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Parasites of seabirds: a survey of effects and ecological implications

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Abstract

Parasites are ubiquitous in the environment, and can cause negative effects in their host species. Importantly, seabirds can be long-lived and cross multiple continents within a single annual cycle, thus their exposure to parasites may be greater than other taxa. With changing climatic conditions expected to influence parasite distribution and abundance, understanding current levels of infection, transmission pathways and population-level impacts are integral aspects for predicting ecosystem changes, and how climate change will affect seabird species. In particular, a range of micro- and macro-parasites can affect seabird species, including ticks, mites, helminths, viruses and bacteria in gulls, terns, skimmers, skuas, auks and selected phalaropes (Charadriiformes), tropicbirds (Phaethontiformes), penguins (Sphenisciformes), tubenoses (Procellariiformes), cormorants, frigatebirds, boobies, gannets (Suliformes), and pelicans (Pelecaniformes) and marine seaducks and loons (Anseriformes and Gaviiformes). We found that the seabird orders of Charadriiformes and Procellariiformes were most represented in the parasite-seabird literature. While negative effects were reported in seabirds associated with all the parasite groups, most effects have been studied in adults with less information known about how parasites may affect chicks and fledglings. We found studies most often reported on negative effects in seabird hosts during the breeding season, although this is also the time when most seabird research occurs. Many studies report that external factors such as condition of the host, pollution, and environmental conditions can influence the effects of parasites, thus cumulative effects likely play a large role in how parasites influence seabirds at both the individual and population level. With an increased understanding of parasite-host dynamics it is clear that major environmental changes, often those associated with human activities, can directly or indirectly affect the distribution, abundance, or virulence of parasites and pathogens.

Keywords

Bacteria, bird, ectoparasite, endoparasite, helminth, marine, pathogen, parasitism, seabird, virus

Introduction

Parasites, defined as organisms that live at the expense of their hosts (Combes 2001; Poulin and Forbes 2012), form diverse and ubiquitous components of all ecosystems, and include both macroparasites (e.g., helminths, arthropods) and microparasites (e.g., bacteria, viruses, fungi, protists). While most ecological studies focus on megafauna, these organisms can exert a significant influence on ecosystem composition and function via their diversity, abundance and impact on other members of the community (Thomas et al. 2005). While much is known regarding parasites in some taxa (i.e. captive mammals), considerably less is known in others. Given that changing climatic conditions are expected to influence parasite distribution and abundance, understanding current levels of infection, transmission pathways and population-level impacts are integral aspects for predicting ecosystem changes (eg. Leger et al. 2013). Seabirds are a particularly interesting group to study in this respect as they often traverse large distances along their migratory routes, and thus may be exposed to, and disperse, many more parasites when compared to other groups (Boulinier et al. 2016). Additionally, seabirds are long-lived and typically breed in large, dense colonies, traits that can favour parasite maintenance within populations (McCoy et al. 2016). Finally, some species of seabirds frequently come into contact with humans (e.g., gulls or harvested species), and thus may be a source of zoonotic disease.

Although the impact of parasites on captive (e.g., poultry) and terrestrial (e.g., Passeriformes) bird species has been relatively well-studied, less has been done on seabird parasites. Recent research has provided an overview of some of these relationships (e.g. Granoth-Wilding et al. 2014; Provencher et al. 2017), whereas others, such as Grimaldi et al.

(2015), focused on the impact of parasites in specific bioregions and orders/genera. Except under extreme conditions where the presence of a parasite has a devastating impact causing widespread mortality (e.g. avian cholera; Butler et al. 2011; Descamps et al. 2012; Friend and Franson, 1999), little is known about how interactions with these organisms alter seabird health, reproductive success, and ultimately, seabird population viability and evolution. The impact of a parasite will depend on the nature of the parasite in question, and may be influenced by interactions with other local environmental factors, such as the quantity and quality of food resources, levels of local pollution, habitat quality, and presence of predators, competitors and/or other parasites (e.g., Provencher et al. 2016; Butler et al. 2011).

Understanding seabird-parasite interactions is particularly important in regions that are expected to experience great degrees of change in the near future. For example, Polar Regions are expected to warm at a more rapid rate than temperate or tropical regions (Francis and Vavrus, 2015). Generally, parasitism is thought to be relatively depauperate in polar regions because of the lower diversities of suitable intermediate hosts, coupled with conditions that may be unsuitable for certain parasite groups (Brooks et al. 2014; Davidson et al. 2011, Kutz et al. 2014). However, with changing climatic conditions, and corresponding distributional changes in different taxonomic groups, parasite diversity in the polar zones may increase substantially. There is already evidence to suggest increased parasitism in northern wildlife due to changing climatic conditions (Brooks and Hoberg, 2007; Kutz et al. 2009, 2012). Additionally, novel parasites may extend their ranges in polar regions, or potentially expand to new hosts introducing new interactions within ecosystems (Davidson et al. 2011; Galaktionov, 2017).

The purpose of the present work is to give an overview of known parasite taxa in the seven aforementioned seabird orders, to survey their current distributions, and examine the known effects on seabird populations worldwide. By doing so, we hope to identify the gaps in our current knowledge and shed light on the relationships between parasites and their seabird hosts, and how changing conditions and other stressors may alter the seabird host-parasite relationships.

Methods

This purpose of this paper is to provide a survey of available literature documenting parasites of seabirds, and their effects. We used a literature scanning approach using Web of Science Core Collection and Google Scholar as our main databases. Queries entered into both databases were a combination of general and taxon-specific search terms. All search results were scanned for relevance related to the diversity, abundance and relationships of parasites with seabird hosts. Publications that did not achieve these goals, or had more specific research focuses were not included. All relevant journal articles were coded and entered in a spreadsheet for further examination. For each article, the following information was recorded: the parasitic organism studied, a short summary of the article, any effects of the parasite on the birds, the seabird order and species infected by the parasite, the location where the study was conducted, the methods used in the study, the year the study was conducted, and citation information. All search terms used for this review can be found in Table 1.

For the purpose of this study, we consider seabirds as defined by Gaston (2004), with updated classifications proposed by the International Ornithological Committee World Bird List

(Gill and Donsker, 2018). This includes gulls, terns, skimmers, skuas, auks and selected phalaropes (Charadriiformes), tropicbirds (Phaethontiformes), penguins (Sphenisciformes), tubenoses (Procellariiformes), cormorants, frigatebirds, boobies, gannets (Suliformes), and pelicans (Pelecaniformes) as the main species. We also include, to a limited extent, seaducks and loons (Anseriformes and Gaviiformes) in this review, as they fulfill a very similar ecological niche.

Results

A total of 258 journal articles on the taxonomy, distribution, prevalence and abundance of parasites in seabirds were reviewed. Of these, 98 articles housed information on the impacts of parasites on seabirds specifically. Research results gathered on each of the parasite groups are summarized below.

Macroparasites

Ectoparasites

Ticks

Ticks are blood-feeding arachnids belonging to the order Parasitiformes, sub-order Ixodida and include approximately 900 described species (Guglielmone et al. 2010). All species require at least one bloodmeal to complete the life cycle, feeding on a wide range of mammals, birds, reptiles and amphibians. Among arthropods, ticks transmit the greatest variety of infectious agents, including viruses, bacteria, protozoa and even helminths, but most research to date on seabirds has focused on *Ixodes* spp. vectors of Lyme disease bacteria (*Borrelia burgdorferi* s.l.; Dantas-Torres et al. 2012; Jongejan and Uilenberg, 2004; Table 1). Ticks can be

divided into two distinct categories; hard ticks (Ixodidae) and soft ticks (Argasidae). Hard ticks have a single long bloodmeal in each of their three life stage (larva, nymph, adult), whereas soft ticks take several short bloodmeals in nymphal and adult stages and have a variable number of nymphal instars (Dietrich et al. 2011). In both groups, the duration of attachment on the host determines the likelihood of disease transmission (Dantas-Torres et al. 2012).

Of the 17 identified species of hard ticks found on seabirds, all but one (*Amblyomma loculosum*) belong to the genus *Ixodes*. Of these, *Ixodes uriae* has the largest distribution, and is the most studied species (Figure 1a; Coulson et al. 2009; McCoy et al. 2003; Munoz-Leal and Gonzalez-Acuna, 2015; Olsen et al. 1993). Hard ticks have been recorded feeding on seabirds belonging to the orders Charadriiformes, Phaethontiformes, Sphenisciformes, Procellariiformes, and Suliformes (Dietrich et al. 2011; Gauthier-Clerc et al. 2003; Ramos et al. 2005). However, no observations of hard ticks on wild individuals from Pelicaniformes, Gaviiformes, or Anseriformes have been reported to date. The taxonomic status of most seabird hard ticks is well-established, though work has shown that these ticks may form isolated host specific populations, even when different seabird species breed in sympatry (e.g., McCoy et al. 2003); the potential for host-associated speciation may be high in this group and overall diversity as measured using traditional morphological criteria may underestimate true diversity (Moon et al. 2015).

The 12 known species of soft ticks exploiting seabirds all belong to the genera *Argas* and *Ornithodoros* (*Carios*), and tend to be restricted to tropical and sub-tropical zones (Figure 2). Soft ticks have been found parasitizing Charadriiformes, Phaethontiformes, Sphenisciformes, Procellariiformes, Suliformes, and Pelicaniformes (Dietrich et al. 2011; Duffy, 1983; Feare, 1976;

Figure 1); we found no study that reported the presence of soft ticks on wild individuals of Gaviiformes or Anseriformes. However, due to the short time that these ticks require for blood-feeding (i.e., minutes) and their nocturnal activity, they are difficult to observe under natural conditions and their diversity, prevalence and local abundance in seabird colonies is surely underestimated. In addition, general questions related to their systematics remain open (Guglielmo et al. 2010; Dupraz et al. 2016), and much basic observational work is still required to clarify their diversity, specificity and impact on seabird population dynamics.

Many studies on tick-seabird systems have focused on the prevalence of human pathogens such as Soldado virus and *B. burgdorferi* within ticks, with few discussing the circulation of these agents among ticks and seabirds (e.g., Gylfe et al. 1999; Main et al. 1976; but see Nunn et al. 2006a and Gomez-Diaz et al. 2010). As most research has targeted known pathogenic agents, the presence and diversity of other microparasites transmitted via ticks (or other potential vectors) remain to be investigated. The effect of known tick-borne pathogens on seabird populations is also poorly understood (Dietrich et al. 2011). We discuss these pathogens in more detail in later sections.

Some work has evaluated the direct impact of ticks on seabird health, reproductive success, and population dynamics in relation to hyperinfestations (e.g., Boulinier et al. 1996; Duffy, 1983; Monticelli et al. 2008; Ramos et al. 2001, 2005). Results vary greatly among species and orders, and are often related to other factors, such as food access and supply. For example, Ramos et al. (2001) and Monticelli et al. (2008) reported that in years of poor food supply, populations of Roseate Terns (*Sterna dougallii*) experienced massive chick mortality and breeding failure in areas of high tick (*Amblyomma loculosum*) densities. However, similar

studies conducted on White-tailed Tropicbirds (*Phaethon lepturus*) in the same region found no significant effect of tick parasitism/interference competition on productivity (Ramos et al. 2005).

There is evidence to suggest that species size may influence the effect that ticks have on individuals and populations. In a study conducted in the Huaura Islands, Peru nest desertion due to ticks was more common for Guanay Cormorant (*Phalacrocorax bougainvilli*) and Peruvian Booby (*Sula variegata*) populations than for the larger Peruvian Brown Pelican (*Pelecanus occidentalis aymbius*; Duffy, 1983). However, post-mortem investigations of three dead King Penguins (*Aptenodytes patagonicus*) found on the Crozet archipelago in the Sub-Antarctic region led researchers to conclude that hyperinfestation by ticks during incubation (when birds do not feed) was the most likely cause of death (Gauthier-Clerc et al. 1999). Although no difference in body mass or behaviour of breeding King Penguins was found with respect to more commonly observed levels of tick infestation (Gauthier-Clerc et al. 2003), some impact on reproductive success has been suggested (Mangin et al. 2003). No such observations have been made for smaller penguin species.

A relatively well-studied aspect of tick-seabird systems is the cyclical dynamics of seabird populations in relation to tick abundance. As the number of ticks in a given colony increases, the likelihood of nest desertion and chick mortality increases (Boulinier and Danchin, 1996; Duffy, 1983; Monticelli et al. 2008; Ramos et al. 2001; Ramos and Drummond, 2017). Conversely, breeding failures at the colony level also may also have a detrimental impact on local tick populations (Danchin, 1992; Dietrich et al. 2011; Monticelli et al. 2008; Olsen et al. 1993; Ramos et al. 2001). This type of dynamic interaction between seabirds and ticks will also

have consequences for the local transmission and large-scale circulation of infectious agents (Boulinier et al. 2001).

Mites

Although these are also small arachnids, unlike ticks, only a small fraction of mite species parasitize animals. Species exploiting seabirds as hosts belong to the orders Mesostigmata, Trombidiformes, and Sarcoptiformes. Among the Mesostigmata, it is species of the superfamily Dermanyssoidea (e.g., *Dermanyssus gallinae*, *Ornithonyssus bursa*) that are among the most studied. Species in this group have been reported to agitate adult birds, causing interruption in egg incubation, reducing nestling growth rates, and reducing overall reproductive success (Clayton and Thompkins, 1995; Moller, 1990). It is the cohort *Astigmatina* (order Sarcroptiformes) however that houses the greatest diversity of bird-associated mites, including feather mites (*Psoroptidia*).

While there is no doubt on the parasitic status of blood-feeding mites, the status of feather mites as parasites is still debated. These mites are thought to mainly consume feather pith or skin, and in some cases, feather oils (Stefan et al. 2015). In domestic birds, mites that feed on feather pith can weaken feathers and cause premature breakage and skin lesions (Proctor, 2003). Hyperinfestation can also result in severe itching, causing birds to pull feathers (Proctor, 2003). However, studies by Blanco et al. (1997; 2001a; 2001b) suggest that feather mites may help boost body condition by removing excess body oils and fungi.

Mite abundance on a bird host can be affected by season, temperature, light, humidity, and host body condition (Proctor, 2003). Mites are typically transmitted between hosts by close

body contact, which can be frequent in colonial nesting seabirds (Proctor, 2003). Feather mites have been found on species belonging to the order Procellariformes, Gaviiformes, Pelecaniformes, Anseriformes, and Charadriiformes (Proctor, 2003; Stefan et al. 2015). A study by Stefan et al. (2015) determined that a single bird can play host to multiple species of mites (*Microspalax brevipes* and *Zachvatkinia ovate*) due to resource partitioning and spatial segregation amongst the species. Indeed, a more recent study found up to 8 different mite species exploiting Cape Verde Shearwaters (*Calonectris edwardsii*) and Bulwer's Petrels (*Bulweria bulwerii*; Stefan et al. 2018). However, the effects of mites on wild seabirds are largely unknown. Studies on mite-seabird interactions have focused on the phylogeny and co-evolution of mites and their hosts, rather than the impact of mite infestation itself (Choe and Kim, 1987, 1988, 1989; Coulson et al. 2009; Stefan et al. 2018).

Fleas

Fleas are small (adults ~3mm), flightless, insects of the order Siphonaptera that parasitize mammal and bird populations worldwide. Of the 2,500 identified species, only those belonging to the genera *Ceratophyllus*, *Parapsyllus*, *Mioctenopsylla*, and *Xenopsylla* have been reported on seabirds (Coulson et al. 2009; Kane et al. 2012). Flea parasitism probably occurs in most seabird species and has been reported in wild seabirds belonging to the orders Sphenisciformes, Charadriiformes, Anseriformes, Procellariformes, and Suliformes (Alonso and Garrido, 2009; Choe and Kim, 1987; Kristjansson et al. 2016). The egg, larval, and pupal stages of most fleas live off the host's body, but adults are obligate blood-feeders. Because a large part of the life cycle occurs in the habitat used by the host, the presence and abundance of fleas is closely related to the conditions of their breeding environment (Gómez-Díaz and

González-Solís, 2010). Fleas can act as disease vectors for several bacteria, viruses and helminths (Bitam et al. 2010; Kane et al. 2012). Although poorly studied in relation to seabirds, they are known mechanical vectors for avipoxviruses (Kane et al. 2012).

Many studies on fleas in seabird colonies focus on examining the diversity and trophic relationships within arthropod communities, rather than the effects of flea parasitism itself (Alonso and Garrido, 2009; Choe and Kim, 1987; Coulson et al. 2009). Gómez-Díaz and González-Solís (2010) analyzed host-parasite relationships by reporting on nitrogen and carbon enrichment in fleas from host species; however, the effects of parasitism on birds themselves were not discussed. A direct effect of fleas on seabirds was reported in a recent study by Kristjansson et al. (2016), examining the presence of the flea *Ceratophyllus garei* in Common Eider (*Somateria mollissima*) colonies. The authors noted a positive relationship between the age of nest bowls, and the number of fleas found within them. Hyper-parasitism by fleas led to irritation in adults, which resulted in agitated egg incubation. Blood cover on eggs was also positively correlated to flea infestation (Kristjansson et al. 2016) suggesting a potential cost in terms of blood loss. These results fall in line with observations in passerine birds (eg. Fitze et al. 2004).

Lice

Lice are obligate parasites belonging to the insect order Phthiraptera. Lice are further subdivided into two main groups: sucking lice (suborder Anoplura) and chewing lice (suborders Ischnocera, Amblycera and Rhynchophthirina). Anoplura are obligate blood-sucking parasites found almost exclusively on mammalian hosts. In contrast, species of chewing lice are commonly found on bird species, feeding on hair, feathers and epidermal skin/scales (Clay and

Morby, 1967). Unlike ticks and fleas, lice spend their entire life cycle on a single host. Females lay their eggs, commonly known as nits, by gluing them to the hairs or feathers of their hosts through a secretion created in their accessory glands. Lice are typically host-specific, rather than geographically-specific, which makes estimating their global distribution challenging (Clay and Morby, 1967). Factors influencing the presence and abundance of lice on seabirds are not extensively studied. Rivera-Parra et al. (2014) sampled five seabird species across seven islands in the Galapagos, and found a connection between host density and louse infestation levels. However, the study also pointed out the need for further research on the impact of local weather conditions and host density on lice loads; factors which have been found to affect louse loads in other bird groups (Clayton et al. 2015).

Louse-seabird interactions are generally studied by collecting lice present on individual birds or in bird nests (Alonso and Garrido, 2009; Coulson et al. 2009; Gomez-Diaz and Gonzalez-Solis, 2010; Rivera-Parra et al. 2014). The most common methods of louse collection include dust ruffling with an insecticide and agitating the feathers until parasites fall off (Mallory et al. 2006; Rivera-Parra et al. 2014), or collecting invertebrates from active nests (Alonso and Garrido, 2009; Coulson et al. 2009). Although lice are prevalent in six of the eight main seabird orders that we consider here (Procellariiformes, Charadriiformes, Pelicaniformes, Anseriformes, Suliformes, Sphenisciformes), most research on louse-seabird interactions has been focused on the co-evolution or phylogeny of lice species in relation to their hosts (Paterson et al. 1993, 2000; Page et al. 2004).

Although rarely studied in seabirds, evidence suggests that lice can reduce host fitness in numerous ways (thermoregulatory stress due to feather condition, grooming costs related to

higher metabolic rates, predator vigilance, etc.; Clayton et al. 2015). We found one study that measured the impacts of louse loads on wild seabirds; Daunt et al. (2001) measured loads of *Eidmanniella pellucida* on breeding European Shags (*Phalacrocorax aristotelis*) and their chicks, and found no measurable effect of louse load on offspring growth.

Flies

Hippoboscid flies (order Diptera), commonly known as louse flies, are the most common family of parasitic flies found on birds and mammals. The Hippoboscidae are divided into three main subfamilies, only two of which (Ornithomyiinae and Hippoboscinae) include obligate parasites of birds (Duvallet & Baldacchino, 2017). As hippoboscid flies are highly mobile (some species are winged) and can spend part of their lifecycle off host, host to host transmission can be very high (Bequaert, 1953). Factors affecting the parasitism by Hippoboscidae in seabirds are not well understood, and many species may have co-evolved with their specific hosts (Bailey, 1967; Levin and Parker, 2013). However, as mentioned above, humidity and oily plumage can be related to the prevalence of louse flies on seabirds (Bequaert, 1953). The annual colonial nesting behavior of seabirds may also be a key aspect supporting the maintenance and spread of hippoboscid flies (Bastien et al. 2014; Levin and Parker, 2013).

Hippoboscid flies have been recorded on seabirds belonging to the orders Suliformes, Procellariiformes, Pelecaniformes, and Charadriiformes (Bastien et al. 2014; Bequaert, 1953; Whiteman et al. 2006). *Olfersia aenescens* most commonly parasitizes Charadriiformes, Procellariiformes, and Pelecaniformes. However, information on hippoboscid flies in other avian orders is less clear. For example, no reports were found of hippoboscids on any members of

Anseriformes in this review; this is thought to be due to their oily plumage and damp nesting habitat preferences (Bequaert, 1953). Within avian orders, the diversity of hippoboscids can vary greatly from family to family. Among Pelicaniformes, all members of the family Fregatidae share the species *Olfersia spinifera*, whereas *O. aenescens*, *O. fossulata* and *O. sordida* parasitize Phalacrocoracidae, Sulcidae and Pelicanidae (Bequaert, 1953).

The impact of Hippoboscidae on seabirds is also sparsely understood. Bequaert (1953) suggested that since many louse fly species are host-specific, they are more dependent on host survival than other, more generalist, ectoparasites. However, their relatively high mobility may limit constraints on virulence. Recent studies on the impact of Hippoboscidae on seabirds have focused on the transmission of microparasites such as haemosporidia, rather than the direct impact of parasitism itself (Bastien et al. 2014; Levin and Parker, 2013). The impact of these microparasites on seabirds is discussed in a later section.

Mosquitoes

There are approximately 3,500 named species of mosquitoes (Diptera: Culicidae), of which seven known genera (*Aedes*, *Anopheles*, *Culex*, *Mansonia*, *Haemagogus*, *Psorophora*, and *Sabethes*) transmit disease to animals, including humans (Fang, 2010; Gubler, 2009). Culicidae are the most prolific disease vectors within the order Diptera, and can transmit a range of parasites (e.g., *Plasmodium relictum*), viruses (alphaviruses, flaviviruses, etc) and helminthes within bird populations worldwide (more details outlined below). Of the four stages of their life cycles, mosquitoes spend the egg, larval and pupal stages in aquatic habitats, and only

parasitize hosts as adults. Only the females bite and can transmit infectious agents (Gulber, 2009).

Mosquitoes are known to parasitize species belonging to Charadriiformes, Suliformes, Procellariiformes and Pelecaniformes. In studies relating to wild seabirds, only *Aedes taeniorhynchus* has been identified as a parasite (Anderson, 1989; Anderson and Fortner, 1988). Most studies conducted on mosquito-bird systems have focused on birds acting as reservoirs for, or direct transmitters of, viruses and diseases that affect humans (Parkinson and Butler, 2005; Reed et al. 2003; Tsiodras et al. 2008). Like other macroparasites, the direct impact of mosquitos on their hosts will depend on their relative abundance. Although factors affecting mosquito abundance are largely unknown, heat, humidity, and the availability of stagnant water for breeding are key determining factors (Wegbreit and Reisen, 2000). Heat has been identified as a particularly important factor affecting mosquito parasitism of seabirds (Gaston et al. 2002; Gaston and Elliott, 2013).

The colonial and often synchronized nature of seabird breeding supports the spread of mosquitoes among hosts within populations; birds born later in the breeding season can be prone to higher degrees of mosquito exposure due to a reduction in nestling hosts (Caillouet et al. 2013). In seabird populations, mosquito parasitism has been positively correlated with egg neglect in Waved Albatrosses (*Diomedea irrorata*) in the Galapagos Islands (Anderson and Fortner, 1988). In Hudson Bay, adult mortality and egg loss in a population of Thick-billed Murres (*Uria lomvia*) were also positively correlated with mosquito parasitism (Gaston et al. 2002; Gaston and Elliott, 2013).

Endoparasites

Helminths

Helminths are a group of worms that are often parasitic in birds and include flatworms - which further separate into cestodes (tapeworms) and trematodes (flukes) - nematodes (roundworms), and acanthocephala (thorny-headed worms; Galaktionov, 2017; Galaktionov and Bustnes, 1997). The life cycle and transmission pathways of helminths are often complex, with both direct transmission (i.e., from parent to chick during feeding), and indirect transmission via intermediate hosts or vectors. Helminths are typically studied in seabirds through carcass collection (e.g., Mallory et al. 2007), although some studies have used regurgitation, endoscopic techniques, and anti-helminth treatments in seabirds, to assess parasitism in the gastro-intestinal tract and their effects (Fonteneau and Cook, 2013; Granroth-Wilding et al. 2017; Provencher et al. 2017). Information on the impact of helminths on some species are more available because they are hunted or often beach cast, but overall the need for carcasses poses a challenge to explore helminth-seabird relationships in wild populations, as lethal sampling is most often used. In situations where carcasses are available, a range of helminths have been found in host species (e.g. Mallory et al. 2007, Tourangeau et al. 2018).

Cestodes and Trematodes

Cestodes and trematodes (Phylum Platyhelminthes) are characterized by their lack of a body cavity, hermaphroditism, and the use of suckers (borthridia) to attach themselves within their host (Galaktionov, 2017). Flatworms can be most easily distinguished by the segmentation in their bodies; trematodes have unsegmented, smooth bodies, whereas cestodes have segmented bodies (Galaktionov, 2017). The lifecycle of trematodes and cestodes often involves two, sometimes three, intermediate hosts (e.g., copepod infected by feeding on cestode eggs,

which in turn are ingested by cephalopods or fish) before reaching maturity within a seabird (Galaktionov, 2017). However, only trematodes require the obligatory participation of molluscs to complete their lifecycle (Galaktionov, 2017).

The prevalence and impacts of cestodes and trematodes vary by species, region, and sex. In Double-crested Cormorants (*Phalacrocorax auritus*) in southern Canada, Robinson et al. (2008) found that males had significantly higher levels of the trematode *Drepanocapalus spathans* when compared with females. Mallory et al. (2007) found a higher frequency of occurrence of cestodes in Northern Fulmars (*Fulmarus glacialis*) during the post-breeding season as compared with the pre-breeding season. The diversity of cestodes and trematodes has been shown to vary across a host species range. For example, birds inhabiting the southern extent of the Common Eider (*Somateria mollissima*) range in the North Sea have as many as 15 trematode species, whereas at the northern extent of the range in Franz Josef Land only, a single trematode species has been reported (Galaktionov, 1996, 2017). In terms of the impact of these worms on seabird health and condition, as for most macroparasites, it is expected that negative impacts may only occur at very high parasite loads (see Galaktionov, 1996), but detailed studies in seabirds are limited and difficult to attribute to cestodes and trematodes in particular.

Nematodes

Nematodes or roundworms (phylum Nematoda) are characterized by their round body shape and the presence of a body cavity. Nematodes also have distinct male and female organisms (Galaktionov, 2017), similar to cestodes and trematodes, however, the prevalence of nematodes in seabirds is highly variable. Even individuals nesting at nearby colonies can exhibit

strong differences in parasitism levels. Fonteneau and Cook (2013) found that Kerguelen Shags (*Phalacrocorax verrucosus*) nesting approximately 25 km from each other had significantly different prevalence and infection loads of the nematode *Contracaecum rudolphii*. The authors attributed this result to differences in diet between the two colonies, highlighting how local diet can be a significant factor for parasitism in seabirds. Sex bias was also identified by Robinson et al. (2008) in Double-crested Cormorants in Canada, where males had significantly higher levels of the nematode *Contracaecum* spp. when compared with females. Experimental removals of gastrointestinal nematode parasites was found to alter resource allocation in European Shags in relation to local breeding conditions (Granroth-Wilding et al. 2015, 2014; Reed et al. 2008), highlighting the importance of the interaction between parasites and local environmental factors in determining parasite impacts (Granroth-Wilding et al. 2014).

Acanthocephalans

Much like cestodes and trematodes, acanthocephalans are parasitic worms that lack a mouth, and instead attach to their hosts using a proboscis that is covered with spiny hooks (Galaktionov, 2017; Hoberg, 1986). Acanthocephalans also have distinct male and female sexes, and their life cycle requires intermediate hosts, most commonly thought to be benthic crustaceans (Galaktionov, 2017). Although acanthocephalans have been identified in many Antarctic and Arctic seabird fauna (Charadriiformes, Sphenisciformes, Anseriformes; Brandao et al. 2014; Hoberg, 1986), they are best studied as one of the most prolific parasites of Common Eiders in the northern hemisphere (Galaktionov, 1996; Provencher et al. 2016, 2018; Figure 3). A sex bias in the prevalence of acanthocephalans in seabird species has been identified, and may be attributable to differing life history strategies between males and females, especially

during the breeding season, caring of young and feeding in distinct areas during the moulting season (Skirnisson, 2015). Similar to the other parasitic worms, the distribution and number of species in acanthocephalans vary by region, with the number of species of acanthocephalans being higher in the sub-Arctic regions than in Arctic environments (Galaktionov, 1996). Again, there is very little work done on how this particular group may negatively affect seabirds given the co-occurrence with other species, and the difficulty of examining this group in isolation in relation to potential impacts on species.

Helminths interactions

While a single host can be affected by the number of helminths it carries, there is no clear relationship demonstrated in the literature on how helminths may interact with respect to each other within a host. For example, Robinson et al. (2008) found no correlation between the most abundant helminths (nematodes and cestodes) in Double-crested Cormorants. In contrast, Provencher et al. (2016) found that the abundance of cestodes and acanthocephalans were negatively correlated with each other in Common Eiders, and suggested a possible negative interaction between helminth species within a host, at least in some species. Northern Fulmars from the high Canadian Arctic harboured several helminth species including cestodes, trematodes, nematodes, and acanthocephalans in varying levels of infection (Mallory et al. 2007). Tourangeau et al. (2018) similarly found that Common Eiders in northern Canada to have several cestodes and acanthocephalans with varying levels of infection in relation to age and sex. Due to the difficulty in obtaining reliable estimates of parasite diversity and loads, the impact of these species on seabird health and population dynamics have received relatively little attention.

In some cases, only the presence or absence of helminths is reported without any additional information. For example, in Provencher et al. (2014), helminths are reported in Arctic Terns (*Sterna paradisaea*), but specific parasite identification and enumeration were not possible during the dissection of the birds. Globally, the lack of trained parasite taxonomists may also be hampering the identification and reporting of seabird parasites (Hopkins and Freckleton, 2002). Furthermore, some of the most comprehensive parasite publications are only available in Russian where there is still a strong tradition of parasitologists interested in systematics and natural history (e.g., Kuklin, 2017).

Microparasites

Arboviruses

Although there are cases where viruses are transmitted by direct contact with an infected individual, most viruses in wild seabird populations are vector-borne (see Van Riper et al. 2002). Arboviruses, or arthropod-borne viruses, comprise close to 50 different viruses that have been identified in wild seabirds (Beckham and Tyler, 2015; Nuttall, 1984; Mackenzie and Williams, 2009). This section focuses on some of the most common types of arboviruses found in seabirds.

Avipoxviruses

Avipoxviruses, a subgroup of poxviruses, are most notable for causing avian pox in birds around the globe (Bolte et al. 1999). Ectoparasites such as mosquitoes are the most common mechanical vectors for this group of viruses in wild seabirds, although a flea species (*Parapsyllus longicornis*) has been suggested as a possible vector as well (Kane et al. 2012).

Avian pox is a slow-developing disease, the effects of which vary by species. The most common form of avian pox affects the skin, where the development of warts around featherless regions of birds (face, legs, and feet) is a common occurrence (Tripathy, 1993). These lesions often disappear with time but can leave behind scarred and damaged skin. However, in cases where these warts become enlarged and clustered, loss of sight, breathing impairment, and difficulty feeding are common side effects. It is in the case of secondary infections due to a dampened immune system, and the development of scar tissue, where avian pox can contribute to bird mortality (Friend and Franson, 1999; Kane et al. 2012).

Infections are also highest during wet seasons and virus transmission is mostly host-density dependent (Van Riper et al. 2002). This is a key factor to note in the spread of avipoxviruses among seabird populations, many of which form dense breeding colonies. Avian pox has been reported in Sphenisciformes, Anseriformes, Charadriiformes, and Procellariiformes. A study of Magellanic Penguins (*Spheniscus magellanicus*) from two colonies in Argentina revealed 108 chicks with avian pox lesions; however, the prevalence of lesions was 0.002 infected chicks to every handled chick. Of the afflicted chicks, 18 were found dead, but whether the cause of death was due to avian pox or secondary infections is unknown (Kane et al. 2012). Avian pox is also the most common viral infection in albatrosses and large petrels (Uhart et al. 2017). It has been reported from Wandering Albatross (*Eudiptes chrysocome*) in the Prince Edward Islands in the Indian Ocean, to Laysan Albatross (*Phoebastria immutabilis*) on Oahu, Hawaii (Young and VanderWerf, 2008), suggesting that albatross populations may be exposed to these viruses worldwide.

Flaviviruses

Flaviviruses (family: Flaviviridae) have been mostly studied for their impacts on human health, in particular, dengue fever, yellow fever, Japanese encephalitis, Zika virus, and West Nile virus (Gaunt et al. 2001; Jaeger et al. 2016). Ticks and mosquitoes are the most common vectors for flaviviruses (Gaunt et al. 2001; George et al. 1985).

Although West Nile virus has been well studied in some bird populations, it is important to note that the most common flaviviruses isolated from seabirds do not include West Nile virus. Most research on West Nile virus in birds has focused on relatively common terrestrial species such as American Crows (*Corvus brachyrhynchos*), Common Grackles (*Quiscalus quiscula*), Blue Jays (*Cyanocitta cristata*), and House Sparrows (*Passer domesticus*; Rappole and Hubalek, 2008; LaDeau et al. 2007). In wild seabird populations, West Nile virus has been identified in post-mortem analyses of American White Pelicans (*Pelicanus erythrorhynchos*), and is suggested to have caused mortality in adults and nestlings (Rocke et al. 2005). Antibodies known to neutralize West-Nile virus were also detected in blood sera from adult Great Frigatebirds (*Fregata minor*) in the Western Indian Ocean, with no apparent sign of disease (Jaeger et al. 2016).

In wild seabirds, flaviviruses such as Meaban virus, Usutu virus, Saumarez Reef virus, Tyuleniy virus, and Gadget's Gully virus have been identified in species belonging to Charadriiformes and Sphenisciformes (Gaunt et al. 2001; George et al. 1985; Mackenzie and Williams, 2009, Arnal et al. 2014; Jaeger et al. 2016). Only the pathogenicity of Saumarez Reef virus has been tested in seabirds through small-scale experimental infections of Little Blue Penguins (*Eudyptula minor*). Wild-captured individuals inoculated with the virus succumbed to

disease and mortality within 9-13 days of the infection (Morgan et al. 1985). Although research on factors affecting the spread of flaviviruses amongst wild seabirds is lacking, one can presume that warm weather, damp/wet habitats, and host density favour the transmission of these vector-borne viruses (Van Riper et al. 2002).

Other Arboviruses

There are at least 40 other types of arboviruses identified from seabird ticks alone, with their pathogenicity and spread in wild seabird populations largely unknown (Nuttall 1984). Lab tests of the Avalon nairovirus isolated from Black-legged Kittiwakes (*Rissa tridactyla*) on suckling mice exhibited little to no effect (Quillien et al. 1986; Spence et al. 1985). Sakhalin virus, named after the location it was first discovered (Sakhalin Island, Sea of Okhotsk), was pathogenic in lab-tested suckling mice after intracerebral inoculation, but the effects of the virus on the host Common Murres (*Uria aalge*) are unidentified (L'Vov et al. 1972). Other arboviruses isolated directly from wild seabirds include Nugget virus, Tagart virus, and an unnamed species identified in Black-legged Kittiwakes in Brittany (Chastel et al. 1987; Doherty et al. 1972). The effects of any of these viruses on their host populations are also unknown.

Avian Influenza

The first isolation of Influenza A virus (Orthomyxoviridae) in wild birds was reported in 1961, following an epizootic among Common Terns (*Sterna hirundo*) in South Africa (Rowan, 1962; Becker, 1966). Since that date, Influenza A viruses have been detected in more than 60 seabird species worldwide, mostly in gulls and terns (see Arnal et al. 2014 and Lang et al. 2016 for review in gulls and other seabirds, respectively). Birds of the Anseriformes and Charadriiformes orders are the main hosts for influenza A viruses (Olsen et al. 2006). Significant

variation in virus prevalence have been found between closely related species, but also season and bird colony, suggesting that the transmission dynamics of avian influenza are strongly associated to the ecology of their hosts. Annual epidemics have been found in Black-headed Gulls (*Chroicocephalus ridibundus*), with peaks of transmission during the breeding season and, in particular, fledgling birds (Verhagen et al. 2014). This supports the idea that bird age is an important factor involved in influenza virus infection. Investigations of virus transmission on tropical oceanic islands have also shown that terns could be involved in the introduction and maintenance of avian influenza viruses in these remote locations (Lebarbenchon et al. 2015).

Among the 16 described avian influenza virus hemagglutinin subtypes, H13 and H16 are associated to seabirds (Olsen et al. 2016). Although low pathogenic virus subtypes do not induce clinical signs of disease (Brown et al. 2012; Verhagen et al. 2015), infection with highly pathogenic avian influenza viruses (H5 and H7 subtypes) can induce severe clinical signs. These subtypes can cause cloudy eyes, ruffled feathers, weakness, a lack of coordination, torticollis, and mortality (Brown et al. 2006). To date, there is only limited evidence that these poultry-adapted viruses can be maintained in wild birds for long periods of time (Krauss et al. 2016; Lebarbenchon et al. 2010). The increasing number of spillover events nevertheless highlights the need to further investigate the role of seabirds in the spread of both low and highly pathogenic avian influenza viruses during epizootics.

Although it is likely that other directly transmitted viruses affect seabird populations, particularly in dense breeding colonies where contact rate is very high, current knowledge on these pathogens remains very limited. In addition to avian influenza, other viruses have been documented in seabirds in the past, such as the one causing puffinosis in Manx Shearwaters

(*Puffinus puffinus*) in Europe (Harris, 1965; Macdonald et al. 1967), or coronaviruses in gulls in the Bering Strait area (Muradrasoli et al. 2010). The epidemiology, ecology and evolution of these viruses would require further investigation in order to precisely assess the physiological and behavioural effects in their natural hosts.

Bacteria and Parasites

Avian Cholera

Avian cholera is a highly contagious disease resulting from infections of the *Pasteurella multocoda* bacterium. DNA fingerprinting has resulted in the identification of at least 16 different serotypes of *P. multocoda* (Friend and Franson, 1999). Avian cholera has become the most prolific infectious disease of waterbirds, even though it first appeared in North America as recently as 1944. Since then, the disease has expanded globally, and outbreaks have increased in frequency since the 1970s (Friend and Franson, 1999). One of the key reasons avian cholera has been so successful in its spread is due to the multitude of ways *P. multocoda* can make its way into a host's system. Bird-to-bird contact, ingestion of carcasses or contaminated food/water, insect bites, and even the aerosolization of the bacteria in heavily contaminated regions can all lead to avian cholera in wild birds (Friend and Franson, 1999). Infections of *P. multocoda* can be acute or chronic, but in most species studied to date, infections result in death within 24-48 hours. Mortality in 6-12 hours has also been reported in wild birds, with peak mortality exceeding more than 1,000 birds a day in some cases (Friend and Franson, 1999).

Avian cholera is identified in wild seabirds almost exclusively through necropsies, and has been reported in species belonging to Anseriformes, Procellariiformes, Phaethontiformes,

Sphenisciformes, Suliformes, Pelicaniformes and Charadriiformes (Crawford et al. 1992; Friend and Franson, 1999; Leotta and Giacobani, 2006). Environmental contamination from diseased birds is a primary source of infection. Due to the dense nesting colonies formed by wild seabirds, and the highly contagious nature of the disease, avian cholera can lead to rapid colony death and even extinction. The only known way to control its spread in these populations is by removing afflicted and dead birds from the region (Descamps et al. 2012; Friend and Franson, 1999).

Avian cholera has been responsible for annual colony collapses in Common Eiders in Nunavut (Figure 4), Cape Cormorants (*Phalacrocorax capensis*) in South Africa, Common Murres in the Baltic Sea, Yellow-Nosed and Amsterdam Albatrosses (*Diomedea chlororhynchos* and *D. amsterdamensis*) on Amsterdam Island, and Macaroni Penguins (*Eudyptes chrysolophus*) in the Antarctic (Cooper et al. 2009; Crawford et al. 1992; Descamps et al. 2012; Osterblom et al. 2004; Waller and Underhill, 2007; Weimerskirch 2004). Long term the effects of these annual outbreaks is still being studied, but at least in some cases colonies persist but at reduced numbers.

Lyme Disease

Lyme disease, caused by the bacteria of the complex *Borrelia burgdorferi* sensu lato is the most widespread tick-borne disease in North America and Europe. The transmission of the infectious agent is best understood in terrestrial systems involving humans, wild birds and small mammals, and *Ixodes ricinus* and *I. scapularis* ticks (Anderson et al. 1986; Kurtenback et al. 2006). Lyme disease symptoms in humans and dogs range from complex mix of neurological disorders, cardiac-associated complications, joint pain, and skin rash in humans, to lameness,

vomiting, diarrhea, lack of appetite, weight loss, and inflammation in dogs (Klempner et al. 2001; Littman et al. 2006). Despite having now been isolated from dozens of wild terrestrial birds, the effects of *B. burgdorferi* in these populations is not well understood. Most research on bird-tick systems studying the disease focus on the role of wild birds as reservoirs, with the potential to spread it across large spatial scales (Clow et al. 2017; Smith et al. 1996).

In seabirds *B. burgdorferi* has been isolated from *I. uriae* ticks in the Northern and Southern hemispheres exploiting species belonging to Charadriiformes, Procellariiformes, and Sphenisciformes (Gylfe et al. 1999; Olsen et al. 1995; Duneau et al. 2008). More generally, evidence of the widespread presence of this infectious agent in seabirds is accumulating (Gasparini et al. 2001; Gomez-Diaz et al. 2011; Staszewski et al. 2008). However, for now, no evidence suggests a pathogenic effect of infection for the birds; in particular, a long-term capture-mark-recapture analysis of breeding Black-legged kittiwakes found no association between exposure to *B. burgdorferi* s.l. and survival (Chambert et al. 2012).

Avian Botulism

Bacteria belonging to the genus *Clostridium* are responsible for an immense amount of wild bird deaths. *Clostridium botulinum* is the most prevalent species of bacteria from this genus found in wild birds, causing mortality through infecting hosts with botulinum toxins. Although there are seven types of botulinum toxins created by this bacterium - labeled A to G - it is the Type C botulinum toxin that has caused the highest mortality in wild birds (Friend and Franson, 1999). Before avian cholera outbreaks increased in frequency in the past quarter century, avian botulism was considered the most destructive disease in wild birds (Friend and Franson, 1999). Botulism outbreaks can regularly result in the death of thousands of waterbirds

and shorebirds in a region and up to a million birds have been lost in a single outbreak of the disease (Friend and Franson, 1999). Blood samples from live birds are needed to identify the toxin in populations, making the study of avian botulism in wild birds a resource dependant endeavour (Friend and Franson, 1999).

Factors affecting the spread of botulism in wild birds include colony density, water-level changes, water quality, and the prevalence of *C. botulinum* toxins in food or water (Friend and Franson, 1999). Temperature also plays a critical role in the spread of botulism, with most outbreaks taking place during summer and fall (Friend and Franson, 1999). In wild seabirds, botulism has been isolated from species belonging to Charadriiformes, Pelecaniformes, and Anseriformes (Friend and Franson et al. 1999; Neimanis et al. 2007; Rocke et al. 2005). The symptoms of the disease in wild seabirds (e.g, Herring Gulls; *Larus argentatus*) include decreased physical coordination, paralysis of legs and wings, dehydration, and a decrease in food consumption. Avian botulism has caused mass mortality in Herring Gulls in Sweden, and American White Pelicans in North America (Neimanis et al. 2007; Rocke et al. 2005).

Chlamydiosis

Chlamydiosis is an infection associated with bacteria belonging to the genus *Chlamydia*, which typically live within animal cells. *Chlamydia psittaci* is the most common species associated with the disease in wild birds. Chlamydiosis can range in pathogenicity in wild birds from inapparent infections to an acute disease with high mortality, depending on the strain of *C. psittaci* affecting the individual/population (Friend and Franson, 1999). Symptoms in wild birds range from decreased food consumption, pus discharges from the eyes and nares, and bloody diarrhea, to becoming rigid and motionless (Friend and Franson, 1999). *Chlamydia*

species can remain active in the tissues, feces, discharges, and even plumage of affected birds, and can be transmitted between individuals by direct contact. The only known way to control the spread of the disease in wild birds is by the removal of dead or affected birds from colonies (Friend and Franson, 1999).

Although waterfowl, pigeons, herons and parrots are the most commonly infected wild birds, chlamydiosis has been reported in over 150 species belonging to 20 orders. The most common wild seabirds infected by the disease include gulls and fulmars (Charadriiformes and Procellariiformes; Franson and Pearson, 1995; Hermann et al. 2006). Studies have also isolated *C. psittaci* from Red-footed (*Sula sula*) and Nazca Boobies (*Sula granti*; Padilla et al. 2004). However, since chlamydiosis in wild birds is often inapparent, the effect of the disease on these populations has not been discussed in any of the studies we found. In outbreaks recorded in wild gulls (species unidentified), chlamydiosis has been fatal for adults, though fledglings reportedly died at a much higher rate (Friend and Franson, 1999).

Haemosporidia

Haemosporidia, or blood parasites, are vector-borne parasites that have been well-studied (e.g., Padilla et al. 2004; Valkiunas, 2004; Vanstreels et al. 2017). They are transmitted to wild birds primarily by midges (*Culicoides* spp.), mosquitoes (*Culex* and *Aedes* spp.) and flies (*Simulium* and *Hippoboscidae* spp.; Friend and Franson, 1999; Vanstreels et al. 2017). There are currently four primary types of haemosporidia identified in seabirds, each carried by a different type of vector. *Plasmodium* species are carried by mosquitoes, and are associated with diseases such as malaria in humans (Friend and Franson, 1999; Vanstreels et al. 2017). *Haemoproteus* species are carried by midges, and *Leucocytozoon* species are carried by flies (Friend and

Franson, 1999). It is unconfirmed what vectors carry *Babesia* spp., but it is assumed to be ticks (Earle et al. 1992; Yabsley et al. 2009). Although many groups of birds are known hosts of various haemosporidian parasites, often with high prevalence in populations (e.g., passerines, waterfowl), in detailed surveys of North America birds, Greiner et al. (1962, 1975) considered seabirds to be “nearly hematozoan-free”.

Haemosporidia have been found in wild seabirds belonging to the orders Charadriiformes, Suliformes, Sphenisciformes, and Procellariiformes, and in some cases certain parasites (e.g., *Plasmodium relictum*) have been associated with high mortality (e.g., wild penguins; Friend and Franson, 1999). However, in the majority of studies, there is little evidence of mortality of wild seabirds caused by haemosporidia (Padilla et al. 2004; Parsons et al. 2017; Peirce and Parsons, 2012; Yabsley et al. 2009). Temperature, migration, and local climatic conditions supporting ectoparasites are key considerations in determining the spread of haemosporidia amongst wild seabirds (Friend and Franson, 1999; Van Riper et al. 2002), and help explain regional prevalence levels (e.g., Grenier et al. 1975; Bennett et al. 1992). For example, Vanstreels et al. (2017) found no evidence of haemosporidia in Magellanic Penguins in the Sub-Antarctic region of Argentina, and Mallory et al. (2007) also found no haemosporidia in Northern Fulmars from the high Arctic. It is also thought that many haemosporidia are host species specific. For example, *Babesia shortii* is the only *Babesia* spp. known to cause pathogenicity in birds (Peirce, 2000). However, it is best studied in Falconidae, and experimental transmissions of the parasite into other terrestrial species have failed in producing pathogenic responses (Peirce, 2000).

Discussion

While our review focused on eight orders of seabirds (Procellariiformes, Phaethontiformes, Suliformes, Charadriiformes, Sphenisciformes, Pelicaniformes, and select Gaviiformes, and Anseriformes), we found that species belonging to the order Charadriiformes were the most represented in the parasite and pathogen literature (Table 2). Although Anseriformes have been studied more extensively in terms of parasites, our focus on parasites in seaducks resulted in far fewer study results. The research done in the eight orders is generally representative of the number of species within each order; Charadriiformes and Procellariiformes have the most numerous species and resulted in the more parasite studies found in the literature, while Phaethontiformes and Gaviiformes have the fewest species, and we found the fewest parasite studies (Table 2).

The focus on parasites and pathogens in colonial nesting seabirds, such as those belonging to Charadriiformes and Procellariiformes, may be because they are easier to study due to their high population densities during the breeding season. This colonial nature lends these species to parasite related studies as larger sample sizes can be accessed relatively easily. On the other hand, species belonging to Gaviiformes are found in lower densities on the landscape, making population-wide analyses more resource- and time-intensive. Important to note is that the colonial nature of some species of birds may also make them more vulnerable to higher levels of parasites and pathogens as compared with birds that breed in isolation because of the contact between individuals at bird colonies (e.g. Boulinier et al. 2001, 2016; McCoy et al. 2016). For example, in some cliff-nesting seabird species where there is little to no

vegetation cover individuals may literally be covered in the faeces of those nesting above them (Figure 5); these faeces are a potential vector for a number of parasites.

The impact of ectoparasites on seabirds are studied through two main metrics; the impact on seabird populations through direct parasitism, and the potential for seabird ectoparasites to act as disease vectors. The impacts of direct parasitism on wild seabirds can depend on the age, sex, and body condition of the host (e.g., Granroth-Wilding et al. 2014; Provencher et al. 2016). Although adult mortality can be caused by ectoparasites (e.g., Gaston and Elliott, 2013), this occurs most often in cases of hyper-infestations. The most commonly reported impact of ectoparasites on adult seabirds is that of reduced parental care due to parasitism (e.g., Duffy et al. 1983; Dietrich et al. 2011). Nest abandonment and inconsistent/slower offspring development are the most well-known outcomes. Mortality in fledglings due to parasitism is much more likely, and has been reported in species belonging to six of the eight orders studied here (Table 2).

The effect of endoparasites on seabirds is much more diverse (Table 2). Flaviviruses, *Chlamydophillia* spp., haemosporidia and *Borrelia burgdorferi* s.l. seem to be asymptomatic in seabirds, which makes understanding their relationships with their hosts difficult. In contrast, highly pathogenic avian influenza and avian cholera can cause mass mortality and colony collapses (e.g., Allison et al. 2015; Descamps et al. 2012). Except for these exceptional cases when such massive die-offs are reported, the physiological and behavioral effects of viral and bacterial infections in seabirds remain largely unknown, at both the individual and population levels. This limitation is mostly associated with the inherent properties of viruses and other microparasites. In particular, field investigation of infectious status and prevalence in

populations usually requires strict conservation procedures of biological material. Laboratory-based techniques (e.g. molecular biology, virus isolation) in sometimes high security laboratories such as for highly pathogenic avian influenza and West-Nile viruses is needed, and certain biological safety precautions are required by law in some regions (e.g., Allison et al. 2015; Lebarbenchon, 2010, 2015).

Effects of certain parasites and pathogens may also be subtle and difficult to measure with respect to the impact of other environmental factors, and choosing the appropriate traits to measure requires clear information on the biological system (Sanchez et al. 2018). For example, the effects of a parasite may only be detectable during times of physiological stress (e.g. breeding or migration), but not during other parts of the annual cycle (Provencher et al. 2017). Identifying the links between such basic epidemiological information and host physiological and behavioural traits, in order to assess the precise effects of infection on host fitness, therefore remains very challenging. Experimental approaches in the field can also be somewhat limited; ethics and biosafety considerations naturally preclude the manipulation of the infectious status of natural migratory hosts with parasites (although this may be easier for helminths than viruses and bacteria).

Understanding the interactions between different parasite types affecting seabirds is also lacking, but has been shown to be essential in other animal groups (e.g., Graham, 2008). Additional observational and experimental studies from a larger range of seabirds aimed at specific parasitic groups would greatly enhance our understanding of these interactions. New methods for investigating the diversity of endoparasites using metabarcoding analyses of faeces may facilitate our understanding of the diversity and distribution of these organisms at

different spatial scales (e.g., McInnes et al. 2017), and may enable us to incorporate parasite dynamics into long-term population survey data. Although there are limitations to metabarcoding approaches to studying effects of parasites as metrics beyond presence and absence will be difficult to quantify. Control measures for the spread of parasites are also rudimentary and resource/time intensive. One way to control their spread in seabirds is by the selective removal of afflicted or dead birds from colonies (e.g., Friend and Franson, 1999). Vaccination has also been recently proposed as an effective measure to protect endemic albatrosses from avian cholera (Bourret et al. 2018), and may be an important conservation consideration for seabirds of particular conservation concern, but is not likely a viable solution for more metropolitan species.

Due to the biological connection between many endo- and ectoparasites, it is important to note that the factors influencing their spread are intrinsically connected. Research shows that abiotic conditions such as heat and humidity, and biotic conditions such as host body condition and colony density, are key factors determining in the spread of parasites within seabird colonies (Caillouet et al. 2013; Monticelli et al. 2008; Proctor, 2003; Ramos et al. 2001). Discussing the spread of these parasites on a global scale is more complex, however. Factors such as migration, climate change, and range extension/change for seabirds and parasites alike need to be taken into consideration. Seabirds are often long-lived and highly migratory, so it should come as no surprise that they can act as effective parasite reservoirs and transporters. There is already evidence showcasing range and species expansions for parasites, although the exact factors involved are as yet unknown (de Souza Peterson et al. 2017; Kane et al. 2012). Changing seasonal temperatures and water levels due to climate change can also extend the

time period that seabirds can be parasitized by ectoparasites, potentially resulting in increased local abundances and subsequently higher chances of pathogenicity. Increasing anthropogenic pollution and higher water levels due to climate change can further contribute to the spread of devastating diseases such as botulism and cholera (Friend and Franson, 1999; Garamszegi et al. 2011; Parkinson and Butler, 2005). The interaction between different environmental stressors and parasitism is only recently starting to be considered for understanding the overall impact on seabird populations.

There is clearly a bias toward research interest in seabird parasites that have the capacity to parasitize or infect human beings (i.e., zoonoses). Evidence of this comes from the comparatively extensive research on West Nile virus and Lyme disease, which can be transmitted to humans through vectors such as ticks and mosquitoes. Although direct transmission of pathogens from birds to humans is considered uncommon, little work has been done to assess seabird pathogens in humans and thus this relationship is likely underestimated. Vectors carried by migratory birds can play a role in the transmission of at least 10 different human pathogens (Tsiodras et al. 2008), but a much better understanding of this phenomenon is still required. Recent work by Fossadal et al. (2018) has shown a positive association between handling *C. psittaci* infected juvenile Northern Fulmars - a species hunted for human consumption - and human psittacosis disease in the Fulmar Islands. It is possible that other commonly harvested species, such as eiders and murrens may present similar correlations in future works. The aforementioned control measures for diseases such as cholera and influenza also expose human beings to these parasites. With the increased risk of outbreaks in seabirds

due to climate change and range expansions, pathogen spillover events will likely become more frequent.

Beyond their zoonotic implications, the impact of parasites on seabirds and human beings have economic and cultural implications. Commonly harvested birds such as Common Eiders and murrelets have experienced pathogenicity, mortality, and even annual colony collapse due to increased parasitism (Gaston et al. 2002, 2013; Kristjansson et al. 2016; Lovvorn et al. 2009). Anthropogenic activities such as overfishing and oceanic pollution are also evolving factors contributing to reduced health in seabirds (Braune et al. 2006; Sydeman et al. 2017). The long-term impacts of these changes can contribute to increased, additive mortality caused by parasites in seabird colonies. Changing climatic conditions and food availability have also resulted in seabirds being preyed upon by novel predators (Iverson et al. 2014; Smith et al. 2010). More research on cumulative effects from parasitism, reduced food availability due to anthropogenic activity, and changing predatory interactions is needed to understand the collective impact these factors can have on parasite-host relationships in seabird colonies (Dey et al. 2018; Iverson et al. 2014; Ramos et al. 2005,). Understanding these interrelations becomes even more crucial when we consider endemic or naïve species of seabirds that may be experiencing increases in multiple stressors due to changing conditions in their habitats. For example, increasing numbers of non-native species in Hawaii have introduced parasites that have led to mass mortality in native songbirds (Van Riper et al. 2002). Expanding ranges for parasites and disease vectors have raised similar concerns in Antarctic seabird populations (Grimaldi et al. 2015).

It is clear that the colonial nature of seabirds makes them effective reservoirs and hosts for parasites. Not all seabirds come in direct contact with each other in these colonies, however, because of strong territoriality. More research is needed to understand the impact of localized separation in colonial nesting seabirds on the spread of parasites. Colonial nesting might indeed yield some benefits to hosts against certain parasites. For example, Douglas et al. (2005) showed evidence of aldehydes created by Crested Auklets (*Aethia cristatella*) can effectively repel ectoparasites. There are also studies to suggest that certain species of wild birds can slow the spread of pathogens like West Nile virus (Levine et al. 2016). The role of seabird diversity and abundance in suppressing zoonotic disease is a worthwhile avenue for further study.

Concurrently, most ecosystems are warming under climate change (Walther et al. 2002), and evidence suggests that increased parasitism is linked with warmer weather (Bellard et al. 2012; Kutz et al. 2008). Therefore, there is a need to understand current level of parasites in seabirds to understand changing patterns and trends in the future. In particular, we stress that studies examining parasitism in bird populations should publish results, regardless of the outcome (e.g., no infection found in seabirds). These baseline studies are essential for documenting the effect of shifting environmental conditions on bird-parasite relationships and teasing apart the questions 'is this new?' or 'new to us?'; a critical question to understanding how environmental changes will impact biota.

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1 TABLES

2 Table 1. All search terms used in Web of Science and Google Scholar to survey data on seabird parasites.

Search Terms Used	Acanthocephalans seabird	Babesia seabird	Haemoproteus seabird	Nematode seabird	Protists Seabird
	Arbovirus seabird	Babesia seaduck	Helminths seabird	Orbivirus seabird	Protozoa sea suck
	Avian Botulism	Bacteria seabird	Hemosporidia	Parasite sea duck	Tick sea duck
	Avian botulism seabird	Cestode seabird	Leucocytozoon seabird	Parasites seabird	Tick seabird
	Avian Cholera	Chlamydiosis	Lice seabird	Pathogens seabird	Trematode seabird
	Avian cholera seabird	Chlamydiosis seabird	Lyme Disease	Phlebovirus seabird	Virus Sea duck
	Avian Influenza	Flavivirus seabird	Lyme disease seabird	Plasmodium seabird	Virus Seabird
	Avian influenza seabird	Flea seabird	Mites seabird	Protist sea duck	Virus seaduck
	Avipoxvirus seabird	Flies seabird	Mosquitoes seabird	Protists Sea duck	Virus seafowl

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4 Table 2. Summary table for known seabird parasites, their taxonomic breakdown, and their documented effects on seabird
 5 populations as studied across seabird life stage.

Parasite type	Taxonomy and diversity*	Life stage			Does the parasite have potential to cause colony collapse or abandonment? (Yes/No/Unknown)	Seabird order(s) affected	Known distribution in seabirds	Key references
		Egg	Fledgling	Adult				
Ticks	Arthropoda, Acari ≥17 species of hard tick (Ixodidae): 16 Ixodes sp. and Amblyomma loculosum ≥12 species of soft tick (Argasidae): Argas and Ornithodoros (Carios) genera	Hyperinfestation of adults can cause inconsistent incubation of the egg.	Vector for numerous viruses and bacteria. Can cause reduction in parental care due to parasitism. In severe cases of infestation, can cause mortality.	Vector for numerous viruses and bacteria. Hyperinfestation can lead to over preening and reduced bodily condition. In severe cases of infestation, can cause mortality.	Yes	Anseriformes Charadriiformes Pelicaniformes Phaethontiformes Sphenisciformes Suliformes	Worldwide Temperate and polar zones: hard ticks (most colonies, except the Canadian high Arctic and continental Antarctica) Tropical and temperate zones: soft ticks	(Dietrich et al., 2011; Muñoz-Leal and González-Acuña, 2015)

Mites	Species from six feather mite families (Astigmata): Alloptidae, Avenzoariidae, Dermationidae, Epidermoptidae, Xolalgidae and Freyanidae. One skin mite (Epidermoptidae; <i>Myialges caulotoon</i>)	No known impact	No known impact	No known impact	Unknown	Anseriformes Charadriiformes Gaviiformes Pelecaniiformes Procellariiformes	Worldwide	(Proctor, 2003; Stefan et al., 2015; Whiteman et al., 2006)
Fleas	Arthropoda, Insecta, (Siphonaptera) <i>Ceratophyllus vagabundus</i> , <i>C. garei</i> , <i>Parapsyllus spp</i> , <i>Mioctenopsylla arctica arctica</i> , <i>Xenopsylla gratioiosa</i>	Hyperinfestation of adults can cause inconsistent incubation of the egg and positively correlated with blood cover on eggs.	Vector for poxviruses. Can cause irritation.	Vector for poxviruses. Can cause irritation.	Unknown	Anseriformes Charadriiformes Procellariiformes Sphenisciformes Suliformes	Precise distributions unknown	(Coulson et al., 2009; Kane et al., 2012; Kristjansson et al. 2016)
Lice	Insecta: Phthiraptera Both groups of chewing lice known on seabirds (Amblycera & Ischnocera)	No known impact	No known impact	No known impact	Unknown	Anseriformes Charadriiformes Pelecaniformes Procellariiformes Sphenisciformes Suliformes	Worldwide	(Clay and Morby 1967; Clayton et al., 2015; Daunt et al. 2001; Rivera-Parra et al., 2014)

Flies	Hippoboscidae (Olfersia and Ornithomyiinae s)	No known impact	Vector for haemosporidia.	Vector for haemosporidia.	Unknown	Charadriiformes Pelecaniformes Procellariiformes Suliformes	Temperate and tropical zones	(Bastien et al., 2014; Bequaert 1953; Levin and Parker, 2013; Whiteman et al., 2006)
Mosquitoes	(Diptera; Culicidae) Aedes taeniorhynchus Aedes aegypti	Hyperinfestation of adults can cause inconsistent incubation of the egg.	Vector for alpha and flaviviruses (e.g, West Nile Virus). Can cause irritation due to parasitism. Can cause reduced parental care due to irritation. Can cause mortality due to parasitism.	Vector for alpha and flaviviruses (e.g, West Nile Virus). Can cause irritation due to parasitism. Can cause mortality due to parasitism.	Unknown	Charadriiformes Pelecaniformes Procellariiformes Suliformes	Worldwide	(Anderson and Fortner 1988; Gubler 2010; Gaston and Elliott, 2013; Rocke et al. 2005)
Helminths	Cestoda, Trematoda, Nematoda, Acanthocephalans**	No known impact	No known impact	Can cause modification of digestive enzymes (Alcidae, Laridae). Can alter behavioural interactions. Can reduce overall body condition.	Unknown	Charadriiformes Suliformes	Northern hemisphere	(Granroth-Wilding et al., 2016, 2015; Kuklina and Kuklin, 2012; Kuklin, 2013; Provencher et al., 2017)

Avipoxviruses	CNPV, canarypox virus FWPV, fowlpox virus	No known impact	Warty nodules that can cause scarring and discomfort. Can lead to secondary bacterial or fungal infections, which can cause mortality.	Warty nodules that can cause scarring and discomfort. Can lead to secondary bacterial or fungal infections, which can cause mortality.	Unknown	Anseriformes Charadriiformes Phaethontiformes Procellariiformes Sphenisciformes	Argentina, South-Western Indian Ocean	(Friend and Franson 1999, p. 163-169; Kane et al. 2012 ; Schoombie et al. 2018)
Flaviviruses	West Nile virus Gadget's gully virus Tyuleniy virus Saumarez Reef virus Meaban virus Precarious point virus SAZ virus	Unknown	Unknown	Unknown in wild birds; mortality caused in experimentally infected birds, and virus isolated postmortem	Unknown	Charadriiformes Pelicaniformes Sphenisciformes	Worldwide	(Gaunt et al. 2001; Mackenzie and Williams 2009; Morgan et al. 1985)
Other Arboviruses	Nuggets virus Sakhalin virus Taggerts virus	Unknown	Unknown	Unknown	Unknown	Charadriiformes Sphenisciformes	Precise distributions unknown	(Chastel et al. 1987; Doherty et al. 1972; L'Vov et al. 1972)
Avian Influenza	H13, H16 subtypes (seabird associated viruses) and other low pathogenic viruses. Also cases of infection by highly pathogenic	Unknown	H5 and H7 Subtypes can cause cloudy eyes, ruffled feathers, overall weakness, reduced coordination, torticollis. In rare cases can also lead to	H5 and H7 Subtypes can cause cloudy eyes, ruffled feathers, overall weakness, reduced coordination, torticollis. In rare cases can also lead to death.	Unknown	Charadriiformes Procellariiformes Sphenisciformes	Worldwide for low pathogenic viruses. Precise distributions for highly pathogenic viruses unknown	(Arnal et al. 2014; Lang et al. 2016)

	viruses (H5 and H7 subtypes)		death.					
Avian Cholera	Pasteurella multocida	Unknown	Can cause mortality within 6 to 48 hours depending on bird sex, age, previous exposure, nutritional status, concurrent infection, and strain virulence and dosage.	Can cause mortality within 6 to 48 hours depending on bird sex, age, previous exposure, nutritional status, concurrent infection, and strain virulence and dosage.	Yes	Anseriformes Charadriiformes Pelicaniformes Phaethontiformes Sphenisciformes Suliformes	Worldwide	(Cooper et al. 2009; Descamps et al. 2012; Waller and Underhill 2007)
Lyme Disease	Borrelia burgdorferi s.l.	Can lead to higher levels of antibodies to <i>B. burgdorferi</i> in eggs, if parent a host for <i>B. burgdorferi</i> .	Unknown	Unknown	Unlikely given very high exposure rates in juvenile and adult birds	Charadriiformes Procellariiformes Sphenisciformes	High latitudes in northern and southern hemispheres	(Dunea et al. 2008; Gasparini et al. 2001; Lobato et al. 2012; Olsen et al. 1993, 1995)
Avian Botulism	Type C botulinum toxin from Clostridium botulinum bacteria	Unknown	Lack of coordination and weakness. Severe flaccid paralysis of legs and wings. Dehydration and lack of appetite. Mortality.	Lack of coordination and weakness. Severe flaccid paralysis of legs and wings. Dehydration and lack of appetite. Mortality.	Yes	Anseriformes Charadriiformes Pelicaniformes	Worldwide	(Friend and Franson 1999, p. 271-281; Neimanis et al. 2007)
Chlamydioses	Chlamydophilia psittaci Chlamydophilia abortus	Unknown	Often inapparent. Can cause mortality.	Often inapparent. Can cause mortality.	Unknown	Charadriiformes Procellariiformes Suliformes	Pacific Ocean, North Atlantic Ocean, South Atlantic Ocean	(Hermann et al. 2000, 2006; Padilla et al. 2004)

Haemosporidia	<i>Babesia</i> spp. <i>Haemoproteus</i> spp. <i>Leucocytozoon</i> spp. <i>Plasmodium relictum</i>	Unknown	Can cause mortality	Can cause mortality	Unknown	Charadriiformes Procellariiformes Sphenisciformes Suliformes	North Pacific Ocean, South Atlantic and South Pacific Ocean	(Earle, 1992; Padilla et al. 2004; Parsons et al. 2017; Vanstreels et al. 2017; Yabsley et al. 2009)
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6 FIGURES

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9 Figure 1: Ticks (*Ixodes uriae*) on a black kittiwake chick in northern Norway. Photograph by T.

10 Boulinier.

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13 Figure 2: The soft tick *Ornithodoros maritimus* (Argasidae) in the nest of a yellow-legged gull

14 (*Larus michahellis*) in Mediterranean. Photograph by K.D. McCoy.

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18 Figure 3: Acanthocephalans (*Profiliculus* sp.) removed from the intestinal section of a single

19 Common Eider Duck (*Somateria mollissima*) from Arctic Canada. Photograph by J. Provencher.

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23 Figure 4: Female Common Eider (*Somateria mollissima*) carcasses found on a colony after
24 cholera outbreak during the breeding season in northern Hudson Bay, Nunavut. Photograph by
25 G. Gilchrist.

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29 Figure 5: Faecal matter on thick-billed murrelets (*Uria lomvia*) nesting below others at a seabird

30 colony on Coats Island, Nunavut where tens of thousands of the birds nest on vertical cliffs

31 above the ocean. Photograph by J. Provencher.

32