 2). Prevalence of fleas was significantly higher on Black-legged Kittiwake chicks than on both kittiwake adults [X^2 (1, N = 523) = 133.4, $p < 0.00001$] and Pelagic Cormorant chicks, [X^2 (1, N = 348) = 52.4, $p < 0.00001$]. Conversely, Pelagic Cormorant chicks had a lower prevalence to their adult counterparts [X^2 (1, N = 154) = 49.6, $p < 0.00001$]. Adult Pelagic Cormorants had higher

prevalence than both Common Murre adults and Black-legged Kittiwake adults [X^2 (1, N = 154) = 129.5, $p < 0.00001$ and X^2 (1, N = 329) = 98.8, $p < 0.00001$, respectively]. Prevalence in Black-legged Kittiwake adults was higher than that of Common Murre Adults [X^2 (1, N = 348) = 22.4, $p < 0.00001$].

Feather lice (Order: Phthiraptera) (n=31 from 2014 and n=50 from 2015) were collected from Pelagic Cormorants, Black-legged Kittiwakes, and Common Murres (Table 3). Because lice were opportunistically collected and observed in low numbers, no comparisons of lice numbers and hosts were conducted. However, seven species of lice were identified, including: *Autromenopon transversum*, *Eidmaniella pellucida*, *Pectinopygus insularis*, *Quadraceps obliquus*, *Quadraceps ornatus*, *Saemundssonia calva*, and *Saemundssonia lari*. Only *A. transversum* and *E. pellucida* were found on more than one host species, although both were found predominately on one host species (Table 3).

To assess the occurrence of potential pathogens associated with seabird ticks and fleas, 85 *Ixodes uriae and* 22 *Ixodes signatus* were tested for *Babesia*, *Rickettsia*, and *Borrelia* spp. and 119 fleas for *Rickettsia* spp. No *Babesia* or *Borrelia* were detected in the ticks tested. However, an appropriately sized band consistent with *Rickettsia* was detected for 37 (43.5%) *Ixodes uriae* and 6 (27.3%) *Ixodes signatus*. Sequences (364-407 bp) from 21 I. uriae and four *I. signatus* samples shared a 91.9-100% consensus identity with *R. amblyommatis*. A total of 8 of 119 fleas were positive for *Rickettsia* including 5/47 (10.6%) *Mioctenopsylla artica hadweni*, 3/18 (16.7%) *Mioctenopsylla traubi traubi*, and 3/54 (5.6%) *Ceratophyllus vagabundus vagabundus. Rickettsia* sequences (355-408 bp) from four fleas (two *C. vagabundus vagabundus* and one each of *M. artica hadweni* and *M. traubi traubi*) were 100% similar to each other and were 100% identical to numerous *R. felis* sequences.

Discussion

In this survey of ectoparasites associated with seabirds breeding on Middleton Island, we detected two species of ticks, three species of fleas, and seven species of lice. Only *Ixodes uriae* has been previously reported from Black-legged Kittiwakes at Middleton Island (McCoy et al., 2005; Hahn et al., 2020). Although *Ixodes uriae* has been previously found on all species we sampled at various locations throughout each species' respective range, this is the first report of this tick on Pelagic Cormorants, Tufted Puffins, and Rhinoceros Auklets inhabiting Middleton Island. We only found *I. signatus* associated with Pelagic Cormorant hosts; however, they have been previously found on Black-legged Kittiwakes, Common Murres, Pelagic Cormorants, and Tufted Puffins at other locations within their range (Choe & Kim, 1987; Danchin, 1992; Price et al., 2003; Khan et al., 2019; Hahn et al., 2020). While there is no evidence of host specificity in these ticks, there may be host preference towards individuals in family Phalocrocoracidae in mixed colonies (Guglielmone et al., 2014), as is further supported by our results.

In previous studies on seabird species in the North Pacific, the prevalence of *I. uriae* varies considerably (4-97%) among hosts and locations (Ballard and Ring, 1979; Choe and Kim, 1987a). Choe and Kim (1987a) reported prevalence and mean number of *I. uriae* per infested Black-legged Kittiwakes in Alaska was 90.9% and 129.1, respectively, and 96.6% and 99.2, respectively, in Common Murres; however, no ranges were reported. This study also examined the prevalence of *I. signatus* in these species and found 27% and 28% of birds to harbor one or more parasites of this species, respectively. Mean number of *I. signatus* per infested host was 4.8 and 8.8 in these species, respectively; however, no range was reported for these ectoparasites either. Our prevalence of *I. uriae* on Black-legged Kittiwakes is consistent with that of Choe and Kim and is on high end of the overall range in the North Pacific; however, average burdens were

much lower than in the aforementioned study. Conversely to Choe and Kim, our study did not find *Ixodes* associated with Common Murres. Overall, our current study provided new data on abundance and infestation rates of *Ixodes* spp. on all the various host species breeding on Middleton Island.

We noted large variability in prevalence and abundance of *Ixodes* spp. parasitizing nesting seabirds in our study. Prevalence and abundance of ticks were significantly higher on chicks versus their adult counterparts in all species, which is logical given the nidicolous life history of these ectoparasites (Eveleigh & Threlfall, 1975, Steele et al., 1990). They were also more common and numerous in chicks of species using natural nesting material such as grasses, twigs, and mud (i.e., Black-legged Kittiwakes and Pelagic Cormorants) than those species using underground burrows (i.e., Rhinoceros Auklets and Tufted Puffins) or those without nesting materials (i.e., Common Murres and Glaucous-winged Gulls). Furthermore, more parasitized species were those using man-made nesting sites (i.e., Black-legged Kittiwakes and Pelagic Cormorants), which may create additional refugia for ticks (Eveleigh & Threlfall, 1974; Dietrich et al., 2011).

Our survey is consistent with previous species reports of *C. vagabundus vagabundus* and *M. traubi traubi* fleas in Black-legged Kittiwakes and Pelagic Cormorants in other portions of their species' range (Traub et al., 1983; Khan et al., 2019). However, our study provides new host associations for *C. vagabundus vagabundus* on Common Murres and new associations for *M. artica hadweni* on Pelagic Cormorants, providing further evidence for classifying these as generalist species. Although studies on prevalence of fleas among seabirds are limited, a wide range of prevalence (9-90%) of *M. artica* on Black-legged Kittiwakes in Norway and Alaska has been reported, but sample sizes were limited (Choe and Kim, 1988; Pilskog et al., 2014). Our

study similarly demonstrated a wide variation in prevalence depending on species and life stage (0.9-80%). Our study further provides new data on the prevalence of fleas on several species of seabirds where prevalence data had been previously unreported.

Avian chewing lice are generally host-specific, and our data lends further support to this theory. Interestingly, we identified *Eidmaniella pellucida* on Black-legged Kittiwakes breeding on the tower on Middleton Island. *Eidmaniella pellucida* is commonly associated with members of Phalacrocoracidae and, therefore, likely was opportunistically parasitizing the Black-legged Kittiwakes that were nesting in close proximity to the Pelagic Cormorants also nesting on the tower. With the exception of this new host association, our other data on lice species and the hosts they occurred on were consistent with host associations from other regions (Price et al., 2003; Khan et al., 2019).

We did not find evidence for *Borrelia* or *Babesia* in *Ixodes uriae* or *Ixodes signatus* ticks parasitizing breeding seabirds on Middleton. Although non-seabird associated *Ixodes* spp. are considered the main vector of the *Borrelia burgdorferi* senso lato group to humans, *I. uriae* and *I. signatus* have been hypothesized to be vectors among avian hosts (Olsén et al., 1993; Glyfe et al. 1999; Glyfe et al., 2001; Smith et al., 2006). For example, *Borrelia garinii* was detected in 33% of *I. uriae* from nests of breeding seabirds in the North Pacific (Olsén et al., 1995), but there is geographic variation as no evidence of *Borrelia* was detected in ticks associated with nesting Tufted Puffins on Egg and St. Lazaria Islands, Alaska (Hoberg & Wehle, 1982). Little is known about the effects of *Babesia* infections on avian species. Clinical disease in seabird infections has been associated with anemia, leukocytosis, and reduced hepatic function in African penguins (*Spheniscus demersus*). as well as reduced survival and acute mortality in Common Murres from California USA and Cape Cormorants (*Phalacrocorax capensis*) and King Penguins

(*Aptenodytes patagonicus*) from South Africa (Yabsley et al., 2009; Vanstreels et al., 2015; Parsons et al., 2016; Parsons et al., 2018). Many of these cases were admitted to rehabilitation centers, often for other reasons such as oiling. Although we did not detect *Babesia* in ticks sampled from the island, various seabirds are susceptible to infection and can develop disease, so further research is needed to elucidate the host and vector associations as well as the geographic range of *Babesia*.

We found *Rickettsia* spp. in both fleas and ticks parasitizing seabirds on Middleton Island. Although *Rickettsia* has most commonly been found among mammal ectoparasites, there are relatively few reports from avian ectoparasites. For example, *Rickettsia africae* has been detected in *Ceratophyllus* fleas associated with passerines, and *R. helvetica* was detected in the hen flea *Ceratophyllus gallinae*, a common avian ectoparasite, associated with a cat (Gilles et al., 2008; Sekeyová et al., 2012).

In this study, we identified *R. felis* in *Ceratophyllus vagabundus vagabundus* and two species of *Mioctenopyslla* fleas. *Rickettsia felis* is a spotted fever group emerging human pathogen found nearly worldwide. Fleas are most commonly associated with transmission (Reif and Macaluso, 2009), but recently there has also been increasing evidence that ticks (e.g., *Riphicephalus*, *Haemophysalis*, *Amblyomma*, and *Ixodes* spp.) can be vectors (Zavala-Velázquez et al. 2002; Ishikura et al., 2003; Cardosa et al., 2006; Pérez-Osorio et al. 2008; Oliveira et al., 2008; Brown and Macaluso, 2016). Little research has been conducted to understand the host or taxa specificity of *Rickettsia* species, and many *Rickettsia* species are not obligatory to a specific vertebrate host, so birds may be a possible amplifying host of *R. felis* (Weinert et al., 2009). This study highlights the need for more research to understand the host and vector associations for *R. felis*. Furthermore, humans working with seabirds on Middleton Island may be accidental hosts

for these fleas, as bites sometimes occur. However, it is unknown if seabird ectoparasites inhabiting the avifauna of Middleton Island take blood meals when biting humans; thus, the risk of zoonotic pathogen transmission is unknown.

Although *Rickettsia* has previously been found in Argasidae ticks associated with seabirds, only one previous study has potentially detected *Rickettsia* in a seabird-associated *Ixodes* species (Reeves et al., 2006; Takano et al., 2009; Kawabata et al., 2013; Wilkinson et al., 2014; Dietrich et al., 2014; Lafri et al., 2015). In that study, an uncharacterized *Rickettsia*-like species (no molecular confirmation) was isolated from an *Ixodes uriae* tick parasitizing a penguin inhabiting Mayes Island within the sub-Antarctic Kerguelen Archipelago (Chastel et al., 1993). In our study, all *Rickettsia* sequences of sufficient quality for species identification were identical or most similar to *R. amblyommatis*. Attempts to sequence some *Rickettsia*-positive ticks failed, possibly due to DNA degradation between the time that PCR was conducted and when sequencing was attempted. *Rickettsia amblyommatis* was first described from *Amblyomma americanum* but has since been found in numerous tick genera throughout the Western hemisphere (Burgdorfer et al., 1974, 1981; Mays et al., 2014; Sayler et al., 2014; Karpathy et al., 2016; Cleveland et al., 2019).

Our investigation has broadened the scientific knowledge regarding ectoparasites of breeding seabirds inhabiting Middleton Island, Alaska, through the identification of two species of ticks, three species of fleas, and seven species of lice among the six species of seabirds sampled. Further research on the ectoparasites affecting breeding seabirds, including those inhabiting the North Pacific Basin, would further elucidate the distribution and host associations of these ectoparasites. We also identified *Rickettsia* infections among two species of *Ixodes* ticks and three fleas sampled. Ticks were infected with *R. amblyommatis*, and fleas were infected with

R. felis, both of which have previously been associated with numerous tick and flea species. Although these *Rickettsia* spp. are not known to be avian pathogens, *R. felis* is zoonotic, and *R. amblyommatis* is suspected to be zoonotic. This information on the prevalence, diversity, and burdens of ectoparasites in seabird populations creates a baseline for further research to understand the effects of parasitism on seabird populations. Furthermore, this study helps elucidate pathogen transmission potential for ectoparasite species identified among seabirds on Middleton Island and highlights the further need to understand the vector associations and distribution of currently recognized *Rickettsia* species.

Acknowledgments

We would like to thank Morgan Walker, Mason Stothart, Josh Cunningham, Shirel Khane-Rapport, Elsa Kern-Lovick, and Angelike Aleksieva for their field collection efforts. This research was funded, in part, by the U.S. Geological Survey through the Wildlife Program of the Ecosystems Mission Area and the Georgia Ornithological Society. Additional support was provided by the wildlife management agencies of the Southeastern Cooperative Wildlife Disease Study member states through the Federal Aid to Wildlife Restoration Act (50 Stat. 917) and by a U.S. Department of the Interior Cooperative Agreement and the Daniel B. Warnell School of Forestry and Natural Resources. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Figure 3.1. (a) Location of Middleton Island, Alaska (59°44’ N, 146°33’ W) indicated by red arrow (Data from Google Maps © 2020) (b) Tower and (c) interior of tower used by nesting Black-legged Kittiwakes (*Rissa tridactyla*) and Pelagic Cormorants (*Phalacrocorax pelagicus*) on Middleton Island, Alaska.

Table 3.1. Total number, prevalence, and abundance of *Ixodes uriae* identified from nesting seabirds and the surrounding environment on Middleton Island, Alaska.

Species	No. Positive/No. Sampled (%)			Avg. No Ticks/Host (Range)			Total Ticks Identified			
							Adult Ticks		Nymphs	
	2014	2015	Total	2014	2015	Total	2014	2015	2014	2015
Black-legged Kittiwake (BLKI)										
Chicks	127/198 (64.1)	46/81 (56.8)	173/279 (62.0)	3.75 (0-40)	4.28 (0-32)	4.02 (0-40)	507	652	75	95
Adults	13/117 (11.1)	10/127 (7.8)	23/244 (9.4)	0.21 (0-6)	0.14 (0-5)	0.18 (0-6)	28	3	6	3
Pelagic Cormorant (PECO)										
Chicks	29/41 (70.7)	24/28 (85.7)	53/69 (76.8)	4.12 (0-23)	3.57 (0-16)	3.85 (0-23)	84	120	7	10
Adults	9/56 (16.1)	5/29 (17.2)	11/85 (12.9)	0.63 (0-10)	0.39 (0-5)	0.51 (0-10)	54	3	2	5
Tufted Puffin (TUPU)										
Chicks	NS	2/17 (11.8)	2/17 (11.8)	NS	0.19 (0-3)	0.19 (0-3)	NS	1	NS	0
Adults	0/3 (0)	0/3 (0)	0/6 (0)	-	-	-	0	0	0	0
Rhinoceros Auklet (RHAU)										
Chicks	NS	1/10 (10.0)	1/10 (10.0)	NS	0.9 (0-9)	0.9 (0-9)	NS	6	NS	3
Adults	0/43 (0)	0/72 (0)	0/115 (0)	-	-	-	0	0	0	0
Common Murre (COMU)										
Chicks	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Adults	0/33 (0)	0/75 (0)	0/108 (0)	-	-	-	0	0	0	0
Glaucous-winged Gull (GWGU)										
Chicks	NS	0/50 (0)	0/50 (0)	NS	-	-	NS	0	NS	0
Adults	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

Total	**178/491 (36.3)**	**88/489 (18.0)**	**266/980 (27.1)**	**2.18 (0-40)**	**1.32 (0-32)**	**1.75 (0-40)**	**675**	**791**	**93**	**119**

Table 3.2. Prevalence and total fleas (Order: Siphonoptera) identified on nesting seabirds and from the surrounding environment (nest material or near nesting sites) on Middleton Island, Alaska (superscripts indicate significant differences).

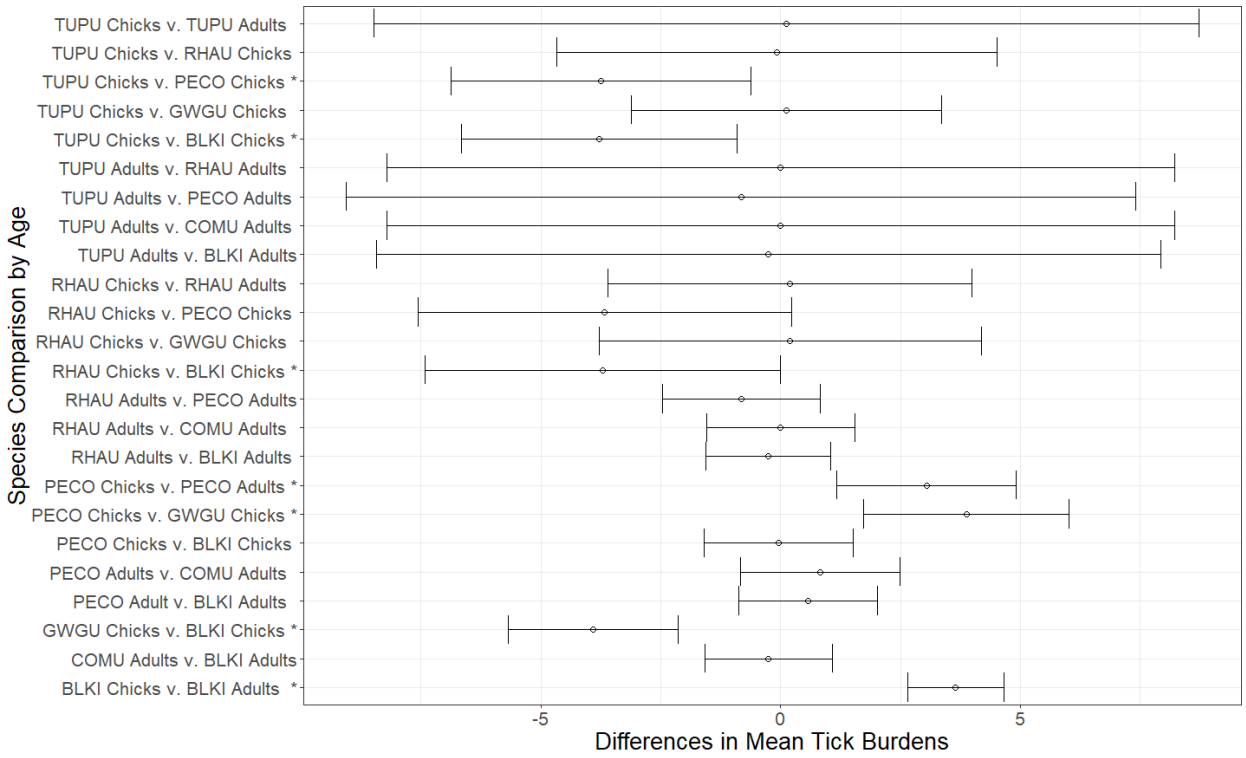
		No. Positive/No. Sampled (%)			*Ceratophyllus vagabundus vagabundus*		*Mioctenopyslla artica hadweni*		*Mioctenopyslla traubi traubi*	
Species		2014	2015	Total	2014	2015	2014	2015	2014	2015
Black-legged Kittiwake (BLKI)					41	27	12	3	3	0
	Chicks	144/198 (72.7)	53/81 (65.4)	197/279 (70.1)[a,b]	30	22	10	2	3	0
	Adults	34/117 (29.1)	15/127 (11.8)	49/244 (20.1)[a,c,d]	11	5	2	1	0	0
Pelagic Cormorant (PECO)					0	0	12	4	5	6
	Chicks	8/41 (19.5)	8/28 (28.6)	16/69 (23.2)[b,e]	0	0	4	3	1	6
	Adults	46/56 (82.1)	22/29 (75.8)	68/85 (80)[c,e,f]	0	0	8	1	4	0
Common Murre (COMU)					1	0	0	0	0	0
	Adults	1/33 (3.0)	0/75	1/108 (0.9)[d,f]	1	0	0	0	0	0
Environmental					0	36	0	70	0	18
Total					**42**	**63**	**24**	**77**	**8**	**24**

Table 3.3. Total lice (Order: Phthiraptera) identified from nesting seabirds on Middleton Island, Alaska, and their host associations ([1]Indicates found on species only in 2015)

Species	Host (n)	Tot. Fleas Identified	Range
Austromenopon transversum	Black-legged Kittiwake (6)	13	1-4
	Glaucous-winged Gull[1] (1)	1	1
Eidmaniella pellucida	Pelagic Cormorant (15)	24	1-5
	Black-legged Kittiwake[1] (1)	1	1
Pectinopygus insularis	Pelagic Cormorant (1)	2	2
Quadraceps obliquus	Common Murre (13)	17	1-3
Quadraceps ornatus	Black-legged Kittiwake (6)	6	1
Saemundssonia calva	Common Murre (2)	3	1-2
Saemundssonia lari	Black-legged Kittiwake (11)	15	1-4

Supplementary Table 3.1. PCR primer pairs used to perform molecular screening for selected pathogens in ectoparasites nesting on Middleton Island, Alaska.

Pathogen	Gene Target	Forward Primer	Reverse Primer
Borrelia	Flagellin (flab)	ACATATTCAGATGCAGACAGAGGT	GCAATCATAGCCATTGCAGATTGT
		AACAGCTGAAGAGCTTGGAATG	CTTTGATCACTTATCATTCTAATAGC
Babesia	18S rRNA	CCTGGTTGATCCTGCCAGTAGT	TGATCCTTCTGCAGGTTCACCTAC
		GAGGTAGTGACAAGAAATAACAATA	TCTTCGATCCCCTAACTTTC
	18S rRNA	CGGGATCCAACCTGGTTGATCCTGC	CCGAATTCCTTGTTACGACTTCTC
		ACCTCACCAGGTCCAGACAG	GTACAAAGGGCAGGGACGTA
	18S rRNA	GAAATTAGAGTGTTTC	ACCCTATTTAGCAGGTTAAG
	18S rRNA	TCGTAGTTGAACTTCTGCTG	ATTGCCTCAAACTTCCTTGC
	ITS-1	CGATCGAGTGATCCGGTGAATTA	GCTGCGTCCTTCATCGTTGTG
		AAGGAAGGAGAAGTCGTAACAAGG	TTGTGTGAGCCAAGACATCCA
Rickettsia	17kDa antigen	GCTTTACAAAATTCTAAAAACCATATA	TGTCTATCAATTCACAACTTGCC
		GCTCTTGCAACTTCTATGTT	CATTGTTCGTCAGGTTGGCG



Supplementary Figure 3.1. Pairwise comparison of the differences of mean tick burdens on species of seabirds nesting on Middleton Island, Alaska by age (BLKI = Black-legged Kittiwakes [*Rissa tridactyla*], COMU= Common Murre [*Uria aalge*], GWGU= Glaucous-winged Gull [*Larus glaucescens]*, PECO = Pelagic Cormorant [*Phalacrocorax pelagicus*], RHAU= Rhinoceros Auklet [*Cerorhinca monocerata*], and TUPU= Tufted Puffin [*Fratercula cirrata*]), (*Indicates significant differences at $p < 0.05$ by Tukey HSD).

CHAPTER 4

EXPERIMENTAL REMOVAL OF ECTOPARASITES INCREASES FLEDGE SUCCESS OF BLACK-LEGGED KITTIWAKES (*RISSA TRIDACTYLA*) ON MIDDLETON ISLAND, ALASKA[1]

[1] Williams, B.M., A.M. Ramey, S.A. Hatch, and M.J. Yabsley. To be submitted to *International Journal for Parasitology: Parasites and Wildlife*.

Abstract

Nesting bird colonies on Middleton Island, Alaska, have undergone population fluctuations, including a decline of breeding Black-legged Kittiwakes (*Rissa tridactyla*) since the 1980s. These population fluctuations are likely due to a variety of factors. However, ectoparasites could be a contributing factor, as studies on other bird species indicate fitness may be reduced with high tick burdens. From June-August 2014 and 2015, we experimentally treated Black-legged Kittiwake nest sites with a mild insecticide to determine if treatment would reduce parasite loads and/or result in increased growth or survival of nestlings in treated nests compared to those in control nests. Black-legged Kittiwake chicks from treated nest sites (n=139) had significantly lower average tick body burdens across years compared with Black-legged Kittiwake chicks from untreated sites (n=151; $F(1,53)=20.6$, $p<0.005$ by ANOVA). No differences in growth rate, hematocrit, or heterophil:lymphocyte ratios were noted, except for differential tarsus measures beginning at day 15 post-hatch ($F(9, 35)=2.4518$, $p= 0.02776$). Fledge success, as measured by survival to day 35, was significantly higher in treated nests versus untreated nests ($p=0.03$ by logistic regression), and those individuals in untreated nest sites were 43.3% (95% CI [0.33, 0.95]) less likely to survive to day 35. Information from this study may be used to guide management of nesting seabirds of conservation concern as treatment of nests with a mild insecticide appears to be a possible strategy for reducing tick infestation of chicks and improving fledging success.

Introduction

Group living and communal nesting, common in nesting seabirds, provide survival advantages, including protection from predators, increased food availability through sharing of information on foraging conditions, and increased breeding success; however, close proximity

linked with cohabitation also increases the risk of pathogen and ectoparasite exposure (Ward and Zahavi, 1973; Alexander, 1974; Stearns, 1980; Bayer, 1982; Møller, 1993). In addition, the risk of pathogen transmission from one year to the next may increase with high levels of interspecific contact and high nesting site fidelity, characteristics common in seabirds (Brown and Brown, 1986; Hatch et al., 2009). While growing, knowledge about seabird parasites and pathogens and their effects on hosts is still limited.

High levels of ectoparasites, such as ticks, can change the behavior and physiology of seabirds and other hosts, potentially impacting the reproduction and survival of young (Aeschlimann, 1991; Duffy, 1983). Ticks can also have direct negative effects on avian hosts, such as exsanguination, anemia, predisposition to secondary infections, direct skin damage, and death in severe cases (Campbell, 1988; Sheldon and Verhulst, 1996; Wanless et al., 1997; Gauthier-Clerc et al., 2003; Sonenshine and Roe, 2014). Along with individual mortalities and behavioral changes associated with hyperparasitism, effects on reproductive productivity, such as lower nest success, reduced growth rates of nesting chicks, and increased chick mortality, may have the potential to lead to colony-level effects (Anderson and May, 1978; Morbey, 1996; Gauthier-clerc et al., 1998; Bergström et al., 1999; Bosch et al., 1997; Bosch and Figuerola, 1999; Ramos et al., 2001; Mangin et al., 2003). For example, in England, high *Ixodes uriae* loads were correlated with reductions of Black-legged Kittiwakes; however, the study did not investigate the effects of ticks on individual birds (Boulinier and Danchin, 1996). There are also reports that high nest ectoparasite burdens caused cormorants, boobies, and pelicans to abandon nests (King et al., 1977a; King et al., 1977b; Duffy, 1983; Norcross and Bolen, 2002). Indirect effects associated with ectoparasites include accumulation of toxins, lowered resistance to toxins,

and pathogen transmission (Gothe et al., 1979, Nuttal, 1984). Tick-borne disease has been associated with breeding failures for seabirds and abnormal development of chicks (Feare, 1976).

Field-based experimental studies where ectoparasites were removed from nesting sites have shown that high ectoparasite loads may lead to reduced body mass, early fledging, lowered hematocrit, and higher polychromasia (Brown and Brown, 1986; Lehman, 1993; McKilligan, 1996; Alves, 1997; Bosch and Figuerola, 1999; Szép and Møller, 1999; Szép and Møller, 2000). One study that experimentally evaluated the impacts of ectoparasites (i.e., fleas, mites, and ticks) on nesting Storm Petrels (*Hydorbates pelagicus*) found that growth rate and hematocrit was negatively correlated with abundance of fleas and ticks (Merino et al., 1999). Additional experimental approaches to investigate the effects of ectoparasites on nesting pelagic seabirds would be help understand the potential detrimental effects on the health and reproductive success of breeding seabirds, potentially helping to guide management decisions as to whether antiparasitic interventions may help to increase survivorship and breeding success.

Middleton Island, Alaska, represents a unique field site conducive to the experimental investigation of the effects of ectoparasites on nesting pelagic seabirds. Middleton island is a small island of approximately 13 km^2 located south of Prince William Sound in the Gulf of Alaska. At least six species of pelagic seabirds breed on the island, including Black-legged Kittiwakes (*Rissa tridactyla*), Pelagic Cormorants (*Phalacrocorax pelagicus*), Glaucous-winged Gulls (*Larus glaucescens*), Common Murres (*Uria aalge*), Rhinoceros Auklets (*Cerorhinca monocerata*), and Tufted Puffins (*Fratercula cirrata*) (Rausch, 1958; Birdlife International, 2019). Because these birds are pelagic, most of the birds breeding on Middleton Island are not found on land outside of the breeding season (approximately mid-March to late August).

In this investigation, we used an experimental approach to evaluate the effect of ectoparasites on the health and breeding success of Black-legged Kittiwakes to determine if treatment with a mild insecticide would improve health parameters and increase fledge success. Like many other seabird species, Black-legged Kittiwakes nest in colonies that may include thousands of individuals. Nest material is composed of grasses, twigs, mud, and other natural materials, all of which can create habitat for nidicolous ectoparasites (Cullen, 1957; Maunder and Threlfall, 1972).

Black-legged Kittiwakes practice asynchronous egg-laying, with 1-3 eggs laid approximately 2-3 days apart (Gill and Hatch, 2002; Maunder and Threllfall, 1972). Siblicide is common, and the first hatched chick often kills other hatchlings by pushing them out of the nest or pecking the scalp until death occurs (Braun and Hunt, 1983). Chicks weigh 30-44g at hatch, then grow rapidly, gaining approximately 400g by day 30, then reduce weight slightly before fledging (Maunder and Threllfall, 1972). Chicks, when flighted, leave the nest on first excursions between days 32-50 (Nysewander, 1983). Full fledge occurs between days 34-58, but chicks often return to the nest to beg parents for food for the remainder of the breeding season (Maunder and Threlfall, 1972).

Black-legged Kittiwakes among the most numerous gull species, with a worldwide distribution of 14.6-15.7 million (Birdlife International, 2019). However, some Black-legged Kittiwake populations are in decline, and therefore, this species is considered to be vulnerable by the International Union for the Conservation of Nature (Descamps et al. 2017; BirdLife International 2019). Long-term studies of breeding Black-legged Kittiwakes on Middleton Island indicate annual variation in reproductive success, with cohorts experiencing significant mortality or complete failure in some years (Hatch et al. 1993). Although food availability has been

associated with reproductive success of Black-legged Kittiwakes at Middleton Island, it is unknown if other factors, such as parasitism by ectoparasites, may also play some role (Roberts and Hatch, 1993; Frederiksen et al., 2004; Österblom et al., 2008). This study aims to determine if a reduction in parasite loads results in improved hematological metrics or increased growth of Black-legged Kittiwake nestlings and greater fledge success using an experimental approach.

Study Site

The United States Air Force previously used Middleton Island. Following decommission in the early 1960s, seabirds began using various structures, including the main communications radar tower (CRT), as nesting habitat. The CRT was modified by the United States Geological Survey-Biological Resources Division (USGS-BRD) and U.S. Fish and Wildlife Service to allow researchers access to nesting adults and chicks via removable window panels (Figure 1). This CRT is divided into two levels covered by 20 panels, each allowing observation of and access to approximately 25 individual nesting sites. Nesting Black-legged Kittiwakes and Pelagic Cormorants use these sites.

Study Design

To assess the impact of ixodid ticks and other ectoparasites on the health of Black-legged Kittiwake chicks hatched and reared on the CRT, we selected two blocks of approximately 25 nests to be used as experimental units for nest treatment (Figure 1). We focused primarily on ixodid ticks because collection efforts limited the scope of the study, and the negative effects of ticks in avian species have been widely documented (Khan et al., 2019). Before the nesting season, nest sites were cleared of previously accumulated materials and treated with approximately 20 grams of Carbaryl (Sevin®-5 Ready-To-Use 5 % Dust (1-naphthyl methylcarbamate), Bayer AG, Leverkusen, Germany), a mild powdered insecticide, to kill

ectoparasites. Once adults began to nest, nest sites with two treatment blocks were retreated with another 20 grams of Carbaryl to reduce ectoparasites on the adult birds. An additional two blocks of approximately 25 nests served as controls and were cleared of nesting material as described previously but were not treated with insecticide prior to or during the nesting period. Experimental and control nest sites were monitored daily throughout the breeding period to assess nest contents and measure chick growth. Upon hatch, all nestlings were captured every five days to determine the ectoparasite burden of each individual, and Carbyl treatment was reapplied to nests when ticks were observed on chicks in either experimental block. Furthermore, basic morphometric measurements were taken for each chick, including weight, wing chord, tarsus-metatarsus, and tail length. Chicks were assumed to fledge when a live chick was observed on or after day 35 per the chick fledge age convention outlined in the standardized protocols for annual seabird monitoring in the Alaska Maritime National Wildlife Refuge (Alaska Maritime National Wildlife Refuge, 2019).

Whole blood from each bird was collected by brachial venipuncture (Owen, 2011). Blood samples were first collected from chicks on day 15 when they had reached a sufficient weight, and then every five days thereafter. A thin blood smear was made, and the remaining blood was stored in heparinized collection vials (BD Mictrotainer® Blood Collection Tubes, Becton Dickinson, Franklin Lakes). Blood smears were fixed with methanol and stained with a modified Giemsa (Dipquick, Jorgensen Laboratories, Inc., Loveland, CO). All capture and sample procedures were reviewed and approved by the University of Georgia's IACUC committee.

To investigate chronic stress, a heterophil:lymphocyte ratio was calculated based on differential leukocyte, and total white blood cell (WBC) counts on thin blood smears. The leukocyte differential count was performed by examining the percent of each WBC type out of

100 (Clark et al., 2009). Relative percentages of heterophils and leucocytes were also calculated. Whole blood was used to calculate a packed cell volume (PCV, i.e., hematocrit) by centrifuging a heparinized microhematocrit tube (StatSpin Microhematocrit tubes; StatSpin Technologies Inc., Westwood, MA USA) at 10,000 rpm for 10 min.

Data Analysis

We assessed differences in average tick burdens, morphometric measurements (i.e., weight, wing chord, culmen, tarsus-metatarsus, and tail length), and health parameters (i.e., hematocrit and heterophil:lymphocyte ratio) for chicks at discrete time points between treated and untreated nest sites using an analysis of variance (ANOVA). Information on other ectoparasites observed was not incorporated into analyses because consistent observation of other ectoparasites was not feasible via our methods. Growth rate was determined by the average change in individual morphometric measurements between five-day measurements. A repeated measures ANOVA was used to determine if the treatment of nest sites altered growth rate. We analyzed fledge success by comparing the survival of chicks at treated and untreated sites to day 35, the chick fledge age convention as outlined by the Alaska Maritime National Wildlife Refuge (2019), using logistic regression. All data was conducted using Program R (Version 1.1.456 – © 2009-2018 RStudio, Inc.)

Results

Tick burdens averaged 0.33/chick in treated nests (n=139) and ranged from 0-7, while tick burdens on chicks in untreated nests (n=113) averaged 4.05/chick and ranged from 0-42 ticks per individual. Other ectoparasites observed included fleas and lice though the burdens of these parasites were not quantified as part of this investigation. Tick burdens did not differ significantly between the two years for treated and untreated blocks. Compared to untreated

nests, chicks from treated nest sites had significantly lower tick body burdens between years ($F(1,53)=20.6$, $p<0.005$; Figure 2). No effect of nest treatment was identified for morphometric measures of weight, wing chord, culmen, and tail length at discrete time periods (Figure 3) or the average growth rate of these measurements (Figure 4). However, chicks from treated nests had longer tarsus-metatarsus lengths after day 15 ($F(8, 35)=2.4518$, $p= 0.02776$), but we observed no difference in the average growth rate of this measure (Figure 5).

Average hematocrit values for chicks were not significantly different between treated and untreated nests in either year (Figure 6). However, hematocrit was higher for chicks in both treated and untreated nests in 2015 than in 2014 at day 25 ($F(9, 18)=2.746$, $p= 0.03578$). Furthermore, there was no significant difference between average heterophil:lymphocyte ratio between treated and untreated nests or between years (Figure 7).

Overall, chicks in treated nest sites (n=139) exhibited a higher probability of fledge, as measured by survival to day 35 in both years ($p=0.03$ by logistic regression) compared with chicks from untreated sites (n=113) (see Figure 8). Individuals in untreated nest sites were 29.3% (95% CI [0.33, 0.95]) less likely to survive to day 35 than their counterparts in treated sites. However, when accounting for year, chicks from untreated nest sites in 2014 were not significantly different from chicks in treated nests from either year; thus, a treatment effect was only noted in 2015. Average fledge success as inferred as survival to day 35 in treated nests was 44.7% (34/76) in 2014 and 41.3% (26/63) in 2015, whereas in untreated nests, average fledge success was 30.6% (23/75) and 21.1% (8/38), for each year, respectively. Overall, of the 139 chicks in treated nest sites, 60 (43.2%) fledged over both years, while in untreated sites, only 31 of 113 (27.4%) fledged.

Discussion

In our study, we successfully manipulated the tick burden of Black-legged Kittiwake chicks hatched on anthropogenically constructed nesting habitat to assess potential effects of parasites on hematological parameters, growth, and fledging. Though we found *I. uriae* ticks on chicks hatched on treated and untreated (control) panels of the CRT at Middleton Island, burdens were higher on control panels than those treated with a mild insecticide. In the case of control panels, tick burdens were higher than some previous reports of seabirds in Alaska but lower than reports from other regions (Choe and Kim, 1987a; 1987b; Dietrich et al., 2011). High tick burden may, at least partially, have been a function of the availability of refugia for ectoparasites provided by the CRT when they were not attached to a host. Refugia is important to ixodid, nidicolous tick species, such as those found on nesting seabirds, as they take a blood meal while the host is present and then spend the rest of their lives (up to four years) in surrounding materials (Dietrich, 2011).

We found that our experimental treatment of nest sites with a Carbaryl insecticide significantly reduced the number of ticks parasitizing nesting Black-legged Kittiwake chicks. Average tick burdens for treated nest sites in both years were less than a single tick per chick, while in untreated nests, tick burdens were more than ten times higher. Tick burdens peaked in the middle of the nestling period, between days 20-30 post-hatch, which corresponds with the first (pre-juvenile) molt, at which point chicks may be the most vulnerable to ectoparasites (Cramp and Simmons, 1983). Carbaryl is one of the most commonly used insecticides in experimental studies on avifauna for the removal of ectoparasites, and other studies that have used either powdered or liquid Carbaryl have seen similar reductions in ectoparasite counts (Collison et al., 1981; Fauth et al., 1991; Beyer and Mock, 1999; Cristinacce et al., 2010; Jones

and Merton, 2012; Causton and Lincago, 2014). Use of any insecticide raises concerns about negative effects on avian species, such as inhibition of important neurological enzymes and mortality (Bednarek and Davidson, 1967; Zinkl et al., 1977). However, previous studies found no evidence of increased risk of mortality, negative health effects of chicks in nests, or reduction of the overall population when exposed to Carbyl (DeWeese et al., 1979; Loomis et l., 1979; Collison et al., 1981; George et al., 1992; Johnston et al., 1994; Fair et al., 1995). Similarly, we did not find evidence of a negative effect of Carbaryl on chick development or fledging success. To the contrary, our study supports the notion that treatment with Carbaryl is an effective strategy for reducing ectoparasite burdens and may improve survivorship of chicks to day 35 post-hatch.

Though we successfully lowered tick burdens on Black-legged Kittiwake nestlings in insecticide-treated nest sites, we generally did not detect evidence that tick burdens from untreated sites led to compromised health, as evidenced through hematological metrics or decreased growth. For example, we did not find a correlation between higher levels of ectoparasitism on untreated nest sites with an increased heterophil:lymphocyte ratio, a metric used to indicate chronic stress (Tompkins et al. 2006; Davis et al., 2008). However, we did find that the average length of the tarsus-metatarsus was longer in chicks in treated nests after day 15. This timing coincides with when the tarsus length plateaus in growth and when it reaches approximately 90% of the adult size (Maurander and Threlfall, 1972). Thus, despite a lack of evidence that tick parasitism affects blood parameters, other effects may be influencing skeletal development. Several studies have reported similar results in the increase of tarsus length with food supplementation, but these studies did not demonstrate an increase in growth rate (De Neve et al., 2004; Cleasby et al., 2011; Lok et al., 2014). Reduced ectoparasitism on chicks and adults

may reduce the necessary time for preening, thus allowing for greater parental foraging and feeding of chicks which may be converted to skeletal growth, a parameter closely related to survival and adult breeding success in passerines (Alatavo and Lundberg, 1986; Bize et al., 2006; Jensen et al., 2008). However, for seabirds, correlations between breeding success and tarsus length have not been made.

Untreated nest sites on the CRT were associated with higher ectoparasitism of nestlings with ticks and reduced probability of survival to day 35 in at least one year of our study. This result is consistent with other studies which found that ectoparasitism reduced the likelihood of fledging and increased chick mortality (Monticelli et al., 2008)**.** This reduced fledging success of parasitized birds can be interpreted as ectoparasites causing detrimental effects to chicks. Such effects may be pronounced in Black-legged Kittiwake populations with high tick burdens, such as those in Europe, where previous studies found average number of ticks per chick in a nest as high as 10.85, which is over two times higher than what we found on Middleton Island (Boulinier and Danchin, 1996). While fledge success does not indicate survival probability to adulthood and subsequent breeding success, it is the first major life hurdle. Studies on other seabirds have suggested that increased parasitism can increase the likelihood of mortality post-fledging, and long-term survival may be compromised (Ramos et al., 2001; Monticelli et al., 2008). Furthermore, repeated nest treatments, such as in our experiment, may further increase breeding success in birds.

We did not observe a significant effect of nest treatment in both years of our study. It is likely that with increased temperature and lowered food availability in 2015, ectoparasitism exacerbated breeding pressure on Black-legged Kittiwakes. Specifically, from late 2013 to 2016, an anomalous warm patch of water extended up the West Coast of North America into the Gulf

of Alaska, creating sea surface temperatures to rise in excess of 6°C and mass die-offs in forage fisheries (Bond et al., 2015; Peterson et al., 2016; Jones et al., 2018; Piatt et al., 2020). Nutritional declines of 44% in Pacific sand lance (*Ammodytes personatus*), a major food source for Black-legged Kittiwakes nesting on Middleton Island, was attributed to breeding failures in the Gulf of Alaska (Gill and Hatch, 2002; Walsh et al., 2018; von Biela et al., 2019). Another marine heatwave emerged in the North Pacific at the end of 2019, highlighting the need for additional studies on the effects of ectoparasites on nesting Black-legged Kittiwake population to determine subsequent benefits of reduced ectoparasitism on survivorship in conjunction with the population impacts of climate change (Amaya et al., 2020).

Our general lack of evidence that ectoparasitism affects growth, except for tarsus length and hematological parameters among Black-legged Kittiwakes on Middleton Island, may suggest that other factors also play important roles in the successful maturation of chicks. That is, tick burdens alone may not explain fledging success. Other stressors such as infection with arboviruses or bacteria transmitted by ectoparasites, higher energetic costs of host functions on account of ectoparasites, food scarcity, and competition with other individuals may all contribute to the lowered probability of nestling survival and fledging success. Although our data suggest that insecticide treatments are unlikely to improve the physiological health or growth of chicks in colonial nesting seabirds, the moderately positive effects on the survival of chicks to date of probable fledging success we observed may have important implications for the management of seabird populations. Ectoparasites may further compound the effects of climate change and food availability, an increasingly important factor for breeding seabirds. Thus, in managed populations where a species is of conservation concern, high tick burdens have been identified,

and it is logistically possible (i.e., nest sites are accessible) treatment of nests with a mild insecticide may be beneficial for improving fledging success.

Conclusions

In our study, we successfully manipulated the ixodid tick burden of Black-legged Kittiwake chicks in nests on an artificial structure on Middleton Island, Alaska, to evaluate the effects of ectoparasitism on the health, growth, and chick maturation. Although we did not find evidence for an effect of ticks on Black-legged Kittiwake chick growth (except for tarsus length), hematocrit, or leucocyte:heterophil ratio on Middleton Island, Alaska, we did find a reduced likelihood of survival to day 35 after hatch for nestlings in nests untreated with a mild insecticide in one of two years. Our results provide evidence that ectoparasitism may contribute to decreased productivity in long-lived seabirds and that nest site treatment, when logistically possible, maybe a management option to increase chick fledging success.

Acknowledgements

We would like to thank Morgan Walker, Mason Stothart, Josh Cunningham, Shirel Khane-Rapport, Elsa Kern-Lovick, and Angelike Aleksieva for field assistance. This project was funded, in part, through the U.S. Geological Survey through the Species Management Program of the Ecosystems Mission Area and the Georgia Ornithological Society. Additional support was provided by the wildlife management agencies of the Southeastern Cooperative Wildlife Disease Study member states through the Federal Aid to Wildlife Restoration Act (50 Stat. 917), by a US Department of the Interior Cooperative Agreement with SCWDS, and the Daniel B. Warnell School of Forestry and Natural Resources. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Figure 4.1. The decommissioned main communications radar tower (CRT), and interior of thereof, used by nesting Black-legged Kittiwakes (*Rissa tridactyla*) and Pelagic Cormorants (*Phalacrocorax pelagicus*) on Middleton Island, Alaska.

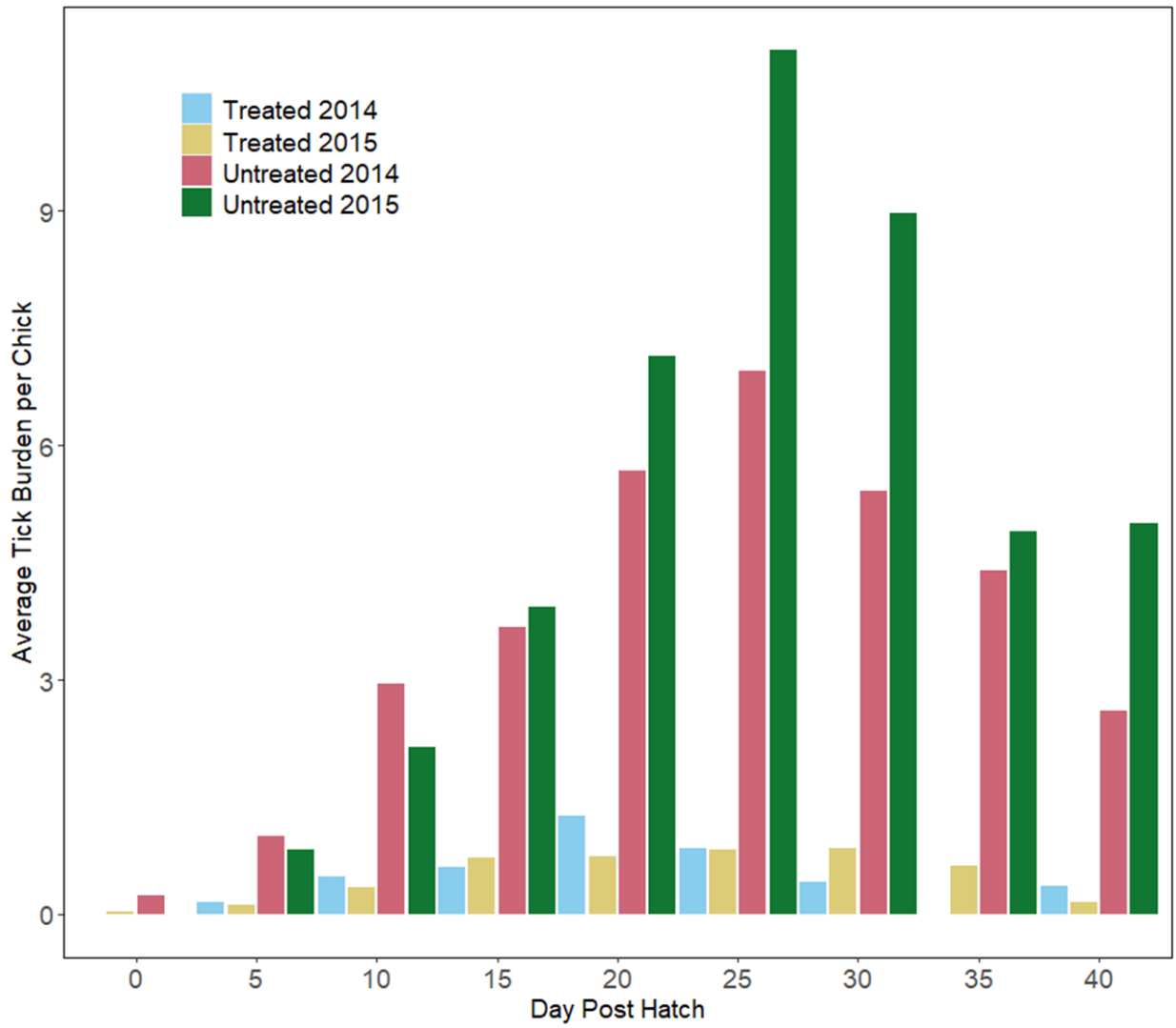

Figure 4.2. Average tick burden per Black-Legged Kittiwake (*Rissa tridactyla*) chick every 5 days post-hatch by nest treatment with a mild insecticide and year.

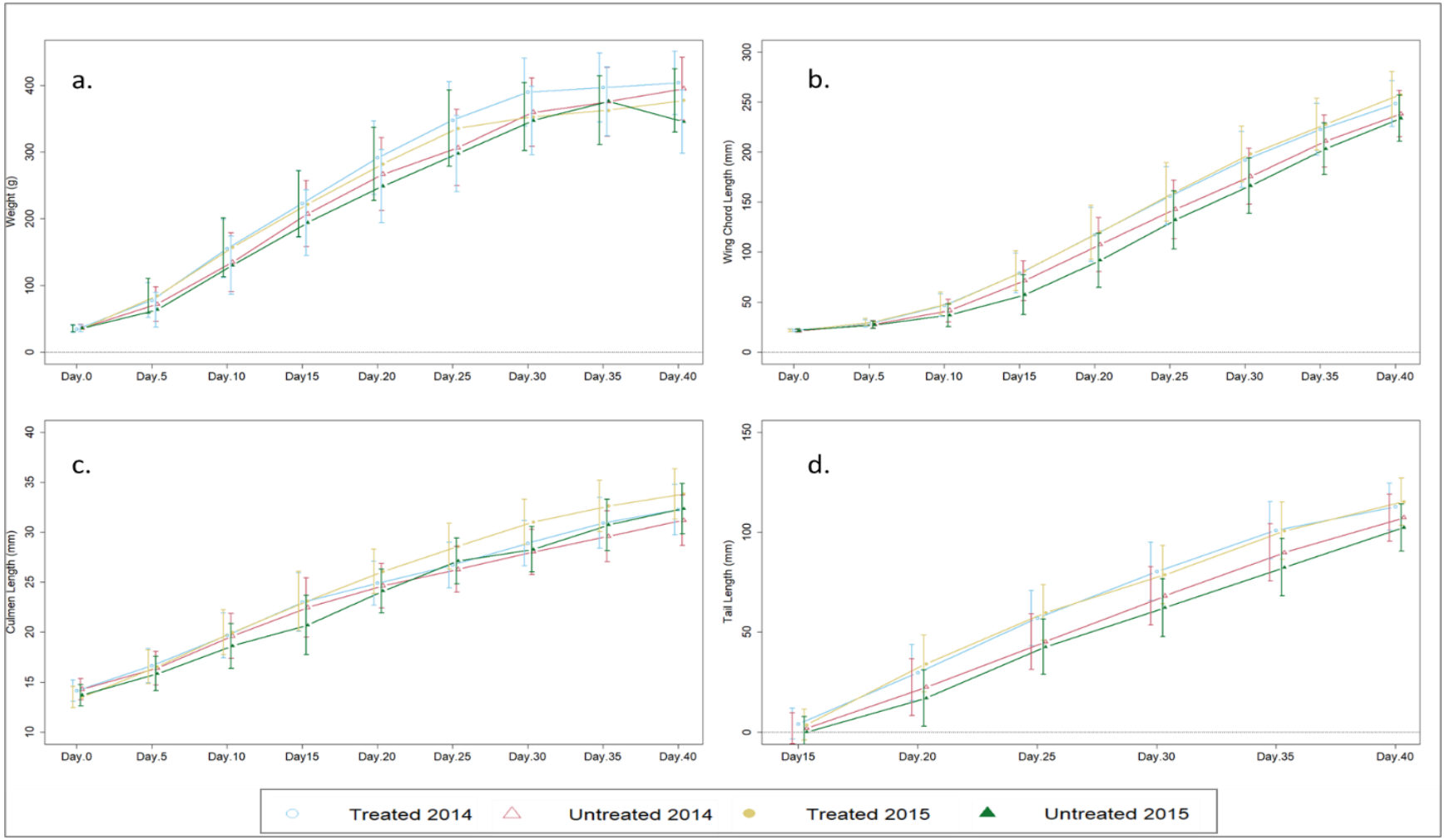

Figure 4.3. Average discrete measurement of morphometric measurements (a. weight in g; b. wing chord length in mm; c. culmen length in mm; and d. tail length in mm) for Black-legged Kittiwakes (*Rissa tridactyla*) chicks every 5 days post hatch by nest treatment with a mild insecticide and year. The standard errors are shown as error bars.

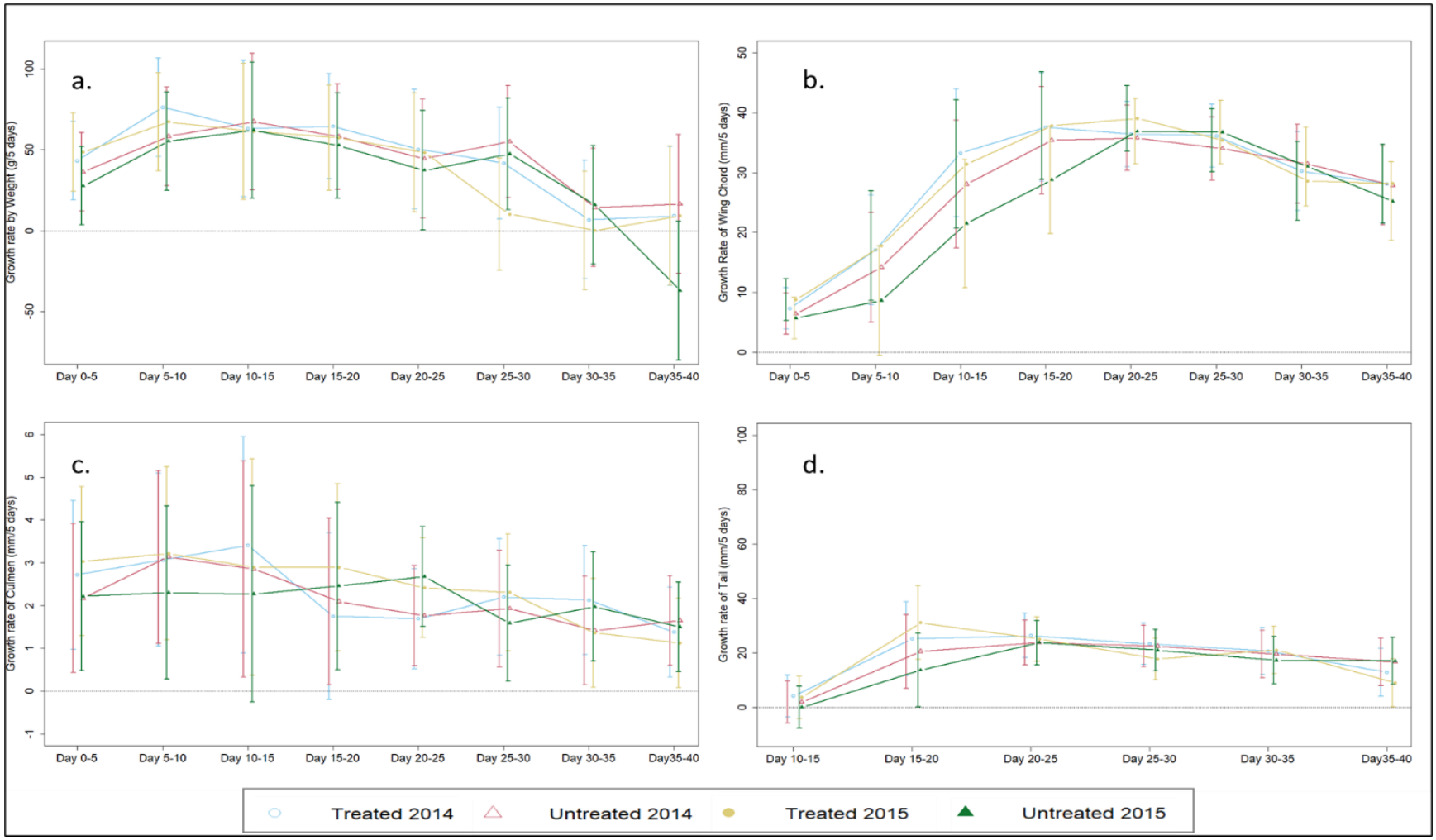

Figure 4.4. Average growth rate of morphometric measurements (a. weight in g; b. wing chord length in mm; c. culmen length in mm; and d. tail length in mm) for Black-legged Kittiwakes (*Rissa tridactyla*) chicks every 5 days post-hatch by nest treatment with a mild insecticide and year. The standard errors are shown as error bars.

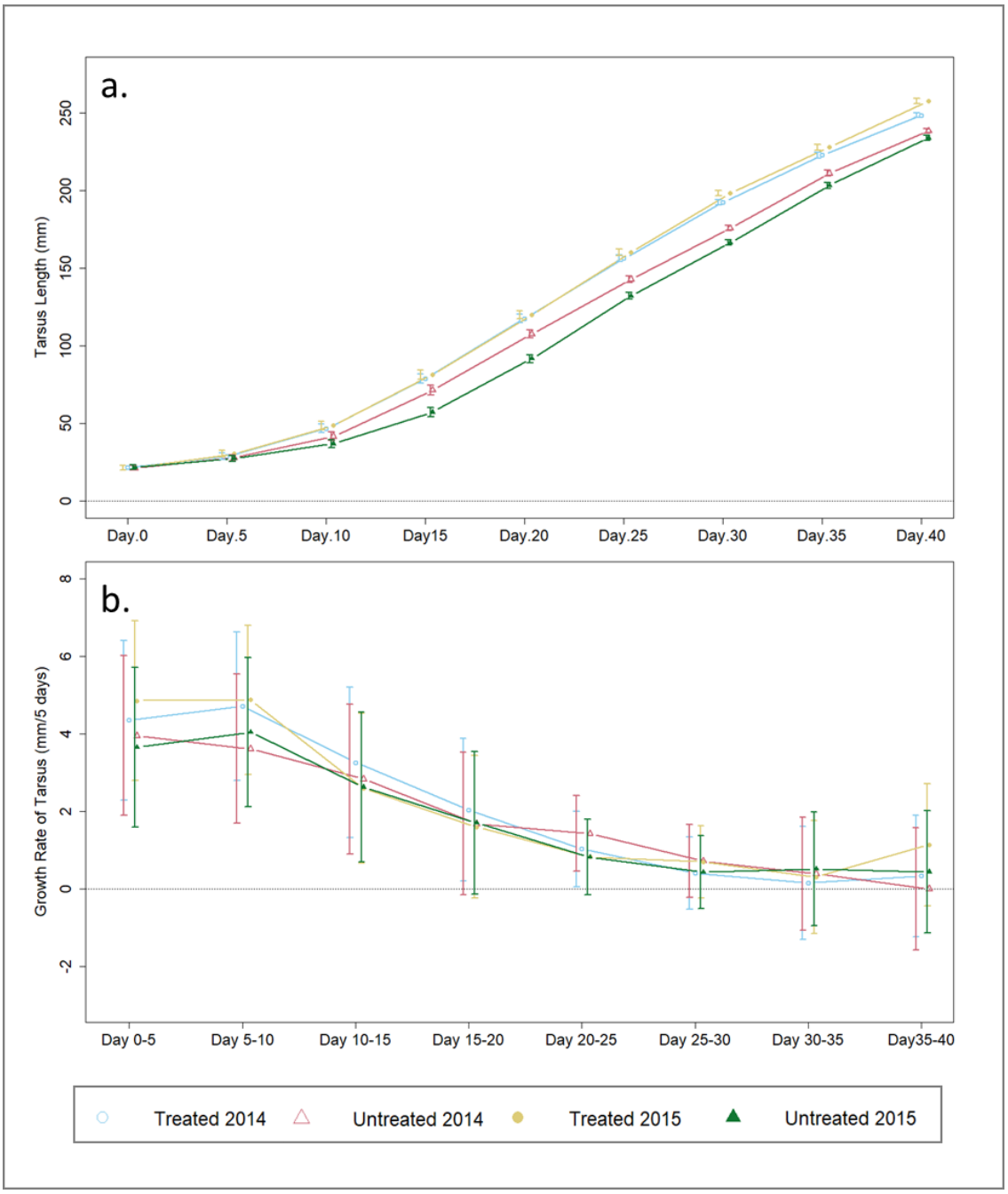

Figure 4.5. a. Average discrete measurements of tarsus-metarsus in mm for Black-legged Kittiwake chicks every 5 days post-hatch by nest treatment with a mild insecticide and year. b. Average growth rate of tarsus-metarsus in mm for Black-legged Kittiwake chicks every 5 days post-hatchby nest treatment with a mild insecticide and year. The standard errors are shown as error bars.

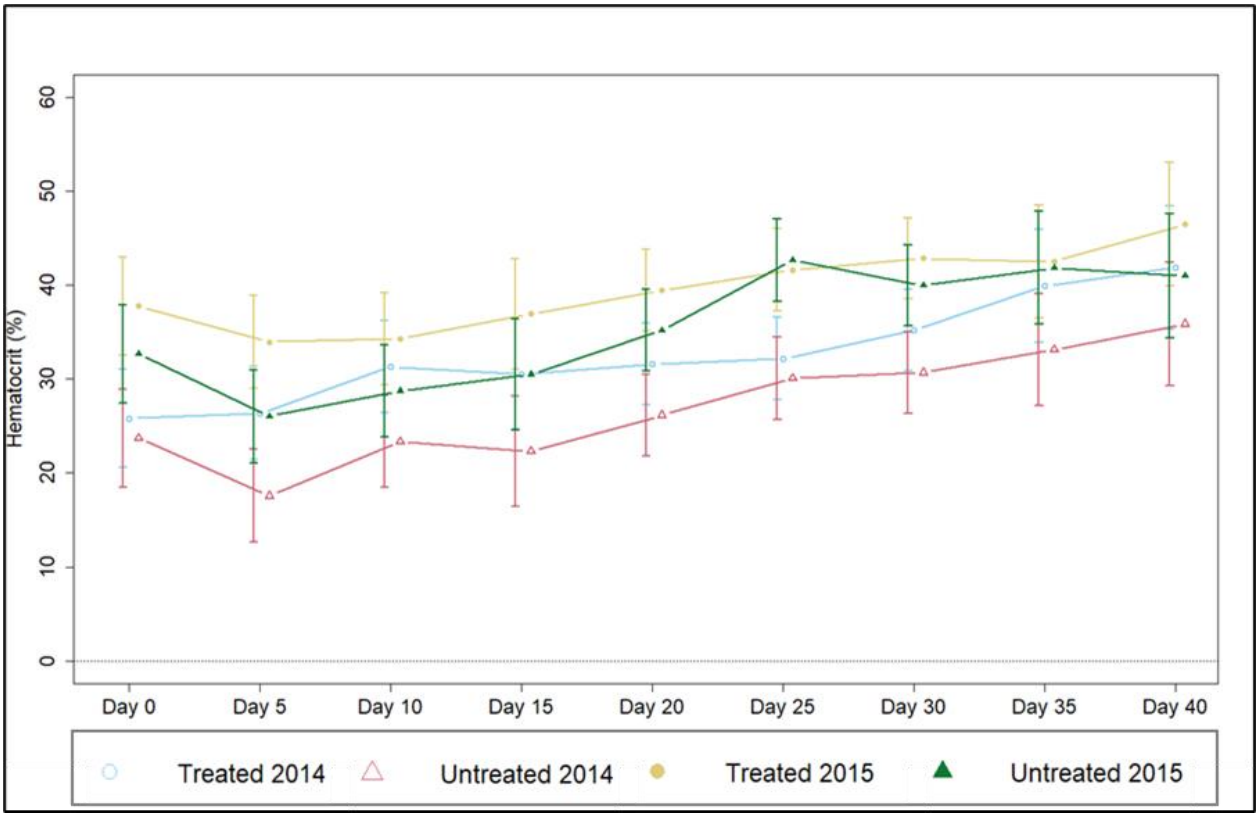

Figure 4.6. Average percent hematocrit of nesting Black-legged Kittiwake (*Rissa tridactyla*) chicks every five days post-hatch by nest treatment with a mild insecticide and year. The standard errors are shown as error bars.

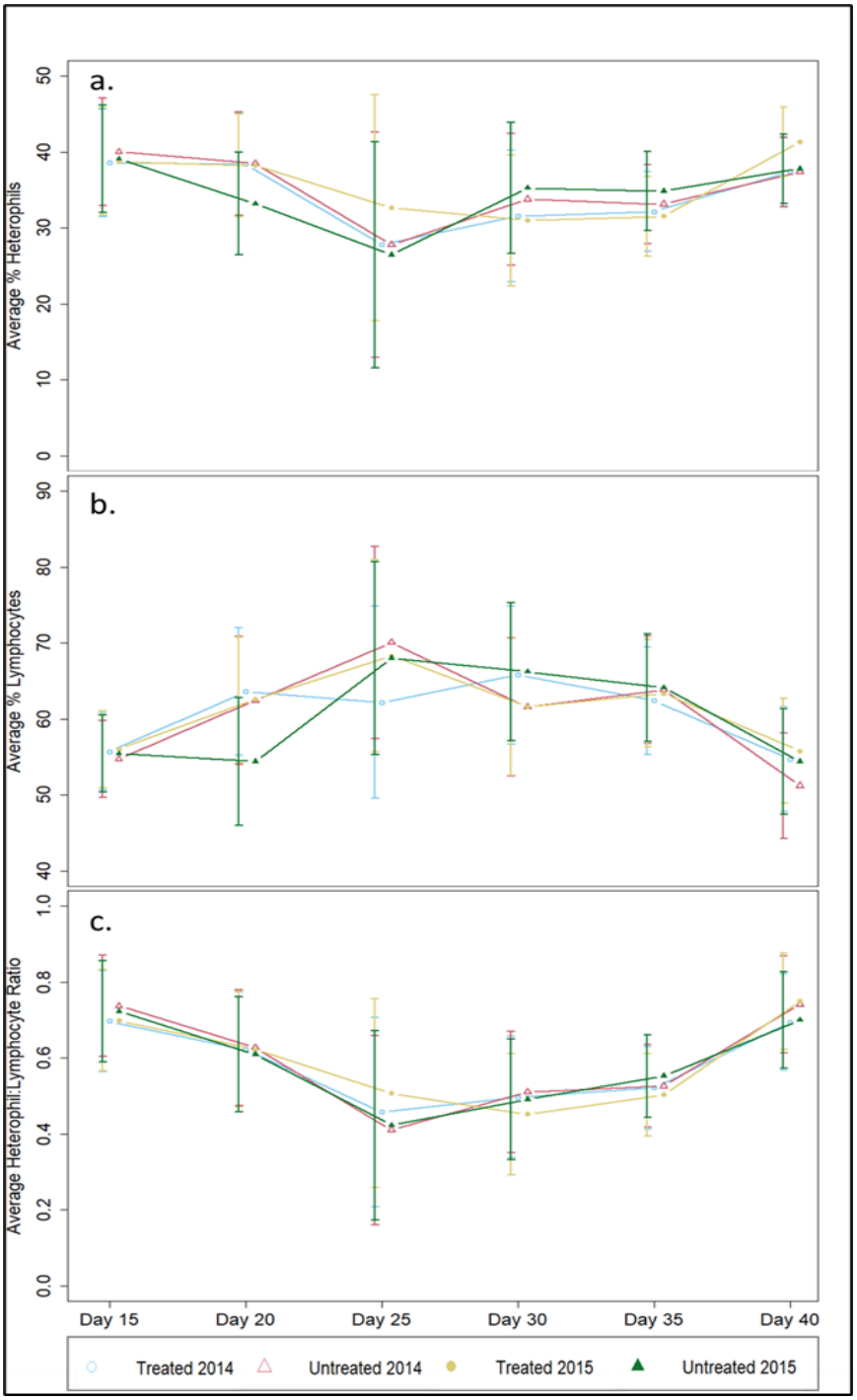

Figure 4.7. Average percentage of lymphocytes (a.), average percentage of heterophils (b.), and average heterophil: leucocyte ratio (c.) of Black-legged Kittiwake (*Rissa tridactyla*) chicks every five days post-hatch by nest treatment with a mild insecticide and year. The standard errors are shown as error bars.

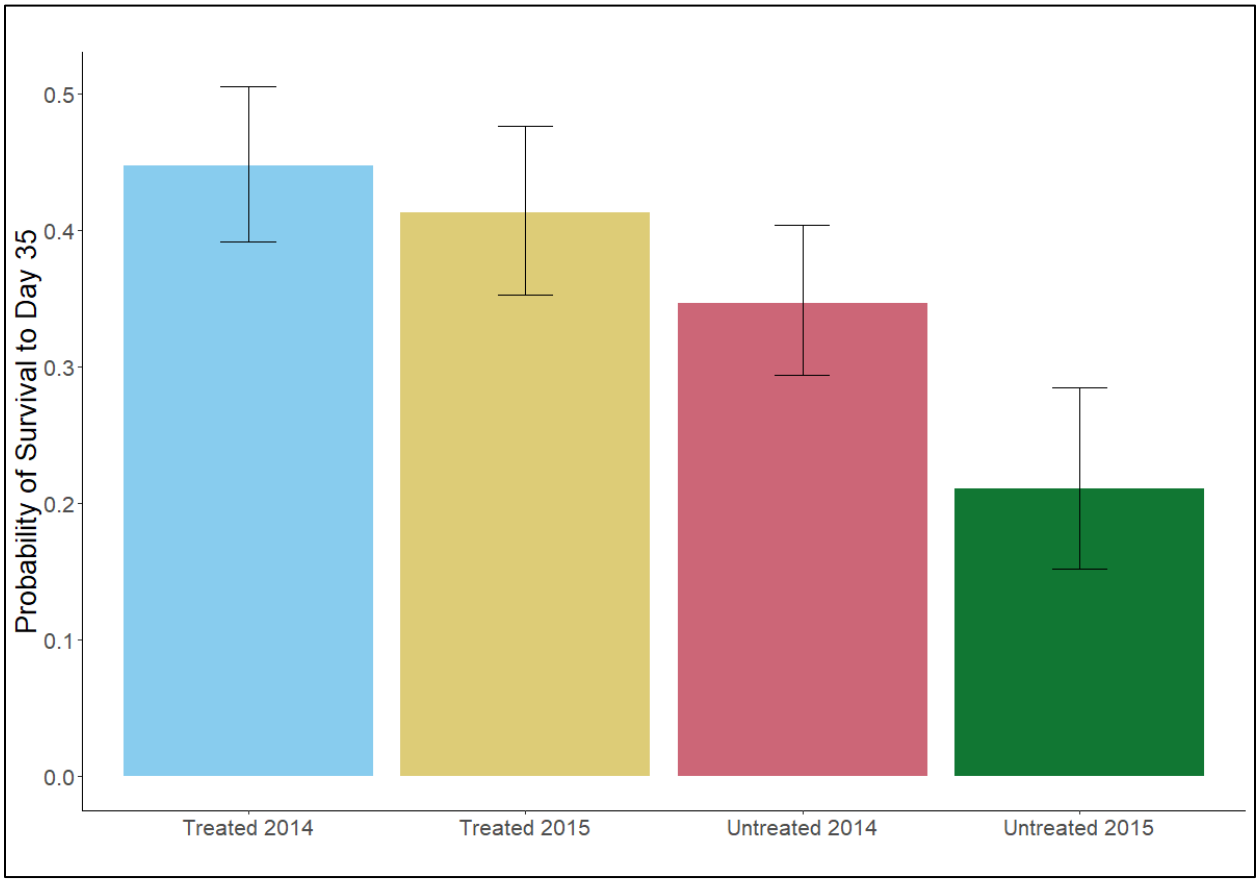

Figure 4.8. Average probability of survival to day 35 post-hatch of Black-legged Kittiwake (*Rissa tridactyla*) chicks on Middleton Island, Alaska in nests treated with a mild insecticide. The standard errors are shown as error bars.

CHAPTER 5

APPARENT ABSENCE OF VECTOR-BORNE PATHOGENS IN SEABIRDS INHABITING MIDDLETON ISLAND, ALASKA[1]

[1] Williams, B.M., A.M. Ramey, M. Walker, S.A. Hatch, and M.J. Yabsley. To be submitted to *Journal of Wildlife Diseases.*

Abstract

Though hematozoa infections have been associated with negative consequences and lowered reproductive success in some avian species, information on the distribution, prevalence, and diversity is limited for arctic and subarctic breeding pelagic seabirds. We sampled six species of seabirds, including black-legged kittiwakes (*Rissa tridactyla*), common murres (*Uria aalge*), glaucous-winged gulls (*Larus glaucescnens*), pelagic cormorants (*Phalacrocorax pelagicus*), rhinoceros auklet (*Cerorhinca monocerata*), and tufted puffins (*Fratercula cirrhata*) nesting on Middleton Island, Alaska for the presence of blood parasites such as *Haemoproteus*, *Plasmodium*, *Leucocytozoon*, *Babesia* and *Borrelia* spp. All samples were negative. The apparent lack of blood parasites in seabirds breeding on Middleton Island may be a function of the limited time these species are present on land and associated with vectors outside of the breeding season. Furthermore, the low tree cover, relatively low temperatures, and persistent winds at this high-latitude breeding site likely limit parasite transmission or development within insect vectors. Our data provide useful baseline information for future ecological change assessments at this site.

Hematozoa infections are associated with negative consequences to the health and fitness of numerous avian hosts, sometimes leading to clinical disease (i.e., lethargy, leukocytosis, lymphocytosis, anemia, myocarditis, nephritic disease, fluid in the coelomic cavities, hepatic disease), reduced immune function, lowered reproductive success, reduced survival rate, and lowered life expectancy (Sorci and Møller, 1997; Sol et al., 2003; Marzal et al., 2004; Cannell et al. 2013; Ashgar et al., 2015). However, information on the distribution, prevalence, and diversity of blood parasite infections is limited for arctic and subarctic breeding pelagic seabirds (Engström et al., 2000). The prevalence of hematozoa infections varies considerably among seabird species and sampling locations, but species associated with warmer climates generally have higher prevalence (Quillfeldt et al., 2011). Therefore, we sought to obtain information on avian blood parasite infections from a sub-arctic island in Alaska that may be useful for better understanding seabird health in northern breeding areas.

Middleton Island (MDO), Alaska, is an isolated island of approximately 16 km^2 in the Gulf of Alaska. The importance of MDO for breeding seabirds was noted in the 1950s (Rausch, 1958). Currently, breeding colonies of Black-legged Kittiwakes (*Rissa tridactyla*), Common Murres (*Uria aalge*), Glaucous-winged Gulls (*Larus glaucescnens*), Pelagic Cormorants (*Phalacrocorax pelagicus*), Rhinoceros Auklets (*Cerorhinca monocerata*), and Tufted Puffins (*Fratercula cirrhata*) occur on the island. Hematozoa have previously been identified from bird species inhabiting MDO, or their close relatives, at other locations, including *Babesia uriae* in Common Murres, *B. bennetti* in several gull species, *B. ungwidiensis* in cormorants, *Leucocytozoon vanderbrandeni* in cormorants, *Haeamproteus larae* and *H. passeris* in gulls, and *Borrelia garinii* in Common Murres, Black-legged Kittiwakes, and Tufted Puffins (Quillfeldt et al., 2011; Peirce and Parsons, 2012).

Seabirds were captured and sampled on MDO during May to August in 2014 and 2015 per procedures reviewed and approved by the University of Georgia's IACUC committee (A201401-006). Whole blood was collected by brachial venipuncture. A thin blood smear was made, and the remaining was stored in heparinized collection vials. Plasma was separated by centrifugation at 2000–3000 × g for 15 minutes. Red blood cells and plasma were stored in separate vials at -20°C. Blood smears were fixed with methanol and stained with a modified Giemsa (Dipquick, Jorgensen Laboratories, Inc., Loveland, CO). Blood smears were analyzed under 1000x, and ~40,000 erythrocytes/slide were examined to determine infection status for piroplasms, spirochetes, and hematozoa. DNA was extracted from whole blood using the Qiagen DNA Purification Kit (Germantown, MD) following the manufacturer's protocol. Samples were screened by nested polymerase chain reaction (PCR) for *Haemoproteus*, *Plasmodium*, *Leucocytozoon,* and *Borrelia* spp. (Hellgren et al. 2004; Yabsley et al. 2012) (Supplemental Table 1). Only a subset of samples was tested for *Babesia,* given financial and labor constraints using protocols targeting the 18S rRNA and ITS-1 rRNA gene targets (Holman et al., 2003; Jefferies et al., 2007; Yabsley et al., 2009). Amplicons were visualized on 0.8% agarose gels stained with Gel Red Nucleic Acid Gel Stain 10,000X in DMSO (Biotium, Hayward, CA). Amplicons of the appropriate size were bi-directionally sequenced at the University of Georgia Genomics Facility (Athens, Georgia). Sequences were compared with related sequences using the nucleotide BLAST function available through the National Center for Biotechnology Information (NCBI). A sample was considered positive if the sequence shared at least a 95% identity with the expected parasite group.

No parasites were observed on blood smears, and all samples were negative by PCR for *Haemoproteus*, *Plasmodium*, *Leucocytozoon*, and *Borrelia* (Table 1). A subset of 375 samples from 2014 tested negative for *Babesia* via PCR (Table 1).

The lack of blood parasites in MDO seabirds is consistent with previous studies conducted at high latitudes in seabird species (Quillfedlt et al., 2011). Two main hypotheses have been previously proposed for the lack of vector-borne pathogens in seabirds, including (1) potential inherent resistance of Charadriiformes to blood parasites and (2) environmental limits for vector and/or parasite development (Service, 1980; Bennett et al. 1992). While high immunocompetence and chemical defense has been demonstrated in seabirds which may reduce host susceptibility to hematozoa, multiple studies contradict the hypothesis for inherent resistance, including prior detection of hematozoa in members of the groups Sphenisciformes (penguins), Procellariiformes (petrels and shearwaters), Suliformes (frigate birds, boobies, and cormorants), and Charadriiformes (skuas, noddies, gulls, and terns (Bennett et al., 1993; Martin et al., 2001; Tella et al. 2002; Esparza et al., 2004; Douglas et al., 2005; Quillfeldt et al., 2011; Levin & Parker, 2012; Levin et al., 2012; Quillfeldt et al., 2014; Khan et al., 2019). Furthermore, blood parasites have been detected in penguins' and gulls' sub-artic nesting areas, so there is evidence for transmission among these birds at selected sites (Quillfeldt et al., 2010).

Habitat use of the seabird species sampled may better explain our lack of detection of avian hematozoa at MDO. The species sampled at MDO are mainly pelagic, coming to shore mainly to breed in the summer (Billerman et al., 2020). Though two of the species sampled, Pelagic Cormorants and Glaucous-winged Gulls, often inhabit coastal areas during the non-breeding season, the partially or largely pelagic behavior of the species sampled likely limits the time individuals breeding on MDO are exposed to blood parasites and appropriate vectors.

Previous sampling of swans for hematozoa on mainland Alaska provides evidence that sparse tree cover, relatively low temperatures, and persistent wind may contribute to the low prevalence of hematozoa (Ramey et al., 2012). Furthermore, high precipitation and low temperature are negatively correlated with some vector development (i.e., *Culex* and *Ixodes* spp.) and parasite development within vectors; however, the relationships are often complex (Gardner et al., 2012). Given the relatively high precipitation, low temperatures (1-15°C), sparse tree cover, and persistent winds (4.7-8.7 meters/second) at MDO (Adapted from Weather Spark and Western Region Climate Center), these environmental variables may also contribute to the apparent low or zero prevalence of hematozoa in seabirds breeding MDO.

In conclusion, we did not find evidence for infection of seabirds breeding on MDO with selected blood parasites. This data may provide useful baseline information for future assessments of ecological change at this site, given the prediction that ranges for parasites and vector-borne pathogens may increase northward with a warming climate (Van Hemert et al., 2014).

Acknowledgments

We would like to thank Morgan Walker, Mason Stothart, Josh Cunningham, Shirel Khane-Rapport, Elsa Kern-Lovick, and Angelike Aleksieva for their field collection efforts. This research was funded, in part, by the U.S. Geological Survey through the Wildlife Program of the Ecosystems Mission Area and the Georgia Ornithological Society. Additional support was provided by the wildlife management agencies of the Southeastern Cooperative Wildlife Disease Study member states through the Federal Aid to Wildlife Restoration Act (50 Stat. 917) and by a U.S. Department of the Interior Cooperative Agreement and the Daniel B. Warnell School of

Forestry and Natural Resources. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Table 5.1. The species and number of seabirds sampled on Middleton Island during 2014-2015 for avian hematozoa. The number of each species screened for *Babesia* is indicated in parentheses. All samples were considered negative for *Haemoproteus, Plasmodium, Leucocytozoon, Borrelia*, and *Babesia*.

Species		2014	2015	**Total**
Black-legged Kittiwake (*Rissa tridactyla*)	Chick	59 (43)	50 (22)	**109 (65)**
	Adult	100 (84)	127 (73)	**227 (157)**
Pelagic Cormorant (*Phalacrocorax pelagicus*)	Chick	41 (41)	22 (11)	**63 (52)**
	Adult	44 (44)	29 (13)	**73 (57)**
Tufted Puffin (*Fratercula cirrhata*)	Chick	0 (0)	17 (17)	**17 (17)**
	Adult	3 (3)	2 (2)	**5 (5)**
Rhinoceros Auklet (*Cerorhinca monocerata*)	Chick	0 (0)	10 (10)	**10 (10)**
	Adult	41 (41)	72 (43)	**113 (84)**
	Chick	0 (0)	0 (0)	**0 (0)**
Common Murre (*Uria aalge*)	Adult	32 (30)	75 (45)	**107 (75)**
Glaucous-winged Gull (*Larus glaucescnens*)	Chick	0 (0)	50 (50)	**50 (50)**
	Adult	0 (0)	0 (0)	**0 (0)**
Total		**320 (288)**	**454 (286)**	**774 (574)**

Table 5.2. PCR primer pairs used to perform molecular screening for selected pathogens in seabirds nesting on Middleton Island, Alaska.

Pathogen	Gene Target	Forward Primer	Reverse Primer
Haemoproteus/Plasmodium	Cytochrome b	CATATATTAAGAGAAITATGGAG	ATAGAAAGATAAGAAATACCATTC
		ATGGTGCTTTCGATATATGCATG	GCATTATCTGGATGTGATAATGGT
Luecocytozoon	Cytochrome b	CATATATTAAGAGAAITATGGAG	ATAGAAAGATAAGAAATACCATTC
		ATGGTGTTTTAGATACTTACATT	CATTATCTGGATGAGATAATGGIGC
Borrelia	Flagellin (flab)	ACATATTCAGATGCAGACAGAGGT	GCAATCATAGCCATTGCAGATTGT
		AACAGCTGAAGAGCTTGGAATG	CTTTGATCACTTATCATTCTAATAGC
Babesia	18S rRNA	CCTGGTTGATCCTGCCAGTAGT	TGATCCTTCTGCAGGTTCACCTAC
		GAGGTAGTGACAAGAAATAACAATA	TCTTCGATCCCCTAACTTTC
	18S rRNA	CGGGATCCAACCTGGTTGATCCTGC	CCGAATTCCTTGTTACGACTTCTC
		ACCTCACCAGGTCCAGACAG	GTACAAAGGGCAGGGACGTA
	18S rRNA	GAAATTAGAGTGTTTC	ACCCTATTTAGCAGGTTAAG
	18S rRNA	TCGTAGTTGAACTTCTGCTG	ATTGCCTCAAACTTCCTTGC
	ITS-1	CGATCGAGTGATCCGGTGAATTA	GCTGCGTCCTTCATCGTTGTG
		AAGGAAGGAGAAGTCGTAACAAGG	TTGTGTGAGCCAAGACATCCA

CHAPTER 6

INFLUENZA A VIRUS IN BREEDING SEABIRDS ON MIDDLETON ISLAND, ALASKA[1]

[1] Williams, B.M., A.M. Ramey, R.L. Poulson, S.A. Hatch, D.E. Stallknecht, and M.J. Yabsley. To be submitted to *PLOS One.*

Abstract

Our understanding of the natural history of influenza A virus (IAV) in seabirds (gulls, terns, cormorants, and alcids) is incomplete. From June - August 2014 and 2015, we sampled six species of seabirds breeding on Middleton Island, including the Pelagic Cormorant (*Phalacrocorax pelagicus*), Glaucous-winged Gull (*Larus glaucescens*), Black-legged Kittiwake (*Rissa tridactyla*), Common Murre (*Uria aalge*), Rhinoceros Auklet (*Cerorhinca monocerata*), and Tufted Puffin (*Fratercula cirrata*), for IAV and IAV antibodies. We did not detect IAV from cloacal swabs and environmental fecal samples for any of the six species sampled using virus isolation and/or RRT-PCR. We detected high prevalence of IAV antibodies in Black-legged Kittiwake [106/219 (48.4%)] and Common Murre adults [90/107 (84.1%)] and low prevalence in Black-legged Kittiwake [3/92 (3.3%)] and Glaucous-winged Gull [18/49 (36.7%)] chicks, Rhinoceros Auklet [43/112 (38.4%)] and Tufted Puffin [2/20 (20%)] adults, and Pelagic Cormorant chicks [10/72 (13.9%) and adults [15/62 (24.2%)]. There was no evidence of IAV antibodies in Rhinoceros Auklet and Tufted Puffin chicks. Antibodies reactive to five hemagglutinin (HA) subtypes (H1, H4, H5, H13, and H16) were detected from plasma collected from seabirds sampled on Middleton Island using hemagglutinin inhibition. Our data are consistent with previous reports of IAV in gulls and alcids, but suggest that the prevalence of IAV infection may be relatively low at this site during the breeding season.

Introduction

Middleton Island, Alaska, is 13km^2 and is located south of Prince William Sound in the Gulf of Alaska; it emerged from the sea approximately 4,300 years ago during a period of tectonic shifting (Miller, 1953). Seabird habitat at this site includes cliffs, beaches, soil bluffs, vegetated slopes, and a decommissioned United States Air Force communications radar tower

modified by the United States Geological Survey-Biological Resources Division (USGS-BRD) and U.S. Fish and Wildlife Service to provide nesting habitat. The tower allows researchers to easily monitor and capture nesting adult and hatchling seabirds via removable window panels. Species of pelagic seabirds that annually nest on Middleton Island from April to August include the Pelagic Cormorant (*Phalacrocorax pelagicus*), Glaucous-winged Gull (*Larus glaucescens*), Black-legged Kittiwake (*Rissa tridactyla*), Common Murre (*Uria aalge*), Rhinoceros Auklet (*Cerorhinca monocerata*), and Tufted Puffin (*Fratercula cirrata*) (Rausch, 1958). Furthermore, over 100 species of migrants have been documented to use Middleton Island as a migration stopover site, highlighting the importance of this island habitat to the avifauna of Alaska (DeCicco et al., 2017).

Avian origin influenza A virus (IAV) was first isolated from a Common Tern (*Sterna hirundo*) in 1961 in South Africa. Subsequently, most wild bird related IAV research and surveillance has focused on Anseriformes and Charadriiformes birds (Becker, 1966; Olsen et al., 2006). Our understanding of the natural history of IAV in seabirds, including gulls and terns (Laridae), alcids (Alcidae), and cormorants (Phalacrocoracidae), remains limited (Arnal et al., 2015; Lang et al., 2016). Seabirds have diverse life-history traits and are found on every continent worldwide but can be defined by being obligatory in some portion of their life to marine environments (del Hoyo, 1996). Research on seabirds can be challenging because of their propensity for marine environments, hard-to-access breeding or stopover sites, and limited time spent on land (Lang et al., 2016). While providing survival advantages, the colonial nesting behavior of these birds could also increase the risk of pathogen transmission (Clancy et al., 2006). While most IAV is unlikely to cause clinical disease in these species, recent evidence shows some populations may be susceptible to severe morbidity and mortality if infected with

viruses of the A/Goose/Guangdong/1/96 (Gs/Gd HP H5) lineage of highly pathogenic avian influenza (HPAI) (Abolnik et al., 2019; Molini et al., 2019; Banyard et al., 2022). Pelagic seabirds are also often long-distance migrants, which could facilitate intercontinental exchange of viruses (Wallensten et al., 2005; Ramey et al., 2010; Wille et al., 2011).

Infections with multiple subtypes of IAV, including all 16 avian HA subtypes and eight avian NA subtypes, have been detected from more than 60 seabird species worldwide, mostly from members of Laridae and Alcidae (Arnal et al., 2015; Lang et al., 2016). Despite a low IAV detection rate from these birds, IAV antibody prevalence can be high with seroprevalence, up to 90%. The general hemagglutinin subtypes found in gulls are H13 and H16, and IAV of these subtypes show limited ability to replicate in non-gull hosts (Fouchier et al., 2005, Hinshaw et al., 1982, Brown et al., 2012). Outside of gulls, the largest number of different subtypes have been isolated from Lesser Noddy (*Anous tenuirostris*), Wedge-tailed Shearwater (*Puffinus pacificus*), Common Murre, and Thick-billed Murre (*Uria lomvia*) (Lang et al., 2016).

Of the species sampled for this study, most previous research conducted on IAV ecology has been on Common Murres. Alcids generally exhibit low prevalence of infection with IAV. Viruses reported from Common Murres include those of diverse subtypes; H1, H2, H3, H4, H6, H10, H11, and H12 (Sazonov et al., 1977; Wallensten et al., 2005; Munster et al., 2007; Ip et al., 2008; Ramey et al., 2010; Granter et al., 2010; Wille et al., 2014; Huang et al., 2014; Lang et al., 2016). Black-legged Kittiwakes and Glaucous-winged Gulls have also been extensively studied worldwide for IAVs, and overall low IAV prevalence estimates have been reported (Munster et al., 2007; Ip et al., 2008; Wille et al., 2014; Lee et al., 2020). Black-legged Kittiwakes are primarily infected with gull-adapted H13 and H16 strains and H4 viruses (Tøennessen et al., 2011; Hall et al., 2013). Meanwhile, a high diversity of IAV subtypes has been reported from

Glaucous-winged gulls, including H1, H3, H4, H5, H11, H13, and H16 (Winker et al., 2008; Wille et al., 2011; Ramey et al., 2015; Reeves et al., 2018). Very few studies have reported IAV from cormorants, and only two have attempted isolation from Pelagic Cormorants with negative results (Walhgren et al., 2008; Ip et al., 20008). Studies on Suliformes worldwide show low prevalence of IAV antibodies (0-2%) (Laver and Webster, 1972; Artois et al., 2002; Lebarbenchon et al., 2015). There a no reports of IAV in Rhinoceros Auklets and Tufted Puffins but there have been few studies, all with low sample sizes (1-7) (Jessup et al., 2009; Siembieda et al., 2010; Knowles et al., 2019; Jones et al., 2019).

The importance of Middleton Island to the ecology of IAVs in migratory birds inhabiting Alaska is unknown. As transmission of IAV in other gulls, such as the Black-headed Gull (*Chroicocephalus ridibundus*), has been linked to the breeding season, Middleton Island offers a unique opportunity to sample seabirds throughout the breeding period (Verhagen et al., 2014). Alaska has been repeatedly documented as an important mixing ground for Eurasian and North American IAVs (Koehler et al., 2008; Ramey et al., 2010; Ramey et al., 2018). For northern hemisphere seabirds, intercontinentally reassorted IAVs with gene segments of both Eurasian and North American lineages have been reported from gulls, Common Murres, and Thick-billed Murres (Wallensten et al., 2005; Lebarbenchon et al., 2009; Ramey et al., 2010; Wille et al., 2011; Van Borm et al., 2012; Hall et al., 2013; Huang et al., 2014; Arnal et al., 2015).

The introduction of Gs/Gd HP H5 IAV from Eurasia to North America through Alaska is an ongoing concern (USDA, 2006; Winker et al., 2007; Koehler et al., 2008; Winker and Gibson, 2010; Harris et al., 2016; Ramey et al., 2022). Such an introduction was first realized in 2014 with the detection of Gs/Gd HP H5 IAVs in North America (Lee et al., 2015; Ip et al., 2015; Lee et al., 2015; Pasick et al., 2015; Torchetti et al., 2015; Lee et al., 2016 Ramey et al., 2016; Zhou,

2016; Lee et al., 2017; Hill et al., 2017). The outbreak resulting from this introduction was the largest in the history of the United States and led to a loss of an estimated 50 million domestic poultry (Ramos et al., 2017). There is evidence of ongoing intercontinental exchange of avian influenza viruses, including those causing HPAI, such that risks to the population health of both wild and domestic birds from similar introductions are enduring (Jeong et al., 2019; Ramey et al., 2018; Lycett et al., 2020; Ramey et al., 2022; Gerlach, 2022).

In this study, we sampled breeding seabirds on Middleton Island, Alaska, to determine the prevalence of avian influenza antibodies and IAV infection during the 2014 and 2015 seasons and characterized the hemagglutinin subtypes to which antibodies were reactive within these birds. The goal was to determine the role that seabirds inhabiting Middleton Island may play in the ecology of IAVs in Alaska. Because our sampling effort occurred just prior to and following an outbreak of Gs/GD HP H5 IAV in North America that was purportedly introduced from East Asia to North America via Alaska, we also tested samples to evaluate previous exposure to such viruses.

Methods

Sample Collection

Six species of seabirds that use Middleton Island for breeding were sampled from May to August in 2014 and 2015. These included Black-legged Kittiwakes (n=163 [2014],148 [2015]) Pelagic Cormorants (n=81, 53), Tufted Puffins (n=3, 7), Common Murres (n=33, 76), Rhinoceros auklets (n=41,76), and Glaucous-winged Gulls (n=50 in 2015). Birds from the communications radar tower (Black-legged Kittiwakes and Pelagic Cormorants) were captured by hand using a wire hook inserted through an opening in the nest boxes looped around the bottom leg for restraint. Individuals from the surrounding areas were captured by hand (Black-

legged Kittiwakes, Glaucous-winged Gull chicks, and Rhinoceros Auklet adults), using a noose pool (Common Murres), or by evacuating a small opening in nest burrows (Tufted Puffins and Rhinoceros Auklet chicks) and manually restrained. Whole blood was collected by brachial venipuncture and stored in heparinized collection vials (Owen, 2011). As part of a concurrent study, whole blood was taken from Black-legged Kittiwake chicks serially every five days beginning day 15 after hatch. Hatch date was unknown for other chick species included in the study. Blood samples were centrifuged at 2000–3000 × g for 15 minutes (World Health Organization, 2002), and plasma was retained in non-heparinized vials at -20 C for use in this study.

Cloacal swabs were obtained from a subsample of birds using sterile cotton-tipped swabs and placed in a brain heart infusion (BHI) medium (Becton Dickinson and Co., Sparks, MD, USA) supplemented with penicillin G (1000 units/ml), streptomycin (1 mg/ml), kanamycin (0.5 mg/ml), gentamicin (0.25 mg/ml) and amphotericin B (0.025 m/ml) (Sigma Chemical Company, St Louis, MO, USA) in 1.5 mL cryogenic collection tubes (Hanson et al., 2008). Samples were stored in a liquid nitrogen-charged dry shipper during field studies and then at -80° C until testing was performed. Fecal samples from beach environments were collected from Glaucous-winged gulls in 2015 and stored as described for cloacal swabs. All capture and sample procedures were reviewed and approved by the University of Georgia's IACUC committee (A2014 01-006).

Virus detection

Isolations were performed in 9-11-day old pathogen-free embryonated chicken eggs incubated at 37°C; three eggs per sample were inoculated by allantoic route at 0.3 mL per egg (Krauss et al., 2004). Prior to inoculation, swab samples were thawed at room temperature,

vortexed thoroughly, and centrifuged at 1500 x g for 15 minutes. Amnioallantoic fluid (AAF) was harvested five days post incubation. All AAF samples were tested at a 1:2 through 1:16 dilution by hemagglutinin (HA) assay using a 0.5% suspension of specific pathogen-free chicken red blood cells in phosphate-buffered saline according to previously described protocols (Thayer and Beard, 1998; Stallknecht et al., 1990a). All HA assays where AAF samples did not exhibit hemagglutination were considered negative. Those that showed partial agglutination were passaged a second time at a 1:10 dilution of the AAF through chicken eggs.

To further evaluate the presence of influenza A virus in swab samples, viral RNA for a subset of samples was extracted using a modified commercial protocol (Ambion MagMAX AI/ND Viral RNA Isolation Kit, Applied Biosystems, Foster City, California, USA) via the Kingfisher semiautomated purification and extraction instrument per the manufacturer's protocol (KingFisher 24, Thermo Fisher Scientific Inc., Waltham, MA) as described by Das et al. (2006). Prior to extractions, swab samples were thawed at room temperature, vortexed thoroughly, and 50µL of media was used for extraction. Modifications to reduce inhibitors included an exchange of the lysis binding buffer for 15µL of bovine serum albumin (BSA) and 870 µg sodium sulfite and the use of a 2 M NaCl and 2 mM EDTA wash step. A nuclease water negative control was added for each extraction. Extracted RNA samples were maintained at -20 C until real-time reverse transcriptase polymerase chain reaction (RRT-PCR) was performed for amplification of the AIV matrix (M) gene as described (Spackman et al., 2002; Das et al., 2006).

RRT-PCR was conducted on a SmartCycler real-time PCR machine (SmartCycler, Cepheid Corp, Sunnyvale, CA). A 101 bp region of the AIV matrix gene was amplified using a 1-step RRT-PCR master mix and primers M+25 (5'-AGATGAGTCTTCTAACCGAGGTCG) and M-124 (5'- TGCAAAAACATCTTCAAGTCTCTG) and M+64 probe (5'-

TCAGGCCCCCTCAAAGCCGA) as described (Spackman et al., 2002). In addition to the extraction water control, a template-free nuclease-free water sample and a sample containing IAV RNA were included in each real-time RRT-PCR batch. Amplification was visualized using the FAM (fluorophore 6-carboxyfluorescein) channel, and amplification below a cycle threshold (C_t) value of 40 was considered positive.

Antibody Detection

Plasma samples were screened for IAV nucleoprotein (NP) antibodies using a commercially available blocking enzyme-linked immunosorbent assay kit. (bELISA; AI MultiS-Screen Avian Influenza Virus Antibody Test Kit, IDEXX Laboratories, Westbrook, Maine, USA). We used a sample to negative ratio (S/N) ratio of >0.7 as a cutoff for negative results as it has been proposed as an informative threshold for wild bird antibodies to IAV (Brown et al., 2009; Shriner et al., 2016). Any sample falling below that threshold was considered positive. Those samples that fell between the manufacturer's 0.5 S/N ratio and the proposed threshold were retested for quality assurance and interpreted as previously described (Brown et al., 2009). For Black-legged Kittiwake chicks that were repeatedly sampled through time, testing was first conducted using samples collected on day 40 post-hatch. Samples from the same bird that were negative at this time point were not further tested, but for those individuals testing positive at day 40, additional testing was conducted using samples collected from all earlier time points.

Samples that were positive by bELISA were also tested by hemagglutinin inhibition assay (HI) against antigens representing several commonly reported HA subtypes, including H1, H4, H5, H13, and H16 (Beard, 1980; Pederson, 2014). Virus antigens included: A/Mallard/Minnesota/AI12-4823/2012 (H1N1), A/blue-winged teal/North Dakota/Sg-00706/2008 (H4N6), recombinant virus North America H5 LPAI A/blue-winged

teal/Texas/AI12-4150/2012 (H5N2) (LP-rgBWT/TX), A/ruddy turnstone/New Jersey/UGAI14-1436/2014 (H13N6), and A/gull/New Jersey/UGAI15-3414/2015 (H16N3). Two additional antigens provided by the National Veterinary Services Laboratory (NVSL), USDA, Ames, Iowa, representing the Gs/Gd HP H5 2.2.4.4. lineage (inactivated GsGD-H5 HPAI A/gyrfalcon/Washington/41088-6/2014 (H5N8) (HP-GYR/WA) and inactivated GsGD A/turkey/Minnesota/9845/2014 (H5N2) (HP-TKY/MN) were also used. Prior to HI testing, plasma samples were treated at a 1:4 dilution with receptor-destroying enzyme (Denka Seiken Co., LTD, Tokyo, Japan) and then treated with a 1:4 dilution of packed turkey erythrocytes to remove nonspecific agglutinins (Beard, 1980). Plasma (25 μL) samples were initially screened by HI using turkey red blood cells at a serum dilution of 1:16 against the previously listed viruses at four HA units each according to a slightly modified protocol adapted from Gilbert et al. (2014) and Poen et al. (2016).

Samples that were positive for antibodies to any of the H5 IAV at a 1:16 dilution were further titrated and tested to differentiate between antibodies to clade 2.3.4.4 GsGD HP H5 and North American lineage LP H5 IAV. Plasma dilutions from 1:16-1:512 were simultaneously tested against a panel of LP-rgBWT/TX, HP-GYR/WA, and HP-TKY/MN antigens. Samples were considered antibody biased to 2.3.4.4 GsGD-HP-H5 if the titer against HP-GYR/WA or HP-TKY/MN exceeded the titer against LP-rgBWT/TX by two or more dilutions (Stallknecht et al., 2020).

Results

Virus isolation was performed on 328 and 353 cloacal swabs collected during 2014 and 2015, respectively, and 50 environmental fecal samples at Glaucous-winged Gull colonies collected during 2015 (Table 1). No IAVs were isolated. Furthermore, to verify negative virus

isolation results, matrix RRT-PCR was conducted for a subsample of 279 swabs, all of which were negative.

A total of 320 and 407 plasma samples were collected from 2014 and 2015, respectively. We detected NP antibodies from all species (Table 2). Seroprevalence estimates ranged between 3.3-84.1% among species and life stage (Table 2) as follows: Black-legged Kittiwake chicks (3/92, 3.3%), Pelagic Cormorant chicks (10/72, 13.9%), Tufted Puffin (2/20, 20%) adults, Pelagic Cormorant adults (15/62, 24.2%), Glaucous-winged Gull chicks (18/49, 36.7%), Rhinoceros Auklet adults (43/112, 38.4%), Black-legged Kittiwake adults (106/219, 48.4%), and Common Murre adults (90/107, 84.1%). The three Black-legged Kittiwake chicks that were positive by bELISA (one from 2014 and two from 2015) all seroconverted between day 35 and day 40 after hatch.

A subsample of 237 of the 288 samples that were antibody positive by bELISA was further tested by HI. Sera were reactive to antigens of all five HA subtypes, with samples most commonly reactive to viruses of the H5 and H16 HA subtypes (Figure 1; Table 3). We identified 115 individuals for which antibodies were reactive to one or more different antigens. Sera from Black-legged Kittiwakes and Common Murres, the species from which the largest number of samples were obtained and tested, were reactive to viruses of all five HA subtypes. Adult Black-legged Kittiwakes and Common Murres consistently demonstrated the highest diversity of subtype-specific antibodies. For the single Black-legged Kittiwake chick plasma sample that was positive by HI, antibody response was consistent with exposure to a virus of the H13 IAV subtype.

Sera from all species were reactive to antigens of the H5 HA subtype. Of the 93 samples that were reactive to H5 HA subtype antigens, 38 were tested to differentiate between antibodies

to clade 2.3.4.4 GsGD HP H5 and North American lineage LP H5 IAV (Table 3). All results were biased to the North American LP serotype, with antibody titers exceeding those observed for the 2.3.4.4 GsGD HP H5 antigens by two or more plasma dilutions.

Discussion

We did not isolate or detect IAV from any breeding seabirds on Middleton Island, Alaska, which is not unprecedented for investigation of IAVs in seabirds (Huang et al., 2014), but contrasts reported results from gulls (Velarde et al., 2010; Verhagen et al., 2014; Lomakina et al., 2009). We detected relatively low antibody prevalence among chicks during the breeding season, which indicates limited infections with IAV on Middleton Island during the breeding season and/or maternal transfer of antibodies to offspring. Several studies have detected antibodies in the eggs of Yellow-legged Gulls suggesting that maternal transfer of antibodies may commonly occur among some seabirds (Pearce-Duvet et al., 2009; Hammouda et al., 2011; Hammouda et al., 2012; Hammouda et al., 2014); however, there is insufficient information available to estimate how long maternal antibodies to IAV can be detected in seabird chicks. The three Black-legged Kittiwake chicks that were bELISA positive for IAVs in this study all seroconverted after day 35, suggesting that limited transmission of IAVs on the island at least partially explains the antibodies detected in Black-legged Kittiwake, Pelagic Cormorant, and Glaucous-winged Gull chicks.

In contrast to the relatively low antibody prevalence among chicks on Middleton Island, adults had higher prevalence of antibodies to IAVs, which is generally consistent with previous research (Wallensten et al., 2005; Granter et al., 2010; Tønnessen et al., 2011; Hall et al., 2013; Huang et al., 2014). Although infection rates at discrete time periods, such as the breeding season, may be low, repeated exposures over the bird's life span could explain the high antibody

prevalence (Wilson et al., 2013). Furthermore, it has been theorized that antibodies may persist longer in species within Laridae compared to ducks due to longer lifespans that favor a long-lasting acquired immunity (Lee, 2006). As elevated levels of host population immunity can limit infection and the efficiency of IAV transmission, the relatively high antibody prevalence estimates that were observed in adults of at least two seabird species, specifically Black-legged Kittiwake and Common Murre, may help to explain the negative virus isolation results during the breeding season on Middleton Island (Webster et al., 1992; Costa et al., 2010; Jourdain et al., 2010; Segovia et al., 2018).

While most transmission of IAVs in wild waterfowl purportedly takes place through a fecal-oral route where water contaminated with fecal material is ingested during foraging behaviors, oral transmission also may be important in the maintenance of IAVs within gull populations. Avian IAVs primarily utilize α2, 3-linked sialic acids (SA) as receptors (Suzuki, 2005; Nicholls et al., 2008). In gulls, α2, 3-linked SA are strongly expressed in the ciliated epithelium of the upper respiratory tract (Ellstrom et al., 2009; Franca et al., 2013). Although IAV shedding in gulls occurs by both the OP and CL routes, OP shedding has been reported to predominate (Costa et al., 2011; Brown et al., 2012; Curran et al., 2013; Froberg et al., 2019; Criado et al., 2021). Because of this, our sampling method that relied on cloacal swabs may have reduced sensitivity for detecting IAV infection (Bahl and Pomeroy, 1977; Velarde et al., 2010).

Seasonality of IAV prevalence in avian populations also may be an important factor when evaluating virus isolation and serologic results. Birds of the family Laridae may demonstrate peaks in IAV prevalence associated with the post-breeding and fall migration periods. For example, peak prevalence in black-headed gulls in the Netherlands occurred after the breeding season, coinciding with the onset of fledging, where susceptible juveniles were

increasingly co-mingling (Verhagen et al., 2014). Thus, most of our sampling effort, which occurred throughout the nesting, incubation, and brooding periods, may not have corresponded with peak transmission among these species in Alaska. That is, our sampling effort concluded each year just as fledging was getting underway and before large concentrations of juvenile birds were consistently observed. Furthermore, three Black-legged Kittiwake chicks showed evidence of seroconversion between days 35 and 40, which may indicate that a peak of infection was beginning at the conclusion of our sampling efforts.

Our study also resulted in a wide range of prevalence estimates for IAV antibodies among species breeding on Middleton Island, which may be due to differences in life history (e.g., habitat use and diet). A more varied diet that includes feeding at inshore, coastal, and freshwater habitats (i.e., Glaucous-winged Gulls) may result in greater IAV transmission versus species that have exclusively pelagic feeding habitats, which would presumably limit environmental exposure to highly virally contaminated surface water where IAV may persist (Hinshaw et al., 1980; Halvorson et al., 1983; Ito et al., 1995; Brown et al., 2008; Ramey et al., 2020; Ramey et al., 2022). That is, fecal-oral transmission among birds using seabird colonies may be limited by the volume of water in adjacent pelagic habitats and salinity of aquatic environments used. The former may dilute virions below infectious titers, and the latter may reduce persistence (Brown et al., 2009, Stallknecht et al., 1990b).

The prevalence of IAV antibodies in Pelagic Cormorants breeding on Middleton Island (14% among adults, 24% among chicks) is seemingly higher than previously reported data on this and similar species. Lebarbenchon et al. (2015) found approximately 2% antibody prevalence in Suliriformes, and other studies have not detected seropositive cormorants (Laver and Webster, 1972; Artois et al., 2002; Albini et al., 2014). Only one study has attempted

isolation of IAV from pelagic cormorants (n=11), and all samples were negative, but this group did not perform serological assays (Wahlghren et al., 2008). Pelagic Cormorants on Middleton Island may be exposed to IAV at Middleton Island through breeding in close proximity to Black-legged Kittiwakes (Gilbert et al., 2014; Poen et al, 2016). Plausible exposure routes outside of the breeding season are less clear.

Our subtype-specific serology data are consistent with previously published studies on exposure of seabirds to IAVs. Wild waterfowl are most often infected with IAV subtypes H1-H12 and rarely by H13 and H16 IAV, which are gull-associated. (Hinshaw et al., 1982; Stallknecht, 2003; Fouchier et al., 2005). Although H13 and H16 are the most commonly isolated serotypes from Laridae, gulls can be infected with all avian IAV HA subtypes (Arnal et al., 2015). The H13 and H16 subtypes have been the predominant subtype reported from Black-legged Kittiwakes but reported isolates also include IAV representing H4 (Tøennessen et al., 2011; Hall et al, 2013). H1, H3, H4, H5, H11, H13, and H16 have been reported from Glaucous-winged Gulls (Huang et al., 2014; Ramey et al., 2015; Lang et al., 2016; Reeves et al., 2018). Numerous IAV HA subtypes also have been reported from Common Murres (e.g., H1, H2, H3, H4, H6, H10, H11, and H12), but there are no reports of IAV in the other alcids included in this study or Pelagic Cormorants (Sazonov et al., 1977; Wallensten et al., 2005; Munster et al., 2007; Ip et al., 2008; Winker et al., 2008; Ramey et al., 2010; Granter et al., 2010; Wille et al., 2011; Wille et al., 2014). Based on our HI results, individual birds appear to have been infected with multiple subtypes.

Concurrent with this study, clade 2.3.4.4 GsGD HP H5 was detected throughout large portions of western and central North America, and it was purported to have been introduced through Alaska via waterfowl (Ip et al., 2015; Lee et al., 2015; Pasick et al., 2015; Torchetti et

al., 2015; Ramey et al. 2016). Because of this, we used HI to evaluate if antibodies reactive to H5 viruses were associated with infections by North American or clade 2.3.4.4 GS/GD HP H5 viruses. Although sufficient HI antibody titers were obtained for less than half (41.2%) of all H5 positive samples to make comparisons, all of these were consistent with North American lineage LP H5 IAV exposure.

In conclusion, we found limited evidence that IAV was circulating on Middleton Island during nesting, incubation, and brooding periods in the sampled species. We did, however, find evidence that seabirds may be permissive hosts of IAV on Middleton Island, including those of the H5 subtype. Thus, it may be important to continue to monitor seabird populations in Alaska for IAVs and exposure thereto, given changing epidemiological dynamics pertaining to GsGD HP H5 IAV and the potential for future outbreaks in wild birds.

Acknowledgments

We would like to thank Morgan Walker, Mason Stothart, Josh Cunningham, Shirel Khane-Rapport, Elsa Kern-Lovick, and Angelike Aleksieva for field assistance. Partial funding for this research came from the United States Geological Survey through the Species Management Program of the Ecosystems Mission Area and the Georgia Ornithological Society. Additional support was provided by the wildlife management agencies of the Southeastern Cooperative Wildlife Disease Study member states through the Federal Aid to Wildlife Restoration Act (50 Stat. 917), by a US Department of the Interior Cooperative Agreement with SCWDS, and the Daniel B. Warnell School of Forestry and Natural Resources. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Table 6.1. Number and species of seabirds sampled on Middleton Island, Alaska that were tested for influenza A virus by virus isolation in embryonated chicken eggs (VI) and matrix gene real-time reverse transcriptase PCR (RRT-PCR) by year. All samples were negative for influenza A virus in both tests.

		VI		rRT-PCR	
Species	Age	2014	2015	2014	2015
Black-legged Kittiwake	Adult	82	60	25	26
	Chick	79	43	6	2
Common Murre	Adult	33	75	10	25
	Chick	0	0	0	0
Glaucous-winged Gull	Adult	0	0	0	0
	Chick	0	50	0	25
Pelagic Cormorant	Adult	51	26	51	13
	Chick	38	38	38	11
Rhinoceros Auklet	Adult	42	50	12	25
	Chick	0	0	0	0
Tufted Puffin	Adult	3	1	1	1
	Chick	0	10	0	8
Total		**328**	**353**	**143**	**136**

Table 6.2. Seroprevalence of influenza A virus (IAV) nucleoprotein (NP) antibodies in seabirds nesting on Middleton Island, Alaska by year (NS indicates age groups not sampled).

		Prevalence of IAV NP Antibody (%)		
Species	Age	2014	2015	**Total**
Black-legged Kittiwake	Adult	45/100 (45)	61/119 (51.3)	**106/219 (48.4)**
	Chick	1/63 (2)	2/29 (7)	**3/92 (3)**
Common Murre	Adult	24/33 (73)	64/74 (45)	**88/107 (82.2)**
Glaucous-winged Gull	Chick	NS	18/49 (37)	**18/49 (37)**
Pelagic Cormorant	Adult	7/43 (16)	3/29 (10)	**10/72 (14)**
	Chick	14/38 (37)	1/24 (4)	**15/62 (24)**
Rhinoceros Auklet	Adult	11/41 (27)	32/71 (45)	**43/112 (38)**
	Chick	NS	0/5 (0)	**0/5 (0)**
Tufted Puffin	Adult	1/3 (33)	1/3 (33)	**3/6 (33)**
	Chick	NS	0/4 (0)	**0/4 (0)**
Total		**104/320 (32.5)**	**184/407 (45.2)**	**288/727 (39.6)**

Table 6.3. Summary of subtype specific antibodies detected among sera collected from six species of seabirds on Middleton Island, Alaska. Samples were screened using a hemagglutinin inhibition (HI) assay against a panel of five antigens with titers of 1:16 considered to be positive.

	Tot. Indiv. Screened		No. Pos. by Hemagglutinin (HA) Subtype by Year (%)									
			H1		H4		H5		H13		H16	
Species	2014	2015	2014	2015	2014	2015	2014	2015	2014	2015	2014	2015
Black-legged Kittiwake	41	44	8 (20)	0	4 (10)	1 (25)	16 (39)	3 (7)	5 (12)	5 (11)	29 (71)	39 (89)
Common Murre	22	62	1 (5)	3 (5)	0	3 (14)	18 (82)	41 (66)	3 (14)	3 (5)	3 (14)	13 (21)
Glaucous-winged Gull	NS	11	-	0	-	1 (9)	-	1 (9)	-	2 (18)	-	5 (46)
Pelagic Cormorant	21	2	5 (24)	0	2 (10)	0	8 (38)	0	1 (5)	0	0	0
Rhinoceros Auklet	9	23	0	0	0	3 (13)	5 (56)	0	0	0	0	5 (22)
Tufted Puffin	1	1	0	0	0	0	1 (100)	0	0	0	0	0
Total	**94**	**143**	**14 (15)**	**3 (2)**	**6 (2)**	**8 (6)**	**48 (6)**	**45 (51)**	**9 (10)**	**10 (7)**	**32 (34)**	**62 (43)**

Table 6.4. Number of birds sampled on Middleton Island, Alaska testing positive via Hemagglutinin Inhibition (HI) assay for antibodies reactive to antigens of one or more Hemagglutinin (HA) subtypes.

		No. of Indiv. Pos. for antibodies reactive to antigens of One or More Different HA Subtypes (%)			
Species	n	1	2	3	4
Black-legged Kittiwake	77	50 (65)	22 (29)	4 (5)	1 (1)
Common Murre	62	42 (68)	15 (24)	4 (7)	1 (2)
Glaucous-winged Gull	7	5 (71)	2 (29)	0 (0)	0 (0)
Pelagic Cormorant	10	6 (60)	2 (20)	2 (20)	0 (0)
Rhinoceros Auklet	12	11 (92)	1 (8)	0 (0)	0 (0)
Tufted Puffin	1	1 (100)	0 (0)	0 (0)	0 (0)
Total	183	**115 (63)**	**42 (23)**	**10 (6)**	**2 (1)**

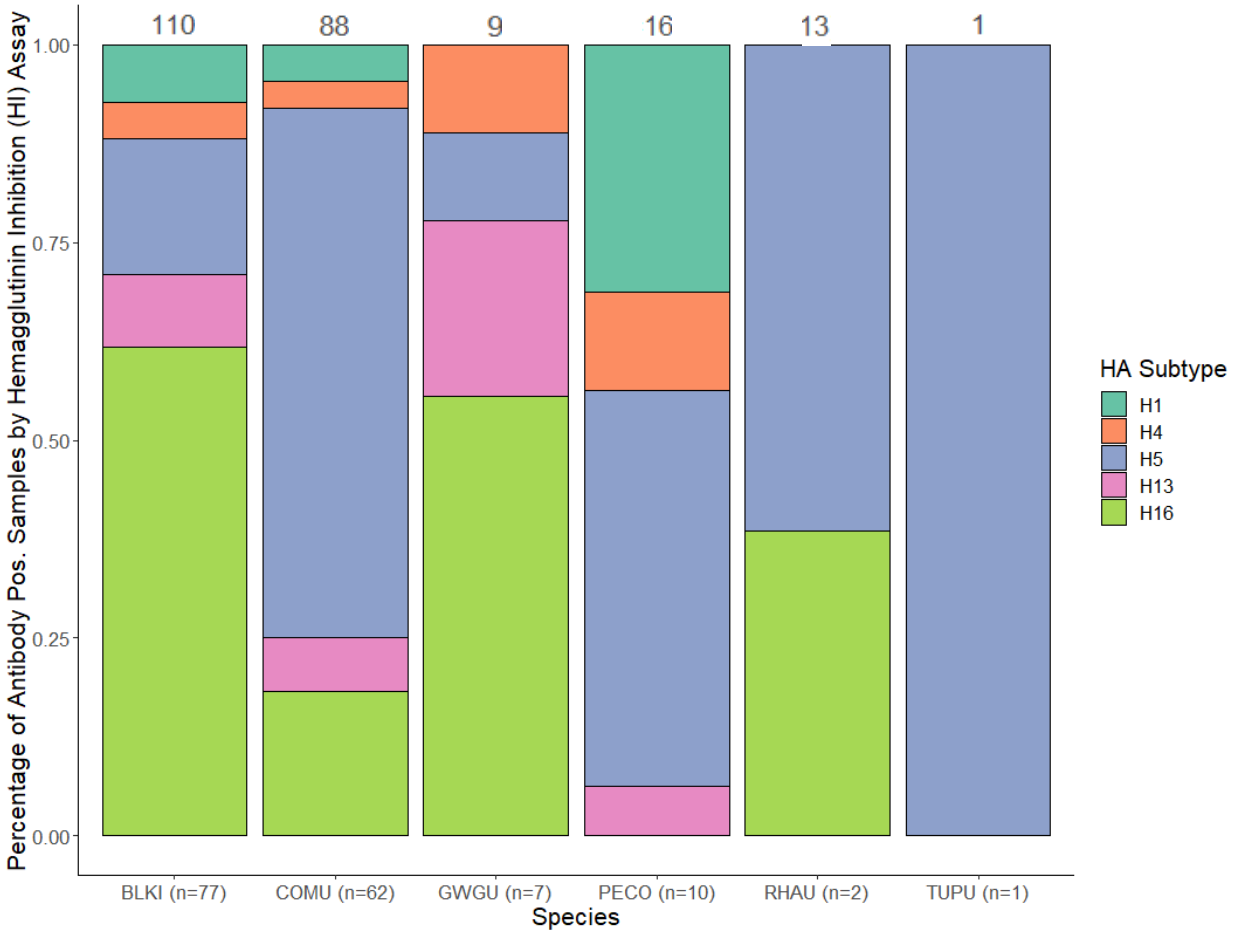

Figure 6.1. Percentage of antibody positive sera samples (total number positive by HA indicated at top) reactive to antigens of five hemagglutinin subtypes via hemagglutinin inhibition (HI) assay per species (Black-legged Kittiwake [*Rissa tridactyla*, BLKI, n=77], Common Murre [*Uria aalge*, COMU, n=62], Glaucous-winged Gull [*Larus glaucescens*, GWGU, n=7], Pelagic Cormorant [*Phalacrocorax pelagicus*, PECO, n=10], Rhinoceros Auklet [*Cerorhinca monocerata*, RHAU, n=2], and Tufted Puffin [*Fratercula cirrata*, TUPU, n=1]) on Middleton Island, Alaska. The denominator, indicated at top, includes the total number of antibodies reactive by HI assay accounting for those samples reactive to more than one subtype.

CHAPTER 7

SUMMARY AND CONCLUSIONS

Seabirds (e.g., gulls, terns, cormorants, and alcids) are globally distributed and among the most numerous groups of birds. They exhibit diverse life-history traits but are generally characterized by adaptation to marine environments, being long-lived, iteroparous breeders in large colonies, and they often migrate long distances. Seabird species have been extensively studied as they are indicators for long-term and large-scale marine ecosystem health. The biological importance of Middleton Island, Alaska (59°44’ N, 146°33’ W) to nesting seabird populations has been recognized for decades. Because of the isolated nature, large colonies, and abandoned structures that have been modified for nesting seabirds, this location provides a unique opportunity to study otherwise difficult seabirds. Long-term studies of these bird colonies indicate that populations undergo fluctuations in reproductive success, with cohorts experiencing significant mortality or complete failure in some years.

Furthermore, many of these populations are experiencing an overall marked decline at this site and/or worldwide. While multiple studies have examined growth parameters and nesting success of bird species on Middleton Island, minimal research has been conducted on disease ecology and its effects on breeding birds at this site. This study was designed to determine if parasites and selected potential pathogens are present and affect the health and survival of seabirds at this location.

In chapter 3, I identified the ectoparasites associated with the breeding seabird colony on Middleton Island, Alaska. I examined them for evidence of selected pathogens, including

Rickettsia, *Borrelia*, and *Babesia* within ticks and fleas. Knowledge about ectoparasites associated with seabird colonies is limited, with most studies investigating the effects of *Ixodes uriae* on nesting populations. Incidences of fleas and mites are often reported in conjunction with other studies, and identification is convoluted. Many of the same species have been reported as different species from multiple hosts based on the assumption of strong host specificity. Furthermore, ticks and fleas have been implicated in the transmission of vector-borne diseases previously associated with seabirds. Ectoparasites have been found on Middleton Island seabirds and could contribute to observed population fluctuations and declines at this site. However, studies of parasites associated with birds nesting on Middleton Island have been limited in scope with low sample sizes.

I opportunistically collected ectoparasites from the bodies of seabirds and the surrounding environment, including nests. All ectoparasites were identified using appropriate dichotomous keys. DNA from fleas and ticks was extracted, and a subsample of ticks was screened by PCR for *Babesia*, *Borrelia*, and *Rickettsia*. A subsample of fleas was screened by PCR only for *Rickettsia*. I identified a total of 2,089 ectoparasites from seabirds or the surrounding environment. Two species of ticks, *Ixodes signatus* and *Ixodes uriae*, three species of fleas, *Ceratophyllus vagabundus vagabundus Mioctenopsylla artica hadweni*, and *Mioctenopsylla traubi traubi*, and seven species of feather lice *Autromenopon transversum*, *Eidmaniella pellucida*, *Pectinopygus insularis*, *Quadraceps obliquus*, *Quadraceps ornatus*, *Saemundssonia calva*, and *Saemundssonia lari*, were identified. These identifications are consistent with previously reported taxa in seabird colonies but represent new location associations. *Ixodes signatus* was only associated with Pelagic Cormorants (*Phalacrocorax pelagicus*), further indicating a strong preference of this species to members of

Phalacrocoracidae. This study is the first report of *Eidmaniella pellucida* associated with Black-legged Kittiwakes (*Rissa tridactyla*).

Unlike previously published studies, I did not find evidence of the circulation of *Borrelia* or *Babesia* in tick populations associated with breeding seabird colonies. While it has been theorized that seabirds may play a more prominent role in the transmission of some vector-borne pathogens, there is little evidence that the tick vector and vector-borne diseases may be moved from one place to another. The lack of these pathogens indicates that the Middleton Island tick population may be naïve. Thus, further monitoring is important for early detection and understanding of the movement of the pathogens. Conversely, my study found evidence of two *Rickettsia* species associated with fleas and ticks. Sequenced data from both species of ticks shared a 91.9-100% consensus identity with *Rickettsia amblyommatis*, while fleas shared a 100% consensus identity with *Rickettsia felis*. The study of flea-borne rickettsiosis is poorly understood outside of mammalian parasites, but further research to better understand the relationships of this group and the role other hosts may play is needed.

In Chapter 4, I experimentally examined the effects that tick parasitism has on nesting Black-legged Kittiwake (*Rissa tridactyla*) chicks. Monitored Black-legged Kittiwake nests at this site have experienced dramatic declines since 1981. While increasing, knowledge about seabird ticks and their effects on their hosts is still limited. However, ticks can have direct negative impacts, including exsanguination, anemia, predisposition to secondary infections, direct skin damage, changes in behavior, and death in severe cases. Furthermore, population-level effects include lower nest success, reduced growth rates of nesting chicks, nest abandonment, and overall reductions. Ectoparasites are known to occur on Middleton Island seabirds and could contribute to population declines observed at this site.

I treated two blocked subsamples of Black-legged Kittiwake nests within the main communications radar tower and treated nest sites with a mild powered insecticide (Carbaryl). Chicks from these nests and two blocked control units were monitored every five days from hatch to day 40-45. I analyzed the differences in average tick burdens, morphometric measurements (i.e., weight, wing chord, culmen, tarsus-metatarsus, and tail length), and health parameters (i.e., hematocrit and heterophil: lymphocyte ratio) at discreet time points between treated and untreated nest sites. Furthermore, I analyzed the growth rate, or the average change in individual morphometric measurements, between each five-day sampling period. Finally, I analyzed fledge success, as measured by survival to day 35 after hatch, as a function of treatment.

I found relatively high tick burdens (mean 2.19, range 0-42) on nesting Black-legged Kittiwake chicks than some previously studied populations in Alaska but lower than others globally. However, treatment significantly reduced the number of ticks parasitizing nesting Black-legged Kittiwake chicks. Despite the reduction of ectoparasites, we found that treatment did not affect morphometric measurements at discrete time periods or the average growth rate of these measurements, except that chicks from treated nests had longer tarsus-metatarsus lengths after day 15. Furthermore, average hematocrit or heterophil:lymphocyte ratio was unaffected by treatment. Importantly, chicks in treated nest sites demonstrated a higher probability of survival to day 35, significantly so in 2015.

While Carbaryl is one of the most commonly used insecticides in experimental field studies, my study further supports that treatment is an effective strategy for reducing ectoparasite numbers. Furthermore, despite the lack of evidence that certain of our parameters were unaffected by treatment, the increase in fledge success indicates that ectoparasitism is causing

some detrimental effects on chicks. While fledge success is not necessarily an indication of survival probability to adulthood and subsequent breeding success, it is the first major hurdle in a bird's life. It has been theorized that increased parasitism can increase the likelihood of mortality post-fledging, and long-term survival may be compromised. Long-term studies on the nesting Black-legged Kittiwake population, and other populations, are needed to determine the subsequent benefits of reduced ectoparasitism on survivorship. However, our study indicates that treatment against ectoparasitism may be an effective, although laborious, strategy to increase breeding success in these birds.

In chapter 5, I surveyed for vector-borne pathogens, including *Babesia*, *Borrelia*, *Haemoproteus*, *Plasmodium*, and *Leucocytozoon*, circulating through six species breeding seabird colonies on Middleton Island, Alaska. Seabirds can be hosts to numerous vector-borne pathogens, and some of these can cause morbidity and mortality. However, information on the distribution, prevalence, and diversity of blood parasite infections is limited for arctic and subarctic breeding pelagic seabirds.

I sampled 774 thin blood smears by microscopy and DNA extracted from whole blood by PCR from birds on Middleton Island for *Borrelia*, *Haemoproteus*, *Plasmodium*, and *Leucocytozoon*. A subsample of 375 DNA samples extracted from whole blood was screened by PCR for *Babesia*. I did not find evidence that vector-borne pathogens were circulating on Middleton Island. These results are similar to previous studies that found low to no prevalence in pelagic seabirds, as well as studies that have been conducted in similar locations. However, the effect of climate change on vectors and vector-borne pathogens is a growing concern, especially in the northernmost latitudes where effects are likely to be amplified. My data will be useful for

future assessments of ecological change at this site concerning range expansion of blood parasites and potential effects to pelagic seabird hosts.

In chapter 6, I assessed the potential for the circulation of influenza A viruses (IAVs) on Middleton Island, Alaska. It has been theorized that the role seabirds play in the global circulation of IAVs differs from that of the better-studied waterfowl hosts. However, our knowledge of the ecological role of these birds is understudied. The importance of Middleton Island to the transmission of IAVs in migratory birds is relatively unknown, and because transmission of IAV in gulls has been linked to the period immediately following breeding, this site offered a unique opportunity to sample seabirds throughout the breeding period. Only one previous study has attempted isolation from Glaucous-winged Gulls (*Larus glaucescens*) from Middleton Island but was unsuccessful. Furthermore, Alaska has been repeatedly documented as an important mixing ground for Eurasian and North American lineage IAVs. Furthermore, the introduction of IAV from Eurasia to North America through Alaska is an ongoing concern related to the potential introduction of Gs/Gd HP H5 lineage viruses causing highly pathogenic avian influenza (HPAI)

I sampled six breeding seabirds to detect IAVs by cloacal swabs or environmental fecal samples tested by virus isolation in embryonated chicken eggs, and results were validated with RRT-PCR. That is, we could not isolate any viruses from breeding seabird colonies, and all subsamples were negative by RRT-PCR. I tested IAV antibodies from plasma samples by a commercially available bELISA kit. Antibody-positive samples were then tested by hemagglutination inhibition (HI) and analyzed to determine subtyped exposure against five hemagglutinin (HA) subtypes (H1, H4, H5, H13, and H16). Those that were consistent with H5 exposure were further tested to differentiate between antibodies to clade 2.3.4.4 GsGD HP H5

and North American lineage LP H5 IAV. Antibodies were detected among birds to antigens of subtypes tested, but H16 and H5 were the most predominant. All antibodies to H5 detected were consistent with exposure to North American lineage LP H5 IAV. Interestingly, I found antibody exposure in three Black-legged Kittiwake chicks showing evidence of seroconversion after day 35.

This detection of very low antibody prevalence in chicks during the breeding season indicates that while there may be circulation of IAV on Middleton Island during the breeding season, it is probably very low. In contrast to the low antibody prevalence in chicks on Middleton Island, adults demonstrated high seroprevalence of antibodies to IAVs, which is consistent with previous research. My study also demonstrated wide variation in the prevalence of antibodies in species breeding on Middleton Island. Seabirds are long-lived species, and even with low exposure at discrete time periods, immunity to various subtypes is likely to build over time. However, differences in the life history of certain species in the utilization of habitat and diet or in the frequency of infection and shedding patterns of the individual species at the breeding site may account for these variances.

My data on seropositivity of birds to different IAV subtypes are generally consistent with previously published studies on seabird exposure to IAVs. All subtypes have been found in members of Laridae, except those specific to bats. However, my study marks the first recorded instances of exposure and subtype-specific antibodies in Pelagic Cormorant (*Phalacrocorax pelagicus*), Rhinoceros Auklet (*Cerorhinca monocerata*), and Tufted Puffins (*Fratercula cirrata*). It also represents the first indication of H5 specific antibodies in Black-legged Kittiwakes. Furthermore, the lack of association with clade 2.3.4.4 GsGD HP H5 indicates that the Middleton Island breeding seabird colonies unlikely played any role in recent HPAI

outbreaks. However, it is also important to note that GsGD HP H5 IAVs have been found in members of Laridae on the Atlantic coast of Canada and in Alaska, highlighting the importance of continued surveillance of these species in conjunction with outbreaks.

Recently, studies have begun to focus on the role Charadriiformes may play in the ecology of IAVs, but knowledge on seabirds is lacking. Alaska has been an area target of influenza research for decades; however, transmission of IAVs in migratory birds breeding on isolated island communities with large populations of densely aggregated birds, like Middleton Island, is relatively understudied. Further research to help understand potential off-island transmission of IAVs among seabirds using Middleton Island helps elucidate the role these species may play in the larger picture of global IAV dynamics.

It has been theorized that, overall, seabirds are the most threatened group of avian fauna and that declines have become more pronounced over the last several decades. There are many hypotheses about the reasons for declines, such as habitat degradation, lack of food or changes in food availability, competition with invasive species, and disease. These issues are compounded by a rapidly changing climate which has been predicted to increase atmospheric humidity, rising sea levels, coastline erosion, increase in oceanic acidity, and cause shifts in plant and animal communities, including increasing the range and abundance of ectoparasite vectors. The effects of climate change are a growing concern, especially in the northern-most latitudes where effects are likely to be amplified. It is increasingly important to monitor vulnerable seabird populations, such as those on Middleton Island, for long-term changes in ectoparasitism and pathogens and their potential effects.