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Original article

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 to 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 dissemination of parasites and pathogens. The Iles Eparses provide breeding and feeding grounds for more than 3 million breeding pairs of seabirds including 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 suggests 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.

1. 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. When combined with increasingly mild winters, these repeated dispersal events have enabled the tick vectors and their associated pathogens

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to establish at higher latitudes (Ogden et al., 2008a, 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 studying 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, 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.

1.1. Seabirds as 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 (breeding site fidelity; Furness and Monaghan, 1987). The high density of individuals within colonies and their predictable seasonal occurrence make these vertebrates good 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 3–6 years old, once reaching maturity, these birds will typically attempt to breed for 20–30 years (Furness and Monaghan, 1987). Given this longevity, chronic infections of non-lethal parasites may be maintained and transmitted over very long periods of time (e.g., *Borrelia* spp. bacteria; Gylfe et al., 2000). In the case of temporary ectoparasites, such as fleas, ticks, or flies, the parasite has to be able to survive in the nest area when birds are absent and will feed again when the birds return to breed. If successful, 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 long-distance movements, with the extreme example being the Arctic tern that flies from 60,000 to 81,000 km during its yearly migration (Egevang et al., 2010). Indeed, although seabirds show high colony fidelity for reproduction, individuals may wander over vast distances to forage and prospect for future breeding sites, and notably during the non-breeding periods of their life cycle. These movements can favor parasite and pathogen dissemination at very large spatial scales.

Past descriptions of seabird parasites and pathogens have suggested that 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 *Uria lomvia*) and large gulls (*Larus argentatus*, *Larus 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).

1.2. 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 (Fig. 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 of frigatebirds, 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 seabird species present on these islands and their approximate population sizes.

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 limits poaching and other human activities that may disturb breeding (e.g., Beale and Monaghan, 2004). 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