Management for Amphibians in Complex Ecosystems

MANAGEMENT FOR AMPHIBIANS IN COMPLEX ECOSYSTEMS

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ABSTRACT

Effective conservation is becoming more difficult as threats to wildlife increase. Natural resource managers are pressured to make difficult decisions with limited resources, and in many instances, some degree of uncertainty. Scientists and managers tasked with the conservation of a species need tools to help guide efficient decision making. Often, information for management decisions is insufficient. Tools that help to inform decision makers and address uncertainty will be invaluable to effective conservation initiatives. Here, we create two models to help managers navigate the complexities associated with decision making. The objective our first study was to create a model to best predict Eastern red-spotted newt (*Notophthalamus viridescens viridescen;* ERSN) breeding occurrence across the northeastern United States. We estimated relationships between breeding ERSN field survey data and landscape-level covariates. We then used those relationships to map predictions of ERSN breeding occupancy across the northeastern U.S. Our estimates accounted for imperfect detection and were used to make spatial predictions of occupancy. This analysis will provide a foundational tool upon which managers can develop management strategies for ERSN. Our second model is a Bayesian belief network intended to guide decision making for wood frog (*Lithobates sylvaticus*) persistence when two pathogens, ranavirus and *Batrachochytrium dendrobaditis,* are present within a pool. Both models help to inform and guide managers faced with the difficult task of managing wildlife populations in the face of multiple threats.

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1.1. Introduction

Of the 7,212 amphibian species recognized by the IUCN, 1,184 (16%) are deemed 'Data Deficient' (IUCN 2021). The IUCN describes Data Deficient species as not having adequate information on the abundance or distribution of a species to make an extinction risk assessment (Adams et al. 2013). The lack of baseline occupancy estimates for many amphibian species is problematic for accurately studying shifting species distributional trends in the face of oncoming threats (Adams et al. 2013). Even species not deemed Data Deficient by the IUCN may lack information that would be valuable for managers and ecologists (Howard and Bickford 2014), improving conservation planning (Sterrett et al. 2019).

Amphibians face multiple, and potentially interacting, threats (Stuart et al. 2004; Cushman 2006; Alford 2011; Hof et al. 2011; Walls et al. 2016). These include anthropogenic land-use changes, pathogens (including *Batrachochytrium dendrobatidis* (Bd), the pathogen which causes the disease chytridiomycosis), climate change, and environmental pollution (Hof et al. 2011). Sensitivity to these threats varies across geographic space (Gibbs 1998; Grant et al. 2016), so predictions about how amphibian populations may respond requires an understanding of species distributions. For under-sampled taxa, we are forced to rely on range maps which are derived with a combination of observed populations and expert judgement (IUCN 2021). Range maps appear as polygons encompassing regions in which a species may occur, and often do not account

for small-scale variation in geography, habitat type, or latitude. These generalized range maps are too imprecise for informing local-level conservation decisions.

Knowledge of site-level occupancy is missing especially for common species (Sterrett et al. 2019), such as Eastern red-spotted newts (*Notophthalmus viridescens viridescens* Rafinesque; Waddle et al. ERSN), which are widely distributed throughout the Eastern United States (Petranka 1998; Lannoo 2005). Commonality may not result in robust populations (Lindenmayer et al. 2011). Often, because a species is common, threats to that species may be unknown or underestimated, and the species may not be thought of as 'vulnerable' until declining population trends are observed (Gaston 2010; Adams et al. 2013; Sterrett et al. 2019). Eastern red-spotted newts have a wide-spread distribution and are locally abundant in portions of their range, though their occurrence is expected to decline as urbanization (and the loss of forest cover) increases (Hecnar and M'Closkey 1996; Gibbs 1998; Guerry and Hunter 2002; Herrmann et al. 2005; Rinehart et al. 2009). Though newts are locally abundant in portions of their range, their regional patterns of occupancy and association with landscape features are poorly understood, making it challenging to assess local population sensitivity to large-scale threats (Rinehart et al. 2009).

An ominous future threat to red-spotted newts is the expected introduction of the pathogen *Batrachochytrium salamandrivorans* (Bsal) to the United States, a close relative to Bd (Martel et al. 2013; Gray et al. 2015; Yap et al. 2017). Bsal causes the disease chytridiomycosis in salamanders and has shown to be lethal to infected red-spotted newts (DiRenzo et al. 2021). Bsal is currently decimating some populations of

European salamanders, and it is expected to make its way to the United States (Martel et al. 2014), though it has not been detected in free-ranging populations (Waddle et al. 2020). If this disease establishes in the United States, it could have a devastating impact on ERSN populations. An understanding of areas with high probability of occupancy can give managers a chance to make proactive management decisions to protect regions of high occupancy from both Bsal and other threats (Sterrett et al. 2019), and to focus Bsal surveillance efforts (Waddle et al. 2020). Combined with studies on areas of high risk for introduction of Bsal (e.g., Richgels et al. 2016; Grear et al. 2021), a detailed understanding of newt occupancy could be a powerful tool to prevent the spread of this dangerous pathogen.

A statistically based understanding of species occurrence and habitat associations can help target management to areas with greatest probability of occupancy. The objective of this study is to create a model to best predict ERSN breeding occurrence across the northeastern United States. We first estimated relationships between breeding ERSN field survey data and landscape-level covariates (Table 1). We then used those relationships to map predictions of ERSN breeding occupancy across the northeastern U.S. Our estimates accounted for imperfect detection and were used to make spatial predictions of occupancy. This analysis will provide a foundational tool upon which managers can develop management strategies for ERSN.

1.2. Methods

1.2.1 Site Selection

The sampling for this project was part of a nationwide investigation led by the US Geological Survey's Amphibian Research and Monitoring Initiative (ARMI) to survey for the salamander fungus (Bsal; *Batrachochytrium salamandrivorans*) in wild amphibian populations across the U.S. Sample sites (ponds or wetlands) were chosen to maximize the probability of detecting Bsal if present; sites were stratified according to the risk of Bsal presence at the county level following Richgels et al. (2016) and described in Waddle et al. (2020). Some sites were selected outside of the high-risk counties where Bsal was unlikely to occur, even if it had invaded the US. Sites were selected from state and public lands, and accessibility was also considered when choosing each sampling site. Wetlands on public lands within the risk map were identified using the U.S. Fish and Wildlife Service's National Wetlands Inventory (NWI).

1.2.2 Field

We sampled 264 sites from New Hampshire to Virginia in 2016 – 2017 during the months of March – August (Fig. 1.1). At least two observers visited each site at least once over the course of this period. Adult newts were captured at wetland sites via aquatic funnel traps, visual encounter surveys (VES), or dipnet surveys.

1.2.3 Hypotheses

ERSN occurrence is expected to be negatively related to habitat fragmentation and road density (Hecnar and M'Closkey 1996; Gibbs 1998; Guerry and Hunter 2002;

Herrmann et al. 2005; Rinehart et al. 2009). The Human Interference Index (HII; Wildlife Conservation Society, 2005) is a compilation of nine data layers, and encapsulates multiple forms of human influence on the landscape. These layers include land use and infrastructure, built-up areas, nighttime lighting, land use, land cover, coastlines, roads, railroads, and navigable rivers.

We hypothesized that breeding newt occupancy would be higher in deciduous forests because these forests tend to have more leaf litter, lower pH, and higher relative soil moisture than coniferous forests (Rinehart et al. 2009). We used the US Forest Service's "Forest Groups in the Northeast" layer and reclassified the layer into coniferous or deciduous forest (USDA Forest Service 2008). We double checked the U.S. Forest Service data against Google Earth Historical data and satellite imagery because the Forest Service data was not fine enough to pick out small patches of coniferous forest within larger tracts of deciduous forest.

Finally, we expected that we would not detect ERSNs on every visit, even if they were present at a site. Because we used multiple survey methods, and visited different sites across the season, we hypothesized that survey method type and time of year would influence our ability to detect newts. We used both active and passive survey methods. Active sampling included both dip-netting and visual encounter surveys. Passive sampling was conducted using aquatic funnel traps fitted with a glow stick (Antonishak et al, 2017). Traps were set and left in pools overnight and checked for ERSNs after ~12 hours. We expected that passive sampling would result in higher detection probabilities because traps were in the pool longer than surveyors, and success of active sampling is

dependent upon the surveyor's skill. We predicted there would be a negative relationship between detection probability and day-of-year; breeding begins in early spring and continues through the beginning of summer, with activity slowing down mid – to late summer (Petranka 1998).

1.2.4 Analysis

To identify the relative importance of hypothesized drivers of newt occupancy across the northeastern United States, we fit single-species single-season occupancy models in Program R (R Core Team 2020) using package RPresence (Hines 2015), a formula-based interface for program PRESENCE (Hines 2015). Occupancy models use detection/non-detection data to estimate species occurrence while accounting for imperfect detection probability, which requires some form of replication of observations (e.g., multiple surveys, multiple methods, multiple observers; MacKenzie et al. 2006). We used survey method as replicate observations to estimate detection probability; each observer and trap were counted as single, separate surveys for a total of 385 total surveys. We specified *a priori* models reflecting our biological hypotheses about newt occurrence and detection (described above), and fit single effect as well as additive models (Table 2).

We evaluated models using Akaike's Information Criterion corrected for small sample size ('AICc'; Burnham and Anderson 2002). We then used model averaging, along with the HII raster and forest type shapefile, to create visual maps of predicted newt occupancy across the northeastern United States based upon the top models.

1.3 RESULTS

We visited 264 sites across the northeastern United States throughout 2016 – 2017 during the months of March – August (Fig. 1.1). Our total number of surveys was 385 and our team detected newts 169 times. The maximum number of visits per site was 3, and the minimum number of visits was 1; of the 264 sites, only 15 were visited twice and 4 were visited three times. Traps were used for 60 visits and 325 visits were conducted using dipnet and VES techniques. Naïve occupancy (i.e., the proportion of sites where ERSNs were observed) was 51% (134 sites).

The most parsimonious model (AICc weight = 0.42) suggested that newt breeding occupancy varied with HII (Table 3). There was a negative relationship between HII and newt breeding occupancy ($\hat{\beta}$ = -0.46; 95% CI: -0.61 - -0.31, Table 4, Fig. 1.2. Forest type was present in the third most highly ranked model and predicted coniferous forests to have lower probabilities of occupancy than deciduous ($\hat{\beta}$ = -0.28; 95% CI: -0.78 – 0.22, Table 4).

For detection probability, survey method and date were in the most parsimonious models (AICc weight > 0.1; Table 3), suggesting both survey method and time of year were influential in detection of newts. We found that passive sampling (i.e., traps) was less effective than active sampling (VES and dipnet) methods for detecting newts (Table 4). We found time of year had a negative effect on detection probability ($\hat{\beta}$ = -0.77; 95% CI: -1.01 - -0.53; Table 4); detection probability was highest at the start (March) of the sampling season and lowest near the end (August; Fig. 1.3).

We predicted ERSN occupancy across the entire northeastern United States using the mean estimated regression coefficients from model averaging the top three models.

1.4 DISCUSSION

We provide an estimate of site-occupancy across the northeastern range of ERSNs (Fig. 1.4). We found, as expected (Hecnar and M'Closkey 1996; Gibbs 1998; Guerry and Hunter 2002; Herrmann et al. 2005; Rinehart et al. 2009), human land use is inversely related to the probability a wetland is occupied by breeding newts. Since ERSNs, especially juvenile efts, are highly dispersive, they have a greater risk of becoming isolated in fragmented habitats and may thus be at greater risk for stochastic local extinction. The dependence upon both terrestrial and aquatic habitats is expected to result in sensitivity of ERSN to human activity in either environment (Cushman 2006; Roe and Grayson 2008).

Although forest type did not occur in our top model, we believed it is still important to consider and therefore model averaged the top three models to include forest type. We believe newts prefer deciduous forest types because coniferous forests tend to have drier soil, less organic matter, and more acidic soils, whereas deciduous forests will have moister soils with more organic material and less acidity (Rettig et al. 2011). Soil and organic matter composition are greatly varied between the two forest types. The organic layer is important to amphibians since it retains moisture and offers refuge (Rettig et al. 2011). In our study, 240 sites were classified as deciduous and only 25 were classified as coniferous. This uneven dispersal of site type may account for the large

standard error around our forest type occupancy estimate. It may also reflect the distribution of wetlands across different forest types.

In the Northeast, ERSN breeding activity begins in March, though exact dates vary by latitude (Petranka 1998) and local conditions. Emigration from pools is triggered by drying, reduction in food resources, or when newts move to overwintering habitat (Gill 1978, Petranka 1998). Our detection probability reflects this pattern. Julian day of year relates to pond hydroperiod and other phenological changes across the breeding season and as hypothesized was an important detection covariate in this study.

We were surprised to find active sampling, i.e. dipnet and visual encounter surveys, to have a higher detection rate than trapping. Traps were left in pools for a minimum of 12-24 hours, while active sampling surveys typically lasted from 0.5- 2 hours, thus allowing traps a much longer capture period. Despite this extended sampling period for traps, active sampling may have performed better because surveyors were not restrained to a specific location within the pool but instead sought out newts to capture.

Though forest type did not occur in our top model, it was still informative (i.e., it had AICc weight = 0.11; Table 1.3). We found that deciduous forests with low human interference have the highest probability of newt breeding occupancy, while coniferous forests with similar levels of human interference have reduced probability of occupancy by newts. Newts may prefer deciduous forest types because coniferous forests tend to have drier soil, less organic matter, and more acidic soils, whereas deciduous forests will have moister soils with more organic material and less acidity (Rettig et al. 2011). The

organic layer retains moisture, which is important for maintaining water balance during terrestrial stages, and deciduous forests tend to have deeper organic layers than coniferous forests (Harper and Guynn 1999; Faccio 2003; Rettig et al. 2011). In our study, 239 sites were classified as deciduous and only 25 were classified as coniferous. This uneven sampling of site type may account for the large standard error around our forest type occupancy estimate. Because the study from which these data were derived preferentially visited sites with suspected or known newt occupancy, we may have undersampled sites within coniferous forests.

Characteristics of a wetland, such as the hydroperiod, substrate, and vegetation, are known to be important for ERSN occurrence (Petranka 1998; Rinehart et al. 2009). We were unable to use region-wide, remotely-sensed wetland layers (e.g., NWI, U.S. Fish and Wildlife Service, 2019), as a most of our sites did not fall within the wetland polygons of the layer. Our trouble with this GIS layer showcases issues of using GIS to determine habitat for animals with small home ranges. Many of the vernal pools we surveyed are too small to be picked up by satellite imagery and even if the GPS coordinates are only a few meters off, wetland types could change in that space.

This study was part of a nationwide investigation led by the USGS Amphibian Research and Monitoring Initiative (ARMI) to determine if Bsal is present in wild amphibian populations within the U.S. Though this study was not specifically designed to estimate the range-wide patterns of red-spotted newt breeding occupancy, we believe its insight on red-spotted newt persistence is nonetheless valuable. Site selection was biased towards pools with historical ERSN observations, but despite this our team of

experienced field scientists failed to detect newts at half of our sites. Our analysis gives insight into newt persistence within historically occupied areas. We have several interpretations for the observed absences at these historically occupied sites. First, newts may have been present at these sites, but not detected by our team. Though we know that this is possible (i.e., or detection probability was not = 1.0), we do not believe our team would have missed such a large percentage of occupied sites, especially since our rates of detection according to our model were relatively high (1.69; Table 1.4). Second, changes in landscape since the initial observations may have occurred between the observation in these databases and our survey events. If habitat has become more developed or fragmented, newts may no longer be able to occupy these sites, and thus these are true local extinctions. Third, environmental changes, such as climate change, may be causing amphibians to shift their distributions (e.g., Amburgey et al. 2018). Our study emphasizes a need for routine monitoring of amphibian species, especially common species that may otherwise be overlooked or given less priority in lieu of species classified as 'vulnerable' or 'threatened' (Sterrett et al. 2019).

Without foundational knowledge of species occupancy patterns, it is difficult to understand the effect present and future threats may have upon a species, and therefore the best management practices for that species (Sterrett et al. 2019). In the face of multiple, interacting threats to amphibians, scientists still need to gather foundational knowledge on many common species, including eastern red-spotted newts (Gaston 2010). Despite their commonness, we lack a comprehensive understanding of red-spotted newt occupancy, and its drivers, across their range. The findings presented here give us a

baseline occupancy map for red-spotted newts throughout areas historically occupied by newts across the Northeast United States. This information can be used in management plans to prioritize areas for monitoring and management, and for forecasting future newt population trends.

1.6 Figures

Figure 1.1: Location of sampling sites. Sites were selected in areas of predicted high risk of BSAL introduction to wild amphibian populations according to Richgels et al 2016. Areas of lower risk were also included as controls.

Figure 1.2: Effect of human interference on red-spotted newt occupancy estimates. The human interference index has been standardized. Values for human interference were obtained from the Wildlife Conservation Society's Human Interference Index.

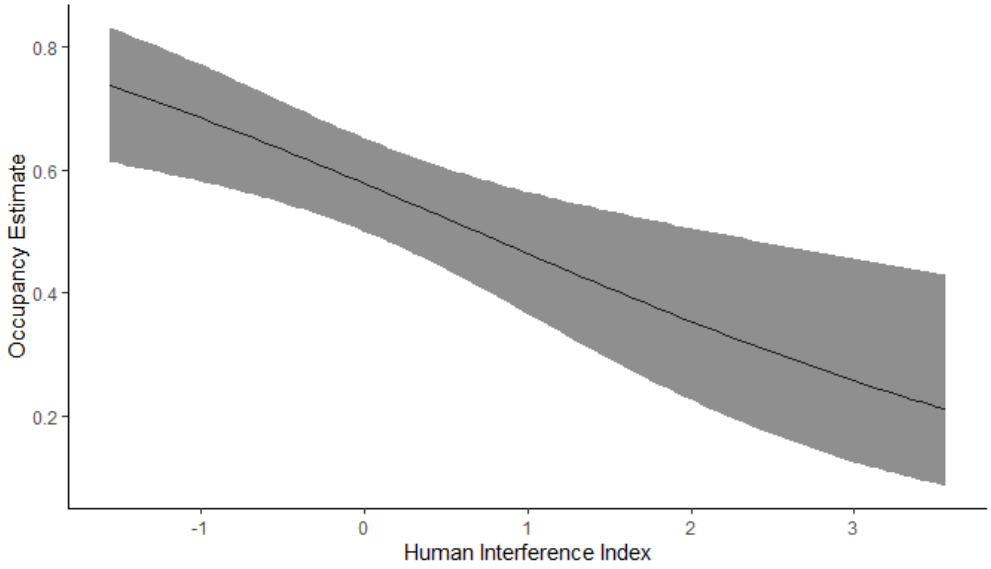


Figure 1.3: Effect of method type and day of year on red-spotted newt detection estimates.

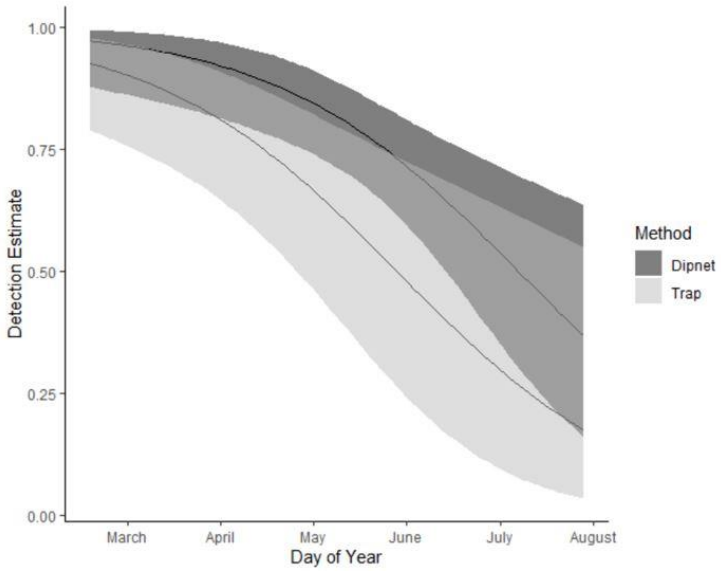
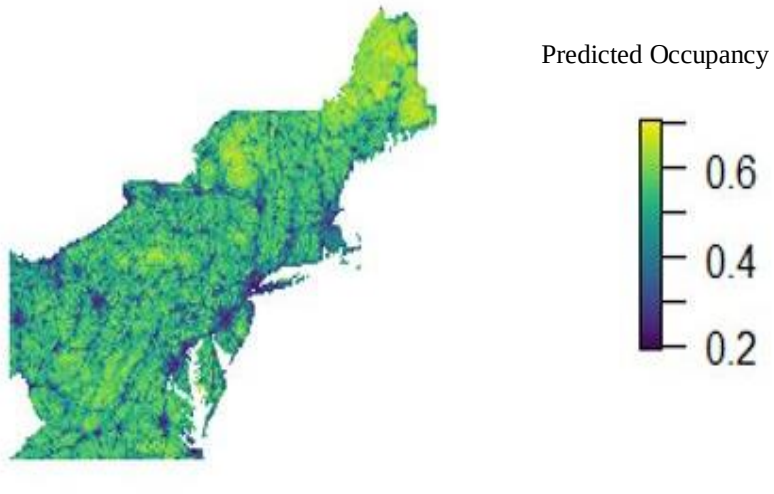


Figure 1.4: Predicted red-spotted newt occupancy based upon model averaged results of top three occupancy models. Top models included forest type and human interference index to predict occupancy. The Wildlife Conservation Society's Human Interference Index (HII) data was utilized to create this map. The HII is a compilation of nine data layers and encapsulates multiple forms of human influence on the landscape. These layers include land use and infrastructure, built-up areas, nighttime lighting, land use, land cover, coastlines, roads, railroads, and navigable rivers. Forest type was divided into coniferous and deciduous forest types.



1.7 Tables

Table 1.1: Definitions for detection and occupancy covariates used in our models. We hypothesized the effect of each covariate before fitting the models and categorized the covariates by whether they were expected to influence detection or occupancy parameters.

Model Covariates			
Covariate	**Definition**	**Parameter**	**Hypothesized Effect**
Human Interference Index (HII)	Global dataset comprised of nine layers: human population density, human land use and infrastructure (built-up areas, nighttime lights, land use/land cover), and human access (coastlines, roads, railroads, navigable rivers).	Occupancy	Occupancy probability will decrease as HII increases.
Forest Type	US Forest Service's data "Forest Groups in the Northeast" and reclassified the layer into coniferous or deciduous forests.	Occupancy	Occupancy probability will be greater in deciduous forests.
Method	Passive or active sampling techniques; passive includes traps set overnight with glowsticks, active includes dip-netting and visual encounter surveys.	Detection	Detection probability will be greater with the trapping method.
Date	Day of year the survey was completed between March and August.	Detection	Detection probability will fluctuate with seasonal breeding patterns; highest detection will occur from March to mid-summer and then begin to decline.

Table 1.2: A priori model set. Each covariate was run in a model separately and against each other covariate or combination of covariates. Constant models, in which no covariates were used, were run as controls.

Covariates	
Occupancy	Detection
Forest Type	Method
HII	Method
Forest Type and HII	Method
Forest Type	Constant
HII	Constant
Forest Type and HII	Constant
Forest Type	Date
HII	Date
Forest Type and HII	Date
Forest Type	Date and Method
HII	Date and Method
Forest Type and HII	Date and Method
Constant	Date
Constant	Method
Constant	Date and Method
Constant	Constant

Table 1.3: The candidate model set and AICc rankings for our occupancy models based on environmental (HII and forest type) and detection (method, day of year) covariates.

Model	AICc	Negative Log-likelihood	Number of Parameters	Delta AICc	Model Likelihood	Model Weight
Method, Date, and HII	467.97	457.74	5.00	0.00	1.00	0.42
Date and HII	468.95	460.80	4.00	0.98	0.61	0.26
Total	469.76	457.43	6.00	1.79	0.41	0.17
Date, HII, and Forest	470.73	460.49	5.00	2.76	0.25	0.11
HII, Constant	475.03	468.94	3.00	7.07	0.03	0.01
Date, Method, and Constant	476.40	468.25	4.00	8.43	0.01	0.01
HII, Forest, and Constant	476.84	468.69	4.00	8.87	0.01	0.01
Method and HII	476.89	468.74	4.00	8.92	0.01	0.00
Date and Constant	477.45	471.36	3.00	9.49	0.01	0.00
Method, Date, and Forest	478.43	468.20	5.00	10.46	0.01	0.00
Method, Forest, and HII	478.71	468.48	5.00	10.74	0.00	0.00
Date and Forest	479.47	471.32	4.00	11.50	0.00	0.00
Constant	481.26	477.22	2.00	13.30	0.00	0.00
Method and Constant	483.00	476.91	3.00	15.03	0.00	0.00
Forest and Constant	483.29	477.20	3.00	15.33	0.00	0.00
Method and Forest	485.05	476.89	4.00	17.08	0.00	0.00

Table 1.4: Results from the top three models determined by the AICc. Our most parsimonious model included the detection parameters method and date and the occupancy parameters of HII. The second model included date as the detection parameter and HII as the occupancy parameter. The third model include both data and method as detection parameters and HII and forest type as occupancy parameters. Estimates and standard errors were included for each model.

Top Three Model Outputs

Method, Date, & HII

	Estimate	Error
Detection Intercept	1.69	0.33
Date	-0.77	0.24
Method - Traps	-1.01	0.57
Occupancy Intercept	0.32	0.16
HII	-0.46	0.15

Date & HII

	Estimate	Error
Detection Intercept	1.35	0.25
Date	-0.58	0.20
Occupancy Intercept	0.37	0.17
HII	-0.47	0.15

Method, Date, HII, & Forest Type

	Estimate	Error
Detection Intercept	1.69	0.33
Date	-0.77	0.24
Method - Traps	-1.01	0.57
Occupancy Intercept	0.34	0.17
HII	-0.48	0.15
Forest Type - Coniferous	-0.28	0.50

CHAPTER 2: MANAGING FOR MULTIPLE PATHOGENS SIMULTANEOUSLY IN COMPLEX ECOSYSTEMS

2.1 Introduction

Ecosystems are highly variable, difficult to observe, and often understudied. Interactions in the ecosystem, among both biotic and abiotic elements, add to the complexity. It is incredibly difficult, if not impossible, to eliminate uncertainty when trying to understand ecological systems; therefore, it is difficult to accurately model natural systems and determine best management actions for the system in question (Runge et al. 2011; Bolam et al. 2019; Smalling et al. 2019). Ever-increasing pressure from threats (e.g., climate change, habitat degradation, urbanization) make timely and effective conservation decision making crucial; however, decisions are often held up because of uncertainty about the system. Additionally, collected data may not be informative for the decision at hand, thus taking valuable time and resources away from finding a management solution. Though the data may be of high quality and informative, it may not be helpful in answering a specific management question (Martin et al. 2012b; Bolam et al. 2019). Empirical data from field observations or mathematical models may not always be readily available and can be difficult, costly and timely to obtain, but tools that combine both empirical and qualitative data (i.e., privileged knowledge gained from experience), while accounting for uncertainty, can fill gaps in empirical data sets (Borsuk et al. 2006; Runge et al. 2011; Brown et al. 2013; Côté et al. 2016; Schwartz et al. 2018; Converse and Grant 2019; Smalling et al. 2019).

To improve conservation strategies, scientists and managers need to develop tools and models that combine existing empirical data, expert opinion, and associated uncertainties. Models for environmental management decisions should directly link to management objectives, predict effects of management alternatives without bias, estimate prediction uncertainty, and be easily understood by scientists and managers alike (Schuwirth et al. 2019). Multiple protocols are available that combine quantitative and qualitative data including structured decision making (SDM), expert elicitation (EE), and Bayesian belief networks (BBNs). Each method has a rigorous, standardized protocol to help researchers avoid common heuristics and collect qualitative data in a methodical, repeatable, and standardized fashion (Runge et al. 2011; Schwartz et al. 2018). Here, we create a framework for a Bayesian belief network using a combination of quantitative data from the literature and expert opinion to understand interactions between two co-occurring amphibian pathogens.

Emerging infectious diseases are an increasingly common threat to wildlife (Dobson and Foufopoulos 2001; Cunningham et al. 2017; Russell et al. 2017). Sometimes, multiple pathogens co-occur, making it even harder to determine best management strategies. Pathogens interact with hosts, but also respond to varying environmental conditions (Hoverman et al. 2011; Bienentreu and Lesbarrères 2020; Bienentreu et al. 2022). One pathogen effect on a host may be amplified by a certain environmental condition, but another effect diminished.

Pathogens may also affect each other; when a pathogen's effect is amplified by a second pathogen's presence, synergy occurs. An antagonistic relationship happens

when the effect of one pathogen is reduced by the presence of a second pathogen (Brown et al. 2013; Côté et al. 2016; Bosch et al. 2020). To best manage for the effect pathogens have on their hosts, we must understand how the pathogens interact with each other, their hosts, and the environment. Disease management strategies often include habitat manipulation to decrease pathogen growth. For example, the amphibian pathogen that causes chytridiomycosis, *Batrachochytrium dendrobatidis* (Bd), does not thrive in temperatures above 28◦C. A suggested management strategy is canopy removal above pools infected with Bd to increase light and temperature in these pools (Roznik et al. 2015). This method may decrease Bd growth in the pool but increase the environmental suitability for ranavirus, another amphibian pathogen (Gahl and Calhoun 2010).

Here we explore interactions between ranavirus, Bd, wood frog larvae, and the vernal pool environment (Longcore et al. 1999; Gray et al. 2009). The framework provides the foundation for a model to help identify management strategies that minimize disease risk to wood frog larvae in vernal pools in the presence of Bd and ranavirus. We first provide a literature review to determine environmental variables that influence Bd and ranavirus, and then fill gaps in the literature with expert elicitation. We then provide a framework for a Bayesian belief network (BBN) that incorporates the empirical data found in the literature with the results from the elicitation. This framework will be used by scientists at the U.S. Geological Survey to guide managers on optimal disease management strategies.

We focus on the co-occurrence of ranavirus and Bd in temporary pools within deciduous forests on protected lands in the Northeastern United States. We use wood

frogs as our study species since it is susceptible to both Bd and ranavirus and widespread throughout this region. The objective for this model is to act as a framework for disease management decisions.

2.2 Literature Review

The goal of this literature review was to identify environmental variables which influence Bd and ranavirus prevalence and intensity. We used 'Google Scholar' and the following search terms in our initial search: ("amphibian" AND "ranavirus"), ("amphibian" AND "*Batrachochytrium dendrobatidis*"), and ("chytrid" OR "*Batrachochytrium dendrobatidis*" AND "ranavirus" AND "co-infection"). To focus in on environmental variables of interest and narrow our search, we added search terms ("salinity" AND "wood frogs"), ("ranavirus" OR "*Batrachochytrium dendrobatidis*" AND "vegetation"), ("ranavirus" OR "*Batrachochytrium dendrobatidis*" AND "salinity"), and ("ranavirus" OR "*Batrachochytrium dendrobatidis*" AND "temperature"). Since our focus is on vernal pool amphibians in the northeastern United States, we targeted literature whose studies are based in the northeastern United States. Our target species are wood frogs, with priority given to studies using wood frogs.

In total, we reviewed 108 papers investigating wood frogs, disease, and environmental factors. Bd was investigated in 70 papers, ranavirus in 36, effect of temperature in 46, and effect of salinity in 17. Other covariates mentioned included vegetation (3), age class (1), hydroperiod (7), pesticides/herbicides/insecticides (7), genetics (2), pH (4), Dissolved organic carbon (DOC)/Nitrate/Phosphate (2), and recreation (3; Fig. 2.1).

When thinking about environmental factors affecting Bd, ranavirus, and wood frog survival, we were interested in factors that could be manipulated and influenced each pathogen. During our initial literature search, both temperature and salinity were repeatedly mentioned in the literature and met these criteria (Fig. 2.1). As we refined our literature search, we focused on the effects of salinity and temperature on Bd, ranavirus, and wood frogs. Though there is ample literature on interactions between each organism and environmental factor and each pathogen on wood frogs, data for a holistic understanding of the system are lacking. Our understanding of how salinity levels and/or temperatures affect wood frog persistence in the presence of both Bd and ranavirus is uncertain.

In the northeast United States, temperature fluctuates between seasons and across environments. Summer temperatures rise above 32^{o}C and winters drop below (-18^{o}C). Along with temporal fluctuations, temperature is affected by landscape variables like elevation, latitude, or habitat type. Temperature variance across seasons and landscapes has implications for both pathogen and wood frog growth (Raffel et al. 2006; Talbott et al. 2018; Bradley et al. 2019).

Bd can survive freezing, and experiences optimal growth between 17-25^{o}C, but fails to grow above 28^{o}C (Johnson et al. 2003; Piotrowski et al. 2004; Kriger and Hero 2008). It is capable of overwintering in amphibian hibernacula and, despite lowered reproduction rates, it can withstand prolonged exposure to temperatures as low as 4^{o}C, (Piotrowski et al. 2004; Bosch et al. 2007). Within a pool, the canopy cover, aquatic

vegetation, and depth all create microhabitats with varying temperatures that act as refuge from (or for) Bd (Heard et al. 2015; Scheele et al. 2017).

As temperatures rise, so does the rate of ranavirus replication. Wood frogs are highly susceptible to ranavirus induced mortality, especially at warmer temperatures. Ranavirus replication is most rapid between 28^{o}C – 32^{o}C, but is capable of causing fatal disease below this temperature threshold (Echaubard et al. 2014; Brand et al. 2016; Hall et al. 2018). Numerous laboratory studies have reported >90% mortality of wood frog tadpoles infected with 10^{3}PFU/ml^{-1} of frog virus 3 (FV3) when temperatures were 23^{o}C or higher (Haislip et al. 2011; Hoverman et al. 2011; Brand et al. 2016). However, Brand et al. (2016) reported 100% survival of wood frog tadpoles at temperatures of 10^{o}C and found that even a 2^{o}C difference (10^{o}C vs 12^{o}C) caused a drastic change in mortality rates (0% compared to 90%).

In the Northeast, deicing salts are commonly applied to roads in the winter, and the effect of road run-off on amphibians has been extensively studied (Karraker et al. 2008; Karraker and Gibbs 2011; Hall et al. 2020). Road salt exposure increases energy demands for osmoregulation in frogs, thus taking resources away from body growth and reducing a frog's immunocompetence (Hall et al. 2020; Donald 2021). Despite extensive study, it is still not entirely clear what concentrations of NaCl deleteriously affect wood frogs. A study by Clemmer et al. (2011) found NaCl concentrations of 500 and 1000 mgL^{-1} (~1,000-2,000µScm^{-1}) had no effect on wood frogs; but studies by Sanzo and Hecnar (2006) and Karraker et al (2008) found NaCl concentrations of 1,400 mgL^{-1} (~3,000µScm^{-1}) to have deleterious effects, while Petranka and Doyle (2010) observed no

deleterious effects until NaCl concentrations reached 4,500 mgL^{-1} (~8,000μScm^{-1}). It is possible that wood frog susceptibility to NaCl concentrations varies substantially over geographic range, or that a variety of other environmental factors may also be influencing findings (Clemmer et al. 2011).

In the same way that elevated salinity negatively impacts wood frog growth, salinity also impacts Bd. As salinity levels increase, Bd reallocates resources from growth and motility to osmoregulation, making Bd zoospores less mobile and infectious (Stockwell et al. 2012). Clulow et al. (2018) hypothesize that increased salinity levels do not have a curative effect on amphibians infected with Bd, but instead prohibit Bd's ability to move through an aquatic environment, thus decreasing transmission. Exposure to salinity levels of 3,900μScm^{-1} may provide substantial refuge to susceptible amphibians from Bd; however, this level of salinity could have fatal consequences on wood frogs (Karraker et al. 2008; Stockwell et al. 2015). Stockwell et al. (2012) found concentrations as low as 1,500μScm^{-1} may significantly decrease Bd infection risk. Managers could use this information to increase salinity levels in pools to inhibit Bd growth, but not to the deleterious effect on wood frogs.

The interaction between ranavirus and salinity is less understood. Ranavirus is not an organism, and therefore does not go through the process of osmoregulation and may not be affected by increased salinity levels. Wood frog larvae in pools with high salinity levels are at higher risk of contracting ranavirus because of the depressive effect salinity has on their immune systems (Hall et al. 2020). Hall et al. (2020) found that elevated salinity levels (800-1,600$mgL^{-1}Cl^{-}$, ~1,600-3,000 μScm^{-1}) increased larval infection

intensity by 10-fold and increased viral shedding rates by 5-fold, possibly increasing transmission rates.

Though wood frogs are susceptible to both Bd and ranavirus, their mortality rates when infected by one pathogen or the other differ. On average, Bd-infected wood frogs experience a 27% mortality rate (Bradley et al. 2015). Ranavirus infection in a wood frog population usually results in >90% mortality (Haislip et al. 2011; Hoverman et al. 2011; Brand et al. 2016). However, there are situations when ranavirus persists in an environment, but only 10% or less of the wood frog population may experience mortality. From our literature review findings, we believe this pattern is influenced by both temperature and salinity (Brand et al. 2016; Hall et al. 2020). Though elevated salinity decreases Bd zoospore growth and motility, it increases the infectiousness of ranavirus. Salinity does not directly affect ranavirus but decreases immune function and causes wood frogs to become more susceptible to ranavirus at lower PFUs (plague forming units) exposure (Hall et al. 2020). Temperatures 10^{o}C and below are outside the optimal temperatures for Bd growth and ranavirus replication (Piotrowski et al. 2004; Brand et al. 2016). Wood frogs are a cold-adapted species and are acclimated to temperatures of 10^{o}C and lower (Arietta et al. 2020). Decreasing temperatures may not decrease immune function within wood frogs, but consideration should be given to the effect that prolonged cold temperatures may have on other species co-habituating with wood frogs. Since ranavirus can cause >90% mortality in wood frog populations, management should make sure not to increase environmental conditions for ranavirus reproduction.

2.3 Background

2.3.1 Pathogens

Bd is a globally distributed fungus identified in 1997 and named in 1999 (Longcore et al. 1999). Distributed worldwide on every continent except Antarctica, Bd has caused the largest amphibian species declines throughout the tropics, and the extinction of species, such as the Golden Toad (*Incilius periglenes*) and Panamanian Golden Frog (*Atelopus zeteki*) (Lips et al. 2006; Fisher et al. 2009). Some amphibian species are highly sensitive to this pathogen, others are tolerant and may act as reservoirs. Bd infects the keratinized tissue within amphibian skin and larval mouthparts (Daszak et al. 1999). If infected as a tadpole, most larvae will survive through metamorphosis. After larvae complete metamorphosis and become juveniles, Bd infects the skin, disrupts osmoregulation and causes mortality (Berger et al. 1998). Despite Bd's widespread presence in the northeastern states, scientists are unsure of its true impact on amphibian populations throughout this region (Longcore et al. 2007).

Ranavirus (Frog Virus III) is found in the Americas, Europe, Asia, and Australia and has been implicated in large die-offs of fish, reptiles, and amphibians (Daszak et al. 1999; Lesbarrères et al. 2012). Ranavirus is a double-stranded DNA virus that causes systemic hemorrhagic disease in amphibians and is responsible for mass amphibian die-offs on five continents with the greatest number of mortality events occurring in North America and Europe (Daszak et al. 1999; Gray et al. 2009; Miller et al. 2011). Ranaviruses are known to infect 72 amphibian species, with the majority of susceptible species in the family Ranidae (Hoverman et al. 2011; Miller et al. 2011). Hoverman et al. (2011) tested the susceptibility of 19 North American amphibian species to ranavirus and found wood

frogs (*Lithobates sylvaticus*) and Gopher frogs (*Lithobates capito*) to be the most susceptible. Susceptibility to ranavirus varies with life stage and species; individuals are most susceptible to ranavirus during periods of larval development when their immune systems are compromised (Gray et al. 2009; Miller et al. 2011).

2.3.2 Wood Frog Life History

Of pond-breeding amphibians in North America, wood frogs are the most widely distributed (Lannoo 2005). Populations in the northeastern U.S. have suffered declines, even in protected areas, and are listed as a species of greatest conservation need in multiple State Wildlife Action Plans (Miller and Grant 2015). The exact causes of these declines are unknown, further complicating management action. Climate change, habitat degradation, and disease are all thought to contribute to declining populations (McCann et al. 2006; Marcot et al. 2006). Wood frogs are affected by both Bd and ranavirus, and are one of the most susceptible amphibian species to ranavirus in North America (Hoverman et al. 2011).

2.4 Methods

2.4.1 Expert Elicitation

Ideally, to answer questions about the effects of environmental variables (e.g., salinity and temperature) on pathogens and wood frogs, we would look to estimates from empirical data. Though there is information on salinity, temperature, Bd, ranavirus, and wood frogs, the data focus on the effect that one factor has on either one pathogen or wood frogs, but not the holistic system. Currently, there is uncertainty surrounding the impacts that salinity and temperature have on ranavirus, Bd, and wood frogs, especially

when considering all three organisms simultaneously. To better understand the holistic effect of these two system parameters, we organized an expert panel to elicit parameter estimates with associated uncertainty using a structured elicitation process.

An expert is someone who holds substantial knowledge of a particular subject and can give insightful information based upon their experience. Experts gain their knowledge through training, research, skill development, and personal experiences (Burgman et al. 2011; Martin et al. 2012a). We tracked authors of informative papers during the literature review for consideration in the elicitation process; however, this was not the only criteria for recruiting experts. It is difficult to identify the best experts to give judgements based on number of publications, and groups of multiple experts almost always perform better than individual experts (Burgman et al. 2011). Casting a diverse set of experts is always important as this will increase cognitive diversity (Hemming et al. 2018a,b). Expert judgement is most useful when data are absent or incomplete, and linguistic uncertainty, contextual biases, and a variety of heuristics often result in mistakes by experts but can be minimized during a carefully structured elicitation process. Heuristics include anchoring, availability bias, representativeness, groupthink, overconfidence, and difficulty communicating knowledge in the forms of numbers and probabilities (Hemming et al. 2018a,b).

As a result, we recruited experts from multiple backgrounds, of differing education levels, ages, and agencies or institutions. If experts could not participate, they offered recommendations for additional experts to follow up with. Using a diverse group of experts reduces biases (Hemming et al. 2018a,b), and aggregating the information

provided using structured elicitation protocols further reduce these biases by treating each step as a process of formal data acquisition.

In our expert elicitation, we used the modified Delphi protocol, IDEA, and the 4-point elicitation protocols (Speirs-Bridge et al. 2010; Hemming et al. 2018a,b). The acronym IDEA from the modified Delphi protocol stands for "Investigate", "Discuss", "Estimate", and "Aggregate" (Hemming et al. 2018a,b). In the "Investigate" portion of the protocol, experts are asked to independently explore relevant literature and answer each given question. During the "Discuss" step, experts are shown anonymous answers and encouraged to discuss their thought processes, individual and group outcomes, and any uncertainties they have about the questions. For the "Estimate" step, experts are asked to revise their answers based on the group discussion. We next averaged the low, best, and high quantiles for each answer, and then generated an aggregate (mean) distribution of the responses (Runge et al. 2011; Hemming et al. 2018a,b). Each answer followed the 4-point elicitation protocol to minimize overconfidence and account for uncertainty. In the 4-point elicitation protocol, experts are asked for a realistic low, high, and central value for the question at hand. Experts are also asked to rate the confidence interval created by their low and high estimates, allowing us to measure uncertainty (Speirs-Bridge et al. 2010). For example, one of our training questions asked experts "Out of 100 randomly selected pools in the Northeastern United States, on average how many are occupied by wood frogs?" Experts gave us their lowest estimate, best estimate, and highest estimate. Next, they rated their confidence that the true answer fell within this range.

After recruiting experts, we asked experts to complete a set of training questions designed to calibrate experts to the questions and have them practice thinking in probabilities. Each training question had known values from empirical data. Upon completion of the training questions, experts attended a conference call to discuss the training questions. At this first meeting, we provided experts with the empirical answer for each question, and asked them to discuss their thought processes, discuss any uncertainties, and for recommendations for better question phrasing. After this first conference call, we sent out the first round of our elicitation questions. Experts had time to individually answer these questions using any resources at their disposal. After returning their answers, we aggregated the results and shared these at our second conference. During this meeting, we discussed results and cleared up linguistic and other uncertainties about the questions. Experts were asked to explain their thought processes and re-think any questions, without feeling pressure to change their answers. After this meeting experts were given time to revise their answers before sending them back to us for aggregation and interpretation (Runge et al. 2011; Hemming et al. 2018a,b).

2.4.2 Bayesian Belief Network

To model interactions between pathogens and the environment, we create the framework for a Bayesian belief network (BBN) model. Bayesian belief networks are models that represent correlative and causal effects of variables graphically and probabilistically (Marcot et al. 2006; McCann et al. 2006; Smalling et al. 2019). A BBN can incorporate both expert opinion and empirical data into a graphical representation, which also accounts for multiple, possibly interacting, stressors. Ecologists and wildlife

managers can use BBNs to track interactions that habitat or environmental predictor variables have on ecological response variables, helping managers to understand the impact that potential management actions might have on their system (Marcot et al. 2006; McCann et al. 2006; Smalling et al. 2019).

The process of creating a Bayesian belief network (BBN) can be broken into three steps (McCann et al. 2006). The first step is to create a conceptual diagram that identifies the key system variables and the hypothesized interactions between these variables. Each of the potential interactions found in our literature review will be included in the conceptual diagram. The next step is to revise the conceptual diagram to produce a beta-level BBN (Marcot et al. 2006). To create the beta-level BBN, we revisit the literature to identify the most influential variables in the conceptual diagram and prioritize those that are easy to measure quantitatively and manipulate because these will be most useful from a management perspective. The final BBN will have an updated model structure and conditional probability tables for each component.

Nodes in the BBN comprise three types (*utility*, *chance*, and *decision*). The utility node contains the fundamental objective that will guide management actions, in our case, the persistence of wood frog populations in the northeastern United States which is a common goal of northeastern refuge managers. In our BBN, we used survival of wood frog larvae as a proxy measurement for persistence. Management strategies that result in zero to low survival (<33%) were the least valued management outcomes (utility = 0), medium survival (33-60%) was highly valued (utility = 0.75), while high survival (>60%) was the most valued outcome (utility = 1). Decision nodes represent actions that

influence salinity and temperature. While we do not specify management actions within our BBN, we know salinity and temperature can be manipulated within a pool and use these two variables as our decision nodes (Stockwell et al. 2015; Beranek et al. 2020). Mangers can specify salinity and temperature values in the BBN's decision and observe the resulting effects on the utility node displaying overall wood frog persistence. We hypothesized that the intensity of ranavirus and prevalence of Bd would drive survival.

Decisions nodes have a direct effect on chance nodes which contain conditional probabilities for a specific condition within the model. Bd prevalence and ranavirus lethal intensity are depicted as chance nodes in our model. Each chance node has a corresponding conditional probability table (CPT) that gives the probability for a specific threshold based upon the decision nodes. To create the CPT for the survival chance nodes, we used empirical data from the literature to determine the probabilities for Bd prevalence and ranavirus intensity based on environmental conditions (i.e., values set in the decision nodes). The chance nodes for ranavirus intensity and Bd prevalence directly impacted the chance node determining wood frog survival. Again, using empirical data from the literature, we created a CPT for each chance node. To account for uncertainty, we divide survival into probability brackets. When data were not available empirically, we used expert knowledge and a specified rule set to allocate probabilities (Table 2.2).

Software

We developed our Bayesian belief network models using GeNIe Academic software from BayesFusion, LLC (http://www.baysefusion.com/), a program made available by BayesFusion Downloads for Academia.

2.5 Results

2.5.1 Conceptual Model I

In the initial conceptual model, we mapped each variable found in the literature to influence ranavirus or Bd within a vernal pool (Fig. 2.2). After listing all variables, we thought about potential interactions between variables. Arrows indicate dependence of a child node to the associated parent node; but the absence of an arrow does not necessarily indicate independence between nodes. For example, 'pH' and 'Vegetation in Pool' do not share an arrow, but we cannot be sure they do not influence one another.

2.5.2 Conceptual Model II

After creating an initial conceptual model, we refined the model to create a second conceptual diagram, or the Beta BBN (Fig. 2.3). We first eliminated any parent nodes whose child nodes were equally informative. For example, 'Proximity to Agriculture' effects 'Fertilizer', 'Dissolved Oxygen', 'Pesticide and Herbicides', 'Nitrogen', 'Water Quality', 'Phosphorus', and 'Vegetation in Pool.' Each of the above child nodes could be measured during a pool visit, and so calculating the pool's proximity to agriculture may not be necessary, and so we removed the node 'Proximity to Agriculture'. Next, we revisited the literature and culled any variables that did not have sufficient support or were too ambiguous. For example, 'Weather' was cut from the model because there was not enough information and cited data to ascertain its importance, and because weather can change so rapidly (e.g., hourly, daily), we did not think it would be a useful metric for management.

2.5.3 Values for Bayesian Belief Network

We broke temperature into 3 ranges, low (<10^{o}C), medium (11-27^{o}C), and high (28^{o}C-32^{o}C). In the low temperature range, wood frogs have a higher probability of surviving ranavirus exposure and Bd growth is slowed, also lowering the probability of a lethal infection (Piotrowski et al. 2004; Brand et al. 2016). The medium range provides optimal growth temperatures (17-25^{o}C) for Bd. While this temperature range is not optimal for ranavirus replication, the pathogen is lethal within this range. In the high temperature range, 28^{o}C – 32^{o}C, ranavirus replication is most rapid, but Bd growth is halted or severely slowed (Piotrowski et al. 2004; Echaubard et al. 2014; Hall et al. 2018).

When determining salinity parameter values for the BBN model, we were interested in a value that reflected natural salinity levels within forested pools in the northeast, a value whose impact was uncertain with respect to wood frog survival but would decrease Bd prevalence, and a salinity value on the edge of wood frog tolerance but could provide refuge from Bd. We chose such a range because we are interested in finding salinity values that decrease Bd growth with minimal deleterious effects on wood frogs.

We chose the value of 18.6 µScm^{-1} to reflect natural salinity levels within forested pools; Karraker et al. (2008) found this to be the average value for a group of forested pools at least 0.5k from State Highway 28N in the Adirondack State Park, New York. We chose the value of 1,500 µScm^{-1} for salinity to reflect an increased salinity value that was not fatal to wood frogs, but decreases Bd prevalence (Stockwell et al. 2012). We chose the value of 3,000 µScm^{-1} as the upper limit for salinity, assuming this value to further decrease Bd growth; however, Hall et al. (2020) found that wood frog larvae exposed to

high salinity treatments experienced 2.85x the mortality rates due to ranavirus of larvae raised in freshwater. Karraker et al. (2008) also found that exposure to salinity of 3,000 μScm^{-1} caused wood frog populations to decline to extinction over time.

We broke Bd prevalence into three categories, low (26%), medium (38%), and high (50%). These categories were based upon field studies looking at Bd prevalence across wood frog populations in northeastern North America. We averaged low, medium, and high prevalence rates found in the literature to determine this values (Forzán et al. 2010; Richards-Hrdlicka et al. 2013; Lenker et al. 2014).

Ranavirus is endemic throughout the northeast United States, and has widespread occurrence (Hoverman et al. 2012; Crespi et al. 2015; O'Connor et al. 2016) Ranavirus has been detected within pools that do not experience mass die-offs, or within pools where >90% of the wood frog population succumbs to ranavirus. We broke ranavirus intensity into two categories, high and low, based on expert observation that ranavirus occurs ubiquitously across the landscape, but that epidemics (>90% mortality) are either experienced, or they are not (<10% mortality). If ranavirus infection intensity is high, we assumed an epidemic would occur; if ranavirus infection intensity was low we assumed an epidemic would not occur.

Interactions between ranavirus and Bd have not been extensively studied. Larvae infected with a lethal intensity of ranavirus will die before completing metamorphosis, but those infected with Bd will not experience mortality until 10 days post-metamorphosis (Berger et al. 1998). We assumed larvae lethally infected with ranavirus will not have the opportunity to die from Bd. In our model, we assume a

synergistic relationship (i.e., the combined effect of pathogens is greater than additive effect), but between pathogens only when ranavirus intensity and Bd are both low.

To calculate survival, we first considered ranavirus intensity. If intensity was low, we assumed 90% of the individuals survived, if the intensity is high, we assumed 10% survival. The larvae that survive ranavirus infection are then considered for Bd infection and we assumed that 27% of the infected larvae would survive Bd (Gahl et al. 2012; Bradley et al. 2015). Persistence was based directly upon estimates of survival. Low persistence (<33%) of wood frog population was given a utility vale of 0 and high persistence (>60%) was given a utility of 1. Medium persistence (33-60%) was also a valued outcome, and therefore given a utility of 0.75.

2.5.4 Final Model

After running the BBN to explore combinations of temperature and salinity, assuming no interaction between pathogens, we re-ran the model for each combination assuming the pathogens did interact (Fig. 2.5). We found, regardless of interaction, environmental conditions with low temperatures (under $10^{o}C$) and low salinity levels ($18.6\mu Scm^{-1}$) produced the highest utility values (utility = .81). High salinity and high temperatures produced the lowest utility values (utility = .10). The probability of high Bd prevalence was minimal at high salinity levels; however, the probability of a high intensity of ranavirus was 50-90% when salinity was high, regardless of temperature. Low temperatures reduced the probability of high ranavirus intensity and slightly decreased the probability of high Bd prevalence.

2.5.5 Model Assumptions

Our model has several assumptions. First, it does not account for mortality outside of disease. The model also assumes that both pathogens exist within the system, individuals are co-infected, and that larvae will experience mortality from ranavirus before metamorphosing and that mortality from Bd will occur 10 days post-metamorphosis (Berger et al. 1998; Haislip et al. 2011). We also assume Bd cannot grow in temperatures 28^{o}C and above, nor in salinity above 3,000µScm^{-1} (Piotrowski et al. 2004; Stockwell et al. 2015). Our last assumption is that overall wood frog persistence is based upon larval survival past 10 days post-metamorphosis.

2.6 Discussion

Conservation of amphibian populations requires estimates of interactions that amphibians have with potential threats, along with interactions between those threats to make useful predictions. Uncertainty surrounding stressor response, possible interactions amongst stressors, and the potential to increase the severity of one stressor while controlling for another adds to the complexity of amphibian conservation. This complexity makes it difficult to establish management strategies and determine areas where additional research may be most impactful. Management tools, like Bayesian belief networks, can help clarify best management practices amidst complexity.

Managers in the northeast are interested in wood frog persistence throughout their range, and are interested in managing for pathogens affecting wood frogs. We considered the effects of manipulating temperature and salinity on Bd prevalence and ranavirus intensity, and the probabilistic effect of these two pathogens on wood frog persistence within a vernal pool. We found ranavirus to have a greater effect on wood

frog persistence compared with Bd, and that temperature had a larger influence on the system than salinity (Fig. 2.4). From our literature review, we found pathogen interaction did not heavily influence the system and that high amounts of uncertainty surround knowledge of pathogen interactions. The highest wood frog persistence (utility = .81) occurred when salinity and temperature were both low (18.6µS; <10^{o}C). The lowest wood frog persistence (utility = .1) occurred when temperature was set to high (28-32^{o}C), regardless of salinity level, and when temperature was set to medium (11-27^{o}C) and salinity to high (3,000µS). Our results indicate pool temperature plays a consequential in the expected mortality from each pathogen.

Understanding and predicting the ecological consequences of management actions is increasingly important for environmental management decision making (Schuwirth et al. 2019). Model goals for ecological management and ecological inference are not always the same. As a result, modelers must collaborate with environmental decision-makers, a common understanding must be developed, and the transfer of knowledge between science and implementation needs to occur (Schuwirth et al. 2019). Often, ecological models produce results that are unable to be translated into management actions. While creating this model, our objective was to create a tool that managers could use to make decisions within their jurisdiction, and our choice of environmental variables were constrained to those that could be measured and manipulated. For example, while aspects such as genetics and pH appeared in the literature, we did not consider them for our model because we do not believe they are practical for management. Wood frog genetics would be difficult to measure, and even

more challenging, and possibly dangerous, to manage. Though pH is directly measurable, it would be difficult to manipulate in a field environment. Vegetation and hydroperiod were often cited as influential in the literature; however, both can be encapsulated by our temperature node. Temperature may be manipulated by adding or removing vegetation surrounding the pool (Roznik et al. 2015). If a management action decreases temperature, it may also increase the pool's hydroperiod. Shade cloths can be used to reduce temperature within a pool, while canopy removal can be used to increase pool temperatures (Skelly et al. 2002). Salinity can be increased or decreased within a pool by preventing road run-off from salinizing the pool, or by purposefully adding salt to a pool.

Though knowledge about a system may be lacking, the creation of models for management action is still essential for conservation (Russell et al. 2017; Smalling et al. 2019). Despite a lack of empirical data, conservation decisions still need to be made in a timely fashion, especially under the pressure of threats like climate change and urbanization. Complex systems, such as our study system, typically have little empirical information to guide the parameterization of models. To fill in gaps of missing information, expert opinion can be collected and incorporated into models (Martin et al. 2012a). Our team is in the process of a structured elicitation process and will update our model as we gain the elicitation results. BBNs are a valuable tool to overcome the challenges of managing for complex systems as they accommodate unbiased priors to guide management decisions in areas of high uncertainty. Uncertainty can paralyze the process of making a management decision. Tools that help to define uncertainties of most importance, or highest expected value of information, can guide future research

initiatives and reduce knowledge gaps in important areas (Runge et al. 2011; Bolam et al. 2019). As new information is acquired, our BBN can easily be updated to incorporate new knowledge (Smalling et al. 2019).

Our model gives insight into future directions for amphibian disease research and management. Our model results indicate ranavirus has a greater impact on wood frog persistence than Bd, but there is uncertainty about how the two pathogens may affect each other, especially if there is a low intensity of ranavirus and low Bd prevalence. There is also uncertainty regarding wood frog tolerance to elevated salinity levels. Tolerance seems to fluctuate across populations within the wood frog's range; however, the drivers of tolerance are unclear. Additional studies analyzing Bd presence in vernal pools with varying salinities throughout the Northeast may also provide additional insight into Bd disease risk patterns; however, because high salinity is associated with higher ranavirus mortality in wood frogs, using salinity as a disease management action may not be advisable (Hall et al. 2020). Future areas of research that would be most impactful to amphibian disease management may include tested field methods to manipulate vernal pool temperatures, further investigate environmental drivers of ranavirus, and testing the effect of deicing salts on Bd prevalence and growth.

2.5 Figures

Figure 2.1: Results from a literature review investigating factors affecting ranavirus, Batrachochytrium dendrobatidis, and wood frogs.

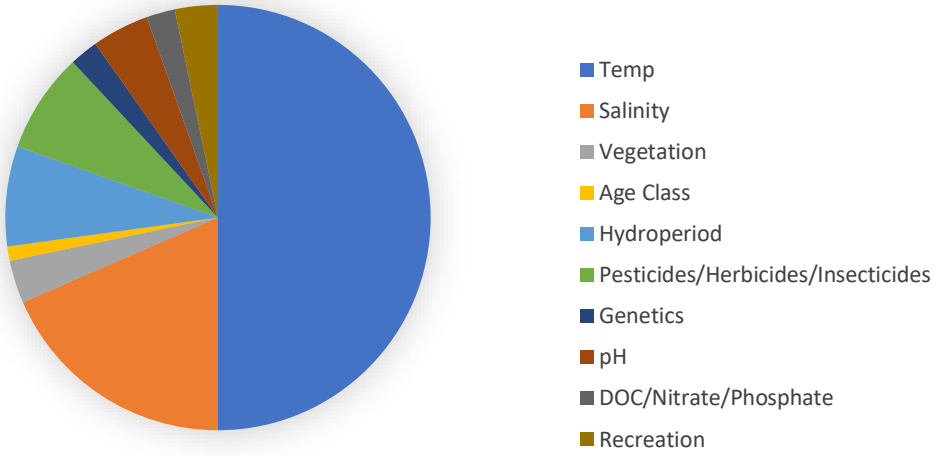


Figure 2.2: Conceptual diagram including each interaction between ranavirus, Batrachochytrium dendrobatidis, and environmental factors determined to be influential during our literature review.

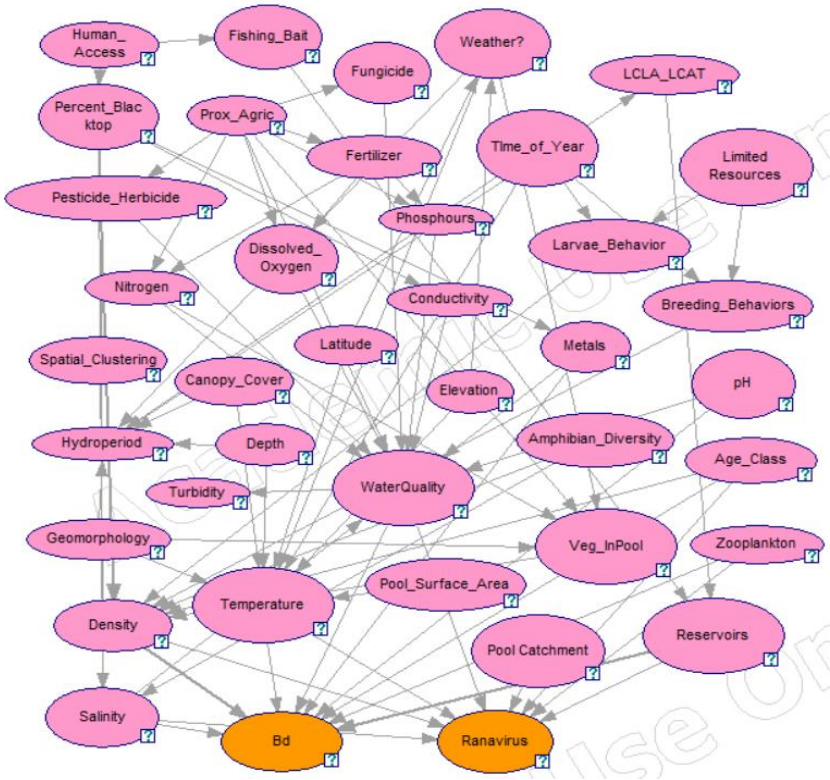


Figure 2.3: Beta-level BBN, a revised conceptual diagram containing most influential environmental variables from the literature, as well as an interaction variable. These environmental variables can be measured quantitatively and manipulated by management action.

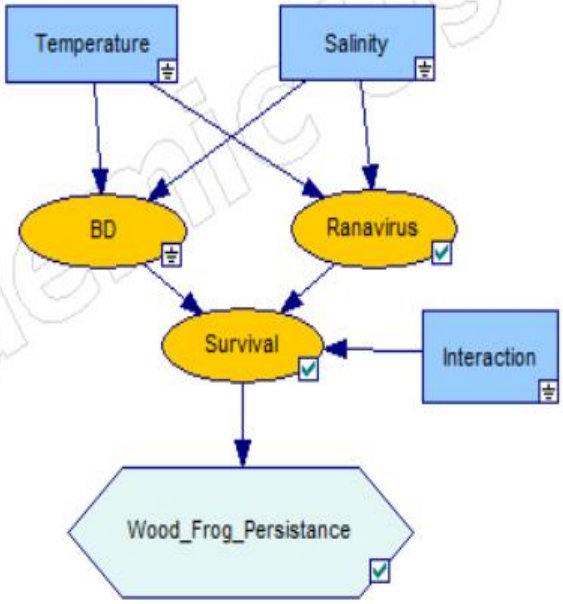


Figure 2.4: Finalized Bayesian Belief network containing variables from Beta-level BBN. Conditional probability tables are associated with yellow chance nodes and light blue utility node. Dark blue nodes represent decision nodes that can be manipulated by decision-makers. The model is currently set at low temperature and low salinity, producing the highest utility value.

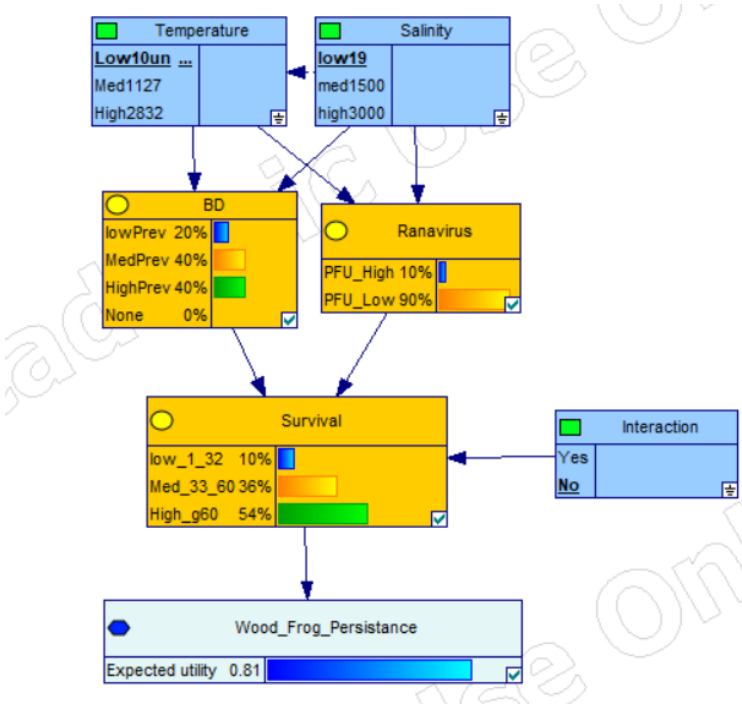


Figure 2.5: A) Utility values produced at low, medium, high temperature and low, medium, high salinity; an interaction between pathogens is not considered. B) Utility values produced at low, medium, high temperature and low, medium, high salinity; an antagonistic interaction between pathogens is considered. C) Probability of high ranavirus intensity under different salinity and temperature scenarios. D) Probability of high Bd prevalence under different salinity and temperature scenarios.

A. Expected Utility w/ No Interaction

Temperature \ Salinity	low	med	high
low	0.81	0.48	0.49
med	0.41	0.47	0.10
high	0.10	0.10	0.10

B. Expected Utility w/ Interaction

Temperature \ Salinity	low	med	high
low	0.74	0.38	0.44
med	0.41	0.39	0.09
high	0.10	0.10	0.10

C. Ranavirus - Pr(High Intensity)

Temperature \ Salinity	low	med	high
low	0.1	0.5	0.5
med	0.5	0.5	0.9
high	0.9	0.9	0.9

D. Bd - Pr(High Prevalence)

Temperature \ Salinity	low	med	high
low	0	0	0
med	1	0.2	0
high	0	0	0

Table 2.1: We broke survival into three groups, low (0-32%), medium (33-60%), and high (>60%). To account for uncertainty surrounding survival, we created brackets and associated probabilities for survival based upon estimated numbers of individuals surviving Bd and ranavirus.

	Survival Probability		
Number Surviving (x)	**Low**	**Medium**	**High**
x < 10	1.00	0.00	0.00
10 < x < 20	1.00	0.00	0.00
20 < x < 32	0.75	0.25	0.00
32 < x < 40	0.25	0.75	0.00
40 < x < 50	0.00	1.00	0.00
50 < x < 60	0.00	0.75	0.25
60 < x < 70	0.00	0.25	0.75
x > 70	0.00	0.00	1.00

Table 2.2: Overview of each node in Bayesian Belief network. Possibly values for each node, justifications, and citations are listed.

	Parameter Value	Justification	Citation
Salinity	Low (18.6 μScm^{-1})	Representative of natural vernal pool salinity in northeastern United States.	Karraker et al. 2008
	Medium (1,500 μScm^{-1})	Uncertainty surrounding impacts on wood frogs, estimated to decrease Bd growth.	Sanzo and Hecnar 2006; Karraker et al. 2008; Petranka and Doyle 2010; Clemmer et al. 2011
	High (3,000 μScm^{-1})	Edge of wood frog's tolerance to salinity, estimated to drastically decrease Bd growth.	Karraker et al. 2008; Petranka and Doyle 2010
Temperature	Low (<10^{o}C)	Ranavirus not as lethal to wood frogs at low temperatures; Bd growth may slow at low temperatures, but is still infectious.	Brand 2016; Piotrowski et al. 2004
	Medium (11-27^{o}C)	Optimal temperature range for Bd growth.	Piotrowski et al. 2004; Johnson et al. 2003; Kriger and Hero 2008
	High (28-32^{o}C)	Optimal temperature range for ranavirus replication.	Echaubard et al. 2014; Brand et al. 2016; Hall et al. 2018
Bd Prevalence	None	If temperatures are high, and salinity is high, Bd growth may completely stop.	Piotrowski et al. 2004; Johnson et al. 2003; Kriger and Hero 2008; Stockwell et al. 2012; Stockwell et al. 2015; Clulow et al. 2018
	Low	High temperature and/or high salinity will slow Bd growth and its' ability to infect individuals.	
	Medium	Bd tolerant to low temperatures, and possibly medium salinity levels.	
	High	Ideal growth for Bd is low salinity, and medium temperatures.	
Ranavirus Intensity	Low	Intensity is low at low temperatures. Salinity does not affect ranavirus, but compromises wood frog's ability to withstand ranavirus infection.	Brand et al. 2016; Hall 2020
	High	Salinity is high and temperatures are high.	Echaubard et al. 2014; Brand et al. 2016; Hall et al. 2018; Hall 2020
Interaction	Yes/No	Uncertainty surrounding knowledge of interactions between ranavirus and Bd. We include this here to determine if a synergistic interaction between pathogens affects wood frog survival.	
Survival	Low	Less than 33% of the larvae survive into metamorphosis.	
	Medium	Between 33-60% of larvae survive into metamorphosis.	
	High	Over 60% of the larvae survive into metamorphosis; ranavirus intensity must be low and Bd prevalence must be none or low.	

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