DR. DEBORAH BOWER (Orcid ID : 0000-0003-0188-3290)

Article type   : Research Article

A review of the role of parasites in the ecology of reptiles and amphibians

Deborah S. Bower[1, 2], Laura A. Brannelly[3], Cait A. McDonald[4], Rebecca J. Webb[5], Sasha E. Greenspan[6], Mathew Vickers[1], Michael G. Gardner[7,8], Matthew J. Greenlees[9].

Affiliation:

[1]College of Science and Engineering, James Cook University, Townsville, 4811, Queensland, Australia, deborah.bower@gmail.com, +61(0) 413334587, (Corresponding author)

[2]School of Environmental and Rural Science, University of New England, Armidale, New South Wales 2350, Australia.

[3] Department of Biological Sciences, University of Pittsburgh, Pittsburgh, Pennsylvania 15260, United States of America

[4] Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14853, United States of America

[5]College of Public Health, Medical and Veterinary Sciences, James Cook University, Townsville, Queensland 4811, Australia

[6] Department of Biological Sciences, University of Alabama, Tuscaloosa, Alabama 35487, United States of America

[7]College of Science and Engineering, Flinders University, GPO Box 2100, Adelaide, South Australia 5001, Australia

[8]Evolutionary Biology Unit, South Australian Museum, North Terrace, Adelaide 5000 South Australia, Australia.

Author Manuscript

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/aec.12695

This article is protected by copyright. All rights reserved

[9] School of Life and Environmental Sciences, University of Sydney, New South Wales 2006 Australia

Key words:

Pathogen, Parasite, Disease, Behaviour, Physiology,

Abstract:

A great diversity of parasites, from viruses and bacteria to a range of remarkable eukaryotic organisms, exploit reptile and amphibian hosts. Recent increases in the emergence of infectious disease have revealed the importance of understanding the effects of interactions between hosts and their parasites. Here we review the effects of parasite infection on a range of demographic, behavioural, genomic and physiological factors in reptile and amphibian species. Reviewing these parasite roles collectively, and prioritising areas for research, advances our ecological understanding and guides direction for conservation in a time of rapid species decline. Poorly resolved systems include Gymnophionan amphibians and Crocodilian hosts, in addition to viral and bacterial parasites. Future research should seek to understand processes enabling population recovery and examining synergistic interactions of parasites with fragmentation, climate change and other processes that threaten species persistence.

Author Manuscript

1. **Introduction**

Parasites have been historically underrepresented in ecological studies but are slowly gaining recognition. The difficulties involved in visual identification and classification (McManus and Bowles 1996), lack of statistical power owing to small sample size, and poor preservation of hosts for subsequent examination, has hindered our ability to quantify parasite and thus incorporate their effects into ecological research. Perhaps owing to the comparative ease of accounting for competing ecological processes such as those in predator-prey systems, parasite systems have received comparatively less attention (Raffel *et al.* 2008). Recent advances in genomic technology and recognition of the severe impacts of parasites have catalysed research that was not previously possible or prioritized (Huggins *et al.* 2017; McKnight *et al.* 2017).

Reptiles and amphibians are a paraphyletic group of vertebrates (Field *et al.* 2014) united by their ectothermic physiology and primarily terrestrial habits. Unlike taxa that serve as important

This article is protected by copyright. All rights reserved

human food resources such as fish, or aesthetically appealing groups such as mammals and birds, amphibians and reptiles (e.g. snakes, lizards and frogs) are less valued by society (Czech *et al.* 1998); this is reflected by their disproportionately lower representation in published literature (Hecnar 2009). Understanding reptiles and amphibians is important because they are species rich with almost 8000 described amphibian species and over 10000 reptile species. They can obtain high biomass and play important roles in the ecosystem including as prey, consumers, pollinators, dispersers, nutrient cycling and bioturbators of soil (Godínez-Álvarez 2004; Iwai and Kagaya 2007; Lovich *et al.* 2018; Sin *et al.* 2008). Reptiles and amphibians have become increasingly vulnerable to extinction and thus research focused on understanding threatening factors to aid in conservation has recently become a priority (Gibbon *et al.* 2000; Meredith *et al.* 2016).

In conservation, the paucity of ecological knowledge in the context of amphibian disease ecology became evident during the global amphibian decline (Collins and Storfer 2003). Biologists were not prepared for disease-induced declines, and pioneering studies on parasites became invaluable to understand host physiology and behaviour, as well as broad ecological processes. The increased emergence of infectious disease over the past two decades has only served to consolidate the importance of understanding the ecological interactions between hosts and parasites (Bower *et al.* 2017b). As the importance of research that quantifies the effects of parasites is increasingly recognised, a review of these studies is timely.

A leader in this field was the late Professor Michael Bull, and his pioneering work arises repeatedly throughout the various subtopics of our review. Here we aim to pay homage to the foresight and dedication of Michael Bull by demonstrating the importance of parasites in the ecology of reptiles and amphibians. We draw from the available literature to highlight the diversity and extent to which parasites and hosts are intertwined in fundamental ecological processes. Specifically, we focus on summarising our knowledge of parasite impacts on reptiles and amphibians, and highlight challenges we face in continuing to unravel these complex relationships.

2. **Diversity of parasites**

Author Manuscript

This article is protected by copyright. All rights reserved

The term parasite encapsulates a taxonomically diverse selection of organisms. They are physiologically dependent on other organisms and, unlike predators, have higher reproductive potential than their host (Crofton 1971). Here we take the ecological definition of parasites as ‘any organism that decreases the fitness of its host by infecting it’ and include both micro-parasites (e.g., viruses and bacteria) and macro-parasites (e.g., worms) (May and Anderson 1990; Méthot and Alizon 2014). Parasites can have a range of effects that differ according to host species, host physiology, host behaviour and environment. There are several taxa of parasites that use reptile (crocodiles, turtles, tuatara, amphisbaenians, lizards and snakes) and amphibian (frogs, salamanders and caecillians) hosts.

2.1 Viruses

Owing to their miniscule size, viruses were not described until long after their effects were known and their role in ecology remains poorly understood. They are intracellular parasites and cannot replicate outside a host. Transmission can occur directly through contact with infected hosts or reservoir surfaces, or via vectors such as ticks and mosquitoes (Marschang 2011). Spanning an extreme spectrum of effects, viruses can range in impact from appearing benign in populations to causing mass mortality events. They also vary from being highly specific to broad in host range and can be zoonotic (transmissible from animals to humans), though pathogenicity toward different hosts is not well understood for most viruses (Ariel 2011). Despite their ability to significantly hinder conservation efforts, some suspected pathogenic viruses remain unresolved as causal agents (e.g. chelonid fibropapilloma associated herpesvirus). The recent characterization of the shingleback nidovirus (O’Dea *et al.* 2016) highlights just how little we know about virology in comparatively well-studied reptile species, in this case sleepy lizards (*Tiliqua rugosa*), variously known as shinglebacks, or bobtails. Associated with the disease syndrome coined ‘bobtail flu’, globally this is the first report of such a virus in a lizard. Other viruses (e.g ranavirus) have been the subject of ecological studies because they threaten populations of reptiles and amphibians and in these cases, much has been documented on transmission and susceptibility (Gray *et al.* 2009).

2.2 Bacteria

Author Manuscript

This article is protected by copyright. All rights reserved

Bacteria are receiving increasing attention for the role they may play in host ecology. Exploration into the function of microbiomes has accelerated this research field, owing in part to the inhibitory effects of bacteria on other pathogens such as the amphibian chytrid fungus (*Batrachochytrium dendrobatidis*, *Bd*) (Jani and Briggs 2014). From an ecological perspective, the ubiquitous nature of bacteria make them problematic for detection and quantification, and understanding when bacteria are pathogenic and under what circumstances continues to challenge researchers (Ramakrishnan *et al.* 1997). Species that cannot be cultured *in vitro* make Koch's postulates difficult to fulfill though sequencing is a powerful tool that is allowing us to unravel interactions among bacteria that we could not previously examine (Byrd and Segre 2016). We do not know how bacteria interact in wild populations for many species, despite their ability to cause bacterial septicemia in captive populations (e.g. *Aeromanas hydrophila*, (Mauel et al. 2002; Pasquale et al. 1994)), and the lack of histopathological confirmation leaves uncertainty surrounding the cause of some wild die-offs. Pioneering research has demonstrated the importance of social networks (Bull *et al.* 2012) and reservoir species in transmission and population biology of specific bacteria (Giery and Ostfeld 2007). Bacterial zoonotic diseases have been the subject of some experimental ecological studies, e.g., those demonstrating antibiotic resistance in human-disturbed sites (Wheeler *et al.* 2012). *Salmonella* spp. infections can potentially spill over in the pet trade (Whiley *et al.* 2017), but the threat from wildlife appears low (Parsons *et al.* 2010).

2.3 Blood (Erythrocytic) parasites

Blood parasites are a paraphyletic group of eukaryotic organisms that occur in the blood stream of hosts (e.g. phylum Apicomplexa). Some of the most extensive long term ecological studies have quantified the effects of blood parasites on the behavior and physiology of squamate hosts (Otero *et al.* 2017; Schall 1982). These have incorporated the paradoxical trade-off in sacrificing parasitic defenses to increase fitness opportunity, only to pay associated costs of increased parasite intensity (Bouma *et al.* 2007). Generally, lizards and blood parasites (e.g Malaria) have proved useful models to address evolutionary questions of diversification and adaptation.

Despite comprehensive ecological studies on squamates and blood parasites, amphibians have received relatively little attention. Recent work demonstrating sexual differences in trypanosome

Author Manuscript

This article is protected by copyright. All rights reserved

prevalence (*Trypanosoma tungarae*) in túngara frogs (*Physalaemus pustulosus*) suggests interesting ecological interactions are at play; frog-biting midges that find their host by male mating calls may be a vector in this system (Bernal and Pinto 2016). The ecological role of other parasites such as Perkinsea-like protists also correlate with mass declines and disease of tadpoles, and are widely distributed throughout the globe (Chambouvet *et al.* 2015). Other parasites such as Mesomycetozoeans (fungal-like opisthokonts) are little known (Rowley *et al.* 2013) though declines of at least one frog species are correlated with an outbreak (Di Rosa *et al.* 2007). As technologies are applied to these understudied groups, further relationships between host and parasites are likely to be revealed.

2.4 Fungi

The global emergence of fungal diseases and associated mass die-offs in a diversity of reptile and amphibian species has brought mycoses (diseases caused by fungi) to the forefront of research and conservation. The number of extirpation events caused by fungi has increased in recent decades, and many losses of amphibian species are included in these events (Fisher *et al.* 2012). The emergence of two distinct species of chytrid fungi (*Batrachochytrium dendrobatidis* and *B. salamandrivorans*) has caused multi-continental amphibian declines, which led to an explosion in ecological studies incorporating these parasites (Bower *et al.* 2017a). Additionally, an emerging fungal disease (associated with *Ophidiomyces ophiodiicola*) causing epidemics in snakes is receiving increasing attention (Allender *et al.* 2015). Marine turtles have also suffered disease associated with *Fusarium* spp. infection causing mass mortality in nests, particularly in stressful environmental conditions (Sarmiento-Ramírez *et al.* 2010). While other potentially lethal fungi have been identified (e.g. *Mucor amphibiorum, Paranannizziopsis australasiensis*), research has been restricted to quantifying prevalence (Masters *et al.* 2016; Speare *et al.* 1994). A potentially deadly fungus, Lecanicillium spp., was diagnosed in a captive colony of endangered Guthega skinks (*Liopholis guthega*) causing cutaneous and systemic mycosis and provided the first report of this infection in reptiles. Beyond these few examples, ecology of fungal pathogens in reptiles and amphibians is little known.

2.5 Animals

Endoparasites

Author Manuscript

This article is protected by copyright. All rights reserved

A diversity of animals parasitise reptiles and amphibians. Myxosporean parasites (Cnidarians) are mostly known from fish, but will also infect reptile and amphibian species (Eiras 2005). Comprehensive ecological studies detailing prevalence and effects in wild populations are lacking (Okamura *et al.* 2018), though myxosporean parasites can reach high loads and cause disease in captive frogs (Hartigan *et al.* 2011), and they may have emerged in distribution recently (Hartigan *et al.* 2010).

Helminths such as pentastomids (respiratory tract), cestodes, trematodes, nematodes, and acanthocephalans are a diverse group of animals clustered together by their worm like appearance and featuring as important parasites in reptile and amphibian health (Koprivnikar *et al.* 2012). Studies of parasitic worms have moved beyond taxonomic description to incorporation into occupancy modelling (Campião *et al.* 2012), behaviour (Gyawali *et al.* 2013; Pfennig and Tinsley 2002), and physiological costs of infection (Goater and Ward 1992), as well as how infection interacts with the environment (Soliman 2012).

Ectoparasites

Studies on the behavioural and physiological interactions of ectoparasites such as ticks and mites in reptile and amphibian ecology have also been extensive, forming a substantial component of the life work of Michael Bull (Godfrey and Gardner 2017). Ticks (*Bothriocroton hydrosauri*) on sleepy lizards (*T. rugosa*) and other bluetongues (*T. spp.*) have been identified as vectors for the bacterial agent causing spotted fever (i.e. the bacteria *Rickettsia* sp.) (Stenos *et al.* 2003; Whiley *et al.* 2016). Flies and mosquitoes have also received some attention in ecological studies, both as direct parasites and vectors (Bernal *et al.* 2007). Additionally, the ecological interactions of leeches have been explored in salamanders (Lunghi *et al.* 2018) and turtles, which can harbor high densities of over 150 leeches on a single turtle (Graham *et al.* 1997). They further act as vectors for blood parasites e.g. for haemogregarines and trypanosomes (Siddall and Desser 1992).

3. Environmental Interactions

The environment of the host can strongly influence parasite dynamics. Reptiles and amphibians are ectotherms, and as such, their physiological processes are governed by ambient temperature.

Author Manuscript

This article is protected by copyright. All rights reserved

Author Manuscript

Behavioural thermoregulation is a consequence of parasite infection in both reptiles (Schall & Sarni 1987, Main & Bull 2000) and amphibians (Lefcort & Eiger 1993, Lefcort & Blaustein 1995, Richards-Zawacki 2009). Their immune system is at the mercy of environmental conditions, and sub-optimal temperature can cause immunosuppression in many species. For example, in cold stunned Kemp's ridley sea turtles (*Lepidochelys kempii*) in Massachusetts, most of the pathological changes observed were associated with bacteria and or fungi. These were suspected to be opportunistic infections due to host immunosuppression caused by the cold temperatures (Innis *et al.* 2009). Prolonged exposure to low temperatures during hibernation resulted in weakened immune systems in leopard frogs (*Lithobates* [*Rana*] *pipiens*) (Cooper *et al.* 1992), and a lizard called the sandfish skink (*Scincus scincus*) had reduced lymphoid tissues and immune response in winter (Hussein *et al.* 1979). In other cases, suboptimal temperatures may elicit an increased immune response resulting in better resistance to disease. Green Tree frogs (*Litoria caerulea*) experimentally acclimated to low temperatures had lower infection intensities when exposed to the amphibian chytrid fungus (*B. dendrobatidis)* than those acclimated to higher temperatures (Greenspan *et al.* 2017b). The individuals exposed to sub-optimal temperature were better able to fight the pathogen because their immune parameters were already adjusted to cope with the challenging environmental conditions. The cool-exposed individuals had a higher neutrophil:lymphocyte ratio, a response also seen in leopard frogs (*L. pipiens*) (Maniero and Carey 1997).

Along with temperature, other external factors can influence the immune system of hosts and their ability to resist infection. Juvenile leopard frogs (*L. pipiens*) experimentally exposed to agricultural pesticides experienced lower lymphocyte proliferation which have a central role in pathogen defense. Higher nematode burdens (Christin *et al.* 2003) and trematode infection can increase exposure and susceptibility by augmenting intermediate snail hosts and reduce liver eosinophil (disease-fighting blood cells) counts, indicative of a reduced immunity (Rohr *et al.* 2008). In addition, UVB radiation causes immunosuppression in amphibians and increases susceptibility to disease (Little and Calfee 2010). Heavy metal toxicity can also cause immunosuppression. For example, mercury concentrations were correlated with reduced lymphocyte proliferation and activity in Loggerhead sea turtles (*Caretta caretta*) (Day *et al.* 2007). The viral disease ‘green turtle fibropapillomatosis’ affects all sea turtle species, and

This article is protected by copyright. All rights reserved

infected individuals also present with reduced lymphocyte proliferation and activity, suggesting that heavy metal contamination such as mercury may make turtles more susceptible (Grillitsch and Schiesari 2010).

Stress-induced physiological changes may increase the incidence of disease in reptiles and amphibians. Environmental stressors such as desiccation of ponds cause tadpoles to metamorphose faster, and this can have a trade off in terms of immunocompetence. Wood frog (*Lithobates sylvaticus*) tadpoles exposed to experimental desiccation have fewer lymphocytes and reduced responses to immune challenge after metamorphosis (Gervasi and Foufopoulos 2008). Newly metamorphed amphibians are disproportionally more vulnerable to the amphibian chytrid fungus (*B. dendrobatidis)* infection, so immune suppression due to environmental stressors can have a dramatic effect on susceptibility (Gervasi and Foufopoulos 2008). The effects of stress on host susceptibility may also have conservation implications. For example, the stress of capture and release into an unfamiliar environment caused a higher rate of disease in translocated Timber Rattlesnakes (*Crotalus horridus*) compared to resident animals (Reinert and Rupert Jr 1999). High densities can reduce immunity and this can be age dependent within a species. For example, higher densities of adults of the lizard (*Zootoca vivipara*) experienced increased local inflammation and high densities of tick infestation (*Ixodes ricinus*) whereas yearlings did not experience inflammation or increased tick infestation (Mugabo *et al.* 2015). Habitat features can also affect parasites differently. In a Mediteranean lizard (*Psammodromus algrius*), the prevalence and infection load of blood parasites was higher in a high elevation deteriorated habitat whereas prevalence and infection load of ticks (Ixodes sp) showed the reverse pattern (Carbayo *et al.* 2018).

4. Behaviour

Amphibians have formed a significant focus of research into behavioural effects of parasites. Much attention has been devoted to understanding the ways in which parasites manipulate their hosts following infection (Finnerty *et al.* 2018; Klein 2003; Moore 1984; Smith Trail 1980). Where the effects of parasites on hosts are deleterious, behavioural strategies that help the host avoid initial infection should be favoured by evolution. Amphibians can recognise and avoid both physical and chemical cues from some potential parasites. Frogs adopt various strategies

Author Manuscript

This article is protected by copyright. All rights reserved

such as foot-stomping, jumping, and wiping their hands over their bodies to prevent mosquito bites, which minimises transmission of mosquito-borne parasites (Ferguson and Smith 2012). Grey tree frogs *Dryophytes* [*Hyla*] *versicolor* discriminated between water bodies based not only on the presence and density of a gastropod vector that carries a trematode parasite of their tadpoles, but also on whether or not the snails were infected, laying less frequently and fewer eggs in treatments with a higher likelihood of infection (Kiesecker and Skelly 2000). There is species-specific variation in the behaviour of tadpoles toward the presence of trematodes (*Echinoparyphium* sp.) (Koprivnikar *et al.* 2014). Permanent pond breeding frogs that were more likely to encounter trematodes (*Echinostoma* spp.) modified their activity in the presence of these parasites. Conversely, ephemeral breeding frog species that encountered less trematodes also lacked the behavioural response, suggesting selection may occur on such behavioural traits (Szuroczki and Richardson 2012). Parasite avoidance behaviour is complex and interacts with predators, whereby tadpoles (*L. pipiens*) preferred areas without trematodes (*Ribeiroia ondatrae)* unless their alternative was predator exposure by larval odonates (Koprivnikar and Penalva 2015). American toad tadpoles (*Bufo americanus*) fleed from the touch of a trematode (*Echinostoma sp.*) (Taylor *et al.* 2004), and tadpoles adopted behaviours that influenced the site in which infection occurred and thus decreased the pathological consequences of infection (Kiesecker *et al.* 1999; Sears *et al.* 2013). Selection against cannibalism is thought to have evolved as a behaviour to minimise parasite transmission between intraspecific hosts. For example, larval tiger salamanders (*Ambystoma tigrinum*) avoided preying on conspecifics with bacterial infection (*Clostridium* sp. bacteria) (Pfennig *et al.* 1998; Pfennig *et al.* 1991). In other cases tadpoles (*Pseudacris regilla* and *Anaxyrus boreas*) did not adopt behaviours to minimise transmission by snails infected with a trematode parasite (*R. ondatrae),* but once infected, decreased their activity and escape distance (Preston *et al.* 2014). Interestingly, the same study showed two less virulent trematodes (*Echinostoma* sp. and *Alaria* sp.) caused no such effects.

Surprisingly, few studies have revealed behaviours that minimise or reduce potential transmission of ectoparasites in reptiles, despite the negative physiological consequences (Aubret *et al.* 2014; Biaggini *et al.* 2009; Godfrey *et al.* 2006). Although one exception in the usually monogamous sleepy lizard (*T. rugosa*) showed that males that are abandoned by females

Author Manuscript

This article is protected by copyright. All rights reserved

between mating seasons have higher tick loads than males that retain their partners, thereby reducing infection potential for females (Bull and Burzacott 2006). As many endoparasites of reptiles are transmitted via their prey, the potential for avoidance may be difficult. Notably, several studies on blood parasites (*Hepatozoon* sp.) in snakes that demonstrated negative effects on nutritional status, reproduction and survival (Madsen *et al.* 2005*)* revealed little effect on behaviour. Keelback snakes *(Tropidonophis mairii*) infected with parasites (Family: Haemogregarinidae and Gnathostomidae) had similar performance (e.g. ‘sprint’ speed) and fitness measures (e.g. escape distance) to uninfected individuals (Brown *et al.* 2006).

Many of the studied behavioural changes in hosts are investigated as a limited single species comparison (Damas-Moreira *et al.* 2014; Daniels 1985; Oppliger *et al.* 1996). These studies often explore only the alteration in behaviour without examining underlying mechanisms. However, there are a number of notable studies that explore complex interactions that note both changes in behaviour of the host and the consequences of these changes for ecology and evolution. These complex interactions have often been demonstrated using lizards, specifically *Lacerta*, *Anolis* and *Sceloporus* spp., as model organisms. These studies demonstrated that *Plasmodium* sp. infection altered male social behaviour (Schall 1982), in part due to altered thermoregulatory and perching behaviour of hosts (Schall and Sarni 1987). Similarly, *Plasmodium* sp. infection altered the outcome of competitive interactions between two species of lacertid lizard, ultimately playing a critical role in determining the distribution of each species on a landscape scale (Schall 1992; Schall and Vogt 1993). Finally, ectoparasites (ticks *Aponomma hydrosauri* and *Amblyomma limbatum*) can affect simple behaviours in sleepy lizards (*T. rugosa*) such as the time spent basking, moving and ultimately dispersing (Main and Bull 2000) but under natural conditions these hosts appear adapted to the ticks and movement is more strongly explained by sex and body condition independent of ticks (Taggart *et al.* 2018). Effects can be intergenerational, in female common lizards (*Z. vivipara*), parasitism by mites (Family: Lealapidae) effected the dispersal behaviour of the offspring (Sorci *et al.* 1994). Such studies highlight the importance of parasites in shaping behaviours that intricately influence the ecology of animals and suggest that any ecological study that wishes to quantify behaviour should attempt to account for possible influences of parasites.

Author Manuscript

This article is protected by copyright. All rights reserved

Some of the most detailed behavioural studies have arisen as a result of specific threats to the persistence of species, thus much research has been invested in understanding the amphibian chytrid fungus (*B. dendrobatidis)* (Pounds *et al.* 2006). The disease (chytridiomycosis) caused by the fungus (*B. dendrobatidis)* has, in some cases, selected for species and individuals that behave in a particular way. For example, the thermal history of different rainforest frog species strongly affected their probability of infection (Rowley and Alford 2013) and this related to the thermal sensitivity of the *B. dendrobatidis* (Daskin *et al.* 2011; Greenspan *et al.* 2017c). Exposure to the *B. dendrobatidis* changed host behavior, reducing escape capacity and foraging in different tadpole species (Han *et al.* 2011; Venesky *et al.* 2009).

Another prominent behaviour of anurans, and an obvious subject of such research with profound consequences for ecology and life history, is reproductive calling. Seasonal patterns of calling resulted from interactions between infection by *B. dendrobatidis* and body condition in the Common mist frog *Litoria rheocola* (Roznik *et al.* 2015). Similarly, Japanese tree frogs *Dryophytes* [*Hyla*] *japonicas* called more rapidly and for longer when infected with the *B. dendrobatidis* (An and Waldman 2016). Contrary to these results, calling was reduced in Brazilian subtropical treefrog (*Hypsiboas prasinus*) infected with helminth parasites and this was exacerbated in smaller individuals (Madelaire *et al.* 2013). Conversely, Grey Treefrog (*H. versicolour*) calling characteristics remained unchanged, though males with greater parasite loads achieved more amplexus (Hausfater *et al.* 1990). In spadefoot toads (*Scaphiopus couchii*), males parasitised by a monogenean worm (*Pseudodiplorchis americanus*) had more attractive calls to females, thereby skewing female choice (Pfennig and Tinsley 2002). While calling duration in Cururu toads (*Rhinella icterica*) was not affected by nematode lungworms (*Rhabdius sp*.), locomotory performance was reduced and this may have played some role in the capacity of toads to find and mate with females (Moretti *et al.* 2014; Moretti *et al.* 2017).

Another model system in the study of the effects of parasites on anuran movement is the infamous invasion of cane toads (*Rhinella* [*Bufo*] *marina*) in Australia (Shine 2010). As is the case with many invasive species, use of ‘natural’ parasites has been explored for potential capacity in control for toads specifically, to mitigate the rate of invasion (Tingley *et al.* 2017). Survival and growth rate of metamorph cane toads (*R. marina*) was reduced, alongside impaired

Author Manuscript

This article is protected by copyright. All rights reserved

locomotory performance and reduced prey intake when infected with *Rhabdius pseudospaheracephala*) (Kelehear *et al.* 2009) and toads showed no tendency to avoid areas inhabited by a lungworm, nor demonstrated the capacity to avoid infection (Kelehear *et al.* 2011). However, infection did not affect dispersal behaviour of adult toads (Brown *et al.* 2016). A bacteria *(Ochrobactrum anthropi)* was also explored as a causative agent of spinal arthropathy in cane toads (*R. marina*) (Brown *et al.* 2007; Shilton *et al.* 2008), though the effects on toads appear to relate to climate and growth (Bower *et al.* 2018).

Original theoretical frameworks of disease ecology assumed that parasite burden and effects were directly related to parasite abundance and distribution within the host population, with all individuals having an equal, random chance of infection (Anderson 1978). More recently, emphasis has shifted towards a social network style of analysis (Bull *et al.* 2012; Godfrey 2013), with evidence that context and interactions between individuals strongly effect parasite transmission and parasite species assemblages. For example, social association in the sleepy lizard (*T. rugosa*) had a stronger link to parasite sharing and transmission than did common resource use (Bull *et al.* 2012; Sih *et al.* 2017). Similarly, tick infestation (*Amblyomma sphenodonti*) and a blood parasite (*Hepatozoon tuatarae*) transmitted by the tick in the tuatara (*Sphenodon punctatus*) was significantly related to social interaction (Godfrey *et al.* 2010). We suggest that theoretical models and predictions of parasite transfer, and the demographic effects of parasites should be updated in response to these findings.

Studies examining how parasites affect the behaviours of reptiles and amphibians are neither complete nor comprehensive in taxonomic coverage. For example, Corethtrellid flies (*Corethrella* sp.) use frog calls to locate potential hosts (Bernal *et al.* 2006), yet despite several studies describing the prevalence of parasitism of anuran amphibians by these and Batrachomyia flies (*Batrachomyia sp.*) (Elkan 1965; Hoskin and McCallum 2007; Kraus 2007), we still do not have a strong understanding of how myiasis (infection with fly larva) influences behaviours of amphibian hosts. Additionally, studies are lacking for entire taxonomic groups; little research has explored the effects of parasites on the behaviour of Gymnophionan amphibians (Caecilians) and surprisingly, Crocodilians. Opportunities certainly exist to improve our understanding of the role of parasites in shaping behaviour, which plays a critical role in ecology.

Author Manuscript

This article is protected by copyright. All rights reserved

5. Physiology

Evidence of the adverse effects of parasites on the physiological condition of reptile and amphibian hosts is mounting (Koprivnikar *et al.* 2012; Martín *et al.* 2008; Oppliger *et al.* 1996; Schall *et al.* 1982; Van Rooij *et al.* 2015). Parasites that consume or destroy red blood cells, such as ticks and hemogregarine protozoa, can reduce hemoglobin concentrations and the capacity for blood to deliver oxygen to tissues (Dunlap and Mathies 1993; Martín *et al.* 2008; Oppliger *et al.* 1996). Trematodes (*Ribeiroia* sp.) encyst in the developing limb buds of amphibians, causing abnormal cellular growth, leading to limb abnormalities (Johnson *et al.* 2001; Johnson *et al.* 1999; Stopper *et al.* 2002) and in garter snakes (*Thamnophis sirtalis*) trematodes (*Alaria* sp.) cause extensive muscle damage (Uhrig *et al.* 2015) . The fungal chytrid genus *Batrachochytrium* damages the permeable skin of amphibians, causing loss of water and electrolyte equilibrium (Voyles *et al.* 2009).

Disruption of physiological processes by parasites can influence individual performance and interactions within and between species. At times, interference with physiological processes causes direct mortality, as in tadpoles of Leopard frogs (*L. pipiens*) with trematode (Family: Echinostomatidae) infections (Schotthoefer *et al.* 2003), toads (*R. marina*) with tick infestations (Lampo and Bayliss 1996), and many frog species infected with the fungus *B. dendrobatidis* (Berger *et al.* 1998). Altered physiology from parasitism may also influence other measures of fitness such as body condition. Western fence lizards, (*Sceloporus occidentalis*) with malaria (*Plasmodium mexicanum*) exhibited decreased fat storage (Schall 1983), as did desert toads (*Scaphiopus couchii*) infected with a monogenean blood parasite *Pseudodiplorchis americanus*, after emergence from hibernation (Tocque 1993). Similarly, tick-infection in cane toads (*R. marina*) reduced their ability to gain weight (Lampo and Bayliss 1996). Decreases in mass or fat deposition could result from allocation of energy to immune defenses, or decreases in aerobic activities such as foraging or defense of foraging territories, as postulated for western fence lizards (*Sceloporus occidentalis*) with heavy tick (*Ixodes pacificus*) loads (Dunlap and Mathies 1993).

Author Manuscript

This article is protected by copyright. All rights reserved

Although comparatively light tick loads (*I. pacificus*) do not appear to influence the body condition of western fence lizards (*S. occidentalis*), co-infection with malarial protozoa (*P. mexicanum*) had a negative effect on host condition because both parasites reduced hemoglobin concentrations by different pathways, leading to further physiological costs (Dunlap and Mathies 1993).

The physiological effects of parasites may also increase the risk of host predation. In pacific tree frogs (*Hyla regilla*) with trematode infections (*Ribeiroia* sp.), limb abnormalities hindered the mobility necessary for predator avoidance (Goodman and Johnson 2011a; b; Johnson *et al.* 1999). Similarly, running stamina was reduced in malaria-infected (*P. mexicanum*) western fence lizards (*S. occidentalis*) (Schall et al. 1982). In common lizards (*Z. vivipara*) infected with hemogregarines, (*Haemogregarina* sp.) locomotor speeds were lowered (Oppliger *et al.* 1996), and rates of tail regeneration (an important mechanism of predator escape) were slower (Oppliger and Clobert 1997). Another pathway by which parasites may alter host physiology is by reducing host thermal tolerance, as with spotted tree frogs (*Litoria spenceri*) infected by the fungus *B. dendrobatidis* (Greenspan *et al.* 2017a) and newts (*Notophthalmus viridescensa*) infected with mesomycetozoan parasite (described as an *Ichthyophonus*-like organism) (Sherman 2008), a reminder that anthropogenic environmental factors, such as climate variability associated with global change and environmental contaminants, can exacerbate the harmful physiological effects of infection (Chatfield *et al.* 2013; Marcogliese *et al.* 2009).

Altered host physiology by parasites can also influence reproductive processes. Malaria-infected (*P. mexicanum*) lizards (*S. occidentalis*) had reduced clutch and testis sizes (Schall 1983). In European green lizards (*Lacerta viridis*) with high tick (*Ixodes ricinus*) burdens, females had more saturated chest coloration, which may have indicated avoidance of highly aerobic interactions such as courtship and mating (Václav *et al.* 2007). European green lizards (*Lacerta viridis*) parasitized by ticks (*I. ricinus*) (Václav *et al.* 2007) and wall lizards (*Podarcis muralis*) infected with hemogregarine blood protozoa (family Haemogregorinidae) (Martín *et al.* 2008) had less-saturated throat coloration, indicating that resources were allocated to other physiological processes such as immunity, at the expense of processes associated with breeding coloration that help to attract females (Václav *et al.* 2007)..

Author Manuscript

This article is protected by copyright. All rights reserved

While there are a number of examples where infection with a parasite led to decreased reproductive effort, there are cases where infection led to increased reproductive effort. In frogs infected with fungus (*B. dendrobatidis*), male leopard frogs (*R. pipiens*) had increased testis size, male southern corroboree frogs (*Pseudophryne corroboree*) and alpine tree frogs (*Litoria verreauxii alpina*) had increased sperm production (Brannelly *et al.* 2016; Chatfield *et al.* 2013), and female alpine tree frogs (*L. v. alpina*) had increased gonad size as well as an increased number of developed eggs inside the ovaries (Brannelly et al 2016). Further, the energetic costs of reproduction can lead to a situation in which immune function is decreased in a trade-off favouring reproductive processes. Wild female tree lizards (*Urosaurus ornatus*) in Arizona had reduced immune function during egg production (vitellogenesis) (French and Moore 2008). Controlled experiments demonstrated that this decrease in immune function only occurs when food resources become limited, suggesting that this is a facultative response (French and Moore 2008). This trade-off between reproduction and immune response could conceivably result in increased susceptibility to disease.

Parasites can also influence the phenotypes of host offspring through physiological tradeoffs (Poulin and Thomas 2008). Common lizards *(Z. vivipara*) in poor condition from blood parasite infection (family Haemogregarinidae), allocated a higher proportion of resources to offspring locomotory performance than to other aspects of offspring performance, which increased sprint speed and survival rates of female offspring, presumably serving to preadapt female offspring to challenging environmental conditions (Sorci *et al.* 1996). In addition, the physiological costs of blood parasites may reduce the competitive ability between species. On a Caribbean island with malaria-susceptible Anole lizards, *Anolis gingivinus* out-competed *Anolis wattsi* in the absence of infection by *Plasmodium azurophilum*; therefore the two species co-occur only in areas with malaria (Schall 1992). In some cases, an individual's own physiological processes may cause immunosuppression, leaving them at risk of parasite invasion. Experimentally elevated levels of the hormone testosterone correlated with increased tick (*Ixodes ricinus*) load in free living male sand lizards (*Lacerta agilis*) and large psammodromus lizards (*Psammodromus algirus*) (Olsson *et al.* 2000; Salvador *et al.* 1996). The ticks negatively reduced the relative number of white blood cells and hemoglobin and increased hematocrit of *P. algirus*, and males with

Author Manuscript

This article is protected by copyright. All rights reserved

experimentally elevated testosterone levels experienced higher mortality. Although there is debate on this topic, there is evidence showing that increased testosterone causes immunosupporession (Foo *et al.* 2017). This provides support for the immunocompetence-handicap hypothesis (ICHH), as testosterone levels are correlated with increased sexual signals (such as colour) and males demonstrate their true fitness by surviving the detrimental effect of increased parasite load (Olsson *et al.* 2000). This hypothesis may explain why brightly coloured male Aruban Whip tail lizards (*Cnemidophorus arubensis*) were more likely to be infected with a hemogregarine blood protozoa (family Haemogregorinidae) than dull males of the same body size (Schall 1986). Similarly, Anole lizards (*Anolis sagrei)* that tolerated infection by *Plasmodium* parasites displayed better body condition than uninfected individuals and were not negatively affected in mortality, stamina and immunocompetence (Bonneaud *et al.* 2017).

6. **Genomics**

At a population level, host genetic diversity can influence parasite load, and consequently disease dynamics. Studies across taxa have demonstrated that host genetic variation dictates parasite susceptibility; populations with greater genetic diversity tend to respond more variably to infection, while homogenous populations suffer from the ‘monoculture effect,’ making them more susceptible to disease (Altermatt and Ebert 2008; Coltman *et al.* 1999; King and Lively 2012; O'Brien *et al.* 1985; Thorne and Williams 1988; Whiteman *et al.* 2006). This increased parasite susceptibility with a loss of genetic diversity has been seen in the Italian agile frog (*Rana latastei)* exposed to ranavirus, where decreased survival correlated with population genetic depletion (Pearman and Garner 2005). Disease outbreaks in inbred and bottlenecked populations may be particularly severe due to a loss of adaptive capacity, the potential loss of alleles conferring resistance, and accumulation of those that are deleterious.

In the evolutionary arms race between pathogen and host, one component of the genome involved in rapid adaptation to pathogen-mediated selection is the highly polymorphic Major Histocompatibility Complex (MHC). Depending on the disease context, MHC allele distributions may be maintained by negative frequency-dependent selection, heterozygote advantage, and/or fluctuating selection (Borghans *et al.* 2004; Doherty and Zinkernagel 1975; Hedrick 2002; Spurgin and Richardson 2010). A recent hypothesis is that diversity of MHC and/or other

Author Manuscript

This article is protected by copyright. All rights reserved

immune genes may have facilitated the evolution of group living in members of the Egerniinae lizards, but this remains untested (Bull *et al.* 2017). The relationship between MHC polymorphism and parasite load is unclear in reptiles. In the Ornate dragon (*Ctenophorus ornatus)*, tick load was positively correlated with MHC diversity in undisturbed habitats, though no relationship was evident in disturbed areas (Radwan *et al.* 2014).

In amphibians, both diversifying and directional selection contribute to MHC diversity (Savage and Zamudio 2011; Teacher *et al.* 2009; Wang *et al.* 2017). Among populations of Black-spotted pond frogs (*Pelophylax nigromaculatus),* MHC class Ia genetic diversity was positively correlated with viral abundance and richness. Moreover, there were significant correlations between MHC functional supertypes and either *Frog virus 3* or *Ambystoma tigrinum virus,* suggesting that these supertypes may have conferred resistance (Wang *et al.* 2017). By comparing ranavirus-infected and uninfected populations of the European Common Frog (*Rana temporaria*), directional selection for specific MHC supertypes in diseased populations was demonstrated (Teacher *et al.* 2009). Similarly, both MHC class IIb heterozygosity and presence of the specific Q allele were associated with increased survival in Lowland leopard frogs (*Lithobates yavapaiensis*) experimentally infected with fungus (*B. dendrobatidis*) (Savage and Zamudio 2011). Directional selection for survival-associated alleles was further confirmed in natural populations of *L. yavapaiensis,* suggesting evolution of tolerance to *B. dendrobatidis* in this species (Savage and Zamudio 2016). Finally, while the relationship between parasite burden and MHC alleles is unclear in the critically endangered corroboree frog (*Pseudophryne corroboree),* recent evidence demonstrates both high MHC class Ia diversity and signatures of positive selection at the peptide binding region, indicating that this locus may be important in adaptation to disease (Kosch *et al.* 2017).

In addition to adaptation, plasticity in host response to a disease can dictate parasite load. Interpreting host response at the level of gene expression is particularly useful when genomic resources are limiting, as in amphibians, where large genome sizes have precluded assembly in all but three taxa (Hellsten *et al.* 2010; Session *et al.* 2016; Sun *et al.* 2015). Microarray and RNA-sequencing in experimental infection trials was most extensively undertaken in the amphibian chytrid fungus (*B. dendrobatidis)* system (Ellison *et al.* 2014a; Ellison *et al.* 2014b;

Author Manuscript

This article is protected by copyright. All rights reserved

Grogan *et al.* 2018; Rosenblum *et al.* 2012a; Rosenblum *et al.* 2012b; Rosenblum *et al.* 2009). Among susceptible species, infection led to decreased expression of transcripts related to skin integrity—such as those in the keratin and elastin pathways—while resistant species upregulated skin integrity-related transcripts (Ellison *et al.* 2014b; Rosenblum *et al.* 2012b; Rosenblum *et al.* 2009). Central American frogs with varied responses to fungal (*B. dendrobatidis)* infection exhibited species-specific differences in gene expression, with highly susceptible species demonstrating both increased expression of transcripts related to inflammation and suppression of lymphocyte activation and proliferation pathways (Ellison *et al.* 2014a; Ellison *et al.* 2014b). Such differences in gene expression not only dictate host infection outcomes, but may also influence parasite evolutionary trajectory. For example, when grown *in vivo* in a susceptible species versus in culture, the fungus (*B. dendrobatidis)* simultaneously increased expression of transcripts involved in proteolysis, transmembrane transport, and cilium morphogenesis, and exhibited a shift in expressed genotype frequencies (Ellison *et al.* 2017). Disentangling the extent to which host genomic and transcriptomic variation may influence rapid evolution in parasite populations holds great promise for refining our understanding of disease dynamics.

7. Conservation

Parasite infection and disease is often not the sole cause of extinction or even the major contributor to declines in many species of amphibians and reptiles (Gibbon *et al.* 2000; Lafferty and Gerber 2002). However, when combined with other stressors, such as population fragmentation or invasive species, a parasite can rapidly devastate a population (Gibbon *et al.* 2000; Tompkins *et al.* 2015). Parasites can affect population viability by causing death, or increasing susceptibility to predators or other stressors, thereby decreasing reproductive capacity and population growth (Cunningham 1996; Lafferty and Gerber 2002). Disease often affects endangered species and those with small populations more dramatically than abundant species (May 1988). One such example is the flattened musk turtle (*Sternotherus depressus)*, a species threatened by habitat change. One population experienced a massive decline (decrease of 50%) over twelve months, primarily caused by septicemia (Dodd Jr 1988). Compounded further by localised poaching of turtles, the severity and impact of that particular disease outbreak was attributed to a weakened immune function due to environmental stress (Dodd Jr 1988). Septicemia does not seem to cause similar effects in other turtle species or populations, further

Author Manuscript

This article is protected by copyright. All rights reserved

suggesting that environmental stressors can exacerbate the effects of disease in threatened species.

Disease is a greater threat generally for endangered and rare species; therefore, management tools used for conservation need to incorporate disease and risk thereof into conservation strategy. Some examples of where such considerations are vital are when managing captive assurance colonies, reintroductions and translocations. Understanding disease is an important component of bringing animals into captivity, as well as the implications of releasing them into the wild. In the past, animal releases have caused more harm than good when parasites were relocated with the target species (Cunningham 1996; Deem *et al.* 2001; Viggers *et al.* 1993). Most current management practices follow strict guidelines for quarantining animals intended for reintroduction/translocation programs and screen for parasites before release (Cunningham 1996). However, continued movement of wildlife for the pet trade and food provides a less regulated, ongoing risk (Gratwicke *et al.* 2010) Improved biosecurity and disease quarantine protocols increase the success of reintroductions (Germano and Bishop 2009), and reduce movement of parasites between locations because disease can impact the target species as well as sympatric species (Cunningham 1996; Viggers *et al.* 1993). However, by removing parasites prior to translocation, host-parasite interactions may be disrupted to the detriment of the host (Northover *et al.* 2018), and more research is needed to understand the risks here.

While most parasites that affect reptiles and amphibians do not result in mass mortality in wild populations, stressful conditions in captivity can cause high morbidity and mortality that would otherwise have minimal impact in the wild (Pessier 2008). One such disease is mucormycosis, which is caused by the fungus *Mucor amphibiorum*. Mucormycosis is rare in wild frog populations (Berger *et al.* 1997; Speare *et al.* 1997), but has on occasion caused 80% mortality in captive colonies in Australia and Germany (Creeper *et al.* 1998). Another example is boid inclusion body disease, which is likely caused by a retrovirus and causes central nervous system abnormalities and death in affected captive boid snakes (Chang and Jacobson 2010). While boid inclusion body disease is a global issue, it has only been reported in captivity (Chang and Jacobson 2010; Hetzel *et al.* 2013). A third example is the bacteria *Pseudomonas* sp, which caused an outbreak of necrotic dermatitis in a captive colony of the critically endangered western

Author Manuscript

This article is protected by copyright. All rights reserved

swamp turtle (*Pseudemydura umbrina*). This caused high mortality in the captive population (Ladyman *et al.* 1998), but similar infections have not been detected in wild populations. Diseases such as those described above can delay or prevent reintroduction attempts, as well as reducing the number of precious individuals in captive insurance populations. Simply due to spatial constraints, animals brought into captivity are often maintained at higher than natural population densities, potentially resulting in stressful conditions that may lower the immune capacity to respond to infection. Captive disease outbreaks might therefore be minimized by developing a better understanding of how these are mediated by captive husbandry (e.g. nutrition, housing) of reptiles and amphibians (Pessier 2008).

The impacts of the disease chytridiomycosis on amphibians has been well-studied and reviewed (Bower *et al.* 2017a; Scheele *et al.* 2014; Woodhams *et al.* 2011), and mitigating risk of the spread of this pathogen has been incorporated into policy governing the management of threatened and declining amphibian species (Commonwealth of Australia 2016). However, the same research and management effort has not been undertaken for other diseases. Where diseases do not directly cause species extinction, populations can still be negatively impacted by parasites, particularly in small populations. For example, ranavirus is widespread in amphibian and reptile species globally, and while it can cause mass declines, it often does not. However, only after a long-term study exploring many different ranavirus-positive and ranavirus-negative populations is it clear that ranavirus has an overall negative effect on population growth over time (Teacher *et al.* 2010).

The extent to which parasites can act as a threatening process is unclear in many cases. Long term population level effects of Fibropapillomatosis are unknown in most regions, but Hawaiian green turtle populations have recovered from initial declines despite disease presence (Chaloupka and Balazs 2005; Jones *et al.* 2016). While myxosporea and sparganosis cause disease in amphibians, and occur in many locations around the globe, prevalence in amphibian communities and impact of disease on populations is essentially unknown (Berger *et al.* 2009). Most diseases described in reptiles and amphibians are reported as case studies, often without information of disease prevalence or population impact.

Author Manuscript

This article is protected by copyright. All rights reserved

A greater understanding of basic ecology such as population level dynamics and impacts of disease is required for a more thoroughly informed effort in undertaking conservation of declining reptiles and amphibians. Presently, there is relatively little research being conducted to address such questions for a majority of known parasites. Furthermore, many parasites regulate host populations without necessarily causing conservation concern. This may manifest through effects on coexistence, competition, predation and herbivory that help maintain diversity in the system through a complex set of interactions (Hatcher *et al.* 2012). Disease is often not the ultimate cause of extinction; therefore, minimising other stressors, such as habitat fragmentation and pollution, will increase the resilience of populations and their ability to tolerate diseases in the future. However, there is also a clear need to understand how parasites and their hosts interact with each other and the environment if we are to be best prepared to manage the inevitable consequences of ongoing anthropogenic activity. Threatening factors are not limited to hosts, parasites themselves may be up to ten times more vulnerable than host baseline extinction rate (Colwell *et al.* 2012). Given the infancy of our understanding of parasite ecology from species diversity through to functional roles, and the lack of current capacity for parasite conservation, these impacts are difficult to predict (Cizauskas *et al.* 2017). The increasing appreciation of a global decline in biodiversity, particularly of amphibians and reptiles (Gibbon *et al.* 2000) suggests that future research is certain to further unravel mechanisms that allow us to understand the role played by parasites in ecology and evolution.

Acknowledgements

We thank Dr. Astrid Vachette for generously donating her time and expertise to translate the abstract to French, Dale Burzacott and Wesley Neely for providing photographs and the Winifred Violet Scott Charitable Trust for providing financial support.

Literature Cited

Allender M. C., Raudabaugh D. B., Gleason F. H. & Miller A. N. (2015) The natural history, ecology, and epidemiology of *Ophidiomyces ophiodiicola* and its potential impact on free-ranging snake populations. *Fungal Ecol.* **17**, 187-96.

Altermatt F. & Ebert D. (2008) Genetic diversity of *Daphnia magna* populations enhances resistance to parasites. *Ecol Lett* **11**, 918-28.

Author Manuscript

This article is protected by copyright. All rights reserved

An D. & Waldman B. (2016) Enhanced call effort in Japanese tree frogs infected by amphibian chytrid fungus. *Biol Lett* **12**, 20160018.

Anderson R. (1978) The regulation of host population growth by parasitic species. *Parasitology* **76**, 119-57.

Ariel E. (2011) Viruses in reptiles. *Vet Res* **42**, 100.

Aubret F., Tort M., Michniewicz R. J., Blanvillain G. & Coulon A. (2014) Cooperate or compete? Influence of sex and body size on sheltering behaviour in the wall lizard, *Podarcis muralis*. *Behaviour* **151**, 1903-20.

Berger L., Skerratt L. F., Zhu X.-Q., Young S. & Speare R. (2009) Severe sparganosis in Australian tree frogs. *J Wildl Dis* **45**, 921-9.

Berger L., Speare R., Daszak P., Green D. E., Cunningham A. A., Goggin C. L., Slocombe R., Ragan M. A., Hyatt A. D., McDonald K. R., Hines H. B., Lips K. R., Marantelli G. & Parkes H. (1998) Chytridiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. *Proc Natl Acad Sci U S A* **95**, 9031-6.

Berger L., Speare R. & Humphrey J. (1997) Mucormycosis in a free-ranging green tree frog from Australia. *J Wildl Dis* **33**, 903-7.

Bernal X. E., Page R. A., Rand A. S. & Ryan M. J. (2007) Cues for eavesdroppers: do frog calls indicate prey density and quality? *Am. Nat.* **169**, 409-15.

Bernal X. E. & Pinto C. M. (2016) Sexual differences in prevalence of a new species of trypanosome infecting túngara frogs. *International Journal for Parasitology: Parasites and Wildlife* **5**, 40-7.

Bernal X. E., Rand A. S. & Ryan M. J. (2006) Acoustic preferences and localization performance of blood-sucking flies (Corethrella Coquillett) to túngara frog calls. *Behav Ecol* **17**, 709-15.

Biaggini M., Berti R. & Corti C. (2009) Different habitats, different pressures? Analysis of escape behaviour and ectoparasite load in *Podarcis sicula* (Lacertidae) populations in different agricultural habitats. *Amphib-Reptilia* **30**, 453-61.

Bonneaud C., Sepil I., Wilfert L. & Calsbeek R. (2017) Plasmodium infections in natural populations of Anolis sagrei reflect tolerance rather than susceptibility. *Integr Comp Biol* **57**, 352-61.

Author Manuscript

This article is protected by copyright. All rights reserved

Author Manuscript

Borghans J. A., Beltman J. B. & De Boer R. J. (2004) MHC polymorphism under host-pathogen coevolution. *Immunogenetics* **55**, 732-9.

Bouma M. J., Smallridge C. J., Bull C. M. & Komdeur J. (2007) Susceptibility to infection by a haemogregarine parasite and the impact of infection in the Australian sleepy lizard *Tiliqua rugosa*. *Parasitol Res* **100**, 949-54.

Bower D., Mengersen K., Alford R. & Schwarzkopf L. (2017a) Using a Bayesian network to clarify areas requiring research in a host–pathogen system. *Conserv Biol* **31**, 1373-82.

Bower D. S., Lips K. R., Schwarzkopf L., Georges A. & Clulow S. (2017b) Amphibians on the brink: Preemptive policies can protect amphibians from devastating fungal diseases. *Science* **257**, 8-9.

Bower D. S., Yasumiba K., Trumbo D. R., Alford R. A. & Schwarzkopf L. (2018) Spinal arthritis in cane toads across the Australian landscape. *Sci. Rep.* **8**, 12458.

Brannelly L. A., Webb R., Skerratt L. F. & Berger L. (2016) Amphibians with infectious disease increase their reproductive effort: evidence for the terminal investment hypothesis. *Open biology* **6**, 150251.

Brown G., Shilton C. & Shine R. (2006) Do parasites matter? Assessing the fitness consequences of haemogregarine infection in snakes. *Can J Zool* **84**, 668-76.

Brown G. P., Kelehear C., Pizzatto L. & Shine R. (2016) The impact of lungworm parasites on rates of dispersal of their anuran host, the invasive cane toad. *Biol Invasions* **18**, 103-14.

Brown G. P., Shilton C., Phillips B. L. & Shine R. (2007) Invasion, stress, and spinal arthritis in cane toads. *Proceedings of the National Academy of Sciences* **104**, 17698-700.

Bull C., Godfrey S. & Gordon D. (2012) Social networks and the spread of Salmonella in a sleepy lizard population. *Mol Ecol* **21**, 4386-92.

Bull C. M. & Burzacott D. A. (2006) The influence of parasites on the retention of long-term partnerships in the Australian sleepy lizard, *Tiliqua rugosa*. *Oecologia* **146**, 675-80.

Bull C. M., Gardner M. G., Sih A., Spiegel O., Godfrey S. S. & Leu S. T. (2017) Why is social behavior rare in reptiles? Lessons from sleepy lizards. *Adv Study Behav* **49**, 1-26.

Byrd A. L. & Segre J. A. (2016) Adapting Koch's postulates. *Science* **351**, 224-6.

Campião K. M., Delatorre M., Rodrigues R. B., Da Silva R. J. & Ferreira V. L. (2012) The effect of local environmental variables on the helminth parasite communities of the pointedbelly

This article is protected by copyright. All rights reserved

Author Manuscript

frog *Leptodactylus podicipinus* from ponds in the Pantanal wetlands. *J Parasitol* **98**, 229-35.

Carbayo J., MARTIN J. & Civantos E. (2018) Habitat type influences parasite load in Algerian Psammodromus lizards (Psammodromus algirus). *Can J Zool* **Early online**.

Chaloupka M. & Balazs G. (2005) Modelling the effect of fibropapilloma disease on the somatic growth dynamics of Hawaiian green sea turtles. *Mar. Biol.* **147**, 1251-60.

Chambouvet A., Gower D. J., Jirků M., Yabsley M. J., Davis A. K., Leonard G., Maguire F., Doherty-Bone T. M., Bittencourt-Silva G. B. & Wilkinson M. (2015) Cryptic infection of a broad taxonomic and geographic diversity of tadpoles by Perkinsea protists. *Proceedings of the National Academy of Sciences* **112**, E4743-E51.

Chang L.-W. & Jacobson E. R. (2010) Inclusion body disease, a worldwide infectious disease of boid snakes: a review. *J Exot Pet Med* **19**, 216-25.

Chatfield M. W., Brannelly L. A., Robak M. J., Freeborn L., Lailvaux S. P. & Richards-Zawacki C. L. (2013) Fitness consequences of infection by *Batrachochytrium dendrobatidis* in northern leopard frogs (*Lithobates pipiens*). *EcoHealth* **10**, 90-8.

Christin M. S., Gendron A. D., Brousseau P., Ménard L., Marcogliese D. J., Cyr D., Ruby S. & Fournier M. (2003) Effects of agricultural pesticides on the immune system of *Rana pipiens* and on its resistance to parasitic infection. *Environ Toxicol Chem* **22**, 1127-33.

Cizauskas C. A., Carlson C. J., Burgio K. R., Clements C. F., Dougherty E. R., Harris N. C. & Phillips A. J. (2017) Parasite vulnerability to climate change: An evidence-based functional trait approach. *Royal Society open science* **4**, 160535.

Collins J. P. & Storfer A. (2003) Global amphibian declines: sorting the hypotheses. *Divers Distrib* **9**, 89-98.

Coltman D. W., Pilkington J. G. & Smith J. A. (1999) Parasite-mediated selection against inbred soay sheep in a free-living island population. *Evolution* **53**, 1259-67.

Colwell R. K., Dunn R. R. & Harris N. C. (2012) Coextinction and persistence of dependent species in a changing world. *Annu. Rev. Ecol. Evol. Syst.* **43**, 183–203.

Commonwealth of Australia. (2016) Draft Threat abatement plan for infection of amphibians with chytrid fungus resulting in chytridiomycosis, http://www.environment.gov.au/biodiversity/threatened/publications/tap/infection-amphibians-chytrid-fungus-resulting-chytridiomycosis.

This article is protected by copyright. All rights reserved

Cooper E. L., Wright R. K., Klempau A. E. & Smith C. T. (1992) Hibernation alters the frog's immune system. *Cryobiology* **29**, 616-31.

Creeper J., Main D., Berger L., Huntress S. & Boardman W. (1998) An outbreak of mucormycosis in slender tree frogs (*Litoria adelensis*) and white-lipped tree frogs (*Litoria infrafrenata*). *Aust Vet J* **76**, 761-2.

Crofton H. (1971) A model of host-parasite relationships. *Parasitology* **63**, 343-64.

Cunningham A. A. (1996) Disease risks of wildlife translocations. *Conserv Biol* **10**, 349-53.

Czech B., Krausman P. R. & Borkhataria R. (1998) Social construction, political power, and the allocation of benefits to endangered species. *Conserv Biol* **12**, 1103-12.

Damas-Moreira I., Harris D. J., Rosado D., Tavares I., Maia J. P., Salvi D. & Perera A. (2014) Consequences of haemogregarine infection on the escape distance in the lacertid lizard, *Podarcis vaucheri*. *Acta Herpetol* **9**, 119-23.

Daniels C. B. (1985) The effect of infection by a parasitic worm on swimming and diving in the water skink, *Sphenomorphus quoyii*. *J Herpetol* **19**, 160-2.

Daskin J. H., Alford R. A. & Puschendorf R. (2011) Short-term exposure to warm microhabitats could explain amphibian persistence with *Batrachochytrium dendrobatidis*. *PLoS ONE* **6**, e26215.

Day R. D., Segars A. L., Arendt M. D., Lee A. M. & Peden-Adams M. M. (2007) Relationship of blood mercury levels to health parameters in the loggerhead sea turtle (*Caretta caretta*). *Environ Health Perspect* **115**, 1421.

Deem S. L., Karesh W. B. & Weisman W. (2001) Putting theory into practice: wildlife health in conservation. *Conserv Biol* **15**, 1224-33.

Di Rosa I., Simoncelli F., Fagotti A. & Pascolini R. (2007) Ecology: The proximate cause of frog declines? *Nature* **447**, E4.

Dodd Jr C. K. (1988) Disease and population declines in the flattened musk turtle *Sternotherus depressus*. *Am Midl Nat* **119**, 394-401.

Doherty P. C. & Zinkernagel R. M. (1975) Enhanced immunological surveillance in mice heterozygous at the H-2 gene complex. *Nature* **256**, 50.

Dunlap K. D. & Mathies T. (1993) Effects of nymphal ticks and their interaction with malaria on the physiology of male fence lizards. *Copeia* **1993**, 1045-8.

Author Manuscript

This article is protected by copyright. All rights reserved

Author Manuscript

Eiras J. C. (2005) An overview on the myxosporean parasites in amphibians and reptiles. *Acta Parasitol* **50**, 267-75.

Elkan E. (1965) Myiasis in Australian frogs. *Ann Trop Med Parasitol* **59**, 51-4.

Ellison A. R., DiRenzo G. V., McDonald C. A., Lips K. R. & Zamudio K. R. (2017) First in vivo *Batrachochytrium dendrobatidis* transcriptomes reveal mechanisms of host exploitation, host-specific gene expression, and expressed genotype shifts. *G3: Genes, Genomes, Genetics* **7**, 269-78.

Ellison A. R., Savage A. E., DiRenzo G. V., Langhammer P., Lips K. R. & Zamudio K. R. (2014a) Fighting a losing battle: vigorous immune response countered by pathogen suppression of host defenses in the chytridiomycosis-susceptible frog *Atelopus zeteki*. *G3: Genes, Genomes, Genetics* **4**, 1275-89.

Ellison A. R., Tunstall T., DiRenzo G. V., Hughey M. C., Rebollar E. A., Belden L. K., Harris R. N., Ibáñez R., Lips K. R. & Zamudio K. R. (2014b) More than skin deep: functional genomic basis for resistance to amphibian chytridiomycosis. *Genome Biol. Evol.* **7**, 286-98.

Ferguson L. V. & Smith T. G. (2012) Reciprocal trophic interactions and transmission of blood parasites between mosquitoes and frogs. *Insects* **3**, 410-23.

Field D. J., Gauthier J. A., King B. L., Pisani D., Lyson T. R. & Peterson K. J. (2014) Toward consilience in reptile phylogeny: miRNAs support an archosaur, not lepidosaur, affinity for turtles. *Evol Dev* **16**, 189-96.

Finnerty P. B., Shine R. & Brown G. P. (2018) The costs of parasite infection: Effects of removing lungworms on performance, growth and survival of free-ranging cane toads. *Funct Ecol* **32**, 402-15.

Fisher M. C., Henk D. A., Briggs C. J., Brownstein J. S., Madoff L. C., McCraw S. L. & Gurr S. J. (2012) Emerging fungal threats to animal, plant and ecosystem health. *Nature* **484**, 186.

Foo Y. Z., Nakagawa S., Rhodes G. & Simmons L. W. (2017) The effects of sex hormones on immune function: a meta-analysis. *Biological Reviews* **92**, 551-71.

French S. S. & Moore M. C. (2008) Immune function varies with reproductive stage and context in female and male tree lizards, *Urosaurus ornatus*. *Gen Comp Endocrinol* **155**, 148-56.

This article is protected by copyright. All rights reserved

Germano J. M. & Bishop P. J. (2009) Suitability of amphibians and reptiles for translocation. *Conserv Biol* **23**, 7-15.

Gervasi S. S. & Foufopoulos J. (2008) Costs of plasticity: responses to desiccation decrease post-metamorphic immune function in a pond-breeding amphibian. *Funct Ecol* **22**, 100-8.

Gibbon J. W., Scott D. E., Ryan T. J., Buhlmann K. A., Tuberville T. D., Metts B. S., Greene J. L., Mills T., Leiden Y. & Poppy S. (2000) The Global Decline of Reptiles, Déjà Vu Amphibians: Reptile species are declining on a global scale. Six significant threats to reptile populations are habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable use, and global climate change. *Bioscience* **50**, 653-66.

Giery S. T. & Ostfeld R. S. (2007) The role of lizards in the ecology of Lyme disease in two endemic zones of the northeastern United States. *J Parasitol* **93**, 511-7.

Goater C. & Ward P. (1992) Negative effects of *Rhabdias bufonis* (Nematoda) on the growth and survival of toads (*Bufo bufo*). *Oecologia* **89**, 161-5.

Godfrey S. S. (2013) Networks and the ecology of parasite transmission: a framework for wildlife parasitology. *International Journal for Parasitology: Parasites and Wildlife* **2**, 235-45.

Godfrey S. S., Bull C. M., Murray K. & Gardner M. G. (2006) Transmission mode and distribution of parasites among groups of the social lizard *Egernia stokesii*. *Parasitol Res* **99**, 223-30.

Godfrey S. S. & Gardner M. G. (2017) Lizards, ticks and contributions to Australian parasitology: C. Michael Bull (1947–2016). *International Journal for Parasitology: Parasites and Wildlife* **6**, 295-8.

Godfrey S. S., Moore J. A., Nelson N. J. & Bull C. M. (2010) Social network structure and parasite infection patterns in a territorial reptile, the tuatara (*Sphenodon punctatus*). *Int J Parasitol* **40**, 1575-85.

Godínez-Álvarez H. (2004) Pollination and seed dispersal by lizards: a review. *Rev Chil Hist Nat* **77**, 569-77.

Goodman B. A. & Johnson P. T. (2011a) Disease and the extended phenotype: parasites control host performance and survival through induced changes in body plan. *PLoS ONE* **6**, e20193.

Author Manuscript

This article is protected by copyright. All rights reserved

Goodman B. A. & Johnson P. T. (2011b) Ecomorphology and disease: cryptic effects of parasitism on host habitat use, thermoregulation, and predator avoidance. *Ecology* **92**, 542-8.

Graham T., Saumure R. & Ericson B. (1997) Map turtle winter leech loads. *The Journal of parasitology* **83**, 1185-6.

Gratwicke B., Evans M. J., Jenkins P. T., Kusrini M. D., Moore R. D., Sevin J. & Wildt D. E. (2010) Is the international frog legs trade a potential vector for deadly amphibian pathogens? *Front Ecol Environ* **8**, 438-42.

Gray M. J., Miller D. L. & Hoverman J. T. (2009) Ecology and pathology of amphibian ranaviruses. *Dis Aquat Org* **87**, 243-66.

Greenspan S. E., Bower D. S., Roznik E. A., Pike D. A., Marantelli G., Alford R. A., Schwarzkopf L. & Scheffers B. R. (2017a) Infection increases vulnerability to climate change via effects on host thermal tolerance. *Sci. Rep.* **7**, 9349.

Greenspan S. E., Bower D. S., Webb R. J., Berger L., Rudd D., Schwarzkopf L. & Alford R. A. (2017b) White blood cell profiles in amphibians help to explain disease susceptibility following temperature shifts. *Dev Comp Immunol* **77**, 280-6.

Greenspan S. E., Bower D. S., Webb R. J., Roznik E. A., Stevenson L. A., Berger L., Marantelli G., Pike D. A., Schwarzkopf L. & Alford R. A. (2017c) Realistic heat pulses protect frogs from disease under simulated rainforest frog thermal regimes. *Funct Ecol* **2017**, 1-17.

Grillitsch B. & Schiesari L. (2010) The Ecotoxicology of Metals in Reptiles. In: *Ecotoxicology of amphibians and reptiles* (eds D. W. Sparling, G. Linder, C. A. Bishop and S. Krest). CRC Press, Second Edition. Boca Raton: CRC Press 337-448.

Grogan L. F., Cashins S. D., Skerratt L. F., Berger L., McFadden M. S., Harlow P., Hunter D. A., Scheele B. C. & Mulvenna J. (2018) Evolution of resistance to chytridiomycosis is associated with a robust early immune response. *Mol Ecol* **27**, 919-34.

Gyawali P., Khanal S. & Shrestha B. (2013) Intestinal helminth fauna in sleepy lizard (*Tiliqua rugosa*) in Australia. *International Journal of Veterinary Science* **2**, 17-20.

Han B. A., Searle C. L. & Blaustein A. R. (2011) Effects of an infectious fungus, *Batrachochytrium dendrobatidi*s, on amphibian predator-prey interactions. *PLoS ONE* **6**, e16675.

Author Manuscript

This article is protected by copyright. All rights reserved

Hartigan A., Fiala I., Dyková I., Jirků M., Okimoto B., Rose K., Phalen D. N. & Šlapeta J. (2011) A suspected parasite spill-back of two novel Myxidium spp.(Myxosporea) causing disease in Australian endemic frogs found in the invasive cane toad. *PLoS ONE* **6**, e18871.

Hartigan A., Phalen D. N. & Šlapeta J. (2010) Museum material reveals a frog parasite emergence after the invasion of the cane toad in Australia. *Parasites & vectors* **3**, 50.

Hatcher M. J., Dick J. T. & Dunn A. M. (2012) Diverse effects of parasites in ecosystems: linking interdependent processes. *Front Ecol Environ* **10**, 186-94.

Hausfater G., Gerhardt H. C. & Klump G. M. (1990) Parasites and mate choice in gray treefrogs, *Hyla versicolor*. *Am Zool* **30**, 299-312.

Hecnar S. J. (2009) Human bias and the biodiversity knowledge base: An examination of the published literature on vertebrates. *Biodiversity* **10**, 18-24.

Hedrick P. W. (2002) Pathogen resistance and genetic variation at MHC loci. *Evolution* **56**, 1902-8.

Hellsten U., Harland R. M., Gilchrist M. J., Hendrix D., Jurka J., Kapitonov V., Ovcharenko I., Putnam N. H., Shu S. & Taher L. (2010) The genome of the Western clawed frog *Xenopus tropicalis*. *Science* **328**, 633-6.

Hetzel U., Sironen T., Laurinmäki P., Liljeroos L., Patjas A., Henttonen H., Vaheri A., Artelt A., Kipar A. & Butcher S. J. (2013) Isolation, identification, and characterization of novel arenaviruses, the etiological agents of boid inclusion body disease. *J. Virol.* **87**, 10918-35.

Hoskin C. J. & McCallum H. (2007) Phylogeography of the parasitic fly Batrachomyia in the Wet Tropics of north-east Australia, and susceptibility of host frog lineages in a mosaic contact zone. *Biol J Linn Soc* **92**, 593-603.

Huggins L. G., Michaels C. J., Cruickshank S. M., Preziosi R. F. & Else K. J. (2017) A novel copro-diagnostic molecular method for qualitative detection and identification of parasitic nematodes in amphibians and reptiles. *PLoS ONE* **12**, e0185151.

Hussein M., Badir N., El Ridi R. & El Deeb S. (1979) Effect of seasonal variation on immune system of the lizard, *Scincus scincus*. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology* **209**, 91-6.

Innis C., Nyaoke A. C., Williams III C. R., Dunnigan B., Merigo C., Woodward D. L., Weber E. S. & Frasca Jr S. (2009) Pathologic and parasitologic findings of cold-stunned Kemp's

Author Manuscript

This article is protected by copyright. All rights reserved

Author Manuscript

ridley sea turtles (*Lepidochelys kempii*) stranded on Cape Cod, Massachusetts, 2001–2006. *J Wildl Dis* **45**, 594-610.

Iwai N. & Kagaya T. (2007) Positive indirect effect of tadpoles on a detritivore through nutrient regeneration. *Oecologia* **152**, 685-94.

Jani A. J. & Briggs C. J. (2014) The pathogen *Batrachochytrium dendrobatidis* disturbs the frog skin microbiome during a natural epidemic and experimental infection. *Proceedings of the National Academy of Sciences* **111**, E5049-E58.

Johnson P. T., Lunde K. B., Haight R. W., Bowerman J. & Blaustein A. R. (2001) *Ribeiroia ondatrae* (Trematoda: Digenea) infection induces severe limb malformations in western toads (*Bufo boreas*). *Can J Zool* **79**, 370-9.

Johnson P. T., Lunde K. B., Ritchie E. G. & Launer A. E. (1999) The effect of trematode infection on amphibian limb development and survivorship. *Science* **284**, 802-4.

Jones K., Ariel E., Burgess G. & Read M. (2016) A review of fibropapillomatosis in green turtles (Chelonia mydas). *The Veterinary Journal* **212**, 48-57.

Kelehear C., Webb J. & Shine R. (2009) Rhabdias pseudosphaerocephala infection in *Bufo marinus*: lung nematodes reduce viability of metamorph cane toads. *Parasitology* **136**, 919-27.

Kelehear C., Webb J. K., Hagman M. & Shine R. (2011) Interactions between infective helminth larvae and their anuran hosts. *Herpetologica* **67**, 378-85.

Kiesecker J. M. & Skelly D. K. (2000) Choice of oviposition site by gray treefrogs: the role of potential parasitic infection. *Ecology* **81**, 2939-43.

Kiesecker J. M., Skelly D. K., Beard K. H. & Preisser E. (1999) Behavioral reduction of infection risk. *Proceedings of the National Academy of Sciences* **96**, 9165-8.

King K. & Lively C. (2012) Does genetic diversity limit disease spread in natural host populations? *Heredity* **109**, 199.

Klein S. L. (2003) Parasite manipulation of the proximate mechanisms that mediate social behavior in vertebrates. *Physiol Behav* **79**, 441-9.

Koprivnikar J., Marcogliese D. J., Rohr J. R., Orlofske S. A., Raffel T. R. & Johnson P. T. (2012) Macroparasite infections of amphibians: what can they tell us? *EcoHealth* **9**, 342-60.

This article is protected by copyright. All rights reserved

Koprivnikar J. & Penalva L. (2015) Lesser of two evils? Foraging choices in response to threats of predation and parasitism. *PLoS ONE* **10**, e0116569.

Koprivnikar J., Redfern J. C. & Mazier H. L. (2014) Variation in anti-parasite behaviour and infection among larval amphibian species. *Oecologia* **174**, 1179-85.

Kosch T. A., Eimes J. A., Didinger C., Brannelly L. A., Waldman B., Berger L. & Skerratt L. F. (2017) Characterization of MHC class IA in the endangered southern corroboree frog. *Immunogenetics* **69**, 165-74.

Kraus F. (2007) Fly parasitism in Papuan frogs, with a discussion of ecological factors influencing evolution of life-history differences. *J Nat Hist* **41**, 1863-74.

Ladyman J., Kuchling G., Burford D., Boardman W. & Raidal S. (1998) Skin disease affecting the conservation of the western swamp tortoise (*Pseudemydura umbrina*). *Aust Vet J* **76**, 743-5.

Lafferty K. D. & Gerber L. R. (2002) Good medicine for conservation biology: the intersection of epidemiology and conservation theory. *Conserv Biol* **16**, 593-604.

Lampo M. & Bayliss P. (1996) The impact of ticks on *Bufo marinus* from native habitats. *Parasitology* **113**, 199-206.

Little E. & Calfee R. (2010) Solar UV radiation and Amphibians. Factors Mitigating Injury. In: *Ecotoxicology of amphibians and reptiles* (eds D. W. Sparling, G. Linder, C. A. Bishop and S. Krest). CRC Press, Second Edition. Boca Raton: CRC Press 449-471.

Lovich J. E., Ennen J. R., Agha M. & Gibbons J. W. (2018) Where have all the turtles gone, and why does it matter? *Bioscience* **68**, 771-81.

Lunghi E., Ficetola G. F., Mulargia M., Cogoni R., Veith M., Corti C. & Manenti R. (2018) Batracobdella leeches, environmental features and Hydromantes salamanders. *International Journal for Parasitology: Parasites and Wildlife* **7**, 48-53.

Madelaire C. B., José da Silva R. & Ribeiro Gomes F. (2013) Calling behavior and parasite intensity in treefrogs, *Hypsiboas prasinus*. *J Herpetol* **47**, 450-5.

Madsen T., Ujvari B. & Olsson M. (2005) Old pythons stay fit; effects of haematozoan infections on life history traits of a large tropical predator. *Oecologia* **142**, 407-12.

Main A. R. & Bull C. M. (2000) The impact of tick parasites on the behaviour of the lizard *Tiliqua rugosa*. *Oecologia* **122**, 574-81.

Author Manuscript

This article is protected by copyright. All rights reserved

Maniero G. D. & Carey C. (1997) Changes in selected aspects of immune function in the leopard frog, *Rana pipiens*, associated with exposure to cold. *Journal of Comparative Physiology B* **167**, 256-63.

Marcogliese D. J., King K. C., Salo H. M., Fournier M., Brousseau P., Spear P., Champoux L., McLaughlin J. D. & Boily M. (2009) Combined effects of agricultural activity and parasites on biomarkers in the bullfrog, *Rana catasbeiana*. *Aquat. Toxicol.* **91**, 126-34.

Marschang R. E. (2011) Viruses infecting reptiles. *Viruses* **3**, 2087-126.

Martín J., Amo L. & López P. (2008) Parasites and health affect multiple sexual signals in male common wall lizards, *Podarcis muralis*. *Naturwissenschaften* **95**, 293-300.

Masters N., Alexander S., Jackson B., Sigler L., Chatterton J., Harvey C., Gibson R., Humphrey S., Rawdon T. & Spence R. (2016) Dermatomycosis caused by Paranannizziopsis australasiensis in five tuatara (Sphenodon punctatus) and a coastal bearded dragon (Pogona barbata) in a zoological collection in New Zealand. *N Z Vet J* **64**, 301-7.

Mauel M. J., Miller D. L., Frazier K. S. & Hines M. E. (2002) Bacterial pathogens isolated from cultured bullfrogs (*Rana castesbeiana*). *J Vet Diagn Investig* **14**, 431-3.

May R. M. (1988) Conservation and disease. *Conserv Biol* **2**, 28-30.

May R. M. & Anderson R. M. (1990) Parasite—host coevolution. *Parasitology* **100**, S89-S101.

McKnight D. T., Schwarzkopf L., Alford R. A., Bower D. S. & Zenger K. R. (2017) Effects of emerging infectious diseases on host population genetics: a review. *Conserv Genet* **18**, 1-11.

McManus D. & Bowles J. (1996) Molecular genetic approaches to parasite identification: their value in diagnostic parasitology and systematics. *Int J Parasitol* **26**, 687-704.

Meredith H., Van Buren C. & Antwis R. E. (2016) Making amphibian conservation more effective. *Conserv Evid* **13**, 1-6.

Méthot P.-O. & Alizon S. (2014) What is a pathogen? Toward a process view of host-parasite interactions. *Virulence* **5**, 775-85.

Moore J. (1984) Parasites that change the behavior of their host. *Sci Am* **250**, 108-15.

Moretti E. H., Madelaire C. B., Silva R. J., Mendonça M. T. & Gomes F. R. (2014) The relationships between parasite intensity, locomotor performance, and body condition in adult toads (*Rhinella icterica*) from the Wild. *J Herpetol* **48**, 277-83.

Author Manuscript

This article is protected by copyright. All rights reserved

Moretti E. H., Titon Jr B., Madelaire C. B., de Arruda R., Alvarez T. & Gomes F. R. (2017) Behavioral, physiological and morphological correlates of parasite intensity in the wild Cururu toad (*Rhinella icterica*). *International Journal for Parasitology: Parasites and Wildlife* **6**, 146-54.

Mugabo M., Perret S., Decencière B., Meylan S. & Le Galliard J.-F. (2015) Density-dependent immunity and parasitism risk in experimental populations of lizards naturally infested by ixodid ticks. *Ecology* **96**, 450-60.

Northover A., Lymbery A., Wayne A., Godfrey S. & Thompson R. (2018) The hidden consequences of altering host-parasite relationships during fauna translocations. *Biol Conserv* **220**, 140-8.

O'Brien S. J., Roelke M. E., Marker L., Newman A., Winkler C., Meltzer D., Colly L., Evermann J., Bush M. & Wildt D. E. (1985) Genetic basis for species vulnerability in the cheetah. *Science* **227**, 1428-34.

O’Dea M. A., Jackson B., Jackson C., Xavier P. & Warren K. (2016) Discovery and partial genomic characterisation of a novel nidovirus associated with respiratory disease in wild shingleback lizards (*Tiliqua rugosa*). *PLoS ONE* **11**, e0165209.

Okamura B., Hartigan A. & Naldoni J. (2018) Extensive uncharted biodiversity: the parasite dimension. In: *Integr Comp Biol* pp. 1-14, Measuring Biodiversity and Extinction: Present and Past” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2018 at San Francisco, California.

Olsson M., Wapstra E., Madsen T. & Silverin B. (2000) Testosterone, ticks and travels: a test of the immunocompetence-handicap hypothesis in free-ranging male sand lizards. *Proceedings of the Royal Society of London B: Biological Sciences* **267**, 2339-43.

Oppliger A., Celerier M. & Clobert J. (1996) Physiological and behaviour changes in common lizards parasitized by haemogregarines. *Parasitology* **113**, 433-8.

Oppliger A. & Clobert J. (1997) Reduced tail regeneration in the common lizard, *Lacerta vivipara*, parasitized by blood parasites. *Funct Ecol* **11**, 652-5.

Otero L., Schall J. J., Cruz V., Aaltonen K. & Acevedo M. (2017) The drivers and consequences of unstable Plasmodium dynamics: A 26-year study of three malaria parasite species infecting a tropical lizard. *bioRxiv*, 189696.

Author Manuscript

This article is protected by copyright. All rights reserved

Author Manuscript

Parsons S. K., Bull C. M. & Gordon D. M. (2010) Low prevalence of *Salmonella enterica* in Australian wildlife. *Environ. Microbiol. Rep.* **2**, 657-9.

Pasquale V., Baloda S. B., Dumontet S. & Krovacek K. (1994) An outbreak of *Aeromonas hydrophila* infection in turtles (*Pseudemis scripta*). *Appl Environ Microbiol* **60**, 1678-80.

Pearman P. B. & Garner T. W. (2005) Susceptibility of Italian agile frog populations to an emerging strain of Ranavirus parallels population genetic diversity. *Ecol Lett* **8**, 401-8.

Pessier A. (2008) Management of disease as a threat to amphibian conservation. *Int Zoo Yearb* **42**, 30-9.

Pfennig D., Ho S. & Hoffman E. (1998) Pathogen transmission as a selective force against cannibalism. *Anim Behav* **55**, 1255-61.

Pfennig D. W., Loeb M. L. & Collins J. P. (1991) Pathogens as a factor limiting the spread of cannibalism in tiger salamanders. *Oecologia* **88**, 161-6.

Pfennig K. S. & Tinsley R. (2002) Different mate preferences by parasitized and unparasitized females potentially reduces sexual selection. *J Evol Biol* **15**, 399-406.

Poulin R. & Thomas F. (2008) Epigenetic effects of infection on the phenotype of host offspring: parasites reaching across host generations. *Oikos* **117**, 331-5.

Pounds J. A., Bustamante M. R., Coloma L. A., Consuegra J. A., Fogden M. P., Foster P. N., La Marca E., Masters K. L., Merino-Viteri A. & Puschendorf R. (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439**, 161.

Preston D. L., Boland C. E., Hoverman J. T. & Johnson P. T. (2014) Natural enemy ecology: comparing the effects of predation risk, infection risk and disease on host behaviour. *Funct Ecol* **28**, 1472-81.

Radwan J., Kuduk K., Levy E., LeBas N. & Babik W. (2014) Parasite load and MHC diversity in undisturbed and agriculturally modified habitats of the ornate dragon lizard. *Mol Ecol* **23**, 5966-78.

Raffel T. R., Martin L. B. & Rohr J. R. (2008) Parasites as predators: unifying natural enemy ecology. *Trends Ecol Evol* **23**, 610-8.

Ramakrishnan L., Valdivia R. H., McKerrow J. H. & Falkow S. (1997) *Mycobacterium marinum* causes both long-term subclinical infection and acute disease in the leopard frog (*Rana pipiens*). *Infect. Immun.* **65**, 767-73.

This article is protected by copyright. All rights reserved

Reinert H. K. & Rupert Jr R. R. (1999) Impacts of translocation on behavior and survival of timber rattlesnakes, *Crotalus horridus*. *J Herpetol* **33**, 45-61.

Rohr J. R., Schotthoefer A. M., Raffel T. R., Carrick H. J., Halstead N., Hoverman J. T., Johnson C. M., Johnson L. B., Lieske C. & Piwoni M. D. (2008) Agrochemicals increase trematode infections in a declining amphibian species. *Nature* **455**, 1235.

Rosenblum E. B., Poorten T. J., Joneson S. & Settles M. (2012a) Substrate-specific gene expression in *Batrachochytrium dendrobatidis*, the chytrid pathogen of amphibians. *PLoS ONE* **7**, e49924.

Rosenblum E. B., Poorten T. J., Settles M. & Murdoch G. K. (2012b) Only skin deep: shared genetic response to the deadly chytrid fungus in susceptible frog species. *Mol Ecol* **21**, 3110-20.

Rosenblum E. B., Poorten T. J., Settles M., Murdoch G. K., Robert J., Maddox N. & Eisen M. B. (2009) Genome-wide transcriptional response of *Silurana* (*Xenopus*) *tropicalis* to infection with the deadly chytrid fungus. *PLoS ONE* **4**, e6494.

Rowley J. J. & Alford R. A. (2013) Hot bodies protect amphibians against chytrid infection in nature. *Sci. Rep.* **3**, 1515.

Rowley J. J., Gleason F. H., Andreou D., Marshall W. L., Lilje O. & Gozlan R. (2013) Impacts of mesomycetozoean parasites on amphibian and freshwater fish populations. *Fungal Biol. Rev.* **27**, 100-11.

Roznik E. A., Sapsford S. J., Pike D. A., Schwarzkopf L. & Alford R. A. (2015) Condition-dependent reproductive effort in frogs infected by a widespread pathogen. *Proc. R. Soc. B* **282**, 20150694.

Salvador A., Veiga J. P., Martin J., Lopez P., Abelenda M. & Puertac M. (1996) The cost of producing a sexual signal: testosterone increases the susceptibility of male lizards to ectoparasitic infestation. *Behav Ecol* **7**, 145-50.

Sarmiento-Ramírez J. M., Abella E., Martín M. P., Tellería M. T., Lopez-Jurado L. F., Marco A. & Diéguez-Uribeondo J. (2010) *Fusarium solani* is responsible for mass mortalities in nests of loggerhead sea turtle, *Caretta caretta*, in Boavista, Cape Verde. *FEMS Microbiol. Lett.* **312**, 192-200.

Savage A. E. & Zamudio K. R. (2011) MHC genotypes associate with resistance to a frog-killing fungus. *Proceedings of the National Academy of Sciences* **108**, 16705-10.

Author Manuscript

This article is protected by copyright. All rights reserved

Savage A. E. & Zamudio K. R. (2016) Adaptive tolerance to a pathogenic fungus drives major histocompatibility complex evolution in natural amphibian populations. *Proc. R. Soc. B* **283**, 20153115.

Schall J. (1983) Lizard malaria: parasite-host ecology. In: *Lizard ecology: studies of a model organism* (eds J. Baker, R. Muller and D. Rollinson) pp. 84-100. Harvard University Press, Cambridge.

Schall J. J. (1982) Lizards infected with malaria: physiological and behavioral consequences. *Science* **217**, 1057-9.

Schall J. J. (1986) Prevalence and virulence of a haemogregarine parasite of the Aruban whiptail lizard, *Cnemidophorus arubensis*. *J Herpetol* **20**, 318-24.

Schall J. J. (1992) Parasite-mediated competition in Anolis lizards. *Oecologia* **92**, 58-64.

Schall J. J., Bennett A. F. & Putnam R. W. (1982) Lizards infected with malaria: physiological and behavioral consequences. *Science* **217**, 1057-9.

Schall J. J. & Sarni G. A. (1987) Malarial parasitism and the behavior of the lizard, *Sceloporus occidentalis*. *Copeia* **1987**, 84-93.

Schall J. J. & Vogt S. P. (1993) Distribution of malaria in Anolis lizards of the Luquillo Forest, Puerto Rico: implications for host community ecology. *Biotropica* **25**, 229-35.

Scheele B. C., Hunter D. A., Grogan L. F., Berger L., Kolby J. E., McFadden M. S., Marantelli G., Skerratt L. F. & Driscoll D. A. (2014) Interventions for Reducing Extinction Risk in chytridiomycosis-threatened amphibians. *Conserv Biol* **28**, 1195-205.

Schotthoefer A. M., Cole R. A. & Beasley V. R. (2003) Relationship of tadpole stage to location of echinostome cercariae encystment and the consequences for tadpole survival. *J Parasitol* **89**, 475-82.

Sears B., Snyder P. & Rohr J. (2013) Infection deflection: hosts control parasite location with behaviour to improve tolerance. *Proceedings of the Royal Society of London B: Biological Sciences* **280**, 20130759.

Session A. M., Uno Y., Kwon T., Chapman J. A., Toyoda A., Takahashi S., Fukui A., Hikosaka A., Suzuki A. & Kondo M. (2016) Genome evolution in the allotetraploid frog *Xenopus laevis*. *Nature* **538**, 336.

Sherman E. (2008) Thermal biology of newts (*Notophthalmus viridescens*) chronically infected with a naturally occurring pathogen. *J Therm Biol* **33**, 27-31.

Author Manuscript

This article is protected by copyright. All rights reserved

Shilton C., Brown G., Benedict S. & Shine R. (2008) Spinal arthropathy associated with *Ochrobactrum anthropi* in free-ranging cane toads (*Chaunus [Bufo] marinus*) in Australia. *Vet Pathol* **45**, 85-94.

Shine R. (2010) The ecological impact of invasive cane toads (*Bufo marinus*) in Australia. *The Quarterly Review of Biology* **85**, 253-91.

Siddall M. E. & Desser S. S. (1992) Alternative leech vectors for frog and turtle trypanosomes. *The Journal of parasitology* **78**, 562-3.

Sih A., Spiegel O., Godfrey S., Leu S. & Bull C. M. (2017) Integrating social networks, animal personalities, movement ecology and parasites: a framework with examples from a lizard. *Anim Behav* **136**, 195-205.

Sin H., Beard K. H. & Pitt W. C. (2008) An invasive frog, Eleutherodactylus coqui, increases new leaf production and leaf litter decomposition rates through nutrient cycling in Hawaii. *Biol Invasions* **10**, 335-45.

Smith Trail D. R. (1980) Behavioral interactions between parasites and hosts: host suicide and the evolution of complex life cycles. *Am. Nat.* **116**, 77-91.

Soliman M. (2012) Heavy metal pollution across sites affecting the intestinal helminth communities of the Egyptian lizard, *Chalcides ocellatus* (Forskal, 1775). *Environ Monit Assess* **184**, 7677-85.

Sorci G., Clobert J. & Michalakis Y. (1996) Cost of reproduction and cost of parasitism in the common lizard, *Lacerta vivipara*. *Oikos*, 121-30.

Sorci G., Massot M. & Clobert J. (1994) Maternal parasite load increases sprint speed and philopatry in female offspring of the common lizard. *Am. Nat.* **144**, 153-64.

Speare R., Berger L., O'Shea P., Ladds P. & Thomas A. (1997) Pathology of mucormycosis of cane toads in Australia. *J Wildl Dis* **33**, 105-11.

Speare R., Thomas A., O'Shea P. & Shipton W. (1994) Mucor amphibiorum in the toad, *Bufo marinus*, in Australia. *J Wildl Dis* **30**, 399-407.

Spurgin L. G. & Richardson D. S. (2010) How pathogens drive genetic diversity: MHC, mechanisms and misunderstandings. *Proceedings of the Royal Society of London B: Biological Sciences* **277**, 979–88.

Author Manuscript

This article is protected by copyright. All rights reserved

Stenos J., Graves S., Popov V. L. & Walker D. H. (2003) *Aponomma hydrosauri*, the reptile-associated tick reservoir of *Rickettsia honei* on Flinders Island, Australia. *The American journal of tropical medicine and hygiene* **69**, 314-7.

Stopper G. F., Hecker L., Franssen R. A. & Sessions S. K. (2002) How trematodes cause limb deformities in amphibians. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology* **294**, 252-63.

Sun Y.-B., Xiong Z.-J., Xiang X.-Y., Liu S.-P., Zhou W.-W., Tu X.-L., Zhong L., Wang L., Wu D.-D. & Zhang B.-L. (2015) Whole-genome sequence of the Tibetan frog *Nanorana parkeri* and the comparative evolution of tetrapod genomes. *Proceedings of the National Academy of Sciences* **112**, E1257-E62.

Szuroczki D. & Richardson J. M. (2012) The behavioral response of larval amphibians (Ranidae) to threats from predators and parasites. *PLoS ONE* **7**, e49592.

Taggart P. L., Leu S. T., Spiegel O., Godfrey S. S., Sih A. & Bull C. M. (2018) Endure your parasites: sleepy lizard movement is not affected by their ectoparasites. *Can J Zool*.

Taylor C. N., Oseen K. L. & Wassersug R. J. (2004) On the behavioural response of Rana and Bufo tadpoles to echinostomatoid cercariae: implications to synergistic factors influencing trematode infections in anurans. *Can J Zool* **82**, 701-6.

Teacher A., Cunningham A. & Garner T. (2010) Assessing the long-term impact of ranavirus infection in wild common frog populations. *Anim Conserv* **13**, 514-22.

Teacher A. G., Garner T. W. & Nichols R. A. (2009) Evidence for directional selection at a novel major histocompatibility class I marker in wild common frogs (*Rana temporaria*) exposed to a viral pathogen (Ranavirus). *PLoS ONE* **4**, e4616.

Thorne E. & Williams E. S. (1988) Disease and endangered species: the black-footed ferret as a recent example. *Conserv Biol* **2**, 66-74.

Tingley R., Ward-Fear G., Schwarzkopf L., Greenlees M. J., Phillips B. L., Brown G., Clulow S., Webb J., Capon R. & Sheppard A. (2017) New weapons in the Toad Toolkit: a review of methods to control and mitigate the biodiversity impacts of invasive cane toads (*Rhinella marina*). *The Quarterly Review of Biology* **92**, 123-49.

Tocque K. (1993) The relationship between parasite burden and host resources in the desert toad (*Scaphiopus couchii*), under natural environmental conditions. *J Anim Ecol*, 683-93.

Author Manuscript

This article is protected by copyright. All rights reserved

Tompkins D. M., Carver S., Jones M. E., Krkošek M. & Skerratt L. F. (2015) Emerging infectious diseases of wildlife: a critical perspective. *Trends Parasitol* **31**, 149-59.

Uhrig E. J., Spagnoli S. T., Tkach V. V., Kent M. L. & Mason R. T. (2015) Alaria mesocercariae in the tails of red-sided garter snakes: evidence for parasite-mediated caudectomy. *Parasitol Res* **114**, 4451-61.

Václav R., Prokop P. & Fekiač V. (2007) Expression of breeding coloration in European Green Lizards (*Lacerta viridis*): variation with morphology and tick infestation. *Can J Zool* **85**, 1199-206.

Van Rooij P., Martel A., Haesebrouck F. & Pasmans F. (2015) Amphibian chytridiomycosis: a review with focus on fungus-host interactions. *Vet Res* **46**, 137.

Venesky M. D., Parris M. J. & Storfer A. (2009) Impacts of *Batrachochytrium dendrobatidis* infection on tadpole foraging performance. *EcoHealth* **6**, 565-75.

Viggers K., Lindenmayer D. & Spratt D. (1993) The importance of disease in reintroduction programmes. *Wildl Res* **20**, 687-98.

Voyles J., Young S., Berger L., Campbell C., Voyles W. F., Dinudom A., Cook D., Webb R., Alford R. A. & Skerratt L. F. (2009) Pathogenesis of chytridiomycosis, a cause of catastrophic amphibian declines. *Science* **326**, 582-5.

Wang S., Liu C., Wilson A. B., Zhao N., Li X., Zhu W., Gao X., Liu X. & Li Y. (2017) Pathogen richness and abundance predict patterns of adaptive MHC variation in insular amphibians. *Mol Ecol* **Volume26**, 4671-85.

Wheeler E., Hong P.-Y., Bedon L. C. & Mackie R. I. (2012) Carriage of antibiotic-resistant enteric bacteria varies among sites in Galapagos reptiles. *J Wildl Dis* **48**, 56-67.

Whiley H., Custance G., Graves S., Stenos J., Taylor M., Ross K. & Gardner M. G. (2016) Rickettsia detected in the reptile tick *Bothriocroton hydrosauri* from the lizard *Tiliqua rugosa* in South Australia. *Pathogens* **5**, 41.

Whiley H., Gardner M. G. & Ross K. (2017) A review of Salmonella and squamates (lizards, snakes and amphisbians): implications for public health. *Pathogens* **6**, 38.

Whiteman N. K., Matson K. D., Bollmer J. L. & Parker P. G. (2006) Disease ecology in the Galapagos Hawk (*Buteo galapagoensis*): host genetic diversity, parasite load and natural antibodies. *Proceedings of the Royal Society of London B: Biological Sciences* **273**, 797-804.

Author Manuscript

This article is protected by copyright. All rights reserved

Woodhams D. C., Bosch J., Briggs C. J., Cashins S., Davis L. R., Lauer A., Muths E., Puschendorf R., Schmidt B. R. & Sheafor B. (2011) Mitigating amphibian disease: strategies to maintain wild populations and control chytridiomycosis. *Front Zool* **8**, 8.

Author Manuscript

This article is protected by copyright. All rights reserved