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ARTICLE
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Trade network surveillance strategies

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Abstract

The global success of the wildlife trade industry has led to the emergence of novel pathogens over the past two decades. The introduction of *Batrachochytrium dendrobatidis* to naive amphibian species has been a cause of global population decline and species extinction. A second chytridiomycosis causing fungus, *Batrachochytrium salamandrivorans* (Bsal), has been identified in the Netherlands, and there is a risk of it being introduced to new regions via the wildlife pet trade. Current regulations governing wild animal trade make it difficult to identify carriers before they enter the trade network, so we seek to provide an early-warning surveillance system to aid in searching the pet trade network for infectious animals. We represent the wildlife trade network as a tiered, directed graph with nodes representing facilities housing animals and edges representing trade relationships. We then propose two novel methods for determining optimal surveillance for the identification of facilities housing infected animals in the event that Bsal is identified within the network. In doing this, we account for the assumption that surveillance has an associated cost representing monetary cost and/or difficulty. The first of these methods utilizes limited information about local network topology and

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prioritizes surveillance that provides more information about network topology. The latter uses only the cost of surveillance and prioritizes surveilling at as many facilities as possible. We test the methods with simulated networks and outbreaks. The surveillance method that considers the network structure generally identifies a greater proportion of facilities housing infectious animals given a fixed cost and generally has a lower total cost than the method that only considers the cost of surveillance. The practice of choosing testing sites based on convenience and prioritizing the number of sampling sites may ultimately be more costly than identifying optimal sites for testing.

KEYWORDS
Batrachochytrium salamandrivorans, chytridiomycosis, conservation, epidemic preparedness, network topology

INTRODUCTION

Wildlife trade is an expansive and lucrative industry, but its global success has led to the emergence of novel pathogens over the past two decades (Karesh et al., 2005; Pavlin et al., 2009). The animals traded are typically transported and stored in a confined and crowded manner, elevating their stress and lowering their innate immunity to any pathogens they harbored before capture (Baker et al., 2013; Pohlin et al., 2021). These conditions also increase their direct and sustained contact with individuals of other species, which exposes them to new pathogens (Cardoso et al., 2021). Finally, the movement of these animals across international borders, often across the globe from where they are native, serves as a potent vector for global pathogen spread (Ogden et al., 2019). Together, these factors have made the wildlife trade a principal concern for the spread of pathogens into naive populations, as the majority of emerging infectious diseases originate in wildlife (Daszak et al., 2008).

Over 11 million live animals were exported from 189 countries between 2012 and 2016 (Özgün et al., 2019) with the majority of these animals, roughly 92%, supplying demand for exotic pets (Smith et al., 2009, 2017). It is estimated that six major pathogen outbreaks stemming from trade in exotic pets between 1997 and 2009 resulted in at least $80 million in losses across a range of industries (Smith et al., 2019). Here, we explore strategies for a rapid response to a potential outbreak via surveillance of a domestic pet animal trade network, with the US exotic pet trade as our case study. In this context, surveillance involves efforts to identify infected facilities rapidly after the initial infection is observed. Our approach recognizes the difficulty in ever knowing all network entities, and their connections, within a dynamic trade network such as that of the pet trade. The topology of the network is an important factor in effective surveillance in trade networks. Because of that, imperfect information about the trade network has been a persistent barrier to optimized surveillance. Moslonka-Lefebvre et al. (2012) provided a method for reducing the spread of disease by reducing the number of highly connected facilities, that is, hubs. Unfortunately this technique (as well as the similar techniques of Colman et al., 2019; Guinat et al., 2016; Herrera et al., 2016 discussed in *Discussion*) requires complete or nearly complete knowledge of the network in question, and, due to lack of regulation in the pet trade and the likelihood that participants in the trade are temporally dynamic, such knowledge is generally not available. Our main contribution is to show that network pathogen surveillance is still feasible and efficient absent this full network knowledge, and point toward key next-steps for moving this early-warning and rapid response system toward implementation.

Amphibians are particularly vulnerable to emerging pathogens associated with trade networks. In recent years, chytridiomycosis, caused by the aquatic fungus *Batrachochytrium dendrobatidis* (Bd), has emerged as one of the major causes of a global amphibian population decline and species extinction (Scheele et al., 2019; Wake & Vredenburg, 2008). A massive mortality event among fire salamanders (*Salamandra salmandra*) between 2010 and 2013 in The Netherlands led to the discovery of a second fungus with an etiologic role for chytridimycosis, *Batrachochytrium salamandrivorans* (Bsal) (Martel et al., 2013). In 2013, Martel et al. determined that Bsal originated in Asia where salamanders likely serve as a reservoir and that the fungal infection is lethal in many salamander species native to North and Central America (Gray et al., 2023; Martel et al., 2014; Olson et al., 2024). In 2014, Martel et al. determined that the international pet trade is the most likely cause of the introduction of the Bsal to Europe and

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noted that 2.3 million individuals of a salamander native to Asia, *Cynops orientalis*, known to serve as a potential reservoir for Bsal, were imported to the United States between 2001 and 2009 (O'Hanlon et al., 2018; Yuan et al., 2018). Nguyen et al. (2017) showed that Bsal is also present in toads, *Bombina microdeladigitora*, from Vietnam and suggested that Bsal containment efforts should not be limited to urodeles. Given the obvious threat of Bsal to salamanders and other amphibians, both globally and in North America, a group of organizations requested that the US Fish and Wildlife Service take action to prevent the spread of Bsal in the United States and initiated a general call to action to prevent the spread of Bsal (Gray et al., 2015).

Based on experiences in the United States with Bd, one important method of protecting native populations from invasive pathogens is the prevention of introduction, but a rapid response is necessary if introduction does occur (Langwig et al., 2015). Examining best practices used in international and domestic trade can provide a path forward. Within the livestock industry, for example, controlling for pathogens like hoof-and-mouth disease involves surveillance and testing as well as public policies that support disease mitigation (Ferguson et al., 2001). Such surveillance is not conducted for most animals imported for the pet trade in the United States. Mandatory testing exists in the United States only for psittacosis, foot-and-mouth disease, Newcastle disease, and avian influenza. Screening for diseases is the responsibility of the importer for non-livestock animals, including those destined for the pet trade (Pavlin et al., 2009). There is little oversight in the United States for the pet amphibian trade, and existing oversight focuses on conservation status rather than disease prevention (Grant et al., 2017; Smith et al., 2017).

Because of the diffuse and deregulated nature of the pet trade, present strategies for controlling infectious disease in these trade networks suffer from a lack of information about the network itself. We seek to aid in a rapid response to a potential introduction of Bsal (or any pathogen) into the US amphibian pet trade by providing a methodology that efficiently and effectively surveils facilities within the pet trade network in search of the pathogen in question. To accomplish this goal, we treat the pet trade network as a tiered, directed graph whose nodes represent ports, distributors, and retailers housing potentially infected animals and whose edges represent trades between facilities. Each node is assigned a numerical value that represents the cost of conducting surveillance at the facility, including both resources and effort. We provide two iterative methods that allow surveillance at a few locations in any given step restricted to facilities within 1 or 2 degrees of separation from an infected facility and subject to a cost-based constraint. One of these methods depends on the network topology local to an infected facility and the other does not. By comparing the effectiveness and efficiency of the methods based on their performance in the face of a limited budget, we can make recommendations for surveillance strategies in pet trade networks.

MATERIALS AND METHODS

A network's topology and characteristics will impact the spread of disease on the network (Shirley & Rushton, 2005), and, therefore, any surveillance method being considered on a trade network may be sensitive to the characteristics of that network. Thus, we first provide a detailed description of the characteristics of the graphs we use to model the amphibian pet trade network in *Materials and methods*: *Network description*. After establishing the necessary network terminology and concepts, we describe the simulated infection process on those graphs in *Materials and methods*: *Infection process*, and then discuss the proposed algorithms in *Materials and methods*: *Surveillance algorithms*. A rigorous discussion of the network characteristics and surveillance methods is provided in Appendix S1.

We begin by assuming a facility housing infected host animals has been identified and focus on a scheme for determining subsequent facilities for surveillance or sampling. As there is currently no surveillance scheme in place for the US domestic amphibian pet trade network, we propose two methods here and compare their performance on a sample population of graphs. Both approaches are iterative and are used in a network for which we initially have no knowledge of the graph topology. In addition, we assume there is a cost associated with sampling at a node that may impact decisions about which nodes to sample and may outright prevent sampling at some nodes. The iterative nature of our algorithms allows for progressive sampling that in turn allows us to gain more knowledge of the network. The gain in knowledge from sampling provides a mechanism to begin a systematic search for infected animals without the need to fully determine all of the network's characteristics and topology.

Unlike much of the work done on pathogen transmission in networks, we focus our attention on the facilities housing animals that are in turn acting as hosts rather than focusing on the animals themselves. Although transmission of pathogens between facilities can occur through multiple pathways, including fomites, we focus on transmission as the result of transportation of the host animals between facilities. This assumption holds for

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pathogens which survive well outside of their hosts, but would need to be adjusted in settings with high incidental transmission (e.g., as has been observed in live-stock surveillance between farms) (Ferguson et al., 2001). Since containment and sanitation practices are likely unknown until after infected animals are being transported within the network, we use a macro-scale model that ignores the proportion of infected animals at a facility like that seen in Moslonka-Lefebvre et al. (2012).

Finally, we provide an efficient network surveillance method that captures difficulties that should be expected while investigating an animal trade network. To this end, both iterative methods allow surveillance at a few facilities in any given step restricted to facilities within 1 or 2 degrees of separation from an infected facility and subject to a cost-based constraint. We begin the surveillance process at a non-port facility. The choice to focus on identification of a pathogen at a mid-network facility allows us to consider a scenario in which widespread transmission of a pathogen may have already occurred, rather than only recommending stopping introduction of pathogens at ports. We note that since nearly half of all declared live amphibian imports between 2000 and 2013 came through just three US ports, testing animals at the time of import may represent a practical control strategy (Smith et al., 2017) if a sufficient percentage of incoming animal volume can be assessed. However, no government agency is currently responsible for such testing and testing would currently require permission from importers; so, a strategy that assumes that some level of network spread has already occurred may be more practical.

The specific description of each part of the model allows us to simulate the model to these specifications. The simulations were written in MATLAB R2024b and can be accessed here: Wright et al. (2026).

Network description

Given the level of uncertainty related to the US domestic amphibian pet trade network, we establish a set of general assumptions about the network's characteristics. We then test our surveillance algorithms on a sample of 500 graphs that meet the general characteristics of this network population to ensure robust results. As established in Pautasso et al. (2010), globalization has increased the importance of small-sized trade networks when considering invasion in biological systems and zoonoses; so we restrict our consideration to relatively small directed networks of 100 facilities, with each acting as a port, distributor/wholesaler, or retailer.

We represent the trade network using directed graphs whose nodes represent facilities housing animals within the network and edges represent movement of animals or contaminated material between facilities. Graphs are assumed to be static and are created with all recent trades captured, where "recent" is dependent on a time-scale dependent on the pathogen in question, trade rates, and surveillance timelines. The node set of the graphs is divided into three categories: sources, distributors, and retailers. *Sources* represent ports or breeders within the network whose suppliers cannot be surveilled (e.g., wild caught animals), meaning their indegree is 0 while their outdegree is positive. *Distributors* may represent distributors, warehouses, and wholesalers that house animals between sources and retailers. Thus, distributors must have a positive indegree and outdegree. Finally, *retailers* capture consumer-level retailers whose customers cannot be surveilled, and thus have positive indegree and 0 outdegree (see summary in Table 1). These categories form three tiers with sources only connecting to distributors, distributors connecting to any kind of facility, and retailers connecting only to distributors. Within our sample of graphs used for comparison, 10% of nodes are sources and, on average, the remaining nodes are 40% distributors and 50% retailers. We do not allow for multi-edges within these graphs as edges represent that trade has occurred and no additional knowledge is gained from tracking repeated trades. Similarly, we assume there are no self-edges (an edge connecting a node to itself) within these graphs.

We construct our sample graphs with a heterogeneous degree distribution like that of a scale-free network in which most nodes have a small number of connections and a few nodes have a large number of connections, similar to that by Moslonka-Lefebvre et al. (2012) and Pautasso et al. (2010). The details of the graph construction, degree distribution, and density are given in Appendix S1: Section S1.

When sample graphs are created, each node is assigned a numerical value representing the cost

TABLE 1 The three types of nodes used in our sample graphs.

Node	Examples	Indegree	Outdegree	Notes
Sources	Ports, breeders	0	>0	Suppliers cannot be surveilled
Distributors	Warehouses, wholesalers	>0	>0	
Retailers	Consumer level stores	>0	0	Customers cannot be surveilled

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associated with surveillance at the node. This cost refers both to the resources necessary for surveillance and the time and effort required. We separately draw costs from both a uniform distribution and an exponential distribution. The uniform distribution provides enough variability in node cost to ensure the surveillance algorithms can effectively use node cost as part of their decision making while limiting the maximum cost ratio of any two nodes. The exponential distribution allows node costs that are large enough that the algorithms are forced to sample no more than one node in a round of sampling, thus capturing facilities that are exceedingly difficult to surveil either because of a large size or a lack of willingness on the part of owners or managers. Thus, the same network topologies can be analyzed when considering either cost distribution. In trade networks with large distributors and small pet shops, the cost distribution is more likely to be exponential than uniform, but exploring both distributions allows us to test the method under a wider range of conditions.

When node costs are drawn from a uniform distribution, the range $(0.2,0.8)$ is used. For the shifted exponential distribution, a node's cost is a random variable $X = Y + 0.25$ where Y is an exponentially distributed random variable with mean 0.25. We avoid probability distributions whose lower bound is 0 as it would suggest that sampling costs at some facilities is infinitesimally small and that the cost ratio of any two facilities is potentially unbounded. That is, for the uniform distribution on $(0.2,0.8)$, we are assuming that the surveillance at the most costly facility is no more than four times the cost of the least costly facility. When using the exponential distribution for node costs, it is possible for the cost of sampling a single node to exceed the allotted cost for a round of sampling making surveillance at the facility impossible. However, for the population of networks used, only two networks have one node each that exceed the allotted cost for the network. Thus, situations in which many facilities cannot be sampled due to cost or non-participation may not be well-represented by these results. It is also of note that we are assuming that the cost of sampling is independent of position in the network. This is unlikely to be true but it serves as a valid way to test the method.

Infection process

To test the surveillance algorithms, some nodes within the sample graphs must represent facilities housing animals infected with the pathogen. Thus, we designate some nodes as "infected" to indicate that they represent such a facility. The sample graphs must have nodes designated as "infected," meaning animals or materials carrying the pathogen can be detected at the facility the node represents to test the surveillance algorithms. All other nodes are considered not to be infected and are referred to as "susceptible." We consider only a static infection state on the network. That is, each node is determined to be susceptible or infected, and that status does not change during the surveillance process.

We assume that the pathogen will be introduced to the trade network via a source node and then be spread to its partners according to edge direction. To capture this with our model, we assigned nodes to be infected in the sample graphs by randomly selecting a source node and assigning that node and all of its descendants to be infected. This choice represents a purely deterministic infection process and would be a worst-case scenario for the spread of infection within the network. The infection process was run on each of the 500 networks in our sample population a single time and the assigned node status was used for all analyses.

Surveillance algorithms

We assume the pathogen has been discovered at an initial facility and concentrate on a scheme for determining subsequent facilities for surveillance or sampling. We assume that subsequent discovery of the pathogen in question requires targeted surveillance of a facility and that surveillance has an associated cost (that may represent effort required and actual monetary cost). We further assume that a limited number of facilities in terms of overall size of networks (5%–15%) can be surveilled in one round of surveillance. Both algorithms proceed via iterative rounds of sampling on a graph using newly found infected nodes and node costs to inform the algorithms about how to surveil in future rounds.

Once an initial facility is identified as infected, the process of determining the infection status of additional facilities begins by identifying all facilities within 2 degrees of separation from the initial facility. In terms of the graphs representing the trade network, this means we identify all nodes within two edges (ignoring direction) of the initial node. We refer to the initial node as the focus, and the subgraph as the 2-neighborhood of the focus (Figure 1). Both algorithms depend on the formation of the 2-neighborhood of the focus, and both algorithms assume that the 2-neighborhood is found with no missing nodes or edges. After the formation of the 2-neighborhood, both algorithms will select additional nodes for testing from those present in the 2-neighborhood using different methods. However, both algorithms are limited in their ability to sample nodes by the total cost that can be spent in a round of sampling. We separately consider scenarios in which both methods can spend no more than 5%, 10%, or 15% of the network cost in a round of sampling.

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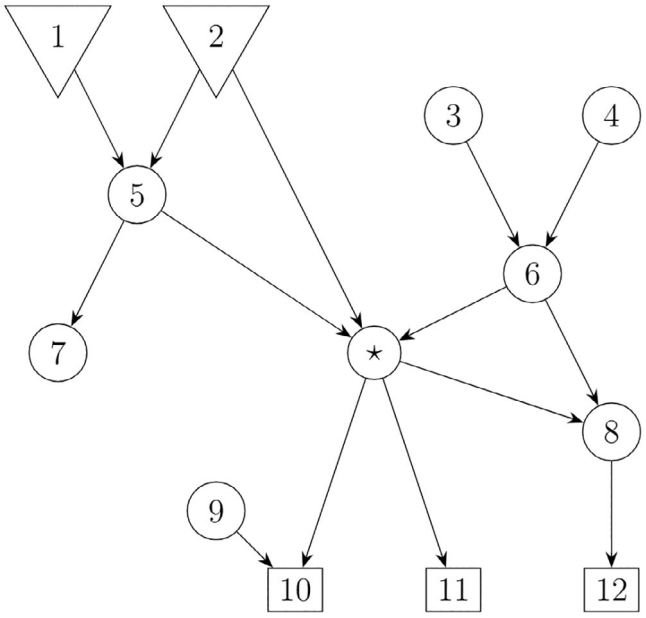


FIGURE 1 An example of a 2-neighborhood whose focus node is marked with a star. Node markers indicate node types with triangles representing sources/ports, circles representing distributors, and squares representing retailers. The number in each marker corresponds to the node number in Appendix S1: Table S2. The focus node is not numbered because it will not be reconsidered in the next round of sampling. The layout of the 2-neighborhood does not correspond to the geographical locations of the facilities in the network.

Our primary algorithm, henceforth referred to as the Informed Method, leverages the information provided by the 2-neighborhood to choose optimal nodes for sampling by considering the probability that a node is infected, the information to be gained by identifying a node as infected, and the cost of sampling the node. It does this by classifying all nodes according to the equivalence classes described in Appendix S1: Section S3. This classification considers factors such as distance from a focal node in both the forward and backward directions as well as indegree and outdegree and sorts each node into a class labeled from class 0 to class 8. In turn, each class is assigned an information score or *weight* allowing the nodes in the 2-neighborhood to be weighted based on how beneficial it will be to sample them, with higher weights corresponding to more important nodes.

We use an ad hoc method for determining appropriate weights for the equivalence classes. For all analysis, we use the weights for equivalence classes based on the following: Class 0, 0; Class 1, 3; Class 2, 1; Class 3, 0.25; Class 4, 1; Class 5, 1; Class 6, 0.1; Class 7, 0.1; Class 8, 0.1.

More information about the weights can be found in Appendix S1: Section S4. After all nodes are classified and weighted, the algorithm chooses the nodes that maximize the sum of the weights being selected subject to the cost constraint. The selected nodes are then sampled to determine their infection status. If a node is not identified as infected, the algorithm assumes the results could be false negative and will draw no conclusions from the result (though it will not sample the node again). If a node is identified as infected, a 2-neighborhood is formed around it and those nodes are classified in the same manner. In the next round of sampling, the algorithm will consider the union of all the 2-neighborhoods. The process then repeats until a stopping condition is met. These stopping conditions are discussed in *Materials and methods*: *Comparison conditions*.

The second algorithm, referred to as the Cost-Focused Method, is meant to act as a control in relation to the Informed Method and represent choosing nodes for sampling based on cost and convenience while ignoring the graph topology information presented in the 2-neighborhood. An example of how these two methods differ can be seen in Figure 2.

Convenience sampling is a common practice for wildlife surveillance (Nusser et al., 2008) and is frequently used during livestock outbreaks. Starting with the 2-neighborhood of the initial facility, the Cost-Focused Method maximizes the number of nodes being sampled subject to the cost constraint. Once additional infected nodes in the 2-neighborhood are identified, the Cost-Focused Method works over the union of their 2-neighborhoods. Mathematically, the Cost-Focused Method is equivalent to using a version of the Informed Method in which each node is assigned the same weight.

For the purposes of testing our methods, an initial focus node was determined. After assigning nodes their infection status, as discussed in *Materials and methods*: *Infection process*, a focus node was selected by randomly choosing an infected non-port node from the infected population. Each graph's initial focus node was determined and stored before the surveillance algorithms were tested on the sample networks.

Comparison conditions

With the population of sample networks constructed with all necessary features, we may compare our surveillance methods. For this comparison, we use two stopping conditions each with their own valuation measure, one which terminates after a certain percentage of successful identifications and one which terminates after a certain total cost.

In the first case, we do not allow another round of sampling if some percentage, T_I, of the total number of

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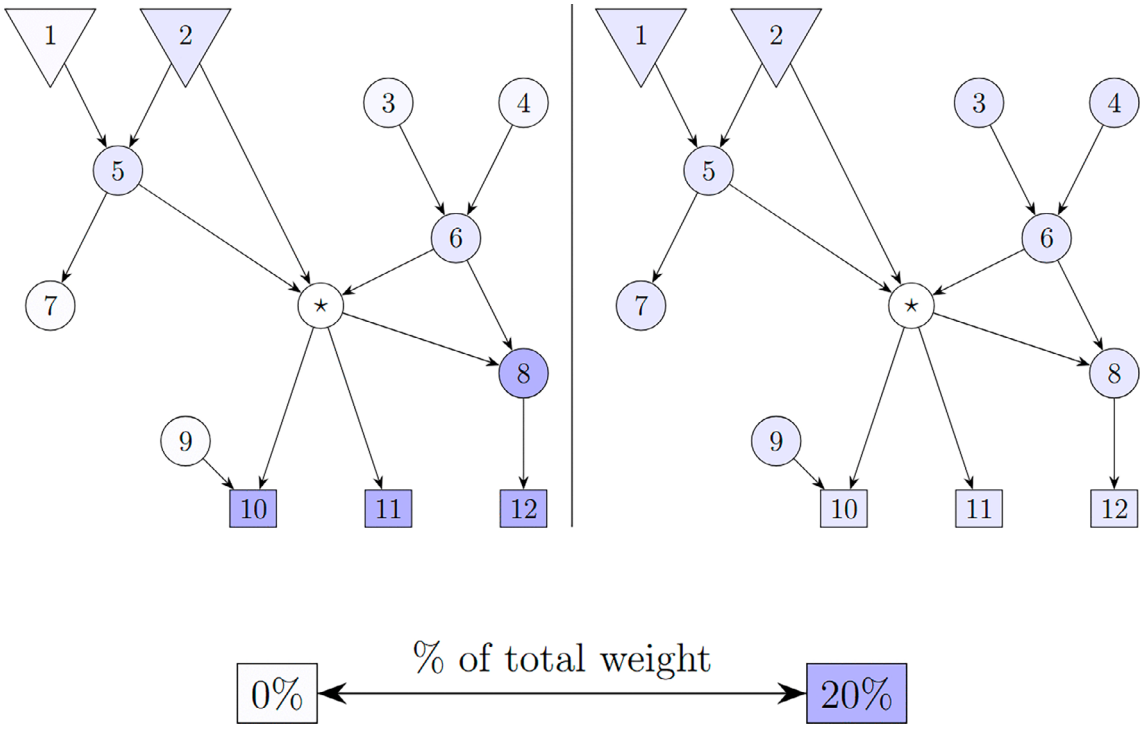


FIGURE 2 A comparison between the Informed Method on the left and the Cost-Focused Method on the right. In the Informed Method, nodes are weighted as more important for surveillance by their probability of becoming infected and by their probability of being infected given that the focal individual ($\star$) is infected and that goods are traveling through the network as the arrows show. In the Cost-Focused Method, each vertex is considered equally important for surveillance.

infected nodes has been identified and use the total cost of sampling to compare the methods. Since sampling is not adjusted as the proportion of identified infected nodes approaches T_I, it is possible for either method to identify a proportion larger than T_I. This case allows us to examine how the methods compare to one another at the very beginning of the surveillance process when few infections have been identifies versus at the end of the process when most of the infections have been identified.

In the second method we do not allow another round of sampling if some percentage, T_c, of the total network cost has been exceeded and use the proportion of the infected nodes found to compare the methods. Under this stopping condition, both methods are likely to exceed T_cN_c, where N_c denotes the total node cost of a graph, in their last round of sampling and another round is not allowed.

Note that an analysis considers either the uniform cost of all nodes in the sample population or the exponential cost, but never both at the same time. Results from both cost distributions are presented together for the sake of comparison. The allotted cost for a round of sampling in a graph is specific to the graph and given by C_pN_c where C_p denotes the percentage of the total network cost that may be spent during a round. In our comparisons we use C_p-values of 0.05, 0.1, and 0.15.

In order to compare the informed method with the cost first method, we simulated infection and surveillance on many synthetic trade networks. A sample population of 500 networks was constructed with the characteristics described in *Materials and methods*: *Network description* with each node preassigned costs from both uniform and exponential distributions. Then, the infection process described in *Materials and methods*: *Infection process* was run on each network in the sample population to create a population of infected nodes within each individual network. As described in *Materials and methods*: *Surveillance algorithms*, an initial focus node was selected from each network's infected population to act as the location of the initial pathogen discovery. All of these steps were done once with all information stored and used during the analysis reported in *Results*. Finally, the surveillance methods described in *Materials and methods*: *Surveillance algorithms* are run on the sample networks with appropriate stopping conditions and the results recorded.

RESULTS

The Informed Method generally has a lower total cost than the Cost-Focused Method for T_I-values greater than 0.5 regardless of the cost distribution (Figure 3). That is, if

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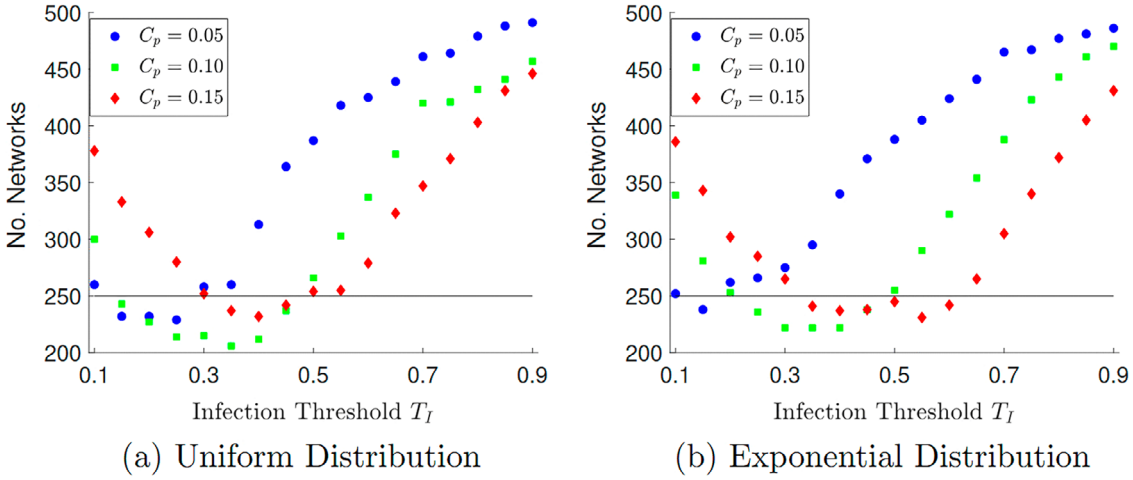


FIGURE 3 The number of networks in the population of 500 networks for which the Informed Method's total cost is less than or equal to that of the Cost-Focused Method with $T_I \in [0.1,0.9]$, $C_p = 0.05$, $C_p = 0.1$, and $C_p = 0.15$. Note that a marker greater than 250 (above the horizontal line) indicates that the Informed Method costs less than or equal to the Cost-Focused Method in more than half of the networks. Recall that C_p refers to the allotted budget for a round of sampling. (a) The node costs are randomly sampled from a uniform distribution on (0.2,0.8). (b) The node costs are randomly sampled from a shifted exponential distribution with mean 0.5.

the goal is to find more than 50% of infected nodes in a network, it is expected that the Informed Method will do so with a cost no greater than that of the Cost-Focused Method. It seems likely that in most situations the desire would be to find nearly all of the infected facilities (i.e., $T_I \geq 0.9$) and that the support for a round of surveillance, C_p, will be small in comparison to the total network cost, N_c. The Cost-Focused Method costs less than the Informed Method for a portion of the T_I-range because the Cost-Focused Method is sampling as many of the lowest cost nodes as possible. As a result, Cost-Focused Method may have a lower total cost than the Informed Method even if it requires more rounds of sampling than the Informed Method.

While Figure 3 indicates that the Informed Method generally costs less than the Cost-Focused Method, it does not show how much less the Informed Method may cost than the Cost-Focused Method. To examine this difference in cost, we let the total cost of identifying T_I of a network's infected nodes be denoted by C_{totIM} and C_{totCFM} for the Informed and Cost-Focused Methods respectively and consider $\log_2(C_{\text{totCFM}}/C_{\text{totIM}})$ for the networks in the same population against the total number of infected nodes in the network (Figure 4). When the node cost distribution is uniform (Figure 4a) for our network population, $C_{\text{totIM}} < C_{\text{totCFM}}$ in 472 out of 500 and $C_{\text{totIM}} = C_{\text{totCFM}}$ in five networks. On average across all networks, C_{totIM} is 62% of the value of C_{totCFM} when the node cost has a uniform distribution. If we consider only the networks for which $C_{\text{totIM}} < C_{\text{totCFM}}$, the average value of $C_{\text{totIM}}/C_{\text{totCFM}}$ is 0.5935. For networks for which $C_{\text{totIM}} > C_{\text{totCFM}}$, the average value of $C_{\text{totIM}}/C_{\text{totCFM}}$ is 1.2456.

The Informed Method continues to yield a lower total cost than the Cost-Focused Method in most instances when node costs have a shifted exponential distribution (Figure 4b). In this case, the Informed Method has a lower total cost than the Cost-Focused Method in 464 out of 500 networks and costs roughly 65% of the cost of the Cost-Focused Method on average.

The Cost-Focused Method will have a lower total cost than the Informed Method when $T_I = 0.2$ and $C_p = 0.05$ (Figure 5). However, in this scenario, the Cost-Focused Method narrowly costs less than the Informed Method (Figure 4c,d). For the uniform node cost distribution case, the total cost of the Informed Method is less than that of the Cost-Focused Method in only 135 of the 500 networks and in the exponential case it is 163 of the 500. Notably, for the uniform cost case, the Informed Method costs roughly 1.04 times the total cost of the Cost-Focused Method on average across all networks. For the exponential case, the Informed Method costs 1.01 times the cost of the Cost-Focused Method on average. That is, while the Cost-Focused Method has a lower total cost when T_I is lower, the cost difference between the methods is less substantial.

Under the second stopping condition discussed in *Materials and methods*: *Comparison conditions*, the Informed Method performs at least as well as the Cost-Focused Method in more than half the networks analyzed over a range of T_c-values (Figure 5).

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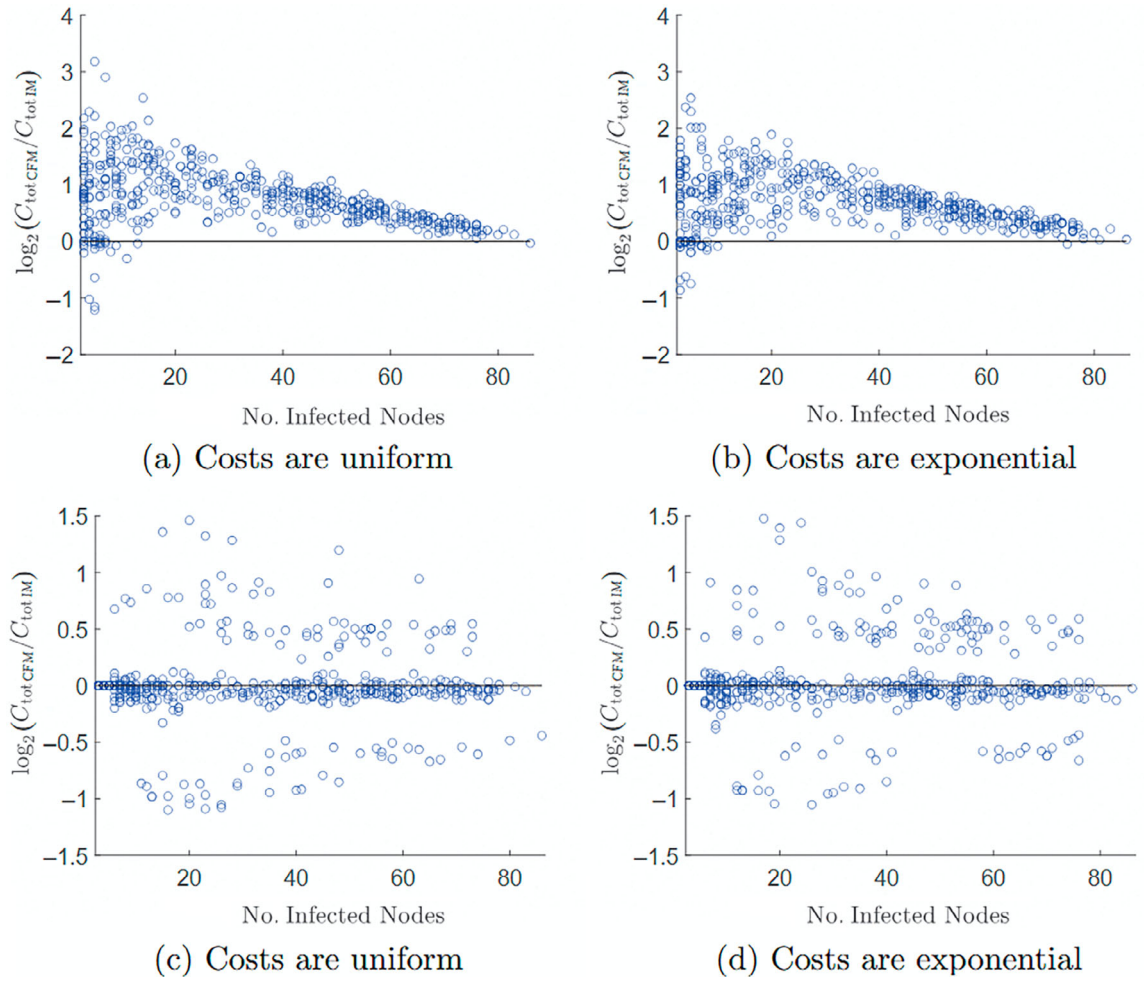


FIGURE 4 The base 2 logarithm of the total cost of finding infected nodes using the Cost-Focused Method (C_{totCFM}) divided by the total cost using the Informed Method (C_{totIM}) versus the total number of infected nodes in the network out of 100 nodes. Sampling uses $C_p = 0.05$. To interpret the $\log_2$ scale on the y axis, note that dot (x,y) with $y > 0$ indicates that, when $x\%$ of the nodes were infected, the Cost-Focused Method costs 2^y times more than the Informed Method. Conversely, a dot (x,y) with $y < 0$ indicates that when $x\%$ of the nodes were infected, the Cost-Focused Method cost 2^y times *less* than the Informed method. (a, b) $T_I = 0.8$ indicates 80% of infected nodes are found. (c, d) $T_I = 0.2$ indicates 20% of infected nodes are found. Note that the scale of the y axis changes between panels (a, b) and (c, d).

For this stopping condition we set the total surveillance cost to be a percentage of the total network cost, N_c.

For most T_c-values, the Informed Method identifies notably more infected facilities than the Cost-Focused Method. When $T_c = 0.5$, in the uniform case, the Informed Method identifies at least as many infected facilities as the Cost-Focused Method in 499 networks. Even when $T_c = 0.2$ the informed method had identified more infected facilities in 88% of the networks examined. By the end of this numerical experiment we find that the total cost of sampling for the Informed Method is 79% of that for the Cost-Focused Method on average. We explicitly examine the cross section in which $T_c = 0.5$ and $T_c = 0.2$ in Figure 6 to demonstrate this point in more detail.

A further discussion of the method's performance in networks with greater edge density is discussed in Appendix S1: Section S6.

DISCUSSION

Surveillance for infection on networks is extremely important in many settings because of the catastrophic effects introduced pathogens can have in settings with many directed interactions. For example, the introduction of Bd to new environments has had a catastrophic effect on both captive and wild amphibian populations worldwide (Scheele et al., 2019; Wake & Vredenburg, 2008). Should Bsal be introduced to the United States, the impacts could be similar (Gray et al., 2015, 2023).

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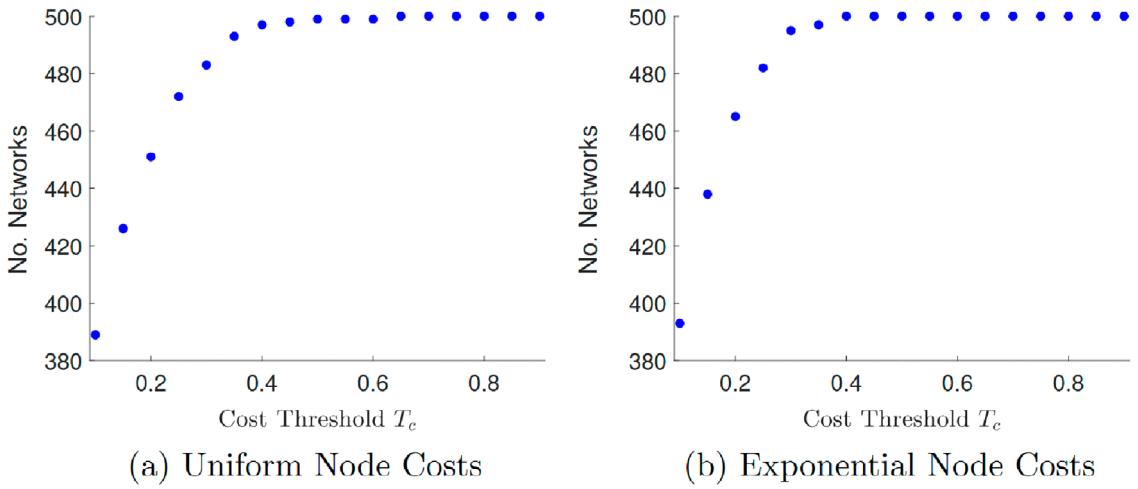


FIGURE 5 Comparisons of the ability of both methods to identify infected nodes across a variety of T_c-values with $C_p = 0.05$. The marker indicates the number of networks for which the Informed Method identified at least as many infected nodes as the Cost-Focused Method.

The international amphibian pet trade has the potential to serve as a conduit for the introduction of Bsal to the United States, which could, in turn, lead to spillover events into native populations. Thus, it is vital that a surveillance system and plan be established to monitor for and respond to the presence of Bsal within the amphibian pet trade network.

We have provided and compared two potential methods for surveilling the US domestic amphibian pet trade network where both require only local knowledge within the network. This situation reflects the likely real circumstances where a pathogen is found within animals housed in a trade facility, and the facility knows the identity of its recent trade partners but does not know the broader trade network that may be affected by the pathogen. We have found that a surveillance algorithm that takes advantage of information about the network topology, even if that knowledge is restricted to local connections, is often more efficient in terms of both overall cost and time to identify facilities housing infected animals than a method that chooses facilities for surveillance based purely on cost and convenience. As it may be overlooked, we mention that the Cost-Focused Method represents not only convenience sampling, but also surveilling as many facilities as possible with a recent connection to a facility where an infection has been identified given cost constraints. The Informed Method sacrifices this widespread surveillance in exchange for more careful selection, and still identifies infected facilities faster and with a lower overall cost than the Cost-Focused Method in most desired cases. Even when the Cost-Focused Method outperforms the Informed Method, the total costs for the two methods are reasonably close, while, when the Informed Method outperforms the Cost-Focused Method, its total cost is often 50%–65% below the cost of the Cost-Focused Method. An additional advantage of the Informed Method comes from the fact that the budgets allotted to each method for a round of sampling are fixed. That is, neither method can utilize leftover resources from a round of surveillance in a future round. As one would expect, the Informed Method typically uses a smaller portion of its surveillance budget than the Cost-Focused Method. If the Informed Method were able to "rollover" the remaining portion of its surveillance budget in each round, it may outperform the Cost-Focused Method by an even wider margin. Importantly, we observe that these results remain true whether the cost distribution is uniform or exponential. This is to be expected because the average cost of sampling a group of nodes will converge to the mean node cost regardless of the initial distribution. Based on these results, our recommendation for surveillance of novel pathogens in the amphibian pet trade network is a scheme like that used by the Informed Method in which local network information is used in conjunction with cost of surveillance rather than a strategy based on surveilling as many facilities as possible.

Importantly, this recommendation comes with the caveat that although global knowledge of the structure of the network is not required, local knowledge of the topology is required in order to carry out the informed method. As pointed out by Salathé and Jones (2010), the structure of a trade network may not be known initially, so there is a need for efficient discovery algorithms that require knowledge of only a portion of the network. Further, construction of a full trade network, especially in the case of the amphibian pet trade, may be quite difficult. In the time taken to inquire about recent trade

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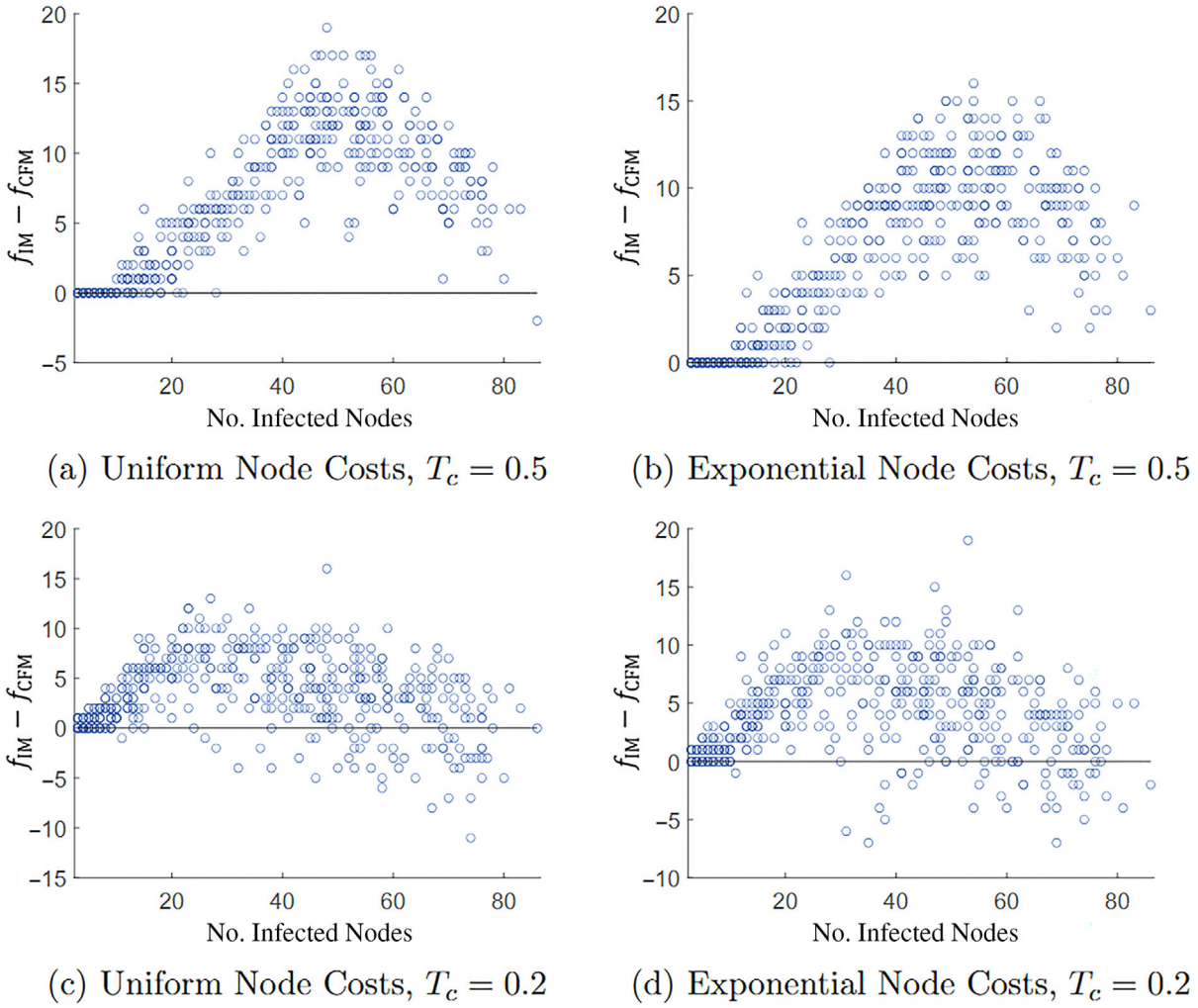


FIGURE 6 Comparison of the number of nodes found by the Informed Method (f_{IM}) versus the Cost-Focused Method (f_{CFM}) using $C_p = 0.05$. (a, b) $T_c = 0.5$. (c, d) $T_c = 0.2$. Denoting the total number of nodes found by the Informed Method by f_{IM} and the total number found by the Cost-Focused Method by f_{CFM}, markers in the plot show $f_{IM} - f_{CFM}$ for given numbers of infected nodes. Thus, $f_{IM} - f_{CFM} > 0$ indicates that the Informed Method has identified more infected nodes than the Cost-Focused Method.

partners and shipping volumes to build a clear picture of the full network, it might be possible for infected animals to pass through the network and arrive in the hands of consumers. The need to identify subsequent infected facilities within such a trade network without having knowledge of the full network is a matter that has seen little attention.

A vast array of literature already exists discussing the transmission of pathogens in networks (see Danon et al., 2011; May, 2006 for a more recent overview). Much of this research focuses on how the network's characteristics and topology affect epidemic characteristics such as transmission rates (i.e., R_0). Other efforts focus on methods for determining which nodes to test for initial pathogen detection or how individual nodes contribute to the spread of infection using methods like Centrality measures. In other previous work, methods for initial pathogen detection driven by modularity (Colman et al., 2019), time dependent hubs (Guinat et al., 2016), or neighborhoods of hubs (Herrera et al., 2016) have been proposed for trade networks but these approaches generally require full knowledge of the network and its topology, which is not available because of the diffuse and unregulated nature of the amphibian pet trade.

There is a comparison to be made to the need for contact tracing like that used for tracking disease spread in social networks with trade facilities taking the role of individuals, shipments taking the role of social interactions (albeit directed), and shipment volumes performing a function similar to exposure time. Methods for constructing transmission networks are discussed by Keeling and Eames (2005), but these methods focus primarily on social connections and cannot account for factors such as trade volumes that

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would vastly impact transmission in a trade network. Buchanan et al. (2020) explore the best practices used internationally for contact tracing during the first year of the COVID-19 pandemic. However, contact tracing efforts are primarily focused on determining proximity to infected individuals and how best to handle data and privacy. Thus, methods related to contact tracing outside of communicating with facilities about their trade partners are not relevant to our goal.

While the Informed Method could be applied as described here, we would recommend further investigation and comparison of both methods. Given the lack of knowledge of the amphibian pet trade network, and the willingness of those involved to comply with surveillance needs, it would be ideal to compare these methods using local neighborhoods of varying sizes and in which some facilities either refuse to disclose trade partners or do so inaccurately (either intentionally because of illegal trade or accidentally because of imperfect reporting). Further, depending on how animals are contained within facilities (i.e., mixing with existing animals or being kept separate), we would recommend the consideration of a different infective dynamics in which infected individuals may not be contagious either by way of quarantine or more detailed pathogenic ecology. Such dynamics may create gaps in the path of infection which are not present in our "worst case scenario" as described in *Materials and methods*: *Infection process*. Finally, given that trade partners are likely to change over time, future work should consider streaming networks. However, such an analysis will only be useful when some understanding of the time needed to collect network topology information and conduct surveillance is known and can be compared to the rate at which the network changes.

Additional work should also be conducted to investigate the weights used by the Informed Method and presented in Appendix S1: Table S1. The weights effectively guide the algorithm in deciding what facilities are most likely to house infected animals given their connection to a known infected facility. For example, a pathogen that causes very rapid mortality may be unlikely to spread to descendants of an infected facility as the animals in question may die before they can be transported, thereby making it more important to conduct surveillance at ancestor facilities. In the same way, ancestor facilities may be weighted more heavily if the pathogen persists in the environment. Contrastingly, a pathogen that spreads easily but causes little or no change to mortality for the host animal may be easier to identify at descendant facilities. Another important example of how the weights may be adjusted to improve performance depends on the statistical needs of the sampling methods. If the sampling effort required to ensure sufficient statistical power for analysis depends on the size or expected prevalence in a node, the weight of such a node should be adjusted. The weights can be ad hoc adjusted for each of these scenarios, but it may be possible to determine optimal weights for a variety of network topologies and pathogens in preparation for the introduction of a novel pathogen.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Code (Wright et al., 2026) is available from Zenodo: https://doi.org/10.5281/zenodo.20330886.

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