





Identifying research needs to inform white-nose syndrome management decisions

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Abstract

Ecological understanding of host–pathogen dynamics is the basis for managing wildlife diseases. Since 2008, federal, state, and provincial agencies and tribal and private organizations have collaborated on bat and white-nose syndrome (WNS) surveillance and monitoring, research, and management programs. Accordingly, scientists and managers have learned a lot about the hosts, pathogen, and dynam-

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ics of WNS. However, effective mitigation measures to combat WNS remain elusive. Host–pathogen systems are complex, and identifying ecological research priorities to improve management, choosing among various actions, and deciding when to implement those actions can be challenging. Through a cross-disciplinary approach, a group of diverse subject matter experts created an influence diagram used to identify uncertainties and prioritize research needs for WNS management. Critical knowledge gaps were identified, particularly with respect to how WNS dynamics and impacts may differ among bat species. We highlight critical uncertainties and identify targets for WNS research. This tool can be used to maximize the likelihood of achieving bat conservation goals within the context and limitations of specific real-world scenarios.

KEYWORDS

bats, influence diagram, *Pseudogymnoascus destructans*, uncertainties, wildlife management

1 | INTRODUCTION

Disease is an increasingly important challenge for wildlife conservation and management (Canessa, Bozzuto, Pasmans, & Martel, 2019; Daszak, Cunningham, & Hyatt, 2000; Deem, Karesh, & Weisman, 2001; Langwig, Voyles, et al., 2015). Threats to wildlife such as Tasmanian devil facial tumor disease (McCallum, 2008), snake fungal disease (Lorch et al., 2016), and amphibian chytridiomycosis (Scheele et al., 2019; Skerratt et al., 2007) demonstrate that emerging infectious diseases of wildlife can cause population declines and even extinction of host species. Furthermore, zoonotic diseases such as West Nile virus and avian influenza highlight the interconnectedness between the health status of the ecosystem and wildlife, human, and domestic animal populations (i.e., One Health; Leibler et al., 2009; Kilpatrick, 2011). There are very few examples of successful pathogen control (e.g., vaccination campaigns in canid species [Knobel et al., 2008; Freuling et al., 2013] and California condors [Chang, Davis, Stringfield, & Lutz, 2007]); for emerging diseases in particular, wildlife managers often have few proven options that can be incorporated into management and mitigation programs (Decker et al., 2006; Deem et al., 2001).

White-nose syndrome (WNS), a disease of hibernating bats caused by the fungus *Pseudogymnoascus destructans* (*Pd*; Lorch et al., 2011; Minnis & Lindner, 2013; Warnecke et al., 2012), has killed over 6 million bats, and led to the extirpation of once common species in many hibernacula in eastern North America (Frick et al., 2015). The fungus was discovered in New York state in 2006 (Blehert et al., 2009) and has since spread throughout the United States and Canada (www.whitenosesyndrome.org/

where-is-wns). *Pseudogymnoascus destructans* affects bat species to varying degrees (Langwig et al., 2012, 2016) ranging from exposure with no signs of disease in some species, to infection resulting in minor to severe lesions and often mortality in numerous other host species (Cryan, Meteyer, Boyles, & Blehert, 2010; Meteyer et al., 2009). As the pathogen continues to spread and invade into new areas across North America, additional species of hibernating bats are likely to be affected.

Since 2008, federal, state, and provincial agencies, and tribal and private organizations in the United States and Canada have collectively spent tens of millions of dollars to fund WNS-related surveillance and monitoring, research, and management activities for bats. These investments have advanced our understanding across diverse disciplines of bat behavior, hibernation physiology, fungal pathogens and disease transmission, as well as provide insight into differences in susceptibility and survival among WNS-affected species (see www.whitenosesyndrome.org/static-page/publishing-science). Despite these advances, methods for stopping the spread of *Pd* or reducing morbidity or mortality of WNS-affected bats are limited (Bernard et al., 2019; Hoyt et al., 2019; Rocke et al., 2019; U.S. Fish and Wildlife Service, 2016). Uncertainties and variations in the ecology of WNS associated with its distribution on the landscape, host species, and time of year make predictions regarding which management actions will achieve desired conservation outcomes, such as host survival and recruitment (Laber, Meyer, Reich, & Pacifici, 2018; Langwig, Voyles, et al., 2015), difficult to estimate. The potential benefits of some types of actions should also be considered against undesirable effects on nontarget organisms (Bernard & Grant, 2019; USFWS, 2016). Identifying critical uncertainties

(i.e., those that, if resolved, would guide selection of optimal management strategies; Runge, Converse, & Lyons, 2011) requires a shared understanding of the state of scientific knowledge and the decision contexts faced by management entities (Grant et al., 2017). This is especially pertinent given the lack of a single regulatory framework, or previously established protocols, used to manage and respond to emerging diseases in wildlife (Langwig, Voyles, et al., 2015). Largely, natural resource management occurs as a patchwork across the landscape due to disjunct jurisdictional boundaries and different agency mandates (Bernard & Grant, 2019).

The WNS community has shared knowledge across disciplines and professions through published and gray literature, professional conferences, and regular WNS-focused meetings. This information sharing has aided research and management efforts for WNS. However, sometimes the research lacks the specificity needed to inform management decisions aimed at maximizing survival and persistence of species of conservation concern (Arlettaz et al., 2010; Lauber, Stedman, Decker, & Knuth, 2011). Owing to the continued threat to North American bat populations and spread of *Pd* into new regions, we conducted a synthesis of the current state of knowledge related to WNS to better identify research priorities, promote research collaborations, and minimize the knowledge-implementation gap (Lauber et al., 2011). We used group expertise to create a conceptual influence diagram of the host-pathogen system, allowing us to work systematically through the mechanisms and dynamics of this disease and identify important remaining uncertainties that may lead to improved management actions.

Influence diagrams are graphical representations of systems used to establish a framework for improving decision-making through a structured, transparent processes by (a) developing a shared understanding of a system and facilitating communication, (b) integrating knowledge from diverse experts, (c) clarifying thinking about processes and relationships of components of a dynamic system, and (d) identifying uncertainties by articulating alternative hypotheses (Howard & Matheson, 2005). Influence diagrams can then be used to estimate the effects of management actions, generate creative and complementary management, improve collaboration across disciplines, evaluate important uncertainties, and prioritize future research to meet shared objectives (e.g., Grant et al., 2018). Key stochastic processes or states (“nodes”) and functional relationships between nodes (“links”) in an influence diagram are often used as a first step to develop quantitative predictive models, such as Bayesian Belief Networks (BBNs, McCann, Marcot, & Ellis, 2006) or path diagrams in structural equation modeling (Grace, Anderson, Olf, & Scheiner, 2010), which can help evaluate effectiveness of

alternative actions on various outcomes of importance (i.e., host survival and pathogen transmission). We focused on creating the foundational structure that can then be used to develop quantitatively robust models.

Here we describe the creation of an influence diagram for WNS that identifies key relationships and uncertainties within the disease system, and which focuses on actionable areas by identifying research priorities most relevant to management decision making. Our objectives were to (a) characterize the state of knowledge about the pathogen (*Pd*) and the disease (WNS) in the context of bat host biology and environmental variation, (b) identify research priorities to aid in the conservation of bat populations under threat from WNS, and (c) provide a framework for prioritizing and resolving system uncertainties that may aid in evaluating and implementing management actions, including the allocation of resources to achieve bat conservation goals.

2 | METHODS

We convened a four-day meeting of subject matter experts (hereafter “participants”) and facilitators (RFB, EHCG, RAK) to create an influence diagram for the host-pathogen system. We used a nominal group technique (NGT) to ensure all participants’ views were considered (Hugé & Mukherjee, 2017). NGT is a structured, in-person elicitation technique that enables participants to provide insight and have their ideas considered by other participants by looping through four key steps: silent idea generation, group sharing, clarification, and voting (i.e., ranking or rating; McMillan, King, & Tully, 2016). The ideal group size for a comprehensive data and knowledge synthesis ranges from 7 to 12, which maximizes the likelihood that all participants are able to play a significant role (Harvey & Holmes, 2012). In total, 15 participants (JCB, JTHC, WFF, DLL, JML, MSM, JDR, ALR, JLS, RST, GGT, MLV, MJV, JPW, CKRW) from a variety of federal ($n = 6$), and state ($n = 2$) agencies, nonprofit organizations ($n = 2$), and academic institutions ($n = 5$) involved in the research or management of North American bats were involved in this project. Participants represented a diverse and inclusive range of scientific and management expertise including, but not limited to, (a) bat ecology and conservation, immunology, and population genetics, (b) fungal ecology and genetics, (c) disease ecology and epidemiology, (d) cave and karst ecology and conservation, and (e) population and disease modeling.

Participants agreed that management objectives identified at the 2015 WNS Disease Management Strategy Workshop (USFWS, 2016) were appropriate root nodes for the diagram: “Maximize bat population persistence” and

“Minimize pathogen spread.” Root nodes are the desired outcomes or objectives that are affected by other variables, events, and links in the model. Participants divided into four multidisciplinary groups to draft a diagram for both objectives. Because of the extent of literature on the effects of WNS on the little brown myotis (*Myotis lucifugus*), participants focused on this species but considered transferability of the diagram to other species of bats expected or known to be vulnerable to the disease.

In developing the diagram, participants identified five constituent sub-diagrams: (a) human-mediated pathogen movement, (b) bat-mediated pathogen movement, (c) within-site bat recruitment, (d) epidemiology, and (e) disease process of WNS. Experts divided into groups based on their topics of interest and created drafts of each sub-diagram. The groups then added evidence (e.g., from scientific literature or expert knowledge) to each diagram to provide support for the hypothesized relationship, identify gaps in knowledge, or determine alternative hypotheses (Grant et al., 2018). Facilitators incorporated the sub-diagrams with the initial influence diagram to create a single comprehensive bat—WNS diagram. Following the in-person meeting, RFB and EHCG conducted two teleconference meetings for each sub-diagram to refine and finalize the influence diagram. Each expert participated in revising one to three diagrams. The objectives for the revision process were to simplify each

diagram without losing important details, minimize redundancy within and among each sub-diagram, ensure links and nodes were correctly represented and defined (Appendix S1), and appropriately link the sub-diagrams to each other (Appendix S2) and to the management objectives (i.e., root nodes, Figure 1).

3 | RESULTS

Here we report the structure and background for each sub-diagram, followed by the uncertainties identified after evaluating the full influence diagram. The uncertainties identified (as denoted by dashed lines in Figures 2–6) herein are not an exhaustive list of all knowledge gaps that remain; rather, they represent important questions identified by the participants.

3.1 | Human-mediated pathogen movement sub-diagram

Humans have the capacity to move pathogens over great distances (Tompkins, Carver, Jones, Krkošek, & Skerratt, 2015). Movement was defined as the translocation of *Pd* to a site. While movement of *Pd* by infected bats is believed to be the primary means of pathogen dispersal in North

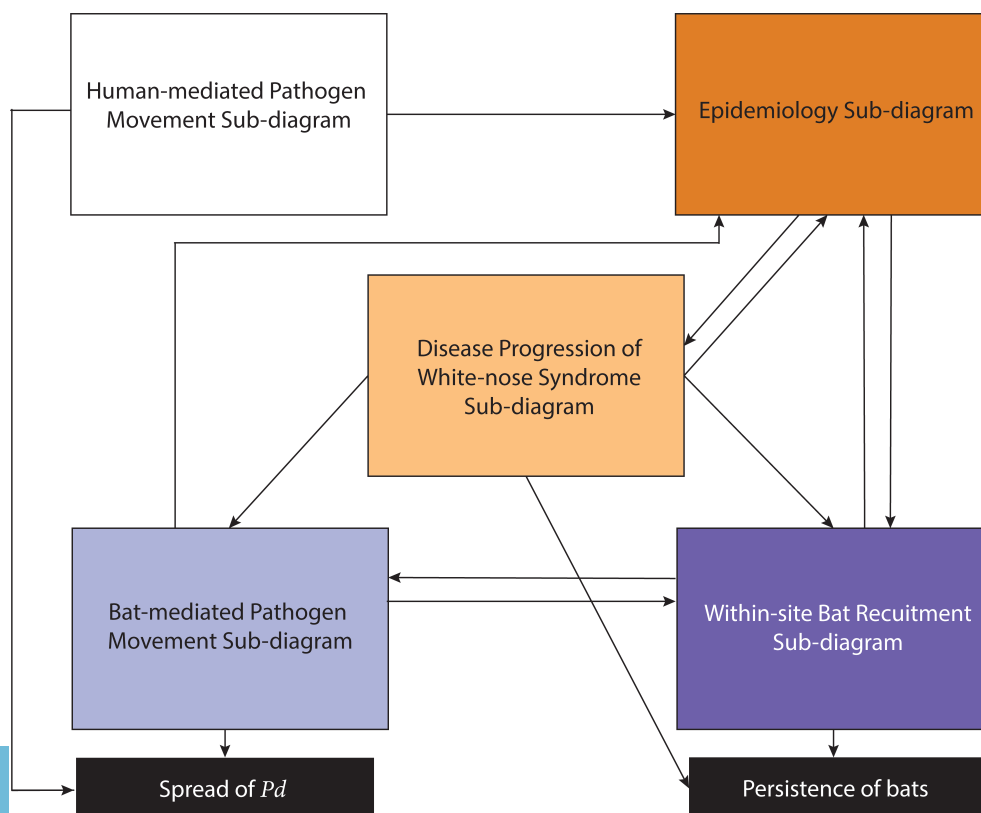


FIGURE 1 General framework for the cogenerated host-pathogen system diagram developed by experts representing state, federal and provincial agencies, academic institutions and nonprofit organizations. White boxes represent each sub-diagram with black boxes representing the two fundamental objectives used as motivation for creating the whole diagram. Arrows between boxes signify the connections between sub-diagrams and fundamental objectives

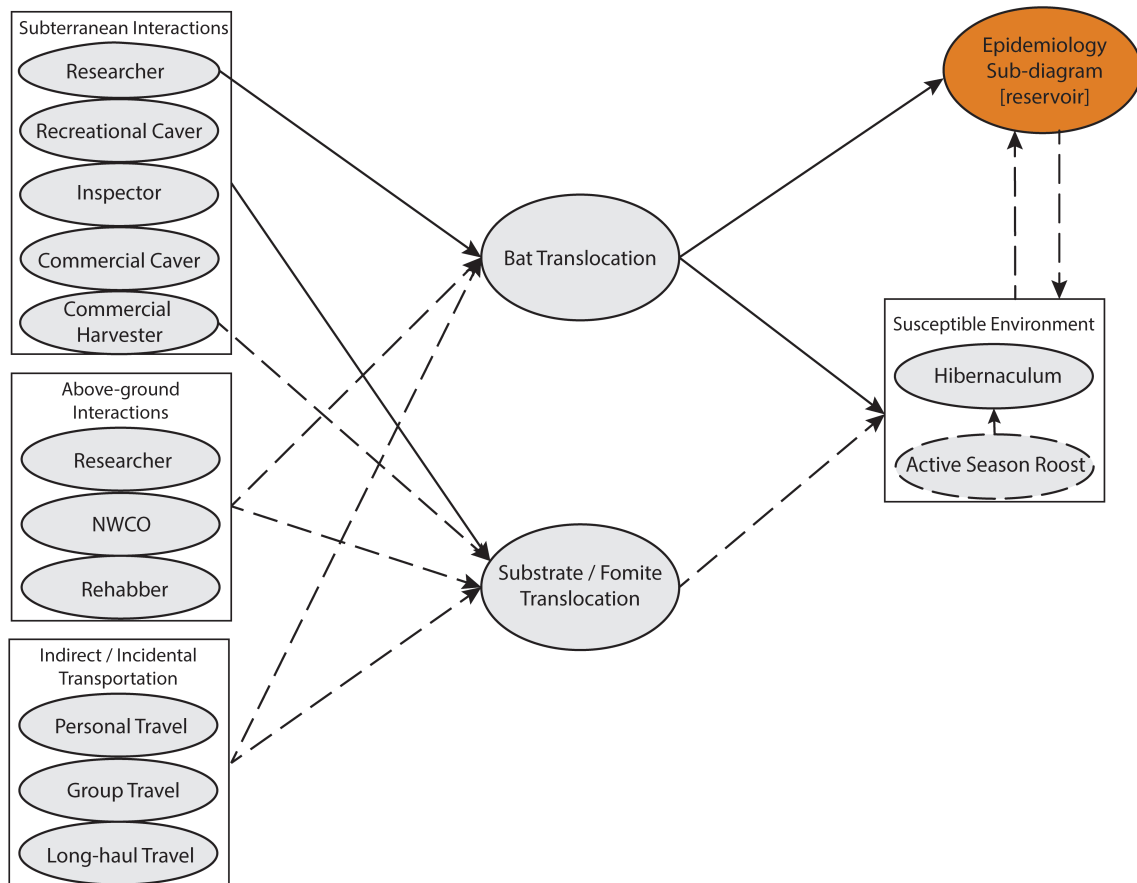


FIGURE 2 Human-mediated pathogen movement sub-diagram. Nodes grouped within boxes (i.e., subterranean interactions, above-ground interactions and indirect/incidental transportation) represent the factors that were expected to jointly contribute to human-mediated movement of the pathogen. Links connected to the themed boxes represent equivalency in contribution of component nodes to the linked node (e.g., nodes within “Subterranean Interactions” contribute to “Substrate/Fomite Translocation”). Links that start from a specific node (parent node) within a group specified that the parent node is assumed to have a different effect from the rest of the nodes to the child node. The only output from this sub-diagram is through the connection to the “Reservoir” node in the Epidemiology sub-diagram. Dashed lines represent where participants identified critical uncertainties or competing hypotheses based on reviews of the literature, whereas solid lines represent known connections. The acronym NWCO stands for Nuisance Wildlife Control Officer

America (Maher et al., 2012; Wilder, Frick, Langwig, & Kunz, 2011), the original arrival of *Pd* from Eurasia is highly suggestive of human translocation of the fungus (Drees et al., 2017; Leopardi, Blake, & Puechmaille, 2015). This sub-diagram (Figure 2) identifies factors considered important for human-mediated movement of *Pd* to new sites: (a) subterranean interactions, (b) above-ground interactions, and (c) indirect or incidental translocation via long-haul and personal or group travel. Researchers, recreational and commercial cavers, inspectors, and other commercial harvester (e.g., mushroom cultivation, cave-aged cheese) were identified as potential sources for *Pd* translocation. Pathogen movement by this mechanism was assumed to occur through substrate/fomite translocation (e.g., fungal spores on equipment transported to a novel environment). Aboveground activities involving interactions with potentially infected bats included researchers, Nuisance Wildlife

Control Operators (NWCO), and wildlife rehabilitators. Translocation of *Pd* could occur through movement of bats (e.g., release of infected bats) or movement of substrates/fomites (e.g., research or wildlife removal equipment).

3.2 | Bat-mediated pathogen movement sub-diagram

Bats play the primary role in extending the range of *Pd* in North America (Wilder et al., 2011). Movements among hibernacula during fall swarming, hibernation and spring migration were identified as important mechanisms for spreading *Pd* among sites (Figure 3). Body condition and reproductive status play important roles in facilitating bat migration over long distances (i.e., to maternity colonies). Maternity colonies are

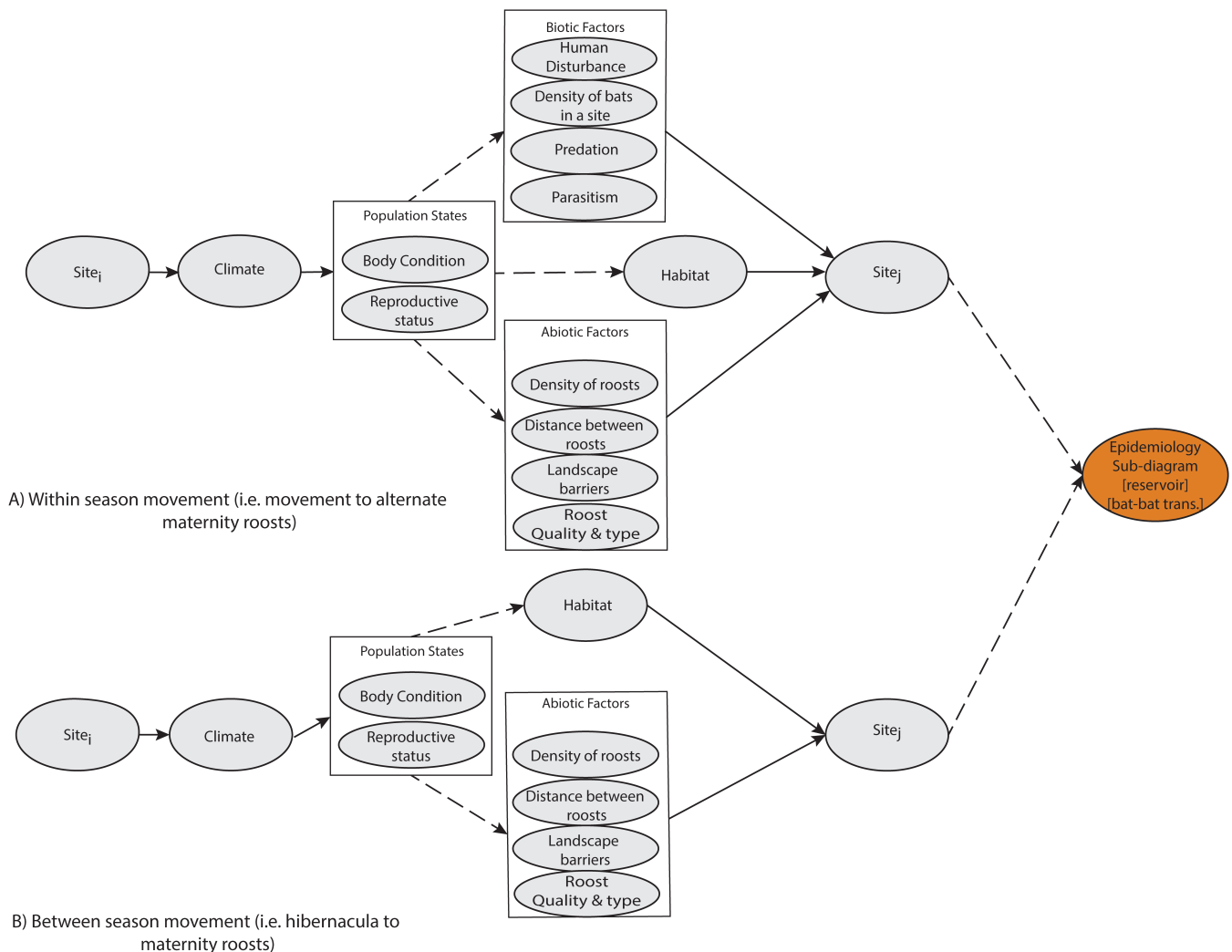


FIGURE 3 Bat-mediated pathogen movement sub-diagram, (a) within season movement. $Site_{i,j}$ represents all sites that may be used during one season and how and why an individual bat or group of individuals may move from one site to another site within a season. Nodes grouped within boxes (i.e., “Population States,” “Biotic Factors,” “Abiotic Factors”) represent the multiple factors that were expected to jointly contribute to the movement of a bat. Links connected to the themed boxes represent equivalency in contribution of component nodes to the linked node (e.g., nodes within “Population States” affect the transition to “Biotic Factors”). An individual must pass through the “Climate” node and “Population States” box prior to moving through either “Habitat,” “Biotic Factors,” or “Abiotic Factors” and to a second site. (b) Between season movement. $Site_{i,j}$ represents all sites that may be occupied and how and why an individual or group of individuals may move from one site to another site between seasons (e.g., summer maternity sites to swarming sites). Nodes grouped within boxes (i.e., “Population States,” “Abiotic Factors”) represent the multiple factors that were expected to jointly contribute to the movement of a bat. Links connected to the themed boxes represent equivalency in contribution of component nodes to the linked node (e.g., nodes within “Population States” affect the transition to “Abiotic Factors”). An individual must pass through the “Climate” node and “Population States” box prior to moving through either “Habitat” or “Abiotic Factors” and to a new seasonal site. The primary outlets of both within and between season movement diagrams are via the “ $Site_j$ ” node to the “Reservoir” and “Bat-bat transmission” node of the Epidemiology sub-diagram. Dashed lines represent where participants identified critical uncertainties or competing hypotheses based on reviews of the literature, whereas solid lines represent known connections

comprised of reproductively active females and are often maintained within an area until young of the year have weaned (Barclay & Harder, 2003).

In late summer, hibernating bat species migrate to swarming sites where mating activity and pre-winter fattening occur (Barclay & Harder, 2003). Over winter,

hibernating bat species engage in periods of reduced activity (i.e., torpor; Speakman & Speakman & Rowland, 1999) influenced by local physical and biological conditions within and surrounding hibernacula (i.e., climate and habitat). The rate at which bats move between sites both within and between seasons is affected by the

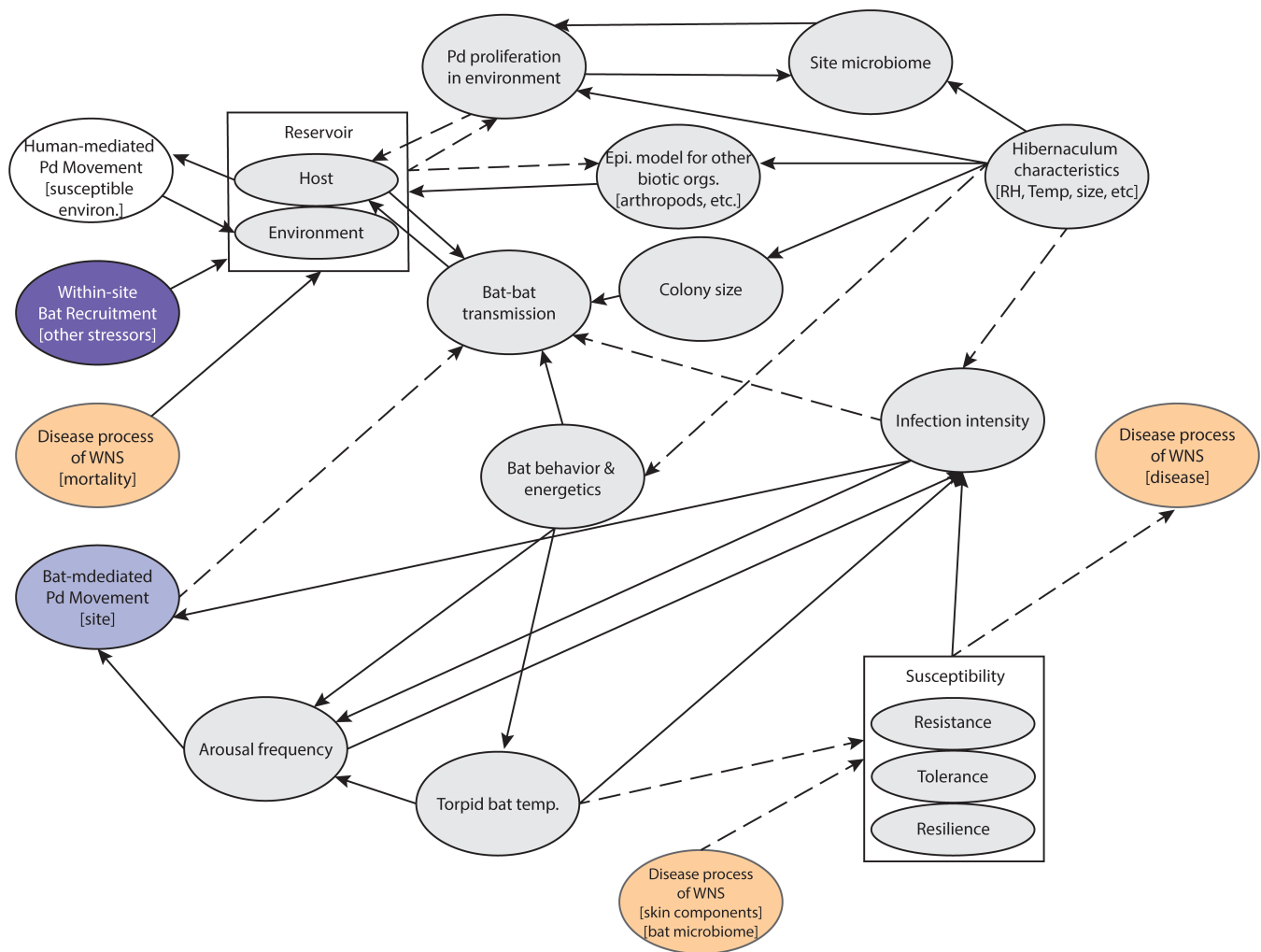


FIGURE 5 Epidemiology sub-diagram. Nodes grouped within boxes (i.e., “Reservoir” and “Susceptibility”) represent the multiple factors that were expected to jointly contribute to disease progression. Links connected to the themed boxes represent equivalency in contribution of component nodes to the linked node (e.g., nodes within “Susceptibility” contribute to “Infection intensity”). There are a number of links between this diagram and the other four sub-diagrams; however, the primary node linking all diagrams is via the “Reservoir” box. Dashed lines represent where participants identified critical uncertainties or competing hypotheses based on reviews of the literature, whereas solid lines represent known connections

exemplified in Peace et al. (2019). Similarly, human activity has the potential to introduce *Pd* to bat populations that have, to date, avoided exposure to the pathogen either by spatial or behavioral separation. Management actions may need to be adapted to address changes to the system associated with added genetic diversity of *Pd* and altered host–pathogen interactions.

Bats alternate between roosts (Davis & Hitchcock, 1965), but fidelity and connectivity among roosts over time remains a key uncertainty. By understanding movement patterns of bats within and among seasons, we may identify management actions that minimize the likelihood of bat-mediated pathogen spread. For example, roost-switching during winter months could be an important driver in local or regional spread, given that it is the

period when bats are most heavily infected with *Pd* (Langwig, Frick, et al., 2015). Furthermore, movement within roosts and increased contact among individuals within a site has recently been identified as a major driver of transmission within infected hibernacula (Hoyt et al., 2018).

3.4 | Within-site bat recruitment sub-diagram

This sub-diagram (Figure 4) captures factors that directly affect reproduction and survival of bats. Due to physiological constraints of hibernation, bats expend their fat reserves, which can affect the survival of an individual

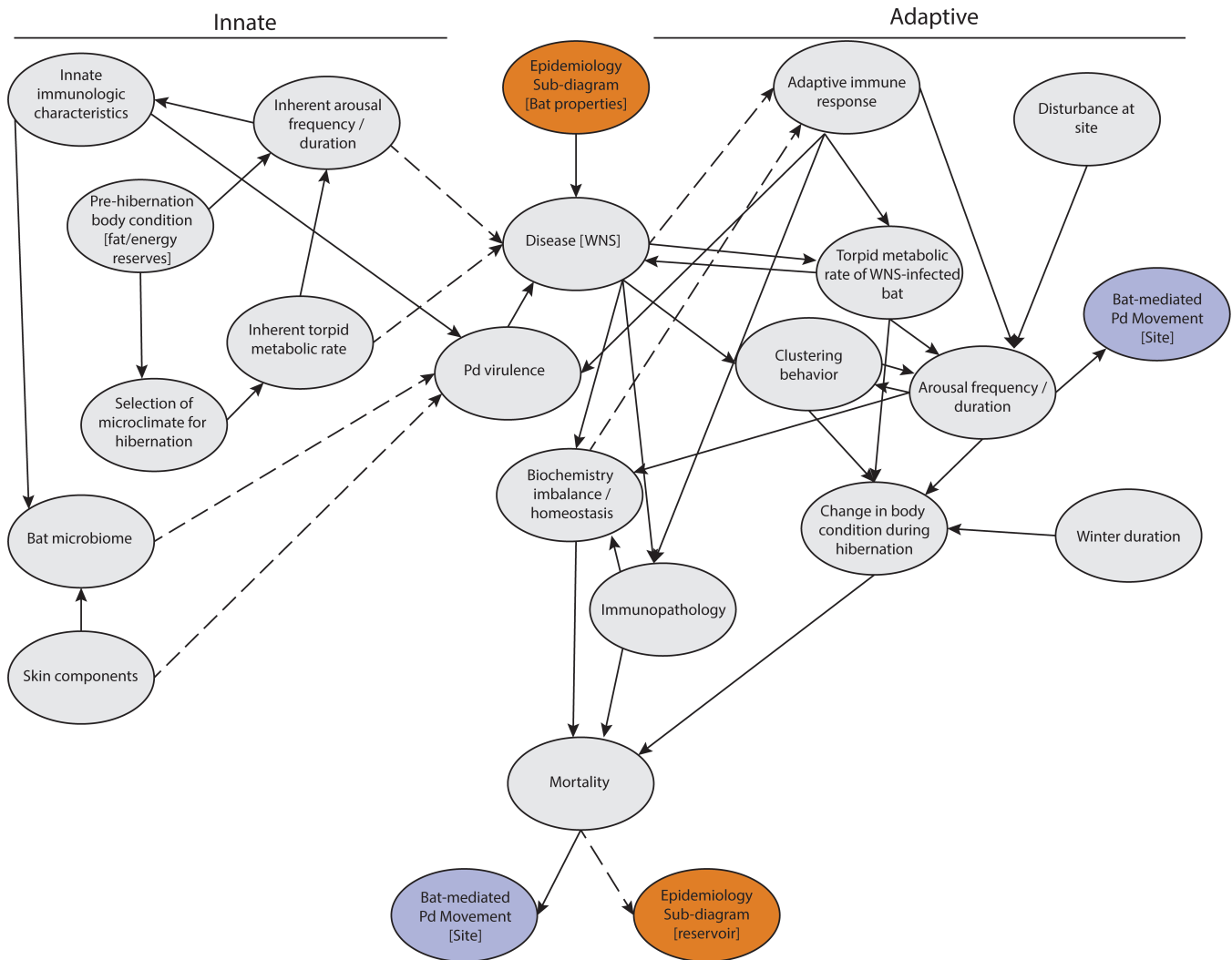


FIGURE 6 Disease progression of WNS sub-diagram. The main input to this sub-diagram is from the “Susceptibility” and “Reservoir” nodes within the Epidemiology sub-diagram. This model reads from left to right, working from pre-disease characteristics, through the disease node, into the post-infection/disease altered characteristics (e.g., “Torpid metabolic rate of a WNS-affected bat” to “Change in body condition during hibernation”). All links funnel through the “Mortality” node where a bat may die due to disease (i.e., $1 - [\text{survival}]$) or continue through the “Bat Movement” sub-diagrams via “Site” or the “Epidemiology” sub-diagram via the “Reservoir” box. Dashed lines represent where participants identified critical uncertainties or competing hypotheses based on reviews of the literature, whereas solid lines represent known connections

(Ruf & Geiser, 2015; van Breukelen & Martin, 2015) as well as their embryos (Barbour & Davis, 1969). Bats with WNS are at a higher risk of mortality due to altered torpor-arousal cycles, physiological perturbations and premature depletion of fat reserves, which often forces midwinter emergence and death from exposure (Verant et al., 2014). If a female survives winter, but has low post-emergence body condition, the likelihood she becomes pregnant is reduced (Jonasson & Willis, 2011). Upon emergence, females require sufficient energy stores for gestation, clearing and healing from infection (Fuller et al., 2011), and migration to a maternity colony or finding viable roosting habitat (O’Keefe & Loeb, 2017). Roost

quality and availability that have minimal disturbance, low predation and parasitism are some of the most important characteristics in neonate and juvenile survival (Webber & Willis, 2018).

3.5 | Uncertainties within the “within-site bat recruitment sub-diagram”

A key uncertainty within this diagram highlights the need to understand the sublethal effects of WNS on recruitment and reproductive success of bats. Possible impacts include reduced pregnancy and birth rates,

which may be affected by hormone levels (such as leptin or cortisol; Davy et al., 2017) needed to sustain all stages of pregnancy, altered fitness and survival of neonates and juveniles caused by low or poor body condition of mothers, and the potential for management actions to bolster reproductive and survival rates in females.

3.6 | Epidemiology sub-diagram

This sub-diagram (Figure 5) describes factors that influence the transmission of *Pd* among potential reservoirs (e.g., bats, other organisms, and the environment). The hibernaculum (e.g., cave, mine, or other suitable hibernation site) is the primary environment where bats encounter *Pd* and develop WNS. Hibernaculum characteristics influence multiple factors related to the epidemiology of WNS and exert strong influences on the proliferation of *Pd* in the environment (Frick et al., 2017; Langwig, Frick, et al., 2015; Langwig, Hoyt, et al., 2015; Reynolds, Ingersoll, & Barton, 2015). These characteristics can also influence the composition and dynamics of microbial communities (Vanderwolf, McAlpine, Forbes, & Malloch, 2012) and the population of bats and other organisms, such as invertebrates, that use caves (Lučan et al., 2016; Zahradníková et al., 2017).

The infection intensity of *Pd* is a key component of WNS epidemiology and is interconnected with multiple host attributes. The intensity of *Pd* infection has been shown to vary by bat species and has been used to identify differences in susceptibility to *Pd* and response to infection within and among species (Davy et al., 2017; Frick et al., 2015). Resistance in bats has been correlated with selection for colder roosting sites (Johnson, Scafani, Sewall, & Turner, 2016) and lower torpid body temperatures (Mayberry, McGuire, & Willis, 2017; McGuire, Mayberry, & Willis, 2017). Higher rates of arousal from torpor and winter activity, such as that observed in the southeastern US, may also contribute to reduced infection intensities (Bernard, Willcox, Parise, Foster, & McCracken, 2017). In contrast, tolerance may be important for survival in sites with high *Pd* prevalence and load. Examples include infection with no mortality in Eurasia (Zukal et al., 2016) and persisting colonies of bats in the US (Frick et al., 2017). Some species of bats develop minimal, to no, apparent pathology following exposure to *Pd* (e.g., *M. grisescens*), with one species, *Corynorhinus townsendii virginianus*, not yet documented with WNS despite living in caves contaminated with *Pd* for almost 10 years (Coleman & Reichard, 2014).

In addition to the infection intensity, the probability of transmission among individuals depends on the encounter rate between individual bats (Hoyt et al., 2018). The

tendency of bats to roost in tight aggregations during hibernation varies by species and has been hypothesized to affect, and be affected by, WNS (Hayman, Pulliam, Marshall, Cryan, & Webb, 2016; Langwig et al., 2016; Wilcox et al., 2014). Clustering behavior has been hypothesized to increase efficiencies in thermoregulation and reduce water loss for hibernating bats and may influence torpid bat temperature and arousal frequency (Boratynski, Willis, Jefimow, & Wojciechowski, 2015; Hayman et al., 2016). However, for WNS-affected bats, clustering may also be disadvantageous due to increased contact rates and disturbance by co-roosting bats (Hoyt et al., 2018; Langwig et al., 2012). Additionally, activity patterns during arousal bouts may also affect transmission rates within a colony. Once a susceptible bat is exposed to *Pd*, the fungus invades the epidermis, resulting in pathological (Meteyer et al., 2009) and physiological changes (Verant et al., 2014; Warnecke et al., 2013) that can alter the frequency of arousal from torpor (Reeder et al., 2012).

3.7 | Uncertainties within the “epidemiology” sub-diagram

WNS affects multiple bat species across North America, therefore, understanding the potential differences between observed or estimated patterns of population growth rate based on annual counts at winter sites and estimating survival rates of bats exposed to *Pd* within and among species in the field (with sufficient sample sizes to ensure acceptable precision) remain two critical information needs. In the case where it is feasible to estimate survival rates, studies that examine the mechanisms (i.e., genetic, physiological, behavioral, or environmental) responsible for increased survival and persistence of bat populations would aid in understanding species-specific risk. Estimating survival rates in populations that persist after the initial mortality and recovery stages of the disease is important to gauge whether these populations are progressing toward recovery.

3.8 | Disease progression of WNS sub-diagram

This sub-diagram (Figure 6) describes the various outcomes of disease in an individual bat that has been exposed to *Pd*. The left side of the diagram represents innate attributes of the host and pathogen that are hypothesized or demonstrated to affect a bat's susceptibility to infection and the subsequent pathology and severity of disease. The right side of the diagram depicts the interrelated adaptive physiologic and behavioral

responses to WNS that affect survival (mortality), movement of bats, and subsequent transmission of *Pd*.

Host-related factors, such as the skin microbiome (Avena et al., 2016), skin chemistry and structure (Pannkuk, Gilmore, Savary, & Risch, 2012), torpor patterns (Moore et al., 2018), microclimate preferences (Langwig et al., 2012), or species-level traits (Langwig, Frick, et al., 2015) could play a role in moderating susceptibility to infection with *Pd*, intensity of infection and progression of epidermal pathology. Development of WNS occurs during hibernation and is a complex, multistage process (Verant et al., 2014). The torpid state creates a favorable environment for *Pd* to proliferate and invade the epidermis of the wing (Meteyer et al., 2009), leading to compromised wing function, which can impede flight (Reichard & Kunz, 2009) and homeostasis (Cryan et al., 2010). Physiologic disturbances documented in bats with WNS include electrolyte imbalances, dehydration, and acidosis (Cryan et al., 2010; Verant et al., 2014; Warnecke et al., 2013; Willis, Menzies, Boyles, & Wojciechowski, 2011). Torpid metabolic rate and evaporative water loss also increase with WNS (McGuire et al., 2017). These responses, in combination with changes in behavior such as increased arousal frequency (Reeder et al., 2012), roost shifts to colder locations or toward entrances of hibernacula (Turner, Reeder, & Coleman, 2011) and changes in clustering behavior (Langwig et al., 2012; Wilcox et al., 2014), contribute to higher rates of energy expenditure and depletion of fat reserves over winter. Ultimately, these physiological and behavioral disturbances lead to a progressive state of morbidity, which can result in death prior to spring emergence (Verant et al., 2014).

Once a bat emerges from hibernation in the spring, activation of the immune system can contribute to worsening of WNS pathology by inducing an immune reconstitution inflammatory syndrome (Meteyer, Barber, & Mandl, 2012). If a bat is able to survive, the lesions in the wing can completely heal several weeks post-emergence (Fuller et al., 2011), although not without some metabolic cost (Meierhofer et al., 2018). The virulence of *Pd* determines the severity of WNS and is thus a key component of the disease process. Virulence factors for *Pd* have been hypothesized to include characteristics identified in other fungal pathogens, such as urease and superoxide dismutase (Smyth, Schlesinger, Overton, & Butchkoski, 2013), as well as a group of subtilisin serine endopeptidases (e.g., PdSP2; destructin-1) that appear to play a role in collagen degradation (O'Donoghue et al., 2015; Pannkuk, Risch, & Savary, 2015). Prehibernation body condition and hibernation behaviors of bats are thought to moderate infection and severity of WNS. Bats with more fat reserves at the start of hibernation may have an increased chance of survival (Czenze, Jonasson, & Willis, 2017; Jonasson & Willis, 2012)

as greater fat stores may ease energetic constraints on beneficial behavior and physiological processes.

3.9 | Uncertainties within the “disease progression of WNS” sub-diagram

Additional research is needed to determine whether interactions between *Pd* and native microbes in the environment, or on the skin of bats, alter relationships between native microbial communities and bat populations using cave roosts. Improved understanding of how *Pd* exists among native microbes in these environments will help determine the long-term interactions of these bacteria, fungi, and viruses, and how these interactions may affect the ability of *Pd* to cause disease. This information will also aid in evaluating the potential effectiveness of possible biotic treatments, such as probiotic treatment (Cheng et al., 2017; Hoyt et al., 2019). For bat hosts, changes in innate and adaptive immune responses or other behavioral or physiologic changes that allow bats to moderate severity of WNS over time may affect the ability of bats to adapt to the disease, while diminishing numbers of hosts may lead to the evolution of less virulent *Pd* in the future.

4 | DISCUSSION

Our influence diagram represents a synthesis of the multidisciplinary knowledge within the North American WNS research community and provides insight into key stochastic processes and functional relationships that underlie host–pathogen dynamics. By synthesizing knowledge across a multidisciplinary team, we created an influence diagram that can help facilitate the direction research can proceed to directly support the decision-making of natural resource managers (Grant et al., 2017, 2018). Responses to wildlife disease is complicated by a lack of information, but also fragmented knowledge that makes it difficult to know which uncertainties should be priorities for research. Additionally, management actions and WNS treatments may be more effectively identified and applied with greater efficacy when the entire system is considered. Our influence diagram sets up the ability to address these research and management challenges.

A considerable amount of research has been conducted on *Pd* and WNS over the last decade, and here we were able to identify important uncertainties within the system that have yet to be addressed. Among the identified uncertainties, we identified research priorities within each sub-diagram to better understand WNS and forecast

the effects of *Pd* and WNS on North American bat populations. Within human-mediated pathogen movement: explore possible outcomes of the impact of an introduction of a novel strain or mating type of *Pd* into North America. For the bat-mediated pathogen movement: determine how host migration and dispersal information can be used to forecast the possible changes in infection status at a site or among regions. For within-site bat recruitment: identify the sublethal effects and impacts WNS has on reproductive success among bat populations. Within the epidemiology sub-diagram: improve estimation of host survival within and among species. And finally, within the disease progression sub-diagram: understand adaptive capacities of bat populations to persist and recover in the presence of *Pd* and consider the potential for attenuation in virulence or reduction in infection intensity of *Pd* over time. Each remaining uncertainty can be addressed from multiple research directions that will require integrating disciplines and techniques such as molecular detection and population genetics, behavior and ecology of the host, ecology of the pathogen, as well as principles of landscape ecology.

Research priorities identified through this assessment represent information needs that, if addressed, may inform and expand potential strategies to manage *Pd* and WNS. Research, particularly in these areas, may help identify areas in the host–pathogen system where new and innovative management may be effective. Estimating the potential efficacy, method and timing of treatments for bats will require understanding how sensitivity to *Pd* varies among individuals, species, and populations, as well as characterizing factors that influence temporal variability in *Pd* growth rates across the life cycle of bats and the ecosystems they occupy. Finally, some populations of bat species susceptible to WNS are persisting despite evidence of the disease (Dobony et al., 2011; Dobony & Johnson, 2018; Frick et al., 2017; Langwig et al., 2017). Research in among-individual and among-population responses to WNS may suggest management actions in these populations to help reduce the impacts of WNS and co-occurring threats, such as mortality from wind turbines, to promote host persistence. Because WNS is predicted to spread to new locations (Maher et al., 2012), understanding variation between host species and among populations of wide-ranging species may help predict which species may be able to coexist with the pathogen. Meanwhile, active management in at-risk regions may be identified to help slow or shorten the epidemic stage of disease invasion.

Improved tools and approaches for surveillance are enhancing our understanding of the distribution of *Pd* on the landscape (Janicki et al., 2015), with early observations aiding studies regarding the ecological (Frick et al., 2015; Langwig, Frick, et al., 2015), behavioral (Bernard et al.,

2017; Hoyt et al., 2018; Langwig et al., 2016), physiological (McGuire et al., 2017; Reeder et al., 2012; Willis, 2015), and genetic (Miller-Butterworth, Vonhof, Rosenstern, Turner, & Russell, 2014) factors that contribute to a species' or individual's vulnerability to infection by *Pd* and the progression of WNS. Empirical data generated from these studies can be used for more robust statistical analyses to quantify relative contributions and interactions of known factors (i.e., uncertainties within the system). Growing knowledge of the ecological preferences of the fungus and how it interacts with other microbes in the environment, along with increasing knowledge of the pathogen's life cycle, and landscape use by potential bat hosts will improve our ability to estimate the range expansion and impacts of *Pd* for novel bat hosts. This information may help managers determine the likelihood that bats in particular areas will be susceptible, and to what extent management actions may be necessary. Our ability to address these information needs will depend on the development and application of new lab and field techniques, along with improvements in collaborative and timely sharing of information and ideas. This may be realized through interdisciplinary collaboration and research focused on shared management objectives using a formal decision-analysis approach (Bernard & Grant, 2019).

Managers can use this diagram as a foundation for working through agency-specific decision problems to explicitly identify and characterize the potential outcome of multiple or sequential management actions (e.g., minimizing spread of *Pd* in winter while improving summer roost habitat; Bernard et al., 2019). Researchers can use the diagram to work with managers to generate novel actions and research priorities, especially for parts of the system where less attention has been focused. The diagram can be used to organize and generate a diverse suite of actions available to a manager, highlight relevant uncertainties and hypotheses specific to management jurisdictions, reveal overlooked management objectives, and identify spatial (local, regional, federal) and temporal (short- vs. long-term) dimensions of a disease management response (Grant et al., 2017). Finally, the diagram can be used to motivate a decision-specific model to predict the effects of proposed actions that may affect elements of the host–pathogen system. Though the ultimate objectives include identifying efficacious actions that may need to be implemented in multiple places in the system, a necessary first step, which we accomplish here, was the organization of current knowledge, identification of knowledge gaps, and specification of research needs. This provides a foundation for conducting research, building predictive models, and evaluating a set of management actions for a specific location on the landscape, all of which are the focus of ongoing work.

The system diagram we present here has already proven to be useful for several agencies faced with managing bat populations affected by *Pd* (see Bernard et al., 2019) and has been used by the USFWS to identify research priorities within their annual funding process. Within the context of a formal decision analysis, influence diagrams are useful for checking the framing of a management decision to ensure that the decision identified will be optimal across all specified management objectives (Bernard & Grant, 2019). Maintenance and updating with new knowledge of this diagram is now one of the tasks of the US WNS Response Team. As such, the model provides promise as the foundation for bat- or disease-related decision problems, such that the framework guides research to inform management goals (i.e., species- or site-specific), identifies actions that achieve their fundamental objectives (e.g., minimize spread of *Pd*; disease progression of WNS diagram), and creates novel alternatives that are specific to their management goals and jurisdiction.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Riley F. Bernard conceived the idea for the workshop, facilitated the in-person workshop, co-led the development of the influence diagram, organized post-workshop conference calls, created the figures and tables, and wrote the manuscript. Jonathan D. Reichard, Jeremy T. H. Coleman, and Rachel A. Katz conceived the idea for the workshop, helped facilitate the in-person workshop and development of influence diagrams, attended conference calls, and assisted with the writing of the manuscript. Julie C. Blackwood, Michelle L. Verant, Jordi L. Segers, Jeffery M. Lorch, J. P. White, and Marianne S. Moore participated at the in-person workshop, on conference calls (8+ hours), and in the writing of the manuscript. Amy L. Russell, Daniel L. Lindner, Rickard S. Toomey, Gregory G. Turner, and Winifred F. Frick participated at the

in-person workshop and on conference calls (1–8 hr) and provided editorial comments. Maarten J. Vonhof and Craig K. R. Willis participated in the in-person workshop and on conference calls (2 hr), respectively, and provided editorial comments. Evan H. C. Grant attained funding for Riley F. Bernard, conceived the idea for the workshop, co-led the development of the influence diagram, participated on post-workshop conference calls, and assisted in the writing and editing of the manuscript.

DATA AVAILABILITY STATEMENT

All data used are accessible in the manuscripts' supplemental documents.

ETHICS STATEMENT

All authors understood how their contributions would be used during the workshop and development of the manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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