Evaluating treatments for North American amphibians under threat of *Batrachochytrium salamandrivorans* with near complete uncertainty

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Significance:

- *Batrachochytrium salamandrovorans* is an emerging infectious disease of salamanders.
  - The pathogen is currently causing dramatic declines in *Salmandra salamandra* populations in Europe.
  - *Bsal* has not been detected in North America, however, areas within the United States are among the most species diverse regions for salamanders.
  - As this pathogen may potentially result in declines in naïve hosts, it is imperative that wildlife managers are aware of potential management actions, and researchers acknowledge and understand the various constraints in making a management decision in the face of extreme uncertainty.

Key words: *Batracochytrium salamandrivorans*, decision science, management, uncertainty, risk, salamanders

Introduction:

Amphibian Populations in Decline.— Over the last four decades, amphibian populations across the world have experienced declines attributed to climate change, habitat alteration, and infectious disease (Daszak et al. 2003; Cohen et al. 2018; Cunningham 2018). Notably, many of these declines have been attributed to the introduction of novel pathogens through human-mediated movement (i.e., "pathogen pollution") to naïve amphibian species or populations (e.g., FV3-like ranavirus, *Batrachochytrium dendrobatidis* and *B. salamandrivorans*; Cunningham 2018). According to a recent International Union for the Conservation of Nature (IUCN) report, 41% of known amphibian species are threatened with extinction, which far outpaces declines in both mammals (25%) and birds (14%; IUCN 2019). For example, within the northeastern United States, wood frogs (*Lithobates sylvaticus*) and spotted salamanders (*Ambystoma maculatum*), of which continuous surveying has occurred in federally protected areas since 2005, are in decline likely due to impacts from climate change and disease (Miller & Grant 2015; Miller et al. 2018; Mosher et al. 2019).

A New Disease Threat.— Batrachochytrium salamandrivorans (*Bsal*) is a newly identified chytrid fungus known to cause erosive skin disease and subsequent mortality in *Salamandra salamandra* populations in northwestern Europe (Martel et al. 2013). Host populations in the Netherlands have been nearly extirpated within seven years of *Bsal* introduction (Spitzen-van der Sluijs et al. 2016). The fungus, endemic to Asia, is likely transported to novel locations via the pet trade (Martel et al. 2014; Cunningham et al. 2015). Susceptibility to *Bsal* varies among species, however based on lab trials, the fungus is expected to be lethal to salamanders in the US from the families Salamandridae and Plethodontidae (DiRenzo et al. *unpublished*.; Martel et al. 2014). Species-specific susceptibility is unknown for the majority of US species.

Responding to emerging infectious diseases of wildlife are commonly challenged by near complete uncertainty regarding specific effects to naïve populations (McCarthy 2014). Because the risk of *Bsal* introduction to North America is high (Richgels et al. 2016), we held a workshop on 30 September 2019 at the Joint Meeting of The Wildlife Society and American Fisheries Society. The goals of the workshop were to work through a list of potential management actions to (1) help managers identify optimal management strategies [to aid in achieving *Bsal* Decision Science, Management and Research Working Group priorities], (2) identify actions that can be included under a categorical exclusion to NEPA [*Bsal* Management Working Group priority], (3) summarize and share knowledge in real time from up-to-date scientific research, and (4) begin to identify current knowledge gaps within the host – pathogen system [*Bsal* Research Working Group priority].

Methods:

Amphibian Community Scenarios

We created hypothetical scenarios to represent real-world amphibian communities located in four high-risk zones identified by Richgels et al. (2016; Supplemental Doc 1). Each amphibian community was comprised of at least one highly competent host (i.e., a species that may suffer mortality from a lethal infection of *Bsal*) and three to ten additional amphibian species with varying degrees of *Bsal* competency (i.e., resistant, tolerant, or susceptible). We used the definitions of *Bsal* susceptibility as described by Martel et al. (2014) and updated by DiRenzo et al. (*unpublished*), where resistant populations do not show signs of infection or clinical disease and experience negative *Bsal* growth rate. Tolerant populations can be infected by *Bsal* but do not show clinical signs of disease. Susceptible hosts exhibit infection resulting in clinical disease with the possibility of subsequent recovery. A host with unknown competency may suffer the effects of *Bsal* but has not been demonstrated to be susceptible to the pathogen in the wild or in laboratory studies. Habitats in each scenario were either a pond or third-order stream, each with varying degrees of human disturbance (i.e., habitat alteration and runoff, urban sprawl, or high human visitation). The scenarios were used to orient participant thinking and help visualize a real-world amphibian community when estimating outcomes for all endpoints for each management action.

Endpoints

Prior to the workshop, participants (principally members of the Decision Science and Research *Bsal* working groups) collaboratively identified nine population demographic endpoints or management outcomes that could be used to evaluate the magnitude and effect of each action (Table 1). Endpoints focused on host survival and reproduction, pathogen transmission, growth and reproduction, and the non-target effects of an action during and after implementation. The definition, interpretation, and explicit timeframe for each endpoint were discussed and agreed upon as a group during a pre-workshop conference call.

Table 1. Endpoints for management actions used during the 2019 TWS *Bsal* Symposium workshop.

Management Endpoints
1. What is the effect of the management action on daily **host survival** given the following life stages: • Egg? • Larval? • Juvenile? • Adult?
2. What is the effect of the management actions on **host reproductive rate** (# eggs/yr)?
3. What is the effect of the management action on weekly ***Bsal* transmission potential on the host within a site**?
4. What is the effect of the management action on weekly ***Bsal* transmission and spread among sites**?
5. What is the effect of the management action on weekly ***Bsal* zoospore growth** (rate to maturity) **and reproduction** (# of zoospores/sporangia)?
6. What is the effect of the management action on weekly **persistence of *Bsal* in the environment**?
7. What is the effect of the management action on weekly **persistence of *Bsal* on the host**?
8. What are the **non-target effects** of the management action **during implementation** on the following: • Non-target biotic (including sensitive and rare species)? • Non-target abiotic (e.g., water quality)? • Human dimensions (i.e., hunting/fishing/cultural resources)?
9. What are the **non-target effects** of the management action over a **monthly time period** on the following: • Non-target biotic (including sensitive and rare species)? • Non-target abiotic (e.g., water quality)? • Human dimensions (i.e., hunting/fishing/cultural resources)?

Management Actions and Treatments

We gave participants in the workshop a list of management actions or treatments that could be used to combat *Bsal* in North America (Table 2), all of which had been discussed by the *Bsal* Research Working Group and in two previous decision analysis workshops (Grant et al. 2017, Canessa et al. 2018). Actions selected were expected to have a measurable effect on one or more endpoints. Most actions considered were developed for *Bd* and have been tested on select amphibians in the lab, but most management actions listed in the table have not been implemented in the field nor have been tested for the management of *Bsal*. Many of these treatments are currently in varying stages of research and development for use against *Bsal* infection.

Table 2. *Bsal* management actions considered, detailed descriptions of the actions, type of action (proactive, reactive, and state independent), and citations. This list of actions was developed using notes from the workshops described in Grant et al., 2017 (Frontiers in Ecology and the Environment), Canessa et al., 2018 (Journal of Applied Ecology), the Research Working Group *Bsal* Management Table, and Thomas et al., 2019 (Amphibia-Reptilia).

Action	**Description**	**Type of Action**	**Citations**
Actions on Animals			
Pre-emptive removal – high thinning	Removal of 90% of individuals prior to entry of *Bsal*	Proactive	Canessa et al. 2018, Spitzen-van der Sluijs et al. 2018
Antifungal treatment	A course of topical treatments of itraconazole on individuals captured at site (100% capture efficiency)	Reactive	Garner et al 2016, Hudson et al. 2016, Geiger et al. 2017, Stegen et al. 2017
Probiotic treatment	A course of treatments for all individuals (captured individuals) using live bacteria and yeasts with anti-fungal properties	Reactive	Woodhams et al. 2011, Bletz et al. 2013, Loudon et al. 2014, Bates et al. 2018, Bletz et al 2018, Schmeller et al. 2018
Improve body condition	Improve body condition of individuals, i.e., by continuous food supplementation for all life stages	Proactive	Cary et al. 2006, Hall et al. 2009
Environmental and Habitat Actions			
Habitat structure manipulation – Min. contact rates via	Create barriers/selectively reduce matrix habitat to minimize migration (by 90%) of susceptible or infected hosts among sites	Proactive	Spitzen-van der Sluijs et al 2018

habitat fragmentation			
Hydrologic manipulation – remove water	Remove water to dry ponds after breeding (to remove pathogen from substrate), allow to refill naturally	Proactive	Woodhams et al. 2011, Bosche et al 2015
Fungicide application – aquatic habitat	Application of a fungicide (a course of applications) to kill pathogen in habitat substrate (including on soils and plants)	Reactive	Woodhams et al. 2011
Heat treatment (via decreased shading of ponds)	Raise temperature of water to kill pathogen (>35C) for 24h	Reactive	Freidenburg and Skelly 2004, Raffel et al. 2010, Forrest and Schlaephfer 2011, Savage et al. 2011, Scheele et al 2014, Heard et al. 2014, Blooi et al 2015
Micropredators – zooplankton treatment	Increase abundance (by 400%) of micropredators that consume zoospores to pond water	Reactive	Buck et al. 2011, Woodhams et al. 2011, Searl et al. 2013, Schmeller et al 2014,
Human Activity Actions			
Reduce public access	Restrict public access (to minimize movement of the pathogen from one pool to the next)	State independent	Hopkins et al. 2018
Create and enforce disinfection stations	Require decontamination protocols for all user groups (i.e., researchers, public, managers), before and after entering habitat	State independent	Bsal TAC reports, Hopkins et al. 2018

The Wildlife Society Workshop

We held a 2.5-hour workshop to identify which management actions had the highest expected effect in preventing the introduction or spread of *Bsal*, as well as those actions which may maintain host persistence and survival. The workshop was advertised within the *Bsal* Task Force, Amphibian Disease list-serve, and to those who presented or attended the '*Batrachochytrium salamandrivorans: The Next Threat to North American Diversity'* special session (hosted by The Wildlife Society). Prior to the workshop, we held one pre-workshop conference call to orient participant thinking and clarify remaining questions regarding the endpoints, actions and scenarios. We, the facilitators, spent the first 20 minutes of the workshop describing the endpoints, actions and scenarios. Participants then self-selected their scenario and split into scenario-based groups. Participants were given a prepared worksheet (Supplemental document 2) and asked to independently estimate the direction (positive or negative) and magnitude of effect (1, 2, or 3, 3 = largest) of each action for each endpoint. If there was complete uncertainty regarding the direction and magnitude of an action on an endpoint, participants were asked to leave a cell blank.

Participants were given 45 minutes to work through their worksheet independently but were allowed to ask clarifying questions of the facilitators. After completing their worksheets, participants were then instructed to discuss their estimates with the group; we facilitated small-group discussions. Following this 30-minute discussion period, participants were allowed to update and change their estimates if desired. In the last 30-minutes of the workshop, each group was asked to discuss and identify their top three actions; these were reported to the facilitators on new worksheets.

Results:

Twenty-four individuals participated in the TWS workshop. Of the four scenarios provided, three were chosen, as no one present in the workshop felt they knew enough about the Southern California newt community. Ten participants worked on the Northeastern eastern red-spotted newt community, seven on the Pacific Northwest rough-skinned newt community, and seven on the Southeastern stream salamander community.

At least one participant provided an estimate for every endpoint and treatment, however, estimates for 'host survival: egg', '*Bsal* zoospore growth', '*Bsal* zoospore reproduction', 'non-target during action: abiotic', and 'non-target after action: abiotic' received over 100 estimates indicating no effect was predicted (Table 3, Figure 1). The total number of blank values by treatment, indicating that effects were completely unknown or that there was complete uncertainty in the true value, ranged from 30 to 72.

Table 3. Total number of estimates (n = participants per direction) provided for the direction of all actions for each endpoint across all scenarios. Participants were asked to provide an estimate of direction for each action and end point. Decreasing (D), Increasing (I), No Effect (0), and blank for uncertain.

Endpoint	**Direction**			
	Decreasing	**Increasing**	**No Effect**	**Uncertain**
1. Host survival: Egg	62	29	128	44
2. Host survival: Larval	71	64	80	47
3. Host survival: Juvenile	56	96	60	47
4. Host survival: Adult	58	99	55	47
5. Host reproductive rate	62	64	70	65
6. *Bsal* transmission on host within a site	132	20	70	41
7. *Bsal* transmission & spread among sites	157	24	34	49
8. *Bsal* zoospore growth	85	13	105	61
9. *Bsal* zoospore reproduction	93	9	102	60
10. Persistence of *Bsal* in environment	119	18	97	30
11. Persistence of *Bsal* on host	107	17	97	43
12. Non-target during action: biotic	38	116	64	46
13. Non-target during action: abiotic	30	53	112	69
14. Non-target during action: human dimensions	39	91	76	58
15. Non-target after action: biotic	35	122	58	49
16. Non-target after action: abiotic	21	66	113	64
17. Non-target after action: human dimensions	32	73	87	72

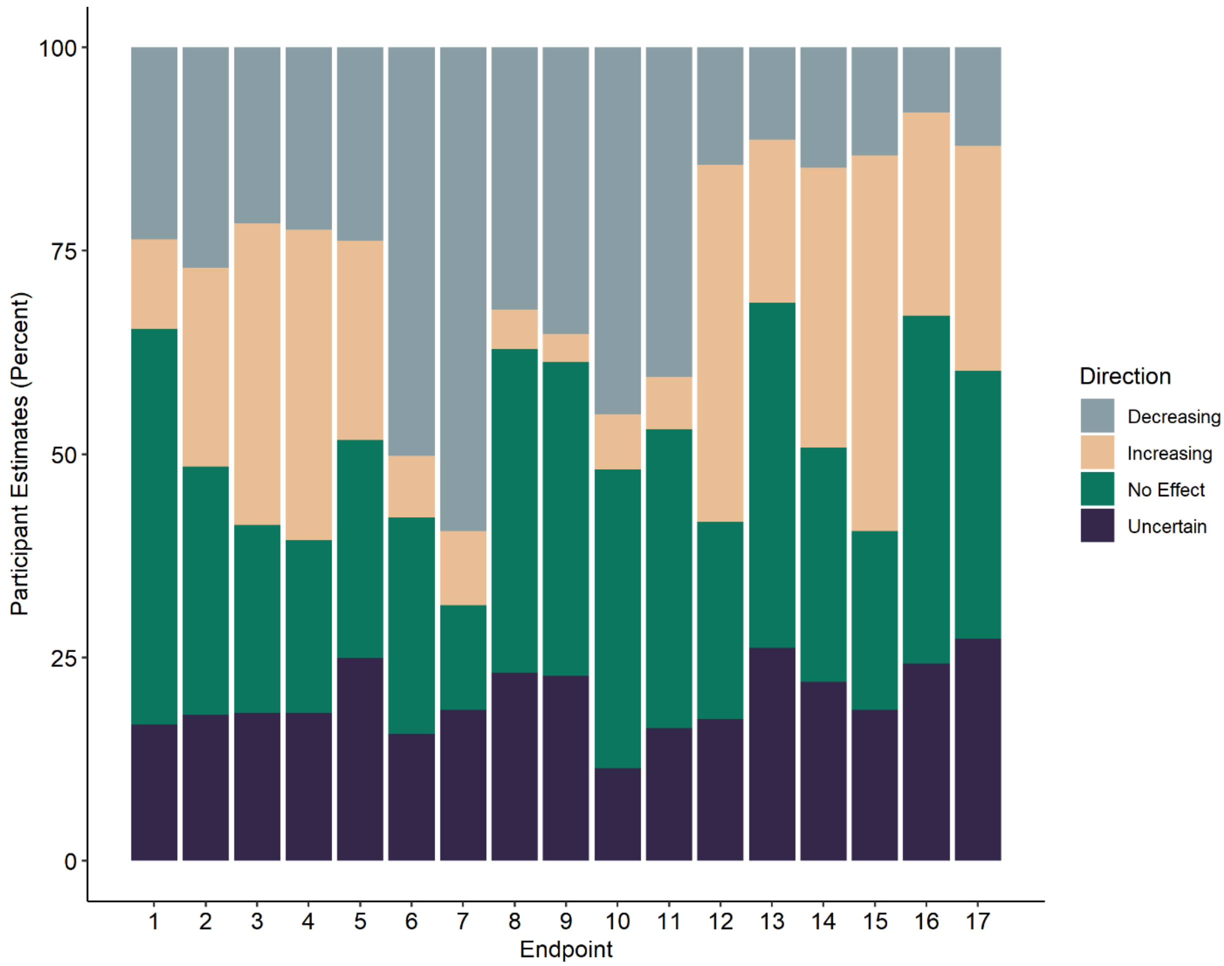

Figure 1. *Graphical representation of Table 3, with bars representing the percent each direction (based on participant estimates) was represented for each endpoint.*

The direction and magnitude of effect of the management actions varied across amphibian community scenarios, as well as among management actions. Predictions for proactive management actions (i.e., creation of barriers, habitat manipulation, preemptive thinning, and improving body condition) were consistent across regional scenarios, with the median direction and magnitude similar for all amphibian communities (Figure 2).

Reactive (post-detection) management actions (Figure 3), such as antifungal treatment, environmental fungicide, heat treatment, micropredators, and probiotic treatments had similar predictions for direction of effect, however the magnitude of effect varied across scenarios. The median reactive alternatives were estimated to be up to 11 times more effective in increasing host survival (egg, larval, juvenile, and adult) and reproduction, than proactive management actions (Appendix 1). A similar pattern was observed across *Bsal*-focused endpoints, with reactive actions expected to perform better than proactive actions on endpoints (e.g., '*Bsal* transmission on host', '*Bsal* transmission among sites', '*Bsal* growth', and '*Bsal* reproduction' Table 4). Participant estimates for 'no effect' or 'uncertain' outcomes were fairly consistent across both proactive and reactive actions. State-independent actions, i.e., disinfection protocols and public access restrictions (Figure 4), which could be implemented both ahead of an invasion and after a detection was observed, were not expected to have much of an impact on host survival and reproduction, nor transmission of the pathogen. They were however, predicted to increase non-target impacts on human-dimensions due to restriction of access to amphibian habitats. Conversely, all other management actions (i.e., all proactive and reactive alternatives) were predicted to have a higher negative magnitude of effect (i.e., increase) on each non-target endpoint.

The top three management actions for each regional amphibian community scenario varied. Participants predicted the most effective management actions for amphibian communities in the Pacific Northwest were 1) preemptive thinning, 2) antifungal treatment, and 3) public access restrictions. The top actions for the Northeast were 1) probiotic treatments, 2) habitat manipulations, and 3) antifungal treatments. Finally, in the Southern Appalachian communities, participants predicted that 1) antifungal treatments, 2) environmental fungicide, and 3) restriction of public access would be most successful in increasing host survival and decreasing pathogen transmission.

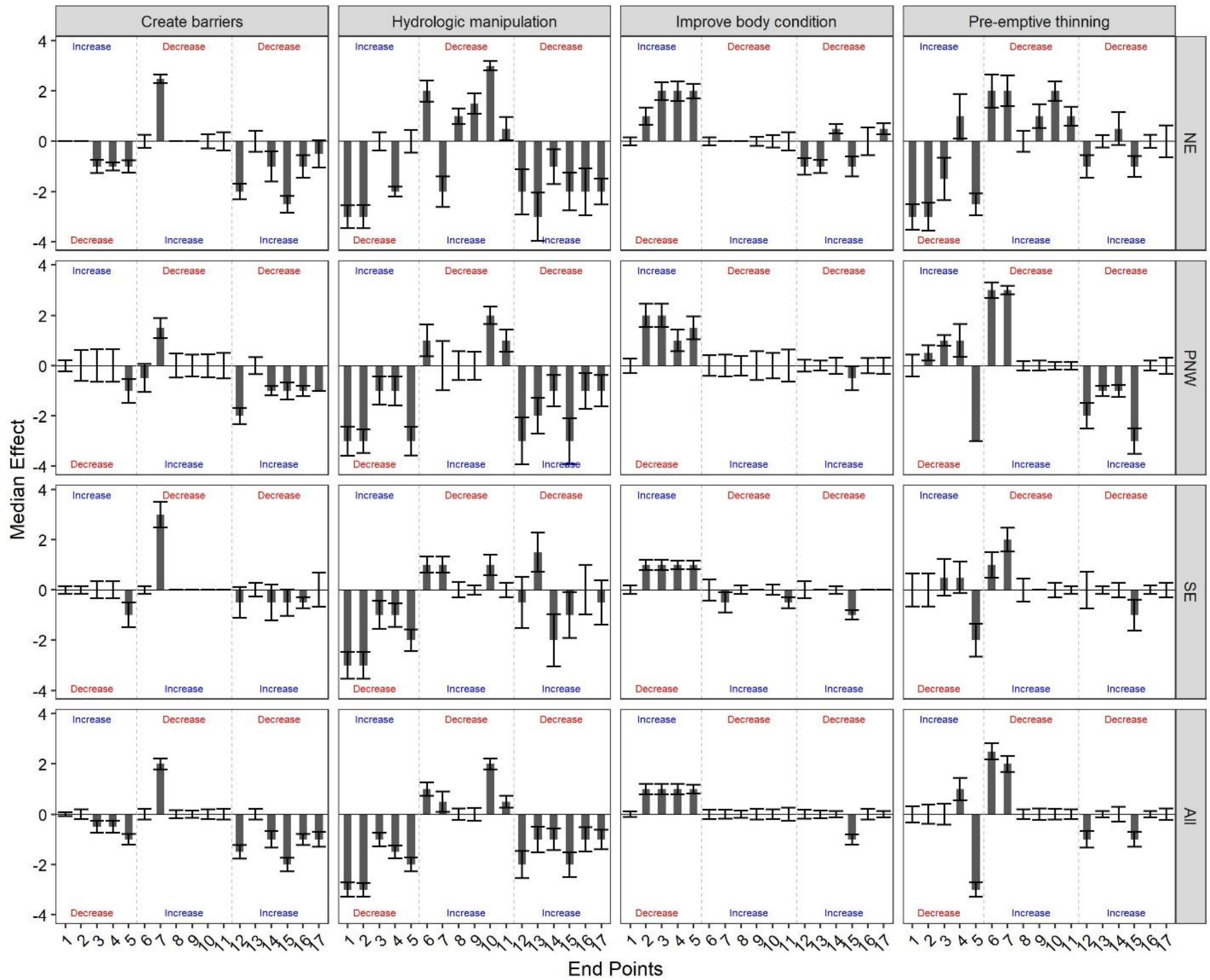

Figure 2. Median magnitude and effect of **proactive** management actions (columns) for each scenario (rows 1 – 3). Proactive actions are described as those that can be implemented *prior* to the arrival of *Bsal* to a site. The overall median magnitude and effect of each action is provided in the bottom row. Direction is denoted in red and blue text and is organized so that values above the 0 line are better for each endpoint. The first five endpoints correspond with host survival (egg, larval, juvenile, and adult) and reproduction. Endpoints 6 – 11 correspond with *Bsal* transmission, spread, growth and reproduction, and persistence. The final 6 endpoints (12 – 17) correspond with the non-target effects of the management action during and after implementation. Error bars are 1-SE from the median.

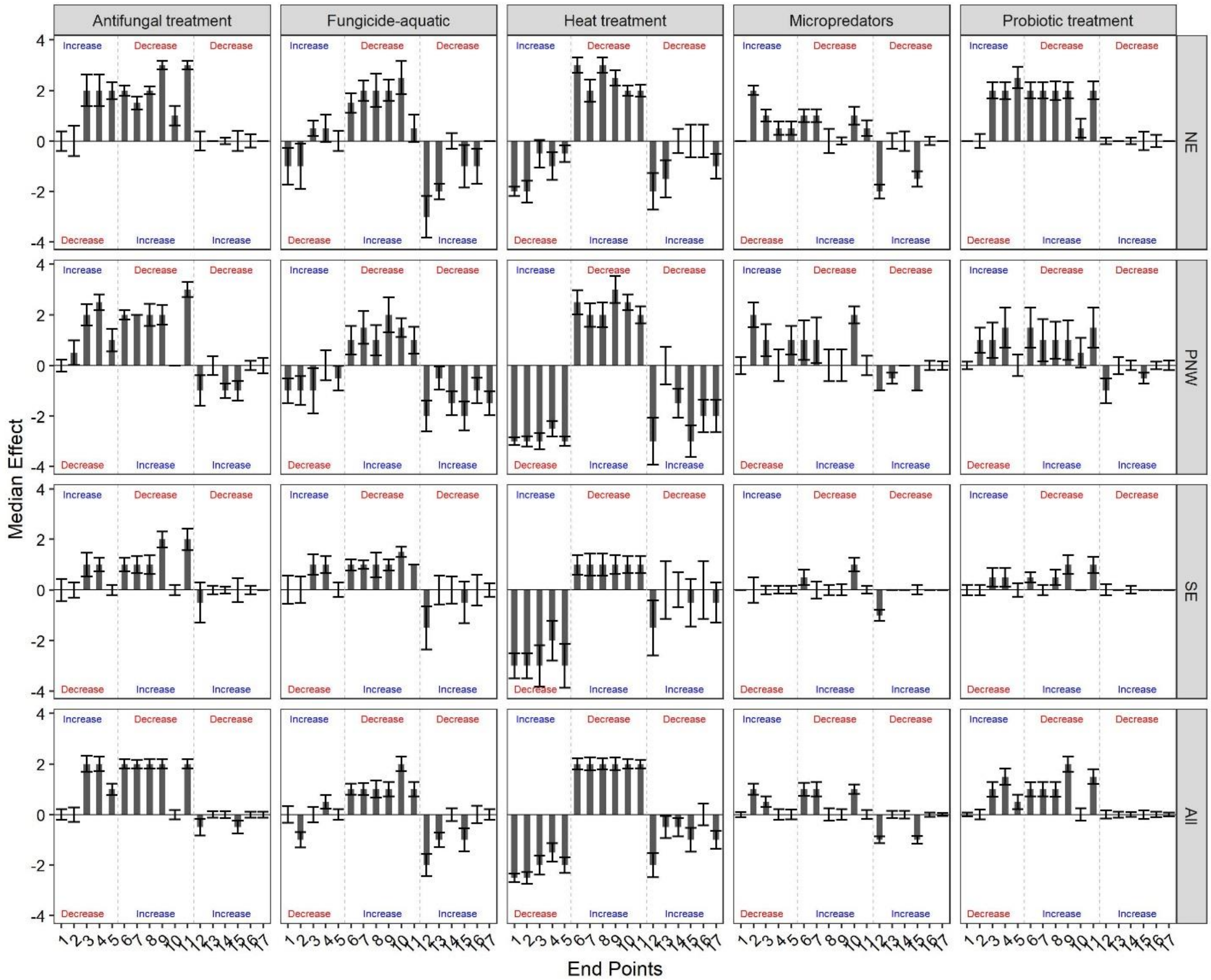

Figure 3. Median magnitude and effect of **reactive** management actions (columns) for each scenario (rows 1 – 3). Reactive actions are described as those that are implemented *after* the arrival of *Bsal* to a site. The overall median magnitude and effect of each action is provided in the bottom row. Direction is denoted in red and blue text. The first five endpoints correspond with host survival (egg, larval, juvenile, and adult) and reproduction. Endpoints 6 – 11 correspond with *Bsal* transmission, spread, growth and reproduction, and persistence. The final 6 endpoints (12 – 17) correspond with the non-target effects of the management action during and after implementation. Error bars are 1-SE from the median.

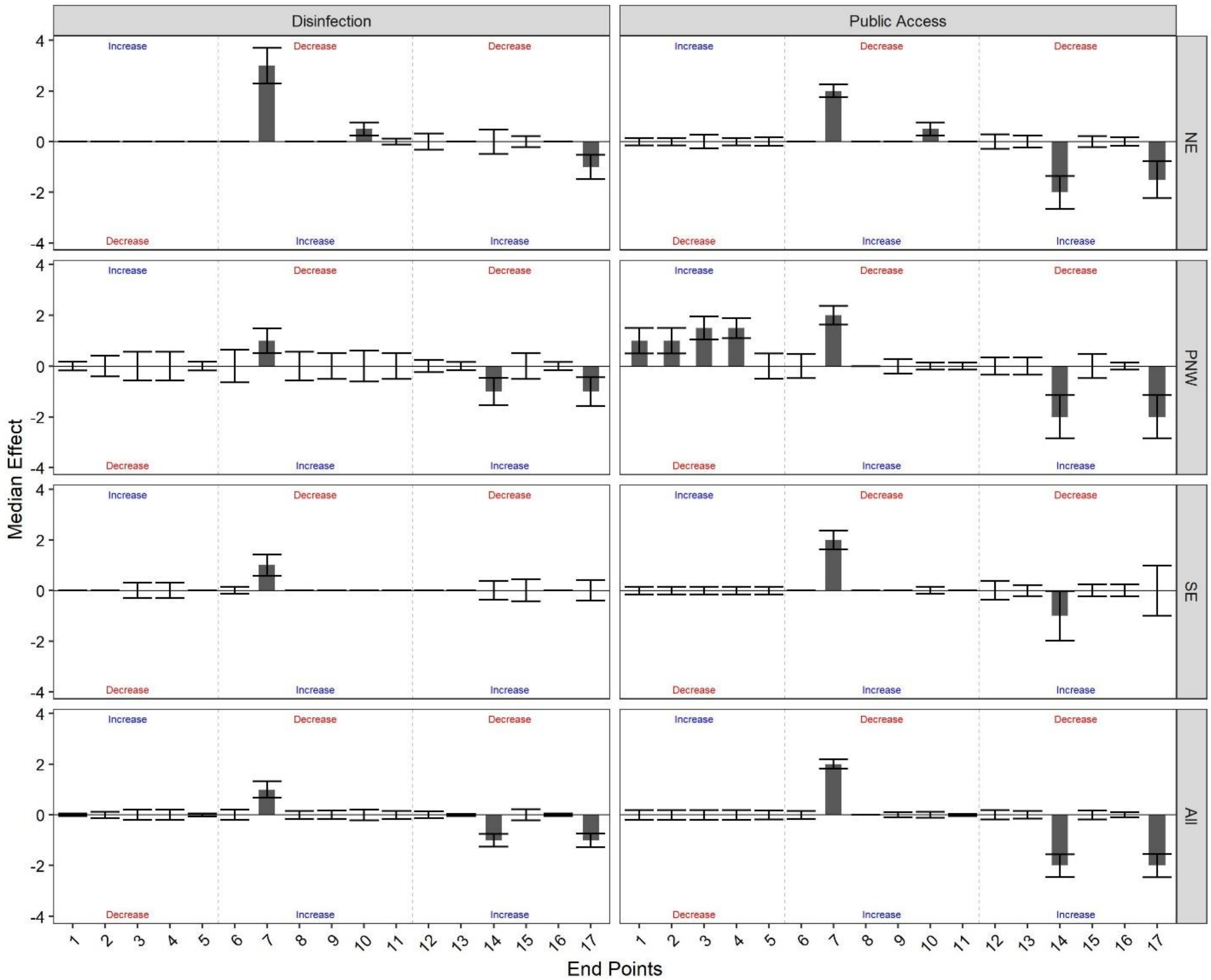

Figure 4. Median magnitude and effect of state independent management actions (columns) for each scenario (rows 1 – 3). State independent actions are described as those that can be implemented *prior* to or *after* the arrival of *Bsal* to a site. The overall median magnitude and effect of each action is provided in the bottom row. Direction is denoted in red and blue text. The first five endpoints correspond with host survival (egg, larval, juvenile, and adult) and reproduction. Endpoints 6 – 11 correspond with *Bsal* transmission, spread, growth and reproduction, and persistence. The final 6 endpoints (12 – 17) correspond with the non-target effects of the management action during and after implementation. Error bars are 1-SE from the median.

Discussion:

Due to the threat of *Bsal* introduction to North America, management agencies and scientific researchers have developed a strategic plan to identify possible routes of pathogen introduction, reduce the risk of entry, increase surveillance and biosecurity strategies, develop diagnostic assays for confirmation of positive samples, identify response and disease intervention strategies and enhance communication and outreach regarding the disease (Gray et al. 2015). With this strategic plan, a prioritized list of research needs was developed to determine host susceptibility, pathogen transmission, and management interventions. For the TWS workshop, the *Bsal* Decision Science Working Group used up-to-date literature and reports (many of which have resulted from research identified as priorities in the 2019 *Bsal* Strategic Plan; p 21 - 23) to collate a list of management actions that are expected to maximize host survival and minimize the introduction and spread of *Bsal*.

Individual experts, in estimating the effects of a management action on a particular system, often create a mental model of that system. In order to minimize among-observer variation due to differing mental models, we created real-world regional amphibian community scenarios for high-risk areas for *Bsal* introduction that participants could visualize while predicting the direction and magnitude of effect each management action was expected to have within a particular scenario. By enabling participants to think about a specific scenario, we were able to truly compare among-observer and among-system variations in management action expectations. Although there were likely still differences within each participant's mental model, this represents true uncertainty in the effects of the proposed management actions.

While there was no particular decision context identified for this workshop (i.e., the participants were not providing estimates for a particular decision maker and their management objectives), the facilitators wanted to incorporate both the goals of the Strategic Plan as well as the range of management objectives described by National Wildlife Refuge managers (a current priority of the *Bsal* Decision Science working group). The endpoints developed incorporated a number of management objectives, epidemiological targets, and were specific to the timing with which benchmarks could be measured (i.e., daily host survival, weekly pathogen transmission rate, or month after implementation). Each endpoint was associated with a parameter in a disease or host population dynamics model. These models have known sensitivity and elasticity so that they can evaluate the expected treatment effects on important parameters (i.e., R_0, occupancy, abundance, survival, turnover). This workshop exercise is a first step in helping identify the parameters that are missing actions, and where additional actions may be added to improve efficacy.

Most management actions for *Bsal* are in varying stages of research and development, however some actions that have been developed to address *Bd* or ranavirus may be useful in combatting the effect of *Bsal* (see literature cited in Table 2). Although research into the various *Bsal* treatments are underway, it was acknowledged that great uncertainty remains within most of the endpoints we developed for this workshop. Ultimately, this uncertainty comes from the difficulty in knowing if a management action for one pathogen is effective for a different, yet similar, pathogen, or how the results from lab studies are transferable to real-world scenarios. During the workshop, participants offered a number of insights into several areas of uncertainty, such as the agreement that some treatments were expected to have very little effect on critical endpoints (i.e., host survival and reproduction), whereas others were expected to have large effects on reducing the persistence and transmission of the pathogen. Several endpoints, such as those focused on the non-target effects of an action were difficult to predict due to either a lack of expertise (i.e., predictions were less informed due to the absence of certain experts), or that estimates were based on how the action should be deployed, versus how it may actually be deployed (i.e., netting off a pond at the beginning of a season vs. multiple treatments of a chemical). Finally, while the actions included within the workshop were distinct, participants were surprised to see that many of them were predicted to have similar effects on the endpoints, suggesting the actions were not as unique as anticipated. It is important to retain these potential actions, as they may have different trade-offs in other management objectives.

This workshop was the first step in explicitly articulating management-specific endpoints, predicting the effect of proposed potential actions, and identifying where uncertainties exist. **Next, we would like each participant to update their response based on the results presented herein.** Following the updating of participant predictions, we will use the results to identify research priorities for the various management actions and end points, especially those of particular interest to natural resource managers. The results we have presented will be used to further develop categorical exclusions under the National Environmental Policy Act (NEPA), a priority project for the *Bsal* Management and Research Working Groups. Finally, we plan to use our endpoints to identify additional actions that may be missing from the current list and facilitate the development of new management alternatives for *Bsal.*

Literature Cited:

Cohen JM, Civitello DJ, Venesky MD, McMahon TA, Rohr JR. 2018. An interaction between climate change and infectious disease drove widespread amphibian declines. Global Change Biology:1–11.

Cunningham AA. 2018. Infectious disease threats to amphibian conservation. The Glasgow Naturalist **27**.

Cunningham AA, Beckmann K, Perkins M, Fitzpatrick L, Cromie R, Redbond J, O'Brien MF, Ghosh P, Shelton J, Fisher MC. 2015. Emerging disease in UK amphibians. Veterinary Record **176**:468.

Daszak P, Cunningham AA, Hyatt AD. 2003. Infectious disease and amphibian population declines. Diversity and Distributions **9**:141–150.

DiRenzo G V., Longo A V., Muletz-Wolz CR, Pessier AP, Goodheart J, Lips KR. (n.d.). Plethodontidae salamanders show variable disease dynamics in response to emerging fungal pathogen infection. In review.

Gray MJ et al. 2015. Batrachochytrium salamandrivorans: The North American Response and a Call for Action. PLoS Pathogens **11**:1–9.

IUCN. 2019. Red list of threatened species. Available from www.iucnredlist.org (accessed July

2, 2019).

Martel A et al. 2013. Batrachochytrium salamandrivorans sp. nov. causes lethal chytridiomycosis in amphibians. Proceedings of the National Academy of Sciences of the United States of America **110**:15325–15329.

Martel A et al. 2014. Recent introduction of a chytrid fungus endangers Western Palearctic salamanders. Science **346**:630–631.

McCarthy MA. 2014. Contending with uncertainty in conservation management decisions. Annals of the New York Academy of Sciences **1322**:77–91.

Miller DAW et al. 2018. Quantifying climate sensitivity and climate-driven change in North American amphibian communities. Nature Communications **9**:3926.

Miller DAW, Grant EHC. 2015. Estimating occupancy dynamics for large-scale monitoring networks: Amphibian breeding occupancy across protected areas in the northeast United States. Ecology and Evolution **5**:4735–4746.

Mosher BA, Brand AB, Wiewel ANM, Miller DAW, Gray MJ, Miller DL, Grant EHC. 2019. Estimating occurrence, prevalence, and detection of amphibian pathogens: Insights from occupancy models. Journal of Wildlife Diseases **55**:563–575.

North American Bsal Task Force. 2019. A North American strategic plan to control invasions of the lethal salamander pathogen *Batrachochytrium salamandrivorans*.

Richgels KLD, Russell RE, Adams MJ, White CL, Grant EHC. 2016. Spatial variation in risk and consequence of Batrachochytrium salamandrivorans introduction in the USA. Royal Society Open Science **3**:150616.

Spitzen-van der Sluijs A et al. 2016. Expanding distribution of lethal amphibian fungus Batrachochytrium salamandrivorans in Europe. Emerging Infectious Diseases **22**:1286–1288.

Appendix 1.

Table 4. Total number of estimates (n = participants per direction) provided for the direction of proactive (P) and reactive (R) actions for each endpoint across all scenarios. Participants were asked to provide an estimate of direction for each action and end point. Decreasing (D), Increasing (I), No Effect (0), and blank for uncertain.

Endpoint	Direction							
	Decreasing		Increasing		No Effect		Uncertain	
	P	R	P	R	P	R	P	R
1. Host survival: Egg	25	38	11	10	49	52	11	20
2. Host survival: Larval	28	43	26	30	28	26	14	21
3. Host survival: Juvenile	31	25	30	55	22	15	13	25
4. Host survival: Adult	34	24	32	56	16	17	14	23
5. Host reproductive rate	43	19	19	39	14	30	20	32
6. *Bsal* transmission on host within a site	38	87	13	5	24	14	21	14
7. *Bsal* transmission & spread among sites	47	71	14	7	13	17	22	25
8. *Bsal* zoospore growth	15	68	6	6	48	22	27	24
9. *Bsal* zoospore reproduction	20	71	4	4	48	19	24	26
10. Persistence of *Bsal* in environment	32	75	13	4	37	31	14	10
11. Persistence of *Bsal* on host	24	79	11	5	41	19	19	17
12. Non-target during action: biotic	15	18	49	59	16	19	16	24
13. Non-target during action: abiotic	11	15	26	25	35	42	24	38
14. Non-target during action: human dimensions	19	11	38	26	18	53	21	30
15. Non-target after action: biotic	13	16	60	53	6	26	17	25
16. Non-target after action: abiotic	9	8	31	31	30	50	26	31
17. Non-target after action: human dimensions	15	7	29	21	27	54	25	38