



Shared resources and disease dynamics in spatially structured populations



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ABSTRACT

Infectious agents are likely to spread among animals that live together, yet we know remarkably little about how infectious agents move among social units. Sharing of resources – such as shared waterholes during a dry season – may provide an efficient route for the transmission of infectious agents among different social groups, and thus could represent an overlooked factor in understanding disease risks in spatially structured populations. We developed a spatially explicit individual-based model to investigate a situation in which multiple individuals of a single species converge at shared resources during periods of resource scarcity (i.e., “lean seasons”). We simulated the transmission of a fecally transmitted infectious agent in a spatially explicit meta-population of 81 social groups distributed on a square lattice. Time steps in the simulation corresponded to “days,” and we simulated disease dynamics over 10 yearly cycles of normal and lean seasons. The duration of the lean season varied across 1000 independent simulation runs, as did 12 other parameters sampled from a Latin hypercube distribution. Seasonal sharing of resources had marked effects on disease dynamics, with increasing prevalence of the infectious agent as lean season duration increased (and thus, duration of resource sharing also increased). Infection patterns exhibited three phases: an initial intermediate prevalence on the normal season home range, a rapid increase in prevalence around the shared resource during the lean season, and then a rapid decline in prevalence upon returning to the normal season range. These findings suggest that seasonal migration increases disease risk when animals congregate around resources, but enables them to escape soil-borne infectious agents upon returning to their original home ranges. Thus, seasonal sharing of resources has both negative and positive effects on disease risk.

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1. Introduction

Infectious agents are ubiquitous in wild animals and can strongly impact their population dynamics. For example, 20 different species of helminths are found among feral Soay sheep on the island of St. Kilda, Scotland (Gulland, 1992), more than 80 species of macroparasites have been reported in zebras in southern Africa (Roberts et al., 2002), and nematodes drive cyclical population dynamics in grouse (Hudson et al., 1998). Importantly, many animals live in social groups, and within a group, individuals interact most commonly and directly with their group-mates while mating, grooming, and raising offspring, and indirectly when they share

shelters, sleeping sites and resources (Krause and Ruxton, 2002). In general, predicting the spread of infections among individuals within groups is likely to be relatively straightforward based on patterns of social and mating behavior, rates of interaction, and sharing of habitats and resources.

In contrast to the spread of disease within groups, movement of infections between groups will be more challenging for parasites that lack other means of movement, such as mobile vectors. Inter-group disease transmission might occur when parasites “hitch a ride” in a dispersing host individual that successfully immigrates to a new social group prior to clearing the infection. An infectious stage of the parasite might also be deposited in an area of range overlap between groups, for example, through fecal contamination in overlap zones. Between-group transmission might also occur through overlap at food sites (Walsh et al., 2007), at sleeping or resting sites, or during aggressive social contacts during inter-group territorial encounters (Nunn and Altizer, 2006). In addition,

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a “bridge” or reservoir host species may move a generalist parasite between two groups of another species, for example if the bridge species has a larger home range that overlaps the ranges of individuals from another species, or when multiple species converge on a single resource. Finally, it is reasonable to expect that seasonal variation in any of these behaviors will influence disease dynamics over time and space, including the spread of infectious diseases between groups, because the life cycles of parasites are adapted to seasonal changes in environmental conditions (Altizer et al., 2006).

Previous authors have modeled this situation of spatially distributed groups in an ecological context. For example, Hess (1996a,b) developed an island meta-population model that investigated both within and among-patch dynamics of a contagious infectious agent. He found that in the absence of host resistance, increased connectivity among patches (i.e., groups) led to a greater likelihood for epidemic spread of a contagious disease. Several other models have shown that specific patterns of sociality reduce parasite risk, for example when large groups are divided into smaller clusters of locally interacting individuals. This suggests that in highly structured populations with limited dispersal, infectious diseases are less likely to become established because infectious agents are effectively contained within subgroups (Salathé and Jones, 2010; Thrall et al., 2000; Watve and Jog, 1997; Wilson et al., 2003). In another recent model of sociality and infectious disease dynamics, Bonnell et al. (2010) developed an agent based model to investigate how the distribution of food resources influences movement and resource sharing by social primates, and how this affects movement of infectious agents through the simulated populations.

Here, we add to the understanding of disease dynamics in spatially structured populations by developing a model that focuses on seasonal shifts in ranges that are associated with sharing of a resource, such as water or food. Shared resources can impact the spread of infectious agents in at least three ways. First, aggregations of animals around resources increase direct and indirect contact rates among individuals, both within and among social groups (Ayeni, 1975; Cooper et al., 2010; Valeix et al., 2007; Vicente et al., 2007). Second, intensified use of resources increases the local density of infectious stages of parasites in the soil (Vicente et al., 2006). Lastly, when animals leave their home ranges in search of resources, they may be exposed to infectious agents not found in their home ranges, including areas used intensively by neighboring groups (Nunn and Dokey, 2006; Stoner, 1996). Conversely, when animals return to their normal ranges, infectious stages of parasites may have cleared from the soil through parasite mortality, and disease risk is further lowered if infected hosts are less able to survive migration back to the range (Altizer et al., 2011; Hausfater and Meade, 1982; Loehle, 1995). Thus, seasonality is likely to have major impacts on the dynamics of infectious organisms, with both positive and negative effects.

In our model, the infectious agent is fecally transmitted and builds up in the environment according to habitat use. The density of infectious material is expected to increase in the environment when group ranges overlap around shared resources. We do not assume that the agent is specifically transmitted in water, food, or in soil, but only that it is gastrointestinal and acquired through ingestion of food or water, or through contact with skin.

Remarkably little is known about the role of shared water sources in wildlife disease ecology. Water sources are expected to impact movement patterns of terrestrial vertebrates (Redfern et al., 2003; Scholz and Kappeler, 2004; Smit, 2011; Smit et al., 2007). Foot-and-mouth disease has been proposed to spread among buffalo and impala through shared drinking resources (Bastos et al., 2000), and waterholes are important in the spread of other parasites and pathogens within species (Vicente et al., 2006, 2007). Much of the effort aimed at investigating the role of waterholes as sources of disease has focused on whether water resources

(and their surroundings) provide a means for infections to move between livestock and wildlife in human-altered habitats (e.g., Bengis et al., 2002), rather than how such situations might alter natural patterns of infection in wild animal populations. In addition, waterholes are interesting because experimental approaches are possible in future extensions of this research – for example, by providing artificial waterholes, using barriers to limit access to particular species, or experimentally reducing levels of infection in water sources (e.g., Hunt et al., 2007). In terms of food resources, Walsh et al. (2007) describe how groups of apes share fruit, including discarded fruit, with potential for disease transmission among social units.

In the research described here, we extended an agent-based model of disease dynamics (Nunn et al., 2011) to investigate how seasonality of resource use and ranging patterns influences disease dynamics. By building on the Nunn et al. (2011) modeling framework, we are able to compare results with and without seasonality, and to assess the role of seasonal ranging in relation to other variables in the previous model. We expected that a longer lean season would increase exposure to infectious agents that accumulate in the soil, resulting in higher population prevalence, a greater number of individuals lost due to disease, and more rapid penetration of the infectious agent into the majority of social groups. We also expected that host behavioral changes related to seasonality – such as ranging patterns – would have strong effects on seasonal variation in infection-related measures, such as prevalence. By systematically varying key environmental, behavioral and disease transmission parameters in the model, we compared the relative importance of seasonal variation with more traditional epidemiological factors, such as disease related mortality and transmission probability. Overall, the model presented here extends the previous model in new directions with additional parameters, while also investigating the previously investigated parameters (Nunn et al., 2011) in the context of seasonality.

2. Materials and methods

2.1. Simulation structure

The model was designed to investigate behavioral, ecological and epidemiological parameters that could potentially influence the spread of an infectious organism in a spatially structured population, specifically in the context of seasonal variation in resources that influence ranging patterns and inter-mingling of social groups. A fecally transmitted infectious organism was introduced at one edge of the habitat. The simulation then tracked the spatial movements of groups of individuals relative to a “core area” of the home range, and the dispersal of individuals among different social groups. Each simulation run consisted of 10 yearly cycles of seasonal change. Groups converged around shared resources during a defined period of resource shortage, which varied in length across simulation runs.

We focus on the aspects of the model involving seasonality and shared resources, but we repeat some model description for clarity and completeness (Nunn et al., 2008, 2011). Model dynamics proceeded in discrete time steps, which represented single days in the lives of host individuals. In each time step several dispersal, infection and demographic processes took place sequentially: (1) ranging and possible infection of hosts through exposure to feces in the ranging matrix, (2) deaths due to the intrinsic mortality rate and disease-related mortality, (3) stochastic dispersal of individuals to neighboring groups, and (4) stochastic births of individuals in groups to replace individuals lost to disease or other factors in those groups over time. These are described below. In addition, each year was divided into “normal” and “lean” seasons, with resources

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