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Behavioural influences on disease risk: implications for conservation and management

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While parasites are fundamental components of ecological systems, emerging infectious diseases are a growing concern for conservation and management. Understanding the drivers and consequences of disease emergence in natural systems is complex because of the diverse array of factors associated with disease dynamics. Host behaviour plays an important role in disease dynamics across multiple scales (individuals to landscapes). Here, we synthesize our current understanding of the interplay between behaviour and disease in the context of conservation. We review the general importance of behaviour for determining the probability of exposure to parasites and the likelihood of infection once exposed. We also discuss the influence of infection on behaviours that affect disease transmission in populations and the potential trait-mediated indirect interactions that can influence disease risk within communities. Furthermore, we present several case studies demonstrating how the incorporation of behaviour into conservation and management strategies is critical for understanding emerging infectious diseases. Given the fundamental relationships between behaviour and infectious disease, there is a need for the development of practical methods for integrating this knowledge into conservation. Establishing a dialogue and forming collaborations between scientists and wildlife managers across multiple scales is an essential step. Ultimately, conservation practices that integrate knowledge of behaviour and infectious diseases will have a greater chance of success.

Host behaviour plays an important role in understanding disease dynamics at multiple scales. For individuals, host behaviour (e.g. activity level, habitat choice) affects the probability of encountering parasites and the risk of infection (Moore, 2002). Behaviour also plays a critical role in the transmission of parasites in populations and communities (Poulin, 2007b). Human modification of the landscape can influence the amount of contact among populations and the movement of populations, which alters both behaviour and disease risk (Dobson & Foufopoulos, 2001). Given that host behaviour is a fundamental component of disease dynamics, conservation and management efforts that account for these effects are necessary. Here, we synthesize our current understanding of the interplay between behaviour and disease in the context of conservation. We begin with a brief overview of the importance of parasites in ecology and evolution. Then, we summarize the significance of behaviour in disease dynamics at different scales (individuals to landscapes). Using a series of case studies, we then discuss how behaviour has or could play a role in conservation within the context of disease. We conclude with future challenges for integrating behaviour into conservation efforts seeking to manage disease risk.

THE IMPORTANCE OF PARASITES

Like free-living species, parasites are fundamental components of natural systems (Kuris et al., 2008; Lafferty et al., 2008). Research over the past several decades has revealed their importance within ecological and evolutionary frameworks (Lafferty et al., 2008; Poulin, 2007a). For instance, given that most free-living species have at least one parasite species, a large portion of biodiversity on the planet is represented by parasites (Dobson, Lafferty, Kuris, Hechinger, & Jetz, 2008). In some communities, parasites can represent a large fraction of the biomass and production (Kuris et al., 2008; Preston, Orlofske, Lambden, & Johnson, 2013). Because many parasites have complex life cycles, they also can play important roles in food webs (e.g. connectance, energy transfer; Lafferty et al., 2008). From an evolutionary perspective, parasites

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can shape the evolution of hosts by placing selection pressures on host populations and regulating host populations (Grenfell et al., 2004; May & Anderson, 1983).

While the importance of parasites in ecology and evolution is increasingly recognized, emerging infectious diseases are a growing concern for humans and wildlife (Daszak, Cunningham, & Hyatt, 2000; Dobson & Foufopoulos, 2001; Jones et al., 2008). Infectious diseases can be classified as emerging for several reasons, including an increase in prevalence or virulence in a host population, spread to a new population or species, or recent evolution of the parasite (e.g. evolved virulence, strain diversification). Emerging infectious diseases such as canine distemper in carnivores, chytridiomycosis in amphibians and white-nose syndrome in bats have received considerable attention due to their devastating effects on host populations (Daszak et al., 2000; Fisher et al., 2012). Many factors can contribute to the emergence of infectious diseases, which has been extensively reviewed (Daszak et al., 2000; Dobson & Foufopoulos, 2001). However, isolating these mechanisms is challenging because of the simultaneous and interacting effects of anthropogenic factors (e.g. climate change, pollution, eutrophication, species loss). Importantly, emerging infectious diseases are one contributor to what is becoming known as the sixth mass extinction (Wake & Vredenburg, 2008). It is imperative that conservation and management practices use a comprehensive approach to combat disease outbreaks, including the consideration of host behaviour in establishing policies for managing infectious diseases. In this review, we focus on host behaviour because very little is known about parasite behaviour, particularly in the context of conservation. However, we acknowledge that behaviour of both hosts and parasites can influence disease outcomes and may be necessary to consider when establishing conservation practices.

BEHAVIOUR AND DISEASE ACROSS SCALES

Individuals and Populations

For individual hosts, a broad range of factors can influence disease risk; age, sex, body size and genetics determine the probability of exposure to parasites or the likelihood of infection once exposed (Schmid-Hempel, 2011). Host behaviours also can influence disease risk (Fig. 1). For instance, parasite burdens tend to be higher in hosts with higher activity levels or with broader home ranges because encounter rates with parasites are greater (Craft, Volz, Packer, & Meyers, 2011). Similarly, parasite burdens can be higher in hosts with extensive contact networks (Craft et al., 2011). Alternatively, hosts can display defensive behaviours to reduce their chances of becoming infected. Antiparasite behaviours such as erratic movement, grooming, migration and self-medication can function to decrease parasite loads (Daly & Johnson, 2011; Hart, 1994, 1997; Taylor, Oseen, & Wassersug, 2004). For instance, ruminants infected with gastrointestinal nematodes will change their diets and selectively consume plants with anthelmintic properties (Villalba, Miller, Ungar, Landau, & Glendinning, 2014).

Once a host is infected, there is a diverse set of potential effects on the host, including changes in growth, development, reproduction, physiology, gene expression, morphology and behaviour (Hart, 1990). While we focus on behaviour, we underscore that these other effects can occur jointly with behaviour and interact to influence disease outcomes (e.g. morbidity, mortality). Sickness behaviours such as lethargy, reduced grooming, loss of appetite and sneezing commonly occur following infection (Hart, 1990; Loehle, 1995; Fig. 1). While many sickness behaviours are simple byproducts of infection rather than adaptations for the host or parasite (Poulin, 1995), they can still be important within the context of populations and communities (see below). Some parasites with complex life cycles alter the behaviour of their hosts to facilitate transmission between host species (Poulin, 1995). For instance, parasite-induced vulnerability to predation has been documented in many systems where the parasite requires both the predator and the prey to complete its life cycle (discussed below).

Because individuals are embedded in populations, the behaviour of individuals can scale up to influence population-level processes in several ways. A regularly observed pattern in host populations is parasite aggregation, in which a small percentage of the population harbours the majority of the parasites (Poulin, 2007a). Such infection heterogeneity is driven by many factors, including variation in host traits such as behaviour (Wilson et al., 2001). For instance, experimental manipulations of behaviour, size and immunity in tadpoles demonstrated that individual-level variation in behaviour (i.e. lower activity levels) was a major driver of trematode aggregation in the population (Johnson & Hoverman, 2014). If infected hosts exhibit sickness behaviours or other trait changes that increase parasite loads, these effects can be amplified, leading to stronger patterns of parasite aggregation in the population (Johnson & Hoverman, 2014). The behaviour of individuals within a population also influences transmission rates, such as with superspreaders. In brief, superspreaders are hosts that are responsible for a disproportionately large number of the transmission events for a population (Lloyd-Smith, Schreiber, & Getz, 2005; Stein, 2011). Hosts that display risky behaviours or have large contact networks are ideal superspreaders in populations. In humans, classic examples of superspreaders include Mary Mallone ('Typhoid Mary') for typhoid fever and Gaetan Dugas for HIV (Hudson, Perkins, & Cattadori, 2008; Paull et al., 2012). As we will discuss below, highly infected individuals or superspreaders are frequently targeted in conservation and management strategies to prevent disease spread in populations.

Communities

Host–parasite interactions are embedded in complex ecological communities. One of the primary goals of disease ecology is to expand beyond single host–parasite interactions to address how other ecological interactions (e.g. competition, predation) influence disease dynamics. Indeed, competition and predation can play pivotal roles in disease dynamics via trait-mediated indirect interactions. Trait-mediated indirect interactions occur when the interaction between two species (e.g. two competitors, a predator and its prey) alters the traits of a species, which in turn change interactions with other species in the community (Werner & Peacor, 2003). From a disease perspective, shifts in the activity or habitat use of hosts induced by the presence of competitors and predators have the potential to influence infection risk (Orlofske, Jadin, Hoverman, & Johnson, 2014; Raffel, Martin, & Rohr, 2008; Szuroczki & Richardson, 2009; Thiemann & Wassersug, 2000; Fig. 1). For instance, research with amphibians and zooplankton (e.g. *Daphnia*) has found that predators induce lower activity levels or shifts in habitat, respectively, leading to increased risk of infection (Decaestecker, De Meester, & Ebert, 2002; Orlofske et al., 2014).

Conversely, parasites can have large effects on ecological processes. In addition to free-living species, parasites can initiate trait-mediated indirect interactions (Fig. 1). Green frog tadpoles, *Lithobates clamitans*, exposed to free-living stages of trematode parasites increased their activity levels as an avoidance response (Marino & Werner, 2013). As a result, tadpoles experienced greater predation rates by larval dragonflies, which target highly active prey. Parasite-induced behavioural changes can have broader implications for the structure and function of communities, particularly when infections significantly alter the behaviour of keystone species or ecosystem engineers. In several systems, parasites alter