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A guide for ecologists: Detecting the role of disease in faunal declines and managing population recovery

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ABSTRACT

Biodiversity is declining at an alarming rate, especially among vertebrates. Disease is commonly ignored or dismissed in investigations of wildlife declines, partly because there is often little or no obvious clinical evidence of illness. We argue that disease has the potential to cause many species declines and extinctions and that there is mounting evidence that this is a more important cause of declines than has been appreciated. We summarise case studies of diseases that have affected wildlife to the point of extinction and bring together the experiences of wildlife managers, veterinarians, epidemiologists, infectious disease specialists, zoologists and ecologists to provide an investigation framework to help ecologists and wildlife managers address disease as a factor in wildlife declines. Catastrophic declines of wildlife may be the result of single or multiple synergistic causes, and disease should always be one factor under consideration, unless proven otherwise. In a rapidly changing world where emerging infectious diseases have become increasingly common, the need to consider diseases has never been more important.

1. Introduction

The world's biological diversity continues to decline at an unprecedented rate (Butchart et al., 2010; Tittensor et al., 2014). The major causes of species declines are attributed to anthropogenic activities, including habitat destruction, over-exploitation, climate change and invasive species, or a combination of these factors (Ducatez and Shine, 2017; Schipper et al., 2008). Infectious disease, although ubiquitous in all species, is rarely investigated, despite compelling and accumulating evidence of disease causing population declines and even species extinctions.

The role of disease as a major factor in species declines has generally been identified when it has appeared as a major emergence event, resulting in the mass morbidity and mortality of large, gregarious or regularly monitored animals. The African rinderpest pandemic in the late 19th century is a seminal example (Daszak et al., 2000), extirpating > 90% of Kenya's buffalo (*Syncerus caffer*) and causing a trophic cascade. Much of Hawaii's endemic avifauna became extinct following the introduction of the mosquito vectors of birdpox and avian malaria (Warner, 1968). Ebola virus eliminated 90–95% of critically endangered western gorillas (*Gorilla gorilla*) in the Congo and Gabon in the early 21st century (Bermejo et al., 2006). Populations of the African wild dog (*Lycaon pictus*) became extinct in the Serengeti in 1991 due to canine distemper and rabies (Daszak et al., 2000). The fungus *Pseudogymnoascus destructans*, white-nosed syndrome (WNS), which was first documented in bats in 2006, has killed millions of bats across north

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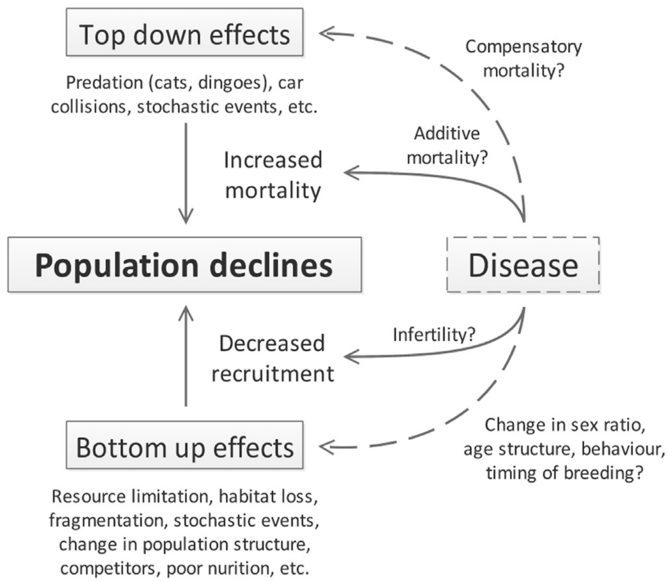

Fig. 1. The influence of disease on demographic parameters can cause population declines. Infectious disease may contribute to population declines directly (solid arrows), and indirectly (dashed arrows) that cause subtle yet fundamental changes in population structure that contribute to population declines.

America and poses an extinction threat to some species, such as the Indiana bat (*Myotis sodalist*) (Thogmartin et al., 2013). In 2015, 62% of the global population of critically endangered saiga antelope (*Saiga tatarica*) died suddenly due to an opportunistic pathogen, the *Pasteurella* bacterium (Milner-Gulland, 2015).

Yet diseases that cause mass mortalities are likely to represent a fraction of the true number of cases in which infectious disease plays a role in population declines (Grogan et al., 2014). We suggest that disease is likely to be an unrecognised contributor to declines as well as an obvious sole cause (De Castro and Bolker, 2005; Pedersen et al., 2007; Reiss et al., 2015; Schloegel et al., 2006; Smith et al., 2006; Tompkins et al., 2015). In this capacity, disease may contribute to population declines through influencing demographic parameters, whereby: (i) an increase in mortality occurs in addition to other top-down effects (additive versus compensatory mortality; Kistner and Belovsky, 2014), (ii) the population cannot compensate for the increased mortality by increasing recruitment (Muths et al., 2011; Scheele et al., 2015); or (iii) a decrease in recruitment is observed (Fig. 1).

Disease can cause population declines through decreased reproductive success, affecting fertility, fecundity, and neonatal survival. Such diseases may be particularly difficult to detect due to subtle or inapparent clinical signs (Scott, 1988). Recent examples include malaria in wild birds (Knowles et al., 2010), porcine reproductive and respiratory syndrome virus in wild boars (*Sus scrofa*) (Reiner et al., 2009), and bacterial infections in wild ungulates (Pioz et al., 2008). Infectious diseases may also increase mortality while decreasing recruitment, exacerbating population-level impacts, for example, chlamydial disease in koalas (*Phascolarctos cinereus*) (Polkinghorne et al., 2013).

Another, and perhaps more insidious, mechanism by which disease may contribute to population declines is through fundamentally altering population structure, and dispersal and migratory patterns (Fig. 1). Pathogens and their vectors often demonstrate tropism, or a specificity for population subgroups, organs, or tissue, potentially leading to changes in population sex ratio, age structure, behaviour, timing of breeding, and dispersal tendencies (Kolby et al., 2010; McDonald et al., 2014), even in populations with high abundance (Lacy, 2000) and therefore triggering detrimental Allee effects (Berec et al., 2007). Furthermore, infections may contribute to altered secondary sex ratios. For example, toxoplasmosis, caused by the parasite *Toxoplasma gondii*, has been reported to increase the proportion of male offspring in rodent species (Kankova et al., 2007).

Multi-disciplinary approaches to identifying and controlling emerging infectious diseases have been developed recently (Daszak et al., 2013; Plowright et al., 2008; Skerratt et al., 2007; Skerratt et al., 2009), but wildlife ecologists do not commonly consider these approaches. Our aims are (1) to develop a framework, directed at wildlife ecologists, for investigation of disease as a potential factor in wildlife population declines, and (2) to demonstrate how wildlife ecologists can apply these approaches to investigating vertebrate declines.

A common challenge in transdisciplinary research is terminology. Here, we define terms that have a common usage but sometimes different meaning across disciplines (Box 1). The term 'disease' is used commonly in the literature, often without much specificity. In a general sense, it can include all pathogenic infectious agents (e.g. bacteria, viruses, and parasites), as well as the resulting individual or population level effects of such infections (e.g. disease outbreaks). The term, 'disease', also encompasses 'non-infectious diseases' (those not caused by infectious agents) such as poisoning, hyperthermia and starvation (Haydon et al., 2002; Porta et al., 2014).

Box 1
Glossary of terms.

'Disease' is any disorder in the health or function of an animal;

'Clinical disease' is an overt or detectable disease, using standard clinical diagnostic techniques such as physical examination;

'Subclinical disease' is one that cannot readily be detected by signs, but is detectable with diagnostic tests, and hosts may be inapparent disseminators of the infectious agent;

'Infection' is an underlying process whereby an infectious agent invades and reproduces in or on an animal host; it does not necessarily imply clinical disease as an outcome; and hosts may be inapparent disseminators of the infectious agent;

'Non-infectious diseases', such as pesticide or heavy metal toxicities, may or may not be associated with anthropogenic risk factors;

'Infectious diseases' are attributed to 'pathogens' (a general term for infectious agents) that include 'micro-parasites' (i.e., viruses, bacteria, fungi, protozoa) and 'macro-parasites' (worms, mites, ticks), although host and environmental factors also play causative roles;

'Epidemic' is the occurrence of a disease in excess of normal expectancy;

'Endemic disease' refers to the constant occurrence of a disease in a region or population;

'Outbreak' is a term typically used to describe an epidemic;

'Reservoir', when used in the context of a target host population, usually refers to a system (host or host stage, vector, or environment) within which the pathogen may be maintained and reproduce indefinitely;

'Host' is a population or individual that carries or is susceptible to an infection.