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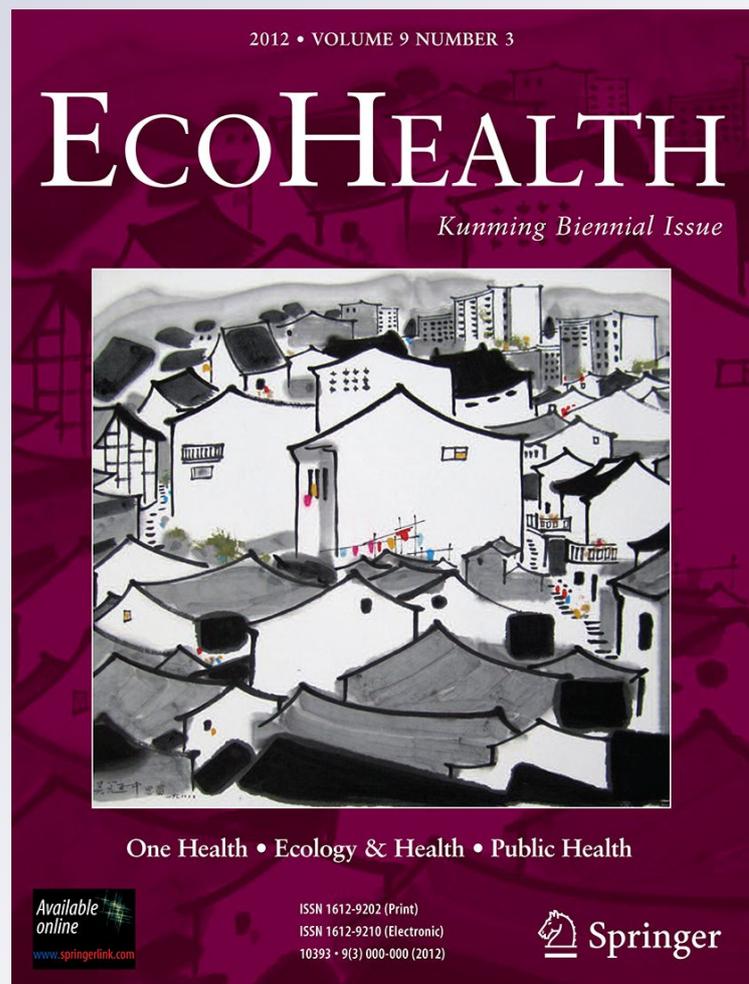
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Review

Macroparasite Infections of Amphibians: What Can They Tell Us?

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Abstract: Understanding linkages between environmental changes and disease emergence in human and wildlife populations represents one of the greatest challenges to ecologists and parasitologists. While there is considerable interest in drivers of amphibian microparasite infections and the resulting consequences, comparatively little research has addressed such questions for amphibian macroparasites. What work has been done in this area has largely focused on nematodes of the genus *Rhabdias* and on two genera of trematodes (*Ribeiroia* and *Echinostoma*). Here, we provide a synopsis of amphibian macroparasites, explore how macroparasites may affect amphibian hosts and populations, and evaluate the significance of these parasites in larger community and ecosystem contexts. In addition, we consider environmental influences on amphibian–macroparasite interactions by exploring contemporary ecological factors known or hypothesized to affect patterns of infection. While some macroparasites of amphibians have direct negative effects on individual hosts, no studies have explicitly examined whether such infections can affect amphibian populations. Moreover, due to their complex life cycles and varying degrees of host specificity, amphibian macroparasites have rich potential as bioindicators of environmental modifications, especially providing insights into changes in food webs. Because of their documented pathologies and value as bioindicators, we emphasize the need for broader investigation of this understudied group, noting that ecological drivers affecting these parasites may also influence disease patterns in other aquatic fauna.

Keywords: parasite, global change, bioindicators, infectious disease, community ecology, malformations, deformities, trematode, helminth, emerging disease

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INTRODUCTION

The rapid and widespread emergence of human and wildlife diseases underscores the importance of determining how environmental change alters host–parasite dynamics as

well as the subsequent impacts of these altered interactions (Daszak et al. 2000; Jones et al. 2008; Ostfeld et al. 2008). With nearly a third of all species extinct or in decline, amphibians have become the most imperiled class of vertebrates worldwide (Stuart et al. 2004; Collins and Crump 2009). Alongside habitat loss and destruction, directly transmitted microparasites, such as ranaviruses and the amphibian chytrid fungus *Batrachochytrium dendrobatidis* (Bd), have been directly linked to population die-offs and species losses (Skerratt et al. 2007; Gray et al. 2009; Kilpatrick et al. 2010). However, macroparasite infections also have the potential to influence amphibian hosts in more subtle and complex ways, as seen in other host taxa. For example, macroparasites influence host growth and reproductive rates, playing a key role in population fluctuations (Hudson et al. 1998; Albon et al. 2002; Holmstead et al. 2005). Additionally, the complex life cycles of many macroparasites makes them effective bioindicators of environmental change (MacKenzie et al. 1995; Marcogliese 2005; Hudson et al. 2006), suggesting that changes in macroparasitic infections also have potential as a conservation tool in amphibian-based research.

Here, we highlight three fundamental reasons why amphibian macroparasites have immediate relevance to the study of amphibians and wildlife disease ecology in general. First, although macroparasites were once thought to cause little pathology in amphibian hosts (Prudhoe and Bray 1982), growing evidence from experimental and field research has revealed important exceptions to this long-held dictum (see Table 1). These parasites can cause pathology directly to individual hosts and/or indirectly through interactions with other pathogens and forms of environmental change (e.g., Koprivnikar 2010). Second, environmental factors such as pesticides, eutrophication, and landscape are important drivers of amphibian macroparasite infections (Kiesecker 2002; Johnson et al. 2007; King et al. 2007; Rohr et al. 2008a; Koprivnikar and Redfern, in press), suggesting that global environmental changes will have significant influences on infections. Third, stemming from the above, macroparasites of amphibians have important potential as biological and environmental indicators. Owing to their complex life cycles and varying dependency on species distributed across multiple trophic levels, many alterations in the food web will affect the parasites moving through it (Marcogliese 2005). Helminths, in particular, can provide an inexpensive yet reliable method of obtaining information about host activity, distribution, and sensitivity to environmental

perturbations while also exhibiting direct vulnerability to factors such as contaminants (Marcogliese and Cone 1997; Pietrock and Marcogliese 2003; Byers et al. 2011).

Our objectives are to (1) provide background on amphibian macroparasites known to cause pathology, (2) review key recent findings regarding drivers of amphibian macroparasite infections and critically assess their complex effects on individuals and populations, and (3) suggest future directions for amphibian–macroparasite research to address pressing gaps in our knowledge of these parasites, particularly with respect to their use as biological indicators. While these objectives have applied significance to understanding amphibian macroparasites, we believe that they have further conceptual importance in exploring the ecology of host–pathogen interactions in the context of global change.

MACROPARASITES AND AMPHIBIANS

Macroparasites typically include helminths (monogeneans, trematodes, cestodes, nematodes, acanthocephalans, nematomorphs) and some arthropods (mites, ticks, copepods, lice). Macroparasites differ from microparasites (e.g., viruses, fungi, bacteria, and protists) by their larger size, their lack of asexual replication in vertebrate hosts, and their intensity-dependent pathology based on the number of parasites infecting a host. Importantly, this means that host pathology (e.g., mortality or morbidity) is most likely to occur under conditions of high infection intensity. Many macroparasites have complex life cycles requiring a period of development in one or more intermediate hosts before maturation in the definitive host. As both generalist predators and prey to larger predators, amphibians function as intermediate and definitive hosts to a variety of parasites in aquatic and terrestrial food webs. Individual frogs may support dozens of macroparasite species and several thousand individual parasites (Sutherland 2005; Schott-hoefer et al. 2011). In most studies, at least half of surveyed amphibians are infected with parasitic helminths (see Supplementary material). However, helminth taxon dominance varies by amphibian host order and ecology (Fig. 1). For example, nematodes are more common in relatively terrestrial amphibian species, while trematodes dominate the macroparasite fauna of ranids, tree frogs, and aquatic amphibians generally. Knowledge of such amphibian helminth infection patterns is crucial for their development as environmental bioindicators (see Table 2).

Table 1. Documented pathologies of common amphibian macroparasites

Parasite taxa	Parasite life stage	Host species	Pathology	Conditions influencing pathology	References
Trematoda					
Echinostomids	Metacercariae	Green frog (<i>Rana clamitans</i>), Northern leopard frog (<i>R. pipiens</i>), American toad (<i>Bufo americanus</i>)	Reduced survival, decreased growth, edema and granulomatous inflammation	Early developmental stage, contaminants, predator cue, and host density	Holland et al. (2007), Schott-hoefer et al. (2003b), Rohr et al. (2010), Fried et al. (1997), Koprivnikar et al. (2008), Shields (1987), and Green and Muths (2005)
<i>Ribeiroia ondatrae</i>	Metacercariae	Green frog, Pacific chorus frog (<i>Pseudacris regilla</i>), Northern leopard frog, Long-toed salamander (<i>Ambystoma macrodactylum</i>), California newt (<i>Taricha torosa</i>), Western toad (<i>B. boreas</i>) Northern red-legged frog (<i>R. aurora</i>), Columbia spotted frog (<i>R. luteiventris</i>), Wood frog (<i>R. sylvatica</i>)	Reduced survival, decreased growth, limb malformations, impaired performance	Early developmental stage and contaminants	Rohr et al. (2010), Johnson et al. (1999), Schotthoefer et al. (2003a), Johnson et al. (2001), Goodman and Johnson (2011a, b), and Kiesecker (2002)
Plagiorchiid	Metacercariae	American toad	Reduced survival		Rohr et al. (2010)
<i>Clinostomum</i> sp.	Metacercariae	Tiger salamander (<i>A. tigrinum</i>)	Scoliosis		Perpinan et al. (2010)
<i>Diplostomulum scheuringi</i>	Metacercariae	Red-spotted newt (<i>Notophthalmus viridescens</i>)	Eye and brain injury		Etges (1961)
<i>Haematoloechus</i> sp. or <i>H. longiplexius</i>	Adult	Bullfrog (<i>R. catesbeiana</i>), Northern leopard frog	Increased white blood cell counts and acetylcholinesterase activity, compression of alveolar tissue, chronic submucosal inflammation, and mild hypertrophy of bronchiolar epithelium		Marcogliese et al. (2009), Shields (1987), and Hsu et al. (2004)
Monostome type—cercariae	Metacercariae	Common hourglass treefrog (<i>Polypedates cruciger</i>)	Reduced survival, decreased growth, malformations	Early developmental stage	Jayawardena et al. (2010) and Rajakaruna et al. (2008)

Table 1. continued

Parasite taxa	Parasite life stage	Host species	Pathology	Conditions influencing pathology	References
Strigeid cercariae	Metacercariae	Tadpole	Reduced survival and edema		Cort and Brackett (1938)
Strigeid metacercariae	Metacercariae	Bullfrog	Increased dehydratorinol		Marcogliese et al. (2009)
<i>Diplostomulum xenopi</i>	Metacercariae	African clawed frog (<i>Xenopus laevis</i>)	Reduced survival and pericarditis and lesions of the heart		Nigrelli and Maraventano (1944)
<i>Telorchis</i> sp.	Metacercariae	Gray tree frog (<i>Hyla versicolor</i>)	Reduced survival and decreased growth	Habitat characteristics	Kiesecker and Skelly (2001)
Monogenea					
<i>Pseudodiplorchis americana</i>	Adult	Desert toad (<i>Scaphiopus couchii</i>)	Reduced energy storage		Toque 1993 and Tocque and Tinsley (1994)
	Oncomiracidia	Desert toad	Lung inflammation with epithelial cell vacuolation, interstitial edema and increases in alveolar exudate, leucocytes and fibrous tissue		Tinsley et al. (2002)
Nematoda					
<i>Rhabdias</i> sp.	Adult	Boreal/western toad	Granulomatous inflammation and nodules, and nematodal pneumonia		Green and Muths (2005)
<i>Rhabdias ranae</i>	Adult	Northern leopard frog	Decreased splenocyte cellularity and phagocytosis	Contaminants	Christin et al. (2003)
<i>Rhabdias bufonis</i>	Adult	European common toad (<i>B. bufo</i>)	Reduced survival, decreased growth, impaired performance	Tadpole density	Goater and Ward (1992) and Goater et al. (1993)
<i>Rhabdias sphaerocephala</i>	Adult	Marine toad (<i>B. marinus</i>)	Reduced survival		Williams (1960)
<i>Rhabdias pseudosphaerocephala</i>	Adult and larvae	Marine toad, Northern water frog (<i>Litoria dahlii</i>), Striped rocket frog (<i>L. nasuta</i>), Green tree frog (<i>L. caerulea</i>), Magnificent tree frog (<i>L. splendida</i>) and Ornate burrowing frog (<i>Opisthodon ornatus</i>)	Reduced survival, decreased growth, impaired performance, reduced stamina, inflammation primarily granulomatous admixed with granulocytes and lymphocytes		Kelehear et al. (2009), Pizzatto et al. (2010), Kelehear et al. (2011), and Pizzatto and Shine (2011)
<i>Rhabdias elegans</i>	Adult	Puerto Rican coquis (<i>Eleutherodactylus coqui</i>)	Impaired performance		Marr et al. (2010)

Table 1. continued

Parasite taxa	Parasite life stage	Host species	Pathology	Conditions influencing pathology	References
<i>Physoccephalus</i> sp.	Larvae	Marine toad	Fibrous cyst formation and cellular infiltration	Non-native host	Kelehear and Jones (2010)
<i>Oswaldocruzia filiformis</i>	Larvae	European common toad	Necrosis and atrophy of stomach mucosa and epithelium		Hendrikx and Van Mop-pes 1983
<i>Capillaria xenopodis</i> or <i>Pseudocapillarioides xenopi</i>	Adults and larvae	African clawed frog	Flaky skin disease, anorexia, intra-epidermal cystic cavities and glomerulosclerosis of the kidney		Cohen et al. (1984) and Brayton (1992)
Cestoda					
<i>Nematotaenia dispar</i>	Adult	European common toad	Gastrointestinal lesions and obstruction		Elkan (1960)
Annelida					
<i>Batrachobdella</i> (<i>Desse-rob-della</i>) <i>picta</i>	Adult	American toad, Wood frog	Reduced survival and decreased growth	Early developmental stage, temperature, tadpole density, and resource availability	Brockelman (1969) and Berven and Boltz (2001)
<i>Hirudo medicinalis</i>	Adult	Smooth newt (<i>Triturus vulgaris</i>), European common toad, edible frog (<i>R. esculenta</i>), marsh frog (<i>R. ridibunda</i>), <i>R. ridibunda-esculenta-lessonae</i> complex, common frog (<i>R. temporaria</i>) moor frog (<i>R. arvalis</i>)	Reduced survival		Meriä and Sterner 2002
Arthropoda					
<i>Lernaea cyprinacea</i>	Adult	Foothills yellow-legged frogs (<i>R. boylii</i>)	Reduced survival, decreased growth and malformations	Temperature and tadpole density	Kupferberg et al. (2009)
<i>Lernaea ranae</i>	Adult	Green frog	External inflammation and bleeding		Stunkard and Cable (1931)

Table 1. continued

Parasite taxa	Parasite life stage	Host species	Pathology	Conditions influencing pathology	References
<i>Hannemania dumni</i> or <i>Hannemania</i> sp.	Larvae	Rich mountain salamander (<i>Plethodon ouachitae</i>) and Caddo Mountain salamander (<i>P. caddoensis</i>), Canyon tree-frogs (<i>H. arenicolor</i>)	Reduced survival, occlusion of nasolabial groove and loss of chemosensory function, ulcerative dermatitis		Anthony et al. (1994) and Sladky et al. (2000)
<i>Argulus americanus</i>	Adult	Southern dwarf siren (<i>Pseudobranchius s. axanthus</i>)	Reduced survival		Goin and Ogren (1956)
<i>Bufo lucilia silvarum</i>	Larvae	American toad, Wood frog	Reduced survival, myiasis		Bolek and Coggins (2002) and Bolek and Janovy (2004)
<i>Bufo lucilia elongata</i>	Larvae	Wood frog	Reduced survival, myiasis		Bolek and Janovy (2004)
Acanthocephala <i>Acanthocephalus ranae</i>	Adult	European common toad	Reduced survival		Elkan (1960)

Representative Groups and Life Cycles

Amphibians can be infected with larval macroparasites as intermediate or paratenic (transport) hosts, or with adult parasites as definitive hosts. As intermediate hosts, amphibians typically become infected by free-living parasite stages during their larval development. For instance, free-swimming trematode stages (cercariae) emerge from snail first intermediate hosts, invade tadpoles, and develop into an encysted stage (metacercaria) or an additional mobile larval stage (mesocercaria). Some larval trematodes, such as *Ribeiroia ondatrae* and the echinostomes, can cause substantial pathology during this process (Table 1; Fig. 2). Amphibian larvae can also become infected by ingesting cercariae (e.g., *Gorgoderina*). As definitive hosts for trematodes, amphibians become infected when they ingest a second intermediate or paratenic host (usually an arthropod or another amphibian) carrying a larval stage (e.g., *Gorgoderina*, *Haematolechus*, and *Halipegus* spp.), or consume cysts found in their own shed skin (e.g., *Glypthelmins* and *Megalodiscus* spp.) or on vegetation (Fig. 3). In these cases, the trematode reproduces sexually within the amphibian and releases reproductive stages (eggs) that leave the host's body.

Nematodes (roundworms), cestodes (tapeworms), and acanthocephalans (spiny-headed worms) are also important and common parasites of amphibians. Amphibians can serve as intermediate or paratenic hosts of spirurid nematodes (e.g., *Spiroxys*, *Gnathostoma*, physalopterids), which are likely acquired by ingesting a wide range of other intermediate or paratenic hosts (Anderson 2000). However, the most common are adult forms that infect the host by direct penetration, ingestion of juveniles/eggs, or ingestion of paratenic hosts (e.g., *Cosmocercoides*, *Gyrinicola*, *Falculstra*, *Oswaldocruzia*, *Rhabdias* spp.). For instance, larval nematodes in the genus *Rhabdias* reside in moist soil and invade the skin of their anuran hosts, subsequently migrating to the lungs. Amphibians are definitive, intermediate, or paratenic hosts for many cestodes (e.g., *Bothriocephalus*, *Cylindrotaenia*, *Distoichometra*, *Mesocestoides*, *Ophiotaenia*, *Proteocephalus* spp.) and acanthocephalans (e.g., *Acanthocephalus*, *Pseudoacanthocephalus*). Virtually all cestodes and acanthocephalans use arthropods as their first intermediate hosts, which are then ingested by the next host in the life cycle.

While endohelminths generally dominate the macroparasite fauna of amphibians, external macroparasites can also be present, particularly monogeneans, although these

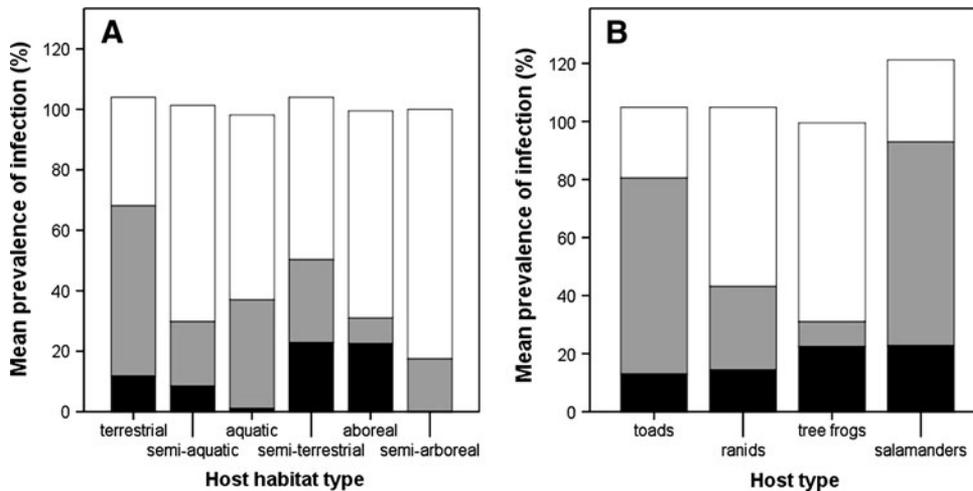


Fig. 1. General helminth diversity in amphibians based on Supplementary material with breakdown of helminth community composition (white bars trematodes, gray bars nematodes, black bars cestodes) based on a amphibian host habitat type, b general host type. Note that data represent only adult and metamorph host stages and the three most common helminths found across studies.

also can be found in organs such as the bladder (e.g., *Polystoma nearcticum*, *Pseudodiplorchis americanus*, *Protopolystoma xenopodis*). Monogeneans have a direct life cycle that does not involve intermediate hosts. Typically, eggs are shed into the water and hatch into a free-swimming stage that locates and infects another host. Arthropods are also known ectoparasites of amphibians. The copepod *Lernaea cyprinacea* has been found to infect tadpoles and mites (e.g., *Hannemania* spp., *Endotrombicula pillersi*) have been reported on adult frogs (Table 1). In addition, flies (e.g., *Bufo lucilia bufonivora*, *Lucilia caesar*) can use amphibians as hosts and leeches (e.g., *Desserobdella picta*) are also often found on both larval and adult amphibians.

KEY FINDINGS FROM STUDIES OF AMPHIBIAN MACROPARASITES

How and When are Amphibian Macroparasite Infections Important?

In contrast to the historical perspective of amphibian macroparasites being relatively benign, recent studies have revealed that some species can exert considerable effects on their hosts (Table 1). For example, trematode metacercariae have traditionally been thought of as “resting” stages causing little host pathology: “Even those parasites that utilize amphibians as intermediate hosts generally seem to do no more than inconvenience their hosts...” (Prudhoe and Bray 1982). This assumption is now being challenged in light of greater recognition that, for certain parasite species and over particular ranges of infection intensity, the pathology associated with macroparasite infections can be considerable. In North America, for instance, *R. ondatrae*

has been linked through field and experimental research to severe limb malformations in amphibian species, which can affect a significant proportion (e.g., 20–100%) of larval and metamorphic individuals in a population (Sessions and Ruth 1990; Johnson et al. 1999, 2002, 2011; Schotthoefer et al. 2003a; Rohr et al. 2010). These malformations impair host mobility and feeding while dramatically reducing the survival of affected individuals to maturity (Johnson et al. 2001; Goodman and Johnson 2011a, b). Similarly, echinostome trematodes that form cysts in tadpole kidneys, which sometimes number in the thousands, can be detrimental for young tadpoles (Fried et al. 1997; Schotthoefer et al. 2003b; Beasley et al. 2005; Holland 2010), causing renal failure and mortality at high infection levels.

Other helminth infections of amphibians also negatively impact their hosts, although considerably less is known about these groups. For example, the large cysts of *Clinostomum* spp. can cause scoliosis and *Diplostomulum scheuringi* can damage host eyes and brain (see Table 1), while adult lung flukes (*Haematoloechus* spp.) commonly found in adult frogs are now known to cause substantial tissue damage (see Table 1; Fig. 2). Such effects also can manifest indirectly through interactions with other factors. For instance, pathology from nematodes such as *Rhabdias* spp. and *Oswaldocruzia filiformis* (Table 1) likely influences host ecology under natural conditions. Cestode infections, such as that of *Nematotaenia dispar*, sometimes result in host pathology and death at high intensities (Elkan 1960) and monogenean infection in desert toads may affect their ability to survive hibernation and breed (Tinsley 1995).

Importantly, the most substantial effects of macroparasites are often sublethal and context dependent (Marcogliese and Pietrock 2011). Both abiotic and biotic

Table 2. Examples of studies examining environmental drivers of amphibian macroparasite infections

Environmental driver	Macroparasite							
	Trematode	Riberoia	Telorchis	General larval	Nematode	Cestode	Monogene	Insect
	Adult	Alaria	Echinostomes	Riberoia	Telorchis	General larval	General direct cycle	Rhabdias
Climate								
Temperature								
Rainfall				+(A2)				0 (A1) -(C3,4), +(A3,4) +(B3,4), +(B3,4)
Nutrients								
Eutrophication								
Phosphate								
Pesticides								
Atrazine								
Mixture								
Other								
Wetland traits								
Patch distance								
Vegetation								
Landscape								
Urbanization								
Forest								
Agriculture								
Water distance								
Biodiversity								
Predators								
Competitors								
Other hosts								
Other								
Stress								

List of environmental drivers assumes an increase/presence of each factor. Impacts on amphibian macroparasite infection denoted as: + increase in host infection, - decrease in host infection, 0 no impact on host infection. Putative mechanisms for effects are indicated by letters with numbered references.

Putative mechanisms: A parasite development, B parasite transmission, C host susceptibility, D host exposure, E parasite survival, F presence of other hosts, ? unknown.

References: 1 Thomas (1937), 2 Paull and Johnson (2011), 3 Tinsley (1995), 4 Tinsley and Jackson (2002), 5 Dare et al. (2006), 6 Raffel et al. (2010), 7 Thiemann and Wassersug (2000), 8 Belden and Wojdak (2011), 9 Johnson et al. (2008), 10 Johnson and Chase (2004), 11 Christen et al. (2003), 13 Griggs and Belden (2008), 14 Kiesecker (2002), 15 Rohr et al. (2008a), 16 Budischak et al. (2008), 17 Koprivnikar et al. (2007), 18 Koprivnikar et al. (2006a), 19 King et al. (2008), 20 Schothoef et al. (2011), 21 King et al. (2010), 22 Koprivnikar et al. (2006b), 23 McKenzie (2007), 24 King et al. (2007), 25 Pounds and Crump (1987), 26 Skelly et al. (2006), 27 Beasley et al. (2005), 28 Belden and Kiesecker (2005), and 29 Orlofske et al. (2012)

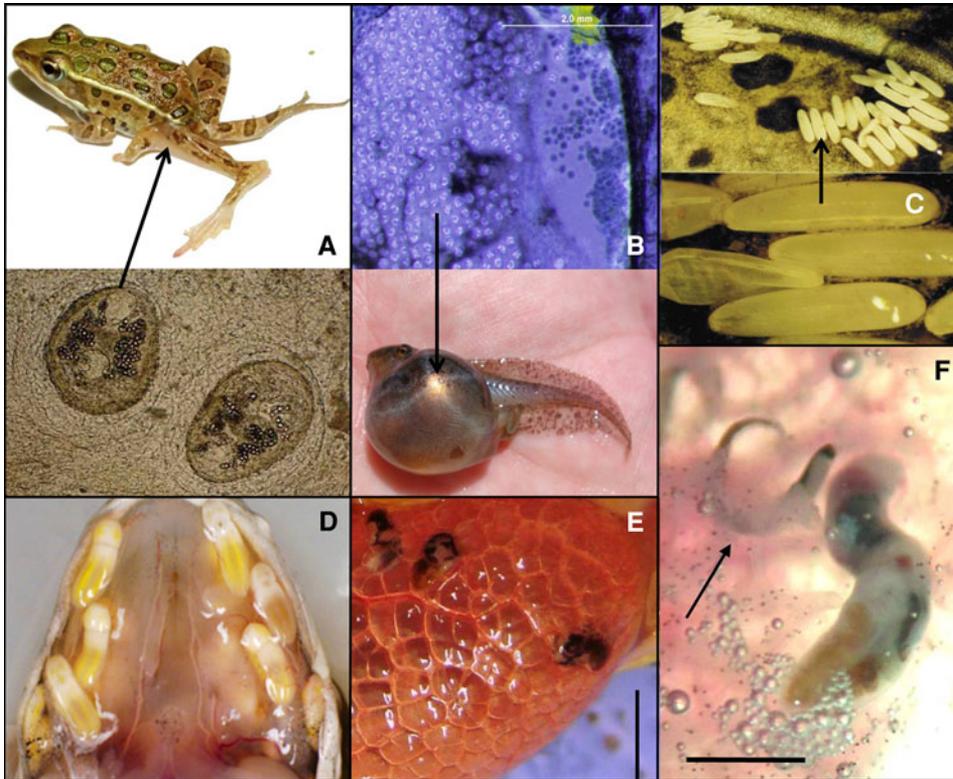


Fig. 2. a Malformed frog and associated *Ribeiroia ondatrae* metacercariae, b Echinostome metacercariae within an amphibian kidney and resulting edema, c Fly eggs on frog skin surface, d *Clinostomum* sp. metacercariae within frog mandible, e External surface of a bullfrog lung with three visible frog lung flukes, *H. floedae*, scale bar mm, f Inside a lung of a bullfrog infected with *H. floedae* and *R. joaquinensis* (arrow), scale bar 2 mm. (photos a–d courtesy of PTJ Johnson, photos e, f courtesy of MG Bolek)

factors can mediate how macroparasites impact their hosts (Lafferty and Holt 2003), with contaminants and predators playing important modulatory roles. For example, echinostome infection rarely has significant negative effects on tadpoles at low intensities (Schotthoefer et al. 2003b; Orlofske et al. 2009), but a combination of infection and pesticide exposure resulted in the decreased mass and survival of tadpoles relative to individuals subjected to stressor alone (Koprivnikar 2010). Similarly, a biomarker of host stress (dehydroretinol) was highest in bullfrogs both exposed to pesticides and infected with strigeid trematode cysts (Marcogliese et al. 2009) and nematode maturation in frog hosts was accelerated by host pesticide exposure (Gendron et al. 2003).

Johnson et al. (2006) reported synergistic increases in salamander malformations and growth impairment when injury from predation and *R. ondatrae* infections were combined, and a combination of trematode infection and predation resulted in lower larval survival than factor alone in another study (Belden and Wojdak 2011). Infection with *R. ondatrae* can result in malformations that significantly decrease frog host ability to respond to predation threats (Goodman and Johnson 2011a, b), similar to the increased vulnerability of helminth-infected red grouse to predators

(Hudson et al. 1992). Such parasite–host–predator dynamics may play a large role in host population fluctuations (Hudson et al. 1992). Other context-dependent effects have also been reported, such as pathology from larval amphibian leech infection depending on rearing temperature, food level, and population density (Berven and Boltz 2001), and many more likely occur, illustrating the need for further study of such interactive effects. Belden and Kiesecker (2005) found greater infection by the trematode *Alaria* spp. in tadpoles exposed exogenously to glucocorticoid stress hormones, indicating the importance of considering other stressors. Accordingly, attempting to elucidate macroparasite effects in isolation of other phenomena occurring in natural settings can lead to a serious underestimation of impacts on hosts and populations given that context dependency with respect to disease is now increasingly recognized as common (Marcogliese and Pietrock 2011).

One of the most important yet largely unexplored questions is whether the effects of macroparasites on individual amphibian hosts translate into population-level effects. Given that amphibians often have highly variable recruitment and substantial mortality in early life stages (e.g., larvae and metamorphs), pathology associated with

macroparasite infections may or may not have significant ramifications for host populations. Because macroparasites are unlikely to cause rapid die-offs or the complete extirpation of host populations, as is sometimes reported for Bd and ranavirus infections (Lips et al. 2006; Gray et al. 2009), detecting any population-level effects associated with macroparasites presents a greater challenge. For instance, even if trematodes, such as *R. ondatrae*, sharply reduce amphibian recruitment through both direct mortality and malformations, as seems likely when malformation frequency exceeds 50%, these effects are nearly impossible to detect without long-term data that accounts for potential “rescue” of affected populations from nearby sites without infection (i.e., source-sink dynamics; e.g., Martínez-Solano and González 2008). Given the ubiquity and diversity of macroparasite infections in amphibians, their potential to occur at very high intensities, and the documented effects of such parasites on other host taxa (Hudson et al. 1992, 1998; Albon et al. 2002), the potential for ecological and evolutionary effects of these parasites on amphibians is considerable. As of yet, no study has directly tackled this topic, which we identify as an important research priority in the continued study of amphibian macroparasites.

What Drives Macroparasite Infection in Amphibians and What Can This Tell Us?

Many environmental factors can affect host susceptibility to infection, transmission pathways via impacts on intermediate/definitive hosts and vectors, parasite development, and survival of parasite infectious stages (see Fig. 3; Table 2). Alterations of food webs or local biodiversity due to environmental stress likely will be reflected by changes in the parasite fauna dependent on them for transmission such that less-disturbed habitats should have a diverse array of species at all trophic levels, and thus a more diverse assemblage of parasites (Marcogliese 2005; Hudson et al. 2006). Owing to their typically complex life cycles, often depending on the co-occurrence of and interactions among multiple host species, macroparasites consequently have much potential for use as indicators of environmental stress, food web structure, and also biodiversity (Marcogliese 2004, 2005) given that host and macroparasite diversity are intricately linked (Hechinger and Lafferty 2005; Thieltges et al. 2011). Simply put, the more complex the life cycle and the greater the degree of parasite specialization on intermediate and definitive hosts, the greater

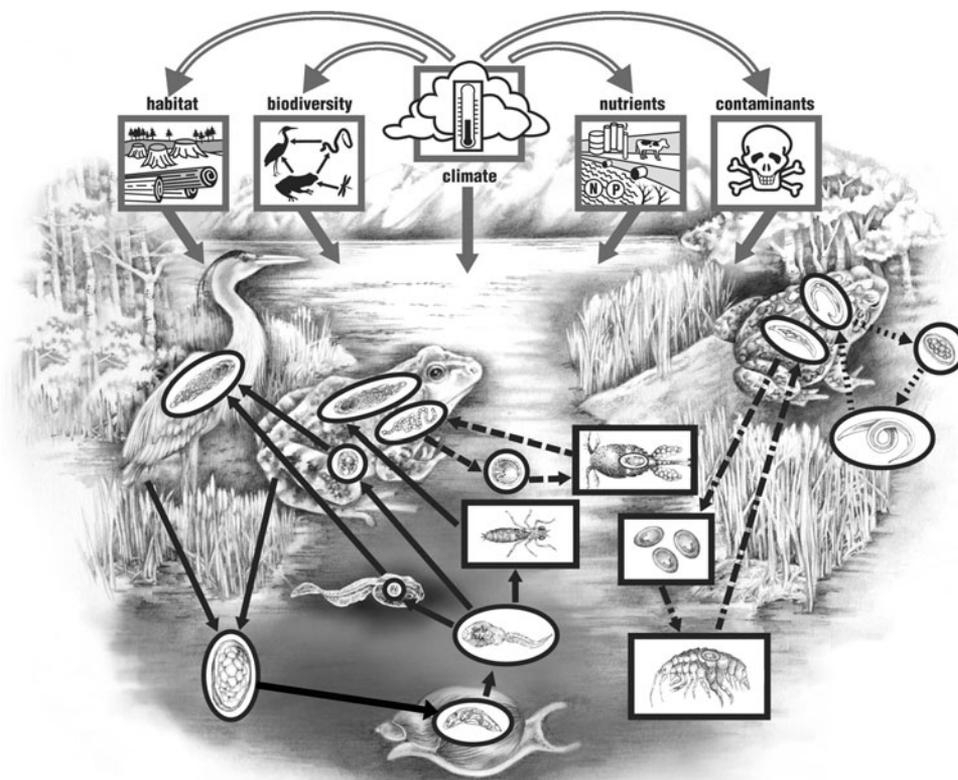


Fig. 3. The potential use of amphibian macroparasites as bio-indicators by virtue of their complex life cycles, varying degrees of host specialization, and capacity for disruption by environmental perturbations (artwork by Mary Jansen). *Solid lines* basic trematode life cycle, *long dashed lines* basic cestode life cycle, *short dashed lines* basic nematode life cycle, *dashed dotted lines* basic acanthocephalan life cycle. Note that in addition to direct effects, climate change has indirect impacts via effects on other environmental drivers (Marcogliese 2001)

the chances that one of the hosts or the parasite itself will be sensitive to a stressor, thus disrupting transmission and preventing the macroparasite from persisting in that habitat (Hudson et al. 1998, 2006; Lafferty and Holt 2003). These ideas have been explored for parasites of fishes in marine and freshwater environments (e.g., MacKenzie et al. 1995; Marcogliese 2004), but have not been widely extended to amphibians and wetland communities.

Because amphibians occur in many habitats (aquatic to terrestrial), have biphasic life cycles, occupy diverse trophic niches, and have a highly permeable integument, they have long been considered sentinel species for environmental perturbations (Hopkins 2007; but see Kerby et al. 2010). We suggest that macroparasites of amphibians could have even greater potential as sensitive bioindicators. This can come in (at least) two primary forms. First, the overall richness and composition of amphibian macroparasite communities can provide valuable information about food web structure and the intact linkages between aquatic and terrestrial ecosystems. Second, the presence and abundance of particular, highly pathogenic parasites can provide information about disease-related threats and, in some cases, forms of environmental perturbation. Below, we highlight the general roles of eutrophication, pesticides, climate change, habitat modification, and biodiversity on amphibian macroparasite interactions and also provide links with similar findings for other wildlife and human diseases.

Eutrophication

Nutrient run-off from erosion, fertilizers, and livestock has demonstrated impacts on amphibian trematode infections. Notably, these effects appear not to be driven by influences on amphibians themselves (Belden 2006), but on other hosts involved in the complex life cycle. Field correlations have been reported among nutrient levels, snail host density, and *R. ondatrae* infection in amphibians (Johnson and Chase 2004), and Skelly et al. (2006) suggested a similar pattern might apply to echinostome infections in amphibians from urban wetlands. Johnson et al. (2007) showed that eutrophication enhanced *R. ondatrae* infection through two related mechanisms: increases in the density of *R. ondatrae*-infected snails and per-snail production of cercariae, both driven by nutrient-mediated increases in algal growth. After controlling for an herbicide, Rohr et al. (2008a) found that phosphate, a common ingredient in fertilizer, was a significant positive predictor

of larval trematode abundance in amphibians. These studies with amphibians have clear applicability to other systems such that environmental nutrient enrichment may play a large role in disease emergence in humans and wildlife (McKenzie and Townsend 2007; Johnson et al. 2010a).

Contaminants

Pesticides can alter patterns of amphibian infection through changes in host immunity, host behavior, or host and parasite abundance (Kiesecker 2002; Christin et al. 2003; Rohr et al. 2008b). The herbicide atrazine has been shown to suppress amphibian immune function, increasing host susceptibility to various parasites (reviewed in Rohr and McCoy, 2010) and this type of effect has now been reported for other pesticides and host–macroparasite systems (e.g., Kelly et al. 2009). Of great concern is the discovery that short-term exposure of amphibian larvae to pesticides can result in their increased susceptibility to trematode infections later in development (Budischak et al. 2008), indicating that chronic contaminant exposure is not necessary. These laboratory-based results using amphibian macroparasites are supported by field observations, a rarity in most systems. Rohr et al. (2008b) reported that atrazine was the most important predictor of overall larval trematode abundance in leopard frogs among 18 Minnesota wetlands, verifying the causal relationship with a mesocosm experiment.

Habitat Alteration

Studies with amphibian macroparasites demonstrate that landscape can have considerable influences not necessarily by impacting amphibians, but other species involved in the often complex life cycles, thereby affecting parasite transmission. Land use, forest cover, and urbanization are significant predictors of trematode, nematode, and ectoparasite infection patterns in amphibians (Westfall et al. 2008; King et al. 2007, 2010; Schotthoefer et al. 2011; Koprivnikar and Redfern, in press). For example, the prevalence of a larval trematode using canids as final hosts in tadpoles is positively correlated with increased forest cover surrounding wetlands whereas that of host–generalist larval trematodes shows a different relationship (King et al. 2007; Schotthoefer et al. 2011; Koprivnikar and Redfern, in press). In addition, mean parasite species richness in individual frogs and total number of parasites were negatively associated with agricultural and

urban area surrounding wetlands (King et al. 2007, 2010). Investigations of human and other wildlife diseases are also increasingly incorporating geospatial tools, recognizing the importance of landscape-level dynamics and processes (e.g., Pfeiffer and Hugh-Jones 2002; Ostfeld et al. 2005).

Climate Change

Environmental changes arising from an altered climate are of general concern for both human and wildlife health, including risks posed by infectious diseases (e.g., Marcogliese 2001, 2008; Harvell et al. 2002; Rohr et al. 2011; Paull and Johnson, in press). These changes may result in catastrophic population-level effects in some systems (e.g., Mouritsen et al. 2005). There is now evidence that amphibian disease caused by microparasites, such as Bd, is linked to changes in temperature variability associated with climate alteration (Rohr and Raffel 2010) and climatic relationships with respect to macroparasites are also likely (Marcogliese 2001, 2008; Rohr et al. 2011). Effects of climate change can be manifested through altered parasite development and survival as well as impacts on amphibian susceptibility and tolerance to disease (Raffel et al. 2006a, 2011). For example, trematode maturation and cercarial production in snails are controlled largely by temperature (Poulin 2006; Morley et al. 2010) and owing to their smaller size and higher metabolic rates, these parasites may respond more strongly to warming than their hosts, with possible corresponding effects on pathology. Paull and Johnson (2011) reported temperature-driven increases in the growth of *R. ondatrae*-infected snails and parasite development, possibly resulting in increased overlap between infected snail and amphibian hosts. Tadpoles would then be exposed to infection risk during earlier and more vulnerable stages of development (Paull and Johnson 2011) without selection pressure on hosts to respond to such changes (Raffel et al. 2011). In addition, small changes in local temperatures may allow for macroparasite life cycle completion in habitats not normally allowing this. This could allow for amphibian macroparasite range expansions if climate change allows introduced parasites to establish and persist, such as the African monogenean *P. xenopodis* in Wales (Tinsley et al. 2011). Changes have also been reported for other macroparasite infections, such as faster within-host development of nematodes and increased prevalence of parasitic copepod infection, following increases in temperature (Griffin 1988; Hakalahti et al. 2006; Kupferberg et al. 2009).

While temperature increases are most commonly associated with global climate change, alterations of precipitation patterns could also have important effects on amphibian–macroparasite dynamics. Notably, the free-living larvae of many nematode species are greatly affected by moisture. Infections with both *Rhabdias hylae* and *R. bufonis* increase in their amphibian hosts during the rainy season (Plasota 1969; Barton 1998) and altered moisture conditions will likely affect interactions with other macroparasites as well. Kiesecker and Skelly (2001) reported that the presence of trematode-infected snails had strong negative effects on gray tree frog survivorship to metamorphosis in temporary but not permanent pools, suggesting that altered water levels may play an additional role.

Biodiversity Change

Recent studies have revealed that amphibian host community composition can play an enormous role in trematode parasite transmission. In lab and mesocosm experiments, Johnson et al. (2008) found that heterospecific amphibian communities containing larvae of two different species supported roughly half as many *R. ondatrae* cysts than did monospecific communities, supporting the “dilution effect” hypothesis which suggests that parasite pathology and abundance increase with decreases in host diversity (e.g., Keesing et al. 2006, 2010). Diverse communities can increase the number of “wasted” transmission events by decreasing the success of parasite infectious stages in finding a suitable hosts, whether due to dead-end hosts, predators, or even interactions with other parasites (Thieltges et al. 2008; Belden and Harris 2007; Johnson and Thieltges 2010). However, changes in host communities could also amplify infection risk to some species through the addition of competent hosts depending on the relationship between competency and order of assembly (e.g., Tompkins et al. 2000).

As previously noted, eutrophication promotes a greater density of gastropods serving as trematode first intermediate hosts. However, a predator-mediated shift in gastropod community composition favoring the species serving as hosts for *R. ondatrae* (Johnson and Chase 2004) illustrates how decreased diversity in this respect can also impact amphibian infection patterns. In addition, competent snail hosts for *R. ondatrae* predominate in low richness assemblages in the field while unsuitable hosts are increasingly present in more diverse snail communities (Johnson et al. 2012). Such findings are directly applicable

to other wildlife and human diseases. For example, Johnson et al. (2009) showed that increased snail diversity also reduces *Schistosoma mansoni* transmission and human infection risk. In addition, the presence of other species not directly involved in macroparasite life cycles, such as predators and conspecifics, can impact exposure to macroparasites by affecting larval amphibian developmental rate, altering anti-parasite behaviors, or consuming parasite infectious stages (Thiemann and Wassersug 2000; Schott-hoefer et al. 2007; Johnson et al. 2010b; Raffel et al. 2010; Koprivnikar et al. 2012; Orlofske et al. 2012).

CONCLUSIONS AND FUTURE DIRECTIONS

Based on the key findings highlighted above, we suggest future directions for research using amphibian–macroparasite systems that are also applicable for other host and parasites. We emphasize throughout the need to incorporate additional scales of inquiry, such as within-host and meta-community aspects.

Macroparasite Effects on Host Individuals

We currently lack a clear mechanistic understanding of how many macroparasites influence the condition of their amphibian hosts yet this is important to better understand potential environmental influences on host–parasite interactions. For instance, the effects of environmental contaminants on hosts may be mediated through pathways also affected by parasite infection (e.g., alterations of certain stress biomarkers and immunity), resulting in multiple stressors with potentially synergistic effects (Marcogliese and Pietrock 2011). Further investigations into sublethal effects of amphibian macroparasites on their hosts, and the circumstances under which these occur (e.g., in combination with predators, contaminants, temperature fluctuations, and other pathogens) are thus sorely needed. Similarly, little is known about the relationship between macroparasites and the amphibian immune system (e.g., Shutler et al. 2009), and examining the extent to which various amphibians possess immune memory (i.e., acquired immunity) to macroparasites will aid in understanding infection patterns (e.g., Raffel et al. 2006b). Distinction between different components of amphibian defenses, including host resistance and host tolerance (see Read et al. 2008; Råberg et al. 2009), will also be helpful in identifying the conditions under which macroparasites

cause pathology, incorporating factors such as the timing and intensity of infection as well as the host's immunity and behavior (e.g., Rohr et al. 2009, 2010; Daly and Johnson 2010; Johnson et al. 2011; Koprivnikar et al. 2012).

Using Amphibian Macroparasites as Bioindicators

To potentially use amphibian macroparasites as bioindicators, we must first determine whether they constitute specific and reliable gauges of their hosts and of impacts on host–parasite interactions resulting from environmental perturbations. This will require a more complete understanding of parasite transmission routes as some amphibian macroparasite life cycles are not yet fully understood (e.g., Bolek and Janovy 2008; Bolek et al. 2009). Such studies are now more feasible due to the development of tools such as “DNA barcodes,” which greatly improve macroparasite identification (e.g., Locke et al. 2011). Furthermore, it will be necessary to mount a concerted effort to establish and test the efficacy of particular macroparasites as bioindicators. Different parasites might be better for indicating different types of environmental perturbations (Blanar et al. 2009). Macroparasites with complex yet relatively host-specific life cycles, including trematode species such as *Halipegus* spp. and *Alaria* spp. (frog and canid final host, respectively), might be optimal for indicating effects on whole communities, whereas those with simpler life cycles, such as *Rhabdias* spp. nematodes, might be preferable for examining effects on amphibian host susceptibility. In addition, are such macroparasites actually more sensitive relative to their hosts? To be effective bioindicators, amphibian macroparasites should demonstrate changes resulting from perturbations before they are observed in more obvious groups. Related to this, it remains to be determined whether it is easier or more cost-effective to simply directly measure the factor of interest. For example, is it easier to sample frog macroparasites and look for *Alaria* spp. than to sample coyotes?

We particularly wish to emphasize that most amphibian macroparasite research efforts to date have largely focused on larval trematodes (mainly *R. ondatrae* and the echinostomes) and nematodes, leaving much opportunity for future research focused on other groups and species. A search in the Web of Science database using the timeframe of August 1899–2011 yielded the following numbers of results for terms combined with amphib*: trematode* (1004), nematode* (1975), cestod* (293), acanthocephal* (211), and monogene* (244). Using more

specific parasite search terms combined with amphib*, 64 results were found for *Ribeiroia**, 92 for echinostom*, and 174 for *Rhabdias**, respectively, illustrating the prominence of certain macroparasite groups and species in the literature.

Identifying the Roles of Amphibian Parasites in Ecological Communities

In addition to studies on individual hosts and parasites, future investigations must tackle questions at larger spatial and temporal scales. For example, there is still considerable debate as to whether the recent apparent increases in *R. ondatrae*-induced amphibian malformations constitute an “outbreak.” There are fewer than 10 published records of mass malformations between 1947 and 1990 but more than 50 mass malformation sites associated with *R. ondatrae* recorded since 1996, suggesting but not demonstrating an increase in parasite-driven amphibian deformities (Johnson et al. 2003). Given that both amphibian hosts and their parasites exhibit dramatic oscillations in abundance over time and among sites/hosts (Pechmann et al. 1991), a thorough evaluation of changes in the prevalence and occurrence of macroparasites in response to environmental perturbations requires the establishment of field sites for long-term monitoring.

Correspondingly, it will be very difficult to determine how macroparasites affect host populations without field studies encompassing significant time periods and geographic ranges. For example, *R. ondatrae* can cause extensive host mortality and pathology (Schotthoefler et al. 2003a; Johnson et al. 2011) and studies have noted a link between high levels of malformations and decreased host performance and survival (Johnson et al. 2001; Goodman and Johnson 2011a, b), but a connection to population-level effects remains conjectural. Ideally, a combination of long-term monitoring, mark-recapture data, and ecosystem-level manipulations (e.g., parasite removal or addition) should be used to address this issue, as has been effective in understanding the effects of macroparasites in other systems (see Hudson et al. 1998). Any such studies must also recognize that population-level effects of parasites on their hosts are likely highly context dependent with the potential to interact with environmental stressors (Lafferty and Holt 2003). In addition, macroparasite effects on host populations, when present, often occur through subtler and more complex pathways, such as increasing predation upon infected hosts (Hudson et al. 1992; Murray

et al. 1997; Hatcher et al. 2006) or decreasing host reproduction (Hudson et al. 1998; Albon et al. 2002).

In the context of amphibian disease, it is particularly important for researchers to be able to extrapolate from empirical studies to field studies and the reverse, especially if the goal is to relate environmental factors with naturally occurring infection patterns. The co-ordination of findings from multiple locations through the development of a centralized and shared database, (e.g., <http://data.whirlingdisease.montana.edu>, www.mammalparasites.org, amphibianparasites.org), would facilitate efforts at large-scale data collection and analysis. This type of database would help researchers examine environmental influences on infection patterns, determine which macroparasites represent emerging diseases, and compile better records regarding parasite range and host use.

Beyond their potential applied importance, amphibians and macroparasites represent an excellent opportunity to address meta-community-level questions about the general role(s) of pathogens in ecological systems (e.g., Leibold et al. 2004; Holyoak et al. 2005; Lafferty et al. 2008). Numerous studies now support the importance of parasites as vital links in communities and ecosystems (Lafferty 2008; Lafferty et al. 2008; Poulin 2010). Because amphibian macroparasites weave into food webs at various levels, they have the potential to exert general effects on both terrestrial and aquatic communities. We must, therefore, improve our understanding of how parasites indirectly influence ecological interactions, such as competition and predation, in addition to studying direct effects on host survival and fitness.

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REFERENCES

- Albon SD, Stien A, Irvine RJ, Langvatn R, Ropstad E, Halvorsen O (2002) The role of parasites in the dynamics of a reindeer population. *Proceedings of the Royal Society of London, Series B* 269:1625–1632
- Anderson RC (2000) *Nematode Parasites of Vertebrates: Their Development and Transmission, 2nd ed.*, Wallingford: CABI Publishing
- Anthony CD, Mendelson JR, Simons RR (1994) Differential parasitism by sex on plethodontid salamanders and histological evidence for structural damage to the nasolabial groove. *American Midland Naturalist* 132:302–307
- Barton DP (1998) Dynamics of natural infections of *Rhabdias cf. hylae* (Nematoda) in *Bufo marinus* (Amphibia) in Australia. *Parasitology* 117:505–513
- Beasley VR, Faeh SA, Wikoff B, Staehle C, Eisold J, Nichols D, et al. (2005) Risk factors and the decline of the cricket frog, *Acris crepitans*: evidence for involvement of herbicides, parasitism, and habitat modifications. In: *Amphibian Declines: The Conservation Status of United States Species*, Lannoo MJ (editor), Chicago: University of Chicago Press, pp 75–87
- Belden LK (2006) Impact of eutrophication on wood frog tadpoles, *Rana sylvatica*, infected with *Echinostoma trivolvis* cercariae. *Canadian Journal of Zoology* 84:1315–1321
- Belden LK, Kiesecker JM (2005) Glucocorticosteroid hormone treatment of larval treefrogs increases infection by *Alaria* sp. trematode cercariae. *Journal of Parasitology* 91:686–688
- Belden LK, Harris RN (2007) Infectious diseases in wildlife: the community ecology context. *Frontiers in Ecology and the Environment* 10:533–539
- Belden LK, Wojdak JM (2011) The combined influence of trematode parasites and predatory salamanders on wood frog (*Rana sylvatica*) tadpoles. *Oecologia* 166:1077–1086
- Berven KA, Boltz RS (2001) Interactive effects of Leech (*Desseirobella picta*) infection on Wood Frog (*Rana sylvatica*) tadpole fitness traits. *Copeia* 2001:907–915
- Blonar CA, Munkittrick KR, Houlihan J, Maclatchy DL, Marcogliese DJ (2009) Pollution and parasitism in aquatic animals: a meta-analysis of effect size. *Aquatic Toxicology* 93:18–28
- Bolek MG, Coggins JR (2002) Observations on myiasis by the calliphorid, *Bufolucilia silvarum*, in the eastern American toad (*Bufo americanus americanus*) from southeastern Wisconsin. *Journal of Wildlife Diseases* 38:598–603
- Bolek MG, Janovy J Jr (2004) Observations on myiasis by the calliphorids, *Bufolucilia silvarum* and *Bufolucilia elongata*, in wood frogs, *Rana sylvatica*, from southeastern Wisconsin. *Journal of Parasitology* 90:1169–1171
- Bolek MG, Janovy J Jr (2008) Alternative life cycle strategies of *Megalodiscus temperatus* in tadpoles and metamorphosed anurans. *Parasite* 15:396–401
- Bolek MG, Snyder SD, Janovy J Jr (2009) Alternative life cycle strategies and colonization of young anurans by *Gorgoderina attenuata* in Nebraska. *Journal of Parasitology* 95:604–616
- Brayton C (1992) Wasting disease associated with cutaneous and renal nematodes. *Annals of the New York Academy of Science* 653:197–201
- Brockelman WY (1969) An analysis of density effects and predation in *Bufo americanus* tadpoles. *Ecology* 50:632–644
- Budischak SA, Belden LK, Hopkins WA (2008) Effects of Malathion on embryonic development and latent susceptibility to trematode parasites in ranid tadpoles. *Environmental Toxicology and Chemistry* 27:2496–2500
- Byers JE, Altman I, Grosse AM, Huspeni TC, Maerz JC (2011) Using parasitic trematode larvae to quantify an elusive vertebrate host. *Conservation Biology* 25:85–93
- Christin MS, Gendron AD, Brousseau P, Ménard L, Marcogliese DJ, Cyr D, et al. (2003) Effects of agricultural pesticides on the immune system of *Rana pipiens* and on its resistance to parasitic infection. *Environmental Toxicology and Chemistry* 22:1127–1133
- Cohen N, Efrige NJ, Parsons SC, Rollins-Smith LA, Nagata S, Albright D (1984) Identification and treatment of a lethal nematode (*Capillaria xenopodis*) infestation in the South African frog, *Xenopus laevis*. *Developmental and Comparative Immunology* 8:739–741
- Collins JP, Crump ML (2009) *Extinction in Our Times: Global Amphibian Decline*, New York: Oxford University Press
- Cort WW, Brackett S (1938) A new strigeid cercaria which produces a bloat disease of tadpoles. *Journal of Parasitology* 24:263–271
- Daly EW, Johnson PTJ (2010) Beyond immunity: quantifying the effects of host anti-parasite behavior on parasite transmission. *Oecologia* 165:1043–1050
- Dare OK, Rutherford PL, Forbes MR (2006) Rearing density and susceptibility of *Rana pipiens* metamorphs to cercariae of a digenetic trematode. *Journal of Parasitology* 92:543–547
- Daszak P, Cunningham AA, Hyatt AD (2000) Emerging infectious diseases of wildlife: threats to biodiversity and human health. *Science* 287:443–449
- Elkan E (1960) Some interesting pathological cases in amphibians. *Proceedings of the Zoological Society of London* 134:275–296
- Etges FT (1961) Contributions to the life history of the brain fluke of newts and fish, *Diplostomulum scheuringi* Hughes 1929 (Trematoda. Diplostomatidae). *Journal of Parasitology* 47:453–458
- Fried B, Pane PL, Reddy A (1997) Experimental infection of *Rana pipiens* tadpoles with *Echinostoma trivolvis* cercariae. *Parasitology Research* 83:666–669
- Gendron AD, Marcogliese DJ, Barbeau S, Christin M-S, Brousseau P, Ruby S, et al. (2003) Exposure of leopard frogs to a pesticide mixture affects life history characteristics of the lungworm *Rhabdias ranae*. *Oecologia* 135:469–476
- Goater CP, Ward PI (1992) Negative effects of *Rhabdias bufonis* (Nematoda) on the growth and survival of toads (*Bufo bufo*). *Oecologia* 89:161–165
- Goater CP, Semlitsch RD, Bernasconi MV (1993) Effects of body size and parasite infection on the locomotory performance of juvenile toads *Bufo bufo*. *Oikos* 66:129–136
- Goin CJ, Ogren LH (1956) Parasitic copepods (Argulidae) on amphibians. *Journal of Parasitology* 42:172
- Goodman BA, Johnson PTJ (2011) Disease and the extended phenotype: parasites control host performance and survival through induced changes in body plan. *PLoS One* 6:e20193

- Goodman BA, Johnson PTJ (2011) Ecomorphology and disease: understanding the cryptic effects of parasitism on host habitat use, thermoregulation, and predator avoidance. *Ecology* 92:542–548
- Gray MJ, Miller DL, Hoverman JT (2009) Ecology and pathology of amphibian ranaviruses. *Diseases of Aquatic Organisms* 87:243–266
- Green D, Muths E (2005) Health evaluation of amphibians in and near Rocky Mountain National Park (Colorado, USA). *Alytes (Paris)* 22:109–129
- Griffin CT (1988) The effect of constant and changing temperatures on the development of the eggs and larvae of *Oswaldocruzia filiformis* (Nematoda: Trichostrongyloidea). *Journal of Helminthology* 62:281–292
- Griggs JL, Belden LK (2008) Effects of atrazine and metolachlor on the survivorship and infectivity of *Echinostoma trivolvis* trematode cercariae. *Archives of Environmental Contamination and Toxicology* 54:195–202
- Hakalahti T, Karvonen A, Valtonen ET (2006) Climate warming and disease risks in temperate regions—*Argulus coregoni* and *Diplostomum spathaceum* as case studies. *Journal of Helminthology* 80:93–98
- Harvell CD, Mitchell CE, Ward JR, Altizer S, Dobson AP, Ostfield RS, et al. (2002) Climate warming and disease risks for terrestrial and marine biota. *Science* 296:2158–2162
- Hatcher MJ, Dick JTA, Dunn AM (2006) How parasites affect interactions between competitors and predators. *Ecology Letters* 9:1253–1271
- Hechinger RF, Lafferty KD (2005) Host diversity begets parasite diversity: bird final hosts and trematodes in snail intermediate hosts. *Proceedings of the Royal Society of London. Series B* 272:1059–1066
- Hendriks WML, Van Moppes MC (1983) *Oswaldocruzia filiformis* (Nematoda: Trichostrongylidae): Morphology of developmental stages, parasitic development and some pathological aspects of the infection in amphibians. *Parasitology Research* 69:523–537
- Holland MP (2010) Echinostome-induced mortality varies across amphibian species in the field. *Journal of Parasitology* 96:851–855
- Holland MP, Skelly DK, Kashgarian M, Bolden SR, Harrison LM, Cappello M (2007) Echinostome infection in green frogs (*Rana clamitans*) is stage and age dependent. *Journal of Zoology* 271:455–462
- Holmstead PR, Hudson PJ, Skorping A (2005) The influence of a parasite community on the dynamics of a host population: A longitudinal study on willow ptarmigan and their parasites. *Oikos* 111:377–391
- Holyoak MM, Leibold A, Mouquet NM, Holt RD, Hoopes MF (2005) Metacommunities: a framework for large-scale community ecology. In: *Metacommunities: Spatial Dynamics and Ecological Communities*, Holyoak M, Leibold MA, Holt RD (editors), Chicago: University of Chicago Press, pp 1–31
- Hopkins WA (2007) Amphibians as models for studying environmental change. *Institute for Laboratory Animal Research Journal* 48:270–277
- Hsu CC, Carter DB, Williams DA, Besch-Williford CL (2004) *Haematoloechus* sp. infection in wild-caught northern leopard frogs (*Rana pipiens*). *Contemporary Topics in Laboratory Animal Science* 43:14–16
- Hudson PJ, Dobson AP, Newborn D (1992) Do parasites make prey vulnerable to predation? Red grouse and parasites *Journal of Animal Ecology* 61:681–692
- Hudson PJ, Dobson AP, Newborn D (1998) Prevention of population cycles by parasite removal. *Science* 282:2256–2258
- Hudson PJ, Dobson AP, Lafferty KD (2006) Is a healthy ecosystem one that is rich in parasites? *Trends in Ecology & Evolution* 21:381–385
- Jayawardena UA, Rajakaruna RS, Navaratne AN, Amerasinghe PH (2010) Monostome cercariae induced malformations in amphibians: effect of infection at the pre-limb-bud stag tadpoles of *Polypedates cruciger* Blyth. *Journal of the National Science Foundation of Sri Lanka* 38:241–248
- Johnson PTJ, Chase JM (2004) Parasites in the food web: linking amphibian malformations and aquatic eutrophication. *Ecology Letters* 7:521–526
- Johnson PTJ, Thieltges DW (2010) Diversity, decoys and the dilution effect: how ecological communities affect disease risk. *Journal of Experimental Biology* 213:961–970
- Johnson PTJ, Lunde KB, Ritchie EG, Launer AE (1999) The effect of trematode infection on amphibian limb development and survivorship. *Science* 284:802–804
- Johnson PTJ, Lunde KB, Haight RW, Bowerman J, Blaustein AR (2001) *Ribeiroia ondatrae* (Trematoda: Digenea) infection induces severe limb malformations in western toads (*Bufo boreas*). *Canadian Journal of Zoology* 79:370–379
- Johnson PTJ, Lunde KB, Thurman EM, Ritchie EG, Wray SW, Sutherland DR, et al. (2002) Parasite (*Ribeiroia ondatrae*) infection linked to amphibian malformations in the western United States. *Ecological Monographs* 72:151–168
- Johnson PTJ, Lunde KB, Zelmer DA, Werner JK (2003) Limb deformities as an emerging parasitic disease in amphibians: evidence from museum specimens and resurvey data. *Conservation Biology* 17:1724–1737
- Johnson PTJ, Preu ER, Sutherland DR, Romansic J, Han B, Blaustein AR (2006) Adding infection to injury: synergistic effects of predation and parasitism on salamander limb malformations. *Ecology* 87:2227–2235
- Johnson PTJ, Chase JM, Dosch KL, Hartson RB, Gross JA, Larson DJ, et al. (2007) Aquatic eutrophication promotes pathogenic infection in amphibians. *Proceedings of the National Academy of Sciences USA* 104:15781–15786
- Johnson PTJ, Hartson RB, Larson DJ, Sutherland DR (2008) Diversity and disease: community structure drives parasite transmission and host fitness. *Ecology Letters* 11:1017–1026
- Johnson PTJ, Lund PJ, Hartson RB, Yoshino TP (2009) Community diversity reduces *Schistosoma mansoni* transmission and human infection risk. *Proceedings of the Royal Society of London. Series B* 276:1657–1663
- Johnson PTJ, Townsend AR, McKenzie VJ, Howarth R, Rejmankova E, Glibert P (2010) Linking environmental nutrient enrichment and disease emergence in humans and wildlife. *Ecological Applications* 20:16–29
- Johnson PTJ, Dobson A, Lafferty KD, Marcogliese DJ, Memmott J, Orlofske S, et al. (2010) When parasites become prey: ecological and epidemiological significance. *Trends in Ecology & Evolution* 25:362–371
- Johnson PTJ, Kellermanns E, Bowerman J (2011) Critical windows of disease risk: amphibian pathology driven by developmental changes in host resistance and tolerance. *Functional Ecology* 25:726–734
- Johnson PTJ, Preston DL, Hoverman JT, Henderson JS, Paull SH, Redmond MD (2012) Species diversity reduces parasite infection through cross-generational effects on host density. *Ecology* 93:56–64
- Jones KE, Patel N, Levy MA, Storeygard A, Balk D, Gittleman JL, Daszak P (2008) Global trends in human emerging infectious diseases. *Nature* 451:990–993

- Keesing F, Holt RD, Ostfeld RS (2006) Effects of species diversity on disease risk. *Ecology Letters* 9:485–498
- Keesing F, Belden LK, Daszak P, Dobson A, Harvell CD, Holt RD, et al. (2010) Impacts of biodiversity on the emergence and transmission of infectious diseases. *Nature* 468:647–652
- Kelehear C, Jones HI (2010) Nematode larvae (Order Spirurida) in gastric tissues of Australian anurans: a comparison between the introduced cane toad and sympatric native frogs. *Journal of Wildlife Diseases* 46:1126–1140
- Kelehear C, Webb JK, Shine R (2009) *Rhabdias pseudosphaerocephala* infection in *Bufo marinus*: lung nematodes reduce viability of metamorph cane toads. *Parasitology* 136:919–927
- Kelehear C, Brown GP, Shine R (2011) Influence of lung parasites on the growth rates of free ranging and captive adult cane toads. *Oecologia* 165:585–592
- Kelly DW, Poulin R, Tompkins DM, Townsend CR (2009) Synergistic effects of glyphosate formulation and parasite infection on fish malformations and survival. *Journal of Applied Ecology* 47:498–504
- Kerby JL, Richards-Hrdlicka KL, Storfer A, Skelly DK (2010) An examination of amphibian sensitivity to environmental contaminants: are amphibians poor canaries? *Ecology Letters* 13: 60–67
- Kiesecker JM (2002) Synergism between trematode infection and pesticide exposure: a link to amphibian limb deformities in nature? *Proceedings of the National Academy of Sciences USA* 99:9900–9904
- Kiesecker JM, Skelly DK (2001) Effects of disease and pond drying on gray tree frog growth, development and survival. *Ecology* 82:1956–1963
- Kilpatrick AM, Briggs CJ, Daszak P (2010) The ecology and impact of chytridiomycosis, an emerging disease of amphibians. *Trends in Ecology & Evolution* 25:109–118
- King KC, McLaughlin JD, Gendron AD, Pauli BD, Giroux I, Rondeau B, et al. (2007) Impact of agriculture on the parasite communities of northern leopard frogs (*Rana pipiens*) in southern Quebec, Canada. *Parasitology* 134:2063–2080
- King KC, Gendron AD, McLaughlin JD, Giroux I, Brousseau P, Cyr D, et al. (2008) Short-term seasonal changes in parasite community structure in northern leopard froglets (*Rana pipiens*) inhabiting agricultural wetlands. *Journal of Parasitology* 94:13–22
- King KC, McLaughlin JD, Boily M, Marcogliese DJ (2010) Effects of agricultural landscape and pesticides on parasitism in native bullfrogs. *Biological Conservation* 143:302–310
- Koprivnikar J (2010) Interactions of environmental stressors impact survival and development of parasitized larval amphibians. *Ecological Applications* 20:2263–2272
- Koprivnikar J, Redfern JC Agricultural effects on amphibian parasitism: importance of general habitat perturbations and parasite life cycles. *Journal of Wildlife Diseases* (in press)
- Koprivnikar J, Forbes MR, Baker RL (2006) Effects of atrazine on cercarial longevity, activity, and infectivity. *Journal of Parasitology* 92:306–311
- Koprivnikar J, Forbes MR, Baker RL (2006) On the efficacy of anti-parasite behaviour: a case study of tadpole susceptibility to cercariae of *Echinostoma trivolvis*. *Canadian Journal of Zoology* 84:1623–1629
- Koprivnikar J, Forbes MR, Baker RL (2007) Contaminant effects on host-parasite interactions: atrazine, frogs, and trematodes. *Environmental Toxicology and Chemistry* 26:2166–2170
- Koprivnikar J, Forbes MR, Baker RL (2008) Larval amphibian growth and development under varying density: are parasitized individuals poor competitors? *Oecologia* 155:641–649
- Koprivnikar J, Gibson CH, Redfern JC (2012) Infectious personalities: behavioural syndromes and disease risk in larval amphibians. *Proceedings of the Royal Society of London. Series B* 279:1544–1550
- Kupferberg SJ, Catenazzi A, Lunde K, Lind AJ, Palen WJ (2009) Parasitic copepod (*Lernaea cyprinacea*) outbreaks in foothill yellow-legged frogs (*Rana boylei*) linked to unusually warm summers and amphibian malformations in northern California. *Copeia* 3:529–537
- Lafferty KD (2008) Ecosystem consequences of fish parasites. *Journal of Fish Biology* 73:2083–2093
- Lafferty KD, Holt RD (2003) How should environmental stress affect the population dynamics of disease? *Ecology Letters* 6: 654–664
- Lafferty KD, Allesina S, Arim M, Briggs CJ, De Leo G, Dobson AP, et al. (2008) Parasites in food webs: the ultimate missing links. *Ecology Letters* 11:533–546
- Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, et al. (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601–613
- Lips KR, Brem F, Brenes R, Reeve JD, Alford RA, Voyles J, et al. (2006) Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. *Proceedings of the National Academy of Sciences USA* 103:3165–3170
- Locke SA, McLaughlin JD, Lapierre AR, Johnson PTJ, Marcogliese DJ (2011) Linking larvae and adults of *Apharyngostrigea cornu*, *Hysteromorpha triloba* and *Alaria mustelae* (Diplostomoidea, Digenea) using molecular data. *Journal of Parasitology* 97: 846–851
- MacKenzie K, Williams HH, Williams B, McVicar AH, Siddall R (1995) Parasites as indicators of water quality and the potential use of helminth transmission in marine pollution studies. *Advances in Parasitology* 35:85–144
- Marcogliese DJ (2001) Implications of climate change for parasitism of animals in the aquatic environment. *Canadian Journal of Zoology* 79:1331–1352
- Marcogliese DJ (2004) Parasites: small players with crucial roles in the ecological theatre. *EcoHealth* 1:151–164
- Marcogliese DJ (2005) Parasites of the superorganism: are they indicators of ecosystem health? *International Journal for Parasitology* 35:705–716
- Marcogliese DJ (2008) The impact of climate change on the parasites and diseases of aquatic animals. *Revue Scientifique et Technique de l'OIE* 27:467–484
- Marcogliese DJ, Cone DK (1997) Parasite communities as indicators of ecosystem stress. *Parasitologia* 39:227–232
- Marcogliese DJ, Pietrock M (2011) Combined effects of parasites and contaminants on animal health: parasites do matter. *Trends in Parasitology* 27:123–130
- Marcogliese DJ, King KC, Salo HM, Fournier M, Brousseau P, Spear P, et al. (2009) Combined effects of agricultural activity and parasites on biomarkers in the bullfrog, *Rana catesbeiana*. *Aquatic Toxicology* 91:126–134
- Marr SR, Johnson SA, Hara AH, McGarrity ME (2010) Preliminary evaluation of the potential of the helminth parasite *Rhabdias elegans* as a biological control agent for invasive

- Puerto Rican coquis, *Eleutherodactylus coqui*, in Hawaii. *Biological Control* 54:69–74
- Martínez-Solano I, González EG (2008) Patterns of gene flow and source-sink dynamics in high altitude populations of the common toad *Bufo bufo* (Anura: Bufonidae). *Biological Journal of the Linnean Society* 95:824–839
- McKenzie VJ (2007) Human land use and patterns of parasitism in tropical amphibian hosts. *Biological Conservation* 137:102–116
- McKenzie VJ, Townsend AR (2007) Parasitic and infectious disease responses to a changing nitrogen cycle. *EcoHealth* 4:384–396
- Merilä J, Sterner M (2002) Medicinal leeches (*Hirudo medicinalis*) attacking and killing adult amphibians. *Annales Zoologici Fennici* 39:343–346
- Morley NJ, Adam ME, Lewis JW (2010) The effects of host size and temperature on the emergence of *Echinoparyphium recurvatum* cercariae from *Lymnaea peregra* under natural light conditions. *Journal of Helminthology* 84:317–326
- Mouritsen KN, Tompkins DM, Poulin R (2005) Climate warming may cause a parasite-induced collapse in coastal amphipod populations. *Oecologia* 146:476–483
- Murray DL, Cary JR, Keith LB (1997) Interactive effects of sublethal nematodes and nutritional status on showshoe hare vulnerability to predation. *Journal of Animal Ecology* 66:250–264
- Nigrelli RF, Maraventano LW (1944) Pericarditis in *Xenopus laevis* caused by *Diplostomulum xenopi* sp. nov., a larval strigeid. *Journal of Parasitology* 30:184–190
- Orlowski SA, Belden LK, Hopkins WA (2009) Moderate *Echino-stoma trivolvis* infection has no effects on physiology and fitness-related traits of larval pickerel frogs (*Rana palustris*). *Journal of Parasitology* 95:787–792
- Orlowski SA, Jadin RC, Preston DL, Johnson PTJ (2012) Parasite transmission in complex communities: predators and alternative hosts alter pathogenic infections in amphibians. *Ecology* 93:1247–1253
- Ostfeld RS, Glass GE, Keesing F (2005) Spatial epidemiology: an emerging (or re-emerging) discipline. *Trends in Ecology & Evolution* 20:328–336
- Ostfeld RS, Keesing F, Eviner VT (2008) *Infectious Disease Ecology: Effects of Ecosystems on Disease and of Disease on Ecosystems*, Princeton: Princeton University Press
- Paull SH, Johnson PTJ (2011) How will climate change affect host-parasite interactions? Understanding differential responses of hosts and parasites *Freshwater Biology* 56:767–778
- Paull SH, Johnson PTJ (2012) Can we predict climate-driven changes to disease dynamics? Applications for theory and management in the face of uncertainty. In: *Wildlife Conservation in a Changing Climate*, Brodie J, Post E, Doak D (editors), Chicago: University of Chicago Press
- Pechmann JHK, Scott DE, Semlitsch RD, Caldwell JP, Vitt LJ, Gibbons JW (1991) Declining amphibian populations: the problem of separating human impacts from natural fluctuations. *Science* 253:892–895
- Perpignan D, Garner MM, Trupkiewicz JG, Malarchik J, Armstrong DL, Lucio-Forster A, et al. (2010) Scoliosis in a tiger salamander (*Ambystoma tigrinum*) associated with encysted digenetic trematodes of the genus *Clinostomum*. *Journal of Wildlife Diseases* 46:579–584
- Pfeiffer DU, Hugh-Jones M (2002) Geographical information systems as a tool in epidemiological assessment and wildlife disease management. *Revue Scientifique et Technique de l'OIE* 21:91–102
- Pietrock M, Marcogliese DJ (2003) Free-living endohelminth stages: at the mercy of environmental conditions. *Trends in Parasitology* 19:293–299
- Pizzatto L, Shine R (2011) The effects of experimentally infecting Australian tree frogs with lungworms (*Rhabdias pseudosphaerocephala*) from invasive cane toads. *International Journal for Parasitology* 41:943–949
- Pizzatto L, Shilton CM, Shine S (2010) Infection dynamics of the lungworm *Rhabdias pseudosphaerocephala* in its natural host, the cane toad (*Bufo marinus*), and in novel hosts (native Australian frogs). *Journal of Wildlife Diseases* 46:1152–1164
- Plasota K (1969) The effect of some ecological factors on the parasitofauna of frogs. *Acta Parasitologica Polonica* 16:47–60
- Poulin R (2006) Global warming and temperature-mediated increases in cercarial emergence in trematode parasites. *Parasitology* 132:143–151
- Poulin R (2010) Network analysis shining light on parasite ecology and diversity. *Trends in Parasitology* 26:492–498
- Pounds JA, Crump ML (1987) Harlequin frogs along a tropical montane stream: aggregation and the risk of predation by frog-eating flies. *Biotropica* 19:306–309
- Prudhoe S, Bray RA (1982) *Platyhelminth Parasites of the Amphibia*, Oxford: Oxford University Press
- Råberg L, Graham AL, Read AF (2009) Decomposing health: tolerance and resistance to parasites in animals. *Philosophical Transactions of the Royal Society B-Biological Sciences* 364:37–49
- Raffel TR, Rohr JR, Kiesecker JM, Hudson PJ (2006) Negative effects of changing temperature on amphibian immunity under field conditions. *Functional Ecology* 20:819–828
- Raffel TR, LeGros RP, Love BC, Rohr JR, Hudson PJ (2006) Parasite age-intensity relationships in red-spotted newts: does immune memory influence salamander disease dynamics? *International Journal for Parasitology* 39:231–241
- Raffel TR, Hoverman JR, Halstead NT, Michel P, Rohr JR (2010) Parasitism in a community context: trait-mediated interactions with competition and predation. *Ecology* 91:1900–1907
- Raffel TR, Lloyd-Smith JO, Sessions SK, Hudson PJ, Rohr JR (2011) Does the early frog catch the worm? Disentangling potential drivers of a parasite age-intensity relationship in tadpoles *Oecologia* 165:1031–1042
- Rajakaruna RS, Piyatissa PMJR, Jayawardena UA, Navaratne AN, Amerasinghe PH (2008) Trematode infection induced malformations in the common hourglass treefrogs. *Journal of Zoology* 275:89–95
- Read AF, Graham AL, Raberg L (2008) Animal defenses against infectious agents: is damage control more important than pathogen control? *PLoS Biology* 6:2638–2641
- Rohr JR, McCoy KA (2010) A quantitative meta-analysis reveals consistent effects of atrazine on freshwater fish and amphibians. *Environmental Health Perspectives* 118:20–32
- Rohr JR, Raffel TR (2010) Linking global climate and temperature variability to widespread amphibian declines putatively caused by disease. *Proceedings of the National Academy of Sciences USA* 107:8269–8274
- Rohr JR, Schotthoefer AM, Raffel TR, Carrick HJ, Halstead N, Hoverman JT, et al. (2008) Agrochemicals increase trematode infections in a declining amphibian species. *Nature* 455:1235–1240

- Rohr JR, Raffel TR, Sessions SK, Hudson PJ (2008) Understanding the net effects of pesticides on amphibian trematode infections. *Ecological Applications* 18:1743–1753
- Rohr JR, Swan A, Raffel TR, Hudson PJ (2009) Parasites, info-disruption, and the ecology of fear. *Oecologia* 159:447–454
- Rohr JR, Raffel TR, Hall CA (2010) Developmental variation in resistance and tolerance in a multi-host–parasite system. *Functional Ecology* 24:1110–1121
- Rohr JR, Dobson AP, Johnson PTJ, Kilpatrick AM, Paull SH, Raffel TR, et al. (2011) Frontiers in climate change–disease research. *Trends in Ecology & Evolution* 26:270–277
- Schotthoefer AM, Koehler AV, Meteyer CU, Cole RA (2003) Influence of *Ribeiroia ondatrae* (Trematoda: Digenea) infection on limb development and survival of northern leopard frogs (*Rana pipiens*), effects of host stage and parasite-exposure level. *Canadian Journal of Zoology* 81:1144–1153
- Schotthoefer AM, Cole RA, Beasley VR (2003) Relationship of tadpole stage to location of echinostome cercariae encystment and the consequences for tadpole survival. *Journal of Parasitology* 89:475–482
- Schotthoefer AM, Labak KM, Beasley R (2007) *Ribeiroia ondatrae* cercariae are consumed by aquatic invertebrate predators. *Journal of Parasitology* 93:1240–1243
- Schotthoefer AM, Rohr JR, Cole RA, Koehler AV, Johnson CM, Johnson LB, et al. (2011) Effects of wetland and landscape variables on parasite communities of *Rana pipiens*: links to anthropogenic changes. *Ecological Applications* 21:1257–1271
- Sessions SK, Ruth SB (1990) Explanation for naturally-occurring supernumerary limbs in amphibians. *Journal of Experimental Zoology* 254:38–47
- Shields JD (1987) Pathology and mortality of the lung fluke *Haematoloechus longiplexus* (Trematoda) in *Rana catesbeiana*. *Journal of Parasitology* 73:1005–1013
- Shutler D, Smith TG, Robinson SR (2009) Relationship between leukocytes and *Hepatozoon* spp. in green frogs, *Rana clamitans*. *Journal of Wildlife Diseases* 45:67–72
- Skelly DK, Bolden SR, Holland MP, Friedenburgh LK, Friedenfelds NA, Malcom TR (2006) Urbanization and disease in amphibians. In: *Disease Ecology: Community Structure and Pathogen Dynamics*, Collinge SK, Ray C (editors), Cary, NC: Oxford University Press, pp 153–167
- Skerratt LF, Berger L, Speare R, Cashins S, McDonald KR, Phillott AD, et al. (2007) Spread of chytridiomycosis has caused the rapid global decline and extinction of frogs. *EcoHealth* 4:125–134
- Sladky KK, Norton TM, Loomis MR (2000) Trombiculid mites (*Hannemania* sp.) in canyon tree frogs (*Hyla arenicolor*). *Journal of Zoo and Wildlife Medicine* 31:570–575
- Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues ASL, Fischman DL, et al. (2004) Status and trends of amphibian declines and extinctions worldwide. *Science* 306:1783–1786
- Stunkard HW, Cable RM (1931) Notes on a species of *Lernaea* parasitic on the larva of *Rana clamitans*. *Journal of Parasitology* 18:92–97
- Sutherland DR (2005) Parasites of North American frogs. In: *Amphibian Declines: The Conservation Status of United States Species*, Lannoo MJ (editor), California: University of California Press, pp 109–123
- Thieltges DW, Jensen KT, Poulin R (2008) The role of biotic factors in the transmission of free-living endohelminth stages. *Parasitology* 135:407–426
- Thieltges DW, Hof C, Dehling DM, Braendle M, Brandl R, Poulin R (2011) Host diversity and latitude drive trematode diversity patterns in the European freshwater fauna. *Global Ecology and Biogeography* 20:675–682
- Thiemann GW, Wassersug RJ (2000) Patterns and consequences of behavioural responses to predators and parasites in *Rana* tadpoles. *Biological Journal of the Linnean Society* 71:513–528
- Thomas LJ (1937) Environmental relations and life history of the tapeworm *Bothriocephalus rarus* Thomas. *Journal of Parasitology* 23:133–152
- Tinsley RC (1995) Parasitic disease in amphibians: control by the regulation of worm burdens. *Parasitology* 111:S153–S178
- Tinsley RC, Jackson JA (2002) Host factors limiting monogenean infections: a case study. *International Journal for Parasitology* 32:353–365
- Tinsley RC, Cable J, Porter R (2002) Pathological effects of *Pseudodiplorchis americanus* (Monogenea: Polystomatidae) on the lung epithelium of its host, *Scaphiopus couchii*. *Parasitology* 125:143–153
- Tinsley RC, York JE, Everard ALE, Stott LC, Chapple SJ, Tinsley MC (2011) Environmental constraints influencing survival of an African parasite in a north temperate habitat: effects of temperature on egg development. *Parasitology* 138:1029–1038
- Toque K (1993) The relationship between parasite burden and host resources in the desert toad (*Scaphiopus couchii*), under natural conditions. *Journal of Animal Ecology* 62:683–693
- Tocque K, Tinsley RC (1994) The relationship between *Pseudodiplorchis americanus* (Monogenea) density and host resources under controlled environmental conditions. *Parasitology* 108:175–183
- Tompkins DM, Draycott RAH, Hudson PJ (2000) Field evidence for apparent competition mediated via the shared parasites of two gamebird species. *Ecology Letters* 3:10–14
- Westfall MC, Cecala KK, Price SJ, Dorcas ME (2008) Patterns of trombiculid mite (*Hannemania dunni*) parasitism among plethodontid salamanders in the western piedmont of North Carolina. *Journal of Parasitology* 94:631–634
- Williams RW (1960) Observations on the Life History of *Rhabdias sphaerocephala* Goodey, 1924 from *Bufo marinus* L., in the Bermuda Islands. *Journal of Helminthology* 34:93–98