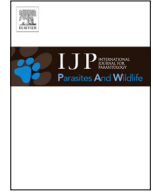




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Invited Review

Neglected wild life: Parasitic biodiversity as a conservation target

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ABSTRACT

Parasites appropriate host resources to feed and/or to reproduce, and lower host fitness to varying degrees. As a consequence, they can negatively impact human and animal health, food production, economic trade, and biodiversity conservation. They can also be difficult to study and have historically been regarded as having little influence on ecosystem organization and function. Not surprisingly, parasitic biodiversity has to date not been the focus of much positive attention from the conservation community. However, a growing body of evidence demonstrates that parasites are extremely diverse, have key roles in ecological and evolutionary processes, and that infection may paradoxically result in ecosystem services of direct human relevance. Here we argue that wildlife parasites should be considered meaningful conservation targets no less relevant than their hosts. We discuss their numerical and functional importance, current conservation status, and outline a series of non-trivial challenges to consider before incorporating parasite biodiversity in conservation strategies. We also suggest that addressing the key knowledge gaps and communication deficiencies that currently impede broad discussions about parasite conservation requires input from wildlife parasitologists.

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1. Introduction

Parasites have few friends. In the vernacular, the term “parasite” connotes free riders and slimy creatures. In nature, they are difficult to study due to their small size, complex life cycles, and

generalized taxonomic impediments. In wildlife biology, parasites have traditionally been either ignored because quantifying their effects on host species is challenging, or antagonized because of the inherent harm they cause their hosts. Many human parasites, often zoonotic, carry important costs that result in morbidity, mortality, and negative effects on the economy (Gallup and Sachs, 2001; Gazzinelli et al., 2012). Wildlife parasites in particular, represent the majority of zoonotic emerging pathogens of humans (Taylor et al., 2001). Animal parasites also impact food security and incomes through their deleterious influences on livestock (Cleveland et al., 2001). Finally, disease can affect conservation efforts, acting as a contributing threat in the endangerment of wildlife hosts, and occasionally causing severe population declines

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(de Castro and Bolker, 2005; Bleher et al., 2009). For all these reasons it is not surprising that parasites are generally viewed through the lens of either direct antagonism or patent disregard.

As a consequence, the maintenance of parasitic biodiversity has not historically been a conservation priority (Gompper and Williams, 1998; Dunn et al., 2009; Griffith, 2012). The stated goal of the field of conservation biology is to maintain biodiversity, including the evolutionary processes that drive and sustain it (Meffe et al., 2006). Yet to ignore the conservation of parasites is to ignore the conservation status of the majority of life on Earth, as parasitism represents the most common consumer strategy on the planet (Poulin and Morand, 2000; Dobson et al., 2008). It also means neglecting a fundamental biological relationship, as infection is fundamental to the ecological and evolutionary drivers of biological diversity and ecosystem organization (Marcogliese, 2004).

Here we argue that wildlife parasites should be considered meaningful conservation targets no less relevant than their hosts. We discuss their numerical and functional importance, current conservation status, and outline a series of non-trivial challenges to consider before incorporating parasite biodiversity in conservation strategies. We use the term “parasite” to refer to both micro and macroparasites. This diverse and multiphyletic group is united by their appropriation of resources from a host in some part of their life cycle. This appropriation creates direct fitness costs to host individuals, although the magnitude of said costs is highly variable and often context-dependent. Despite the increasing visibility of parasite conservation in the scientific literature (Gompper and Williams, 1998; Windsor, 1998; Gómez et al., 2012), this topic has seldom been addressed with specific reference to wildlife parasites. Here we focus on parasites of wildlife and the roles of wildlife parasitologists in discussions about parasite conservation.

2. Is the host-parasite relationship important?

Wildlife parasite studies have traditionally focused on the documentation of parasitic communities in host populations, surveillance for parasitic organisms of animal or human health relevance, or assessments of disease risk to long-term host persistence (Riley et al., 2004; Clifford et al., 2006; Pedersen et al., 2007; Hamer et al., 2012). More rarely are they concerned with the ecological and evolutionary ramifications of host-parasite associations (Gompper and Williams, 1998). However, recent research suggests host-parasite relationships are a fundamentally important driver of ecological structure and function. Parasites are a ubiquitous component of ecosystems in terms of species diversity (Poulin and Morand, 2004), biomass (Kuris et al., 2008), and relevance in food webs (Amundsen et al., 2009; Dunne et al., 2013).

By extracting resources from their hosts, parasites force them to alter their energy balances (Thomas et al., 2009) consequently influencing host fitness even in the absence of clinical signs of infection (Hudson et al., 2002). The resulting impacts of parasitism on host reproductive rate (Schwanz, 2008), growth (Gorrell and Schulte-Hostedde, 2008), movement, and survival (Robar et al., 2010) translate into influences on community and ecosystem organization. At small spatial scales, the differential effects of infection of generalist parasites can modulate competitive interactions. For example, parapoxvirus-mediated apparent competition likely explains the ecological success of introduced gray squirrels (*Sciurus carolinensis*) in the United Kingdom (Tompkins et al., 2002). Nematodes can modulate the coexistence (or lack thereof) of sympatric bird species (Tompkins et al., 2001), and meningeal worm (*Parelaphostrongylus tenuis*) favor white-tailed deer (*Odocoileus virginianus*) in habitats deer share with elk (*Cervus elaphus*) (Bender et al., 2005). Infection can also affect reproductive behaviors and

output, for example causing abortion or sterility. In the most extreme case, parasitic castrators divert the host's metabolism for their own reproductive success, driving changes in host density and maturation rates (Lafferty and Kuris, 2009).

Parasites can also shape patterns of animal distribution and density at larger spatial scales, as seen in the introduction and subsequent removal of the rinderpest virus in East Africa, which dramatically impacted ecosystem structure by influencing ungulate population densities (Thomas et al., 2005). The impacts of rinderpest infection over large-scale ecosystem processes (e.g. wildfire dynamics and the ecology of tree species) are still apparent across the Serengeti ecosystem (Holdo et al., 2009). Parasites are also natural selection agents influencing a variety of host attributes, from phenotypic polymorphism and secondary sexual characters, to the maintenance of sexual reproduction (Wegner et al., 2003; Livey et al., 2004; Blanchet et al., 2009). These effects ultimately drive biological diversification, through influencing host reproductive isolation and speciation (Summers et al., 2003).

Finally, recent discussions of the importance of parasites in food webs (Lafferty et al., 2008a; Britton, 2013; Dunne et al., 2013); as modulators of host behavior (Barber et al., 2000; Lefevre et al., 2009), drivers of community composition (Fenton and Brockhurst, 2008), competitive interactions and biological invasions (Hatcher et al., 2006, 2012; Dunn et al., 2012); and as selective agents (Summers et al., 2003; Nunn et al., 2004), provide multiple lines of evidence for the ecological and evolutionary relevance of parasitic biodiversity.

3. Are wildlife parasites endangered?

In the conservation literature, parasites are most often viewed as threats to their hosts (Nichols and Gómez, 2011), infection often understood as a sign of ecosystem disturbance (Patz et al., 2004), and the loss of wildlife seen as a driver of disease amplification (Randolph and Dobson, 2012). Recent research has shown that most human emerging diseases have a zoonotic reservoir, that reservoirs are most often wildlife species (Jones et al., 2008), and that anthropogenic disturbance is commonly associated with human and wildlife disease emergence events (Daszak et al., 2000). Particularly given the media attention paid to emerging zoonotic disease, it is possible that we live in an age characterized by a generalized perception that parasites must be controlled rather than conserved.

However, parasites are not immune to the threats that affect free-living species and our current biodiversity crisis may well be primarily characterized by the loss of affiliate species (Dunn et al., 2009). Reports of pandemics and emerging disease illustrate one of the consequences of global environmental change but do not preclude the fact that many parasite species are also threatened by it. We now know that ecosystem disturbance creates risks for parasite persistence (Hudson et al., 2006; Lafferty, 2012). For example, land-use change and pollution can both reduce the abundance and diversity of parasite species (Lafferty, 1997; Huspeni and Lafferty, 2004; Bradley and Altizer, 2007). Climate change can restrict parasite transmission (Afrane et al., 2012) and lead to phenological mismatches between parasites and hosts (Rohr et al., 2011). Parasites are also threatened by deliberate attempts to control or eradicate them. In certain circumstances, the extirpation of parasites of public health or veterinary importance can be an unquestionable gain, but control efforts often affect species beyond those initially targeted (Kristensen and Brown, 1999). In other instances, routine veterinary practices can have the unintended effect of eliminating intermediate hosts and thereby interrupt enzootic transmission cycles in species other than those receiving the treatment (Spratt, 1997; Wardhaugh et al., 2001).

Parasites and other associated taxa are threatened not only by direct environmental alteration but are also indirectly affected by

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