The role of seabirds of the Iles Eparses as reservoirs and disseminators of parasites and pathogens

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Abstract

The role of birds as reservoirs and disseminators of parasites and pathogens has received much attention over the past several years due their high vagility. Seabirds are particularly interesting hosts in this respect. In addition to incredible long-distance movements during migration, foraging and prospecting, these birds are long-lived, site faithful and breed in dense aggregations in specific colony locations. These different characteristics can favor both the local maintenance and large-scale transmission of parasites and pathogens. The Iles Eparses provide breeding and feeding grounds for a large portion of seabird biodiversity, with over 3 million breeding pairs of at least 13 species. Breeding colonies on these islands are relatively undisturbed by human activities and represent natural metapopulations in which seabird population dynamics, movement and dispersal can be studied in relation to that of circulating parasites and pathogens. In this review, we summarize previous knowledge and recently-acquired data on the parasites and pathogens found in association with seabirds of the Iles Eparses. These studies have revealed the presence of a rich diversity of infectious agents (viruses, bacteria and parasites) carried by the birds and/or their local ectoparasites (ticks and louse flies). Many of these agents are widespread and found in other ecosystems confirming a role for seabirds in their large scale dissemination and maintenance. The heterogeneous distribution of parasites and infectious agents among islands and seabird species suggest that relatively independent metacommunities of interacting species may exist within the western Indian Ocean. In this context, we discuss how the patterns and determinants of seabird movements may alter parasite and pathogen circulation. We conclude by outlining key aspects for future research given the baseline data now available and current concerns in eco-epidemiology and biodiversity conservation.

Keywords: Avian ecology, Dispersal, Emergence, Infectious agents, Insular ecosystems, Metapopulation dynamics

Introduction

The role of birds as reservoirs and disseminators of parasites and pathogens has received increasing attention over the past several years, as bird migratory movements have been directly implicated in disease emergence (Altizer et al., 2013; Fuller et al., 2012). The most famous example of this is the global circulation of avian influenza A viruses which travel with their bird reservoirs during spring and fall migrations (e.g., Olsen et al., 2006). The increasing occurrence of Lyme disease in North-eastern USA and Canada has also been associated with bird movements; passerine birds naturally carry (infected) ticks north during spring migration, and when combined with increasingly mild winters, these vectors and their associated pathogens are now able to establish and maintain high local population sizes (Ogden et al., 2008a; Ogden et al., 2008b). Indeed, birds often move over large distances, both during seasonal migrations between breeding and over-wintering grounds, and during pre-breeding and post-breeding periods. In many species, such movements occur between areas where individuals aggregate in high densities and where parasite transmission can be facilitated by high contact rates and repeated use (Altizer et al., 2011). In order to understand the epidemiology of avian–associated pathogens and predict disease emergence, it is therefore necessary to understand how these different behaviors and population attributes alter the probability of pathogen maintenance and dispersal. Studying bird-parasite interactions can also provide essential, basic information for understanding the fundamental processes involved in the ecology and evolution of host-parasite interactions.

In this paper, we assess the role of seabirds in the natural circulation of parasites and pathogens in the Iles Eparses, an insular ecosystem of the south-western Indian Ocean that is home to a high diversity of marine birds. We start by discussing why seabirds are excellent model systems for study host-parasite interactions and how they may be involved in disease emergence processes. We then outline the diversity of parasites and pathogens found in association with these birds in the Iles Eparses, summarizing data from the literature and adding some original data. These studies cover most major pathogen groups along with several types of ectoparasites and have involved detailed sampling, morphological typing, molecular screening (both specific and non-specific) and serological analyses. We then discuss what we know about the patterns and determinants of seabird movements in this region and how these movements may affect parasite and pathogen circulation. We finish by outlining some predictions on disease emergence based on current knowledge and suggest key aspects to focus on for future research.

Seabirds as ideal hosts of parasites and pathogens

Marine birds, or seabirds, comprise a vast diversity of species and include members of at least six avian orders (Sphenisciformes, Procellariiformes, Pelecaniformes, Suliformes, Phaethontiformes and Charadriiformes) that all share the characteristic of feeding at sea. These birds are particularly interesting to study in relation to their role as reservoirs and disseminators of parasites and pathogens. First and foremost, the greatest majority of seabirds are colonial breeders, meaning that they aggregate in large numbers for several months per year in order to reproduce. The location of breeding colonies tends to be stable over long periods of time and birds typically return to the same colony (and sometimes to the exact same nest site) year after year to breed (Furness and Monaghan, 1987). The high density of individuals within colonies maximizes infection risk and their predictable seasonal occurrence makes these vertebrates ideal hosts for parasites (Rothschild and Clay, 1961). In addition to being colonial breeders, seabirds are also long-lived hosts. Although reproduction is frequently delayed until a bird is 3 to 6 years old, once reaching maturity, these birds will typically attempt to breed for 20-30 years (Furness and Monaghan, 1987). Given this incredible longevity, chronic infections of non-lethal parasites can be maintained and transmitted over very long periods of time. In the case of temporary ectoparasites, such as fleas, ticks, or flies, the parasite only has to wait for the return of the birds in order to feed. Indeed, large populations of nest-dwelling ectoparasites can build up over time until reproductive success becomes so low that birds abandon the colony (e.g., Danchin, 1992; Duffy, 1983). Seabirds are also the record holders for the greatest long-distance migrations, with the extreme example being the Arctic tern that flies from 60,000 to 81,000km during its yearly migration between its breeding grounds in the north and its overwinter areas at sea in the south (Egevang et al., 2010). Although many seabirds are faithful to their breeding site year after year (breeding site fidelity) and generally return to their natal colony to breed (natal philopatry), these individuals may wander over incredible distances to forage, and notably during the non-breeding periods of their life cycle.

Past descriptions of seabird parasites and pathogens have suggested a wide array of infecting organisms may be associated with these birds. For example, pelagic birds such as common and Brunnich's guillemots (*Uria aalge* and *U. lomvia*) and large gulls (*Larus argentatus*, *L. marinus*) can harbor a rich diversity of avian influenza viruses (Dusek et al., 2014; Huang et al., 2014). Other studies have demonstrated that coronavirus and paramyxovirus infections may also regularly occur in species of Charadriiforme birds (gulls, terns, shorebirds) (Coffee et al., 2010; Mackenzie et al., 1984; Muradrasoli et al., 2010). Apicomplexan parasites have likewise been occasionally recorded in these hosts (Peirce, 2000; Yabsley et al., 2009). A review by Dietrich et al. (2011) outlined that seabirds are parasitized by at least 29 different tick species across the globe and that 60 viruses or variants from approximately eight serogroups have been identified from these arthropods, most of unknown pathogenicity. Diverse bacterial agents are also harbored by ticks, the most important from a human perspective being those of the Lyme disease complex *Borrelia burgdorferi* sensu lato (Duneau et al., 2008), relapsing fever *Borrelia* (Takano et al., 2009) and various *Rickettsia* and *Coxiella* spp. (Kawabata et al., 2006; Reeves et al., 2006).

Seabirds in the Iles Eparses

A high density of seabirds occurs in the western Indian Ocean (WIO), with approximately 31 species and 7.4 million breeding pairs (Le Corre et al., 2012). The main breeding grounds for these birds include the Seychelles, the Mascarene Islands and a particularly abundant (~3 million pairs) and diverse assemblage in the Mozambique Channel (Figure 1). The Iles Eparses, with four permanently emerged coralline islands, provide breeding and feeding grounds for a large portion of this biodiversity. Within this area, diverse seabird species overlap both within colonies (multispecific breeding areas) and in foraging areas at sea (Le Corre et al., 2012). Indeed, Europa alone boasts eight seabird species and more than a million breeding pairs, with some of the last major colonies offrigatebirds, boobies and tropicbirds in the region (Le Corre et al., 2012). Major populations of the sooty tern

(*Onychoprion fuscatus*) breed on Juan de Nova, Les Glorieuses, and Europa; the largest colony in the Indian Ocean occurs on Juan de Nova with approx. 2 million breeding pairs and a very high nest density (5.2 nests/m^2; Le Corre and Jaquemet, 2005). Table 1 outlines the main seabird species present on these islands and their approximate population sizes.

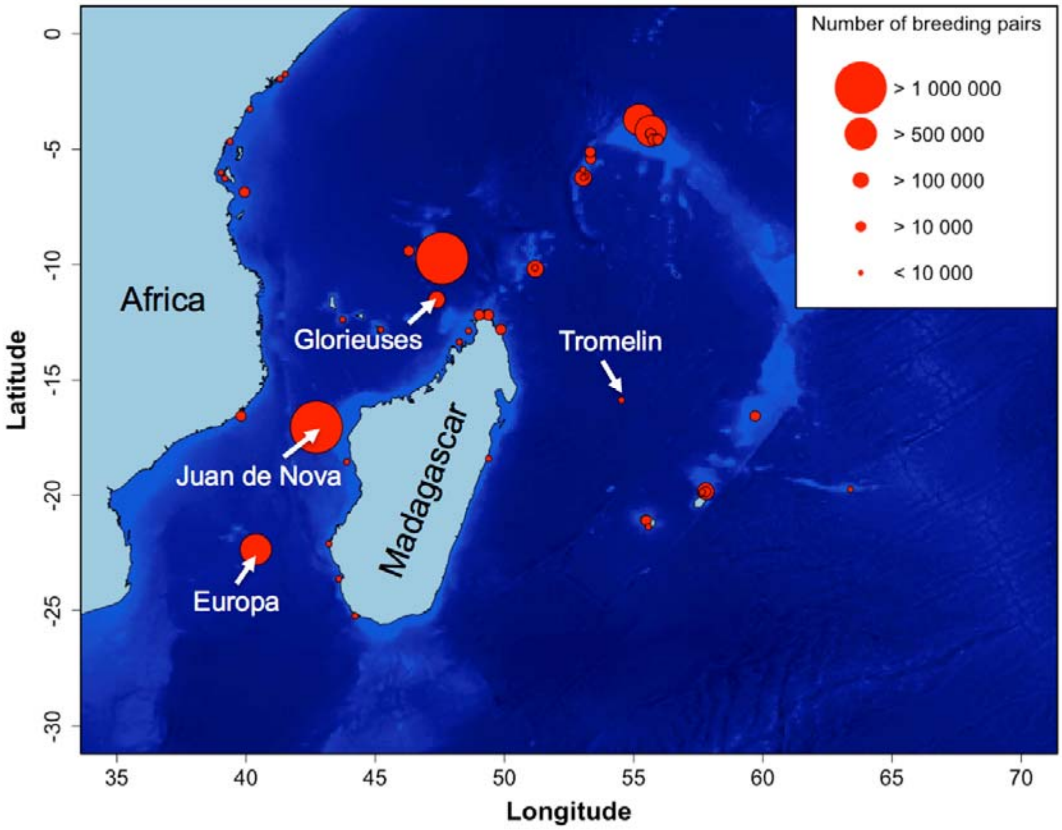


Figure 1: Density of breeding seabirds in the western Indian Ocean, showing the locations of the four emerged islands of the Iles Eparses. Modified from Le Corre et al., 2012.

Table 1: Number of breeding pairs (bp) of each seabird species found on the Iles Eparses. The approximate island size is indicated in brackets. The number of breeding pairs on Europa, Juan de Nova and Les Glorieuses is based on data from Le Corre and Jaquemet (2005). Data for Tromelin are from Le Corre et al. (2015).

	Europa ($28km^2$)	**Juan de Nova** ($5km^2$)	**Les Glorieuses** ($7km^2$)	**Tromelin** ($1km^2$)
Red-footed booby *Sula sula*	3000bp	-	-	855bp
Masked booby *Sula dactylatra*	-	-	-	1090 bp
Brown booby *Sula leucogaster*	-	-	-	1bp
Red-tailed tropicbird *Phaethon rubricauda*	3500bp	-	-	-
White-tailed tropicbird *Phaethon lepturus*	1000bp	-	-	-
Lesser frigatebird *Fregata ariel*	1200bp	-	-	Night roosting only
Great frigatebird *Fregata minor*	1100bp	-	-	Night roosting only
Sooty tern *Onychoprion fuscatus*	760,000bp	2,000,000bp	270,000bp	-
Roseate tern *Sterna dougalli*	-	-	-	Roosting
Brown noddy *Anous stolidus*	-	-	300bp	Night roosting only
Lesser noddy *Anous tenuirostris*	-	-	-	Night roosting only
Greater crested tern *Thalasseus bergii*	-	250bp	-	-
White tern *Gygis alba*	-	-	-	3bp
Caspian tern *Hydroprogne caspia*	10bp	-	-	-
Audubon's shearwater *Puffinus lherminieri*	50bp	-	-	-

In addition to being biodiversity hotspots, the Iles Eparses are relatively wild compared to other tropical island systems. Although this area cannot be called pristine because of traces left by previous human inhabitants (i.e., introduced plants and mammals; Le Corre et al., 2015; Ringler et al., 2015), the only permanent human presence on the islands is temporary military and reserve personnel (and occasionally biologists) which effectively limit poaching and other human activities that may disturb breeding. This aspect is particularly important, as human activities can reduce nesting success, colony persistence (e.g., Beale and Monaghan, 2004) and modify ecosystem functioning (McCauley et al., 2012). The Iles Eparses are also interesting from the perspective of their geographic position. As mentioned above, these islands are nestled within a major zone of seabird biodiversity, and potentially function as part of regional metapopulations for several species. They also lie at the intersection of transoceanic migratory routes between Europe, Africa, Asia, Oceania, and the Subantarctic islands (Boere et al., 2006; Le Corre and Probst, 1997). Because of their use as terrestrial resting zones, these islands may represent key sites of parasite exchange between ecosystems and notably with mainland Africa and Madagascar (Tortosa et al., 2012). The Iles Eparses therefore provide an ideal setting to evaluate the natural presence of different types of parasites and pathogens, their impact on seabird population dynamics, and their links with terrestrial ecosystems.

Parasites and pathogens associated with seabirds in the Iles Eparses

As outlined above, few studies have focused on seabird parasites and pathogens, and even fewer in the region of the Iles Eparses. In this section, we outline the different types of parasitic organisms that are known to occur in the seabirds of this region. This information is based on recently published studies and some original work from our group, along with historical records from the literature.

General sampling procedures

In the Iles Eparses, most work on the detection of infectious agents has been performed on biological material collected relatively recently from seabirds on three of the four emergent islands: Europa, Juan de Nova, and Tromelin (Figure 1). Blood, as well as cloacal and oropharyngeal swabs, have been collected from seven seabird species (Table 1): great frigatebird (*Fregata minor*), lesser frigatebird (*F. ariel*), masked booby (*Sula dactylatra*), red-footed booby (*S. sula*), sooty tern (*Onychoprion fuscatus*), red-tailed tropicbird (*Phaethon rubricauda*), and white-tailed tropicbird (*P. lepturus*). Sampling procedures and sample preservation were conducted as described in Bastien et al. (2014), Lebarbenchon et al. (2013), Lebarbenchon et al. (2015) and Jaeger et al. (2015). Surveys for ectoparasites associated with seabirds were performed in parallel, either while handling the birds, or by searching the nest substrate and surrounding area. Although we are aware that the general approach used cannot detect all parasites present, notably gut endoparasites, it has provided baseline data for future quantification of infestation levels.

Ectoparasites

Two dominant ectoparasites were detected on the birds of the Iles Eparses: the soft tick *Ornithodoros (Carios) capensis* sensu stricto (Argasidae) and the hard tick *Amblyomma loculosum* (Ixodidae) (Figure 2). Seabirds are commonly parasitized by ticks throughout the world (Dietrich et al., 2011) and these nest-dwelling parasites are known to reduce individual reproductive success and, in extreme infestations, to cause colony desertion (e.g., Converse et al., 1975; Duffy and Deduffy, 1986; King et al., 1977; Monticelli and Ramos, 2012; Monticelli et al., 2008; Ramos et al., 2001). In the Iles Eparses, *O. capensis* was recorded on all three islands surveyed (Table 2) and could be found within seabird nests or in the surrounding habitats (e.g., under tree bark or driftwood), when not directly collected on the host. Interestingly, these ticks were not found in association with all available hosts and seabird species-tick associations varied among islands. For example, *O. capensis* was frequent on boobies on Tromelin (30% of birds infested, n = 149 birds), but absent from these hosts on Europa. On Juan de Nova, infestation rates of sooty terns was 39% (n = 260 birds)y, with tick infestation increasing after hatching; chicks were more frequently infested (68%, n = 100 nests) than adult birds (18%, n=160; $^{\chi}2 = 67.38$, df = 1, $p < 0.0001$) and adults with chicks had a higher prevalence of infestation (54%, n = 52) than incubating adults (<1%, n=101; $^{\chi}2 = 62.43$, df = 1, $p < 0.0001$). These data suggest that chicks are the preferred hosts of this tick. However, it should be noted that adult and nymphal stages of this tick feed rapidly (10-60 mins) and may use adult birds at night. Larval stages, which feed the longest among the different life stages (1-2 days), are also more difficult to detect on adult birds, so our survey estimates should be considered with caution. *O. capensis* is known to occur on other islands of the WIO (Dietrich et al., 2011), and is part of a circum-tropical species complex specialized on colonial seabirds. However, the exact global distribution of each species of this complex is unclear at present and requires detailed sampling and morphological/genetic analyses (Gómez-Díaz et al., 2012).

Amblyomma loculosum, a hard tick with a large host spectrum (Figure 2), was only recorded on Tromelin in the Iles Eparses (Table 2). On this island, 149 individuals of masked and red-footed boobies were searched) and a global tick infestation rate of 6% was found. Unlike *O. capensis*, *A. loculosum* is highly mobile, shows aggressive host seeking behavior (Feare and Gill, 1997) and is thus easily found in the host environment when present. The apparent absence of *A. loculosum* from Europa and Juan de Nova (Table 2) is surprising and could be explained by inter-island differences in seabird species communities or in habitat characteristics, each island being quite distinct in terms of size and vegetation (Table 1, Hivert et al, this issue). As *A. loculosum* is known to be widespread in seabird colonies throughout the WIO and beyond (Dietrich et al., 2011; 2014; Feare, 1976; Hoogstraal et al., 1976), the environmental factors linked to its presence and absence in different colonies would be interesting to explore to better understand the factors limiting its colonization success.

Other ectoparasites were also present on the Iles Eparses. In particular, hippoboscid (or louse) flies were frequently found on seabirds. These insects are common obligate ectoparasites on mammals and birds, with only the pupal stage found off-host. Flies were found infesting great frigatebirds on Europa and red-footed and masked boobies on Tromelin, but were absent from red-footed boobies on Europa (Table 2; Bastien et al., 2014). Genetic analyses performed on the flies suggested that those from great frigatebirds were closely related to *Olfersia spinifera,* whereas flies collected on the two booby species of

Tromelin were genetically related to *O. aenescens* (Bastien et al., 2014). *Olfersia spinifer*a and *O. aenescens* have been observed on the Galapagos, infesting frigatebirds and boobies, respectively, and the limited genetic differences found with flies of the Iles Eparses support the presumed high host specificity and dispersal potential of these ectoparasites (Dittmar et al., 2006; Levin and Parker, 2012b, 2013). Feather mites were also found associated with red-tailed tropicbirds on Europa (Table 2), but their role as true parasites is unclear (Walter and Proctor, 2013). No fleas or lice were recorded on the birds, but sampling did not specifically target these ectoparasites. Although large populations of mosquitoes are present on certain islands (Bagny et al., 2009) and likely play a role in the pathogen transmission, mosquitoes are not considered as parasitic organisms *per se* and were therefore not sampled in our surveys. Indeed, mosquitoes likely feed on nesting birds, but the frequency and impact of these bloodmeals are unknown (see for instance Anderson and Fortner, 1988).

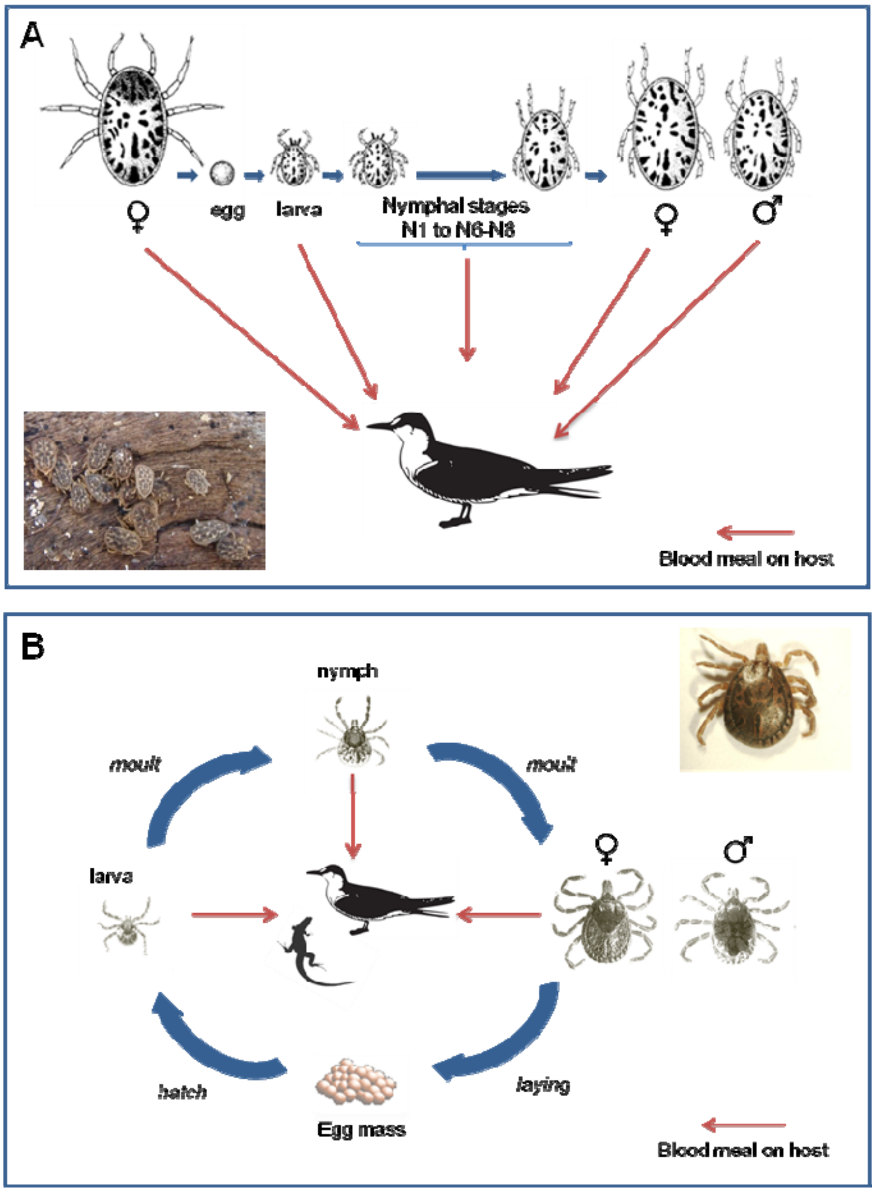
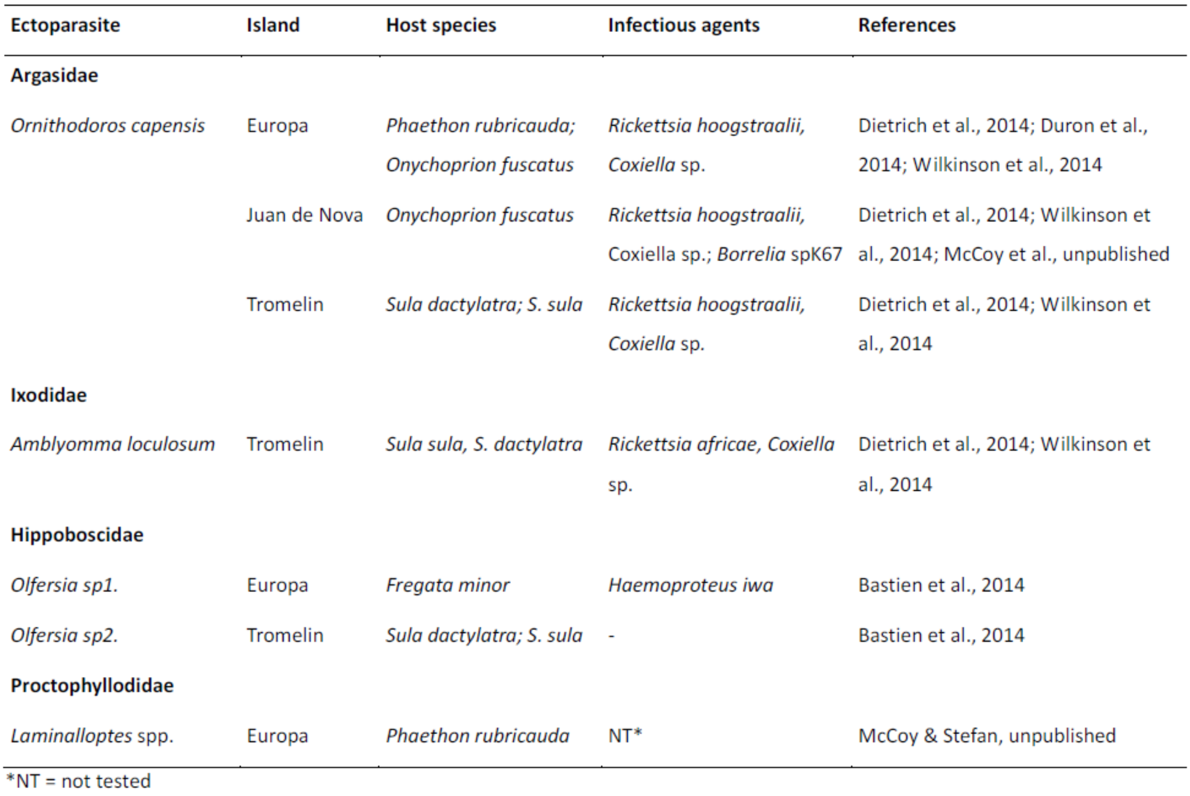


Figure 2: Ticks exploiting colonial seabirds of the Iles Eparses A) the soft tick *Ornithodoros (Carios) capensis* (Family Argasidae) and its basic life cycle. Each active life stage will take several short bloodmeals (10 minutes to 24 hours long), with larval bloodmeals being longer than nymphal and adult meals. The average number of bloodmeals per life stage and the number of nymphal stages is unknown under field conditions, B) the hard tick *Amblyomma loculosum* (Family Ixodidae) and its typical life cycle; there is only a single instar and a single long bloodmeal (3 to 10 days) in each life stage. Under optimal conditions, *A. loculosum* can complete its entire life cycle within 5 months (Hoogstraal et al., 1976), but in order to coincide with the availability of its avian hosts, it likely takes a full year (Feare and Gill, 1997). Drawings of the soft tick are modified from Mehlhorn and Armstrong (2001). Photos: *O. capensis* from wood debris on Juan de Nova by K.D. McCoy; male of *A. loculosum* by M. Dietrich.

Table 2: Ectoparasites, host species and associated vector-borne infectious agents (bacteria and parasites) in the Iles Eparses.



Ectoparasite	Island	Host species	Infectious agents	References
Argasidae				
Ornithodoros capensis	Europa	*Phaethon rubricauda; Onychoprion fuscatus*	*Rickettsia hoogstraalii, Coxiella* sp.	Dietrich et al., 2014; Duron et al., 2014; Wilkinson et al., 2014
	Juan de Nova	*Onychoprion fuscatus*	*Rickettsia hoogstraalii,* Coxiella sp.; *Borrelia* spK67	Dietrich et al., 2014; Wilkinson et al., 2014; McCoy et al., unpublished
	Tromelin	*Sula dactylatra; S. sula*	*Rickettsia hoogstraalii, Coxiella* sp.	Dietrich et al., 2014; Wilkinson et al., 2014
Ixodidae				
Amblyomma loculosum	Tromelin	*Sula sula, S. dactylatra*	*Rickettsia africae, Coxiella* sp.	Dietrich et al., 2014; Wilkinson et al., 2014
Hippoboscidae				
Olfersia sp1.	Europa	*Fregata minor*	*Haemoproteus iwa*	Bastien et al., 2014
Olfersia sp2.	Tromelin	*Sula dactylatra; S. sula*	-	Bastien et al., 2014
Proctophyllodidae				
Laminalloptes spp.	Europa	*Phaethon rubricauda*	NT*	McCoy & Stefan, unpublished

*NT = not tested

Viruses

Wild birds are known to play a central role in the epidemiology of vector-borne flaviviruses such as West-Nile and Usutu viruses (Komar et al., 2003; Vazquez et al., 2011), representing the main amplifying hosts and acting as long distance vectors through their migrations. Other flaviviruses, such as the Meaban virus, a virus transmitted by *Ornithodoros* spp. ticks, have also been widely reported in seabirds (Arnal et al., 2014a; Chastel et al., 1985). We therefore investigated the circulation of these flaviviruses in seabird populations of the Iles Eparses. Direct screening of bird blood for the presence of flaviviruses was conducted using the universal real-time PCR method of Moureau et al. (2007); these analyses did not yield positive results (Table 3), suggesting that either birds were not infected at the time of sampling or that viremia was below the detection threshold (Jaegar et al., 2015). However, results from serology showed an alternative picture; Jaeger et al. (2015) carried out ELISA assays to detect anti-flavivirus antibodies on 855 plasma samples collected from both breeding adults and chicks of nine seabird species distributed across seven islands of the WIO. On Europa, only two of more than 250 birds and five species were seropositive and both of these individuals were adult great frigatebirds. Seroprevalence was higher in sooty terns on Juan de Nova (8.2%) and was highest on Tromelin in masked (42.3%) and red-footed (17.5%) boobies. Sero-neutralisation analyses suggested that the birds had been exposed to the three expected viruses: West Nile, Usutu and Meaban viruses (Jaeger et al., 2015). In particular, two great frigatebirds from Europa carried antibodies against West Nile virus or a closely related flavivirus; as low seroprevalence was measured in adults and no juveniles were carrying antibodies at the time of sampling, birds may have been infected during the non-breeding part of their life cycle. In contrast, Usutu viral antibodies were detected in seabirds of Tromelin and Juan de Nova, both in chicks and adult birds, suggesting that this virus may be endemic to these colonies (Table 3). Only a single adult sooty tern of Juan de Nova was seropositive for the Meaban virus and more sampling will therefore be required to infer possible infection pathways. As these flaviviruses are all vector-borne, the role of blood-feeding arthropods (ticks and mosquitoes) as vectors and reservoirs of these viruses needs to be explored. A phylogenetic study of these viruses is also called for in order to assess their circulation at different spatial scales within the WIO and their potential pathogenicity. As mentioned above, the maintenance of dense populations of several mosquito species on some of the Iles Eparses, in particular on Europa, could favor the circulation of mosquito-borne viruses. Wild birds are recognized as major hosts of alphaviruses, and particularly Sindbis virus, and one could therefore expect such viruses to circulate in seabird communities. Although our preliminary attempt to detect alphaviruses in bird blood with generic nested PCR assays has been unsuccessful (Table 3), we cannot yet exclude a role for seabirds in alphavirus epidemiology. Serology-based methodologies (Lundstrom et al., 2001) could reveal whether seabirds of the Iles Eparses are involved in epidemiological cycles of alphaviruses. Molecular detection and virus isolation in mosquitoes and other types of ectoparasites should also be developed (Brown et al., 2012; Jost et al., 2010).

Wild birds are also reservoirs of numerous directly-transmitted viruses. During the past decade, influenza A virus emergence has been extensively studied, particularly in ducks and seabirds (Olsen et al., 2006). Although seabirds are natural hosts for influenza viruses (Stallknecht and Shane, 1988) the epidemiological position that these hosts occupy in relation to wild ducks, domestic birds and humans has not been assessed (Arnal et al., 2014b). In the Iles Eparses, direct detection by PCR of viral RNA in cloacal swabs did not yield positive results (Lebarbenchon et al., 2013; 2015). However, a more recent investigation that focused on serology-based approaches has shown that terns likely play a significant role in the epidemiology of influenza viruses in the WIO (Lebarbenchon et al., 2015). On Europa and Juan de Nova, the prevalence of sooty terns with influenza virus nucleoprotein antibodies was 1.15% and 10.7%, respectively (Table 3), suggesting significant inter-colony differences in virus circulation. Analyses of the hemagglutinin subtype-specific antibodies indicate that these birds were mainly infected with the H16 virus subtype, a gull-associated subtype (Fouchier et al., 2005). However, H9 subtype-specific antibodies were also found in birds sampled on Juan de Nova and suggest that terns may be in contact with a large diversity of viral subtypes, including viruses usually infecting wild ducks and poultry and thus may represent a potential threat to human and domestic animal health (Lebarbenchon et al., 2015).

Like influenza viruses, avian coronaviruses and paramyxoviruses have been identified in a large diversity of wild bird species, including seabirds (Coffee et al., 2010; Muradrasoli et al., 2010). Current knowledge on the ecology and epidemiology of these viruses is very limited compared to avian influenza (Fuller et al., 2012), but previous studies have demonstrated that their co-circulation regularly occurs and involves complex interactions (Wille et al., 2015). The co-circulation of avian influenza viruses, coronaviruses and paramyxoviruses was investigated in the Iles Eparses using broad target PCR methods, but yielded negative results (Lebarbenchon et al., 2013). This finding may result from (i) the low number of samples tested, (ii) a lack of PCR specificity, (iii) a strong temporal pattern in virus shedding and epidemics that limits detection, or iv) a surprising absence of these viruses in the region.

Bacteria

A high diversity of bacteria is found in avian species. Bacteria of the Pasteurellaceae family are particularly pathogenic for wild birds. *Pasteurella multocida*, the agent of the avian cholera, is a highly contagious disease that can cause significant mortality (Hubalek, 2004). This microorganism has been found in seabirds and is considered responsible for significant population declines in endangered species, such as the Yellow-nosed albatross *Diomedea chlororhynchos* on Amsterdam Island (Weimerskirch, 2004). This pathogen has also been suggested to modify population dynamics and lead to local population extinctions in more abundant species (e.g., the common eider duck; Descamps et al., 2012). In the Iles Eparses, we tested 448 individuals of five species from Europa and Tromelin for the presence of *P. multocida* by PCR amplification following the method of Townsend et al. (1998); none of the bird samples tested positive (Table 3). Furthermore, no mass mortality events have been reported during more than 20 expeditions (45 days each) conducted since 1995 by members of our research consortium, suggesting that *P. multocida* does not circulate in the Eparse colonies.

Ticks are reservoirs and vectors of numerous bacteria of major medical and veterinary importance and can prove useful for screening for host pathogens. Via a meta-genomic approach using universal bacterial primers to amplify a hyper-variable portion of the 16s rRNA gene, we quantified the presence and abundance of bacteria present in ticks sampled from different seabird species on the Iles Eparses (Figure 3). Gammaproteobactera and alphaproteobacteria were identified as two of the most prominent bacterial classes present in both *O. capensis* and *A. loculosum* , and corresponded primarily to *Rickettsia* and *Coxiella* genera, respectively (Wilkinson et al., 2014). Targeted PCR analyses of individual tick extracts showed that both bacteria were at high prevalence in seabird ticks of the Eparses colonies. *Coxiella* bacteria were found to infect almost all *O. capensis* ticks tested (98-100% prevalence) and a slightly lower number of *A. loculosum* (64%) (Table 2). Distinct lineages were associated with each tick species (Wilkinson et al., 2014) and multi-locus analyses have shown them to be closely related to *Coxiella burnetii*, the agent responsible for Q fever, a common infectious disease of humans and domestic animals (Duron et al., 2014). Indeed, *Coxiella* bacteria are found widely in soft ticks of seabirds and, given their prevalence and diversity, are likely tick endosymbionts with vertical transmission (Duron et al., 2015; Wilkinson et al., 2014). *Rickettsia* prevalence was particularly high in *A. loculosum* (93%, n =

14 ticks), but varied among islands for *O. capensis* ($\chi2 = 27.50$, df = 2, $p < 0.0001$), ranging from 16% (n = 43 ticks) on Juan de Nova to 74% (n = 42 ticks) on Europa (Dietrich et al. 2014). Genetic analyses also showed strong host specificity between tick species and different *Rickettsia* lineages. Indeed, *A. loculosum* on Tromelin was infected with *Rickettsia africae*, the agent of African tick-bite fever (Eldin et al., 2011), whereas *O. capensis* harbored lineages related to *R. hoogstraalii*, an infectious agent of unknown pathogenicity (Table 2).

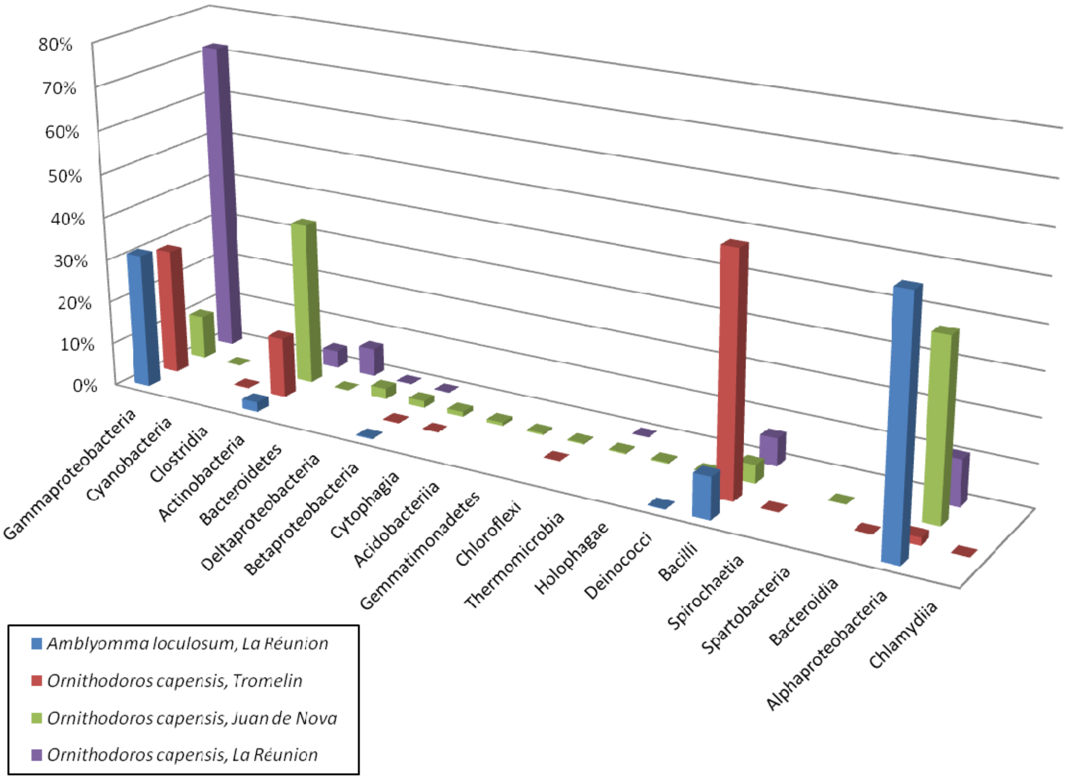


Figure 3: Bacterial diversity in ticks of the western Indian Ocean. Bars represent the percentage of sequences obtained via 16S 454 pyrosequencing that could be classified into each bacterial class. Data adapted from Wilkinson et al. (2014).

The metagenome approach also revealed trace quantities (13 of 24,797 reads) of *Borrelia* spp. in *O. capensis* from Tromelin (Figure 3) (Wilkinson et al., 2014); as mentioned previously, bacteria of this genus are responsible for Lyme disease and relapsing fever in humans. A targeted PCR approach of the conserved *FlaB* gene also identified a positive *O. capensis* tick sampled in the sooty tern colony of Juan de Nova (McCoy et al. unpublished).

Sequence analysis of this isolate suggests that it is very closely related to *Borrelia* sp. K67, a bacterium of the relapsing fever group previously isolated from a seabird tick in Japan, *Ornithodoros sawaii*, and known to be pathogenic for humans (Takano et al., 2009). This same strain seems to be present in penguins of South Africa (Yabsley et al., 2012) and occurs in relatively high prevalence in certain seabird colonies of the North Atlantic Ocean (McCoy et al. unpublished), highlighting the ability of seabirds to spread infectious agents at broad spatial scales.

Parasites

Recent studies have shown that seabirds can be infected with common avian blood parasites of the apicomplexan sub-genera *Haemoproteus* and *Parahaemoproteus* (genus *Haemoproteus*), with prevalence varying among species and geographic locations (Quillfeldt et al., 2011). An investigation of blood parasite infections in seabirds inhabiting Europa and Tromelin was therefore performed using established PCR protocols for the detection of parasites of the *Haemoproteus*, *Plasmodium* and *Leucocytozoon* genera (Hellgren et al., 2004). No evidence of infection with *Leucocytozoon* was found in the tested birds (Table 3). In contrast, 35% of tested frigatebirds were positive for *Haemoproteus* at the time of sampling; this infection was not found in other bird species sampled at the same location and time of the year (Bastien, 2013; Bastien et al., 2014; Table 3). Genetic analyses showed that the detected parasite was closely related to *Haemoproteus iwa*, previously found in frigatebirds of the Pacific and Caribbean Sea (Bastien et al., 2014; Levin and Parker, 2012b; Levin et al., 2011; Merino et al., 2012) and transmitted by hippoboscid flies of the genera *Olfersia* (see above). Only a single fly collected from a frigatebird of Europa was found positive for *H. iwa*, whereas no positive flies were found on boobies of Tromelin, and this despite high infestation levels. These results suggest a wide geographic distribution of *Haemoproteus iwa* among frigatebird breeding sites and demonstrate how specificity in the vector may constraint parasite infection dynamics. Finally, a single infection of *Plasmodium* spp. in a single great frigatebird of Europa was found. Sequencing showed this parasite to be genetically related to a widespread avian *Plasmodium* species with low apparent specificity (herons, penguins, kites) (Bastien et al., 2014). Its transmission on Europa is likely favored by the maintenance of dense populations of several mosquito species on this island (Bagny et al., 2009) that may act as non-specific vectors.

Table 3. Infectious agents in seabirds of the Iles Eparses.

Infectious agent	Island	Hosts	N tested samples (N PCR-positive)	N tested samples (N ELISA-positive)	Reference
Bacteria					
Pasteurella multocida	Europa	Great frigatebird, Red-footed booby, Red-tailed tropicbird, Sooty tern, White-tailed tropicbird	417 (0)	NT	Bastien, 2013
	Tromelin	Red-footed booby	31 (0)	NT	Bastien, 2013
Viruses					
Alphavirus	Europa	Red-footed booby, Red-tailed tropicbird, White-tailed tropicbird	36(0)	NT	Lebarbenchon et al., 2013
Coronavirus	Europa	Great frigatebird, Red-footed booby, Red-tailed tropicbird, White-tailed tropicbird	142 (0)	NT	Lebarbenchon et al., 2013
	Tromelin	Red-footed booby	31 (0)	NT	Lebarbenchon et al., 2013
Flavivirus	Europa	Great frigatebird, Red-footed booby, Red-tailed tropicbird, Sooty tern, White-tailed tropicbird	48 (0)	247 (2[1])	Jaeger et al., 2015
	Juan de Nova	Sooty tern	146(0)	146 (12[2])	Jaeger et al., 2015
	Tromelin	Masked booby, Red-footed booby	115 (0)	115 (33[3])	Jaeger et al., 2015
Influenza A virus	Europa	Great frigatebird, Red-footed booby, Red-tailed tropicbird, Sooty tern, White-tailed tropicbird	418 (0)	457 (5)	Lebarbenchon et al., 2013; 2015
	Juan de Nova	Sooty tern	126 (0)	234 (25)	Lebarbenchon et al., 2015
	Tromelin	Masked booby, Red-footed booby	31 (0)	43 (1)	Lebarbenchon et al., 2013; 2015
Paramyxovirus	Europa	Great frigatebird, Red-footed booby, Red-tailed tropicbird, White-tailed tropicbird	142 (0)	NT	Lebarbenchon et al., 2013
	Tromelin	Red-footed booby	31 (0)	NT	Lebarbenchon et al., 2013
Blood parasites					
Haemoproteus	Europa	Great frigatebird, Red-footed booby, Red-tailed tropicbird, White-tailed tropicbird	153 (17[4])	NT	Bastien, 2013; Bastien et al., 2014
	Tromelin	Masked booby, Red-footed booby	131 (0)	NT	Bastien et al., 2014
Leucocytozoon	Europa	Great frigatebird, Red-footed booby, Red-tailed tropicbird, White-tailed tropicbird	123 (0)	NT	Bastien, 2013
Plasmodium	Europa	Great frigatebird, Red-footed booby, Red-tailed tropicbird, White-tailed tropicbird	153 (1)	NT	Bastien, 2013; Bastien et al., 2014
	Tromelin	Masked booby, Red-footed booby	131 (0)	NT	Bastien et al., 2014

[1] West-Nile virus-specific antibodies were detected in the two positive samples. [2] Usutu virus or Meaban virus-specific antibodies were detected in some of the positive samples. [3] Meaban virus-specific antibodies were detected in some of the positive samples. [4] Parasite species identified as *Haemoproteus iwa*.

Circulation of parasites and pathogens among islands

Seabird movements

To estimate the probability of pathogen dissemination at different spatial scales, it is necessary to possess a clear understanding of seabird movement patterns and seabird behaviors during both breeding and non-breeding periods. Traditionally, information on seabird movement came from ringing data (Furness and Monaghan, 1987). Of course, this type of study requires a monumental effort to ring and recapture birds and, when individuals disappear from the population, it is often difficult to identify the cause (i.e., death or emigration to an unknown location). With the advent of molecular tools and novel tracking devices, more information has become available on the uniqueness of different seabird colonies and the tendency for these colonies to exchange migrants (e.g., Friesen et al., 2007; Ponchon et al., 2013).

Although seabirds are able to disperse at global scales, many genetic studies have shown strong population genetic structure among colonies, and notably in the absence of physical barriers (Friesen et al., 2007). Data in the Iles Eparses are limited to date, but previous studies suggest that the populations of this region may be distinct (Le Corre, 1999; Le Corre and Jouventin, 1999). For example, the population of white-tailed tropicbird from Europa was found to be strongly differentiated from other populations of the Indo-Pacific region and from those of the Atlantic Ocean, both morphologically and genetically (Le Corre and Jouventin, 1999; Humeau et al., unpublished). This structure cannot be explained by dispersal distance *per se*, and is probably linked to a combination of founder effects and natal philopatry leading to strong genetic drift (Humeau et al. unpublished). These results fall in line with observations of tropical seabird species from other areas of the globe. Indeed, significant structure at regional scales has been demonstrated for both masked (Steeves et al., 2005) and brown boobies (*S. leucogaster*) (Morris-Pocock et al., 2011; Morris-Pocock et al., 2010). Nasca boobies (*S. granti*) are likewise strongly structured among islands within the Galapagos Archipelago, with no relationship to the geographic distance among colonies (Levin and Parker, 2012a). However, despite significant population structure in mitochondrial DNA at a global scale in red-footed boobies, structure at regional scales seems to be weaker than in related species, suggesting some gene flow, or secondary contact among previously isolated populations (Morris-Pocock et al., 2010). Migration patterns in frigatebirds tend to differ from these other species and these populations are expected to be less structured. Indeed, frigatebirds are known to move over large distances to forage and rely on terrestrial stop-over sites to rest. A early resighting study of great frigatebirds in the central Pacific found that birds moved regularly within a 600km radius of their colony of origin, and that adult birds could be seen at colonies more than 850km apart (Dearborn et al., 2003). In this study, one bird was even resighted more than 7600 km from where it was marked. Genetic studies using microsatellite and mitochondrial markers have confirmed that high gene flow occurs among colonies of great frigatebirds at the within-archipelago scale (Levin and Parker, 2012a) and large scale dispersal has been inferred for populations of the magnificient frigatebird (*F. magnificens*); although colonies from the Galapagos Islands were distinct, all other populations showed little to no structure, even between ocean basins (Hailer et al., 2011).

Although genetic information is helpful for delineating the limits of seabird populations and can provide information on the relative frequency of exchanges and the distance at which they occur, it is also limited in the sense that we can only evaluate effective dispersal, that is, when a bird has changed colonies and successfully reproduced. There is no genetic signal left for unsuccessful dispersal events. When considering parasite and pathogen transmission probabilities, these unsuccessful events may be as important as successful ones, or even more so if infected individuals have a higher tendency to disperse (see below). Genetic data also does not provide us with information about what birds do during non-breeding periods (post or pre-breeding periods), nor on the timing of their movements. Both of these aspects are essential. Indeed, in order for transmission to occur, an uninfected bird must either come into direct contact with an infected bird, encounter the infective stage in the environment, or be bitten by an infected vector. Fortunately, knowledge on seabird movements at sea and the frequency of occasional visits to other breeding colonies has increased greatly over the last decade as new technologies to track birds at different spatial scales have become available (Ponchon et al., 2013).

Much effort has been made to track birds within the WIO in order to identify general movement patterns and key foraging areas (Le Corre et al., 2012). Since 2003, regional tracking programs have focused on 10 seabird species from 12 different populations using GPS (Global positioning systems) and Argos satellite transmitters for short-term studies (see for instance Kappes et al., 2011; Pinet et al., 2012; Weimerskirch et al., 2005; Weimerskirch et al., 2004; Weimerskirch et al., 2006), and GLS (Global Location Sensors, or geolocators) for year round tracking (see Le Corre et al., 2012 and reference therein, for details on the use of each system for each bird species). A review of these tracking data show that boobies tend to remain within 200km of their breeding colonies (Kappes et al., 2011; Weimerskirch et al., 2005), whereas all other species (great frigatebirds, wedgetailed shearwaters, Barau's petrel, red-tailed and white-tailed tropicbirds) tend to move much greater distances during the breeding season (Le Corre et al., 2012; Pinet et al., 2011; Weimerskirch et al., 2004). In the non-breeding period, red-tailed and white-tailed tropicbirds, great and lesser frigatebirds, wedgetailed shearwaters, sooty terns and Barau's petrels move into the eastern Indian Ocean where they forage at sea (Le Corre et al., 2012). No information is currently available on the post-breeding movements of red-footed and masked boobies of Europa and Tromelin. Because of the need to recover tracking devices, we also lack information on movements of juvenile birds and failed breeders, movements that are of significant importance for breeding site selection and can represent a major period of parasite and pathogen dispersal (Danchin, 1992; Gómez-Díaz et al., 2012; McCoy et al., 2003; Ponchon et al., 2013). Tracking information on seabirds outside the WIO is also lacking, and in particular, along eastern Africa and the northern and central Indian Ocean; information on potential dispersal from these colonies will be necessary in order to make clear predictions on the probability of pathogen emergence within the WIO.

Circulation of ectoparasites and associated pathogens

Complimentary information on seabird dispersal, behavior and population structure can be obtained indirectly by studying the population genetic structure of the parasites and pathogens associated with these birds. Indeed, if the parasite/pathogen is specific to a seabird species, and these hosts represent the only means by which it can be transmitted among colonies, data on their spatial genetic structure will provide information on the role of the host in this process (McCoy et al., 2005; Nieberding and Olivieri, 2007). In the case of nest-dwelling ectoparasites like ticks, a bird must be physically present in the colony in order to be infested by local ectoparasites or to leave an ectoparasite in a location where it is likely to encounter a new host. In temperate-polar regions, for instance, differences in dispersal have been found for ticks associated with seabird species with contrasting within-colony behaviors; gregarious interactions among Atlantic puffins (*Fratercula arctica*) when they visit novel colonies is thought to favor higher dispersal success of *Ixodes uriae* ticks than the more isolated behavior of black-legged kittiwakes (*Rissa tridactyla*), resulting in much stronger inter-colony structure in kittiwake ticks (McCoy et al., 2003). Interestingly, the structure found in kittiwake ticks is in direct contrast with a lack of population structure in this seabird across very wide geographic scales (McCoy et al., 2005); data from the parasite therefore reveal the limits to seabird movement. In the cases of permanent ectoparasites, only direct contact between conspecifics is required for transmission; this can occur either within the colony or during interactions at sea. For example, Gomez-Diaz et al. (2007) found a surprising lack of structure among lice infesting three distinct taxa of Cory's and Cape Verde shearwaters (*Calonectris diomedea diomedea*, *C. d. borealis*, and *C. edwardsii*); lice are typically considered to be very host specific and highly structured (Johnson et al., 2002). As population structure among bird taxa is strong, Gomez-Diaz et al. (2007) hypothesized that the lack of structure in lice could be due to frequent contact among birds during the over-winter period at sea, contacts that favor parasite exchange. Similarly, Levin and Parker (2013) found that population structure in hippoboscid flies tended to be lower than that of their hosts within the Galapagos Archipelago and suggest that this may be linked to among-colony movements of birds during the pre-breeding period. These same type of movements, for which we have almost no data (see above), have also been evoked to explain the surprising mix of *Ornithodoros* tick lineages found within seabird colonies of the Cape Verde Islands (Gómez-Díaz et al., 2012).

The probability of host movement and parasite/pathogen dispersal may depend on the impact of the parasites on the birds themselves. In some cases, a parasite may reduce breeding success and, as an indirect consequence, favor dispersal because failed birds have a higher tendency to prospect new colony locations than successfully breeding birds (Boulinier and Danchin, 1996; Boulinier et al., 2008). In other cases, bird movement may be reduced because of the debilitating effects of a pathogen, limiting its transmission to distant locations (e.g., Descamps et al., 2012). Even the direct movement of the vectors can be affected by their infection status. For example, a recent study by Levin and Parker (2014) demonstrated that the probability of louse flies switching among frigatebird hosts depended on their infection status with *Haemoproteus iwa*; infected flies tended to switch birds less often than uninfected flies, reducing parasite transmission. In contrast, other systems have shown that ectoparasite feeding may be prolonged by an infecting pathogen to increase transmission to the host (van Houte et al., 2013). This type of modification may, in turn, increase the probability of ectoparasite dispersal to distant locations.

II. **Conclusions and Perspectives**

Our review of currently available data has shown that a broad diversity of parasites and pathogens circulate among seabirds in the Iles Eparses. Several of these are widespread in birds, their ectoparasites and in neighboring ecosystems (influenza A, relapsing fever *Borrelia*, *Rickettsia africae*, *Haemoproteus iwa*). The accumulation of knowledge from seabird mark-recapture studies, population genetic analyses and more recent tracking data show that different seabird species are likely to have different propensities to disseminate infectious agents depending on the frequency and distance of their individual movements, but also on their behaviors with conspecifics within colonies and at sea. For example, based on current data, two types of post-breeding movement patterns in seabirds of the Iles Eparses can be discriminated in terms of their probably to disseminate parasites and pathogens: species that carry-out frequent stop-overs on different islands of the region, and notably the two frigatebird species, and species that remain pelagic and only come to land for breeding or by accident, such as red-tailed tropicbirds and sooty terns. Based on this division, we can predict that species such as frigatebirds should disperse parasites and pathogens more readily than strictly pelagic species such as tropicbirds or sooty terns. Directly-transmitted parasites and pathogens should mix at greater spatial scales when their hosts share over-wintering foraging areas, whereas more localized species, such as boobies should be more strongly isolated, particularly when found in monospecific colonies. These hypotheses now require specific testing.

Despite the insight gained by recently-acquired data, work is yet required to fully understand how these systems function under natural conditions and within a metapopulation framework. Such data can provide a more global understanding of the ecology and evolution seabird-parasite interactions and enable informed predictions to be made on the risk of disease emergence. With this goal in mind, we outline below some key aspects to focus on for future research in the region of the Iles Eparses.

Future research directions

- More detailed tracking information is required during the pre-breeding period, when young birds may travel to distant colonies to prospect for future breeding and foraging grounds. This aspect will be particularly challenging as most GPS/GLS tracking systems are temporary and require the bird to be recaptured. Young birds have much higher mortality rates than adult birds and may remain far away from their natal colony for several years.

- Little information is also currently available on detailed movement patterns of smaller seabirds such as sooty terns, a major proportion of the seabird biodiversity of the Iles Eparses. This has been due largely to a lack of precise tracking methods (i.e., GPS) for smaller-bodied birds; the miniaturization of loggers should enable more data to be collected in the near future.

- A more complete inventory of ectoparasites (including fleas, lice, as well as ticks and flies) using standardized sampling and with detailed morphological and molecular characterization is required. This type of data will enable comparative studies of ectoparasite prevalence and abundance on the different seabird species and islands and can be linked with seabird and pathogen dynamics within colonies.

- Screening studies of infectious agents, both in seabirds and in possible vector organisms, need to be completed. This is particularly the case for those agents whose presence is strongly suspected in the WIO based on previous work (e.g., avian coronavirus in seabirds; Muradrasoli et al., 2010) or whose presence was revealed in initial studies (e.g., *Borrelia* spp. in *O. capensis* ticks). Likewise, determining the role of different ectoparasites as potential vectors of the infectious agents found is the next step for understanding their circulation (e.g., testing flaviviruses in *O. capensis* ticks in Juan de Nova and Tromelin). Temporal sampling for serological screening is an ideal way to determine where and how seabirds are exposed to the infectious agents.

- Although, in this article, we emphasize the potential importance of parasites and pathogens of seabirds for human and livestock health, an evaluation of their impact on seabird reproduction success and dispersal is also called for. Indeed, few studies have focused on this question, particularly for infectious bacterial and viral agents. Their impact may need to be considered in light of disease emergence in other ecosystems, but also for the conservation of these key species in the Iles Eparses.

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