Acta Herpetologica 15(1): 39-45, 2020
DOI: 10.13128/a_h-8744

An overview of research regarding reservoirs, vectors and predators of the chytrid fungus *Batrachochytrium dendrobatidis*

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Submitted on: 2019, 8th September; revised on: 2020, 13th January; accepted on: 2020, 15th January
Editor: Fabio M. Guarino

Abstract. This review presents an overview of research from 1998-2018 regarding interactions of *Batrachochytrium dendrobatidis* with both potential hosts and predators. To this end, 23 different studies collected from the Web of Science database along with two external journals were utilized, encompassing numerous taxonomic groups. Numerous groups of animals were identified as potential vectors for the fungus, with crayfish and reptiles standing as the most prominent and consistent non-amphibian hosts warranting their inclusion in any future broadscale distribution surveys. an important area for future research. Additionally, *Daphnia* were noted to serve as predators of the zoospores when exposed in mesocosm scenarios, reducing infection levels in corresponding tadpoles. Caecilians have also been observed to be carriers of *Bd*, though the level as to which the chytrid impacts these organisms needs to be further researched. In total, this review indicates that future research needs to begin including freshwater crustaceans, caecilians and reptiles in field studies for presence/absence, while a broader range of taxa need to be tested to see whether they serve as vectors or hosts in natural scenarios.

Keywords. *Batrachochytrium dendrobatidis*, crayfish, reptiles, *Daphnia*, fish, caecilians, alternate hosts, review.

INTRODUCTION

Since its identification in the late 1990s, amphibian declines have been heavily attributed to a parasitic fungus called *Batrachochytrium dendrobatidis* (Longcore et al., 1999) as it spreads around the globe (Longcore et al., 1999). A member of the fungal division Chytridiomycota, the zoospores encyst in an amphibian's skin, often resulting in deleterious effects, posing especially difficult to eradicate to its ability to persist in areas for years despite an apparent lack in hosts and easy spread via multiple vectors. While anthropogenic actions and naturally resistant amphibian species have long been considered potential vectors for *Batrachochytrium dendrobatidis* (*Bd*), interest has steadily grown over the past decade in whether non-amphibians could serve as either a vector for the disease or potentially as alternative hosts from which the fungus could complete its lifecycle (McMahon et al., 2013). As the zoospores are specifically attracted to highly keratinized cells, such as those in the frog's skin, early studies proposed and investigated whether the fungus would be attracted to keratin from non-amphibious sources such as snakeskin and crayfish with varying results (Longcore et al., 1999; Piotrowski et al., 2004; Rowley et al., 2006). Since then, research into the topic has been few and far between, with the subjects ranging from traditional aquatic species to those who may serve as unconventional vectors such as reptiles.

MATERIAL AND METHODS

In this review, we sought to provide an overview regarding research into the roles that taxa outside of the clade Batrachia

ISSN 1827-9635 (print)
ISSN 1827-9643 (online)

(frogs and salamanders) play as potential hosts or predators of *Bd*. To select studies for inclusion in this review, we combined the Web of Science database along with the journals *Herpetological Review* and *Herpetological Conservation & Biology* to find most of the studies/reports. When searching the database, each major taxa group investigated, combined with the chytrid, were used as keywords, with new taxa being included every time they were first eluded to in a previous study. While it is possible that some studies could have been overlooked due to differences in keywords or not being present in the database, this search method covered a broad range of taxonomic groups and serves as a solid base for this research.

RESULTS

These studies have been conducted in a range of fashions in both the lab and the field on animals ranging from crayfish, to reptiles and even nematodes, with several such individuals found capable of carrying the fungus. All investigated species were selected due to the presence of keratin either on surface structures or internally (such as the gastrointestinal tract), while also being associated with freshwater environments where they could easily contract the pathogen. While macroinvertebrates were the initial focus of this form of study, reptiles have become increasingly more researched.

Potential Reservoirs

When it comes to invertebrates, crustaceans have been the most prominently studied for a potential relationship with *Bd*, with two separate approaches for two distinct groups. Decapods (crayfish and shrimp) were first investigated as carriers for *Bd* in 2006 in a study on both *Caridina zebra* (a shrimp) and *Cherax quadricarinatus* (Queensland Red Claw) in field studies and in lab infection studies that initially reported the presence of the chytrid in both species before being retracted a year later with false positives being attributed to an error in the transcription of raw data (Rowley et al., 2006; 2007). Despite this early controversy, a later study by McMahon et al. (2013) confirmed the presence of zoospores on both the carapace and in the gastro-intestinal tract of three crayfish species; *Orconectes virilis* (Blue Crayfish), *Procambarus alleni* (Blue Crayfish) and *Procambarus clarkii* (Louisiana Crayfish) both in captivity and in the wild. This model study presents a few notable findings, most importantly that tadpoles exposed to infected crayfish were highly susceptible to having the pathogen transmitted to them in captivity (McMahon et al., 2013). Discharge tubules being observed in the gastrointestinal tract of both captive and wild-caught crayfish also indicates that they can serve as reservoir hosts for *Bd* (McMahon et al., 2013). Interestingly, these crayfish were found to be both carriers and victims of *Bd*, with gill recession occurring in individuals who were exposed to either *Bd* filtrates or the zoospores themselves (McMahon et al., 2013). The finding that in the natural systems where crayfish tested positive for *Bd*, all the amphibians were negative, also helps to indicate that the crayfish may act as true alternate hosts in a broader cycle (McMahon et al., 2013).

Some of these findings were corroborated by another study, that identified *Bd* in both wild and farmed populations at 3.31% and 6% prevalence respectively across various *Procambarus* species in Louisiana (Brannelly et al., 2015). Unfortunately, this study was not conducted with a concurrent amphibian survey to assess a potential relationship between infection rates of the crayfish and the amphibians, limiting the ecological importance of this study. Additionally, the close quarters of the farmed populations would easily result in cross-contamination that might have inflated the number of positives found in these populations. Inflated or not, the finding of *Bd*-positive (*Bd*+) individuals pose an interesting potential for disease spread as fishermen will often purchase live crayfish as bait, potentially introducing contaminated individuals to *Bd*-negative (*Bd*-) sites. This potential vector needs to be further explored on a larger scale, as the various methods of transmission must be understood if we are to curb the spread of this disease. These findings of crayfish positivity were not universal, however, as the study by Betancourt-Roman et al. was performed in a similar fashion but found no evidence of gill recession in *Procambarus alleni* and a fairly low prevalence rate (5%) on sampled carapaces (Betancourt-Roman et al., 2016). However, this study was only performed with nine exposed individuals in the lab (small compared to the previous two studies) and the restriction of sampling to the carapace, excluding the GI tract, could have potential resulted in false negatives (Betancourt-Roman et al., 2016).

Research involving crustaceans was not limited to crayfish, as a study by Paulraj et al. (2016) investigated the possibility of *Macrobrachium rosenbergii* (Giant Freshwater Prawn) serving as a vector for *Bd*, due to the prominent commercial species being heavily impacted by fungal infections. A field survey was conducted across 15 culture ponds in South India over the course of four years, with infection being determined through visual inspection and subsequent swabbing (Paulraj et al., 2016). Physical signs of infection noted by the researchers included: dullness of color, abnormal protrusion of scales, tufts of fungal growth, lethargic movement and an overall spongy appearance (Paulraj et al., 2016). This study mirrored previous research on crustaceans with a *Bd* prevalence of 17.4-38.8% being detected across the sampled farming ponds with prevalence noted to be lowest in the months of April, May, June, and highest in October, November and December (Paulraj et al., 2016). These findings continue to support the idea that the infection may transfer from amphibians in the spring to crustaceans in the fall, with this specific scenario needing further study. Another study investigating the presence of *Bd* on the island of Jamaica included two Sesarmid land crabs and 12 crayfish (unidentified) in their survey, with one of each being *Bd*+ (Holmes et al., 2014). Neither of these studies investigated presence within the gastrointestinal tract (which was shown by previous studies to have higher levels in crayfish compared to carapace swabs) and did not directly observe discharge tubules, but the potential that they mirror other decapods means that these species should be investigated in a manner similar to McMahon et al. (2013).

Certain fish have also been shown to function as reservoirs in the laboratory, with samples taken from *Danio rerio* displaying various stages of development, including discharged mature zoosporangia, indicating the ability to reproduce off the larvae (Liew et al., 2017). Infected individuals were found to suffer from fin erosion at the 72-hour mark and later, along with skin blisters, the disruption of muscle striations, and an increased level of degeneration with these same symptoms occurring in larvae exposed to only filtered supernatants (Liew et al., 2017). This damage seems to be similar in nature to the negative impacts of *Bd* on crayfish, with the same symptoms in filtered treatments indicating the presence of some enzyme causing the damage rather than just encystation. The ability for the chytrid to clearly encyst and replicate successfully in *D. rerio* larvae further illustrates why the view of potential hosts for *Bd* needs to be expanded and indicates that this is a knowledge gap that should be focused on more extensively.

Potential Vectors

Reptiles ranging from squamates to those in the clade Aves have been investigated the most, with the first study being undertaken in 2012 (Garmyn et al., 2012). Waterfowl have been of interest due to their consistent exposure to water systems such as ponds and wetlands where they would be likely to encounter *Bd*+ environments and serve as vectors between various sites. All these studies focused on sampling the toe scales of various individuals either through swabs alone or through toe clippings. All living species that have been sampled across two studies (Garmyn et al., 2012; Hanlon et al., 2017) were found to have individuals positive for the chytrid, with 14.9% of *Branta canadensis*, 19.5% of *Anser anser domesticus*, 45% of *Anas strepera*, 50% *Anas carolinensis* and 62% of *Anas platyrhynchos* being *Bd*+. In the laboratory it was also found that spores would adhere and encyst to toe scales after 24-hours while desiccation tests found that spores remained viable after 30 minutes, indicating that the range of transmission would be based off an animal's flight speed over thirty minutes (Garmyn et al., 2012). Furthermore, they were also able to have zoospores produce zoosporangia from Day 4-14 after initial exposure (Garmyn et al., 2012). Notably, in the study by Garmin et al (2012) the feet of sampled waterfowl were rinsed to remove transient spores differently from the study by Hanlon et al (2017) and this could have been the reason for increased levels of positive individuals. The fungus has also been detected from museum specimens of waterfowl, but this appears to be more variable depending on the sampling technique. When comparing specimens from both the La Paz Museum and Seville Museum, 13 individuals were found to be *Bd*+ when performing tissue sampling while only one of those same individuals was positive from swabs (Burrowes and De la Riva, 2017). This study also found that the oldest positive sample dated back to 1982 from an *Anas flavirostris* (Yellow-billed Teal) and a *Plegadis ridgwayi* (Puna Ibis) collected from Ulla Dam, Bolivia (Burrows and De la Riva, 2017). Other species positive for *Bd* include *Anas georgica* (Yellow-billed Pintail), *Rollandia rolland* (White-tufted Grebe), *Fulica ardesiaca* (Andean Coot), *Fulica gigantea* (Giant Coot), *Lophonetta specularioides* (Crested Duck) and *Spatula puna* (Puna Teal), having been collected from various sites across Bolivia (Burrows and De la Riva, 2017).

Squamate reptiles have also been investigated as potential vectors by testing for the fungus on the ventral surface of multiple species and comparing its presence to nearby amphibian populations. *Anolis lionotus* and A. *humilis* were found to be positive for *Bd*, with a prevalence of 9% and 32% respectively among sampled individuals and an overall prevalence of 16% in survey sites in Panama (Kilburn et al., 2011). Three snake species were also positive for the chytrid: *Imantodes cenchoa* (Blunthead Tree Snake), *Nothopsis rugosus* (Rough Coffee Snake) and *Pliocercus euryzonus* (Cope's False Coral Snake), with one individual of each species being tested and a total prevalence of 38% among all sampled snakes (Kilburn et al., 2011). Habitat may have had an influence on which species tested positive for the fungus with the three species of snakes as *A. humilis* routinely encountering wet leaf litter that could retain spores, while *A. lionotus* is specifically noted as being semi-aquatic. It is possible that the snakes may have acquired zoospores through predation upon infected amphibians, while *Bd*+ reptiles may serve as vectors for the spread of this disease by direct contact or indirect environmental spreading. This study is markedly contrasted by a similar study conducted in Australia, which investigated whether *Physignathus lesueurii* (Eastern Water Dragon) juveniles were positive for *Bd* by conducting opportunistic sampling in Murray Upper National Park (Phillott et al., 2009). While all of the *P. leseuerii* were found to be negative, concurrently sampled amphibians in the area were found to be positive for *Bd* showing that the fungus is present in the region (Phillott et al., 2009). The reason infection was not able to set in on these agamids may be due to prolonged periods of desiccation or to the natural cutaneous microfauna present, but neither of these factors were specifically investigated.

The potential for fish to be vectors has also been investigated in two studies in a laboratory setting, including *Poecilia reticulata* (Ornamental Guppies) and *Gambusia holbrooki* (Eastern Mosquitofish) and *Danio rerio* (McMahon et al., 2013; Liew et al., 2017). While both *D. rerio* and *P. reticulata* had high levels of *Bd* shortly after initial exposure, the guppies showed a consistent decrease in the genomic equivalents of *Bd* DNA and the mosquitofish showed no evidence of infection (Liew et al., 2017). The previously mentioned colonization of *D. rerio* in combination with these findings shows that *Bd*'s relationship to fish can vary extensively across taxa, with fish serving as both potential hosts and/or vectors with more extensive research being required to better shape how fish relate to *Bd* ecology. Bacteria were also shown to have a significant effect in mitigating infection of the larvae in exposed zebrafish coinciding with research regarding amphibian microbial communities having an impact on susceptibilities (Liew et al., 2017). Forming a profile of the three fish species' bacterial communities would allow comparison between susceptible and resistant amphibians and may explain why infection was able to persist in *D. rerio* larvae and produce mature zoosporangia while infection waned in the *P. reticulata* and failed in *G. hoolbrooki*. Another important note is that if the mosquitofish reacted to *Bd* in a similar manner to the guppies, the difference in time before sampling between these two studies could be responsible for the differences in susceptibility through false negative readings.

Abiotic factors may also be potential vectors of *Bd* zoospores as explored in a study based in Honduras that investigated zoospore presence in raindrops. Out of the 20 rainfall events that Kolby et al. (2015) sampled in this study, one was found to have a *Bd*+ sample with an extremely low density As the study ensured collection sheets were emplaced in clearings to prevent throughfall of contaminated water from the forest canopy, these zoospores were at least from drops that were windblown off contaminated amphibians and may have even been directly carried by the precipitation (Kolby et al., 2015). This study proposes a potentially game-changing method of transportation if the zoospores can truly be transported through precipitation and definitely requires follow on research to verify these findings and expand upon their possible implications.

Predators

Taxa of the Order Cladocera (Water Fleas) and various other micro-invertebrates have been investigated as predators of the fungus and whether they might be effective as biological controls. Individuals of the genus *Daphnia* have been shown to have a clearly negative impact on zoospore concentrations, reducing genomic equivalents to nearly undetectable levels in a mesocosm experiment combining infected tadpoles with more than ten *Daphnia* (Hamilton et al., 2012). Infected *Rana aurora* (Northern Red-legged Frog) tadpoles were used, with *Daphnia* being noted to have an indirect positive effect on tadpole biomass alongside a negative impact on overall tadpole survivability (Hamilton et al., 2012). To verify that zoospore presence in *Daphnia* intestines was due to predation, another study exposed starved individuals to the zoospores and compared treatments with living and dead individuals, finding significantly higher concentrations in the intestines of living *Daphnia* (Buck et al., 2011). While these studies show evidence that members of *Daphnia* would be beneficial in fighting the chytrid, the reduced scope of these makes it hard to draw any major generalizations, especially regarding natural systems.

Outside of *Daphnia*, microfauna presence in general has been observed to be negatively correlated with zoospore prevalence in natural systems with lab experiments indicating that a portion of this impact comes from the microfauna predating upon the zoospores (Schmeller et al., 2014). One study noted that higher prevalence of microfauna was a significant differentiator between low and high prevalence sites (Schmeller et al., 2014), while another noted the presence of a more diverse rotifer and micro-arthropod community in bromeliads had a more negative impact on *Bd* prevalence than the protist diversity found in the surrounding streams (Blooi et al., 2017). This information coupled with the studies on *Daphnia* illustrate why it is important to consider *Bd*'s role in the ecological community outside of simply being a parasite if we desire to truly understand its distribution pattern along with what may help curb its spread.

Caecilians

Despite being amphibians, the finding that *B. dendrobatidis* can infect caecilians is fairly recent and can potentially provide information regarding the ecology of the fungus that has been long overlooked. While their secluded nature and primarily subterranean lifestyle make them unlikely to serve as vectors, it is interesting to note that this has not precluded them from encountering this fungus. Furthermore, it also continues to demonstrate how broadly ranging this pathogen's potential hosts are, though the full impact of chytridiomycosis on members of order Gymnophiona are hard to determine due to the difficulties of studying members of this taxa. The first study to investigate caecilians for *Bd* specifically sampled both African and South American species, including nearly 200 individuals upon initial capture and an additional 31 being tested after being kept in captivity for two years (Gower et al., 2013). While small in terms of geographic coverage, this study was quite broad regarding taxa diversity, including representatives from 10% of known species and at least one species from 12/34 known genera and 8/10 known families (Gower et al., 2013). While none of the South American species were positive for the chytrid, all African genera tested had at least two positive individuals except *Schistometopum*, showing a broad range of infectivity (Gower et al., 2013). Unfortunately, however, improper sampling techniques initially including handling without gloves could have led to false positives and inflated the present findings. Another recent study also performed in Africa confirmed the prevalence of *Bd* in four species not reviewed in the Gower study, providing confirmation of the pathogen's presence in African species of caecilians (Thorpe et al., 2018). However, this study had small sample sizes making it difficult to extrapolate the range of this disease across the broader population. A third study was also conducted in Africa as a broad survey of caecilians and anurans for the fungus and found it to be present on various caecilians but gave no specific identifications regarding species sampled and which were positive for *Bd* (Hydeman et al., 2017). Overall, members of Gymnophiona should be investigated more thoroughly to determine the presence of *Bd* across the order worldwide, though this may be difficult as a result of their isolated and subterranean nature.

Unclear Relationships

Investigation of invertebrates was not limited to crustaceans, with the nematode species *Caenorhabditis elegans* also being the subject of investigation in two separate studies due to their habitat overlap with amphibians/crayfish and the similarity of function between their tissues. Both studies utilized heat-killed *Bd* as controls and determined mortality by counting both the living and dead individuals present in each treatment (Shapard et al., 2012; Betancourt-Roman et al., 2016). These two studies had contradictory results, however, as Shapard et al. noted an increase in mortality from control to infected treatments, while Betancourt-Roman et al. saw no significant differences between the two groups. While these separate experiments were run as similarly as possible, the Betancourt-Roman study noted that differing lab conditions made the study hard to replicate and that double the concentration of zoospores was used. In the Shapard study, the use of staining dye to mark the zoospores displayed an apparent attachment of *Bd* to the external cuticle of the nematodes, with the cuticle frequently becoming breached afterward (Shapard et al., 2012). Due to the effects of zoospores on the cuticle, it is probable that the zoospores release proteolytic enzymes that serve to degrade the collagen forming the cuticle, however this enzyme was not isolated. This interaction between nematodes and *Bd* warrants further examination, due both to the contradictory findings of these two studies and the potential for use as either vectors or hosts (as indicated by observed encystation in the laboratory).

The potential of other parasites to influence the prevalence of *Bd* in amphibians has also been investigated across many field sites and multiple anuran species. A negative correlation with both parasite abundance and diversity was noted in *Bd* infected *Rana aurora* tadpoles (Nieto et al., 2007). *Echinostoma* sp. specifically were negatively correlated with *Bd* presence across various amphibians while *Ribeiroia ondatrae* was positively correlated with *Bd* presence at the site level (Stutz et al., 2018). This aspect of disease interaction has been largely under-researched and warrants further study to better understand the overall ecology of the chytrid fungus.

DISCUSSION

When looking at this research it seems clear that non-amphibian hosts pose a potentially important role in both transmission and ecology of *Batrachochytrium dendrobatidis* across numerous taxonomic groups. The presence of *Bd* zoospores on the toe scales of waterfowl could allow for the fungus to be spread across a wide range, while the potential for zoospores to be dispersed via rainfall poses an even wider avenue for distribution. While birds are potentially capable of transporting *Bd* the longest distance, the detected presence on some squamate and fish species raises the potential these taxa could serve to distribute among large, interconnected water systems and wetlands. The presence of zoospores in and on crayfish could also allow for a wider spread of the fungus through anthropogenic methods, especially as *Bd* has been observed successfully replicating within their gastro-intestinal tract. Fishing especially could allow for the fungus to be spread easily and much more rapidly than it would naturally, as infected crayfish can be transported long distances to potentially isolated water systems where the zoospores can then become introduced via fecal matter or upon predation of the crayfish. The finding that crayfish can be positive for the disease while amphibians in the same system are negative could also help explain how *Bd* has managed to persist in systems after the initial extirpation of frogs. Predation of the zoospores by various microfauna such as *Daphnia* presents an alternate end of the spectrum by potentially helping to explain how and why certain areas have been more impacted by the presence of *Bd*. Repeatedly, lab studies would also observe that an enzyme produced by the zoospores had a negative impact on non-amphibian species, with gill recession in crayfish, fin erosion in fish and cuticle breaching in nematodes being tied to this enzyme. While none of these studies identified the enzyme, the fact that filtrate has the same deleterious effects as zoospore presence could mean that negative impacts experienced by non-amphibian hosts/vectors are caused primarily by the enzyme, but future research on the subject is needed.

CONCLUSION

Based on these findings, it is clear that an important concern for *Bd* field surveys is the incorporation of other known hosts outside of amphibians. The most likely taxa to be carrying the fungus besides anurans and caudatans seems to be crustaceans such as crayfish species within the genus *Procambarus* which reside in largely the same habitats as anuran species and have been observed to have full lifecycles being conducted through the chytrid. Birds could be a potentially important factor when trying to model the chytrid's spread across broad areas, and should definitely be investigated further to observe whether they are truly viable vectors for the zoospores. This is especially true for waterfowls due to their ability to fly long distances in the thirty minutes required for the zoospores to become susceptible to desiccation, posing a major potential threat to the prevention of this disease's spread. Transportation via rainfall poses a similar potential problem and should continue to be investigated to better determine the prevalence of this phenomenon and how it may impact distribution. Similarly, predation of zoospores by microfauna needs further research, potentially utilizing a mesocosm approach, to test what taxa have the largest impacts and how this interaction relates to how *Bd* fits into the community at a larger scale. Finally, it is important to continue investigating other taxa to help broaden the list of potential hosts, with a special focus on other crustaceans/macroinvertebrates and semi-aquatic reptiles along with caecilian taxa when performing studies in South America or Africa.

ACKNOWLEDGMENTS

We would like to thank the members of Team Salamander at the University of Tennessee: Chattanooga for their continuous support throughout this process, who helped improve the study via valuable discussions and support.

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