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AMPHIBIAN AND REPTILE CONSERVATION IN THE LAKE CHAMPLAIN
BASIN: HUMAN IMPACT, MITIGATION STRATEGIES, AND ECOLOGICAL
INSIGHTS

A Dissertation Presented

by

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ABSTRACT

This dissertation delves into the multifaceted realm of wildlife conservation, with a specific focus on the amphibian and reptile populations inhabiting the Lake Champlain (Abenaki place name Bitawbagok) Basin. Comprising four interconnected chapters, I examine the impact of human activities, the efficacy of mitigation strategies and the importance of systematic monitoring in the pursuit of preserving biodiversity in a changing environment.

Chapter 1 investigates the unintended consequences of human infrastructure, particularly roads on biodiversity and wildlife mortality. Roads, pervasive in the northeastern United States, induce habitat fragmentation, which alters wildlife behavior and causes road mortality. This study, conducted in Monkton, Vermont, evaluates the effectiveness of wildlife underpasses in mitigating amphibian road mortality, offering valuable insights for resource managers facing the challenges of infrastructure development.

Chapters 2 and 3 address the ramifications of globalization, specifically the proliferation of aquatic invasive species (AIS) in the Lake Champlain Basin. Chapter 2 consists of a comprehensive and systematic literature review of the unintended consequences of AIS management and highlights the data gaps that very few studies explore the negative impacts of mechanical AIS management and even fewer explore the negative effects of AIS management on reptile populations. Chapter 3 attempts to fill these data gaps by evaluating the impacts of AIS mechanical harvesters on turtle populations within the Lake Champlain Basin. By quantifying the impact of mechanical harvesting on turtle populations, this research aims to inform targeted and effective aquatic nuisance control permit conditions, contributing Vermont-specific insights with potential broader applications in managing invasive species globally.

Chapter 4 shifts the focus to the global threats of habitat degradation and loss, with a focus on gray treefrogs. This study employs PVC pipes, a passive trapping methodology, to understand habitat associations of gray treefrogs outside of their breeding season. This research not only contributes to filling knowledge gaps in gray treefrog natural history, but also provides a potential tool for long-term monitoring, which is crucial for informed land conservation strategies.

Collectively, these chapters explain the interconnectedness of wildlife conservation, human activities, and ecosystem management. They emphasize the crucial need for evidence-based strategies, systematic monitoring, and proactive conservation measures to protect the delicate balance of herptile populations in the face of human induced environmental challenges. This dissertation contributes to the growing body of knowledge essential for the sustainable management and preservation of biodiversity in ecologically sensitive regions like the Lake Champlain Basin.

CITATIONS

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DEDICATION

This dissertation is dedicated to my wife and daughter, whose love and support have been my guiding light. To my two loyal companions, Aurora and Masie, who bring joy to my days. And to the wildlife of the world, whose intrinsic right to exist inspires this work and my enduring passion for ecology.

Beauty and wonder.
Harmony and perfection.
Nature calls to me.

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Indigenous Land Acknowledgement

The University of Vermont is located on the historic and current land of the Abenaki (Alnôbak) people. The Abenaki have been the stewards of Vermont (N'dakinna) forever, yet they have been the subject of both genocidal and ethnocidal attacks by Vermont's earliest European settlers and their descendants. In the recent past, the University of Vermont and the Government of Vermont had caused unspeakable harm to the Abenaki community. The University played a major role in the attempted eradication of the Abenaki people via the Eugenics Movement. Therefore, the University of Vermont and the State of Vermont should do everything in their power to attempt to dampen the pain that they have caused. The University should provide free tuition to Abenaki students and acknowledge the harm that it has caused. In this dissertation I intend on honoring the Abenaki by using their place names, where possible, and by not forgetting the atrocities that have been committed against them.

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INTRODUCTION

Amphibians and reptiles, collectively known as herptiles, are vital to maintaining ecological balance, yet their populations face significant threats worldwide, especially in sensitive ecosystems like the Lake Champlain Basin. Compared to other vertebrates, a disproportionately high number of reptile and amphibian species are threatened or at risk of extinction (Cox et al. 2022). These species provide essential ecosystem services, such as pest control, and have contributed to advancements in pharmaceutical development. Beyond their ecological and medical importance, herptiles hold cultural, religious, and mythological significance across diverse human societies (Valencia-Aguilar et al. 2013; Hocking and Babbitt 2014). Their preservation is crucial not only for ecosystem health but also for their intrinsic and societal value.

Despite decades of conservation research, significant gaps remain in understanding the unintended impacts of human activities on biodiversity and herptile populations (Grubisic et al. 2019; Mehring et al. 2020). Habitat fragmentation, biological invasions, and data deficiencies in species ecology are particularly pressing concerns for amphibians and reptiles, yet key knowledge gaps persist in evaluating their ecological consequences (IPBES 2023). Roads contribute to habitat fragmentation and wildlife mortality, but the effectiveness of mitigation strategies is not well understood (Fahrig and Rytwinski 2009; de Lima Filho et al. 2021). Similarly, management of aquatic invasive species (AIS) may unintentionally harm native wildlife, though little research has been done to quantify these effects (De Jonge et al. 2012; Morón-López 2021). Finally, conservation efforts often focus on amphibians during breeding seasons, limiting our understanding of their ecology and habitat needs throughout the year (Raithel 2019).

Addressing these challenges is critical for improving conservation outcomes and mitigating human-induced threats to herptile populations.

Roads are a significant driver of habitat fragmentation and wildlife mortality, particularly for amphibians, whose seasonal migrations make them extremely vulnerable to vehicle induced mortality (Guilherme et al. 2007; Dutta 2018). Networks of roads have expanded globally, increasing mortality rates and population isolation, which in turn disrupts genetic connectivity and long-term species viability (Schwartz et al. 2020; Pokorny et al. 2022). Various mitigation techniques, such as road underpasses and fencing, have been implemented to reduce these impacts, but their effectiveness remains poorly quantified. While some studies suggest that road crossing structures benefit amphibian populations, there is a notable lack of before-and-after mortality comparisons that would provide robust evidence for their efficacy (Glista et al. 2008; Gagnon et al. 2011). Without such data, it is difficult to determine whether current mitigation efforts are sufficient or if additional measures are needed to ensure population persistence.

Invasive species are a leading cause of biodiversity loss and ecosystem disruption, prompting widespread management efforts to mitigate their impact (Linders et al. 2019). In aquatic systems, control methods such as mechanical harvesting, chemical treatments, and biological introductions are commonly used to reduce the ecological impacts of AIS populations (Simberloff 2011; Phelps et al. 2017; Codd-Downey et al. 2021). However, these management techniques can have unintended ecological consequences, potentially affecting non-target organisms, altering habitat structure, and disrupting food webs (Simberloff 2011; Phelps et al. 2017; Codd-Downey et al. 2021). Despite the widespread implementation of AIS management strategies, research on their broader ecological

impacts remains limited. In particular, little is known about how mechanical removal methods influence wildlife populations, including rates of bycatch and unintended mortalities. Addressing this knowledge gap is crucial for developing management strategies that minimize harm to native species while effectively controlling invasive species.

Research on amphibian populations has largely focused on their breeding seasons, as individual amphibians are more detectable when they congregate at aquatic sites for reproduction (Raithel 2019). However, this seasonal bias limits our understanding of their ecology for the majority of the year, particularly in terrestrial environments where many species spend significant portions of their life cycle (Johnson et al. 2007). Outside of the breeding season, amphibians disperse across landscapes and use microhabitats that tend to be poorly documented due to logistical challenges in detection. This lack of data on non-breeding habitat use and survival rates hinders conservation planning, particularly in the context of habitat protection and land management (Santos et al. 2020).

This dissertation addresses these gaps through four interconnected studies, each tackling a unique conservation challenge linked to a global herptile threat, but with local context in the Lake Champlain Basin. Chapter 1 focuses on the effectiveness of wildlife underpasses at reducing amphibian mortality during their spring breeding migration. Chapter 2 identifies data gaps surrounding the unintended ecological consequences of AIS management by systematically searching through the available literature. Chapter 3 builds on Chapter 2 by examining the impact of mechanical harvesting of AIS on wildlife populations, with a particular focus on bycatch rates in the Lake Champlain Basin. Lastly, Chapter 4 investigates habitat associations and monitoring methods for a cryptic

amphibian species, emphasizing the importance of adopting a holistic approach to the conservation of common species. Together, these studies underscore the interconnectedness of human activities, wildlife conservation strategies, and broader ecosystem health.

To address these challenges, this dissertation integrates field studies, a systematic review, and data-driven analyses. A before-after control-impact design is used to evaluate mitigation strategies and provide robust evidence for their effectiveness. A comprehensive literature review identified critical gaps in AIS management, while multi-taxa surveys quantify bycatch impacts during AIS mitigation. Lastly, passive monitoring techniques are also employed to inform long-term habitat studies for a cryptic amphibian, offering practical approaches for future research.

By addressing these critical conservation challenges, this dissertation provides actionable insights to support herptile conservation in the Lake Champlain Basin and beyond. Its findings offer practical guidance for policymakers, resource managers, and conservationists in shaping sustainable practices and policies. Furthermore, the methodologies employed in this research serve as a template for biodiversity conservation studies in similar ecosystems worldwide. Ultimately, this work underscores the importance of integrating science-based strategies into management decisions to safeguard amphibian and reptile populations for future generations.

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CHAPTER 1: ASSESSING THE EFFICACY OF WILDLIFE UNDERPASSES IN MITIGATING AMPHIBIAN ROAD MORTALITY: A CASE STUDY FROM THE NORTHEASTERN UNITED STATES

Abstract

Roads pose significant threats to wildlife populations worldwide, leading to habitat fragmentation and high mortality rates among various species. Mitigation strategies such as wildlife underpasses have been implemented to alleviate these impacts, yet few studies have assessed their effectiveness before and after implementation. We conducted a case study in the northeastern United States to evaluate the efficacy of a wildlife underpass complex in mitigating amphibian road mortality. The study area encompassed a 1.3 km stretch of road, where two underpasses were constructed to facilitate amphibian passage. Through a comprehensive survey spanning five years pre-construction and seven years post-construction, we collected data on amphibian mortality and environmental factors. Linear-mixed effects models were used to assess changes in mortality rates before and after underpass construction using a before-after control-impact design. Our findings indicate a substantial reduction in mortality across the entire amphibian community and for non-arboreal amphibians within the treatment areas post-construction. While arboreal amphibian mortality decreased, the difference was not statistically significant. The underpasses effectively facilitated amphibian movement. Overall, our study provides empirical evidence of the effectiveness of wildlife underpasses in reducing amphibian road mortality, highlighting them as a potentially important conservation action. These findings underscore the significance of incorporating underpass structures into transportation planning and infrastructure development to mitigate negative impacts on

wildlife populations. Moreover, our study contributes valuable insights for future research and informs policy initiatives aimed at enhancing habitat connectivity and safeguarding vulnerable amphibian populations in environments bisected by roadways.

Key Words – underpass, wildlife crossing, road mortality, mitigation, migration, amphibian, conservation

Introduction

Human infrastructure tends to have unintended negative consequences on the natural world (Sun and Narins, 2005; Egea-Serrano et al., 2012; Woinarski et al., 2020; Niebuhr et al., 2022). The creation of human infrastructure, such as roads, often leads to habitat fragmentation, degradation, and destruction; which are the primary causes of biodiversity loss globally (Andrén, 1994; Wilson et al., 2016; Crooks et al., 2017; de Lima Filho et al., 2021). As human populations continue to grow, more and more infrastructure will be built (McDonald et al., 2020). Human development and infrastructure may cause unintended negative impacts on many wildlife taxa (Andrén, 1994; Moore et al., 2023).

Roads can have detrimental impacts on wildlife species in multiple ways (Lodé, 2000; Lester, 2015). Roads may cause reduced genetic exchange between populations, change wildlife behavior, and can lead to local extirpations of wildlife populations (Riley et al., 2014; Schwartz et al., 2020; Driessen, 2021; Pokorny et al. 2022). Very few species are immune to the effects of roads. For example, large and mobile species, such as ungulates, are killed in large numbers by vehicular collisions, even at low traffic densities (Riley et al., 2014; Poulin et al., 2023). As human populations continue to grow, more vehicles will be used on roadways. Therefore, the negative impacts of roads on wildlife are likely to increase without implementing mitigation strategies (Riley et al., 2014; Lester, 2015; Schwartz et al., 2020; Pokorny et al. 2022).

Many mitigation techniques have been implemented successfully across the globe to reduce wildlife road mortality. These techniques include drift fences, making bridges and culverts passable by wildlife, tunnels, overpasses, fencing, underpasses, and many

more (Glista et al., 2009). All of these techniques provide opportunities for wildlife to safely cross roads (Bager and Fontoura, 2013; Bellis et al., 2013; Lester, 2015). Large wildlife underpass and overpass complexes, used in tandem with fencing, have been successful in reducing road mortality of large mammals in North America (Sawaya et al., 2014; Sawyer et al., 2016; Simpson et al., 2016). Unfortunately, these techniques are harder to implement in the northeastern United States, where increased human densities and associated infrastructure (e.g., driveways) make it difficult for transportation agencies to install large overpass and underpass structures, especially in tandem with fencing.

Despite record funding for wildlife crossings (Infrastructure Investment & Jobs, 2021), large crossing structures are expensive, ranging from \$500,000 to \$2.7 million for underpasses and \$2.7 million to \$6.2 million for overpasses in the United States; making them challenging for state and local governments to implement (Sugiarto, 2022). However, wildlife crossing structures designed for small wildlife, like amphibians, can be quite small and are relatively easy to install, especially when repairing roads (Fairbank, 2014; Huijser et al., 2016; Seiler et al., 2016). Wildlife underpasses are one of the most implemented infrastructural mitigation techniques used to prevent wildlife mortality on roads (Pimm et al., 2021). Despite this, very few studies have compared wildlife mortality levels before and after the installation of underpasses (Glista et al., 2008; Gagnon et al., 2011). Therefore, there is great importance in evaluating whether wildlife underpasses are an effective means of mitigating road mortality, especially considering the high cost of building them.

Amphibians are the most vulnerable group of vertebrates, with approximately 40.7 % of amphibian species being susceptible to extinction (Wren et al., 2015; Churko et

al., 2020; Luedtke et al., 2023). Roads negatively impact multiple life stages of amphibians (i.e., waterbody salinification via road salt, traffic noise impacting frog mating calls, etc.) (Taylor and Goldingay, 2010; Coelho et al., 2012; Beebee, 2013; Kioko et al., 2015). Temperate amphibians generally have two distinct life stages: an aquatic egg/larval stage and a terrestrial (or semi-terrestrial) adult stage (Gibbs and Shriver, 2005). Therefore, most amphibians require a habitat matrix that includes both wetlands and upland habitats to persist (Bradford, 1983; Lamoureux and Madison, 1999; Joly et al., 2003). The loss and fragmentation of these critical habitats is the most immediate threat to amphibians in the northeastern United States and across the globe (Gibbs, 1998; Cushman, 2006; Guilherme et al., 2007; Gu et al., 2011; Dutta, 2018).

Throughout the northeastern United States, many wetlands are separated from upland habitats due to roads. Fragmentation due to roads can lead to extreme mortality events when amphibians cross roads to breed and return to the uplands on rainy nights in the spring, summer and fall (Mazerolle, 2004; Sterrett et al., 2018). This mortality can be severe enough to cause local extirpations (Gibbs and Shriver, 2005). Conservationists have attempted to reduce road-induced mortality by building amphibian/wildlife underpasses on roads that intersect important habitats for amphibians (Schmidt and Zumbach, 2008; Woltz et al., 2008; Pomezanski, 2018). Very few studies have investigated amphibian mortality before and after the installation of underpasses (Fahrig and Rytwinski, 2009). However, there is some evidence that they are effective at reducing mortality (Jackson, 2000).

In this study, we used linear mixed effects models to analyze amphibian mortality data collected prior to and after the installation of a wildlife underpass complex in

Monkton, Vermont. The objectives of this study were 1) to determine if there was a significant decrease in amphibian mortality in the treatment areas after the construction of the underpasses; 2) to understand whether underpasses are equally effective for all amphibian species; and 3) to determine whether the underpass wing walls in so-called “buffer” areas impacted mortality more like treatment or control areas. We hypothesized that the total amphibian mortality would be significantly less than in control areas after underpass construction, and that reductions in mortality would be most pronounced for non-arboreal species, because arboreal species may climb over the structure. We also hypothesized that buffer areas would act more like control areas than treatment areas. Our research provides resource managers with valuable information about the effectiveness of underpasses for amphibians, which is essential given the concerning impacts of road-induced wildlife mortality and the high cost of these structures.

Methods

Background

In 1997, biologists in Vermont (Abenaki place name, N’dakinna) identified a segment of Monkton Road in the town of Monkton, as one of the State’s most important and vulnerable amphibian crossings. During just two nights in the spring of 2006, more than 1,000 amphibians were estimated to have been killed by automobiles (unpublished data). This prompted the Monkton Conservation Commission and partners to apply for grants, which allowed them to design and construct the underpasses on Monkton Road. The structures were built in 2015 and cost \$342,397. Data were collected for five years prior to construction (from 2011-15) and for seven years post construction (2016–22).

Study Area

The underpasses are located on a 1.3 km stretch of Monkton Road that runs north to south. There is a wetland to the west of the underpasses and upland habitat to the east of the underpasses. The underpass complex is composed of two separate underpass structures about 0.5 km apart, with wing walls on both the upland and wetland sides of the road that are intended to funnel amphibians to the tunnel openings (Figure 1-1). The underpass structures are made of solid concrete. The northern crossing site covers 220.7 linear meters of the road, and the southern crossing site covers 243.3 linear meters of the road. These measurements encompass the entire crossing sites, including the treatment areas (where underpasses and walls were installed), and buffer areas. Each of the eight wing walls end with hard plastic oriented in semi-circles designed to turn amphibians back toward the underpass tunnels. When the underpass structures were installed, issues with rock ledge resulted in some design changes to the wing walls that were intended to guide amphibians to the tunnel openings, making the wing walls on the wetland and upland side unmatched in length and less angled than initially planned. The underpass tunnels form an upside down “U” shape and were partially buried in the substrate. The northern tunnel is ~ 1.5 m tall, while the southern tunnel is ~ 0.9 m tall. Both tunnels are ~ 1.5 m wide and the wing walls are ~ 1 m high.

For the purposes of our study, the crossing site was divided into two crossing areas (north and south), each with controls, treatments, and buffers (located at both ends of the treatment areas) (Figures 1-1 and 1-2). The control areas were referred to as the northern control area (NC) and the southern control area (SC) and were separated from the treatment areas by more than 50 m to maintain independence and avoid potential in

direct effects from the structures. While small control areas (e.g., 50 m or 100 m) could theoretically be used, our approach ensured that the full crossing zone was adequately represented. The treatment areas were referred to as the northern treatment area (NTR) and the southern treatment area (STR). Treatment areas included both the walls and tunnels of the underpass structures. The buffer areas were referred to as the southern buffer 1 (SB1), the southern buffer 2 (SB2), the northern buffer 1 (NB1), and the northern buffer 2 (NB2). NB1 and SB1 were located on the northern side of their respective treatment areas, while NB2 and SB2 were located on the southern side of their respective treatment areas. The purpose of the buffer areas is described in detail below. In total, the walls and tunnels (the structures in the “treatment” and “buffer” areas) account for 18.5% of the total crossing area (Figure 1-1).

The buffers were created to account for the possibility that some animals would turn away from the tunnel openings when encountering the wing walls rather than turning toward the openings and eventually through the underpass tunnels – especially considering that the wing walls angled only slightly and were largely parallel to the road due in part to the design change. Furthermore, the land’s topography may have allowed amphibians to enter the buffer areas from the sides opposite the treatment areas. The buffer areas included both walled and unwalled sections to assess whether amphibians were bypassing the walls in significant numbers. The key distinction between treatment and buffer areas is that treatment areas contain both underpasses and wing walls, whereas buffer areas include only the terminal ends of treatment walls that extend beyond the core treatment zone. Evaluating buffers separately helps determine whether the wing walls effectively extended the functional size of the treatment area. Additionally, If amphibian

mortality is lower in the treatment areas than in the controls, and not higher in the buffer areas than in the controls, we can conclude that the underpass complex was successful.

The habitat to the west of the underpasses is characterized by a marsh with emergent vegetation that drains into a tributary of Little Otter Creek, VT. The habitat to the east of the underpasses is characterized by upland northern hardwood forest that is primarily composed of maple (*Acer* spp.), American beech (*Fagus grandifolia*), birch (*Betula* spp.), and rocky ledges. Monkton Road is a relatively busy, paved two-lane road, with a speed limit of 64 km per hour.

Study Species

We anticipated encountering mole salamanders (*Ambystoma* spp.), eastern newts (*Notophthalmus viridescens*), wood frogs (*Lithobates sylvaticus*), green frogs (*Lithobates clamitans*), pickerel frogs (*Lithobates palustris*), American toads (*Anaxyrus americanus*), gray treefrogs (*Hyla versicolor*) and spring peepers (*Pseudacris crucifer*) based on their known distribution, habitat preferences, and breeding ecology. These species are commonly found in temperate forested landscapes with seasonal wetlands and ponds, similar to our study area (Gibbs 1998). Among these species, spring peepers and gray treefrogs are arboreal and were expected to be able to climb over the underpass structures, thus bypassing their benefit. Animals were handled in accordance with the approved guidelines of the Institutional Animal Care and Use Committee at the University of Vermont.

Survey Methods

The Monkton Road amphibian crossing area was monitored for five years prior to the construction of the underpasses (2011–2015) and seven years after the construction of the underpasses (2016–2022). Surveys were completed in the same manner prior to and after the construction of the Monkton Road underpasses. The monitoring primarily occurred between 20:30 and 22:30 when nighttime, rain, road traffic, and amphibian movement occurred in conjunction. Four to five surveys were conducted each year between late March and early May on nights that it rained, and where temperatures were above 1.67 °C. During the surveys, between one and eight people were involved with data collection. The crossing areas were divided into the eight transects described above (Figure 1-2). Surveyors collected data by walking along the road surface, completing a single pass through each transect from south to north, using the same methodology for each survey. Data collected during each transect included the date, how many minutes were spent completing the surveys, how many cars went by during the surveys, what species were encountered, and whether encountered individuals were dead or alive. We also acquired the minimum and maximum temperature for the survey day, and the total amount of precipitation (rain or snow) that occurred on the survey day from the National Oceanic Atmospheric Administration (NOAA) (Table 1-1).

Statistical Analysis

We transformed the amphibian mortality count data to the number of amphibians killed per meter of road in each transect type, due to the differences in linear sizes among transects. We hypothesized that there may have been a difference in mortality between arboreal and non-arboreal amphibians because arboreal amphibians could climb over the underpass structure rather than pass through it. Therefore, we conducted all analyses on

three subsets of data: total amphibian mortality per meter of road; non-arboreal amphibian (all species except spring peepers and gray treefrogs) mortality per meter of road; and arboreal amphibian (only spring peepers and gray treefrogs) mortality per meter of road. We predicted stronger differences between treatment and control areas for all amphibian and non-arboreal amphibian analyses.

We used the lme4 package in R to perform repeated-measures linear mixed-effects modeling with a Gaussian response variable (Bates et al., 2015; R Core Team, 2021). We were primarily interested in evaluating an interaction between transect type (i.e., control, treatment, or buffer) and period (interaction between pre- and post-construction and transect type), based on our before-after control-impact (BACI) design. However, we also explored covariates including minimum temperature, maximum temperature, and precipitation as fixed effects and day of year (DOY) and year as random effects. DOY and year were treated as random effects to account for the variability in amphibian migration intensity that was associated with each specific day and each specific year that we collected data. We scaled the minimum temperature, maximum temperature, and precipitation covariates. We pooled transect types across the northern and southern crossing areas (i.e., treatment = NTR + STR, control = NC + SC, etc.) during the modeling process. We hypothesized that the treatments would reduce mortality rates, while temperature and precipitation would have a positive relationship with mortality. In other words, we expected that both higher maximum and minimum temperatures, as well as increased precipitation, would correspond to increased mortality rates. We also hypothesized that there would not be an increase in mortality in the buffers after the construction of the underpass complex.

Model Selection

We fit 40 models for all combinations of our covariates for each of the three subsets of data (all amphibians, arboreal amphibians only, non-arboreal amphibians only). We included single random effects and additive and interactive fixed effects of up to six covariates for each model (Table 1-A1). We calculated the Akaike Information Criterion Corrected (AICc) for each model, which is a measure that balances goodness-of-fit and model complexity. Lower AICc values indicate more parsimonious models (Burnham and Anderson 2004). We compared AICc values by calculating the difference in AICc values (ΔAICc) and assessing AICc weights. A difference of two or more in AICc suggests substantial evidence in favor of the model with the lower AICc value (Akaike, 1974). We applied the Bonferroni correction to lower the family-wise error rate and avoid false significant results.

Results

Species Encountered

During the course of the study, 5,273 amphibians were encountered; 3,053 anurans, 2,110 salamanders, and 110 which could not be identified due to damage suffered during the mortality event. In total, 62.9% of all encountered amphibians were dead (69.4% of encountered frogs and 51.6% of encountered salamanders) (Figure 1-3 and Table 1-2). The highest mortality recorded on a single survey night was 167 amphibians across the 464 m of transects. Surveys were conducted on rainy nights; however, we never experienced rainfall heavy enough to wash away carcasses, so weather conditions did not contribute to data loss. There was an 80.2% decrease in total

amphibian mortality, a 94.3% decrease in non-arboreal amphibian mortality, and a 73.6% decrease in arboreal amphibian mortality in the treatment areas during the post-construction period.

We encountered 12 amphibian species during our surveys. These species included: spotted salamanders (*Ambystoma maculatum*), blue spotted salamander complex (*Ambystoma laterale x jeffersonianum*), eastern newts, four-toed salamanders (*Hemidactylium scutatum*), northern two-lined salamanders (*Eurycea bislineata*), wood frogs, spring peepers, northern leopard frogs (*Lithobates pipiens*), pickerel frogs, American toads, green frogs, and gray treefrogs (Table 1-2). Blue spotted salamander complex and four-toed salamanders are classified as uncommon and rare, respectively, in Vermont. We classified spring peepers and gray treefrogs as arboreal amphibians, while the other 10 species were classified as non-arboreal amphibians.

Mixed-effects Modeling

Our best total amphibian mortality model received 39% of the model weight and included the interaction between transect type and period, and maximum temperature as fixed effects; and DOY as a random effect (Table 1-3). This model suggests that there was no difference in total amphibian mortality between transect types during the pre-construction period, and that there was no difference in pre- and post-construction mortality for the control and buffer areas. Although amphibian mortality nearly increased significantly across the entire crossing area during the post-construction period ($p = 0.057$), this increase was primarily driven by higher mortality in the control areas. Meanwhile, total amphibian mortality significantly decreased in the treatment areas during the post-construction period (Table 1-4). The results of our Bonferroni correction

also support that there was a significant decrease in total amphibian mortality in treatment areas between periods (Figure 1-4). The second-best supported model received 32% of the model weight and was identical to the top model except that it included minimum temperature instead of maximum temperature. All top 4 models included a transect by period interaction, supporting the idea that the amount of mortality per transect varied by period.

Our best non-arboreal amphibian mortality model received 49% of the model weight and included the interaction between transect type and period, precipitation, and maximum temperature as fixed effects, and DOY as a random effect (Table 1-3). This model suggests that there was no difference in non-arboreal amphibian mortality between transect types during the pre-construction period, and that there was no difference in mortality in the control and buffer areas in the post-construction period. However, there was a significant decrease in non-arboreal amphibian mortality in the treatment areas from the pre-construction to the post-construction period (Table 1-4). The results of our Bonferroni correction further support that there was a significant decrease in total amphibian mortality in treatment areas between periods (Figure 1-4). The second-best supported model received 22% of the model weight and was identical to the top model except that it included minimum temperature instead of maximum temperature. All top 5 models included a transect by period interaction, supporting the idea that the amount of mortality per transect for non-arboreal amphibians varied by period.

Our best arboreal amphibian mortality model received 48% of the model weight and included transect type, precipitation, and maximum temperature as fixed effects, and year as a random effect (Table 1-3). This model suggests that there was not a statistically

significant reduction in arboreal amphibian mortality between the two study periods (Table 1-4). The results of our Bonferroni correction also supports that transect type did not significantly reduce arboreal amphibian mortality (Figure 1-4). However, the reduction in mortality was almost significant (p-value = 0.056, CI = 7.45 – 0.09), meaning that treatment areas almost differed from control areas significantly due to a large proportion of arboreal amphibians using the underpasses. The second-best supported model received 22% of the model weight, but did not include transect type. However, 3 of the top 4 models included transect type, supporting the idea that the treatment areas are having somewhat of a negative effect on arboreal amphibian mortality (i.e., reducing mortality).

Discussion

Amphibian populations are extremely susceptible to extirpation due to roads intersecting their critical habitat (Fahrig et al., 1995). Biologists and concerned community members have attempted to reduce road induced mortality on amphibian populations by encouraging the construction of wildlife underpasses. However, despite being one of the most implemented mitigation techniques used, very few studies have used a BACI design to evaluate whether these structures are effective at reducing amphibian mortality (Pimm et al., 2021). The question of whether or not structures are the right choice depends on many factors – cost, species impacted, traffic mortality, etc., but should also include consideration of the potential for structure efficacy.

We found that the underpass structures significantly reduced the amount of amphibian mortality on the road, which suggests that amphibian underpasses are an effective mitigation strategy for combating road-related amphibian declines. We saw an

80.2% decrease in mortality in the treatment areas among all amphibians after the underpass structures were constructed, and a 94.3% decrease in mortality among non-arboreal amphibians. However, the underpass structures were not as effective at reducing mortality for arboreal amphibians, the majority of which in our study were spring peepers. Despite this, we still observed a 73.6% decrease in mortality among arboreal amphibians in the treatment areas after the construction of the underpass complex. Arboreal amphibian mortality may be further reduced by modifying the underpass structure design. Hughes et al. (2021) found that fences with aluminum flashing and a 10 cm horizontal lip at the top were effective at preventing Pacific treefrogs (*Hyla regilla*) from getting into agricultural fields. So, perhaps this methodology could be adapted for other crossing structures.

There was some concern that amphibians would work their way to the ends of the walls and onto the road surface, negating the positive impact of the treatment areas and leading to unintended consequences (Meshaka et al., 2007; Gilhooly et al., 2019). However, if this were the case, we would expect to see a significant increase in amphibian mortality in the buffer areas between the two time periods. Instead, we found that the lengths and angles of the walls in our study caused the buffer area to function similarly to a control. While the buffers did not appear to increase road mortality, they also did not extend the benefits of the treatment area. This implies that project managers should ensure that wing walls are angled away from the road, as much as is feasible given other constraints, to funnel amphibians towards tunnel openings in future construction projects focused on reducing amphibian mortality; especially if there are unexpected design changes during the construction phase of the project. Furthermore, project

managers should also ensure that wing walls are matched on both sides of the road to safeguard the passage of amphibians moving both to the breeding pools and to the uplands. Future wildlife underpass studies could look at the effectiveness of “amphibian turnarounds” and what modifications would prevent arboreal amphibians from getting over the underpass wing walls.

Another concern would be whether underpass structures are effective at reducing fall migration mortality, especially considering that many migrating amphibian populations are recruitment-driven (Sterrett et al., 2018). However, Pagnucco (2010) observed that long-toed salamander (*Ambystoma macrodactylum*) mortality was substantially reduced during their fall migration after installing fencing and a tunnel. Therefore, we suspect that underpass structures would be effective for fall migrants, but we only collected data in the spring so further research would need to be conducted to confirm or deny their effectiveness in the fall.

Very few studies have compared wildlife mortality before and after the implementation of wildlife structures (Jackson, 2000; Fahrig and Rytwinski, 2009; Fitzsimmons and Breisch, 2015). Despite this, most studies focus on the effectiveness of crossing structures after they are built. For example: Allaback and Laabs (2003) focused on how far salamanders will travel along a wall before they give up on crossing the road; while Mata (2004) focused on what kind of structures are most used by wildlife. Even though there are a multitude of empirical studies regarding the effectiveness of wildlife crossing structures after construction (Huijser et al., 2016; Simpson et al., 2016; Denneboom et al., 2021), resource managers could greatly benefit from more BACI

design projects focusing on comparing before and after mortality at wildlife crossing structures.

Our BACI study design (Smith et al., 1993) adds strength to the evidence we present that the underpass structures reduced amphibian mortality. Observations were made before and after the underpass construction and we had unimpacted control sites that we compared to impacted treatment sites. This should have accounted for any natural or preexisting differences between the transects, meaning that we should have been able to estimate the “true” effect that the treatments had on mortality (Smith et al., 1993). Based on the assumption of this type of experimental design, the trajectories of the control and treatment areas should have been exactly parallel in the absence of the intervention (Smith et al., 1993).

Crossing structures may also benefit many other wildlife taxa (Caldwell and Klip, 2019). At our study location, wildlife cameras from a different study observed many mammal species, including American black bear (*Ursus americanus*), bobcats (*Lynx rufus*), racoons (*Procyon lotor*), and North American porcupines (*Erethizon dorsatum*) using the underpass complex to safely cross the road. We also observed a few bird species and common gartersnakes (*Thamnophis sirtalis*) using the underpass structures. Additionally, the Lewis Creek Association counted 2,208 amphibians using one of the underpasses via wildlife cameras between March 10th – May 3rd, 2016 (unpublished data).

Because underpasses may attract a large density of amphibians and many species use underpasses, there may be a risk of increased predation (Mata et al., 2020). However, mortality from predations should be much less significant than the mortality caused by

impacts with vehicles (Edwards et al., 2022). Furthermore, there is still a high degree of mortality in nearby areas where there are no underpass structures. So, theoretically the predators would still scavenge on animals that have already been killed (Muszynska et al., 2022). Additionally, predation could be reduced by installing “anti-predation” devices inside of the underpass tunnels (Tissier et al., 2016). In our study area, the underpass complex had large slate slabs in each tunnel and along the wing walls to provide cover for amphibians.

In 2021 the U.S. Senate passed the Infrastructure Investment and Jobs Act that will provide \$350 million to municipalities, states, tribal governments, federal agencies, and nonprofit organizations to fund wildlife underpasses, as well as improving habitat connectivity (Bies, 2021). This study provides valuable information to resource managers and transportation agencies considering the construction of wildlife underpasses in important amphibian crossing areas.

Implications for Management and Design of Amphibian Underpasses

Design Considerations for Maximum Effectiveness

The effectiveness of amphibian underpasses is influenced by their design. The study results suggest that the angle and length of wing walls play a crucial role in guiding amphibians toward tunnel entrances. Walls that angle outward from the road rather than parallel may more effectively funnel individuals toward safe passage through the underpass structures. Additionally, ensuring symmetry in wing walls on both sides of the road is critical to facilitate movement in both directions.

Arboreal amphibians, such as spring peepers and gray treefrogs, showed a smaller but notable reduction in mortality compared to non-arboreal species. This suggests that some individuals bypassed the underpasses by climbing over the wing walls. To improve their effectiveness for arboreal species, modifications such as aluminum flashing with a horizontal lip at the top of the wingwalls, as suggested by Hughes et al. (2021), could be incorporated into future designs to prevent climbing and redirect individuals toward the underpass tunnel entrances.

A key concern in underpass implementation is whether amphibians bypass the tunnels and enter roadways at the end of wing walls, potentially increasing mortality in buffer areas. Our study found no significant increase in mortality in buffer zones, suggesting that amphibians were not disproportionately bypassing the walls. However, buffer zones did not extend the effectiveness of the treatment areas, suggesting that further research should examine whether additional modifications, such as extended wing walls or vegetation barriers, could improve the system's functionality.

Broader Applications for Conservation Planning

These findings provide valuable insights for conservation practitioners, transportation agencies, and policymakers seeking to mitigate amphibian road mortality. When planning new road infrastructure or retrofitting existing roads, incorporating amphibian underpasses should be prioritized. Given the substantial reduction in mortality, the investment in such structures is justified, particularly in areas with known high-density amphibian migrations. Furthermore, these structures will also benefit other taxa of wildlife.

With the passage of the Infrastructure Investment and Jobs Act (2021), significant funding has been allocated for wildlife crossings, providing an opportunity for municipalities, state agencies, and conservation organizations to implement amphibian-friendly infrastructure. The demonstrated effectiveness of underpasses in this study supports their inclusion in transportation planning and policy initiatives aimed at reducing road mortality and enhancing habitat connectivity. Future research should continue refining underpass designs to maximize their efficacy for a broader range of species and environmental conditions.

Conclusion

This study evaluated the efficacy of wildlife underpasses in mitigating amphibian road mortality along a 1.3 km stretch of Monkton Road in Vermont. The construction of underpasses led to an 80.2 % decrease in total amphibian mortality and 94.3 % decrease in non-arboreal amphibian mortality in treatment areas. Although the reduction in arboreal amphibian mortality was not statistically significant, a 73.6 % decrease was observed. The underpasses were effective for various amphibian species, including non-arboreal and arboreal species. However, modifications to the design could further reduce arboreal amphibian mortality. The buffer areas did not increase mortality, indicating that the wing walls effectively funneled amphibians towards the underpasses without causing unintended consequences.

These findings support the incorporation of wildlife underpasses into transportation planning and infrastructure development to enhance habitat connectivity and reduce wildlife mortality. The study provides empirical evidence that can inform policy initiatives aimed at protecting vulnerable amphibian populations. Overall, this

study highlights the importance of wildlife underpasses as a conservation strategy to mitigate the negative impacts of roads on wildlife populations and underscores the need for continued research and policy support to enhance their effectiveness.

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Tables

Table 1-1. Covariates used to predict amphibian mortality at the Monkton Road underpass complex in Monkton, Vermont.

Covariate	Code	Description	Data Source
Transect	Tran	Transect type (treatment, buffer, control).	Field data
Day of year	DOY	The day of year starting from January 1st (day 1) and ending on December 31st (day 365).	Field data
Year	Year	The year of the survey.	Field data
Period	Period	Interaction between period the survey took place (i.e., pre- or post-construction) and transect type.	Field data
Minimum Temperature	TempMn	The minimum temperature of the given survey measured in Celsius.	NOAA*
Maximum Temperature	TempMx	The maximum temperature of the given survey measured in Celsius.	NOAA*
Precipitation	Precip	The total amount of precipitation (rain or snow) of the given survey. Measured in centimeters.	NOAA*

Note: Transect, day of year, year, and period are categorical variables, while minimum temperature, maximum temperature, and precipitation are continuous variables.

Table 1-2. The total number (N) of amphibians encountered at the Monkton Road underpass complex in Monkton, Vermont between 2011-2022.

Species	N	% Dead
Caudata		
<i>Ambystoma laterale x jeffersonianum</i>	184	35.9%
<i>Ambystoma maculatum</i>	1,702	49.2%
<i>Eurycea bislineata</i>	3	33.0%
<i>Hemidactylium scutatum</i>	4	25.0%
<i>Notophthalmus viridescens</i>	217	84.3%
Anura		
<i>Anaxyrus americanus</i>	10	50.0%
<i>Hyla versicolor</i>	5	40.0%
<i>Lithobates clamitans</i>	13	69.2%
<i>Lithobates palustris</i>	7	28.6%
<i>Lithobates pipiens</i>	4	25.0%
<i>Lithobates sylvaticus</i>	469	72.3%
<i>Pseudacris crucifer</i>	2,545	69.2%

Table 1-3. Top 5 models for predicting the total, non-arboreal, and arboreal amphibian mortality at the Monkton Road underpass complex in Monkton, Vermont.

Fixed Effects	Random Effects	N Parameters	AICc	Δ AICc	Weight
Total Mortality					
Tran + MaxTemp + Tran * Period	DOY	9	3454.90	0	0.39
Tran + MinTemp + Tran * Period	DOY	9	3455.29	0.39	0.32
Tran + Precip + MaxTemp + Tran * Period	DOY	10	3456.96	2.07	0.14
Tran + Precip + MinTemp + Tran * Period	DOY	10	3457.35	2.45	0.11
Tran + MaxTemp	DOY	6	3462.15	7.25	0.01
Non-arboreal Mortality					
Tran + Precip + MaxTemp + Tran * Period	DOY	10	2915.41	0	0.49
Tran + Precip + MinTemp + Tran * Period	DOY	10	2916.98	1.57	0.22
Tran + MaxTemp + Tran * Period	DOY	9	2917.43	2.02	0.18
Tran + MinTemp + Tran * Period	DOY	9	2918.94	3.53	0.08
Tran + Precip + Tran * Period	DOY	9	2922.52	7.10	0.01
Arboreal Mortality					
Tran + Precip + MaxTemp	Year	7	3187.27	0	0.48
Precip + MaxTemp	Year	5	3188.81	1.54	0.22
Tran + Precip + MinTemp	Year	7	3190.54	3.27	0.09
Tran + Precip + MaxTemp + Tran * Period	Year	10	3190.60	3.33	0.09
Precip + MinTemp	Year	5	3192.03	4.76	0.04

Table 1-4. Top model results for total, non-arboreal, and arboreal mortality at the Monkton Road underpass complex in Monkton, Vermont. The “Estimate” column contains the regression coefficient estimate while the “95% CI” column includes the 95% confidence interval for the coefficient.

	Estimate	95% CI	t-value	p-value
Total Mortality				
TransTypeControl (Intercept)	11.86	4.58 – 19.18	3.21	0.003
TransTypeBuffer	0.65	-6.28 – 7.58	0.18	0.854
TransTypeTreatment	-3.13	-11.13 – 4.87	-0.77	0.442
TempMxScale	4.30	1.57 – 7.02	3.12	0.002
PeriodPost	7.99	-0.23 – 16.21	1.91	0.057
TransTypeBuffer: PeriodPost	1.27	-7.73 – 10.28	0.28	0.782
TransTypeTreatment: PeriodPost	-12.30	-22.69 – -1.90	-2.32	0.021
Non-arboreal Mortality				
TransTypeControl (Intercept)	4.26	0.68 – 7.82	2.35	0.0200
TransTypeBuffer	1.66	-1.83 – 5.15	0.93	0.351
TransTypeTreatment	-1.70	-5.73 – 2.33	-0.83	0.408
PrecipScale	-1.24	-2.45 – -0.04	-2.05	0.041
PeriodPost	6.97	2.85 – 11.09	3.33	<0.001
TempMxScale	2.11	0.76 – 3.46	3.09	0.002
TransTypeBuffer: PeriodPost	-0.60	-5.14 – 3.94	-0.26	0.796
TransTypeTreatment: PeriodPost	-8.47	-13.71 – -3.22	-3.17	0.002
Arboreal Mortality				
TransTypeControl (Intercept)	8.92	4.28 – 13.56	3.95	0.001
TransTypeBuffer	0.10	-3.17 – 3.36	0.58	0.954
TransTypeTreatment	-3.68	-7.45 – 0.09	-1.92	0.056
PrecipScale	2.48	1.03 – 3.94	3.36	<0.001
TempMxScale	2.69	1.19 – 4.20	3.52	<0.001

Figures

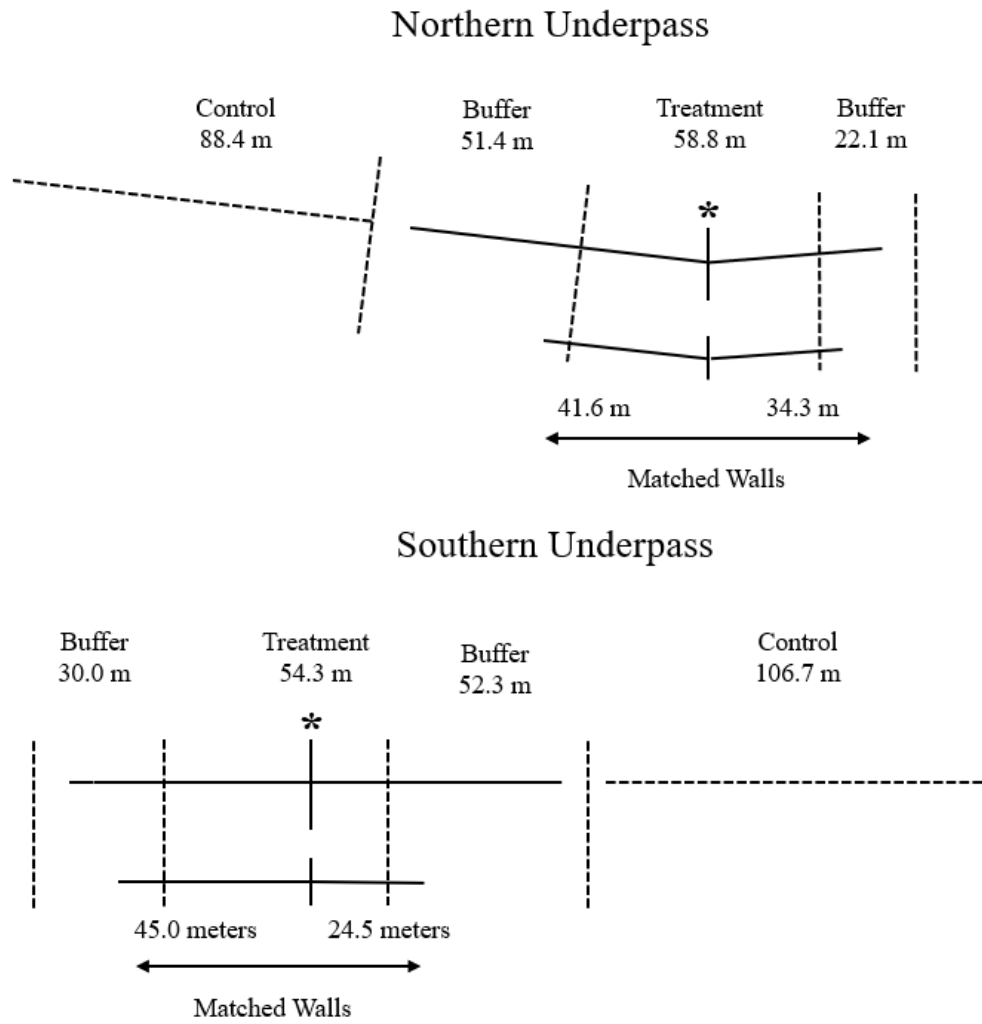


Figure 1-1. Schematic showing the configuration of the Monkton Road, Vermont amphibian underpasses. Solid horizontal lines represent walls, while dashed lines indicate the location of the buffer and control areas. *Indicates the location of the tunnel openings.

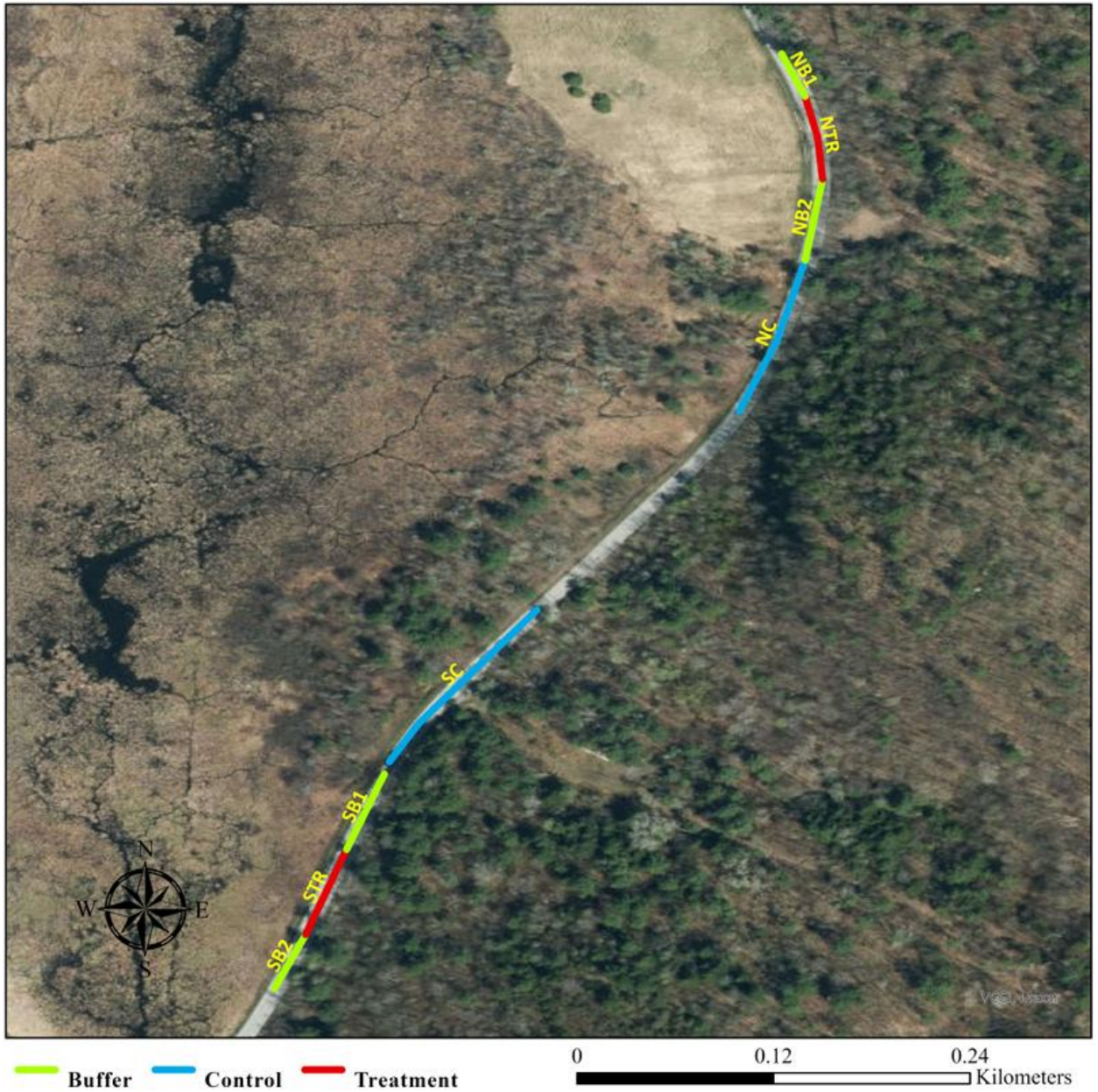


Figure 1-2. Control, treatment, and buffer areas at the Monkton Road, Vermont amphibian underpasses.

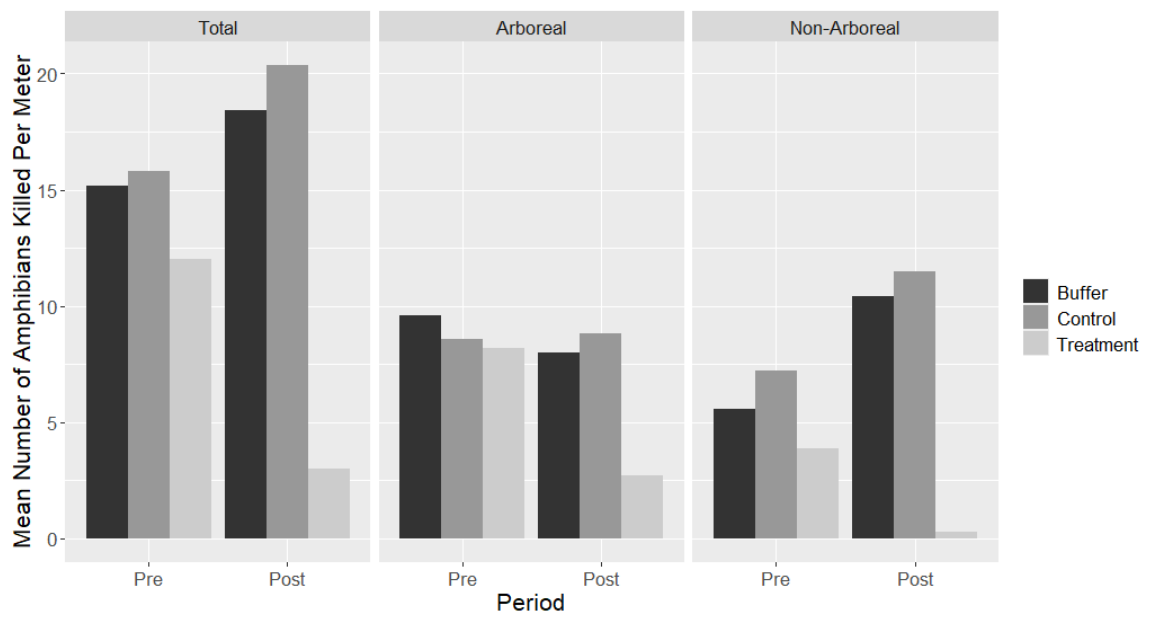


Figure 1-3. Mean number of amphibians killed per meter of road pre- and post-construction at the Monkton, Vermont amphibian underpasses.

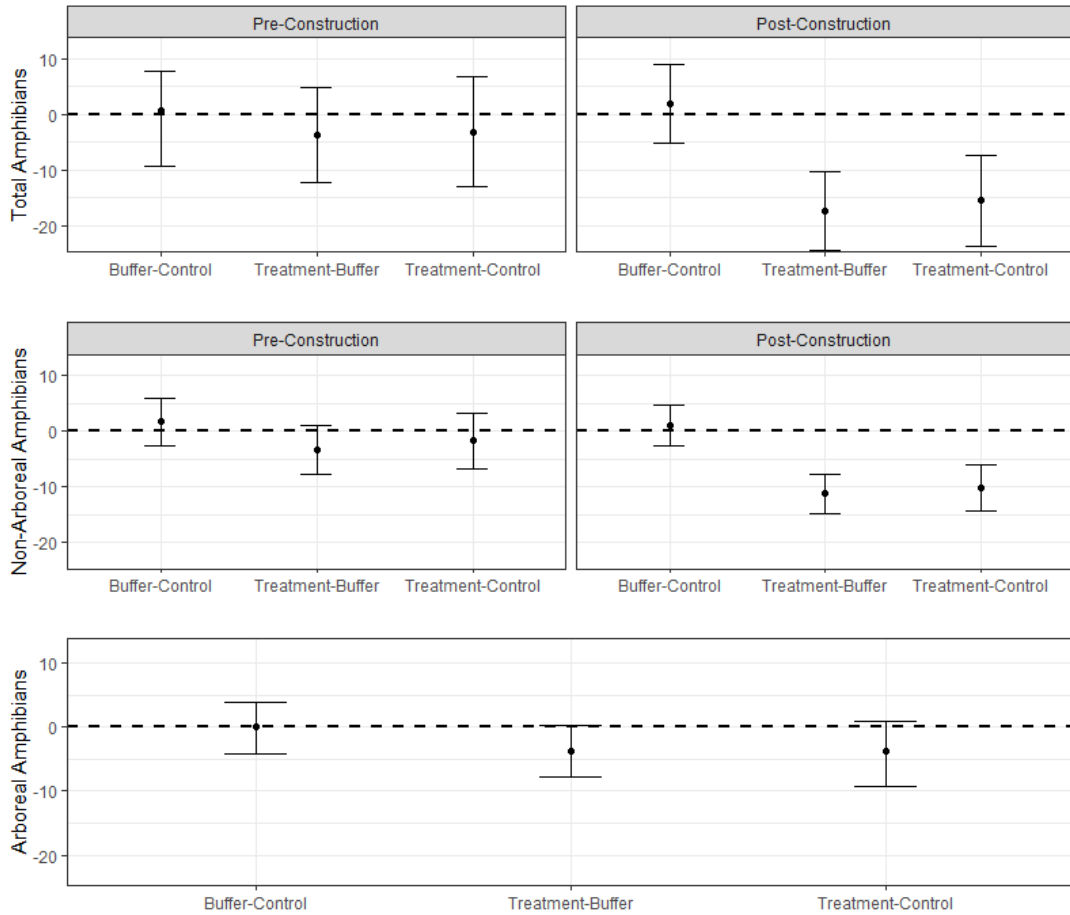


Figure 1-4. Difference in means of top model results after Bonferroni correction for amphibians killed per meter of road at the Monkton, Vermont amphibian underpass. Error bars are 95% confidence intervals for the model estimate.

Appendix

Table 1-A1. All covariate combinations for mixed modeling for amphibian mortality at the Monkton Road underpass complex in Monkton, Vermont.

Fixed Effects	Random Effects
-	Year
TransType	Year
Period	Year
TempMn	Year
TempMx	Year
Precip	Year
TransType + Period	Year
TransType + TempMn	Year
TransType + TempMx	Year
TransType + Precip	Year
TransType + Precip + TempMn	Year
TransType + Precip + TempMx	Year
Precip + TempMn	Year
Precip + TempMx	Year
TransType + TransType * Period	Year
TransType + TempMn + TransType * Period	Year
TransType + TempMx + TransType * Period	Year
TransType + Precip + TransType * Period	Year
TransType + Precip + TempMn + TransType * Period	Year
TransType + Precip + TempMx + TransType * Period	Year
-	DOY
TransType	DOY
Period	DOY
TempMn	DOY
TempMx	DOY
Precip	DOY
TransType + Period	DOY
TransType + TempMn	DOY
TransType + TempMx	DOY
TransType + Precip	DOY
TransType + Precip + TempMn	DOY
TransType + Precip + TempMx	DOY
Precip + TempMn	DOY
Precip + TempMx	DOY
TransType + TransType * Period	DOY
TransType + TempMn + TransType * Period	DOY

TransType + TempMx + TransType * Period	DOY
TransType + Precip + TransType * Period	DOY
TransType + Precip + TempMn + TransType * Period	DOY
TransType + Precip + TempMx + TransType * Period	DOY

CHAPTER 2: COLLATERAL DAMAGE: EVALUATING THE ECOLOGICAL COSTS OF AQUATIC INVASIVE SPECIES MANAGEMENT

Abstract

Aquatic invasive species (AIS) management is essential for preserving ecosystem health and supporting human activities, but it can also have unintended ecological consequences. This systematic review synthesizes existing literature to examine these unintended impacts of AIS management, with a focus on mechanical harvesting. This review identifies critical gaps in understanding the ecological costs of AIS management, particularly regarding less-studied taxa such as reptiles. Mechanical harvesting, while effective for controlling invasive aquatic plants, has limited research assessing its bycatch and effects on long-lived species with slow reproduction rates. Additionally, the literature overemphasizes chemical control methods and studies conducted in North America, neglecting global perspectives and diverse taxa. This study reveals that management strategies often prioritize economic and recreational benefits over ecological integrity. To address these challenges, this review highlights the need for holistic, ecosystem-based approaches that incorporate bycatch monitoring and consider the ecological, economic, and social dimensions of AIS management. By emphasizing the importance of interdisciplinary research and standardized protocols, this work provides a foundation for improving AIS control practices and achieving sustainable ecosystem management.

Key Words – invasive species management, ecological consequences, mechanical harvesting, holistic management, bycatch

Introduction

Globalization and more connected human societies have facilitated and greatly increased the spread of invasive species (Cambray 2003; Meyerson and Mooney 2007; Ram and Palazzolo 2008; Hulme 2009; Thomaz et al. 2014; Bertelsmeier 2021). Invasive species are non-native species that harm ecosystems, local economies, and human health (Beck et al. 2017). These invaders are known to reduce biodiversity and negatively impact ecosystem functioning across the globe (Molnar et al. 2008; Clavero et al. 2009; Linders et al. 2019). Unfortunately for resource managers, invasive species are extremely hard to manage once established (Williams and Grosholz 2008; Büyüktaşkın 2017). Furthermore, there are often unintended negative consequences associated with invasive species management (Bergstrom et al. 2009; Dexter et al. 2013; Coulter et al. 2018; Baquero et al. 2023).

Aquatic invasive species (AIS) management has been particularly salient for resource managers for the past century with billions being spent on management yearly (Marten and Moore 2011). Aquatic invasive plants tend to form dense mats of vegetation that degrade wildlife habitat, reduce biodiversity, and impede anglers and recreational boaters (Marsden and Hauser 2009; Lake George Association 2022). Hoagland and Jin (2006) highlight the importance of integrating both economic benefits and ecological health into management efforts, critiquing instances where economic considerations dominate without adequate ecological grounding. For example, many AIS management projects are implemented primarily for human recreation (i.e., boating, swimming, fishing, etc.) and/or preserving the value of lakeside properties (Zhang and Boyle 2010; Lantry et al. 2015). This has led organizations to implement management techniques

without considering their impact on the entire ecosystem (de Jonge et al. 2012).

Fortunately, this seems to be shifting, and more resource managers are taking all of the complexities associated with a particular ecosystem into account before implementing management programs (Morón-López 2021).

Management programs tend to consist of three different “families” of techniques: chemical, biological, and mechanical. Each type of technique has costs and benefits associated with them. Chemicals, such as herbicides, can be effective at reducing and controlling AIS in waterbodies. However, they aren’t always selective, can pose a risk to humans, and may inadvertently kill wildlife (Mikulyuk et al. 2020; Codd-Downey et al. 2021). Biological controls, when done correctly, can quickly reduce AIS within a waterbody, but can be extremely risky (Simberloff and Stiling 1996; Simberloff 2011). For instance, bighead carp (*Hypophthalmichthys nobilis*), black carp (*Mylopharyngodon piceus*), grass carp (*Ctenopharyngodon idella*), and silver carp (*Hypophthalmichthys molitrix*) were all introduced as biological controls and have themselves become invasive (Phelps et al. 2017). Mechanical control techniques, which can also be quite effective, primarily consist of hand pulling plants and deploying benthic barrier mats. However, both methods are quite expensive (mats need to be maintained and hand harvesting requires many person hours) and tend to be limited to small areas (Boylen et al. 1996; Laitala et al. 2017; Codd-Downey et al. 2021). The aforementioned costs associated with the methodologies above have led resource managers to employ technologies, such as mechanical harvesters, that don’t use chemicals and are able to harvest large amounts of plant materials quickly (Lishawa et al. 2017).

Mechanical harvesters are used to control aquatic invasive plant infestations throughout the globe (Figure 2-1) (Alam et al. 1996; Howard-Williams et al. 1996). They are primarily used to open areas for human recreation (NHDES 2018). Mechanical harvesters work by cutting the plant below the surface of the water and gathering the plant material as its cut. The gathered plant material is stored in the harvester or on a barge, before being disposed of offsite (VTDEC 2008; NHDES 2018). Despite their benefit, mechanical harvesters are not immune to bycatch and can negatively impact fish and wildlife populations (Booms 1999; Sharp et al. 2006; NHDES 2018).

To our knowledge, very few studies have evaluated the impacts of different management techniques on plants and animals. Therefore, we do not know if the ecological costs of various management techniques are greater than the benefits. Theoretically, plants and fast reproducing fish (r-selected) should not be greatly impacted by various management techniques (Chiu and Kuo 2012). However, longer living, slower-reproducing organisms (K-selected) may suffer irreversible damage to their populations (Chiu and Kuo 2012; Li Veli et al. 2024). For example, turtles are long-lived and have fairly slow reproduction rates. Therefore, losing only a few individuals could potentially lead to the decline and extirpation of turtle populations (Nickerson and Pitt 2012; Bougie et al. 2022). In particular, most turtles are proficient swimmers and can likely avoid mechanical harvesters or chemical application sites (Pace et al. 2001). However, small cryptic species may be unable to escape capture and may not be easily seen by the operators or applicators of the various management techniques. For instance, eastern musk turtles (*Sternotherus odoratus*) are poor swimmers that occupy shallow, heavily vegetated areas of waterbodies where they slowly walk along the bottom (Figure

2-2) (Ernst and Lovich 2009). Unfortunately, this makes them highly susceptible to bycatch and other unintended management impacts.

Resource managers must navigate complex ecological and social landscapes when making decisions about AIS management (de Jonge et al. 2012; Morón-López 2021). These decisions are often complicated by scientific uncertainties, competing stakeholder interests, and unintended ecological consequences. Therefore, the objectives of this literature review are: 1) provide an overview of common AIS management techniques, particularly focusing on mechanical harvesting; 2) summarize current knowledge about the unintended consequences of AIS management; and 3) identify gaps in research related to mechanical AIS harvesting. This literature review will help resource managers to think critically about how to best manage AIS in the aquatic ecosystems within their jurisdiction.

Methods

Rationale

A formal literature review was conducted on the existing literature to examine the unintended ecological consequences of AIS management, with a specific focus on mechanical harvesting. The intent of this review was to highlight the existing research on bycatch and non-target impacts to assess whether a significant data gap exists regarding the effects of mechanical harvesting and other AIS management techniques on native species. By synthesizing relevant findings, this review informs the broader context of AIS management impacts and underscores the necessity of incorporating bycatch assessments

into management strategies to ensure that management is beneficial, rather than harmful to native flora and fauna.

Search strategy

To ensure reproducibility and accessibility to those without access to a paid database, we used Google Scholar (Google, Mountain View, CA, USA) to conduct our literature review search. While searching through the literature, we recorded each search term and selected relevant articles based on their titles and abstracts. We then created a brief summary of the article, created an evaluation that recorded the scientific merit and relevance of the study, and recorded any key concepts from each article. To provide a comprehensive evaluation of non-target impacts, we examined mechanical harvesting within the field of ecology as well as adjacent AIS management methodologies and scientific fields, such as economics and toxicology. Additionally, to ensure a comprehensive review, we incorporated studies from multiple disciplines using predefined criteria for relevance and scientific merit. Lastly, we tried to primarily use peer-reviewed publications; however, we also included grey literature (i.e., government and non-government reports, graduate theses and dissertations, conference proceedings, technical reports, etc.). The structure of our literature review ensured that we encompassed different methodologies, historical contexts, and policies; and highlighted any data gaps.

Screening and data extraction

To ensure a comprehensive and relevant literature review on AIS management, particularly focusing on mechanical harvesting, we established the following inclusion

criteria. Studies must specifically address AIS management, and ideally discussed, measured, assessed, or evaluated the unintended consequences of each technique. Our review encompassed research from diverse geographic locations, ensuring a global perspective on AIS management practices within the scope of available literature. The review considered studies examining a wide range of species, including both flora and fauna, to understand the broader ecological impacts. Our review prioritized recent publications to ensure the relevance of findings, while also incorporating older studies when they met our inclusion criteria. Additionally, we included studies that assessed both the intended and unintended ecological consequences of AIS management practices, providing a holistic view of their impacts.

Literature Review and Data Synthesis

We analyzed the number of manuscripts by country, continent, and publication year, as well as by targeted invasive species, AIS control methods, and impacted non-target taxa. Control methods were categorized into five groups: biological (e.g., introduction of species), chemical (e.g., lampricide or herbicide), mechanical (mechanical harvesting), other (e.g., cultural practices or literature reviews), and physical (e.g., barriers such as physical containment, electric, chemical, acoustic, etc.; habitat manipulation; benthic barriers; and removal methods like electrofishing, netting, angling, etc.). Additionally, we quantified the number of studies focusing on mechanical harvesting and the non-target taxa impacted by this method. Then, we calculated the proportion of manuscripts – both overall and those specifically addressing mechanical harvesting – that involved data collection. Finally, we performed Chi-Square tests of independence to determine if any country, continent, targeted AIS, control method, and

impacted taxa were more frequently reported in the literature. If there were any significant results, we conducted post-hoc pairwise comparisons using the RVAideMemoire package in R (Herve 2021) to adjust comparisons and identify specific differences between country, continent, targeted AIS, control method, and impacted taxa.

Results

Our keyword/term search (performed between 2 September 2024 and 21 November 2024) initially generated a list of 1,851,740 articles using broad search terms. This prompted us to use a list of 33 fairly specific search terms (Table 2-A1), that allowed us to narrow this list down substantially (Figure 2-2). We then narrowed this list down to 824 articles by removing any articles that did not include or imply invasive species management in their titles. The next step included reviewing the remaining article abstracts, which eliminated any articles that weren't relevant. Then we reviewed the full text of the remaining 127 articles and evaluated them against the objectives of this literature review (adapted from Larson et al. 2016 and Page et al. 2021). 47 of the 127 articles were included in our systematic literature review, with the remaining 80 being excluded because they didn't mention unintended consequences, or they couldn't be accessed (Figure 2-2). From the 47 articles, we extracted information on the countries and continents where the study occurred, the targeted AIS, the control methodology used, whether data were generated, the consequences discussed (including both unintended and no impact), and the non-target taxa that were affected by management.

Only 37% of publications from our eligible literature were accepted for review (Figure 2-2). Our Chi-Square test indicated that there was a significant relationship between continent of origin and the frequency of publication ($X^2_{(5, N=84)} = 83.14, p <$

0.001). Significantly more manuscripts involved studies in North America ($p < 0.001$) compared to the other continents (Figure 2-3).

There also was a significant relationship between the country of origin and the frequency of publication ($X^2_{(16, N=84)} = 193.26, p < 0.001$). The United States of America (USA) was more frequently represented in the literature compared to other countries ($p < 0.001$) (Table 2-1). Most studies were published after 2010, with very few being published before 2000 (Figure 2-4).

There was a significant relationship between targeted taxa and the frequency of publication ($X^2_{(5, N=48)} = 102.50, p < 0.001$). Aquatic invasive plants were the target of management significantly more than other taxa ($p = 0.01$) (Table 2-2).

There was also a significant relationship between treatment methodology and the frequency of publication ($X^2_{(5, N=75)} = 42.36, p < 0.001$). Chemical control was published significantly more than any other control methodology (Table 2-3). The difference between chemical control and hand-pulling, as well as “other” categories, was highly significant ($p < 0.001$). The differences between chemical control and biological control ($p = 0.01$), physical control ($p = 0.01$) and mechanical harvesting ($p = 0.01$) were also statistically significant.

There was a significant relationship between negatively impacted taxa and the frequency of publication ($X^2_{(7, N=86)} = 80.33, p < 0.001$). Native plants were negatively affected more than other taxa, with fish and invertebrates being negatively impacted in more than a third of studies (Table 2-4). Negative impacts were reported significantly more often for plants compared to reptiles, birds, bivalves, and amphibians ($p < 0.001$).

Additionally, negative impacts were reported significantly more often for fish compared to reptiles, birds, bivalves, and amphibians ($p < 0.001$). Lastly, negative impacts were reported significantly more often for invertebrates, compared to reptiles ($p = 0.001$), birds ($p = 0.004$), bivalves ($p = 0.009$), and amphibians ($p = 0.009$).

Mechanical harvesting negative impacts were only discussed in 27.7% of reviewed manuscripts (Figure 2-5). There was not a significant relationship between mechanical harvesting and unintended impacts, and the frequency of publications ($X^2_{(3, N=23)} = 6.39, p = 0.09$). Most mechanical harvesting studies reported unintended negative consequences on plants and fish, while only 2 manuscripts (4.3% of total manuscripts) discussed negative impacts on reptiles (Figure 2-5). 68.1% of studies actually generated data, while only 46.2% of mechanical harvesting studies generated data.

Discussion

North America, particularly the USA, is more frequently represented in research exploring the unintended consequences of AIS management. This may be due to the USA's substantial annual spending on AIS management (\$166 billion), despite many countries spending a higher percentage of their GDP on AIS management (Diagne et al. 2020; Cuthbert et al. 2021). However, these findings align with the broader trend of underrepresentation of the global south in environmental sciences (Karlsson et al. 2007; Wilson et al. 2016). A lack of comparable resources to the global north most certainly contributes to the disparity between the north and south (Vadrot 2020). However, Blicharska et al. (2017) suggest that a myriad of factors apart from access to monetary resources hinders global southern researchers' ability to secure funding. For example, scientists from the global south may have greater challenges in securing grant funding

and publishing in peer-reviewed literature (which are concentrated in the global north) due to the English language being the primary form of communication in much of the world of science (Blicharska et al. 2017).

Chemical control AIS methods dominated the literature, with two-thirds of manuscripts mentioning their unintended impacts on ecosystems. This is unsurprising due to the relatively low costs of application and the typically immediate impacts on AIS (Marten and Moore 2011; Weidlich et al. 2020). However, we still only found 32 manuscripts that overtly discussed the unintended consequences and the taxa that were negatively impacted due to AIS chemical control. This represents an extremely small portion of manuscripts that focus on AIS management.

We also found that studies largely focused on plants (also the most targeted AIS) and fish, neglecting less charismatic taxa like reptiles. Many AIS management projects are done for economic reasons, such as opening waterways for recreation, increasing angling opportunities and experiences, and raising property values (Zhang and Boyle 2010; Lantry et al. 2015). Therefore, the focus on preventing negative effects on native plants and fishes makes intuitive sense. However, a more holistic and comprehensive approach to AIS management may help ensure the integrity of ecosystems (de Jonge et al. 2012; Morón-López 2021). Additionally, expanding monitoring efforts to include less charismatic taxa could provide a more complete understanding of ecological impacts, particularly given the existing negative biases against these species (Brambilla et al. 2013; Monsarrat and Kerley 2018).

Our findings underscore a critical gap in the literature regarding the broader ecological impacts of mechanical harvesting, particularly its effects on less-studied taxa

such as reptiles. This gap not only limits our understanding of the full ecological cost of invasive species management but also highlights the need for more comprehensive research to guide resource managers in developing holistic and sustainable management strategies. Based on the taxa most frequently reported in the literature, it is possible that mechanical harvesting impacts on K-selected species, such as some reptiles, are understudied. Many of the species affected in this study appear to be r-selected, meaning they are short-lived and reproduce quickly, which may allow their populations to recover more readily from incidental removal (Chiu and Kuo 2012). In contrast, K-selected species, which tend to have lower reproductive rates and longer lifespans, may be more vulnerable to even low levels of bycatch, potentially leading to population declines (Chiu and Kuo 2012; Li Veli et al. 2024). Given these concerns, developing a standardized method for collecting bycatch data during mechanical harvesting operations could help resource managers better assess and mitigate unintended impacts (Savoca et al. 2020).

This formal and comprehensive literature review highlights the critical gaps in understanding the ecological impacts of AIS management, particularly the impacts of mechanical harvesting and the effects on sensitive reptile populations. Furthermore, very few studies have examined the long-term ecological consequences, such as population dynamics and community shifts, of AIS management methods. The lack of substantial global data, especially from the global south, severely limits the comprehensive evaluation of AIS management strategies. This paper illustrates the need for more researchers to overtly study the unintended consequences of AIS control.

With this paper, we have underscored the complexity and importance of taking a “whole-ecosystem” approach to managing AIS. Supporting this approach requires holistic

strategies that balance ecological risks with stakeholder needs. We also recommend that mechanical harvesting protocols include bycatch monitoring to minimize harm to vulnerable taxa. Furthermore, by integrating ecological risk assessments, managers can improve decision-making and align their AIS interventions with conservation goals that benefit the entire ecosystem.

We have effectively provided a starting point for future research. However, in the future, scientists should prioritize research in underrepresented regions and on less-studied taxa. They should also conduct longitudinal studies on the long-term impacts of AIS management, especially mechanical harvesting. Finally, future research should embrace interdisciplinary approaches, combining ecological, economic, and social dimensions, allowing for a more holistic approach to ecosystem management.

Conclusion

This systematic review highlights the significant knowledge gaps in understanding the unintended ecological consequences of AIS management, particularly mechanical harvesting. While AIS control is essential for preserving ecosystem health and human activities, the ecological costs of these interventions remain underexplored. The disproportionate focus on chemical control methods and certain taxa, such as plants and fish, reveals a lack of attention to less-studied species, including reptiles and other non-charismatic fauna. Furthermore, the geographic bias toward North America underscores the need for more research from underrepresented regions to develop globally applicable management strategies.

To address these challenges, future research must prioritize the ecological impacts of mechanical harvesting, particularly on long-lived, slow-reproducing species susceptible to bycatch. Standardized monitoring and data collection protocols are critical to assessing the broader consequences of AIS management techniques. Additionally, resource managers should adopt holistic approaches that consider both ecological and socioeconomic factors to ensure sustainable and effective interventions.

By emphasizing the need for interdisciplinary collaboration and inclusive research efforts, this review provides a foundation for improving AIS management practices. Implementing the recommendations outlined here will enable resource managers to better balance ecological integrity with stakeholder needs, ultimately contributing to healthier and more resilient aquatic ecosystems.

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Tables

Table 2-1. Frequency (N) and percentage of manuscripts by study location.

Location	N	Percent of Manuscripts*
Africa		
Non-specified African Countries	5	10.6%
South Africa	2	4.3%
Asia		
Japan	1	2.1%
Non-specified Asian Countries	5	10.6%
Australasia		
Australia	2	4.3%
New Zealand	3	6.4%
Non-specified Australasian Countries	5	10.6%
Europe		
France	1	2.1%
Non-specified European Countries	6	12.8%
Norway	1	2.1%
United Kingdom	1	2.1%
North America		
Canada	6	12.8%
Non-specified North American Countries	5	10.6%
United States of America	34	72.3%
South America		
Argentina	1	2.1%
Brazil	2	4.3%
Non-specified South American Countries	4	8.5%

*Note: There were 47 manuscripts, some of which contained multiple locations. Therefore, the Percent of Manuscripts column does not add up to 100%.

Table 2-2. Frequency (N) and percent of manuscripts by targeted aquatic invasive species.

Aquatic Invasive Species	N	Percent of Manuscripts*
Fish	5	10.6%
Plant	34	72.3%
Bivalve	3	6.4%
Not Specified	2	4.3%
Invertebrate	3	6.4%
N/A	1	2.1%

**Note: There were 47 manuscripts, some of which contained multiple target invasive species. Therefore, the Percent of Manuscripts column does not add up to 100%.*

Table 2-3. Frequency (N) and percentage of manuscripts by aquatic invasive species control method.

Control Method	N	Percent of Manuscripts*
Biological	11	23.4%
Chemical	32	68.1%
Hand-pulling	4	8.5%
Mechanical	13	27.7%
Other	4	8.5%
Physical	11	23.4%

**Note: There were 47 manuscripts, some of which contained multiple methodologies. Therefore, the Percent of Manuscripts column does not add up to 100%.*

Table 2-4. Frequency (N) and percent of manuscripts by impacted non-target taxa.

Impacted Non-target Taxa	N	Percent of Manuscripts*
Plants	31	66.0%
Fish	22	46.8%
Amphibians	4	8.5%
Reptiles	2	4.3%
Birds	3	6.4%
Bivalves	4	8.5%
Invertebrates	17	36.2%
Didn't Specify	3	6.4%

**Note: There were 47 manuscripts, some of which contained multiple impacted taxa. Therefore, the Percent of Manuscripts column does not add up 100%.*

Figures



Figure 2-1. Aquatic invasive species mechanical harvester in operation taken by Solitude Lake Management. Photo retrieved from <https://www.solitudelakemanagement.com/mechanical-harvesting-control-nuisance-aquatic-weeds/>.

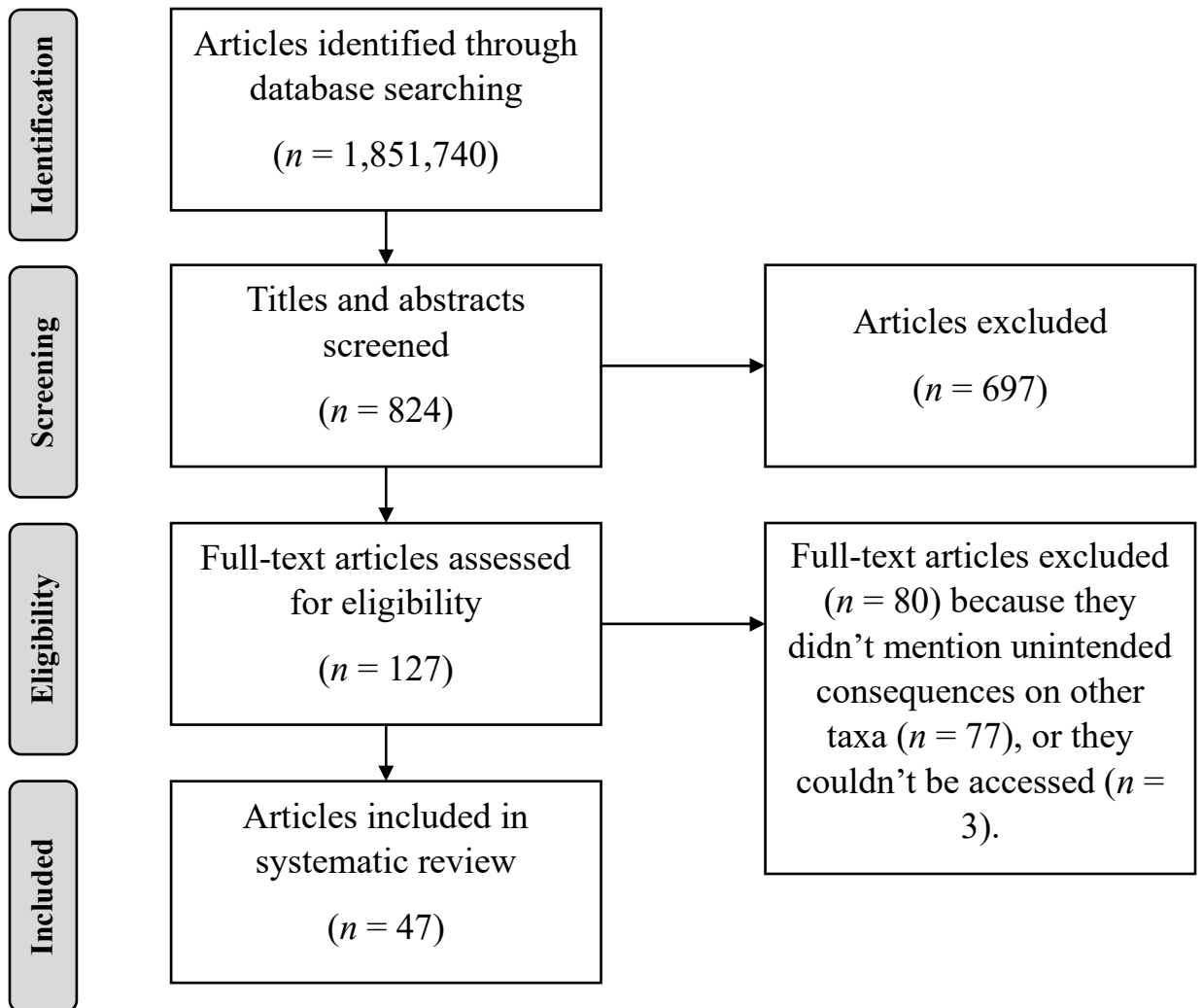


Figure 2-2. PRISMA literature search flow diagram showing the number of articles that were located, kept, and discarded at each stage of the literature review (adapted from Page et al. 2021).

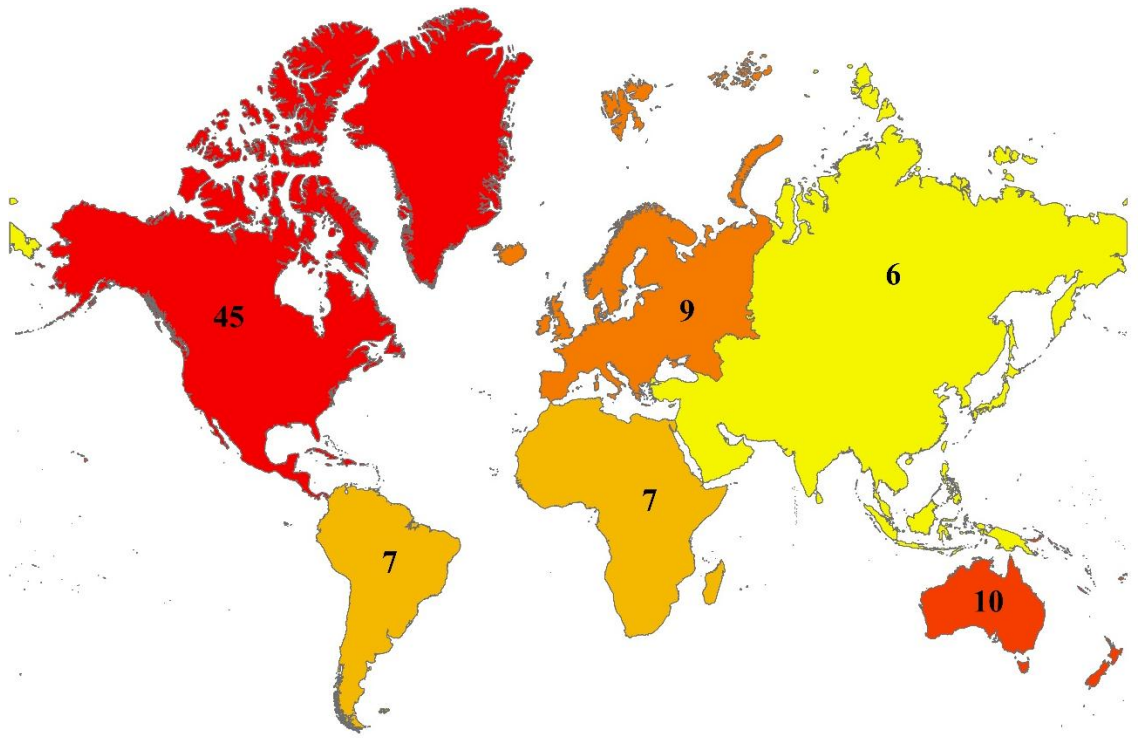


Figure 2-3. The number of publications in the literature review per continent that discussed unintended consequences of aquatic invasive species management.

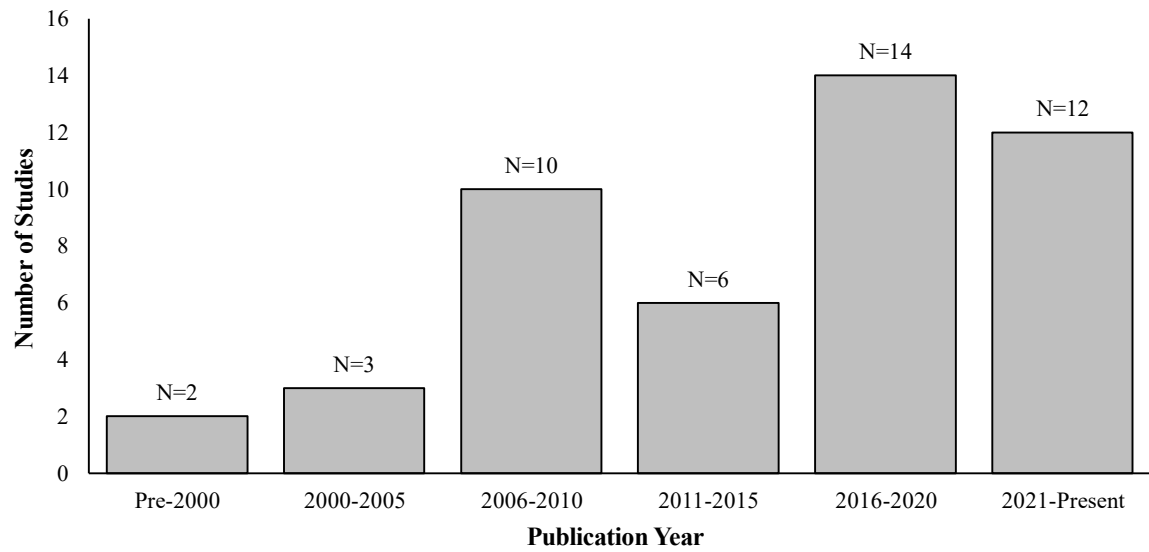


Figure 2-4. The number of publications (47 out of 127) in the literature review that discussed unintended consequences of aquatic invasive species management published over time.

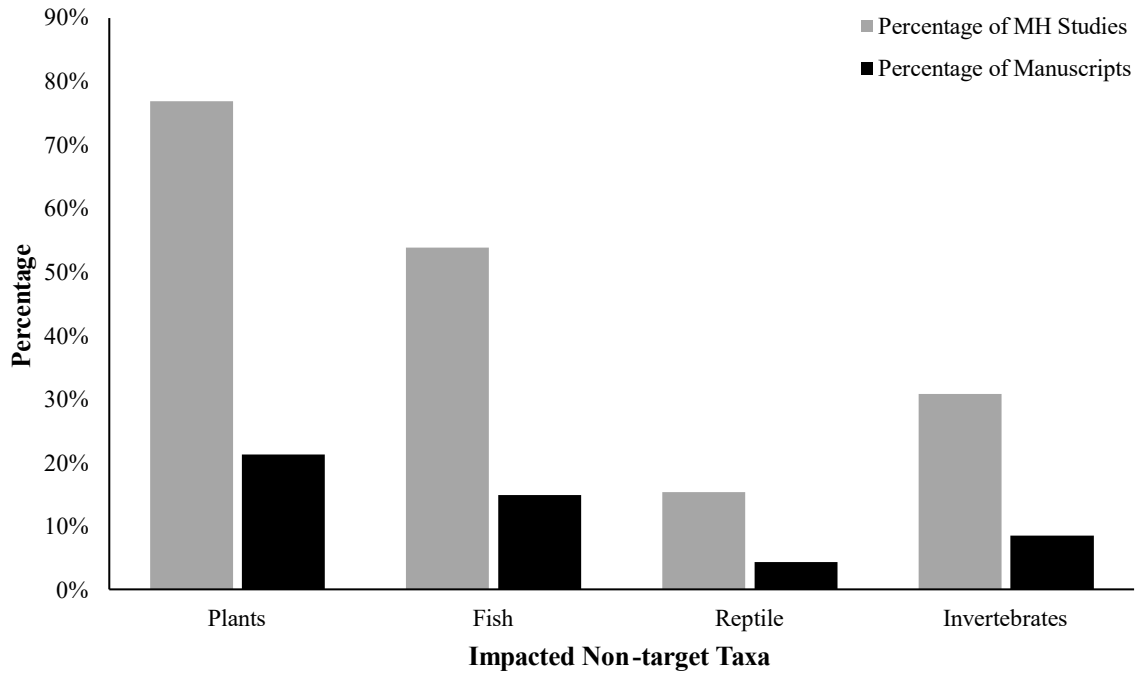


Figure 2-5. Percentage of mechanical harvesting (MH) manuscripts by impacted non-target taxa.
**Note: There were 47 manuscripts (13 mechanical harvester), some of which contained multiple impacted taxa. Therefore, the Percent of MH Studies and Percent of Manuscripts do not add up to 100%.*

Appendix

Table 2-A1. Search terms used to conduct a literature review on the unintended impacts of aquatic invasive species management.

Search Terms
bycatch AND aquatic invasive species management AND native species mortality
bycatch AND invasive plant control AND aquatic AND wildlife
bycatch during aquatic invasive plant management
bycatch rates AND aquatic invasive species management AND native species mortality
nontarget AND management AND aquatic invasive plant AND turtle
nontarget AND management AND invasive AND turtle
nontarget AND management AND invasive plant AND reptile AND aquatic
nontarget AND management AND invasive plant AND turtle
nontarget AND management AND invasive plant AND turtle AND aquatic
nontarget AND mechanical harvesting AND invasive AND wildlife
nontarget AND mechanical harvesting AND invasive
nontarget AND mortality AND aquatic invasive plant management
nontarget AND mortality AND aquatic invasive plant management AND wildlife
consequences AND aquatic invasive plant management AND wildlife
consequences of aquatic invasive plant management AND wildlife
mortality AND invasive plant control AND aquatic AND wildlife
nontarget AND management AND invasive plant AND fish AND aquatic
nontarget AND mechanical harvesting
unintended mortality AND native species AND invasive plant control
bycatch AND aquatic invasive species
mortality AND management AND invasive plant AND wildlife AND aquatic
nontarget AND mortality AND aquatic invasive management
nontarget AND mortality AND aquatic invasive species AND management
nontarget AND mortality AND aquatic invasive species management
impacts of aquatic invasive species mechanical harvesting
unintended mortality AND invasive plant control
impacts of aquatic invasive plant management AND management AND invasive plant AND wildlife AND aquatic
impacts of aquatic invasive plant management AND wildlife
aquatic invasive species management AND native species mortality
nontarget AND aquatic invasive species
mortality AND invasive plant control AND aquatic
impacts of aquatic invasive species chemical treatment
mortality AND invasive plant control

**CHAPTER 3: THE IMPACT OF AQUATIC INVASIVE SPECIES MECHANICAL
HARVESTING ON TURTLE POPULATIONS IN THE LAKE CHAMPLAIN
BASIN**

Abstract

Mechanical harvesting is a widely used aquatic invasive species (AIS) management technique. This method is used in the Lake Champlain Basin to prevent Eurasian watermilfoil (*Myriophyllum spicatum*) and European water chestnut (*Trapa natans*) from degrading native ecosystems and impeding human activities. While effective in reducing invasive plants, this method could pose a risk of unintended bycatch and mortality to non-target species, including turtles. This study investigated the impact of mechanical harvesting on turtle populations, focusing on eastern musk turtles (*Sternotherus odoratus*) and painted turtles (*Chrysemys picta*). We employed self-reported surveys, hand-sorting harvested plant material, and turtle trapping across multiple sites to quantify bycatch across multiple taxonomic groups. Bycatch rates across all taxa were low (< 1 individual/hour), and mortality rates were even lower, suggesting minimal direct impact on turtle populations. However, challenges in tracking tagged turtles limited insights into behavioral interactions with harvesters. Our results highlight the potential for resource managers to collaborate with mechanical harvester operators to refine harvester designs, such as installing excluder devices, to further reduce bycatch. This study provides critical baseline data to inform AIS management strategies that balance invasive plant control with the conservation of native flora and fauna. Continued research, including long-term population monitoring and harvester design improvements, is essential to safeguard vulnerable species in managed aquatic environments.

Key Words – aquatic invasive species, mechanical harvesting, turtle populations, bycatch and mortality, conservation management

Introduction

Increasingly interconnected human societies have significantly facilitated and accelerated the spread of invasive species (Cambray 2003; Meyerson and Mooney 2007; Hulme 2009). Invasive species, which are non-native and detrimental to ecosystems, local economies, and human health, are known to reduce biodiversity and adversely affect ecosystem functioning (Molnar et al. 2008; Clavero et al. 2009; Linders et al. 2019). Unfortunately for resource managers, once invasive species become established, they are extremely difficult to control (Williams and Grosholz 2008; Büyüktaktın 2017). Among the most problematic are aquatic invasive plants, which tend to form dense mats of vegetation that degrade wildlife habitat, reduce biodiversity, and impede anglers and recreational boaters (Marsden and Hauser 2009; Lake George Association 2022). These plants can spread via animals, humans, fragments, roots, and seeds, making them especially challenging to manage (Vander Zanden et al. 2008; Kelly et al. 2012). Additionally, managing invasive species can inadvertently cause negative consequences, such as trophic cascades that rapidly alter ecosystem dynamics (Bergstrom et al. 2009; Dexter et al. 2013; Coulter et al. 2018; Baquero et al. 2023). However, these effects appear to be underrepresented in the published literature (Chapter 2, this dissertation).

The impacts of Aquatic invasive species (AIS) worldwide have led to the development of a variety of control methodologies, each with unique costs and benefits. Benthic barrier mats are effective at reducing rooted aquatic plant infestations in small bodies of water by preventing and inhibiting growth. However, they must be maintained, are not selective, and are ineffective in large lakes (Laitala et al. 2017; Codd-Downey et al. 2021). Hand harvesting can be effective at reducing small patches of AIS close to

shore. Nonetheless, hand harvesting is slow and cost prohibitive, and can inadvertently lead to further infestations if the entire plant (i.e., roots, fragments, etc.) isn't collected (Boylen et al. 1996; Codd-Downey et al. 2021). Herbicides are perhaps the most controversial methodology employed by resource managers. Herbicides can be effective at reducing and controlling AIS in waterbodies. However, herbicides aren't always selective, may pose a risk to humans, and may harm native plants and wildlife (Mikulyuk et al. 2020; Codd-Downey et al. 2021). These challenges have led resource managers to utilize and employ mechanical harvesters, a method that doesn't use herbicides and is able to harvest large amounts of aquatic invasive plants quickly (Lishawa et al. 2017).

The impacts of AIS management on vertebrates appear to vary depending on the control method used, the geographic region, and the taxa involved (Chapter 2, this dissertation). While some vertebrate groups, such as fish, are relatively well-studied, others – particularly long-lived species like turtles – receive far less attention (Brambilla et al. 2013; Monsarrat and Kerley 2018). This gap is especially concerning given that slow-reproducing species may be disproportionately affected by management activities, yet their vulnerabilities remain underexplored in the literature (Chapter 2, this dissertation).

As in many waterbodies across the world, AIS have been present in the Lake Champlain (Abenaki place name Bitawbagok) Basin for over a century, where they are outcompeting native plants and animals in many waterbodies across the basin (Lake Champlain Basin Program 2005; Lake Champlain Basin Program 2021). Furthermore, AIS negatively impact wildlife habitat and cause economic harm within the basin (Marsden and Hauser 2009; Zhang and Boyle 2010). Among the most prolific of these

species are Eurasian watermilfoil (*Myriophyllum spicatum*) and European water chestnut (*Trapa natans*) (VTDEC 2008; VTDEC 2021; APIPP 2022). Eurasian watermilfoil has been present in the Lake Champlain Basin since its discovery in St. Albans Bay in 1962 and has spread throughout the lake and to other inland waterbodies (Marsden and Hauser 2009). European water chestnut (*Trapa natans*) was documented in Lake Champlain in the 1940s and has since spread to other inland waterbodies within the Lake Champlain Basin (Lake Champlain Basin Program 2022a). Millions of federal, state, and local funds have been spent trying to control Eurasian watermilfoil and European water chestnut in the Lake Champlain Basin (Kelting 2010; Lake Champlain Basin Program 2005; Lake Champlain Basin Program 2022a). While waterbodies in the Lake Champlain Basin are managed using various methods (e.g., benthic barriers, diver operated suction harvesting, fragment barriers, hand harvesting, herbicides, hydrotanking, and implementation of spread prevention programs), mechanical harvesting is commonly used due to its ability to quickly remove large swaths of plant material (Hussner et al. 2017; Lake Champlain Basin Program 2022a; VTDEC 2022).

The state of Vermont (Abenaki place name, N'dakinna) allows the use of mechanical harvesters to control Eurasian watermilfoil and European water chestnut in various lakes (Figure 3-1) (VTDEC 2008; VTDEC 2022). These harvesters are mainly employed to create open spaces for recreational activities (NHDES 2018). They operate by cutting the plants below the water's surface and collecting the cut material. The collected plant material is then stored either in the harvester or on a barge before being disposed of offsite (VTDEC 2008; NHDES 2018). However, mechanical harvesters are

not without drawbacks, as they can unintentionally capture and harm fish and wildlife populations (Booms 1999; Sharp et al. 2006).

Most turtles are proficient swimmers (Pace et al. 2001), so many turtle species in the Lake Champlain Basin should be able to escape mechanical harvesters. However, small, cryptic species like the eastern musk turtle (*Sternotherus odoratus*) are poor swimmers that inhabit shallow, densely vegetated areas where they slowly walk along the bottom of the waterbody (Figure 3-2) (Ernst and Lovich 2009). This behavior makes them vulnerable to bycatch. There is concern that eastern musk turtles (and others) may be unintentionally injured or killed by mechanical harvesters due to their size and cryptic coloration. Given that turtles are long-lived, the loss of even a few individuals could potentially lead to the decline and extirpation of their populations (Nickerson and Pitt 2012; Bougie et al. 2022).

Prioritizing the collection of bycatch data when designing AIS mitigation projects is a best practice (Savoca et al. 2020). Understanding the impacts of mitigation will ensure that both short-lived, fast-reproducing and long-lived, slow-reproducing organisms will be safeguarded from any unintended impacts of management (Chiu and Kuo 2012; Li Veli et al. 2024). Therefore, the objectives of this study are to 1) quantify the amount of bycatch harvested by mechanical harvesters, 2) determine how many turtles are captured by mechanical harvesters, 3) determine whether significant turtle mortality occurs during the harvesting process, and 4) understand how turtle behavior is impacted by AIS mechanical harvesters. Ultimately, this study will yield Vermont-specific data and results that will allow the Vermont Agency of Natural Resources to develop targeted and potentially more effective aquatic nuisance control permit

conditions that safeguard turtles, while potentially easing restrictions for permit applicants. Furthermore, to our knowledge, this study will be the first study to explore AIS mechanical harvesting's impact on turtle populations. By addressing these gaps, this study not only provides critical data to inform AIS management strategies in Vermont but also contributes to a broader understanding of how mechanical harvesting affects non-target species, particularly long-lived taxa like turtles. The findings will help guide resource managers in balancing invasive species control with the conservation of native wildlife, ultimately supporting more sustainable and ecologically responsible management practices.

Methods

Study Area

Lake Champlain is a large freshwater lake with a surface area of 1,127 km², a shoreline exceeding 800 km, more than 70 islands, and a relatively large drainage basin with a 19:1 land to lake ratio (Facey et al. 2012; Meltzer et al. 2012). The lake has an average depth of 22 m and a maximum depth of 122 m. The lake is divided into five main basins: Missisquoi Bay, Malletts Bay, the Inland Sea, the Main Lake, and the South Lake. Lake Champlain is an international body of water, lying within the USA (New York and Vermont) and Canada (Quebec).

Lake Bomoseen is Vermont's third largest lake (largest entirely within Vermont) with a surface area of 9.6 km² and a shoreline of ~27 km (Zhang and Boyle 2010; Sheldon 1997). Lake Bomoseen has an average depth of 8 m, and a maximum depth of 20 m. The northern portion of the lake is characterized by deep cool water, while the

southern portion is much shallower and warmer. Both lakes have a mixture of developed and forested shorelines, are popular recreational areas, and are colonized by AIS (VTDEC 2008; VTDEC 2022).

Study Species

Eastern musk turtles are a small turtle with an average carapace length of 8-14 cm, with a grayish-green carapace that is often covered in algae (Lowery 2023). Eastern musk turtles are a long-lived species, with an estimated lifespan of 30 years in the wild, and an average age of sexual maturity at age 3 or 4 in northern latitudes (Ernst and Lovich 2009; Cambell et al. 2020). Eastern musk turtles have a state natural heritage rank of S2 (rare) and are listed as a species of concern in Vermont and a Species of Greatest Conservation Need in Vermont and New York.

Painted turtles (*Chrysemys picta*) are small turtles with an average carapace length of 9-25 cm, with an olive to black carapace with bright yellow and/or red markings (Knipper 2002; Ernst and Lovich 2009). Painted turtles are a long-lived species, with an estimated lifespan of 35 to 40 years in the wild, and an average age of sexual maturity at 3 to 5 for males and 6 to 10 for females in northern latitudes (Ernst and Lovich 2009). Painted turtles have a state natural heritage rank of S5 (common) in Vermont and New York.

Self-Reported Mechanical Harvester Bycatch Survey

We designed a bycatch field form for mechanical harvester operators to use to record any turtles and animals that were inadvertently captured during the harvesting process. The form included fields for waterbody, town, and state (Vermont and New

York) where the harvest occurred, as well as the harvest site(s) and latitude. We requested that harvesters record the total time spent harvesting each day that they recorded data. We also asked them to tally the number of alive and dead turtles that they observed and requested a photograph whenever possible to confirm the species of captured turtles. Lastly, we were primarily interested in turtles during this study, however, we asked the harvesters to record any animal bycatch that they noticed (i.e., fish, invertebrates, birds, etc.).

Hand-Sorted Mechanical Bycatch Survey

We conducted three replicate discarded plant surveys at each of the three sites, which were located in the South Lake and Pelot's Bay of Lake Champlain, as well as in Lake Bomoseen. These surveys involved systematically hand-sorting through discarded plant material unloaded by the harvester operators at the dumping/offloading site. We examined every part of each plant to identify any animal bycatch. While our primary focus was on turtles and other vertebrates, we recorded all animals encountered during the sorting process. We also documented the volume of the plant material, any animals that were found, and the dominant plant species.

Turtle Trapping

To understand how turtles interacted with mechanical harvesters during operation, we attempted to capture and tag eastern musk turtles and painted turtles with global positioning system (GPS) and VHF transmitters. Additionally, we deployed GPS transmitters on mechanical harvesters operating within our study sites. To accomplish the turtle tagging, we trapped turtles using baited hoop traps at 3 locations within Lake

Champlain and 1 location within Lake Bomoseen (Figure 3-3). At each study site, 15 baited hoop traps were deployed (2-inch Sq. mesh treated nylon turtle nets, Memphis Net & Twine Co., Inc., Memphis TN, USA). Each hoop trap was secured in water up to 80 cm in depth with two wooden stakes and baited with canned sardines (Figure 3-4). We ensured that each trap had at least 5.1 cm of net remaining above the water to permit breathing by trapped turtles. Traps were set for a minimum of 12 hours and a maximum of 24 hours before checking. Multiple trap-nights were completed at each site in an attempt to meet our ideal sample size and distribution of turtles across sites.

Measurements and Marking

Each captured turtle was weighed, measured, and sexed. We also marked individuals using the North American Code (Nagle et al. 2017) in case we wanted to conduct future population studies (e.g., see if turtle populations were declining in mechanically harvested areas). The 11 marginal scutes on the right side of the turtle were coded A through K and N through X on the left side (Figure 3-5). A unique identification code was assigned to each turtle by filing a notch on its marginal scutes using a triangular metal file. Each mark was read alphabetically. For example, a turtle with notches on scutes A, H, O, and V had an identification code of AHOV.

Global Positioning System (GPS) Tagging

Eastern musk turtles and painted turtles were tagged with Ecotone STERNA GPS-UHF and VHF transmitters (Ecotone Telemetry, Gdynia, Poland). The total weight of the transmitters was <5% of the body weight of each turtle to avoid significant impact on the behavior of the turtle (Innes et al. 2008). Transmitters were attached to the turtles' rear

marginal scutes using plumbers' putty and fast-drying epoxy (adapted from Christenson and Chow-Fraser 2014). The process of transmitter attachment was slightly different for painted turtles because they have deciduous scutes (i.e., scutes that shed off). So, we secured the GPS and VHF transmitters to the turtles by drilling two small holes in the margin of their carapace to attach the transmitters with wire. We attempted to monitor tagged turtles throughout the field season by downloading GPS data in the field using a Windows tablet and an EP-BS Base Station (Ecotone Telemetry, Gdynia, Poland).

Analysis

We analyzed our self-reported mechanical harvester bycatch survey and hand-sorted mechanical harvester survey data using single-factor ANOVAs to determine if there were differences in the number of turtles caught by species and bycatch between study sites. We also analyzed our turtle trapping data to assess differences in the size of turtles caught between sites. Additionally, we used Tukey's Honestly Significant Difference (HSD) test to compare turtle sizes between sites.

We applied two-sample t-tests to the self-reported mechanical harvester bycatch survey data to compare the number of bycaught living animals to bycaught dead animals. Similarly, we used two-sample t-tests on the hand-sorted bycatch survey data to assess whether bycatch rates differed between native plant-dominated and invasive plant-dominated areas. Lastly, we calculated catch-per-unit-effort (CPUE) for all bycaught organisms in both bycatch datasets.

Results

Self-Reported Mechanical Harvester Bycatch Survey

Mechanical harvester operators reported capturing a total of 43 turtles from four different species over the course of 18 days in the southern portion of Lake Champlain. They captured 23 turtles from 8/2/2023 – 8/15/2023 and 20 turtles from 7/23/2024 – 7/31/2024 (Table 3-1). There was no significant difference in the number of turtles caught among the different species, as indicated by our ANOVA results ($F_{(3, 68)} = 1.73, p = 0.17$). Harvester operators reported that all turtles were returned to the water alive and without injury.

In addition to the turtles detailed above, harvester operators reported capturing 11 additional animals (fish, one snake, and one frog) of which 4 were alive (Table 3-2). The 7 mortalities included 1 common watersnake (*Nerodia sipedon*) and 6 fish. The operators reported that this was the first watersnake they had ever captured. A total of 9 fish were captured by the harvesters. The captured fish included 2 pumpkinseed (*Lepomis gibbosus*), 1 northern pike (*Esox lucius*), 1 common carp (*Cyprinus carpio*), 1 bluegill (*Lepomis macrochirus*), and 5 black crappie (*Pomoxis nigromaculatus*). While onboard of a harvester, we counted 186 minnows being captured on Lake Bomoseen on 7/24/2024 over the course of 3 hours. We excluded them from the analyses because the harvester operators on Lake Champlain focused on larger game fish when completing their self-reported surveys.

Bycatch per hour was relatively low for total bycatch, as well as for turtles, fish, and living and dead individuals (Table 3-2). The average rate of bycatch was 0.38 per hour for all bycatch, 0.33 per hour for living bycatch, 0.05 per hour for dead bycatch, 0.30 per hour for turtles, and 0.06 per hour for fish. These rates are likely higher for fish if you include small fish (i.e., minnows, juveniles, etc.). For example, the rate of bycatch

per hour for minnows with our one sample from Lake Bomoseen was 61.67. However, this number may be inflated because small fish may be able to fall through the grates and back into the water once they are off the conveyor belt and in the harvester's barge. Alive animal capture rates were significantly higher than dead animal capture rates ($t_{(32)} = 3.97$, $p < 0.001$). These results suggest that there are low bycatch rates and even lower mortality, as all living bycatch noticed by harvester operators were returned immediately to the water.

Hand-Sorted Mechanical Harvester Bycatch Survey

We conducted 3 bycatch surveys at Lake Champlain and Lake Bomoseen where we systematically sorted through 1,401 liters of mechanically harvested plant material. Encountered animals included individuals from the orders Odonata and Coleoptera, mayflies (Order Ephemeroptera), zebra mussels (*Dreissena polymorpha*), snails, leeches, crawfish, bluegill, minnows, and shiners. We encountered 1,128 animals, with the vast majority being invertebrates (Table 3). Pelots Bay had the most bycatch, with most individuals being zebra mussels. Bycatch rates remained relatively low between the sites (Table 3-3). As stated before, very few fish were encountered during these surveys, suggesting that most small fish are able to slip through the grates within the barge of the mechanical harvester. There were no differences in bycatch between study sites ($F_{(2, 6)} = 1.52$, $p = 0.29$). There was also no difference between the amount of bycatch found in native plant dominated areas vs invasive plant dominated areas ($t_{(7)} = 1.42$, $p = 0.10$).

Turtle Trapping Results

We caught 220 turtles in hoop traps over the course of 344 trap nights from June-August 2023 and May-August 2024 (Table 3-4). 89.5% of captured individuals were painted turtles. Musk and painted turtles tended to be similar in size between each site (Table 3-A1). However, painted turtles at Benson Landing were significantly heavier than painted turtles at Lake Bomoseen ($p = 0.02$). Male and female turtles within each species were similar in weight between each site, but females did tend to be bigger than males (Table 3-A2). We recaptured 13 turtles between the sites, with 69.2% being males. All turtle recaptures occurred in Lake Champlain, with 1 recaptured painted turtle and 1 recaptured musk turtle at Benson Landing and 11 recaptured painted turtles at Pelots Bay. 210 fish were captured in our hoop traps (Table 3-5). All bluegill and bass (*Micropterus spp.*) survived, however, approximately 30% of the larger fish, including bowfin (*Amia calva*), common carp, common rudd (*Scardinius erythrophthalmus*), and tench (*Tinca tinca*), became entangled in the hoop trap netting and needed to be euthanized. We also had a double-crested cormorant (*Nannopterum auritum*) mortality after it was entangled in a hoop trap. These unexpected mortalities were reported to the Vermont Fish and Wildlife Department.

Turtle Tracking and Interactions with Mechanical Harvesters

We tagged a total of 29 turtles and 3 mechanical harvesters with GPS and VHF transmitters. Unfortunately, we were unable to recover most of the turtles or get close enough to download the data from our transmitters. Despite this, we didn't observe any negative impacts on the turtles from the GPS and VHF transmitters. We believe that the thick, submerged and emergent vegetation where our turtles were found interfered with the receiver's ability to pick up the signal from the transmitters.

Discussion

Few studies document the species and numbers of organisms bycaught during AIS control efforts (Chapter 2, this dissertation). This highlights the critical need for resource managers to systematically record unintended impacts of AIS control during treatments (Chapter 2, this dissertation). Such data are essential to ensure that both short-lived and long-lived organisms can persist in managed environments (Chiu and Kuo 2012; Li Veli et al. 2024). Our study aimed to address this gap by providing a practical framework for resource managers to adapt and implement in their AIS control projects.

Bycatch and bycatch-induced mortality rates were remarkably low in this study. Our CPUE calculations suggest that fewer than one individual is caught per hour across all animal groups, highlighting the minimal impact of this methodology on the integrity of aquatic ecosystems within this study. Notably, we found that relatively few turtles were removed from the water by the mechanical harvesters, and no turtles were found within our hand-sorted samples. However, eastern musk turtles were the most frequently captured species, supporting our hypotheses that small, cryptic, and poor-swimming turtles may be negatively impacted by mechanical harvesting. While bycatch rates were low in this study, it is important to note that our harvester operators were highly engaged and diligently scanned for turtles, returning them to the water when found. In other locations, particularly those with larger harvesting vessels or less conscientious operators, bycatch mortality rates could be higher. Had our operators not noticed and returned captured turtles, the impacts could have been more severe. Additionally, reporting accuracy may be biased (McCormick et al. 2015), but this bias can be reduced by placing cameras on harvesters or deploying observers to monitor the harvesting process. This

highlights the need for further research to assess the vulnerability of long-lived species to mechanical harvesting, particularly in areas where harvesting conditions differ from those in Lake Champlain. Nonetheless, we are fairly confident that bycatch rates in Lake Champlain are low, especially considering that we found no difference in bycatch across the study sites.

Very few studies have explored the unintended impacts of mechanical harvesting, with even fewer focusing on long-lived reptiles (Marcelino and Mosher 2025). To our knowledge, this is the first study to explore the effects of mechanical harvesting on turtle populations. This further emphasizes the need for resource managers to standardize data collection procedures while implementing AIS management (Savoca et al. 2020). We also found that mechanical harvester operators are extremely willing to assist in data collection efforts. Therefore, as long as resource managers supplied mechanical harvester operators with appropriate material, they could collect ecological data fairly quickly and with very little extra effort.

Mechanical harvesters tend to be in service for decades, meaning that the operators must maintain and upgrade them periodically (J. Strong, personal communication, August 6, 2024). This means that harvester operators need to be proficient in fabricating parts for maintenance, as well as parts to make the harvesting process more efficient. Thus, resource managers could work with mechanical harvester operators to improve the design of harvesters to further reduce bycatch. For example, the grates that allow water to drain out of the harvesters could be widened to ensure that small fish are able to escape capture. Another potential method to reduce bycatch rates

would be the development and implementation of an excluder device that could prevent larger fish and turtles from being captured (Brewer et al. 2006).

Monitoring plant communities is expensive and challenging for resource managers, but important in ensuring the health and integrity of an ecosystem (Marsh and Trenham 2008). Because mechanical harvesters tend not to be selective during management, native plants are inadvertently harvested during operation (Sharp et al. 2006). So, mechanical harvester plant bycatch could provide an easy and cost-effective opportunity for resource managers to obtain data on the plant diversity within an area of interest. This would also be a great opportunity for researchers to quantify invertebrate diversity. Therefore, researchers and resource managers would greatly benefit from forming relationships with mechanical harvesting operators.

We were extremely unsuccessful in our efforts to track turtles to see how they interacted with mechanical harvesters. However, we did gain some valuable insights. For example, we found that the North American Code (Nagle et al. 2017) was extremely fast and effective to use for both painted turtles and musk turtles. We were able to quickly mark over 100 turtles at Pelots Bay and would have been able to mark hundreds more without the possibility of running out of unique identifiers. Furthermore, this methodology was easy to teach to technicians and even easier to read and identify recaptured turtles. Additionally, even though our tracking efforts failed, determining how turtles interact with mechanical harvesters would further safeguard their populations. We suggest that extensive testing and potentially new technology development is needed for GPS transmitters to be effective in understanding fine-scale movement and behavior for freshwater turtles in highly vegetated habitats.

Our results suggested that mechanical harvester bycatch was fairly unimpactful on turtle populations. However, to our knowledge, this project is only the first study to attempt to quantify AIS mechanical harvesting impacts on turtle populations. More research must be conducted to understand the effects of AIS control on long-lived organisms. Future research should focus on longer-term monitoring of turtle populations in harvested areas and testing modifications to harvesters to prevent bycatch. These longer-term monitoring projects could include treating the relationship between turtles and mechanical harvesters as a predator-prey interaction. This could be accomplished by using radio telemetry to estimate turtle home ranges (Ouellette and Cardille 2011; Bowers et al. 2021) and comparing them to harvester “home ranges.” If possible, researchers should also attempt to compare “exposure to capture risk” (Hebblewhite and Merrill 2007). Understanding the relationship between turtles and harvesters will allow resource managers to adjust permit conditions to ensure that mechanical harvesters are minimally impacting native species.

Conclusion

This study represents a critical step towards understanding the unintended ecological impacts of AIS mechanical harvesting, particularly on turtle populations in the Lake Champlain Basin. Our findings indicate that bycatch rates, including mortality, were remarkably low across all surveyed sites. This suggests that mechanical harvesting is a relatively low risk AIS management strategy in terms of its impact on non-target aquatic species. While the results are promising, this study also underscores the need for continued monitoring to confirm the long-term safety of mechanical harvesting for vulnerable long-lived species like turtles.

The collaboration with mechanical harvester operators highlighted the potential for resource managers to leverage partnerships for efficient and cost-effective data collection. Additionally, our recommendations for equipment modifications, such as wider grates and excluder devices, present practical opportunities to further minimize bycatch. These insights can inform permit conditions and guide future management practices to better balance invasive species control with the conservation of native wildlife.

However, this research is only the beginning. More comprehensive and long-term studies are needed to fully understand the interactions between mechanical harvesters and native flora and fauna. Future work should focus on assessing population-level impacts, refining harvesters' designs to prevent bycatch, and developing standardized data collection protocols. By addressing these gaps, resource managers can enhance the ecological sustainability of AIS management methodologies.

Ultimately, this study contributes valuable insights to the growing body of literature on AIS control, emphasizing the importance of minimizing unintended ecological consequences while maintaining effective management. By prioritizing both invasive species mitigation and biodiversity conservation, resource managers can safeguard aquatic ecosystems in perpetuity.

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Tables

Table 3-1. The number of turtles captured by mechanical harvesters in the southern portion of Lake Champlain from 8/2/2023 – 8/15/2023 and 7/23/2024 – 7/31/2024.

Year	Musk Turtle	Painted Turtle	Snapping Turtle	Map Turtle	Total
2023	9	4	3	7	23
2024	10	4	6	0	20

Table 3-2. Bycatch rates and the number of living and dead animals captured by mechanical harvesters, based on self-reported data from the southern portion of Lake Champlain across all taxa.

Year	Alive	Dead	Total	Bycatch/Hour	Alive/Hour	Dead/Hour	Turtles/Hour	Fish/Hour
2023	25	5	30	0.42	0.35	0.07	0.32	0.07
2024	22	2	24	0.34	0.31	0.03	0.28	0.06

Animals consisted of turtles, fish, one snake, and one frog.

Table 3-3. Bycatch rates, the number of turtles, invertebrates (Invert.), and fish encountered, as well as the dominant plant species recorded during the hand-sorted bycatch surveys at Lake Champlain and Lake Bomoseen, VT.

Sample	Total	Turtles	Invert.	Fish	Total/Liter	Invert./Liter	Fish/Liter	Dominant Plant
Lake Bomoseen								
1	62	0	60	2	0.41	0.40	0.01	<i>Potamogeton spp.</i>
2	13	0	13	0	0.09	0.09	0.00	<i>Myriophyllum spicatum</i>
3	24	0	20	4	0.16	0.13	0.03	<i>Myriophyllum spicatum</i>
Pelot's Bay, Lake Champlain								
1	45	0	45	0	0.30	0.30	0.00	<i>Elodea spp.</i>
2	148	0	148	0	0.98	0.98	0.00	<i>Elodea spp.</i>
3	652	0	652	0	4.31	4.31	0.00	<i>Elodea spp.</i>
South Lake, Lake Champlain								
1	18	0	17	1	0.10	0.09	0.01	<i>Trapa natans</i>
2	35	0	33	2	0.23	0.22	0.01	<i>Trapa natans</i>
3	131	0	122	9	0.87	0.81	0.06	<i>Trapa natans</i>

Table 3-4. Number of turtles caught in hoop traps from June 2023 to August 2024 at Lake Champlain and Lake Bomoseen, VT.

Site	Map Turtle	Musk Turtle	Painted Turtle	Snapping Turtle	Spiny Softshell
Benson Landing	0	4	9	2	0
Lake Bomoseen	0	0	50	5	0
Pelots Bay	0	2	131	6	3
St. Albans Bay	1	0	7	0	0

Table 3-5. Fish bycatch caught in hoop traps from June 2023 to August 2024 in Lake Champlain and Lake Bomoseen, VT.

Species	Benson Landing	Lake Bomoseen	Pelots Bay	St. Albans Bay	Total
<i>Amia calva</i>	6	3	17	1	27
<i>Cyprinus carpio</i>	1	0	0	0	1
<i>Lepomis macrochirus</i>	0	0	1	0	1
<i>Micropterus dolomieu</i>	0	1	0	0	1
<i>Micropterus nigricans</i>	0	0	2	0	2
<i>Scardinius erythrophthalmus</i>	0	0	22	0	22
<i>Tinca tinca</i>	1	0	50	0	51

Figures



Figure 3-1. Aquatic invasive species mechanical harvester in a Vermont lake. Photo retrieved from <https://dec.vermont.gov/watershed/lakes-ponds/aquatic-invasives/control>.



Figure 3-2. An eastern musk turtle (*Sternotherus odoratus*) basking on a log. Photo retrieved from <https://www.vtherpatlas.org/herp-species-in-vermont/sternotherus-odoratus/>.

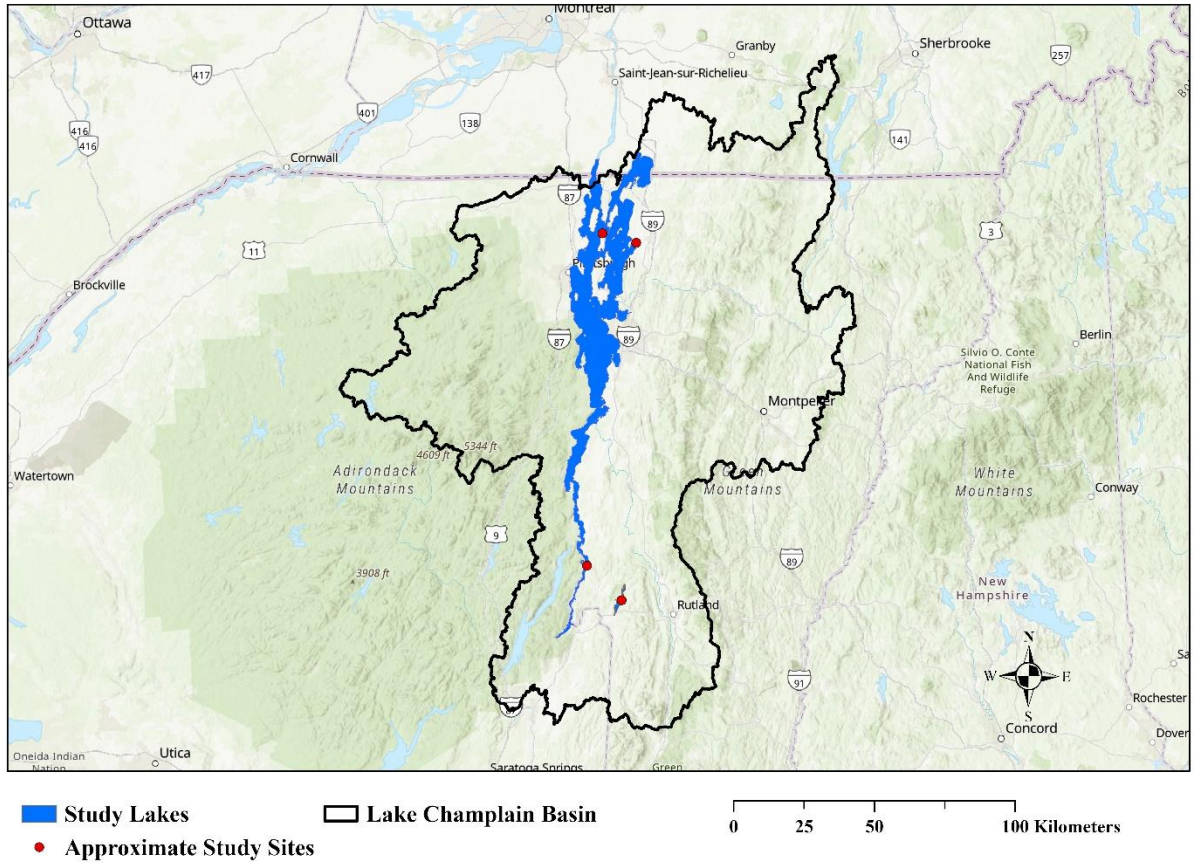


Figure 3-3. Lakes and site locations for studying the impact of aquatic invasive species mechanical harvesting on turtle populations in the Lake Champlain Basin.



Figure 3-4. A baited hoop trap in Lake Champlain.

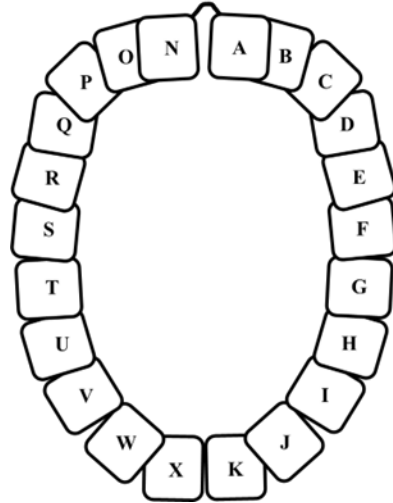


Figure 3-5. North American coding system schematic for kinosternid turtles, as viewed dorsally on the carapace with the anterior end up. Adapted from Nagle et al. (2017).

Appendix

Table 3-A1. Summary statistics of musk and painted turtles caught from June 2023 to August 2024 at Lake Champlain and Lake Bomoseen, VT.

Site	Musk Turtle	Painted Turtle	Total
Benson Landing			
N	4	9	13
Average Weight	281.7	401.7	371.7
Average Carapace Length	124.0	146.4	140.8
Average Carapace Width	83.5	106.3	100.6
Average Plastron Length	81.9	133.8	120.8
Average Plastron Width	44.8	69.1	63.0
Lake Bomoseen			
N	N/A	50	50
Average Weight	N/A	297.6	297.6
Average Carapace Length	N/A	130.6	130.6
Average Carapace Width	N/A	95.1	95.1
Average Plastron Length	N/A	121.7	121.7
Average Plastron Width	N/A	63.4	63.4
Pelots Bay			
N	2	131	133
Average Weight	285	332.7	331.9
Average Carapace Length	123.25	135.6	135.4
Average Carapace Width	81.65	98.5	98.3
Average Plastron Length	84.15	125.8	125.2
Average Plastron Width	43.95	68.8	68.4
St. Albans Bay			
N	N/A	7	7
Average Weight	N/A	360.7	360.7
Average Carapace Length	N/A	151.6	151.6
Average Carapace Width	N/A	102.9	102.9
Average Plastron Length	N/A	128.6	128.6
Average Plastron Width	N/A	66.9	66.9

Table 3-A2. Summary statistics of female and male painted turtles caught from June 2023 to August 2024 at Lake Champlain and Lake Bomoseen, VT.

Site	Female	Male	Unknown
Benson Landing			
N	5	4	N/A
Average Weight	461.00	327.50	N/A
Average Carapace Length	155.40	135.23	N/A
Average Carapace Width	113.00	98.00	N/A
Average Plastron Length	141.20	124.55	N/A
Average Plastron Width	72.60	64.63	N/A
Lake Bomoseen			
N	7	33	10
Average Weight	399.29	269.50	362.5
Average Carapace Length	142.71	127.15	139.6
Average Carapace Width	104.54	92.56	100.95
Average Plastron Length	135.29	117.87	131.8
Average Plastron Width	69.39	61.75	66.7
Pelots Bay			
N	31	95	5
Average Weight	429.35	296.26	430
Average Carapace Length	147.56	131.11	147.8
Average Carapace Width	108.09	95.08	104.075
Average Plastron Length	139.14	120.97	135.2
Average Plastron Width	70.40	68.24	68.25
St. Albans Bay			
N	3	4	N/A
Average Weight	428.33	310.00	N/A
Average Carapace Length	147.33	154.75	N/A
Average Carapace Width	107.00	99.75	N/A
Average Plastron Length	137.00	122.25	N/A
Average Plastron Width	70.67	64.00	N/A

**CHAPTER 4: USING POLYVINYL CHLORIDE PIPES TO BRIDGE
KNOWLEDGE GAPS: COMPREHENSIVE GRAY TREEFROG MONITORING
AND CONSERVATION IN A CHANGING WORLD**

Abstract

Understanding species' habitat associations is crucial for biodiversity conservation, especially in the face of climate change and habitat loss. Gray treefrogs (*Hyla versicolor*), though classified as least concern, have significant knowledge gaps regarding their terrestrial and overwintering behaviors. This study evaluates the effectiveness of Polyvinyl Chloride (PVC) pipes as a monitoring tool for gray treefrogs in the northeastern United States to address these gaps. Over two years, PVC pipe arrays were deployed across eight study sites, capturing 179 individuals with a 10.1% recapture rate. Habitat variables such as basal area, elevation, and maximum temperature significantly influenced capture success, with higher temperatures and later dates in the year correlating to higher capture rates. Additionally, radio telemetry provided initial insights into overwintering behavior, with tracked individuals seeking refuge in tree canopies and brush piles as temperatures approached freezing. Our findings highlight PVC pipes as a cost-effective and scalable method for long-term treefrog monitoring, extending beyond the breeding season to provide critical data on habitat use. While challenges remain in tracking overwintering behaviors, refining telemetry methods and increasing sample sizes could improve our understanding of treefrog ecology in colder climates. Additionally, integrating community science initiatives could enhance monitoring capacity and public engagement in amphibian conservation. This research contributes to broader efforts to safeguard amphibians against climate change and habitat loss by improving knowledge of

seasonal habitat use and refining monitoring techniques for long-term conservation planning.

Key words – winter ecology, conservation, community science, long-term monitoring, radiotelemetry

Introduction

Human-induced climate change and habitat loss are among the greatest threats to biodiversity worldwide, altering ecosystems and reshaping species distributions (Brooks et al. 2002; Malcolm et al. 2006; Sinervo et al. 2010; Bellard 2012; Foden et al. 2013; Warren et al. 2013). As global temperatures and landscapes are fragmented, species must adjust to shifting temperature and moisture regimes, seasonal variations, and habitat availability. One in six species is projected to go extinct if these environmental changes continue unabated (Urban 2015). While governments worldwide are taking steps to mitigate climate change and protect biodiversity (Paris Agreement 2018; Executive Order No. 14,008, 2021; Community Resilience and Biodiversity Act 2023), conservation efforts require a deeper understanding of species' ecological needs and their responses to changing environmental conditions. Studying how wildlife interacts with key climatic and seasonal variables is essential for developing effective conservation strategies in a rapidly changing world (Lathrop and Bognar 1998; Wilson et al. 2006; Belote et al. 2021; Matthipoulos et al. 2023).

Amphibians are particularly vulnerable to the effects of climate change and habitat loss, as their survival depends on specific temperature and moisture conditions (Foden et al. 2013). Rising global temperatures, shifting precipitation patterns, and increased frequency of extreme weather events threaten amphibian populations by altering breeding cycles, drying critical habitats, and exacerbating disease outbreaks (Lawler et al. 2010; Winter et al. 2016). Approximately 41% of amphibian species are at risk of extinction, making them the most threatened group of vertebrates. Additionally, 16% of amphibian species are classified by the International Union for Conservation of

Nature (IUCN) as data deficient, meaning that their conservation status remains uncertain (IUCN Species Survival Commission 2012; Wren et al. 2015; Bland et al. 2016). Despite their vulnerability, amphibians remain underrepresented in conservation planning, in part due to biases favoring mammals and a lack of comprehensive data on their habitat requirements across seasons (Santos et al. 2020). Understanding how amphibians respond to environmental variability is critical for predicting their future distributions and ensuring their persistence in a changing climate.

Gray treefrogs (*Hyla versicolor*) are classified by the IUCN as being a species of least concern (IUCN 2015). However, very little is known about the gray treefrog's natural history. For example, there is uncertainty surrounding gray treefrogs' hibernation strategy and very little is known about how they use terrestrial habitat outside of their breeding season (Johnson and Semlitsch 2003; Johnson et al. 2007; Raithel 2019). We need to keep common species common if we are to ensure biodiversity across the globe. This can only be accomplished by understanding fundamental habitat requirements for persistence and protecting their crucial habitat (Hanauska-Brown et al. 2011; Watson and Watson 2015; Santos et al. 2020).

Many sampling methods are used to monitor gray treefrogs, including nighttime road searches and acoustic monitoring (Mazerolle 2004; Pomezanski 2021). However, due to their cryptic nature, most monitoring efforts only occur during the spring while gray treefrogs are breeding (Raithel 2019). Therefore, passive trapping methodologies, such as using Polyvinyl Chloride (PVC) pipes as artificial refugia, could be important in helping scientists gain a better understanding of the natural history of the gray treefrog outside of the breeding season and in terrestrial habitats. PVC pipes have been used to

monitor various treefrog species throughout the globe (Hoffman et al. 2009; Glorioso and Waddle 2014; McGrath-Blaser 2021). Most of the studies involving PVC pipes have been conducted in the southeastern United States and South America. To our knowledge, the northernmost published PVC pipe studies have occurred in North Carolina and Missouri, USA making it unclear whether PVC is a viable method for studying treefrogs at northern latitudes where shorter active seasons and differences in forest composition might reduce their utility (Glorioso and Waddle 2014).

Currently, gray treefrogs occur throughout much of the eastern United States and southeast Canada (IUCN 2015). However, due to global warming and habitat loss, the gray treefrog's range may change (Titley et al. 2021). Therefore, PVC pipes would allow resource managers to gain a baseline understanding of the distribution of gray treefrogs, and how they use their habitat throughout their current range. Furthermore, this methodology could be adapted to conduct long-term monitoring projects, as well as provide a means for researchers to capture and attach GPS transmitters to frogs for spatial studies. This information can help influence a more holistic approach to land conservation.

The objectives of this study are: 1) to investigate the effectiveness of PVC pipes at capturing and monitoring gray treefrogs in the northeastern United States; 2) determining what habitat variables (i.e., basal area, tree type, weather, etc.) are important for gray treefrog occurrence; and 3) determine gray treefrog winter habitat selection. We hypothesized that more gray treefrogs would be captured in areas with higher basal area, due to trees being smaller and having fewer natural cavities for the frogs to occupy.

Methods

Study Area

There were eight study areas in this project: Macrae Farm Park in Colchester, VT; Porter Point Natural Area in Colchester, VT; Ethan Allen Homestead in Burlington, VT; Centennial Woods in Burlington, VT; the Intervale Center in Burlington, VT; the Watershed Center in Bristol, VT; Birds of Vermont Museum in Huntington, VT; and Raven Ridge in Monkton, VT. Each study area included a matrix of habitats that includes both wetland and upland habitat. Additionally, gray treefrogs had been heard or observed at each survey area before trap deployment.

Study Species

Gray treefrogs have long thin limbs and plump bodies. They have long, partly webbed toes, with large toepads that produce mucous, which allows them to climb many different surfaces (Smith et al. 2006). Gray treefrogs lack dorsolateral folds and the dorsum skin is dotted with numerous dermal glands that produce a toxic secretion (Raithel 2019). Gray treefrog skin coloration varies from green to brownish gray in response to its environment. Their limbs have dark traverse bars, with bright yellow interspersed with dark gray reticulations, on their lower flanks and inner thighs (Brodie and Formanowicz 1981).

There are subtle differences between male and female gray treefrogs. Male gray treefrogs have throats that are very dark or heavily spotted with black, whereas females have throats that are white or have very few black spots. During the breeding season the

male's vocal sac has a balloon-like appearance when it is inflated. When the vocal sac is not inflated it looks like loose skin under their chins (Raithel 2019).

During much of the year gray treefrogs are arboreal. They will often move to the ground during rainy or humid weather to forage and breed (Raithel 2019). In Vermont (Abenaki place name, N'dakinna), gray treefrogs breed from April through July. They typically breed in standing or slow-moving water that has abundant vegetation (Vermont Reptile & Amphibian Atlas 2021). Very little is known about how gray treefrogs use terrestrial habitats outside of the breeding season (Raithel 2019).

Gray treefrogs are capable of using glycerol mobilization to avoid freeze induced mortality (Layne and Jones 2001). However, the extent to which their freeze tolerance protects them, and the duration before cells incur damage, remains relatively unknown (Irwin and Lee 2003). Furthermore, their overwintering location – whether in tree canopies, under bark, or on the ground – remains largely unknown. Prior studies suggest that treefrogs use the aforementioned microhabitats as hibernacula non-randomly up to 340 meters away from wetlands (Johnson et al. 2007; Johnson et al. 2008).

Survey Methods

We set up two PVC pipe arrays at each of the eight study locations. Each study area had two study arrays. One array was placed in an area with low basal area (less than 100 BA/ft²), while the other array was placed in an area with high basal area (more than 100 BA/ft²) (Mississippi Wildlife, Fisheries, & Parks 2021). Each array contained 25 PVC pipes that were attached to trees (Figure 4-1). The pipes were 60 cm long, had a diameter of 3.8 cm, were capped at the bottom, had a hole drilled ~15 cm above the cap

to drain excess water, and had a string inside to ensure that small mammals could escape the trap. Each pipe was hung 2 meters from the ground. Our survey methodology was adapted from Glorioso and Waddle (2014).

We were interested to see whether basal area (BA) impacted capture probability for gray treefrogs. So, BA was measured at each array using a BAF 10 angle gauge (Forestry Suppliers, Mississippi, USA). We also recorded the diameter at breast height (DBH) of each tree that we hung PVC pipes on. Additionally, we recorded the tree type, humidity, maximum temperature, minimum temperature, precipitation, elevation, and day of year (DOY), and quadratic day of year (QDOY) for each site visit.

Trap mortality for this method is negligible because treefrogs can move in and out of the PVC pipes freely. Therefore, there is a great deal of flexibility in checking the traps (Glorioso and Waddle 2014). However, we checked each trap array bi-weekly from early June to late October in 2022 and from late June to late October in 2023. We were unable to completely follow our bi-weekly trap checking schedule during the summer of 2023, due to extreme flooding. Once captured, treefrogs were removed from the pipe by shaking them out of the PVC pipes into a small plastic bag. Frogs were held until they were sexed and snout-vent length (SVL) was measured.

Gray treefrogs were marked with visual implant elastomer (VIE, Northwestern Marine Technology, Inc., Shaw Island, WA, USA) to determine recapture rates and to determine whether VIE was effective for long-term monitoring of gray treefrogs. VIE is a two-part silicone-based material which cures to a pliable consistency, which can be seen using ultraviolet light. Marks were injected using a 29-gauge insulin needle, which was disinfected between individuals using alcohol pads (adapted from Bainbridge et al. 2015).

Previous studies suggested that VIE marks are retained by individuals and that there is little bias in identification of marked individuals (Bailey 2004; Grant 2008). Furthermore, VIE marking has not been found to reduce survival and growth rates of juvenile or adult treefrogs (Sapsford et al. 2014; Bainbridge et al. 2015).

Radio Telemetry

We wanted to determine where gray treefrogs overwintered within their habitat. Therefore, we attempted to capture adult gray treefrogs during the late fall of 2024 at Centennial Woods, Porter Point, and Raven Ridge; and attach VHF transmitters to them using waistbands (adapted from McGarrity and Johnson 2010; Groff et al. 2015). Transmitters that exceed 10% of a frog's mass could negatively impact their health and behavior (McGarrity and Johnson 2010). Therefore, VHF transmitters were under 10% of each tagged frog's bodyweight. The average gray treefrog weighs approximately 7.12 g (Mueller 2006). So, transmitters and waistbelts were under 0.72 g in total mass.

We used a transmitter (Series A1025, Advanced Telemetry Systems, Isanti MN, USA) that weighed approximately 0.65 g, which should have given us a battery life between 28 and 44 days. We tested the fit of the transmitters on captive gray treefrogs at the ECHO Leahy Center for Lake Champlain prior to deployment to ensure that the attachment method would not negatively impact the frogs. We used 1 mm-diameter stretch bead cord to attach transmitters to captured treefrogs. We restrained the treefrog's rear legs and positioned the waistband around the frog's pelvic girdle, ensuring that a 0.25-0.5 cm gap remained between the sacral hump and the waistband when the transmitter was pulled away from the frog's body (adapted from McGarrity and Johnson

2010; Groff et al. 2015) (Figure 4-2). Tracking occurred at each site at least twice a week from early October to early December.

Analysis

We used R to perform negative binomial regression modeling with trap abundance (i.e., number of frogs inside of PVC pipe traps) as our response variable for our site-level model set and binomial regression modeling with probability of capture for our trap-level model set (Venables et al. 2002; R Core Team 2021). We examined the distribution of trap abundance using histograms and performed goodness of fit tests on Poisson and negative binomial models to determine what modeling approach would be most appropriate for our data. The negative binomial model was a better fit and the Akaike Information Criterion Corrected (AICc) was much better compared to the Poisson models.

Our covariates for our negative binomial and binomial regression model sets included BA, humidity, maximum temperature, minimum temperature, precipitation, elevation, DOY, and QDOY for the site-level model set. The trap-level model set included all of the aforementioned covariates, with the addition of DBH and tree type (Table 4-1). We hypothesized that humidity, precipitation, and elevation would have a negative relationship with abundance and probability of capture, while temperature and DOY would have a positive relationship with abundance and probability of capture. Additionally, we hypothesized that trap abundance and probability of capture would decrease as BA increased. Lastly, we hypothesized that DBH would have a negative effect on probability of capture; and that traps on deciduous trees would have a higher likelihood of capture success compared to those on coniferous trees.

For the site-level model set, we fit 256 models for all combinations of our covariates (Table 4-A1). For the trap-level model set, we fit 512 models for all combinations of our covariates (Table 4-A2). We calculated the AICc, which is a measure that balances goodness of fit with model complexity. Lower AICc values are indicative of a more parsimonious model (Burnham and Anderson 2004). We compared AICc values by calculating the difference in AICc values (ΔAICc) and AICc weights. A difference of 2 or more indicates substantial evidence in favor of the model with the lower AICc value (Aikaike 1874). When multiple models had $\Delta\text{AICc} < 2$ and relatively low model weight, we performed model averaging using the MuMIn package in R (Bartoń 2020) to account for model uncertainty and derive averaged parameter estimates. We also completed Chi-Square tests to ensure that our data properly fit our models.

Results

Survey Results

From 2022 to 2023, over the course of 75 total visits at each of our survey sites, we captured 179 gray treefrogs in our PVC pipe traps. We captured at least 1 treefrog in 56% of our site visits. The number of gray treefrogs captured in a single PVC pipe varied from 0 to 3 individuals. The highest number of gray treefrogs captured in a single array during a site visit was 22 individuals. During our study we marked 163 individuals, with 16 individuals being too small to be marked. We recaptured 10.1% of marked individuals at least once. The average SVL for captured treefrogs was 38.8 mm (39 mm for males, 36 mm for females, and 32 mm for unknown individuals). The sex ratio of captured treefrogs was 1.3 males to females.

Trap-level Modeling

Our top 5 trap-level models accounted for 46.8% of the model weight, with the best model receiving 12.3% of the model weight (Table 4-2). The top model included BA, DBH, DOY, elevation, and maximum temperature. This model demonstrates that the aforementioned covariates have a significant impact on PVC trap probability of capture. DOY and maximum temperature had positive effects, while BA, DBH, and elevation had negative effects on probability of capture (Table 4-3). The top model (AIC = 1276.0) was a better fit than the null model (AIC = 1372.9, $X^2_{(5)} = 106.94$, $p < 0.001$).

Given that multiple models had $\Delta AICc < 2$, we used model averaging to account for model uncertainty and obtain more stable coefficient estimates. The averaged trap-level model included BA, DBH, DOY, elevation, humidity, maximum temperature, minimum temperature, precipitation, and tree type, though humidity, minimum temperature, precipitation, and tree type had little influence. Consistent with the top trap-level model, DOY and maximum temperature had positive effects on PVC trap probability of capture, while BA, DBH, and elevation had negative effects (Figure 4-3). These results suggest that treefrog probability of capture in PVC pipe traps increases as the year progresses and with higher maximum temperatures, while it decreases in traps that are attached to larger trees (higher DBH) that are coniferous, in areas with higher BA, and at higher elevations. The model-averaged results reinforce the conclusions from our top model, suggesting that both microhabitat characteristics and broader environmental factors influence gray treefrogs use of PVC pipe traps.

Site-level Modeling

Our top 5 site-level models accounted for 40.8% of the model weight, with the best model receiving 10.8% of the model weight (Table 4-2). The top model included DOY, and elevation. This model suggests that PVC trap abundance is significantly influenced by the previously mentioned covariates. DOY had a positive effect, while elevation had a negative effect on abundance (Table 4-3). The top model (AIC = 417.7) was a better fit than the null model (AIC = 442.67).

Similarly to the trap-level models, multiple models had $\Delta AICc < 2$, so we used model averaging to account for model uncertainty and obtain more robust coefficient estimates. The averaged site-level model included BA, DOY, elevation, humidity, maximum temperature, minimum temperature, precipitation, and QDOY, though precipitation had little influence ($p = 0.74$). The direction and significance of covariates remained consistent with the top site-level model, with DOY and maximum temperature having positive effects on PVC trap abundance, while BA, elevation, and humidity had negative effects. Additionally, QDOY suggests that abundance will be higher before and after the breeding season (Figure 4-3). These results suggest that treefrog abundance in PVC pipe traps increases with warmer temperatures and increases seasonally, while abundance in PVC pipe traps decreases at higher elevations and under more humid conditions. The model-averaged results reinforce the conclusions from our top model, suggesting that these environmental factors significantly shape gray treefrog abundance in PVC traps.

Radio Telemetry

Unlike previous years in this study, inconsistent weather from early October to late November 2024 negatively affected the number of gray treefrogs captured

(unpublished data). Therefore, we were only able to successfully trap and tag four gray treefrogs. Three of the transmitters remained active between 28 – 48 days. However, one of the transmitters only remained active for 9 days. We are unsure whether the transmitter loss was due to battery depletion, the frog leaving the study area, or a predation event. We tracked the three individuals with active transmitters two to three times per week, and none moved more than 40 meters between successive fixes. The tracking period was characterized by dry and cold weather, with temperatures occasionally dropping below freezing. Although we were unable to track the frogs through the winter, we observed that they were either in the tree canopy or within brush piles as temperatures approached freezing.

Discussion

Our study demonstrates that PVC pipes are an effective method for capturing gray treefrogs in the northern parts of their range. The average capture rate of 2.4 individuals per site visit underscores the potential of this method to monitor gray treefrogs outside of their breeding season. Furthermore, the number of captured individuals was consistent with anuran studies in other regions (Johnson et al. 2008; Glorioso and Waddle 2014). Additionally, PVC pipes had relatively low negative impacts on other taxa within the environment. For example, we only observed a total of 9 dead rodents in our traps over the entirety of our study, with our traps being deployed for over 181 days.

Our model results provided evidence that key habitat variables influence PVC pipe trapping success, aligning with ecological expectations. Trapping success was lower in forests with higher BA, likely because larger trees (increased DBH) provide more natural refugia for treefrogs (Johnson et al. 2008). Similarly, forests at higher elevations,

which are more likely to contain coniferous trees, may negatively impact amphibian occurrence due to increased habitat acidification (Freda and Dunson 1986; Wyman 1988; Wyman and Jancola 1992). On days with higher humidity, trapping success was reduced, which may be due to treefrogs being more active and foraging outside of PVC refugia under such conditions (Raithel 2019). Additionally, trapping success increased with DOY, likely reflecting rising temperatures over time. Since higher temperatures are often accompanied by decreased relative humidity (Elovitz 1999), this may create less favorable conditions for treefrog foraging, leading to increased use of PVC pipes.

We observed a substantial increase in capture probability around DOY 230 (mid-August), suggesting a peak in post breeding activity likely driven by increased movement and dispersal from breeding sites. QDOY appeared to suggest a seasonal pattern in capture success: it declined leading up to the breeding season, flattened during peak breeding, and then increased afterward. This indicates that capture probability is relatively stable during the breeding season but is influenced more strongly by seasonal effects before and after this period. Therefore, the model results align with the natural history of gray treefrogs, highlighting distinct seasonal patterns in capture probability. The increase in capture probability post-breeding season suggests that monitoring efforts using PVC pipe traps should be intensified from mid-July to early September to maximize capture rates and gather valuable data on gray treefrog populations.

VIE may provide a relatively straightforward method for conducting amphibian capture-mark-recapture studies with good mark retention (Bailey 2004). However, we found this technique challenging to use on adult gray treefrogs due to their elastic skin, which made it challenging for needle penetration and the administration of VIE beneath

the skin. Additionally, we observed some marks migrating, likely a result of the skin's elasticity. Despite these challenges, we consider VIE a more humane and effective marking method compared to toe-clipping (Heard et al. 2008; Schmidt and Schwarzkopf 2010), particularly for studies that do not require individual frogs to have unique marks.

This study strongly supports the use of PVC pipe trap arrays for long-term monitoring of gray treefrogs across their range. These traps are cost-effective, simple to construct and install, low maintenance, and require minimal personnel hours throughout the year. Furthermore, resource managers could further streamline treefrog population monitoring by leveraging community science (Tulloch et al. 2013; Freiwald et al. 2018). For example, partnerships with local conservation organizations, science centers, and elementary and secondary schools could facilitate the setting up and monitoring of PVC pipe trap arrays by volunteers, who could record observations and contribute data to community science databases. This collaborative approach would not only enhance data collection but also foster community engagement in conservation efforts and raise public awareness about amphibian ecology and habitat conservation (Schuttler et al. 2019; Nance et al. 2024).

Although we were unable to track gray treefrogs until temperatures dropped below freezing, we remain confident that this tracking method is well-suited for future studies. The frogs moved freely and appeared unaffected in their environment, allowing us to reliably track each individual to its specific location during each tracking session. With additional resources, we would purchase additional transmitters to replace those with depleted batteries. This approach would involve trapping and tagging treefrogs earlier in the fall, tracking their movements, and replacing transmitters at regular

intervals. These adjustments would allow us to capture and mark an adequate sample size while extending our tracking efforts into the winter months when temperatures fall below freezing.

This study highlights the utility of PVC pipe traps as a cost-effective and scalable method for monitoring gray treefrog populations across their range, providing critical baseline data on their habitat use and distribution. By increasing our understanding of species' ecological needs, this approach can help inform broader biodiversity conservation efforts aimed at protecting habitat and maintaining ecosystem resilience. Effective habitat monitoring and protection for species like gray treefrogs contribute to preserving ecosystem functionality in the face of climate change and habitat loss, ensuring that conservation strategies are grounded in species-specific ecological data.

Conclusion

This study demonstrates the efficacy of PVC pipe traps as a reliable and scalable method for monitoring gray treefrog populations in the northernmost parts of their range. By capturing critical data on habitat use and environmental factors influencing treefrog abundance, we fill important knowledge gaps about this species' terrestrial and seasonal behavior. Our findings highlight the potential for PVC pipe traps to extend monitoring beyond the breeding season, providing resource managers with a practical tool for long-term amphibian conservation.

While our radio telemetry efforts faced challenges, they provided initial insights into overwintering behaviors, suggesting that treefrogs seek refuge in tree canopies and brush piles as temperatures approach freezing. Future studies should refine tracking

methods, increase sample sizes, and extend monitoring into freezing temperatures to better understand treefrog winter ecology. Additionally, integrating community science efforts could expand long-term monitoring capacity and foster public engagement in amphibian conservation.

By improving our understanding of gray treefrog habitat use across seasons, this study contributes to broader efforts to safeguard amphibian populations in the face of climate change and habitat loss. Continued development of cost-effective and accessible monitoring techniques will be essential for ensuring the persistence of common species like the gray treefrog, which play a vital role in maintaining ecological balance.

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Tables

Table 4-1. Covariates used to predict Polyvinyl Chloride pipe gray treefrog abundance in Vermont.

Covariate	Code	Description	Data Source
Basal area	BA	The basal area of a survey site.	Field data
Diameter at breast height	DBH	The diameter measured at breast height of each tree measured in centimeters.	Field data
Day of year	DOY	The day of year starting from January 1st (day 1) and ending December 31st (day 365).	Field data
Elevation	Elev	The elevation above sea level of an array measured in meters.	Field data
Humidity	Humid	The average humidity of the given survey measured as a percentage.	NOAA*
Minimum temperature	TempMn	The minimum temperature of the given survey measured in Celsius	NOAA*
Maximum temperature	TempMx	The maximum temperature of the given survey measured in Celsius	NOAA*
Precipitation	Precip	The total amount of precipitation (rain or snow) of the given survey measured in centimeters.	NOAA*
Quadratic of Day of Year	QDOY	The quadratic of day of year.	Field data
Tree type	Type	Whether the tree type where a trap was placed was coniferous or deciduous.	Field data

**National Centers for Environmental Information. (Accessed on February 8, 2024). NOAA Climate Data Online (CDO) – Datasets. Retrieved from ncei.noaa.gov/cdo-web/datasets*

Table 4-2. Top 5 models for predicting Polyvinyl Chloride pipe gray treefrog trap capture probability and abundance in Vermont.

Model	N Parameters	AICc	Δ AICc	Weight
Trap-level				
BA + DBH + DOY + Elev + TempMx	6	1276.00	0.00	0.12
BA + DBH + DOY + Elev + TempMx + TempMn	7	1276.20	0.19	0.11
BA + DBH + DOY + Elev + TempMx + Type	7	1276.80	0.78	0.08
BA + DBH + DOY + Elev + TempMx + TempMn + Type	8	1276.90	0.84	0.08
BA + DBH + DOY + Elev + Humid + TempMx	7	1277.20	1.18	0.07
Site-level				
DOY + Elev	4	417.7	0.00	0.11
DOY	3	415.0	0.23	0.10
DOY + Elev + TempMx	5	415.4	0.66	0.08
DOY + TempMx	4	415.8	1.05	0.06
DOY + Elev + QDOY	5	415.8	1.09	0.06

Table 4-3. Top model results for predicting Polyvinyl Chloride pipe gray treefrog capture probability and abundance in Vermont.

	Estimate	z-value	95%CI
Trap-level			
Intercept	-10.091	-8.82	-12.3707 – -7.8827
BA	-0.301	-1.83	-0.6258 – 0.0190
DBH	-0.011	-1.86	-0.0236 – 0.0003
DOY	0.027	8.40	0.0205 – 0.0329
Elev	-0.005	-3.23	-0.0078 – -0.0020
TempMx	0.069	3.65	0.0324 – 0.1064
Site-level			
Intercept	-4.487	-5.17	-6.3125 – -2.7402
DOY	0.022	5.74	0.0141 – 0.0293
Elev	-0.004	-1.72	-0.0085 – 0.0010

Figures



Figure 4-1. Polyvinyl Chloride (PVC) pipe attached to trees at Raven Ridge in Monkton, Vermont.



Figure 4-2. Gray treefrog with a waistband-mounted radio transmitter used to track treefrogs to winter hibernacula during the fall of 2024 (adapted from Groff et al. 2015).

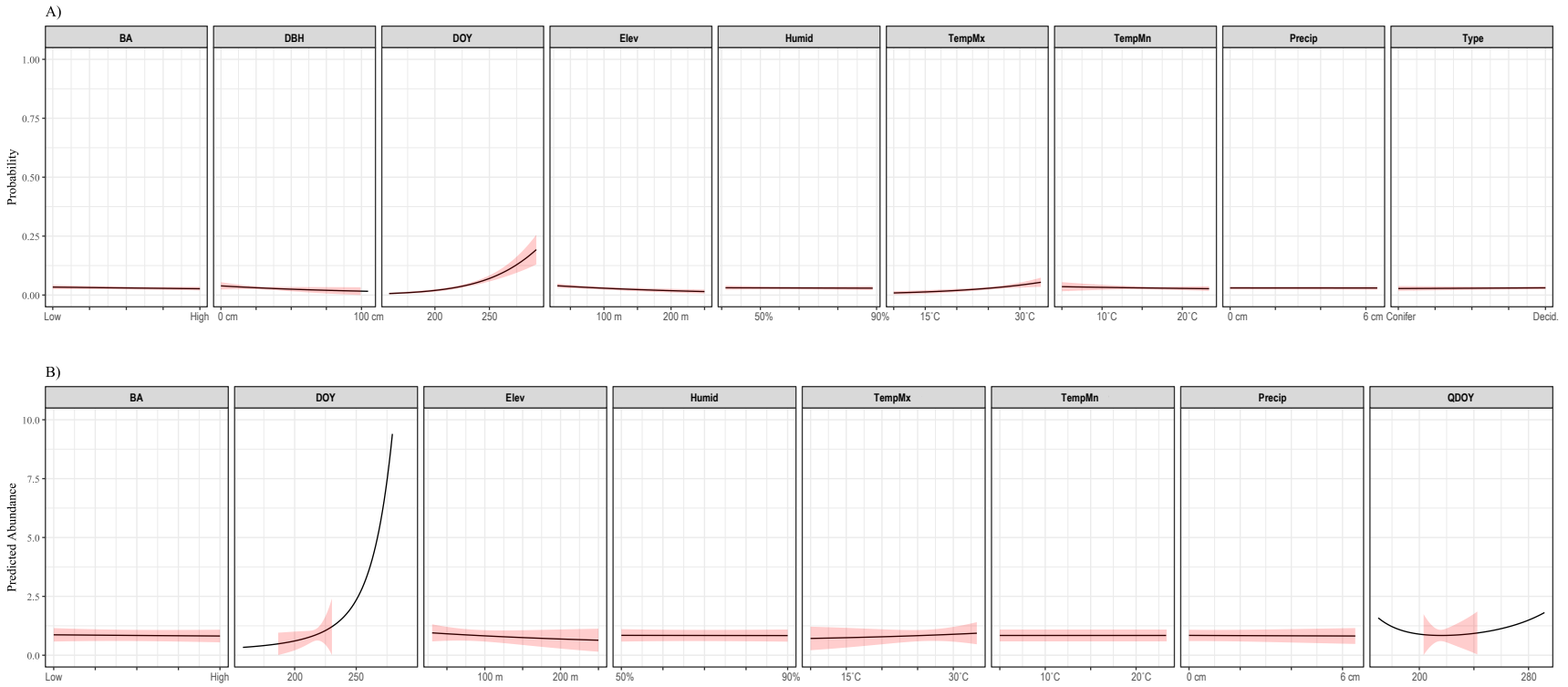


Figure 4-3. Partial dependence plots showing predicted gray treefrog abundance across habitat and climatic variables. (A) Trap-level and (B) site-level model-averaged predictions. Black lines show estimates, with red shading indicating 95% confidence intervals.

Appendix

Table 4-A1. Site-level model set with all covariate combinations for Poisson regression modeling for Polyvinyl Chloride pipe gray treefrog abundance in Vermont.

Model
Null
BA
DOY
Elev
Humid
TempMx
TempMn
Precip
QDOY
BA + DOY
BA + Elev
DOY + Elev
BA + Humid
DOY + Humid
Elev + Humid
BA + TempMx
DOY + TempMx
Elev + TempMx
Humid + TempMx
BA + TempMn
DOY + TempMn
Elev + TempMn
Humid + TempMn
TempMn + TempMx
BA + Precip
DOY + Precip
Elev + Precip
Humid + Precip
TempMx + Precip
TempMn + Precip
BA + QDOY
DOY + QDOY
Elev + QDOY
Humid + QDOY
TempMx + QDOY
TempMn + QDOY
Precip + QDOY
BA + DOY + Elev

BA + DOY + Humid
BA + Elev + Humid
DOY + Elev + Humid
BA + DOY + TempMx
BA + Elev + TempMx
DOY + Elev + TempMx
BA + Humid + TempMx
DOY + Humid + TempMx
Elev + Humid + TempMx
BA + DOY + TempMn
BA + Elev + TempMn
DOY + Elev + TempMn
BA + Humid + TempMn
DOY + Humid + TempMn
Elev + Humid + TempMn
BA + TempMn + TempMx
DOY + TempMn + TempMx
Elev + TempMn + TempMx
Humid + TempMn + TempMx
BA + DOY + Precip
BA + Elev + Precip
DOY + Elev + Precip
BA + Humid + Precip
DOY + Humid + Precip
Elev + Humid + Precip
BA + TempMx + Precip
DOY + TempMx + Precip
Elev + TempMx + Precip
Humid + TempMx + Precip
BA + TempMn + Precip
DOY + TempMn + Precip
Elev + TempMn + Precip
Humid + TempMn + Precip
TempMn + TempMx + Precip
BA + DOY + QDOY
BA + Elev + QDOY
DOY + Elev + QDOY
BA + Humid + QDOY
DOY + Humid + QDOY
Elev + Humid + QDOY
BA + TempMx + QDOY
DOY + TempMx + QDOY
Elev + TempMx + QDOY

Humid + TempMx + QDOY
BA + TempMn + QDOY
DOY + TempMn + QDOY
Elev + TempMn + QDOY
Humid + TempMn + QDOY
TempMn + TempMx + QDOY
BA + Precip + QDOY
DOY + Precip + QDOY
Elev + Precip + QDOY
Humid + Precip + QDOY
TempMx + Precip + QDOY
TempMn + Precip + QDOY
BA + DOY + Elev + Humid
BA + DOY + Elev + TempMx
BA + DOY + Humid + TempMx
BA + Elev + Humid + TempMx
DOY + Elev + Humid + TempMx
BA + DOY + Elev + TempMn
BA + DOY + Humid + TempMn
BA + Elev + Humid + TempMn
DOY + Elev + Humid + TempMn
BA + DOY + TempMn + TempMx
BA + Elev + TempMn + TempMx
DOY + Elev + TempMn + TempMx
BA + Humid + TempMn + TempMx
DOY + Humid + TempMn + TempMx
Elev + Humid + TempMn + TempMx
BA + DOY + Elev + Precip
BA + DOY + Humid + Precip
BA + Elev + Humid + Precip
DOY + Elev + Humid + Precip
BA + DOY + TempMx + Precip
BA + Elev + TempMx + Precip
DOY + Elev + TempMx + Precip
BA + Humid + TempMx + Precip
DOY + Humid + TempMx + Precip
Elev + Humid + TempMx + Precip
BA + DOY + TempMn + Precip
BA + Elev + TempMn + Precip
DOY + Elev + TempMn + Precip
BA + Humid + TempMn + Precip
DOY + Humid + TempMn + Precip
Elev + Humid + TempMn + Precip

BA + TempMn + TempMx + Precip
DOY + TempMn + TempMx + Precip
Elev + TempMn + TempMx + Precip
Humid + TempMn + TempMx + Precip
BA + DOY + Elev + QDOY
BA + DOY + Humid + QDOY
BA + Elev + Humid + QDOY
DOY + Elev + Humid + QDOY
BA + DOY + TempMx + QDOY
BA + Elev + TempMx + QDOY
DOY + Elev + TempMx + QDOY
BA + Humid + TempMx + QDOY
DOY + Humid + TempMx + QDOY
Elev + Humid + TempMx + QDOY
BA + DOY + TempMn + QDOY
BA + Elev + TempMn + QDOY
DOY + Elev + TempMn + QDOY
BA + Humid + TempMn + QDOY
DOY + Humid + TempMn + QDOY
Elev + Humid + TempMn + QDOY
BA + TempMn + TempMx + QDOY
DOY + TempMn + TempMx + QDOY
Elev + TempMn + TempMx + QDOY
Humid + TempMn + TempMx + QDOY
BA + DOY + Precip + QDOY
BA + Elev + Precip + QDOY
DOY + Elev + Precip + QDOY
BA + Humid + Precip + QDOY
DOY + Humid + Precip + QDOY
Elev + Humid + Precip + QDOY
BA + TempMx + Precip + QDOY
DOY + TempMx + Precip + QDOY
Elev + TempMx + Precip + QDOY
Humid + TempMx + Precip + QDOY
BA + TempMn + Precip + QDOY
DOY + TempMn + Precip + QDOY
Elev + TempMn + Precip + QDOY
Humid + TempMn + Precip + QDOY
TempMn + TempMx + Precip + QDOY
BA + DOY + Elev + Humid + TempMx
BA + DOY + Elev + Humid + TempMn
BA + DOY + Elev + TempMn + TempMx
BA + DOY + Humid + TempMn + TempMx

BA + Elev + Humid + TempMn + TempMx
DOY + Elev + Humid + TempMn + TempMx
BA + DOY + Elev + Humid + Precip
BA + DOY + Elev + TempMx + Precip
BA + DOY + Humid + TempMx + Precip
BA + Elev + Humid + TempMx + Precip
DOY + Elev + Humid + TempMx + Precip
BA + DOY + Elev + TempMn + Precip
BA + DOY + Humid + TempMn + Precip
BA + Elev + Humid + TempMn + Precip
DOY + Elev + Humid + TempMn + Precip
BA + DOY + TempMn + TempMx + Precip
BA + Elev + TempMn + TempMx + Precip
DOY + Elev + TempMn + TempMx + Precip
BA + Humid + TempMn + TempMx + Precip
DOY + Humid + TempMn + TempMx + Precip
Elev + Humid + TempMn + TempMx + Precip
BA + DOY + Elev + Humid + QDOY
BA + DOY + Elev + TempMx + QDOY
BA + DOY + Humid + TempMx + QDOY
BA + Elev + Humid + TempMx + QDOY
DOY + Elev + Humid + TempMx + QDOY
BA + DOY + Elev + TempMn + QDOY
BA + DOY + Humid + TempMn + QDOY
BA + Elev + Humid + TempMn + QDOY
DOY + Elev + Humid + TempMn + QDOY
BA + DOY + TempMn + TempMx + QDOY
BA + Elev + TempMn + TempMx + QDOY
DOY + Elev + TempMn + TempMx + QDOY
BA + Humid + TempMn + TempMx + QDOY
DOY + Humid + TempMn + TempMx + QDOY
Elev + Humid + TempMn + TempMx + QDOY
BA + DOY + Elev + Precip + QDOY
BA + DOY + Humid + Precip + QDOY
BA + Elev + Humid + Precip + QDOY
DOY + Elev + Humid + Precip + QDOY
BA + DOY + TempMx + Precip + QDOY
BA + Elev + TempMx + Precip + QDOY
DOY + Elev + TempMx + Precip + QDOY
BA + Humid + TempMx + Precip + QDOY
DOY + Humid + TempMx + Precip + QDOY
Elev + Humid + TempMx + Precip + QDOY
BA + DOY + TempMn + Precip + QDOY

BA + Elev + TempMn + Precip + QDOY
DOY + Elev + TempMn + Precip + QDOY
BA + Humid + TempMn + Precip + QDOY
DOY + Humid + TempMn + Precip + QDOY
Elev + Humid + TempMn + Precip + QDOY
BA + TempMn + TempMx + Precip + QDOY
DOY + TempMn + TempMx + Precip + QDOY
Elev + TempMn + TempMx + Precip + QDOY
Humid + TempMn + TempMx + Precip + QDOY
BA + DOY + Elev + Humid + TempMn + TempMx
BA + DOY + Elev + Humid + TempMx + Precip
BA + DOY + Elev + Humid + TempMn + Precip
BA + DOY + Elev + TempMn + TempMx + Precip
BA + DOY + Humid + TempMn + TempMx + Precip
BA + Elev + Humid + TempMn + TempMx + Precip
DOY + Elev + Humid + TempMn + TempMx + Precip
BA + DOY + Elev + Humid + TempMx + QDOY
BA + DOY + Elev + Humid + TempMn + QDOY
BA + DOY + Elev + TempMn + TempMx + QDOY
BA + DOY + Humid + TempMn + TempMx + QDOY
BA + Elev + Humid + TempMn + TempMx + QDOY
DOY + Elev + Humid + TempMn + TempMx + QDOY
BA + DOY + Elev + Humid + Precip + QDOY
BA + DOY + Elev + TempMx + Precip + QDOY
BA + DOY + Humid + TempMx + Precip + QDOY
BA + Elev + Humid + TempMx + Precip + QDOY
DOY + Elev + Humid + TempMx + Precip + QDOY
BA + DOY + Elev + TempMn + Precip + QDOY
BA + DOY + Humid + TempMn + Precip + QDOY
BA + Elev + Humid + TempMn + Precip + QDOY
DOY + Elev + Humid + TempMn + Precip + QDOY
BA + DOY + TempMn + TempMx + Precip + QDOY
BA + Elev + TempMn + TempMx + Precip + QDOY
DOY + Elev + TempMn + TempMx + Precip + QDOY
BA + Humid + TempMn + TempMx + Precip + QDOY
DOY + Humid + TempMn + TempMx + Precip + QDOY
Elev + Humid + TempMn + TempMx + Precip + QDOY
BA + DOY + Elev + Humid + TempMn + TempMx + Precip
BA + DOY + Elev + Humid + TempMn + TempMx + QDOY
BA + DOY + Elev + Humid + TempMx + Precip + QDOY
BA + DOY + Elev + Humid + TempMn + Precip + QDOY
BA + DOY + Elev + TempMn + TempMx + Precip + QDOY
BA + DOY + Humid + TempMn + TempMx + Precip + QDOY

BA + Elev + Humid + TempMn + TempMx + Precip + QDOY
DOY + Elev + Humid + TempMn + TempMx + Precip + QDOY
BA + DOY + Elev + Humid + TempMn + TempMx + Precip + QDOY

Table 4-A2. Trap-level model set with all covariate combinations for logistic regression modeling for Polyvinyl Chloride pipe gray treefrog abundance in Vermont.

Model
Null
BA
DBH
DOY
Elev
Humid
TempMx
TempMn
Precip
Type
BA + DBH
BA + DOY
DBH + DOY
BA + Elev
DBH + Elev
DOY + Elev
BA + Humid
DBH + Humid
DOY + Humid
Elev + Humid
BA + TempMx
DBH + TempMx
DOY + TempMx
Elev + TempMx
Humid + TempMx
BA + TempMn
DBH + TempMn
DOY + TempMn
Elev + TempMn
Humid + TempMn
TempMx + TempMn
BA + Precip
DBH + Precip
DOY + Precip
Elev + Precip
Humid + Precip
TempMx + Precip
TempMn + Precip
BA + Type

DBH + Type
DOY + Type
Elev + Type
Humid + Type
TempMx + Type
TempMn + Type
Precip + Type
BA + DBH + DOY
BA + DBH + Elev
BA + DOY + Elev
DBH + DOY + Elev
BA + DBH + Humid
BA + DOY + Humid
DBH + DOY + Humid
BA + Elev + Humid
DBH + Elev + Humid
DOY + Elev + Humid
BA + DBH + TempMx
BA + DOY + TempMx
DBH + DOY + TempMx
BA + Elev + TempMx
DBH + Elev + TempMx
DOY + Elev + TempMx
BA + Humid + TempMx
DBH + Humid + TempMx
DOY + Humid + TempMx
Elev + Humid + TempMx
BA + DBH + TempMn
BA + DOY + TempMn
DBH + DOY + TempMn
BA + Elev + TempMn
DBH + Elev + TempMn
DOY + Elev + TempMn
BA + Humid + TempMn
DBH + Humid + TempMn
DOY + Humid + TempMn
Elev + Humid + TempMn
BA + TempMx + TempMn
DBH + TempMx + TempMn
DOY + TempMx + TempMn
Elev + TempMx + TempMn
Humid + TempMx + TempMn
BA + DBH + Precip

BA + DOY + Precip
DBH + DOY + Precip
BA + Elev + Precip
DBH + Elev + Precip
DOY + Elev + Precip
BA + Humid + Precip
DBH + Humid + Precip
DOY + Humid + Precip
Elev + Humid + Precip
BA + TempMx + Precip
DBH + TempMx + Precip
DOY + TempMx + Precip
Elev + TempMx + Precip
Humid + TempMx + Precip
BA + TempMn + Precip
DBH + TempMn + Precip
DOY + TempMn + Precip
Elev + TempMn + Precip
Humid + TempMn + Precip
TempMx + TempMn + Precip
BA + DBH + Type
BA + DOY + Type
DBH + DOY + Type
BA + Elev + Type
DBH + Elev + Type
DOY + Elev + Type
BA + Humid + Type
DBH + Humid + Type
DOY + Humid + Type
Elev + Humid + Type
BA + TempMx + Type
DBH + TempMx + Type
DOY + TempMx + Type
Elev + TempMx + Type
Humid + TempMx + Type
BA + TempMn + Type
DBH + TempMn + Type
DOY + TempMn + Type
Elev + TempMn + Type
Humid + TempMn + Type
TempMx + TempMn + Type
BA + Precip + Type
DBH + Precip + Type

DOY + Precip + Type
Elev + Precip + Type
Humid + Precip + Type
TempMx + Precip + Type
TempMn + Precip + Type
BA + DBH + DOY + Elev
BA + DBH + DOY + Humid
BA + DBH + Elev + Humid
BA + DOY + Elev + Humid
DBH + DOY + Elev + Humid
BA + DBH + DOY + TempMx
BA + DBH + Elev + TempMx
BA + DOY + Elev + TempMx
DBH + DOY + Elev + TempMx
BA + DBH + Humid + TempMx
BA + DOY + Humid + TempMx
DBH + DOY + Humid + TempMx
BA + Elev + Humid + TempMx
DBH + Elev + Humid + TempMx
DOY + Elev + Humid + TempMx
BA + DBH + DOY + TempMn
BA + DBH + Elev + TempMn
BA + DOY + Elev + TempMn
DBH + DOY + Elev + TempMn
BA + DBH + Humid + TempMn
BA + DOY + Humid + TempMn
DBH + DOY + Humid + TempMn
BA + Elev + Humid + TempMn
DBH + Elev + Humid + TempMn
DOY + Elev + Humid + TempMn
BA + DBH + TempMx + TempMn
BA + DOY + TempMx + TempMn
DBH + DOY + TempMx + TempMn
BA + Elev + TempMx + TempMn
DBH + Elev + TempMx + TempMn
DOY + Elev + TempMx + TempMn
BA + Humid + TempMx + TempMn
DBH + Humid + TempMx + TempMn
DOY + Humid + TempMx + TempMn
Elev + Humid + TempMx + TempMn
BA + DBH + DOY + Precip
BA + DBH + Elev + Precip
BA + DOY + Elev + Precip

DBH + DOY + Elev + Precip
BA + DBH + Humid + Precip
BA + DOY + Humid + Precip
DBH + DOY + Humid + Precip
BA + Elev + Humid + Precip
DBH + Elev + Humid + Precip
DOY + Elev + Humid + Precip
BA + DBH + TempMx + Precip
BA + DOY + TempMx + Precip
DBH + DOY + TempMx + Precip
BA + Elev + TempMx + Precip
DBH + Elev + TempMx + Precip
DOY + Elev + TempMx + Precip
BA + Humid + TempMx + Precip
DBH + Humid + TempMx + Precip
DOY + Humid + TempMx + Precip
Elev + Humid + TempMx + Precip
BA + DBH + TempMn + Precip
BA + DOY + TempMn + Precip
DBH + DOY + TempMn + Precip
BA + Elev + TempMn + Precip
DBH + Elev + TempMn + Precip
DOY + Elev + TempMn + Precip
BA + Humid + TempMn + Precip
DBH + Humid + TempMn + Precip
DOY + Humid + TempMn + Precip
Elev + Humid + TempMn + Precip
BA + TempMx + TempMn + Precip
DBH + TempMx + TempMn + Precip
DOY + TempMx + TempMn + Precip
Elev + TempMx + TempMn + Precip
Humid + TempMx + TempMn + Precip
BA + DBH + DOY + Type
BA + DBH + Elev + Type
BA + DOY + Elev + Type
DBH + DOY + Elev + Type
BA + DBH + Humid + Type
BA + DOY + Humid + Type
DBH + DOY + Humid + Type
BA + Elev + Humid + Type
DBH + Elev + Humid + Type
DOY + Elev + Humid + Type
BA + DBH + TempMx + Type

BA + DOY + TempMx + Type
DBH + DOY + TempMx + Type
BA + Elev + TempMx + Type
DBH + Elev + TempMx + Type
DOY + Elev + TempMx + Type
BA + Humid + TempMx + Type
DBH + Humid + TempMx + Type
DOY + Humid + TempMx + Type
Elev + Humid + TempMx + Type
BA + DBH + TempMn + Type
BA + DOY + TempMn + Type
DBH + DOY + TempMn + Type
BA + Elev + TempMn + Type
DBH + Elev + TempMn + Type
DOY + Elev + TempMn + Type
BA + Humid + TempMn + Type
DBH + Humid + TempMn + Type
DOY + Humid + TempMn + Type
Elev + Humid + TempMn + Type
BA + TempMx + TempMn + Type
DBH + TempMx + TempMn + Type
DOY + TempMx + TempMn + Type
Elev + TempMx + TempMn + Type
Humid + TempMx + TempMn + Type
BA + DBH + Precip + Type
BA + DOY + Precip + Type
DBH + DOY + Precip + Type
BA + Elev + Precip + Type
DBH + Elev + Precip + Type
DOY + Elev + Precip + Type
BA + Humid + Precip + Type
DBH + Humid + Precip + Type
DOY + Humid + Precip + Type
Elev + Humid + Precip + Type
BA + TempMx + Precip + Type
DBH + TempMx + Precip + Type
DOY + TempMx + Precip + Type
Elev + TempMx + Precip + Type
Humid + TempMx + Precip + Type
BA + TempMn + Precip + Type
DBH + TempMn + Precip + Type
DOY + TempMn + Precip + Type
Elev + TempMn + Precip + Type

Humid + TempMn + Precip + Type
TempMx + TempMn + Precip + Type
BA + DBH + DOY + Elev + Humid
BA + DBH + DOY + Elev + TempMx
BA + DBH + DOY + Humid + TempMx
BA + DBH + Elev + Humid + TempMx
BA + DOY + Elev + Humid + TempMx
DBH + DOY + Elev + Humid + TempMx
BA + DBH + DOY + Elev + TempMn
BA + DBH + DOY + Humid + TempMn
BA + DBH + Elev + Humid + TempMn
BA + DOY + Elev + Humid + TempMn
DBH + DOY + Elev + Humid + TempMn
BA + DBH + DOY + TempMx + TempMn
BA + DBH + Elev + TempMx + TempMn
BA + DOY + Elev + TempMx + TempMn
DBH + DOY + Elev + TempMx + TempMn
BA + DBH + Humid + TempMx + TempMn
BA + DOY + Humid + TempMx + TempMn
DBH + DOY + Humid + TempMx + TempMn
BA + Elev + Humid + TempMx + TempMn
DBH + Elev + Humid + TempMx + TempMn
DOY + Elev + Humid + TempMx + TempMn
BA + DBH + DOY + Elev + Precip
BA + DBH + DOY + Humid + Precip
BA + DBH + Elev + Humid + Precip
BA + DOY + Elev + Humid + Precip
DBH + DOY + Elev + Humid + Precip
BA + DBH + DOY + TempMx + Precip
BA + DBH + Elev + TempMx + Precip
BA + DOY + Elev + TempMx + Precip
DBH + DOY + Elev + TempMx + Precip
BA + DBH + Humid + TempMx + Precip
BA + DOY + Humid + TempMx + Precip
DBH + DOY + Humid + TempMx + Precip
BA + Elev + Humid + TempMx + Precip
DBH + Elev + Humid + TempMx + Precip
DOY + Elev + Humid + TempMx + Precip
BA + DBH + DOY + TempMn + Precip
BA + DBH + Elev + TempMn + Precip
BA + DOY + Elev + TempMn + Precip
DBH + DOY + Elev + TempMn + Precip
BA + DBH + Humid + TempMn + Precip

BA + DOY + Humid + TempMn + Precip
DBH + DOY + Humid + TempMn + Precip
BA + Elev + Humid + TempMn + Precip
DBH + Elev + Humid + TempMn + Precip
DOY + Elev + Humid + TempMn + Precip
BA + DBH + TempMx + TempMn + Precip
BA + DOY + TempMx + TempMn + Precip
DBH + DOY + TempMx + TempMn + Precip
BA + Elev + TempMx + TempMn + Precip
DBH + Elev + TempMx + TempMn + Precip
DOY + Elev + TempMx + TempMn + Precip
BA + Humid + TempMx + TempMn + Precip
DBH + Humid + TempMx + TempMn + Precip
DOY + Humid + TempMx + TempMn + Precip
Elev + Humid + TempMx + TempMn + Precip
BA + DBH + DOY + Elev + Type
BA + DBH + DOY + Humid + Type
BA + DBH + Elev + Humid + Type
BA + DOY + Elev + Humid + Type
DBH + DOY + Elev + Humid + Type
BA + DBH + DOY + TempMx + Type
BA + DBH + Elev + TempMx + Type
BA + DOY + Elev + TempMx + Type
DBH + DOY + Elev + TempMx + Type
BA + DBH + Humid + TempMx + Type
BA + DOY + Humid + TempMx + Type
DBH + DOY + Humid + TempMx + Type
BA + Elev + Humid + TempMx + Type
DBH + Elev + Humid + TempMx + Type
DOY + Elev + Humid + TempMx + Type
BA + DBH + DOY + TempMn + Type
BA + DBH + Elev + TempMn + Type
BA + DOY + Elev + TempMn + Type
DBH + DOY + Elev + TempMn + Type
BA + DBH + Humid + TempMn + Type
BA + DOY + Humid + TempMn + Type
DBH + DOY + Humid + TempMn + Type
BA + Elev + Humid + TempMn + Type
DBH + Elev + Humid + TempMn + Type
DOY + Elev + Humid + TempMn + Type
BA + DBH + TempMx + TempMn + Type
BA + DOY + TempMx + TempMn + Type
DBH + DOY + TempMx + TempMn + Type

BA + Elev + TempMx + TempMn + Type
DBH + Elev + TempMx + TempMn + Type
DOY + Elev + TempMx + TempMn + Type
BA + Humid + TempMx + TempMn + Type
DBH + Humid + TempMx + TempMn + Type
DOY + Humid + TempMx + TempMn + Type
Elev + Humid + TempMx + TempMn + Type
BA + DBH + DOY + Precip + Type
BA + DBH + Elev + Precip + Type
BA + DOY + Elev + Precip + Type
DBH + DOY + Elev + Precip + Type
BA + DBH + Humid + Precip + Type
BA + DOY + Humid + Precip + Type
DBH + DOY + Humid + Precip + Type
BA + Elev + Humid + Precip + Type
DBH + Elev + Humid + Precip + Type
DOY + Elev + Humid + Precip + Type
BA + DBH + TempMx + Precip + Type
BA + DOY + TempMx + Precip + Type
DBH + DOY + TempMx + Precip + Type
BA + Elev + TempMx + Precip + Type
DBH + Elev + TempMx + Precip + Type
DOY + Elev + TempMx + Precip + Type
BA + Humid + TempMx + Precip + Type
DBH + Humid + TempMx + Precip + Type
DOY + Humid + TempMx + Precip + Type
Elev + Humid + TempMx + Precip + Type
BA + DBH + TempMn + Precip + Type
BA + DOY + TempMn + Precip + Type
DBH + DOY + TempMn + Precip + Type
BA + Elev + TempMn + Precip + Type
DBH + Elev + TempMn + Precip + Type
DOY + Elev + TempMn + Precip + Type
BA + Humid + TempMn + Precip + Type
DBH + Humid + TempMn + Precip + Type
DOY + Humid + TempMn + Precip + Type
Elev + Humid + TempMn + Precip + Type
BA + TempMx + TempMn + Precip + Type
DBH + TempMx + TempMn + Precip + Type
DOY + TempMx + TempMn + Precip + Type
Elev + TempMx + TempMn + Precip + Type
Humid + TempMx + TempMn + Precip + Type
BA + DBH + DOY + Elev + Humid + TempMx

BA + DBH + DOY + Elev + Humid + TempMn
BA + DBH + DOY + Elev + TempMx + TempMn
BA + DBH + DOY + Humid + TempMx + TempMn
BA + DBH + Elev + Humid + TempMx + TempMn
BA + DOY + Elev + Humid + TempMx + TempMn
DBH + DOY + Elev + Humid + TempMx + TempMn
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