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

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31 **Key words:**

32 Pathogen, Parasite, Disease, Behaviour, Physiology,

33 **Abstract:**

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

45

46

47 **1. Introduction**

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

57

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

60 human food resources such as fish, or aesthetically appealing groups such as mammals and birds,  
61 amphibians and reptiles (e.g. snakes, lizards and frogs) are less valued by society (Czech *et al.*  
62 1998); this is reflected by their disproportionately lower representation in published literature  
63 (Hecnar 2009). Understanding reptiles and amphibians is important because they are species rich  
64 with almost 8000 described amphibian species and over 10000 reptile species. They can obtain  
65 high biomass and play important roles in the ecosystem including as prey, consumers,  
66 pollinators, dispersers, nutrient cycling and bioturbators of soil (Godínez-Álvarez 2004; Iwai and  
67 Kagaya 2007; Lovich *et al.* 2018; Sin *et al.* 2008). Reptiles and amphibians have become  
68 increasingly vulnerable to extinction and thus research focused on understanding threatening  
69 factors to aid in conservation has recently become a priority (Gibbon *et al.* 2000; Meredith *et al.*  
70 2016).

71  
72 In conservation, the paucity of ecological knowledge in the context of amphibian disease ecology  
73 became evident during the global amphibian decline (Collins and Storfer 2003). Biologists were  
74 not prepared for disease-induced declines, and pioneering studies on parasites became invaluable  
75 to understand host physiology and behaviour, as well as broad ecological processes. The  
76 increased emergence of infectious disease over the past two decades has only served to  
77 consolidate the importance of understanding the ecological interactions between hosts and  
78 parasites (Bower *et al.* 2017b). As the importance of research that quantifies the effects of  
79 parasites is increasingly recognised, a review of these studies is timely.

80  
81 A leader in this field was the late Professor Michael Bull, and his pioneering work arises  
82 repeatedly throughout the various subtopics of our review. Here we aim to pay homage to the  
83 foresight and dedication of Michael Bull by demonstrating the importance of parasites in the  
84 ecology of reptiles and amphibians. We draw from the available literature to highlight the  
85 diversity and extent to which parasites and hosts are intertwined in fundamental ecological  
86 processes. Specifically, we focus on summarising our knowledge of parasite impacts on reptiles  
87 and amphibians, and highlight challenges we face in continuing to unravel these complex  
88 relationships.

89

## 90 2. Diversity of parasites

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

100

## 101 2.1 Viruses

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

119

## 120 2.2 Bacteria

121 Bacteria are receiving increasing attention for the role they may play in host ecology.  
122 Exploration into the function of microbiomes has accelerated this research field, owing in part to  
123 the inhibitory effects of bacteria on other pathogens such as the amphibian chytrid fungus  
124 (*Batrachochytrium dendrobatidis*, *Bd*) (Jani and Briggs 2014). From an ecological perspective,  
125 the ubiquitous nature of bacteria make them problematic for detection and quantification, and  
126 understanding when bacteria are pathogenic and under what circumstances continues to  
127 challenge researchers (Ramakrishnan *et al.* 1997). Species that cannot be cultured *in vitro* make  
128 Koch's postulates difficult to fulfill though sequencing is a powerful tool that is allowing us to  
129 unravel interactions among bacteria that we could not previously examine (Byrd and Segre  
130 2016). We do not know how bacteria interact in wild populations for many species, despite their  
131 ability to cause bacterial septicemia in captive populations (e.g. *Aeromonas hydrophila*, (Mauel  
132 *et al.* 2002; Pasquale *et al.* 1994)), and the lack of histopathological confirmation leaves  
133 uncertainty surrounding the cause of some wild die-offs. Pioneering research has demonstrated  
134 the importance of social networks (Bull *et al.* 2012) and reservoir species in transmission and  
135 population biology of specific bacteria (Giery and Ostfeld 2007). Bacterial zoonotic diseases  
136 have been the subject of some experimental ecological studies, e.g., those demonstrating  
137 antibiotic resistance in human-disturbed sites (Wheeler *et al.* 2012). *Salmonella* spp. infections  
138 can potentially spill over in the pet trade (Whiley *et al.* 2017), but the threat from wildlife  
139 appears low (Parsons *et al.* 2010).

140

### 141 2.3 Blood (Erythrocytic) parasites

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

149

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

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

161

## 162 2.4 Fungi

163 The global emergence of fungal diseases and associated mass die-offs in a diversity of reptile  
164 and amphibian species has brought mycoses (diseases caused by fungi) to the forefront of  
165 research and conservation. The number of extirpation events caused by fungi has increased in  
166 recent decades, and many losses of amphibian species are included in these events (Fisher *et al.*  
167 2012). The emergence of two distinct species of chytrid fungi (*Batrachochytrium dendrobatidis*  
168 and *B. salamandrivorans*) has caused multi-continental amphibian declines, which led to an  
169 explosion in ecological studies incorporating these parasites (Bower *et al.* 2017a). Additionally,  
170 an emerging fungal disease (associated with *Ophidiomyces ophiodiicola*) causing epidemics in  
171 snakes is receiving increasing attention (Allender *et al.* 2015). Marine turtles have also suffered  
172 disease associated with *Fusarium* spp. infection causing mass mortality in nests, particularly in  
173 stressful environmental conditions (Sarmiento-Ramírez *et al.* 2010). While other potentially  
174 lethal fungi have been identified (e.g. *Mucor amphibiorum*, *Paranannizziopsis australasiensis*),  
175 research has been restricted to quantifying prevalence (Masters *et al.* 2016; Speare *et al.* 1994).  
176 A potentially deadly fungus, *Lecanicillium* spp., was diagnosed in a captive colony of  
177 endangered Guthega skinks (*Liopholis guthega*) causing cutaneous and systemic mycosis and  
178 provided the first report of this infection in reptiles. Beyond these few examples, ecology of  
179 fungal pathogens in reptiles and amphibians is little known.

180

## 181 2.5 Animals

### 182 Endoparasites

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

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

196 Ectoparasites

197 Studies on the behavioural and physiological interactions of ectoparasites such as ticks and mites  
198 in reptile and amphibian ecology have also been extensive, forming a substantial component of  
199 the life work of Michael Bull (Godfrey and Gardner 2017). Ticks (*Bothriocroton hydrosauri*) on  
200 sleepy lizards (*T. rugosa*) and other bluetongues (*T. spp.*) have been identified as vectors for the  
201 bacterial agent causing spotted fever (i.e. the bacteria *Rickettsia* sp.) (Stenos *et al.* 2003; Whiley  
202 *et al.* 2016). Flies and mosquitoes have also received some attention in ecological studies, both  
203 as direct parasites and vectors (Bernal *et al.* 2007). Additionally, the ecological interactions of  
204 leeches have been explored in salamanders (Lunghi *et al.* 2018) and turtles, which can harbor  
205 high densities of over 150 leeches on a single turtle (Graham *et al.* 1997). They further act as  
206 vectors for blood parasites e.g. for haemogregarines and trypanosomes (Siddall and Desser  
207 1992).

208

### 209 **3. Environmental Interactions**

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

212 Behavioural thermoregulation is a consequence of parasite infection in both reptiles (Schall &  
213 Sarni 1987, Main & Bull 2000) and amphibians (Lefcort & Eiger 1993, Lefcort & Blaustein  
214 1995, Richards-Zawacki 2009). Their immune system is at the mercy of environmental  
215 conditions, and sub-optimal temperature can cause immunosuppression in many species. For  
216 example, in cold stunned Kemp's ridley sea turtles (*Lepidochelys kempii*) in Massachusetts, most  
217 of the pathological changes observed were associated with bacteria and or fungi. These were  
218 suspected to be opportunistic infections due to host immunosuppression caused by the cold  
219 temperatures (Innis *et al.* 2009). Prolonged exposure to low temperatures during hibernation  
220 resulted in weakened immune systems in leopard frogs (*Lithobates [Rana] pipiens*) (Cooper *et*  
221 *al.* 1992), and a lizard called the sandfish skink (*Scincus scincus*) had reduced lymphoid tissues  
222 and immune response in winter (Hussein *et al.* 1979). In other cases, suboptimal temperatures  
223 may elicit an increased immune response resulting in better resistance to disease. Green Tree  
224 frogs (*Litoria caerulea*) experimentally acclimated to low temperatures had lower infection  
225 intensities when exposed to the amphibian chytrid fungus (*B. dendrobatidis*) than those  
226 acclimated to higher temperatures (Greenspan *et al.* 2017b). The individuals exposed to sub-  
227 optimal temperature were better able to fight the pathogen because their immune parameters  
228 were already adjusted to cope with the challenging environmental conditions. The cool-exposed  
229 individuals had a higher neutrophil:lymphocyte ratio, a response also seen in leopard frogs (*L.*  
230 *pipiens*) (Maniero and Carey 1997).

231  
232 Along with temperature, other external factors can influence the immune system of hosts and  
233 their ability to resist infection. Juvenile leopard frogs (*L. pipiens*) experimentally exposed to  
234 agricultural pesticides experienced lower lymphocyte proliferation which have a central role in  
235 pathogen defense. Higher nematode burdens (Christin *et al.* 2003) and trematode infection can  
236 increase exposure and susceptibility by augmenting intermediate snail hosts and reduce liver  
237 eosinophil (disease-fighting blood cells) counts, indicative of a reduced immunity (Rohr *et al.*  
238 2008). In addition, UVB radiation causes immunosuppression in amphibians and increases  
239 susceptibility to disease (Little and Calfee 2010). Heavy metal toxicity can also cause  
240 immunosuppression. For example, mercury concentrations were correlated with reduced  
241 lymphocyte proliferation and activity in Loggerhead sea turtles (*Caretta caretta*) (Day *et al.*  
242 2007). The viral disease 'green turtle fibropapillomatosis' affects all sea turtle species, and



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

246  
247 Stress-induced physiological changes may increase the incidence of disease in reptiles and  
248 amphibians. Environmental stressors such as desiccation of ponds cause tadpoles to  
249 metamorphose faster, and this can have a trade off in terms of immunocompetence. Wood frog  
250 (*Lithobates sylvaticus*) tadpoles exposed to experimental desiccation have fewer lymphocytes  
251 and reduced responses to immune challenge after metamorphosis (Gervasi and Foufopoulos  
252 2008). Newly metamorphed amphibians are disproportionately more vulnerable to the amphibian  
253 chytrid fungus (*B. dendrobatidis*) infection, so immune suppression due to environmental  
254 stressors can have a dramatic effect on susceptibility (Gervasi and Foufopoulos 2008). The  
255 effects of stress on host susceptibility may also have conservation implications. For example, the  
256 stress of capture and release into an unfamiliar environment caused a higher rate of disease in  
257 translocated Timber Rattlesnakes (*Crotalus horridus*) compared to resident animals (Reinert and  
258 Rupert Jr 1999). High densities can reduce immunity and this can be age dependent within a  
259 species. For example, higher densities of adults of the lizard (*Zootoca vivipara*) experienced  
260 increased local inflammation and high densities of tick infestation (*Ixodes ricinus*) whereas  
261 yearlings did not experience inflammation or increased tick infestation (Mugabo *et al.* 2015).  
262 Habitat features can also affect parasites differently. In a Mediterranean lizard (*Psammodromus*  
263 *algrius*), the prevalence and infection load of blood parasites was higher in a high elevation  
264 deteriorated habitat whereas prevalence and infection load of ticks (*Ixodes* sp) showed the  
265 reverse pattern (Carbayo *et al.* 2018).

266

#### 267 **4. Behaviour**

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

274 such as foot-stomping, jumping, and wiping their hands over their bodies to prevent mosquito  
275 bites, which minimises transmission of mosquito-borne parasites (Ferguson and Smith 2012).  
276 Grey tree frogs *Dryophytes [Hyla] versicolor* discriminated between water bodies based not only  
277 on the presence and density of a gastropod vector that carries a trematode parasite of their  
278 tadpoles, but also on whether or not the snails were infected, laying less frequently and fewer  
279 eggs in treatments with a higher likelihood of infection (Kiesecker and Skelly 2000).  
280 There is species-specific variation in the behaviour of tadpoles toward the presence of  
281 trematodes (*Echinoparyphium* sp.) (Koprivnikar *et al.* 2014). Permanent pond breeding frogs that  
282 were more likely to encounter trematodes (*Echinostoma* spp.) modified their activity in the  
283 presence of these parasites. Conversely, ephemeral breeding frog species that encountered less  
284 trematodes also lacked the behavioural response, suggesting selection may occur on such  
285 behavioural traits (Szuroczki and Richardson 2012). Parasite avoidance behaviour is complex  
286 and interacts with predators, whereby tadpoles (*L. pipiens*) preferred areas without trematodes  
287 (*Ribeiroia ondatrae*) unless their alternative was predator exposure by larval odonates  
288 (Koprivnikar and Penalva 2015). American toad tadpoles (*Bufo americanus*) fled from the  
289 touch of a trematode (*Echinostoma* sp.) (Taylor *et al.* 2004), and tadpoles adopted behaviours  
290 that influenced the site in which infection occurred and thus decreased the pathological  
291 consequences of infection (Kiesecker *et al.* 1999; Sears *et al.* 2013). Selection against  
292 cannibalism is thought to have evolved as a behaviour to minimise parasite transmission between  
293 intraspecific hosts. For example, larval tiger salamanders (*Ambystoma tigrinum*) avoided preying  
294 on conspecifics with bacterial infection (*Clostridium* sp. bacteria) (Pfennig *et al.* 1998; Pfennig  
295 *et al.* 1991). In other cases tadpoles (*Pseudacris regilla* and *Anaxyrus boreas*) did not adopt  
296 behaviours to minimise transmission by snails infected with a trematode parasite (*R. ondatrae*),  
297 but once infected, decreased their activity and escape distance (Preston *et al.* 2014).  
298 Interestingly, the same study showed two less virulent trematodes (*Echinostoma* sp. and *Alaria*  
299 sp.) caused no such effects.  
300  
301 Surprisingly, few studies have revealed behaviours that minimise or reduce potential  
302 transmission of ectoparasites in reptiles, despite the negative physiological consequences (Aubret  
303 *et al.* 2014; Biaggini *et al.* 2009; Godfrey *et al.* 2006). Although one exception in the usually  
304 monogamous sleepy lizard (*T. rugosa*) showed that males that are abandoned by females

305 between mating seasons have higher tick loads than males that retain their partners, thereby  
306 reducing infection potential for females (Bull and Burzacott 2006). As many endoparasites of  
307 reptiles are transmitted via their prey, the potential for avoidance may be difficult. Notably,  
308 several studies on blood parasites (*Hepatozoon* sp.) in snakes that demonstrated negative effects  
309 on nutritional status, reproduction and survival (Madsen *et al.* 2005) revealed little effect on  
310 behaviour. Keelback snakes (*Tropidonophis mairii*) infected with parasites (Family:  
311 Haemogregarinidae and Gnathostomidae) had similar performance (e.g. 'sprint' speed) and  
312 fitness measures (e.g. escape distance) to uninfected individuals (Brown *et al.* 2006).  
313  
314 Many of the studied behavioural changes in hosts are investigated as a limited single species  
315 comparison (Damas-Moreira *et al.* 2014; Daniels 1985; Oppliger *et al.* 1996). These studies  
316 often explore only the alteration in behaviour without examining underlying mechanisms.  
317 However, there are a number of notable studies that explore complex interactions that note both  
318 changes in behaviour of the host and the consequences of these changes for ecology and  
319 evolution. These complex interactions have often been demonstrated using lizards, specifically  
320 *Lacerta*, *Anolis* and *Sceloporus* spp., as model organisms. These studies demonstrated that  
321 *Plasmodium* sp. infection altered male social behaviour (Schall 1982), in part due to altered  
322 thermoregulatory and perching behaviour of hosts (Schall and Sarni 1987). Similarly,  
323 *Plasmodium* sp. infection altered the outcome of competitive interactions between two species of  
324 lacertid lizard, ultimately playing a critical role in determining the distribution of each species on  
325 a landscape scale (Schall 1992; Schall and Vogt 1993). Finally, ectoparasites (ticks *Aponomma*  
326 *hydrosauri* and *Amblyomma limbatum*) can affect simple behaviours in sleepy lizards (*T. rugosa*)  
327 such as the time spent basking, moving and ultimately dispersing (Main and Bull 2000) but  
328 under natural conditions these hosts appear adapted to the ticks and movement is more strongly  
329 explained by sex and body condition independent of ticks (Taggart *et al.* 2018). Effects can be  
330 intergenerational, in female common lizards (*Z. vivipara*), parasitism by mites (Family:  
331 Lealapididae) effected the dispersal behaviour of the offspring (Sorci *et al.* 1994). Such studies  
332 highlight the importance of parasites in shaping behaviours that intricately influence the ecology  
333 of animals and suggest that any ecological study that wishes to quantify behaviour should  
334 attempt to account for possible influences of parasites.

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

344  
345 Another prominent behaviour of anurans, and an obvious subject of such research with profound  
346 consequences for ecology and life history, is reproductive calling. Seasonal patterns of calling  
347 resulted from interactions between infection by *B. dendrobatidis* and body condition in the  
348 Common mist frog *Litoria rheocola* (Roznik *et al.* 2015). Similarly, Japanese tree frogs  
349 *Dryophytes [Hyla] japonicas* called more rapidly and for longer when infected with the *B.*  
350 *dendrobatidis* (An and Waldman 2016). Contrary to these results, calling was reduced in  
351 Brazilian subtropical treefrog (*Hypsiboas prasinus*) infected with helminth parasites and this was  
352 exacerbated in smaller individuals (Madelaire *et al.* 2013). Conversely, Grey Treefrog (*H.*  
353 *versicolour*) calling characteristics remained unchanged, though males with greater parasite  
354 loads achieved more amplexus (Hausfater *et al.* 1990). In spadefoot toads (*Scaphiopus couchii*),  
355 males parasitised by a monogenean worm (*Pseudodiplorchis americanus*) had more attractive  
356 calls to females, thereby skewing female choice (Pfennig and Tinsley 2002). While calling  
357 duration in Cururu toads (*Rhinella icterica*) was not affected by nematode lungworms (*Rhabdius*  
358 *sp.*), locomotory performance was reduced and this may have played some role in the capacity of  
359 toads to find and mate with females (Moretti *et al.* 2014; Moretti *et al.* 2017).

360  
361 Another model system in the study of the effects of parasites on anuran movement is the  
362 infamous invasion of cane toads (*Rhinella [Bufo] marina*) in Australia (Shine 2010). As is the  
363 case with many invasive species, use of 'natural' parasites has been explored for potential  
364 capacity in control for toads specifically, to mitigate the rate of invasion (Tingley *et al.* 2017).  
365 Survival and growth rate of metamorph cane toads (*R. marina*) was reduced, alongside impaired

366 locomotory performance and reduced prey intake when infected with *Rhabdus*  
367 *pseudospaheracephala*) (Kelehear *et al.* 2009) and toads showed no tendency to avoid areas  
368 inhabited by a lungworm, nor demonstrated the capacity to avoid infection (Kelehear *et al.*  
369 2011). However, infection did not affect dispersal behaviour of adult toads (Brown *et al.* 2016).  
370 A bacteria (*Ochrobactrum anthropi*) was also explored as a causative agent of spinal arthropathy  
371 in cane toads (*R. marina*) (Brown *et al.* 2007; Shilton *et al.* 2008), though the effects on toads  
372 appear to relate to climate and growth (Bower *et al.* 2018).

373  
374 Original theoretical frameworks of disease ecology assumed that parasite burden and effects  
375 were directly related to parasite abundance and distribution within the host population, with all  
376 individuals having an equal, random chance of infection (Anderson 1978). More recently,  
377 emphasis has shifted towards a social network style of analysis (Bull *et al.* 2012; Godfrey 2013),  
378 with evidence that context and interactions between individuals strongly effect parasite  
379 transmission and parasite species assemblages. For example, social association in the sleepy  
380 lizard (*T. rugosa*) had a stronger link to parasite sharing and transmission than did common  
381 resource use (Bull *et al.* 2012; Sih *et al.* 2017). Similarly, tick infestation (*Amblyomma*  
382 *sphenodonti*) and a blood parasite (*Hepatozoon tuatarae*) transmitted by the tick in the tuatara  
383 (*Sphenodon punctatus*) was significantly related to social interaction (Godfrey *et al.* 2010). We  
384 suggest that theoretical models and predictions of parasite transfer, and the demographic effects  
385 of parasites should be updated in response to these findings.

386  
387 Studies examining how parasites affect the behaviours of reptiles and amphibians are neither  
388 complete nor comprehensive in taxonomic coverage. For example, Corethrellid flies  
389 (*Corethrella* sp.) use frog calls to locate potential hosts (Bernal *et al.* 2006), yet despite several  
390 studies describing the prevalence of parasitism of anuran amphibians by these and *Batrachomyia*  
391 flies (*Batrachomyia* sp.) (Elkan 1965; Hoskin and McCallum 2007; Kraus 2007), we still do not  
392 have a strong understanding of how myiasis (infection with fly larva) influences behaviours of  
393 amphibian hosts. Additionally, studies are lacking for entire taxonomic groups; little research has  
394 explored the effects of parasites on the behaviour of Gymnophionan amphibians (Caecilians) and  
395 surprisingly, Crocodylians. Opportunities certainly exist to improve our understanding of the role  
396 of parasites in shaping behaviour, which plays a critical role in ecology.

397

398 **5. Physiology**

399 Evidence of the adverse effects of parasites on the physiological condition of reptile and  
400 amphibian hosts is mounting (Koprivnikar *et al.* 2012; Martín *et al.* 2008; Oppliger *et al.* 1996;  
401 Schall *et al.* 1982; Van Rooij *et al.* 2015). Parasites that consume or destroy red blood cells, such  
402 as ticks and hemogregarine protozoa, can reduce hemoglobin concentrations and the capacity for  
403 blood to deliver oxygen to tissues (Dunlap and Mathies 1993; Martín *et al.* 2008; Oppliger *et al.*  
404 1996). Trematodes (*Ribeiroia* sp.) encyst in the developing limb buds of amphibians, causing  
405 abnormal cellular growth, leading to limb abnormalities (Johnson *et al.* 2001; Johnson *et al.*  
406 1999; Stopper *et al.* 2002) and in garter snakes (*Thamnophis sirtalis*) trematodes (*Alaria* sp.)  
407 cause extensive muscle damage (Uhrig *et al.* 2015). The fungal chytrid genus *Batrachochytrium*  
408 damages the permeable skin of amphibians, causing loss of water and electrolyte equilibrium  
409 (Voyles *et al.* 2009).

410

411 Disruption of physiological processes by parasites can influence individual performance and  
412 interactions within and between species. At times, interference with physiological processes  
413 causes direct mortality, as in tadpoles of Leopard frogs (*L. pipiens*) with trematode (Family:  
414 Echinostomatidae) infections (Schotthoefer *et al.* 2003), toads (*R. marina*) with tick infestations  
415 (Lampo and Bayliss 1996), and many frog species infected with the fungus *B. dendrobatidis*  
416 (Berger *et al.* 1998). Altered physiology from parasitism may also influence other measures of  
417 fitness such as body condition. Western fence lizards, (*Sceloporus occidentalis*) with malaria  
418 (*Plasmodium mexicanum*) exhibited decreased fat storage (Schall 1983), as did desert toads  
419 (*Scaphiopus couchii*) infected with a monogenean blood parasite *Pseudodiplorchis americanus*,  
420 after emergence from hibernation (Tocque 1993). Similarly, tick-infection in cane toads (*R.*  
421 *marina*) reduced their ability to gain weight (Lampo and Bayliss 1996). Decreases in mass or fat  
422 deposition could result from allocation of energy to immune defenses, or decreases in aerobic  
423 activities such as foraging or defense of foraging territories, as postulated for western fence  
424 lizards (*Sceloporus occidentalis*) with heavy tick (*Ixodes pacificus*) loads (Dunlap and Mathies  
425 1993).

426

427 Although comparatively light tick loads (*I. pacificus*) do not appear to influence the body  
428 condition of western fence lizards (*S. occidentalis*), co-infection with malarial protozoa (*P.*  
429 *mexicanum*) had a negative effect on host condition because both parasites reduced hemoglobin  
430 concentrations by different pathways, leading to further physiological costs (Dunlap and Mathies  
431 1993).

432  
433 The physiological effects of parasites may also increase the risk of host predation. In pacific tree  
434 frogs (*Hyla regilla*) with trematode infections (*Ribeiroia* sp.), limb abnormalities hindered the  
435 mobility necessary for predator avoidance (Goodman and Johnson 2011a; b; Johnson *et al.*  
436 1999). Similarly, running stamina was reduced in malaria-infected (*P. mexicanum*) western fence  
437 lizards (*S. occidentalis*) (Schall *et al.* 1982). In common lizards (*Z. vivipara*) infected with  
438 hemogregarines, (*Haemogregarina* sp.) locomotor speeds were lowered (Oppliger *et al.* 1996),  
439 and rates of tail regeneration (an important mechanism of predator escape) were slower  
440 (Oppliger and Clobert 1997). Another pathway by which parasites may alter host physiology is  
441 by reducing host thermal tolerance, as with spotted tree frogs (*Litoria spenceri*) infected by the  
442 fungus *B. dendrobatidis* (Greenspan *et al.* 2017a) and newts (*Notophthalmus viridescens*)  
443 infected with mesomycetozoan parasite (described as an *Ichthyophonus*-like organism) (Sherman  
444 2008), a reminder that anthropogenic environmental factors, such as climate variability  
445 associated with global change and environmental contaminants, can exacerbate the harmful  
446 physiological effects of infection (Chatfield *et al.* 2013; Marcogliese *et al.* 2009).

447  
448 Altered host physiology by parasites can also influence reproductive processes. Malaria-infected  
449 (*P. mexicanum*) lizards (*S. occidentalis*) had reduced clutch and testis sizes (Schall 1983). In  
450 European green lizards (*Lacerta viridis*) with high tick (*Ixodes ricinus*) burdens, females had  
451 more saturated chest coloration, which may have indicated avoidance of highly aerobic  
452 interactions such as courtship and mating (Václav *et al.* 2007). European green lizards (*Lacerta*  
453 *viridis*) parasitized by ticks (*I. ricinus*) (Václav *et al.* 2007) and wall lizards (*Podarcis muralis*)  
454 infected with hemogregarine blood protozoa (family Haemogregarinidae) (Martín *et al.* 2008)  
455 had less-saturated throat coloration, indicating that resources were allocated to other  
456 physiological processes such as immunity, at the expense of processes associated with breeding  
457 coloration that help to attract females (Václav *et al.* 2007)..

458

459 While there are a number of examples where infection with a parasite led to decreased  
460 reproductive effort, there are cases where infection led to increased reproductive effort. In frogs  
461 infected with fungus (*B. dendrobatidis*), male leopard frogs (*R. pipiens*) had increased testis size,  
462 male southern corroboree frogs (*Pseudophryne corroboree*) and alpine tree frogs (*Litoria*  
463 *verreauxii alpina*) had increased sperm production (Brannelly *et al.* 2016; Chatfield *et al.* 2013),  
464 and female alpine tree frogs (*L. v. alpina*) had increased gonad size as well as an increased  
465 number of developed eggs inside the ovaries (Brannelly *et al.* 2016). Further, the energetic costs  
466 of reproduction can lead to a situation in which immune function is decreased in a trade-off  
467 favouring reproductive processes. Wild female tree lizards (*Urosaurus ornatus*) in Arizona had  
468 reduced immune function during egg production (vitellogenesis) (French and Moore 2008).  
469 Controlled experiments demonstrated that this decrease in immune function only occurs when  
470 food resources become limited, suggesting that this is a facultative response (French and Moore  
471 2008). This trade-off between reproduction and immune response could conceivably result in  
472 increased susceptibility to disease.

473

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



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

500

## 501 6. Genomics

502 At a population level, host genetic diversity can influence parasite load, and consequently  
503 disease dynamics. Studies across taxa have demonstrated that host genetic variation dictates  
504 parasite susceptibility; populations with greater genetic diversity tend to respond more variably  
505 to infection, while homogenous populations suffer from the 'monoculture effect,' making them  
506 more susceptible to disease (Altermatt and Ebert 2008; Coltman *et al.* 1999; King and Lively  
507 2012; O'Brien *et al.* 1985; Thorne and Williams 1988; Whiteman *et al.* 2006). This increased  
508 parasite susceptibility with a loss of genetic diversity has been seen in the Italian agile frog  
509 (*Rana latastei*) exposed to ranavirus, where decreased survival correlated with population  
510 genetic depletion (Pearman and Garner 2005). Disease outbreaks in inbred and bottlenecked  
511 populations may be particularly severe due to a loss of adaptive capacity, the potential loss of  
512 alleles conferring resistance, and accumulation of those that are deleterious.

513

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

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

525  
526 In amphibians, both diversifying and directional selection contribute to MHC diversity (Savage  
527 and Zamudio 2011; Teacher *et al.* 2009; Wang *et al.* 2017). Among populations of Black-spotted  
528 pond frogs (*Pelophylax nigromaculatus*), MHC class Ia genetic diversity was positively  
529 correlated with viral abundance and richness. Moreover, there were significant correlations  
530 between MHC functional supertypes and either *Frog virus 3* or *Ambystoma tigrinum virus*,  
531 suggesting that these supertypes may have conferred resistance (Wang *et al.* 2017). By  
532 comparing ranavirus-infected and uninfected populations of the European Common Frog (*Rana*  
533 *temporaria*), directional selection for specific MHC supertypes in diseased populations was  
534 demonstrated (Teacher *et al.* 2009). Similarly, both MHC class IIb heterozygosity and presence  
535 of the specific Q allele were associated with increased survival in Lowland leopard frogs  
536 (*Lithobates yavapaiensis*) experimentally infected with fungus (*B. dendrobatidis*) (Savage and  
537 Zamudio 2011). Directional selection for survival-associated alleles was further confirmed in  
538 natural populations of *L. yavapaiensis*, suggesting evolution of tolerance to *B. dendrobatidis* in  
539 this species (Savage and Zamudio 2016). Finally, while the relationship between parasite burden  
540 and MHC alleles is unclear in the critically endangered corroboree frog (*Pseudophryne*  
541 *corroboree*), recent evidence demonstrates both high MHC class Ia diversity and signatures of  
542 positive selection at the peptide binding region, indicating that this locus may be important in  
543 adaptation to disease (Kosch *et al.* 2017).

544  
545 In addition to adaptation, plasticity in host response to a disease can dictate parasite load.  
546 Interpreting host response at the level of gene expression is particularly useful when genomic  
547 resources are limiting, as in amphibians, where large genome sizes have precluded assembly in  
548 all but three taxa (Hellsten *et al.* 2010; Session *et al.* 2016; Sun *et al.* 2015). Microarray and  
549 RNA-sequencing in experimental infection trials was most extensively undertaken in the  
550 amphibian chytrid fungus (*B. dendrobatidis*) system (Ellison *et al.* 2014a; Ellison *et al.* 2014b;

551 Grogan *et al.* 2018; Rosenblum *et al.* 2012a; Rosenblum *et al.* 2012b; Rosenblum *et al.* 2009).  
552 Among susceptible species, infection led to decreased expression of transcripts related to skin  
553 integrity—such as those in the keratin and elastin pathways—while resistant species upregulated  
554 skin integrity-related transcripts (Ellison *et al.* 2014b; Rosenblum *et al.* 2012b; Rosenblum *et al.*  
555 2009). Central American frogs with varied responses to fungal (*B. dendrobatidis*) infection  
556 exhibited species-specific differences in gene expression, with highly susceptible species  
557 demonstrating both increased expression of transcripts related to inflammation and suppression  
558 of lymphocyte activation and proliferation pathways (Ellison *et al.* 2014a; Ellison *et al.* 2014b).  
559 Such differences in gene expression not only dictate host infection outcomes, but may also  
560 influence parasite evolutionary trajectory. For example, when grown *in vivo* in a susceptible  
561 species versus in culture, the fungus (*B. dendrobatidis*) simultaneously increased expression of  
562 transcripts involved in proteolysis, transmembrane transport, and cilium morphogenesis, and  
563 exhibited a shift in expressed genotype frequencies (Ellison *et al.* 2017). Disentangling the extent  
564 to which host genomic and transcriptomic variation may influence rapid evolution in parasite  
565 populations holds great promise for refining our understanding of disease dynamics.

566

## 567 **7. Conservation**

568 Parasite infection and disease is often not the sole cause of extinction or even the major  
569 contributor to declines in many species of amphibians and reptiles (Gibbon *et al.* 2000; Lafferty  
570 and Gerber 2002). However, when combined with other stressors, such as population  
571 fragmentation or invasive species, a parasite can rapidly devastate a population (Gibbon *et al.*  
572 2000; Tompkins *et al.* 2015). Parasites can affect population viability by causing death, or  
573 increasing susceptibility to predators or other stressors, thereby decreasing reproductive capacity  
574 and population growth (Cunningham 1996; Lafferty and Gerber 2002). Disease often affects  
575 endangered species and those with small populations more dramatically than abundant species  
576 (May 1988). One such example is the flattened musk turtle (*Sternotherus depressus*), a species  
577 threatened by habitat change. One population experienced a massive decline (decrease of 50%)  
578 over twelve months, primarily caused by septicemia (Dodd Jr 1988). Compounded further by  
579 localised poaching of turtles, the severity and impact of that particular disease outbreak was  
580 attributed to a weakened immune function due to environmental stress (Dodd Jr 1988).  
581 Septicemia does not seem to cause similar effects in other turtle species or populations, further

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

584  
585 Disease is a greater threat generally for endangered and rare species; therefore, management  
586 tools used for conservation need to incorporate disease and risk thereof into conservation  
587 strategy. Some examples of where such considerations are vital are when managing captive  
588 assurance colonies, reintroductions and translocations. Understanding disease is an important  
589 component of bringing animals into captivity, as well as the implications of releasing them into  
590 the wild. In the past, animal releases have caused more harm than good when parasites were  
591 relocated with the target species (Cunningham 1996; Deem *et al.* 2001; Viggers *et al.* 1993).  
592 Most current management practices follow strict guidelines for quarantining animals intended for  
593 reintroduction/translocation programs and screen for parasites before release (Cunningham  
594 1996). However, continued movement of wildlife for the pet trade and food provides a less  
595 regulated, ongoing risk (Gratwicke *et al.* 2010) Improved biosecurity and disease quarantine  
596 protocols increase the success of reintroductions (Germano and Bishop 2009), and reduce  
597 movement of parasites between locations because disease can impact the target species as well as  
598 sympatric species (Cunningham 1996; Viggers *et al.* 1993). However, by removing parasites  
599 prior to translocation, host-parasite interactions may be disrupted to the detriment of the host  
600 (Northover *et al.* 2018), and more research is needed to understand the risks here.

601  
602 While most parasites that affect reptiles and amphibians do not result in mass mortality in wild  
603 populations, stressful conditions in captivity can cause high morbidity and mortality that would  
604 otherwise have minimal impact in the wild (Pessier 2008). One such disease is mucormycosis,  
605 which is caused by the fungus *Mucor amphibiorum*. Mucormycosis is rare in wild frog  
606 populations (Berger *et al.* 1997; Speare *et al.* 1997), but has on occasion caused 80% mortality in  
607 captive colonies in Australia and Germany (Creepers *et al.* 1998). Another example is boid  
608 inclusion body disease, which is likely caused by a retrovirus and causes central nervous system  
609 abnormalities and death in affected captive boid snakes (Chang and Jacobson 2010). While boid  
610 inclusion body disease is a global issue, it has only been reported in captivity (Chang and  
611 Jacobson 2010; Hetzel *et al.* 2013). A third example is the bacteria *Pseudomonas* sp, which  
612 caused an outbreak of necrotic dermatitis in a captive colony of the critically endangered western

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

622  
623 The impacts of the disease chytridiomycosis on amphibians has been well-studied and reviewed  
624 (Bower *et al.* 2017a; Scheele *et al.* 2014; Woodhams *et al.* 2011), and mitigating risk of the  
625 spread of this pathogen has been incorporated into policy governing the management of  
626 threatened and declining amphibian species (Commonwealth of Australia 2016). However, the  
627 same research and management effort has not been undertaken for other diseases. Where  
628 diseases do not directly cause species extinction, populations can still be negatively impacted by  
629 parasites, particularly in small populations. For example, ranavirus is widespread in amphibian  
630 and reptile species globally, and while it can cause mass declines, it often does not. However,  
631 only after a long-term study exploring many different ranavirus-positive and ranavirus-negative  
632 populations is it clear that ranavirus has an overall negative effect on population growth over  
633 time (Teacher *et al.* 2010).

634  
635 The extent to which parasites can act as a threatening process is unclear in many cases. Long  
636 term population level effects of Fibropapillomatosis are unknown in most regions, but Hawaiian  
637 green turtle populations have recovered from initial declines despite disease presence  
638 (Chaloupka and Balazs 2005; Jones *et al.* 2016). While myxosporea and sparganosis cause  
639 disease in amphibians, and occur in many locations around the globe, prevalence in amphibian  
640 communities and impact of disease on populations is essentially unknown (Berger *et al.* 2009).  
641 Most diseases described in reptiles and amphibians are reported as case studies, often without  
642 information of disease prevalence or population impact.

643

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

663

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668

669

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