Migration, prospecting, dispersal? What host movement matters for infectious agent circulation?

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Synopsis

Spatial disease ecology is emerging as a new field that requires the integration of complementary approaches to address how the distribution and movements of hosts and parasites may condition the dynamics of their interactions. In this context, migration, the seasonal movement of animals to different zones of their distribution, is assumed to play a key role in the broad scale circulation of parasites and pathogens. Nevertheless, migration is not the only type of host movement that can influence the spatial ecology, evolution and epidemiology of infectious diseases. Dispersal, the movement of individuals between the location where they were born or bred to a location where they breed, has attracted attention as another important type of movement for the spatial dynamics of infectious diseases. Host dispersal has notably been identified as a key factor for the evolution of host-parasite interactions as it implies gene flow among local host populations and thus can alter patterns of coevolution with infectious agents across spatial scales. However, not all movements between host populations lead to dispersal *per se*. One type of host movement that has been neglected, but that may also play a role in parasite spread is prospecting, i.e. movements targeted at selecting and securing new habitat for future breeding. Prospecting movements, which have been studied in detail in certain social species, could result in the

dispersal of infectious agents among different host populations without necessarily involving host dispersal. In this paper, we outline how these various types of host movements might influence the circulation of infectious disease agents and discuss methodological approaches that could be used to assess their importance. We specifically focus on examples from work on colonial seabirds, ticks and tick-borne infectious agents. These are convenient biological models because they are strongly spatially structured and involve relatively simple communities of interacting species. Overall, this review emphasizes that explicit consideration of the behavioral and population ecology of hosts and parasites is required to disentangle the relative roles of different types of movement for the spread of infectious diseases.

Introduction

Although migration, the seasonal movement of animals to different areas of their distribution, is assumed to play a key role in the broad scale circulation of parasites and pathogens (Altizer et al. 2011; Bauer & Hoye 2014), other types of host movements may also come into play in determining eco-epidemiological patterns across spatial scales. In the context of increasing interest for integrative approaches to infectious disease biology (Daszak et al. 2000; Cleaveland et al. 2014), spatial disease ecology builds on a vast array of approaches to address how the distribution and movements of hosts and parasites may condition the dynamics of their interactions within ecosystems (Hess et al. 2002; Holt & Boulinier 2005). The long-standing interest in the roles of host dispersal and spatially structured contact networks in the dynamics of epidemics and the persistence of infectious agents within host communities has led to the development of diverse statistical approaches (Diggle 2000; Keeling et al. 2004; Craft et al. 2009; Fenner et al. 2011), including the analysis

of dispersal gradients and the spatial spread of parasites via travelling waves (Bjørnstad et al. 2002; Mundt et al. 2009). However, the role of different types of host movement in the spreading of diseases remains understudied (Boulinier et al. 2001; Perkins et al. 2009; Plowright et al. 2011, Blackwood et al. 2013). Strong heterogeneity in individual movement patterns can contribute considerably to heterogeneity in the transmission of infectious agents at different scales (Lloyd-Smith et al. 2005; McCallum et al. 2007). With the recent development of the field of movement ecology (Nathan et al. 2008; Morales et al. 2010; Fieberg et al. 2010; Jeltsch et al. 2013), the question of the potential role of non-migratory host movements for disease spread can increasingly include ecological and evolutionary dimensions. Movement ecology has notably stressed that key features in the movements of individuals can be linked to the life histories of the species considered and the landscapes in which they have evolved (Johnston et al. 1992; Boulinier et al. 2008; Morales et al. 2010), and that these features may have critical implications for the dynamics and evolution of subdivided populations (Pulliam 1988; Clobert et al. 2001; Bowler & Benton 2005; Hanski & Gagiotti 2004).

In this manuscript, after reviewing the importance of the spatial dimension of parasite circulation, we outline which type of host movements may especially matter for the dispersal and spread of infectious agents. We then focus on the relatively neglected case of prospecting movements, i.e. visits to breeding patches where an individual is not currently breeding, illustrating insights that have been gained on this topic through the study of seabird-parasites systems. After briefly reviewing other systems in which non-migratory movements may require particular attention, we outline timely research perspectives, potential study designs and available tools to examine questions related to the impact of these alternative types of movement. Here, we exclude human-mediated movements, which

are also well known to lead to the transmission of infectious agents or their vectors over long distances (Cunningham 1996; Adams & Kapan 2009; Stoddard et al. 2009).

Why does the spatial dimension of host-parasite interactions matter?

The spatial dimension is important for the epidemiology, ecology and evolution of the interactions between infectious agents and their hosts. From an eco-epidemiological standpoint, the continental spread of West Nile Virus (Rappole et al. 2000) and *Mycoplasma gallisepticum* (Hochachka & Dhondt 2000) in susceptible bird populations, the northward expansion of Lyme disease in eastern North America (Leighton et al. 2012) or the rapid spread of Phocine Distemper Virus along European coastal areas (Harding et al. 2002) represent examples stressing the need to determine the factors contributing to the spatial dynamics of infectious agents. In the context of climate change, habitat quality can also change and new environments may become available for reservoir hosts, vectors and their parasites. Because of individual differences in exposure and susceptibility, the circulation and local persistence of infectious agents within and among host populations will depend on variation in individual movements and behaviors, as outlined by modeling approaches (Keeling & Rohani 2007; Polowright et al. 2011). Finally, because of effects they will have on host-parasite gene flow, the relative dispersal rates of hosts and parasites in spatially structured populations will also affect the coevolution of populations (Thompson 2005, Louhi et al 2010, Mazé-Guilmo et al. 2016). These epidemiological, ecological and evolutionary processes may all be at play when infectious agents can infect several host species; in that case, the spatial context of the interactions is also very likely to be important

to consider, notably when reservoir species are to be identified and potential management decisions to be taken (Viana et al. 2014).

What types of host movement are important for the spread of infectious disease agents?

Migration

Migratory movements have been clearly identified as being important for the spread of infectious agents over broad spatial scales (Altizer et al. 2011, Bauer & Hoye 2014). This is notable because of the large geographic scale they often encompass and the fact that they can contribute to the contact among individuals from various populations at remotely located stop-over and/or wintering sites (Figure 1). Migration often occurs between high latitude areas, where reproduction takes place in the summer, and wintering areas at latitudes closer to the equator, although seasonal migratory movements may take various other forms (Dingle 2014). Migratory movements often involve large numbers of individuals that gather in high densities at sites where the transmission of infectious agents can occur between infected and susceptible individuals. Migration has thus been identified as a key process in the spread of both directly and environmentally transmitted agents (e.g. avian influenza viruses: Olsen et al. 2006; Gilbert et al. 2006, Hill et al. 2012), and vector-borne agents (e.g. tick-transmitted Lyme disease bacteria, Leighton et al. 2012; or mosquito-transmitted blood parasites, Fuller et al. 2012). Geographic and temporal characteristics of movements are important to consider in this context because the course of infection may simultaneously affect the likelihood of transmission and the ability of sick individuals to move long distances (Gaidet et al. 2014). The physiological stress associated with migration

may also affect host susceptibility, and thus, potentially, disease transmission (Dingle 2014). The fact that a disease involves migratory birds is nevertheless not sufficient in itself to assume that migratory behavior *per se* is the factor responsible for the spread of the infectious agent. Considering where and when transmission is likely to occur in relation to other types of movements and events may also be important (Figure 1).

Foraging

Foraging movements can affect the spatial spread of many infectious agents if they are food-borne agents, trophically-transmitted parasites, or directly transmissible when individuals compete for a focal food resource (Figure 1). Although foraging movements usually occur at relatively much smaller scales than migratory movements, this is not always the case. Like many other seabirds, Scopoli's shearwaters (*Calonectris borealis*) can forage several hundred kilometers from their colony; this is only a slightly smaller spatial scale than that of their winter migration (Péron & Gremillet 2013). Although such distances are impressive, it is unlikely that this mode of foraging will lead to the broad circulation of parasites and infectious agents because the birds do not necessarily interact closely with conspecifics when they forage. Conversely, in some cases, small scale foraging movements could indirectly result in the spread of some agents to another species that, in turn, spreads them on a broader scale. For example, scavenging or predatory birds, such as skuas, may connect host prey populations (Figure 2A) and transfer an infectious agent that may then have a dramatic effect on the dynamics of the prey species and/or spread over long distances via migration.

Dispersal

Dispersal is defined as the movement of individuals between a location where they were born or bred to a new location where they breed (Clobert et al. 2001; Ronce, 2007; Figure 1). Dispersal has attracted attention as another important type of movement for the spatial dynamics of infectious diseases, although empirical work in wild populations has lagged behind theory, possibly because many factors may affect dispersal (Boulinier et al. 2001; Blackwood et al. 2013). In addition to its contribution to understanding the dynamics of host-parasite interactions within metapopulations, where the dispersal of an infected host can lead to inter-patch colonization (Hess et al. 2002; Bjørnstad et al. 2004), host dispersal has been identified as a key factor in the evolution of host-parasite interactions as it implies gene flow among local host populations, which alters local standing genetic diversity and, thus, coevolution with infectious agents (Gandon et al. 1996; Gandon & Michalakis 2002; Thompson 2005). It has been suggested that the relative dispersal rates of hosts and parasites among local populations directly affect local adaptation of the host to the parasites and *vice versa* (Gandon et al. 1996, Lion and Gandon, 2015). But not all movements between host populations lead to dispersal *per se*; an overlooked detail when making generalizations about the dynamics of parasite circulation in subdivided populations (McCoy et al. 2005a; Mazé-Guilmo et al. 2016). For example, some exploratory movements, like prospecting, may not lead to the dispersal of a host individual, but may contribute to the large scale dispersal of a parasite among host populations.

Prospecting

Prospecting movements are defined as visits made by individuals to locations where they are not currently breeding, but where they may settle in the future to reproduce (Reed et al.

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1999; Figure 1). Described for many bird species (Reed et al. 1999), these types of forays outside the birth location or main current breeding site of an individual are usually reported in a context of breeding habitat selection, in which such visits may allow individuals to gather information on the suitability of potential future breeding sites and to initiate access to these sites. Prospecting movements made by individuals before they first breed are reported to occur at much larger scales than prospecting forays made by adult birds that failed their breeding attempt (Reed et al. 1999), although the sometime much more nomadic movements of pre-breeders, especially in very young age classes of long-lived species, are especially difficult to track. Attendance at breeding areas by prospecting individuals usually occurs late in the breeding season in colonially breeding bird species; at that time, individuals are possibly preparing their local recruitment in the next season (Reed et al. 1999, Boulinier et al. 1996). Prospectors often land, walk, enter nesting burrows or land on nests or chicks (in birds) or directly interact with conspecifics (in birds and mammals), although it is often difficult to infer where the prospecting individuals came from. Prospecting forays have also been reported in other taxa, such as in social mammals, in which they are associated with attempts by individuals to seek mating opportunities outside their social group (Young et al. 2005, 2007). In an epidemiological context, these movements have been neglected because they are often secretive and difficult to track, also because they can be brief and involve young and/or unmarked individuals coming from outside a study area. They may however be especially important for the circulation of infectious agents because, as opposed to most dispersal events, they occur within a single breeding season and can involve intimate contact between individuals with very different exposure histories, favoring pathogen exchange.

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Transmission mode of infectious agents and the role of host movement in their dispersal

The transmission mode of infectious agents will determine the potential implications of host movement for their dispersal and transmission. Directly transmitted agents, and in particular sexually transmitted diseases, will require direct contact between susceptible and infectious hosts which can occur at any time, during any type of movement. When environmental transmission is required (for instance, for food-borne infectious agents), transmission chains require individuals to visit specific sites (Roche & Rohani 2009). While these agents may be less likely to be transferred by certain large scale movements, their shedding along a migratory pathway or during visits with another social group could lead to a successful transmission event. The spread of environmentally transmitted infections may also be favored by scavengers or predators whose foraging grounds can be very large and encompass different sub-populations of infected and susceptible hosts (Figure 2A). Their role may be reinforced by the year-round nature of their interactions with their prey, as opposed to the more seasonally variable contact rates that some (especially migratory) species display. Finally, vector-borne agents require the local presence of the vector for transmission to occur, but this condition is not in itself sufficient to ensure transmission, as hosts may not transmit the infectious agent to the vector during close contact, and even a very close contact, such as a bite, may not result in successful infection of a new host. In some cases, when the vector is also a parasite (e.g., ticks, fleas, lice), it can be dispersed by a vertebrate along with the infectious agent (e.g., Comstedt et al. 2006). However, the successful colonization of a new habitat by a vector requires a specific set of conditions, such as suitable environmental conditions and the long-term presence of suitable hosts. Depending

on the dispersed life stage of the vector, one may also expect very different rates of successful colonization.

The case of prospecting: insight using a highly spatially structured seabird system

Why seabirds?

The role of birds as reservoirs and disseminators of parasites and pathogens has received much attention over the past several years due their high mobility. However, the large spatial scales involved and the numerous species that share migratory flyways and breeding or wintering grounds make it difficult to disentangle the potential role of different types of movements for pathogen dissemination. 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 with a limited diversity of host species (Furness & Monaghan 1987; McCoy et al. 2016). These characteristics can favor both the local maintenance and large-scale dissemination of parasites and pathogens, but also makes them ideal model systems to assess the role of different types of movements in spreading disease agents.

Even when breeding in polar areas, seabird populations are exposed to a high diversity of parasites and infections. Here, we focus on a particular system involving *Ixodes uriae*, a tick that commonly exploits colonial seabirds in temperate and polar regions, and the different infectious agents it transmits (McCoy et al. 2005b, Dietrich et al, 2011, Dietrich et al. 2012). Indeed, this tick hosts a suite of viruses (Chastel 1988), among which are several flaviviruses,

that are extensively distributed among seabird species over a wide geographic area (Heinze et al. 2012). The tick *I. uriae* also transmits Lyme disease bacteria to seabirds in both hemispheres (Olsen et al. 1995; Gasparini et al. 2001; Gomez-Diaz et al. 2012). Local infestation levels by *I. uriae* can vary strongly among breeding cliffs (Gasparini et al. 2001) and colonies (McCoy et al. 1999) and the tick relies entirely on its seabird host for inter-colony dispersal; given that seabird breeding phenology is highly seasonal at high latitudes, and that these ticks require about a week to complete a blood meal, inter-colony dispersal of ticks can only occur via the movements made by birds within the breeding season. Indeed, most seabirds, such as the black-legged kittiwake *Rissa tridactyla*, spend the winter at sea, far from land (Figure 2B and Frederiksen et al. 2012).

Which individuals move among colonies during a breeding season should thus be paramount to the transmission of ticks and infectious agents. Young birds at fledging may frequently wander among colonies, and are often heavily infested by ticks. This was noted by Danchin (1992), who reported the occurrence of non-local fledglings parasitized by ticks in nests that were otherwise uninfested. These observations were possible due to detailed survey work of all the nests within a study colony where all the nestlings had been ringed (Danchin 1992). Another category of individuals that may visit different colonies within a breeding season are prospecting individuals that have not bred or that have failed their breeding attempt (Cadiou et al. 1994). Prospecting has been extensively studied in the kittiwake because it is relatively easy to track local movements of marked individuals that breed on vertical cliff faces and because these movements may be associated with the gathering of public information used by individuals to choose a future breeding site (Boulinier & Danchin 1997, Danchin et al. 1998, Boulinier et al. 2008). Prospecting visits occur late in the breeding season (Boulinier et al. 1996), when successful areas typically attract more individuals, potentially favoring the

dispersal of parasites among breeding groups. This type of movement could be especially important in a metapopulation context, among colonies at regional scales. However, tracking marked individuals over large areas and within colonies where thousands of birds breed cannot be easily achieved by traditional capture-mark-resighting methods.

An indirect approach to the role of prospecting

As an indirect way to explore the potential role of prospecting in the dispersal of parasites, the population genetic structure of the kittiwake and its tick *I. uriae* was investigated using a comparable set of genetic markers for each species (microsatellites; McCoy et al. 2005a). For the tick, population genetic differentiation varied over the range of scales considered; little structure among tick populations exploiting kittiwakes was found among colonies separated by up to two hundred kilometers, whereas significant structure was observed beyond this limit and increased with the geographic distance between colonies (Figure 3B). Host populations, in contrast, showed very little evidence of differentiation at a comparable scale (Figure 3A). This suggests prospecting birds move frequently enough between colonies up to 200 kilometers apart that tick populations are able to remain genetically mixed at this spatial scale. When exploring the population genetic structure of ticks sampled from other seabird species across the same scales, for example the Atlantic puffin (*Fratercula arctica*), no structure was found among tick populations isolated by more than 700 km. This might be due to differences in behavior and breeding biology among seabird species. Puffins breed in burrows on the slopes above cliffs (rather on the vertical faces of cliffs) and might be more likely to drop-off or pick-up ticks while prospecting within colonies than kittiwakes (McCoy et al. 2003). The impact of frequent, large scale movements in seabirds and their ticks can be

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seen in patterns of geographic structure in the pathogens they transmit. For example, a phylogeographic study of the most frequently occurring Lyme disease bacterium in seabirds, *Borrelia garinii*, demonstrated large-scale exchange of strains both within and across ocean basins (Gomez-Diaz et al. 2011).

In contrast to hard ticks such as *I. uriae*, soft ticks infesting seabirds, such as *Ornithodoros maritimus* infesting yellow-legged gulls (*Larus michahellis*), may move less among colonies. Indeed, stable differences in the seroprevalence of a tick-borne flavivirus have been recorded between colonies less than 100 km apart (Arnal et al. 2014). In soft ticks, nymphal and adult ticks take very brief blood meals (~10mins), typically at night when birds do not move. Because these ticks may thus rarely be dispersed, even by short movements of prospecting individuals, the study of their population genetic structure is likely to provide less information on the distance and frequency of host prospecting movements than that of hard ticks. Overall, the study of the genetic structure of vector populations and that of infectious agents is important as it allows one not only to infer dispersal rates at different scales, but also to explore whether host specialization plays a role in the circulation of infectious agents. In communities of host species with various levels of mobility, the degree of specialization of vectors could indeed potentially (and dramatically) affect the spread of infectious agents (e.g., see McCoy et al. 2003 and 2005b for the seabird-tick system).

A more direct approach to the role of prospecting

Although prospecting movements were suspected to occur over large spatial scales, the use of GPS tracking tools to record these movements was only recently proposed (Ponchon et al. 2013). GPS loggers are commonly used to track the foraging movements of breeding birds during incubation or chick rearing (e.g., Ponchon et al. 2014). However, their deployment for

studying prospecting movements has lagged, mainly because failed breeders, who are more

likely to prospect, are also more difficult to recapture, especially if they bred in an area

where local breeding success was low (Chambert et al. 2012, Ponchon et al. 2013). The

tracking of individuals that failed their breeding attempt (e.g., that lost their eggs) has

nevertheless been successful (Ponchon et al. 2015 and Figure 2C), notably using UHF-GPS

loggers that do not require the individuals to be recaptured in order to gather location data.

Evidence of repeated prospecting visits by failed breeders to colonies situated tens of

kilometers away is now accumulating, and suggests that those movements may connect

colonies in a broad social network within which parasites/pathogens may be dispersed.

The case of other (social) species

We have shown that prospecting movements may be responsible for disease spread in

seabirds, much more likely than migratory movements, which, even if they occur at much

broader scales might not necessarily lead to successful parasite dispersal given that most

seabird species overwinter at sea. But could such prospecting movements be involved in

superspreading events in other systems? Relatively little is known about prospecting in non-

social bird species (Part & Doligez 2003), but it is likely that prospecting movements by birds

may contribute to the spread of parasites between local host populations, independently of

migratory movements.

In social mammals, forays of individual meerkats (*Suricata suricatta*) among groups other

than their own have been identified as prospecting events (Young et al. 2005, 2008; Drewe

et al. 2009), and are suspected of leading to the dispersal of infectious agents such as

tuberculosis bacteria (Drewe et al. 2010). In such cases, movements appear to be related to

opportunities to mate outside the group, which if successful lead to direct contact among

individuals (Doolan & Macdonald, 1996, Drewe et al. 2010). More generally, the movements of individual mammals among social groups have been related to an increased risk of spreading diseases (Altizer et al. 2003, Craft et al. 2011). Although the spatial scale involved is much smaller than that of highly mobile and colonially breeding mammals, such as some species of bats and seals, this issue has also specific implications in relation to disease management. When the structure of social groups is disrupted, some individuals may venture further from the group, leading to increased transmission of infectious agents among groups and species. This is thought to be the case for tuberculosis bacteria among badgers (*Meles meles*). In fact, badger control efforts in the UK have been suspected to increase dispersal rates of individuals and lead to tuberculosis dissemination (Roggers et al. 1998, Vicente et al. 2007, McDonald et al. 2008). In the case of disease transmission between wild and domestic animals, the behavioral processes affecting the spatial movements of individuals may thus also be critical to consider (Miguel et al. 2013).

Research Perspectives

Pending questions

Many challenging questions remain to be addressed in the field of disease ecology (Tompkins et al. 2011) and we hope that our review emphasizes that integrating movement ecology and parasite transmission will open up new avenues of research. We have suggested that a relatively neglected type of movement, *i.e.* prospecting, may play a significant role in some instances, but its importance for the spread of disease agents in relation to other movements, notably in complex communities of hosts and parasites, remains to be determined. Even in the relatively simple cases we considered, much work is still needed to

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explore whether we can relate the movements of individuals to transmission events and eco-epidemiological dynamics. We have shown that some movements, conditioned by the experience of individuals, have the potential to spread infectious agents, but we still do not fully understand how much this depends on other plastic responses, such as the development of acquired immunity following exposure to infectious agents (Cross et al. 2005). In addition to their current involvement in reproduction, individuals may vary in their propensity to prospect, which could have direct implications for the spread of infectious agents. In particular, their individual exposure history and the timing of events affecting the quality of the environment may be critical. In this context, approaches considering the dynamic dimension of social network could be especially useful (Sih et al. 2009, Craft et al. 2011) and may prove powerful to address related community dynamic questions in heterogeneous landscapes. In addition, one may wonder how the effects of natural *versus* human-induced movements can be related to habitat selection and disease agent transmission.

Available tools

The availability of tools to explore the roles of various types of movements on the dispersal of infectious agents has increased dramatically over the last two decades. In addition to classical capture-mark-recapture/resighting approaches, miniaturized GPS loggers are widely available for use in tracking the movements of vertebrates; these enable research teams to track the movements of individuals with high spatial and temporal precision without requiring recapture (Nathan et al. 2008). This is especially useful as we have seen that roaming movements by non-breeding individuals or individuals that failed their current breeding attempt may be critical when studying transmission of some infectious agents,

even if these are not the easiest to track (Ponchon et al. 2013). The development of radio-frequency identification technology, which allows the efficient tracking of large numbers of individuals simultaneously, will likely continue to generate very useful data to infer social contact networks and enable us to better infer the contribution of different types of movements to disease dissemination (Perkins et al. 2009). Networks of antennas, set-up within breeding groups, may also inform us about the occurrence of key movements, particularly for burrow nesting species which are difficult to directly survey. In some situations, loggers recording the proximity among individuals may be especially useful. More indirect tools are also becoming increasingly available. In addition to classical population genetic approaches for host and parasite populations, the use of microbial genetics may provide useful complementary data about transmission networks (e.g. VanderWaal et al. 2014). More classical methods, such as serological studies or the use of isotope analyses, can also be powerful to address questions related to the histories of individuals in terms of exposure to a community of infectious agents and particular habitats.

Including disease ecology in movement ecology studies

To obtain the most from data gathered to answer questions about movement and disease agent circulation, carefully designed studies should be set-up and implemented in the field. Such designs should allow researchers to account for potential biases that may limit the strength of the inferences to be made. A key issue in disease ecology is, for instance, accounting for the fact that it is difficult to be certain whether an individual has been exposed or not to specific infectious agents; this can now be dealt with using relevant statistical tools in addition to powerful biomedical tools (McClintock et al. 2009). Indeed, it is not because a field sample does not lead to the positive detection of an infectious agent or

specific antibodies that the sampled individuals are not infected or have not been exposed to the agent. Hierarchical sampling designs at appropriate temporal and spatial scales are especially important in this context as they can be used to account for detectability issues across scales. Statistical approaches originally developed in the context of capture-mark-recapture analyses are now increasingly applied to eco-epidemiological situations (Cooch et al. 2012; Choquet et al. 2013), and these should prove useful in such contexts.

Another important issue is the need for replication at relevant spatial scales; this may be especially critical when we consider movements among locations at broad scales (the focal study units become the patches, not necessarily the individuals within patches). As mentioned above, the design of field studies would benefit from *a priori* conceptual work involving participants with complementary skills, notably integrating modelling, laboratory and field based approaches (Restif et al. 2012). Experimental approaches solidly grounded on detailed observational work with the study system may be especially powerful to address some specific questions. In the case of the potential importance of prospecting movements, we have seen that particular environmental and/or social conditions may favor prospecting; the manipulation of these conditions may thus provide a way to address the potential causal link between degradation of local conditions and the occurrence of prospecting movements. In cases where massive breeding failures may be due to local disease outbreaks, vaccination on some host patches could then enable one to address local epidemiological issues, along with issues related to the dispersal of the infectious agent among patches.

Conclusion

We believe that our review of the various types of movements that may be important for the superspreading of infectious agents highlights that, in addition to gathering data on migratory species as part of extensive ringing programs, the specific design and

implementation of field studies addressing original questions about the complex processes that underlie the dynamics of infectious agents in wild populations is required. Such studies must rely on integrative population approaches, and will likely be especially valuable if they are conducted in a spatially explicit context and involve, in addition to classical disease ecology methodologies, the tracking of the individual host histories across environmental conditions.

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Figure legends

Figure 1. Different types of movements may lead to superspreading events. Such movements need to be made between locations where transmission among hosts can occur, thus they often involve the movements of infected hosts towards patches containing susceptible hosts (or the reverse). The timing of movements is also critical to consider in relation to opportunities for superspreading events. Migration as well as dispersal and foraging may be responsible for key spreading events in some cases, but a largely neglected type of movement, prospecting (i.e. visits among breeding groups within a season), may be a critical type of movement for the spatial epidemiology, ecology and evolution of host-parasite interactions, notably in social species.

Figure 2. Different types of movements potentially responsible for superspreading events: (A) Foraging locations of 6 Subantarctic skuas (*Catharacta antarctica*) recorded with GPS-UHF during the breeding season 2015 on Amsterdam Island, southern Indian Ocean. Over 3 days, the tracked individuals foraged close to their breeding colony (white triangle) among several seabird colonies they are preying upon and where they may disperse infectious agents; (B) Migratory movements of Black-legged kittiwakes (*Rissa tridactyla*) breeding on Hornøya, Norway (white star) recorded with satellite transmitters for the winter 2010-2011 (solid lines, n = 5) and 2011-2012 (dashed lines, n = 3). Despite such large scale movements, these pelagic seabirds are unlikely to contribute to the spread of infectious agents because most of them remain at sea during migration and wintering; (C) Movements of 4 failed breeding Black-legged kittiwakes recorded with GPS-UHF during the breeding season 2015. They show prospecting visits to known (solid circles) or suspected (dashed circles) kittiwake

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colonies situated > 40 km away from their nesting colony, in Hornøya, Norway (white star). These often overlooked movements may significantly contribute to the spread of parasite vectors and infectious agents.

Figure 3. Exploration of the population genetic structure of a host species (A), the black-legged kittiwake (*Rissa tridactyla*), and of its tick (*Ixodes uriae*) (B) as an indirect way of inferring the spatial scale of host movements and their potential implication for the circulation of tick-borne agents. The figure shows pairwise genetic distance ($F_{ST}/1-F_{ST}$) as a function of the geographical distance between populations sampled at the scale of the North Atlantic. Both host and parasite showed significant patterns of isolation by distance, but tick populations were not structured when colonies were separated by less than approximately 200 kilometres (~log 2.3), suggesting tick dispersal occurs via the prospecting of individual hosts among colonies situated from ten to a few hundred kilometers apart (redrawn from McCoy et al. 2005a).

(A) Kittiwake

(Mantel test: P = 0.048)

(B) Tick

(Mantel test: P< 0.0001)

(Fst/1-Fst)

Log (distance)

200km