POTENTIAL OF MODELING TO PREDICT THE RE-ESTABLISHMENT OF BAT POPULATIONS AFFECTED BY WHITE-NOSE SYNDROME IN NORTHWESTERN ONTARIO

by

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Major Advisor	Second Reader

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A CAUTION TO THE READER

MAJOR ADVISORS COMMENTS

In somewhat unusual circumstances, I took on the supervision of this thesis in late November after Mr. Nesbitt was well underway. Mr. Nesbitt had already begun work on a topic of interest that was outside my research focus. Fortunately, Dr. Julie Rosenthal, Associate Professor in the School of Outdoor Recreation, Parks and Tourism, had some personal experience with little brown bats in northwestern Ontario and agreed to assist and act as Second Reader. The product of this collaboration is a thesis that asks a useful research question, addresses that question from appropriate perspectives and, in the end, provides an answer. The process of writing a good literature review is demanding. Mr. Nesbitt has succeeded in navigating these sometimes tricky waters to produce a document of which he can be proud and that meets the requirements for an undergraduate thesis in the Faculty of Natural Resources Management.

ABSTRACT

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Keywords: Little brown bat, survival rate, mortality rate, reproductive rate, carrying capacity, hibernacula, direct transmission, swarming

Since the first confirmed case in North America in 2007, white nose syndrome caused by *Pseudogymnoascus destructans* has decimated bat populations in the northeastern US and eastern Canada. Ontario is home to eight species of bat, with four of these being labeled as Endangered, either provincially or federally. Afflicted individuals transmit the fungus through physical contact in roosts or during swarming events. Presence of the host is not required for the fungus to persist in suitable environments such the cool, moist locations chosen as hibernacula. Recently, modeling has been used to better understand this disease and the effects it has on bat populations. Two research questions formed the focus of this thesis: What is the potential of modeling to predict the re-establishment of bat populations in northwestern Ontario? and What information is needed to support a modeling effort?

Current literature was reviewed and five papers that employed the use of models were selected. Papers were compared on the basis of goals, scenarios, outcomes and data used. It was determined that modeling could be useful in the context of northwestern Ontario and that data on bat physiology and hibernacula conditions were the most essential.

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INTRODUCTION

White-nose syndrome is the common name used for an infectious fungal disease that causes mass-mortality events in several bat species found in North America. The fungus that causes white-nose syndrome, first identified as *Geomyces destructans, later Pseudogymnoascus destructans* (Blehert & Gargas) Minnis & D.L. Lindner)*,* was first detected in North America in 2007 when researchers came across a mass mortality of bats in a cave located in New York state (Hoyt et al. 2021). This fungus is naturally found in Eurasia where it also afflicts hibernating bat species but without any of the resulting mass mortality events as seen in North America (Verant et al. 2012). Since the first documented case in New York, the fungus has spread at a rate of 200-900 km per year into other bat populations across eastern North America (Hoyt et al. 2021). Only two years later in 2009, the first documented case of white-nose syndrome in Canada was detected from a cave in southern Ontario (US Fish and Wildlife Service 2020). Over the next few years, cases began to show up throughout other parts of Ontario as well as Quebec, Nova Scotia, New Brunswick and P.E.I, with the first recorded cases from the Thunder Bay District coming in 2014 (Government of Canada n.d.).

In total, Ontario is home to eight different species of bats, four of which are now classified as Endangered according to the Committee on the Status of Species at Risk in Ontario (COSSARO) and/or the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). While bats in Ontario are also threatened by both windmills and climate change, the white-nose syndrome disease outbreak has been identified as the main reason for these bat populations to decline so dramatically over such a relatively short period of time (Laying et al. 2019). Due to the highly contagious nature of this disease and the devastating impact it has on local bat populations, governments and conservation groups have begun to enhance their efforts in tracking and predicting the path of white-nose syndrome as well as using a wide variety of wildlife monitoring practices to evaluate the impact that this fungus has left on bat populations across the continent. Now that this disease has been present in North America for over a decade, researchers have also begun to investigate resistance from remnant populations as well as the potential for recovery after the disease has decimated overall population numbers.

One of the techniques available to develop a better understanding of different biological phenomena including host-pathogen relationships is the use of modeling. Modeling techniques for these kinds of relationships can be adapted for bats based on other wildlife disease scenarios and can help to predict the range of effects of this fungus on bat populations. In this field, modeling is used to help in our understanding of the white-nose syndrome epidemic, including finding any gaps in current data on bat populations, predicting overall recovery and indicating how we may be able to protect Ontario's endangered bat species in the future. This kind of analysis uses a wide variety of data to determine different factors that are important to maintaining self-sustaining populations across a range of established and decreasing populations. In order to use a modeling approach effectively, basic information regarding the host-pathogen relationship needs to be available. Some of the most important factors to consider include bat physiology, the pathogens biology, host behavior and host ecology.

This paper will provide insight on this threat to Northwestern Ontario's Little brown bat population, determine if modeling can be used as a method to better understand the white nose syndrome disease and use informed decision-making to plan for recovery.

In order to achieve this, my research questions are:

a. What is the potential of modeling to predict the re-establishment of bat populations in northwestern Ontario?
b. What information is needed to support a modeling effort?

The Lakehead University Library website and Google Scholar were used to conduct searches for research articles and journals that related to describing bats in Ontario, the causal agent of the disease (*Geomyces destructans* and/or *Pseudogymnoascus destructans*) and modeling efforts that specifically looked into relationships between North American bat populations and the introduced fungus. While few sources focusing on northwestern Ontario were available, all papers included within this process must have focused on this disease's impacts within North America, more specifically in southern Ontario and the northeastern United States. In the process of selecting specific papers, key topics such as population recovery, population decline, habitat selection and influences of landscape conditions were used to refine the search. Modeling papers that included full descriptions of the data were also favored, as they provided a clear and thorough outline of the data included within each modelling effort.

LITERATURE REVIEW

Ontario bats

In total Ontario is home to eight resident bat species: Eastern small-footed bats (*Myotis leibii*), Little brown bats (*Myotis lucifugus*), Northern myotis (*Myotis septentrionalis*), Tricoloured bats (*Perimyotis subflavus*), Eastern red bats (*Lasiurus borealis*), Hoary bats (*Lasiurus cinereus*), Silver-haired bats (*Lasionycteris noctivagans*) and Big brown bats (*Eptesicus fuscus*), all of which belong to the family *Vespertilionidae* (Kagume 2008). More commonly known as evening bats, this family is characterized by their relatively small size as well as being active mostly at dawn and dusk when they are hunting for insects and other small flying invertebrates. Bats that reside in Ontario either remain here year-round by hibernating during winter months or by migrating to more southern latitudes where winters are less intense. Of these eight species, Eastern red bats, Hoary bats and Silver-haired bats all migrate into the more southern parts of the continent throughout the U.S and Mexico, usually leaving Ontario between August and October depending on where in the province they are located (Laying et al. 2019). The other five species (Eastern small-footed bats, Little brown bats, Northern myotis, Tricoloured bats and Big brown bats) remain in Ontario year-round, utilizing various structures and landscapes known as hibernacula where they hibernate during the coldest months until spring (Laying et al. 2019). To survive through the long winter months, Ontario's bat species will feed intensively to build up fat reserves before going into their preferred hibernaculum (most typically caves or abandoned mineshafts) where they remain in torpor for much of the winter excluding a few occasions where they wake up and move around their cave (Czenze and Willis 2015). Table 1 summarizes some relevant behavioral habits of Ontario's four Endangered bat species.

These hibernating species are at the highest risk of contracting white-nose syndrome as the hibernaculum sites are the main area that the causative fungus, *Geomyces destructans*, can be found (Laying et al. 2019). All bat species in Ontario, their at-risk statuses and presence in the Thunder Bay District as well as whether the disease has been detected in these local populations is summarized in Table 1. Excluding the Big brown bat, four of Ontario's five resident hibernating bat species are listed as Endangered in Ontario under the Endangered Species Act from 2007 (Endangered Species Act 2007). Additionally, the Little brown bat, Northern myotis and the Tricoloured bat are listed as federally Endangered according to evaluations done by COSEWIC (Government of Canada 2021).

At both provincial and federal levels, species at risk are defined by COSSARO and COSEWIC using evaluative criteria that consider the native range of a species, its relative abundance and if the species is dependent on specific kinds of habitat (COSEWIC 2019). As noted in the introduction, additional factors, such as windmill collisions and climate change, have contributed to the decline in bat numbers, however Laying et al. (2019) identified white-nose syndrome as the leading cause of their elevation to Endangered status. It is therefore important to understand how bat behavior influences the spread of this disease. Table 2 summarizes some relevant behavioral habits on Ontario's four Endangered bat species. These behaviours are the primary transmission vectors for white nose syndrome between bats. Roosting habitat and the behavior between bats during roosting as well as swarming events are primarily when bats are in close contact with one another and therefore risk spreading the fungus throughout populations.

Table 1. Species status rankings and confirmation of presence in the Thunder Bay District for Ontario's eight bat species.

Species	Status in Ontario (COSSARO)	Status in Canada (COSEWIC)	IUCN status	Present in Thunder Bay District?	WNS identified
Eastern small-footed bat (*Myotis leibii*)	Endangered (2013)	Not Evaluated	Endangered (2018)	No	Yes
Little brown bat (*Myotis lucifugus*)	Endangered (2012)	Endangered (2013)	Endangered (2018)	Yes (Uncommon)	Yes
Northern myotis (*Myotis septentrionalis*)	Endangered (2013)	Endangered (2013)	Near Threatened (2018)	Yes (Uncommon)	Yes
Tricolored bat (*Perimyotis subflavus*)	Endangered (2015)	Endangered (2013)	Vulnerable (2018)	No	Yes
Eastern red bat (*Lasiurus borealis*)	Not Evaluated	Not Evaluated	Least Concern (2015)	Yes (abundance unknown)	No
Hoary bat (*Lasiurus cinereus*)	Not Evaluated	Not Evaluated	Least Concern (2015)	Yes (abundance unknown)	No
Silver-haired bat (*Lasionycteris noctivagans*)	Not Evaluated	Not Evaluated	Least Concern (2018)	Yes (abundance unknown)	No
Big brown bat (*Eptesicus fuscus*)	Not Evaluate	Not Evaluated	Least Concern (2016)	Yes (Common)	Yes

Table 2. Roosting and swarming behavior, as well as preferred summer and winter habitats for Ontario's four Endangered bat species.

Species	Roosting behavior	Preferred summer roosting habitat	Preferred winter roosting habitat	Swarming events	Citation
Eastern small-footed bat (*Myotis leibii*)	Solitary or in small clusters, may pack together tightly in smaller spaces	Caves, mines, hollow trees, under tree bark and rock outcrops	Colder areas closer to the entrances of smaller caves or mineshafts, in crevices or under rocks near the caves floor	Yes, late summer to early fall outside of hibernacula (mate selection, breeding, building up fat reserves)	(Johnson and Gates 2007) (Solari 2018)
Little brown bat (*Myotis lucifugus*)	High concentrations in summer nurseries and hibernacula, small groups in varying locations during summer	Wide variety of sites including in trees, buildings, wood piles, rocks and occasionally small caves	Natural caves and abandoned mines with high humidity and average temperatures below freezing	Yes, late August to October depending on location. Populations mix during swarming, but individuals may not hibernate at this location	(Fenton and Barclay 1980)
Northern myotis (*Myotis septentrionalis*)	Sexes roost separately during the summer, larger clusters in deep crevices during winter	Favors tree roosts, also selects caves, buildings and under tree bark	Natural caves and abandoned mine shafts	Yes, occurs during August and September in the same location, both inside and around hibernaculum	(Caceres and Barclay 2000)
Tricolored bat (*Perimyotis subflavus*)	Sexes roost separately, only coming together during swarming events near cave openings to breed	Rock outcrops, caves, tree foliage and buildings close to open forests near water	Deep in natural caves and abandoned mineshafts	Yes, occurs from August to October and is the only time when both males and females are together (breeding)	(Solari 2018)

Pseudogymnoascus destructans

White-nose syndrome (WNS) is an infectious disease caused by an invasive species of fungus from Eurasia known as *Pseudogymnoascus destructans* (Verant et al. 2012). The fungus is most commonly found in moist environments with low temperatures and relatively high humidity compared to the surrounding landscape, which makes bat hibernaculum sites the perfect location for the fungus to grow and distribute spores (Lilley et al. 2018). Similar to many other fungal pathogens that infect mammalian species, *P. destructans* does not require the host species to be present in order to survive, but the exact length of time that the spores of this species can survive in caves without a host is still uncertain (Lorch et al. 2013). As long as the fungus remains under 20°C during warmer summer months it is capable of growing which helps to limit the fungus growth to deeper portions of caves (Lorch et al. 2013).

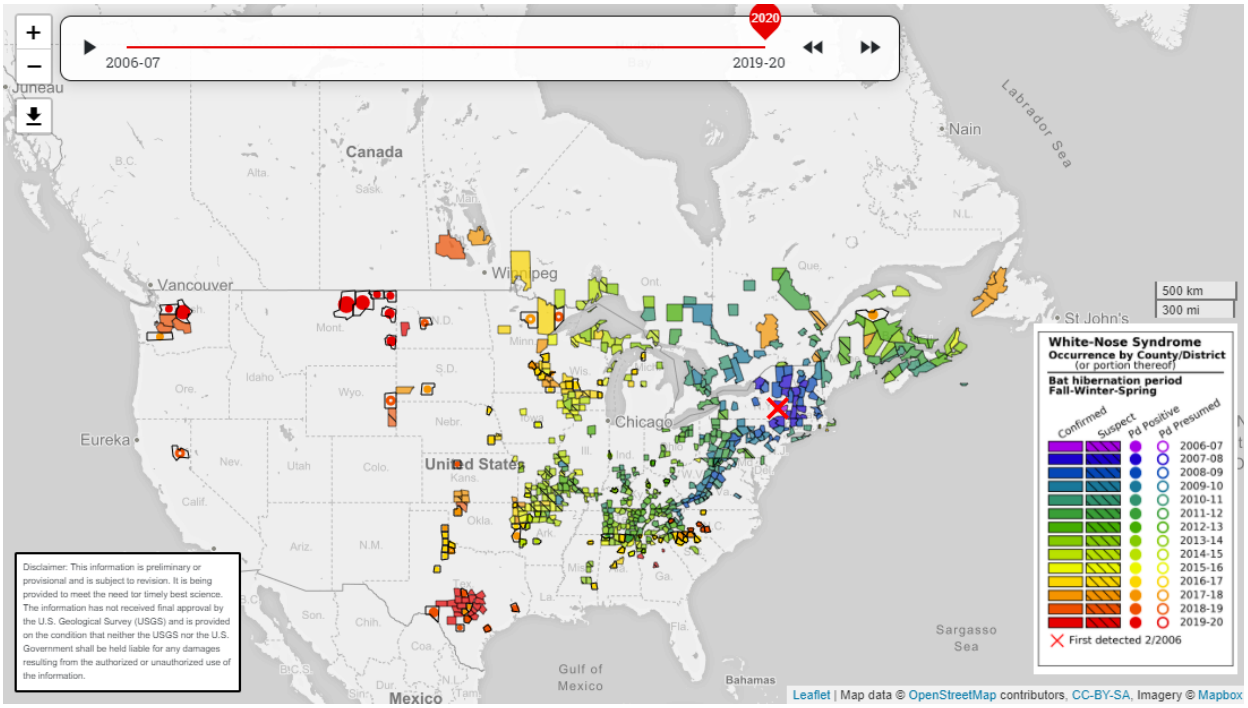
Figure 1. Little brown bat (*Myotis lucifugus*) infected with white-nose syndrome (used with permission from J. Rosenthal).

Presence in Europe

Prior to its emergence in North American bat populations, little research or investigation had been done on *P. destructans* within its native European range. Reports dating back to the 1980's from various countries in Europe had identified distinctive white face covering on hibernating bats, which is indicative of bats infected by this disease. However, these populations lacked the mass mortalities that made the disease so devastating to bat populations in North America (Wibbelt et al. 2010). After its outbreak in North America, surveys in several European countries including Germany, Hungary, Switzerland and the United Kingdom were carried out to gather samples from European bats that showed physical signs of a possible infection such as skin deterioration or the characteristic white fuzz (Wibbelt et al. 2010). These studies concluded that *P. destructans* was present in several of the sampled colonies in Germany, Switzerland and Hungary and that both the North American and European versions of the fungus had the same genetic signature (Wibbelt et al. 2010). Over the course of this study and from previous population counts dating back to the 1930's from across Europe, no mass mortality events anywhere close to the scale at which they occur in North America had been reported (Wibbelt et al. 2010). It is still unknown as to why *P. destructans* has little effect on European bat populations, but many authors including Wibbelt et al. (2010) theorize that European bats had co-evolved alongside the fungus and are thus relatively unaffected by the disease, unlike North American populations. A second study involved isolating *P. destructans* from both New York and Germany and inoculating each into Little brown bats (endemic to North America) where both strains proved to be fatal, further supporting the theory of natural immunity in European bat populations (Verant et al. 2012).

Introduction to North America

The first official documentation of *P. destructans* in North America came from a cave in central New York during the winter of 2006-2007 (Verant et al. 2012). After this point, the fungus continued to spread rapidly across the eastern and Midwest United States as well as north into Canadian provinces including Ontario, Quebec, New Brunswick, Nova Scotia and P.E.I. The first detected case in Canada was found in southern Ontario in the winter of 2009-2010 where, upon further investigation, the fungus was found to be present in several caves across the southern portion of the province (Laying et al. 2019). Only four years later in 2014, the first cases of white-nose syndrome in northwestern Ontario bats were detected from the Terrace Bay section of the Thunder Bay District (Government of Canada n.d.). Since being introduced seventeen years ago, *P. destructans* has been detected over much of eastern North America, with cases occurring throughout the Midwest and even on the Pacific coast in Washington and California, as shown in Figure 2 below (US Fish and Wildlife Service 2020).



Disclaimer: This information is preliminary or provisional and is subject to revision. It is being provided to meet the need for timely best science. The information has not received final approval by the U.S. Geological Survey (USGS) and is provided on the condition that neither the USGS nor the U.S. Government shall be held liable for any damages resulting from the authorized or unauthorized use of the information.

Figure 2. Map of the distribution and spread of white-nose syndrome in North America (US Fish and Wildlife Service 2020).

Since the first recorded death from white-nose syndrome in North America, the fungus has been spreading at a rate of around 200-900 km per year with an estimated 5.7-6 million bats dying by 2018, just 12 years after the disease's first confirmed case on the continent (Lilley et al. 2018).

Impacts of white nose syndrome on bats

Once a bat has become exposed to *P. destructans* and infection has taken place, the fungus produces hyphae that replace the hair follicles and sweat glands on the bat's muzzle and causes deterioration of the skin on the ears and wings (Blehert 2009). Additionally, the presence of this disease within a bat's system disrupts its hibernation cycle and causes it to exit torpor and become active within their hibernaculum leading to dehydration and the overall depletion of fat reserves that must remain high in order for bats to survive the winter with no available food sources (Kramer et al. 2019).

When colonies of a certain bat species are afflicted by white-nose syndrome and experience a decrease in numbers within their environment, other species found within the same area can become more active to fill those niches (Morningstar et al. 2019). The amount of interspecific competition that occurs between bat species depends on the niche overlap between them, which can also be impacted by the presence of white-nose syndrome through changes in diet (Morningstar et al. 2019). When *P. destructans* becomes present within a colony, a reduction in local species abundance as well as localized extinction events for some species causes ecological changes across a larger scale within their environment through the removal of large portions of the population (Frick et al. 2015). Once the fungus has become established within a population for several years, white-nose syndrome can also significantly impact the overall yearly reproductive success for several species (Pettit and O'Keefe 2017). Increases in capture rates of non-reproductive and post-lactating female bats shows that individuals that make it through the winter while infected with WNS will often be unable to reproduce or raise young due to a lack of energy from depleted fat reserves (Pettit and O'Keefe 2017). Part of what makes this disease so dangerous to bat populations is the ease at which it can spread into uninfected hibernacula. Once an uninfected bat has entered an infected hibernaculum or come into contact with an infected individual, fungal spores attach themselves to the bat which begins the initial infection (Lilley et al. 2018). When this occurs, the infected bat has the potential to continue to spread these fungal spores into new uninfected sites through shedding as it moves from a variety of locations or hibernacula prior to entering a permanent hibernation site (Lilley et al. 2018). This disease is spread fastest through direct physical interactions with other uninfected individuals which can occur frequently during hibernation or in swarming events that occur prior to entering hibernacula (Lilley et al. 2018).

Monitoring

In order to gather the data necessary to conduct further research into this disease's impact on current and future bat populations, a wide variety of wildlife monitoring practices specialized for monitoring bats can be used. Some of the most commonly used and most effective methods are acoustic sampling and visual counts through roost surveys and using mist nets. Of these methods, acoustic surveys are one of the most effective ways to track bat activity. By using specialized devices known as bat detectors to record the echolocation calls used by bats during feeding, presence or absence of identified bat species can be determined (Adams et al. 2012). As shown below in Figure 3, the bat detectors can be fixed onto trucks, which allows researchers to cover greater distances and gather specific data from particular areas including high densities of clustered hibernacula or high-quality feeding habitat.

Figure 3. Truck equipped with a bat detector in Sleeping Giant Provincial Park near Thunder Bay, ON (McCaul and Kingston 2020).

This kind of data can be used to determine activity levels during different times of the day and throughout the year, which also helps to locate important sites where roosting or swarming events may occur (Adams et al. 2015). When this data is compiled from summer and winter months, it can be compared with pre-white nose syndrome data to determine if significant changes in activity have occurred. Typically, low summer activity levels from population decline and lack of energy along with high winter activity levels inside hibernacula are additional indicators that white-nose syndrome is present within a given area around a particular hibernaculum (Hicks et al. 2020).

The easiest method to identify if white-nose syndrome is present in an ecosystem is visual observation of live or deceased bats. To do this, two popular methods are employing the use of mist nets or performing roost surveys inside potential hibernaculum locations. Mist nets are effective at capturing flying species such as bats and birds and are commonly used in mark-recapture studies for bats to keep track of specific individuals and monitor their overall health (Flaquer 2007). The main issues involving mist nets include the difficulty of setting them up over bat flyways such as lakes or streams and the biased data obtained from the small portion of individuals from the population that are captured (Flaquer 2007). Mist netting also increases the risk of injury to the bats themselves, especially if the skin membranes of the wings are already deteriorated from the disease's presence. While being fairly straight forward, roost surveying is by far the most effective method to identify the presence of white-nose syndrome in a particular population or region. These surveys involve researchers entering known or predicted bat hibernaculum sites and conducting visual counts to determine which species are present as well as setting a baseline for the estimated populations found within a particular site (Flaquer 2007). Surveying in this manner can yield important data on the conditions within and around hibernacula as well as visually identifying the presence of white-nose syndrome from living or deceased bats found within the site. By bringing data together through models that are designed to account for various sampling methods, more accurate assessments of survival rates can be determined and help to provide some insight on what needs to be done to protect remaining populations or assist with recovery efforts.

Modeling

One of the difficulties with conducting studies on natural phenomena such as disease outbreaks is the wide variety of factors that play a part in specific events.

Multiple different components within an ecosystem work to influence what goes on over the course of a specific natural event which can make events, such as a white nose syndrome outbreak and other disease epidemics, difficult to track or study in the field. With so many different variables at play during these events, one of the best methods to track and predict the possible outcomes of a particular scenario is through the use of modeling. Models involve the compilation of known data from key components of the phenomenon under study and using this information to help researchers design testable hypotheses (Kimmins 2004). While models can be very effective in predicting how components of an ecosystem may respond to an event, they have certain limitations in their ability to perfectly replicate different biological processes (Kimmins 2004).

In general, the goal of using models in the study of the white nose syndrome outbreak in bat populations is to describe and better understand the extent of the outbreak and the dynamics of the disease itself. Researchers are interested in gaining a greater understanding of the different ecological components that are involved in both the spread of the disease and the potential for recovery among affected populations. In order to assess the potential of modeling to predict and better understand the impacts of white nose syndrome on bat populations in northwestern Ontario, five papers that employed the use of models in their studies were selected for analysis. Table 3 summarizes the following information for each paper: the goal, the scenarios conducted, the outcome and the kinds of data that were used to obtain these results. Understanding which kinds of data are the most important to evaluate the effect that this disease has on bat populations is essential in monitoring, predicting and eventually assisting population recovery. As shown in Tables 4, 5 and 6, the five models described here incorporate a range of factors including bat physiology, fungal characteristics and environmental conditions, respectively. This information is employed to create scenarios based on assumptions informed by the knowledge and bias of the modeller (Kimmins 2004). All of the five selected papers focus primarily on Little brown bat populations in eastern North America, primarily due to the size and abundance of this species' populations before the disease outbreak and the severity at which these populations have been impacted.

Table 3. Outline of goals, scenarios, outcomes and data from five modeling papers involving white nose syndrome.

Author	Goals	Scenario	Outcome	Data
Maslo et al. 2015	Determine long-term population viability	24 scenarios (combinations of time-dependent & sex-specific effects on annual survival rates and recapture probability)	Increasing annual survival rates in remnant populations of little brown bat colonies afflicted by WNS indicates resistance to the disease	Annual survival rates and annual demographic trends
O'Regan et al. 2015	Determine if distance between hibernacula and mortality rates at each site will slow down or stop the spread of the fungus	10000 simulations (multi-scale model) until the total number of susceptible hibernacula were infected. 1000 simulations to determine epidemic size	Disease caused mortality at a county level will not limit the spread of the disease. Clustered hibernacula along geographic movement corridors will likely have the highest rate of decline.	Hibernaculum transmission rates, infection histories, (individual hibernaculum sites for micro, county-level rates for macro). Susceptible, infectious and removed hibernacula
Russell et al. 2015	Simulate impacts of WNS and evaluate time to recovery	12 scenarios (combinations of four starting population sizes, three demographic rates after recovery period)	High risk species are not likely to recover from residual surviving populations due to the uncertainty of reduced size population dynamics	Reproductive rates, pre and post WNS survival rates (adults, reproductive females, yearlings) and carrying capacity
Lilley et al. 2018	Model the effect that hibernaculum distribution and environmental conditions have on the spread of WNS	Variations in spatial distance between hibernacula (clustering density) were established to examine and replicate various environmental conditions across a landscape	Pathogens increase faster in poorly connected hibernacula within a clustered landscape (founding the epidemic). Landscape invasion is most successful through long-distance host dispersal	Spatial distribution and temperature of hibernacula, population dynamics (population growth, recovery rates, mortality rates), fungal dispersal and infection rates
Kramer et al. 2019	Linking individual hibernaculum sites to regional scales, determining transmission and severity of the infection to evaluate population declines	100 replications for each of the 2000 parameter sets (including both stochastic and deterministic models for within and among hibernaculum dynamics)	Metapopulation sizes are drastically reduced or become extinct in most cases, with a small percentage of populations persisting past the initial 10-year period	Infection rates (environmental & transmitted; within hibernaculum and swarming), transmission rates, death rates, population growth

Table 4. Comparison of data on bat physiology used in the five selected papers.

	Maslo et al. 2015	O'Regan et al. 2015	Russell et al. 2015	Lilley et al. 2018	Kramer et al. 2019
Scaling factor			x		
Starting population size	x (set at 1000)		x		
Juvenile-Adult ratio	x		x		
Population growth	x	x		x	x
Survival during WNS	x		x		
Reproductive rate adult % of females breeding			x		
Reproductive rate first year born % of females breeding			x		
Adult survival pre & post WNS			x		
First year born survival pre & post WNS			x		
Carrying capacity			x	x	
Bat population reproductive rate				x	
Recovery (infected to exposed)				x	
Recovery (exposed to susceptible)				x	x
Hibernation mortality coefficient				x	
Torpor rate				x	
Arousal rate				x	
Development of symptoms				x	
Mortality rate	x			x	x
Direct transmission		x		x	x
Transition to visibly infected					x
Transition to heavily infected					x
Gradient between frequency dependent & density dependent transmission					x
Probability of avoiding infection from infected hibernacula					x
Migration decay				x	
Adult male & female survival	x				
Juvenile survival	x				
Probability for adult females to return to hibernacula	x				

Table 5. Comparison of data on *Pseudogymnoascus destructans* used in the five selected papers.

	Maslo et al. 2015	O'Regan et al. 2015	Russell et al. 2015	Lilley et al. 2018	Kramer et al. 2019
Environmental contamination (shedding)				x	x
Relative shedding of heavily infected					x
Fungal growth in environment					x
Loss of fungus from environment					x
Infection from environment				x	x
Fungal carrying capacity				x	
Competitor carrying capacity				x	
Fungal growth coefficient				x	
Competitor growth coefficient				x	
Competition strength (pathogen to community)				x	
Competition strength (community to pathogen)				x	

Table 6. Comparison of data on bat hibernacula used in the five selected papers.

	Maslo et al. 2015	O'Regan et al. 2015	Russell et al. 2015	Lilley et al. 2018	Kramer et al. 2019
Distance between hibernacula		x	x		
Number of hibernacula			x		x (visited during swarming)
Landscape clustering coefficient				x	
Hibernaculum temperature info				x	
Hibernacula infection histories		x			
Number of susceptible hibernacula*		x			

*all hibernacula included were assumed to be susceptible

DISCUSSION

The research questions (repeated below) focus on the potential for modeling to assist in understanding and mitigating the impacts of white nose syndrome on bat populations in northwestern Ontario.

a. What is the potential of modeling to predict the re-establishment of bat populations in northwestern Ontario?
b. What information is needed to support a modeling effort?

This discussion presents information derived from the five modeling papers, with information on the biology of the bats, epidemiology of the disease itself and characteristics of hibernacula being used to evaluate and support future modeling efforts.

For each of the five modelling papers selected, a specific aspect of the ecological relationship between Little brown bats and the fungus provided the focus that supported the papers' goal. The data included within each paper's modeling effort was compiled into Tables 4, 5 and 6 based on whether the data is involved with bat physiology, fungal characteristics or conditions of hibernacula. By organizing the data in this manner, the results can be compared from each paper and used to help answer the previously stated research questions.

Consistent in all five papers, uncertainty was included into each of the models. Uncertainty is incorporated to account for natural variation and any other unknown types of data. Each paper utilized uncertainty in a different way. For example, incorporated into a population projection model to conduct a vital rate sensitivity analysis (Maslo et al.

2015), the macroscale spread of white nose syndrome yearly between counties (O'Regan et al. 2015), both spatial and demographic migration rates based on a range of expert opinions (Russell et al. 2015), ambient temperatures from active hibernacula (Lilley et al. 2018) and in treating reproduction and dispersal as stochastic events (Kramer et al. 2019).

Only one paper included any long-term monitoring, which involved a mark-recapture survey from a New Jersey bat colony to acquire data over a four-year period to determine annual survival rates and demographic trends (Maslo et al. 2015). This kind of data allowed the authors to make assumptions about long-term population trends, which is essential in determining the survivability potential of not only a specific population but to all bats that are heavily impacted by white nose syndrome (Maslo et al. 2015).

Russell et al. (2015) focused primarily on including data based on bat physiology. This paper investigated the ability of potentially resistant surviving populations to recover from a catastrophic decline by utilizing data based on changes to population size, post white nose syndrome reproductive rates and changes to demographic rates within these small remnant populations (Russell et al. 2015). O'Regan et al. (2015) also looked into the potential viability of small populations and how these could further spread or impede the spread of the disease across larger landscapes but instead incorporated data on distances between hibernacula and previously recorded infection histories to predict potential spread. Both Lilley et al. (2018) and Kramer et al. (2019) investigated how fungal growth, competition and how different modes of transmission influence overall population decline due to fungal disease outbreaks and the likelihood of continued disease spread across landscapes.

While there is little consistent overlap between the types of data used within each paper, all of them utilized some type of data on bat physiology to simulate modeling scenarios. Papers that focused more on bat populations and their recovery utilized a wider variety of data based on bat physiology with starting population size, the juvenile to adult ratio, population growth, survival rate during white nose syndrome, carrying capacity of local populations, recovery rate from exposed to susceptible individuals, direct transmission rate and mortality rate all used in at least two of the five papers. Population growth was the most commonly used data between all five papers, excluding Russell et al. (2015), which focused more on the potential for recovery of remnant populations after an outbreak of white nose syndrome has occurred. Direct transmission and mortality rates were also important as both were included in three out of the five papers used in this study. These kinds of data are extremely important in working towards predicting re-establishment as they help to provide a baseline on population size, birth rates, death rates and survival rates. Several papers also indicated that the lack of pre white nose syndrome data created problems with effectively determining changing trends to population sizes over time as the disease continues to afflict bats. This factor emphasizes the importance of conducting field work such as roost surveys to accurately establish a baseline upon which to analyze the changes in population dynamics for populations of bats impacted by white nose syndrome.

Of the five papers included in this study, Lilley et al. (2018) and Kramer et al. (2019) were the only two that included data on *P. destructans*. Environmental contamination from shedding and the rate of infection from the environment were included in both papers, which emphasises the importance of understanding the means by which the fungus moves through the environment, either directly between bats or via the surrounding environment and hibernacula (Kramer et al. 2019). Each paper, however, focused on a different aspect of the fungus. Kramer et al. (2019) used data on the spread of the fungus through shedding and its persistence within an environment (growth and loss) to evaluate the rate of infection from the environment and the resulting population decline. Lilley et al. (2018) focused more on the fungus itself and its growth within the environment as well as evaluating the influence of other fungal competitors to growth within selected habitats. By linking these factors to data on bat physiology including reproductive rates, recovery rates, mortality rates, torpor and arousal rates as well as environmental factors such as the landscape clustering coefficient and hibernacula temperatures, a greater understanding of the extent to which particular populations are affected can be achieved.

Understanding the dynamics between the disease and its environment is very important in determining the best methods to work towards population recovery across a larger landscape scale and would be best used supplementally alongside data involving population dynamics to assist in making predictions about how particular populations will be affected by the disease. While specific data on the fungal ecology may not be an essential component of modeling potential recovery, it is invaluable in the overall understanding of this disease outbreak and specifically how the fungus negatively impacts bat populations.

While little data on hibernacula were included in any of the papers, it could be argued that such information is important to determine the rate of spread from individual hibernacula as well as the quality of habitat that remnant populations can utilize for potential recovery. All papers except for Maslo et al. (2015) incorporated some kind of data on hibernacula conditions and histories. Mean temperatures at different points of a hibernaculum site can be of great value when looking at each species of bat in Ontario and their preferred hibernaculum conditions that influence the selection of a winter roosting site. Pairing this data with both the number of and distance between hibernacula would assist in predicting the spread of the fungus through the environment and the potential for recovery of each species based on available suitable hibernacula. Temperature is also an important environmental factor to determine where the fungus itself can persist without the host species, with cooler hibernacula being favoured as an overwintering site by some bats and acting as a threshold limit to fungal growth and spread. Similar to the data on bat physiology, it is beneficial to have baseline data on habitat conditions over time to support the modeling effort. By understanding where the bats live as well as the conditions that would encourage a particular species to inhabit a site, further measures can be taken in working towards determining how bats may become susceptible to contract the disease as they utilize different aspects of their habitat. Identifying and monitoring active hibernacula can also assist in predicting the path of the outbreak across a region and provide more information on continued spread of the disease between these sites. Most importantly is determining which kinds of specific habitats that Ontario’s endangered bat species choose to occupy within regional environments, therefore allowing further data collection and monitoring to occur.

Acquiring the necessary data to conduct informative modeling efforts for northwestern Ontario bat populations effectively would require the most important factors of bat physiology and specific data on active hibernaculum conditions to be gathered using a variety of potential monitoring strategies. Presence of bat species within a specific search area can be determined using bat detectors, which can assist in locating potential hibernaculum or essential habitats based on densities of bat echolocation calls. By employing unobtrusive monitoring practices that help to prevent disturbance to populations as well as reducing the risk of inadvertently spreading the fungus, data on reproductive rates, population size, survival rate, recovery rate and carrying capacity can be obtained. In addition, data on hibernacula conditions such as distribution, total number and temperature would assist in charting the continued spread of the disease.

CONCLUSION

With the right data, modelling can be an effective tool in assisting to predict the re-establishment of bat populations in northwestern Ontario. Some of the most important data is that relating to changes in bat population size such as survival rate, reproductive rate and recovery rate, all of which can be attained through monitoring methods such as roost surveys. Roost monitoring can also provide information about conditions inside hibernacula, which play a key role in disease maintenance and spread. Ideally, data on the key aspects identified should be gathered repeatedly (e.g. on a yearly basis) to quantify long-term trends in bat population dynamics. Models can inform decision-making for the recovery and re-establishment of bat populations affected by the white nose syndrome.

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