Understanding Highly Pathogenic Avian Influenza Outbreaks in the Western Cape Ostrich Industry:

Did Network Dynamics Enhance Vulnerability?

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February 13, 2012

Submitted in partial fulfillment of the requirements for the degree of

Masters of Science in Conservation Biology

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Abstract

Disease outbreaks in both domestic and wild systems in recent years indicate the increasing potential for disease spill-over of generalist pathogens between domestic and wild species. Events of this nature are of considerable threat to rare or endangered species, while also being of significant economic concern for the farming industry. Understanding how disease moves within and between these contrasting systems is vital to prevent large-scale, multi-system epidemics in the future. Within the domestic system, this involves understanding how contact networks created by the movement of livestock between locations contribute to the transmission of disease. This study utilized network analysis to understand how the movement of ostrich stock between farm locations in the Western Cape, South Africa may have contributed an epidemic outbreak of Highly Pathogenic Avian Influenza (HPAI) within the ostrich industry in 2011. A database consisting of source, target, batch size and date of movement for all transfers of ostrich since September 2005 to April 2011 was used to construct an ostrich movement network. This network was analyzed to test if network structure and changes in network properties over time were contributing to the vulnerability of the system to disease epidemic. The network was deemed highly vulnerable to disease epidemics. In addition, network evolution over the time-series indicated that the network was becoming increasingly vulnerable prior to the HPAI outbreak. The cause of this increase in vulnerability is likely the emergent properties associated with self-organization of the network due to economic growth and industry changes following outbreaks in 2004 and 2005. Based on the study, recommendations are made for policy and management interventions that could reduce the epizootic potential in the ostrich industry and reduce the probability of spillover to wild populations.

Acknowledgements

I would like to thank my supervisors Dr. Jasper Slingsby and Professor Graeme Cumming for their support and guidance for the duration of this project. I would also like to thank the South African Ostrich Business Chamber and the Department of Agriculture for the Western Cape for providing me with the data used in this study. In addition, I would like to thank Dr. John Grewar for assisting with cleaning the data, while also being endlessly supportive and helpful in answering my nonstop questions about the ostrich industry and avian influenza epidemiology. Furthermore, the design input from James Moolenshot and statistical support of Dr.Paulo Denti took my project to another level.

Completing this thesis would have been impossible if not for the unwavering support of my mother Denise Trowsdale and my father Alan Moore. Any success I have achieved in this program is a direct result of their love and encouragement. In addition, I could never have made it though without the endless support, humor and belief of my friends in Canada and South Africa , as well as my wonderful digsmates. With countless names to mention, I do feel that Danielle Duplisea, Timothy Moore, Raven Pearson, Maggie Yeomans, and all members of the UCT and Ghost Ultimate Frisbee teams warrant special acknowledgement.

Finally, I would like to thank my classmates who have become my family in South Africa. Through all of the stress, sleepless nights and seemingly endless work load that accompany this degree, you have never failed to make me laugh, show me love and remind me that we were in it together.

Chapter 1.

Literature Review

Although factors such as habitat destruction, urbanization and overexploitation remain the leading drivers of both local and global species extinctions (Sala 2000), conservation biologists must increasingly consider other factors that contribute to species declines. One such factor is disease (Daszak et al. 2000). For example, the American Chestnut *Castanea dentata* dominated the forests of the eastern United States until the late 1800s, when the introduction of a canker pathogen triggered a mass mortality event in over 3.6 million ha of its range (Ellison et al. 2005). There are currently ~833 known extinctions listed by the World Conservation Union (IUCN), of which only 3.7% list infectious disease as a known causal factor (IUCN 2008). However, limitations on evidence and uncertainty surrounding threats to species survival have likely lead to underestimation of the role of disease in species decline (Smith et al. 2009).

Of particular concern is the potential for diseases to act synergistically with other factors and accelerate species decline. Recent years have seen alarming mass declines of reptile and amphibian species and a growing body of research highlights synergistic relationships between global warming and disease as the central cause (Daszak et al. 1999, Pounds et al. 2006, Schloegel et al. 2006, Bosch et al. 2007). Specifically, a pathogenic chytrid fungus and climate change have been implicated in the extinction of over 70 amphibian species in the American tropics alone (Pounds et al. 2006). Another often cited factor leading to species decline is large scale habitat alteration (Sala 2000). This factor is particularly relevant to the spread of disease, specifically when considering intensive agricultural landscapes and the resulting homogeneity and novel connectivity of natural systems. The African rinderpest pandemic of the late 1800's, for example, traversed the African continent in a mere 8 years, wiping out ~90% of cattle in sub-Shararan Africa as well as decimating wild herds of buffalo, giraffe and wildebeest (Daszak et al. 2000; Roeder 2008). This pathogen was introduced in a domestic herd and its virulence largely related to its ability to spread from one diseased species, or reservoir, to another susceptible species. This phenomena has been termed disease spill-over and is becoming an increasing concern as humans continue to convert large tracks of land for intensive farming and reliance on domestic livestock grows with a swelling population. Recent large scale spill-over events, notably Foot and Mouth Disease in the U.K, (Kiss et al. 2006), Bovine Tuberculosis in Europe (Bohm et al. 2009), and Avian Influenza globally (Kilpatrick et al. 2006), underscore the increasing need to focus epidemiological research on understanding disease transmission within and between domestic and wild populations and species.

Traditional methods of analyzing and modeling disease transmission, such as mean field- (Susceptible-Infected-Recovered (SIR)), metapopulation- and lattice-based models have been used for decades (Craft & Caillaud 2011). Although these methods have proven very useful in understanding the behavior of epidemics, they typically assume homogeneity in social relations (ie. familial, co-workers, or acquaintances) or contact within a population. As social and other contact relations are rarely homogeneous, the models are based on an oversimplification of social structure and thus disease dynamics within the population are not accurately modeled (Hamede et al. 2009).

Network analysis addresses some of the shortfalls of traditional disease research approaches (Danon et al. 2011). By focusing on relational interactions within and between populations, network analysis incorporates the heterogeneity missing from traditional models and offers a novel perspective on social, relational and disease dynamics. Although the emergence of network analysis has been relatively recent in biological studies, the technique has a long history of application within the social sciences (Borgatti et al. 2009).

Network Analysis

Network analysis has been utilized in the social sciences to understand the inherent complexity of relational interactions for decades and its foundational principles have been on the cusp of wider applicability for many years (Barabasi 2009). Commonly known as social network analysis, it was initially used to study relationships among social entities and understand the patterns and implications of these relationships. Gaining perspective on political, economic and social relational environments allowed researchers to identify patterns or regularities in relationships among interacting units within the social environment in a quantitative and meaningful way (Wasserman & Faust 1994). This research revealed that common relational structures often governed these interactions, indicating that network analysis could be used to quantify emerging relational patterns regardless of the specific nature of the entities being studied (Barabasi 2003, Cumming et al. 2010). Network analysis was subsequently applied in mathematics and computer science, but in the last decade the utilization of this approach has been become widely applied in a diverse array of fields including medicine (Barabasi et al. 2011), physics (Strogatz 2001) , molecular biology (Vogelstein et al. 2000), ecosystem function (Bascompte 2009), and ecology (Butts 2009). These applications have contributed to a greater understanding of many technological and human based systems including the internet, computer chips and terrorist networks.

In the last decade, network analysis has received growing attention for bridging research fields. Janssen et al. (2006) indicates that basic mathematical representation of social and ecological system can be similar and this allows the opportunity to create a ‘common currency’ of evaluation of relationships within such systems. The universal applicability of network analysis to study many natural and human phenomena indicates that there may be similar laws governing qualitatively different complex networks (Barabasi & Oltavai 2004).

Network analysis is based on graph theory and statistics, aiding investigation of the structure of a system, known in the field as a network (Janssen et al. 2006). The method focuses on how a collection of units interact as a single system (Figure 1) (Meyers et al. 2005; Proulx et al. 2005). A network is represented by a number of constituents, the first of which is termed a node or vertex. These are entities, which are defined by the analyst, typically represent a single element within the system (e.g. an individual, species, habitat patch or farm). In addition, nodes have descriptive attributes which do not directly originate from their relations to other nodes (e.g. body size, age or water chlorination at a farm) (Cumming et al. 2010).

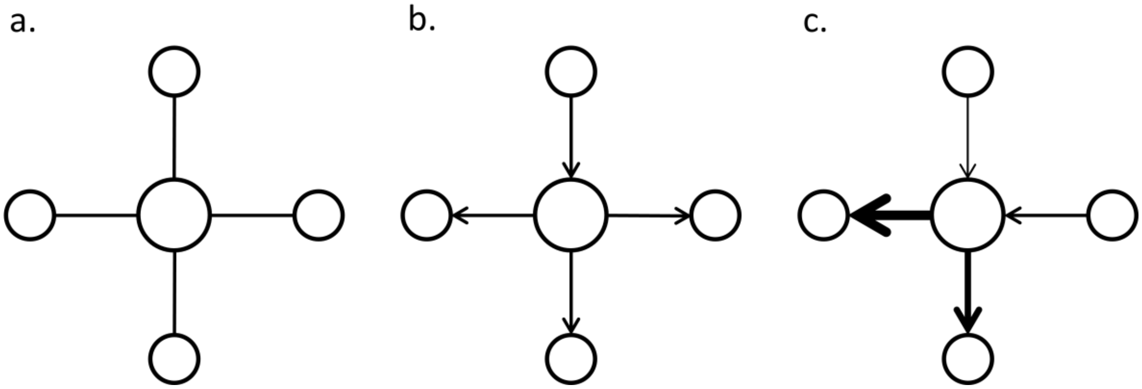

Figure 1. Visual representations of networks, where the circles symbolize nodes or vertices and the lines connecting the nodes represent edges or links. The most basic networks are unweighted and the relationships are considered either present or absent (a) while more complex networks can be directed (b) and/or weighted (c).

The relations between nodes are described as links, ties or edges, which are often depicted by a single line connecting the units. Links can represent a wide range of interaction such as communication, pollen dispersal, movement of farm stock, or contact (Cumming et al. 2010). Links can also reveal further information regarding the system as a whole. Links might, for example, be described as directed or undirected, where directed links describe relationships between two nodes that are not symmetric (Figure 1b), and undirected nodes describe symmetric links (Figure 1a). An example of a directed link within a pastoral system is a link where one farm sells stock to another farm as the flow of resources occurs in one direction only. However, if stock were traded in both directions then the relationship would likely be considered undirected. If the links in a graph are described as directed, then the graph itself would be labeled a directed graph. In directed graphs, links are often depicted as arrows which indicate the direction of the relationship (Hanneman and Riddle 2005). The spread of disease is often depicted as a directed network, as pathogens are passed from an infected individual to a susceptible one (Meyers et al. 2006) . For example, Meyers et al. (2005) modeled the spread of Severe Acute Respiratory Syndrome (SARS) in Canada using a directed network analysis, which allowed the researchers to determine that the central site of disease proliferation had occurred at hospitals in the city of Toronto, due partially to an increase in flow of patients to these sites during the SARS outbreak.

The final constituent of network analysis is identifying the boundary conditions of the network; these conditions are set by the analyst and dictate which entities are included or excluded from a network (Proulx et al. 2005; Cumming et al. 2010). The two most common methods of setting boundary conditions are to take either an egocentric or a full network approach. Networks can be viewed in a number of ways, the most elementary being an egocentric network which focuses on a single node or the ‘ego’. Egocentric datasets are most useful when analyzing an entire network is not possible or when the properties of specific nodes are of particular interest (Hanneman and Riddle 2005).

By analyzing network structure, or how it changes in time, analysts can make inferences about how system being studied functions, and how energy, disease or information flows throughout the system (Cumming et al. 2010). In recent years, the utilization of network analysis to understand biological and environmental phenomena has expanded rapidly. Within biology, common application occurs when networks are formed by a physical structure, such as neural networks (Humphries et al. 2006) or ant nests (Buhl et al. 2004); when they refer to abstract relationships between connected entities, such as food webs (Dunne et al. 2002) or amphibian meta-popultions in ponds (Fortuna et al. 2006); or when they describe processes or flows, such as cellular networks (Jeong et al. 2000) or the Earth’s climate system (Tsonis & Roebber 2004).

The use of networks in biology has been most readily embraced within the sub-disciplines of cell biology, ecology and epidemiology. In an early contribution, Jeong et al

(2000) presented evidence indicating the high level of similarity in network structure of cellular networks across 43 species. In addition, Vogelstein et al. (2000) successfully likened the regulation of the cancer suppressing gene p53 to the functioning of the Internet, displaying further evidence for both the network properties of the cell, as well as the universality of networks in natural systems. Subsequent work has provided further support for the use of network analysis when studying cellular structure and function (Barabasi & Oltvai 2004, Barabási et al. 2011).

The use of network analysis has been embraced in ecology to understand natural processes. Networks have been described as particularly useful descriptors of ecological systems as they show both the composition of multiple elements in ecosystems and the interactions between these elements (Bascompte 2009). The use of network analysis within the field of biology began in the 1950's when Odum & Odum (1953) examined ecosystems as sets of components and modeled how energy flowed through those systems. Consequently, analyzing and visualizing trophic interactions as a complex network of interactions has remained an important field in ecology for decades (Bascompte 2007). Aside from trophic studies, network analysis has remained relatively under-utilized in ecology until recently (Cumming et al. 2010). Recent diverse network-based studies in the field of ecology have further emphasized the value of this technique and have lead to further understanding of species extinction (Dondelinger 2008), habitat fragmentation (Rhodes et al. 2006) and disease dynamics (Shirley & Rushton 2005). Considerable research has been conducted to further understand disease dynamics in contact networks in wild species (Danon et al. 2011).

Network Analysis & Disease

Epidemiological application of network analysis was initially used in studies of disease transmission in humans, with the earliest application focusing on the spread of the HIV/AIDS epidemic in North America and understanding the underlying epidemiological process (Proulx et al. 2005). Within network epidemiology, diseases spread from node to node via edges (Craft & Caillaud 2011). Network analysis can provide insights into individual risk of exposure to disease as well as maximum potential epidemic size (Webb 2006). Researchers are increasingly using the technique to examine disease dynamics in wild populations. It has been most frequently used to provide a novel perspective on social relationships and contact networks, which can have profound implications for contagious disease transmission (Kiss et al. 2006, Hamede et al. 2009, Leibler et al. 2010).

Though Craft and Caillaud (2011) indicate that the technique is still underutilized in wildlife epidemiology, a number of studies have emerged in recent years which display the utility of the method to this field. Hamede et al. (2009) used network analysis to describe the contact network between wild Tasmanian devils, currently threatened by an infectious cancer. The researchers observed a highly connected social group, such that an infection in one individual has the potential to spread throughout the entire population network due to the social behavior relations of the species. Studies which combine biogeographic information with relational data to examine disease spread have also proven highly informative. Using long term data from the Serengeti Lion Project, Craft et al. (2010) were able to characterize the network of interaction between prides, as well as exploring the effect of nomadic individuals that were largely blamed for the spread of the disease. The results of the study indicated that, contrary to previous speculation, the nomadic individuals had very little impact on disease spread throughout the region. However, the system was found to be highly susceptible to epizootics due to the frequent local contact between prides as well as the occasional long range contact due to the long range movements of some lone males interacting with prides a large distance away.

The use of network analysis to understand disease dynamics within natural systems is often limited by the ability to collect the relevant data, such as population structure. The accuracy of network representations is contingent on large amounts of data and the data available on wild systems is often limited (Craft & Caillaud 2011). Pastoral or livestock farming systems offer potential options for understanding animal disease networks, as these systems are highly monitored and resultantly provide a large amount of detailed data. For example, The Cattle Tracing Scheme in Great Britain contains highly detailed information regarding the movement of all cattle within the country. Livestock movements between farms has been identified as a major mechanism for disease transmission and the mapping of these movement networks has proven to be highly informative in understanding disease transmission in animals (Danon et al. 2011). The movement of sheep during 2001 was cited as one of the major catalysts for the outbreak of Foot and Mouth Disease (FMD). Using a highly detailed dataset of the movement of individuals prior to and during the disease outbreak, researchers were able to discover a number of factors that likely contributed to proliferation of the disease. A network analysis of the system revealed a high seasonality of activity within the industry, indicating a higher risk of disease spread during certain times of the year. In addition, the structure of interactions indicated that highly connected nodes or farms should be the points of surveillance in the future to prevent a similar epizootic (Kiss et al. 2006). Though understanding disease in these systems is socioeconomically important to the system itself, it is also important from a biological perspective to understand those pathogens which are more generalist in nature. Diseases such as bovine tuberculosis (bTB) and Highly Pathogenic Avian Invluenza (HPAI) are able to cross-infect multiple host species and epizootics of this nature can have grave implications for both managed and wild populations (Roberton et al. 2006; Bohm et al. 2009).

Potential issues with network analysis/ missing links in research

The use of network analysis for studying diverse and interdisciplinary phenomena continues to expand. However, Butts (2009) cautions against blind acceptance of assumptions in the theoretical representation of empirical phenomena. The use of network analysis commits the analyst to making assumptions about which variables are interacting, the nature of this interaction, and the time scale at which this interaction is taking place. Spurious application of assumptions of actual networks or the study systems themselves could lead to researchers drawing inaccurate conclusions. Thus one must be discerning when choosing whether to apply network analysis to a system or not, and ensure that the network's representation of factors within the system is correct (Butts 2009). Additional challenges have been proposed with specific regard to the use of network analysis in the fields of biogeography and conservation (Cumming et al. 2010). Among the challenges posed is the need to further incorporate the temporal dynamism of ecological and social systems into network analyses. By studying the changes in links, insight can be gained into the potentially non-random changes in systems over time. Another issue is that researchers treat social and biological networks as separate entities, though the systems may be overlapping in both time and space. To further develop the utility of network analysis for investigating conservation problems, ideas must be empirically tested and refined, ideally using large long-term datasets (Cumming et al. 2010). Many of these challenges can be addressed using data from a temporally dynamic social-ecological system for which the potential exists to obtain a large and detailed dataset.

Chapter 2. Understanding highly pathogenic avian influenza outbreaks in the Western Cape Ostrich Industry: Did Network Dynamics Enhance Vulnerability.

1. Introduction

Disease outbreaks have the ability to decimate wild and domestic populations and whole communities of species over large areas, often with devastating cascading effects for biodiversity and ecosystems as a whole (Daszak et al. 2000; Pongsiri et al. 2009). Increasingly connected global markets and modern, production-oriented farming practices greatly facilitate the spread of disease, risking large economic losses and posing an immense threat to the conservation of biodiversity (Holling & Meffe 1996; Daszak et al. 2001; Patz et al. 2004). Pathogens which infect multiple host species are of particular concern, as their proliferation in a single species or system has the potential to ‘spill-over’ to other susceptible populations. Disease spillover between wild and domestic populations is economically costly and poses a significant threat to wild populations (Daszak et al. 2000). In order to understand the disease dynamics of spill-over events, understanding of transmission between and within each contrasting system is vital. Unfortunately, epidemiological data of wild systems is limited and difficult to collect, but data from domestic systems is often abundant and can be used to improve our understanding of the dynamics of disease transmission in metapopulations (interacting but distinct populations of the same species) (Power & Mitchell 2004).

Industrial farming systems can be characterized as high-intensity, high-energy monocultures which are specifically managed to maximize output efficiency. Modern farming converts natural ecosystems, potentially containing dozens or hundreds of species, to large monospecific systems. This decline in diversity makes these systems fundamentally less resilient to perturbations, such as disease outbreaks (Holling & Meffe 1996). Outbreaks of Foot and Mouth Disease (FMD) in the UK cattle and sheep industries highlight the transmission potential of disease within intensive domestic systems. Fundamental characteristics of production, such as the movement of farm stock between locations, facilitate the spread of disease over large geographic distances (Shirley & Rushton 2005). During the 2001 FMD outbreak in the UK, it is estimated that by the time the disease was detected at two farms at least 57 premises in 16 countries had contracted the disease via the movement of farm stock between locations (Shirley & Rushton 2005). The global connectivity of many domestic systems clearly has the potential to transport disease to novel regions undetected. For diseases which are known to infect entire families or genera of species, such as FMD or avian influenza, each domestic shipment of farm stock is a threat to wild populations and can have potentially large impacts.

The African rinderpest pandemic of the late 1800's illustrated the potentially dire consequences of introducing novel viruses to naive wildlife populations, and demonstrated that domestic species can connect wild populations across landscapes and facilitate disease epidemics. The virus was introduced to the horn of Africa in 1889 and reached Cape Town, South Africa within 8 years, wiping out ~90% of cattle in sub-Saharan Africa. The generalist nature of the pathogen facilitated the rapid spread across the continent, infecting and decimating roaming populations of buffalo, giraffe and wildebeest (Daszak et al. 2000; Roeder 2008). The African rinderpest pandemic is an example of large scale 'disease spill-over', where transmission of infection occurs from one (often domestic) reservoir population to another susceptible population (Daszak et al. 2000). Spill-over from domestic species is of growing conservation concern, with an increasing number of wild species including lions, seals and buffalo, being impacted by disease from domestic species (Roelke-Parker et al. 1996; Kennedy et al. 2000; Rodwell et al. 2001).

Most documented domestic spillover events have involved cattle, sheep and other ungulates, but the rapid expansion of global poultry production poses another system with high potential for disease spillover. Human-mediated movement of farm stock coupled with the migratory life history of many wild bird species has created a highly-connected, global-scale interaction system that has lead to a number of outbreaks of Highly Pathogenic Avian Influenza (HPAI) over the past decade. In 2011 alone, HPAI outbreaks were reported in Bangladesh, Cambodia, China, India, Iran, Israel, Japan, Korea, Mongolia, Nepal, Palestine, and South Africa (World Organization for Animal Health website, 2011), each likely resulting in massive culling efforts and considerable economic losses (Mather & Marshall 2010). In addition, fatal infections of HPAI in the last decade have occurred in millions of birds from 11 avian orders, including some globally threatened species (Roberton et al. 2006; Wallace & Fitch 2008) Understanding the factors that increase transmission potential within this system is thus of both economic and ecological importance.

The emergence of HPAI within many contrasting systems further highlights that diverse research approaches are required to understand this disease. While understanding transmission potential between domestic and wild birds is vital, it is also paramount to consider the transmission pathways within the wild and domestic systems independently. Molecular methods have provided insight in cases of spill-over between systems, however there is continued uncertainty regarding the evolution of the disease and specific nature of cross-species transmission (Roberton et al. 2006; Wallace & Fitch 2008). While research in wild systems has detected strains of Low Pathenogenic Avian Influenza, the detection of HPAI is decidedly more difficult due the high mortality rate associated with infection (Cumming et al. 2011). In addition, acquiring the data relevant for epidemiological understanding of a generalist pathogen is notably challenging in wild populations. Determining meaningful contact patterns, the highly structured nature of populations, as well as inadequate sample sizes are just a few factors which complicate the understanding of this disease in wild populations (Craft & Caillaud 2011). While the lack of relevant data currently limits understanding of certain aspects of HPAI spill over, the highly monitored nature of modern farming systems has the potential to provide large amounts of detailed contact data (Kilpatrick et al. 2006).

Understanding the pathogen dispersal potential of wild migratory birds requires study of life history patterns, dispersal rates and ecological drivers in order to improve our ability to predict the risk of spread of avian borne diseases (Gaidet et al. 2010, 2011). Conversely, dispersal or movement within the poultry or ostrich industries is far more relational and dependent on social interactions than ecological. It is dictated by the buying and selling of birds and their movement from breeder to farmer to abattoir and the subsequent relationships among farmers which govern these movements (Leibler et al. 2010). Studying movements within domestic systems requires a technique which addresses relational interactions while also incorporating biological factors. Network analysis is one such technique which has been increasingly used to understand movement and contact networks in domestic industries and disease epidemiology (Kiss et al. 2006; Kao et al. 2007; Robinson et al. 2007).

Network analysis is a relatively new technique to the biological sciences but has had a firm grounding in the social sciences since the 1960's (Barabasi 2003). Typically used to study relationships among social entities, in recent years it has been used to understand a number of biological phenomena, including energy flow in ecosystems (Bascompte 2009), population dynamics (Fortuna et al. 2006) and disease transmission (Hamede et al. 2009). The universal application of network analysis to many kinds of data is due to the commonality of network properties between diverse systems. Measures such as network size (number of entities incorporated into the analysis) or network density (measure of network connectivity) converge in similar ways independent of the age, function or scope of the network being studied (Barabási 2009).

A network approach to epidemiology has aided in understanding a number of disease epizootics within domestic systems. Notably, Kiss et al. (2001) used cattle and sheep movement data to construct a network and perform short simulations of Foot and Mouth Disease (FMD) transmission in the UK. In addition, Natale et al. (2009) produced a static graph of cattle FMD in Italy to inform about disease transmission in that domestic system. Danon et al. (2011), however, question the use of static networks to model very dynamic movement of livestock, and Vernon &

Keeling (2009) concluded that static network representations fail to adequately represent dynamic networks. Many additional network analysis studies of FMD have been conducted and have provided much insight into the disease dynamics of cattle and sheep industries (Shirley & Rushton 2005; Kiss et al. 2006; Kao et al. 2007; Robinson et al. 2007; Jewell et al. 2009).

Despite the global recognition of the pivotal role infected poultry plays in spreading HPAI, the network approach has not been extensively used to study the transmission of avian influenza within a domestic system (Boyce 2007). A study by Leibler et al. (2010) investigated the role of different types of contact between poultry farms in the UK which may heighten the risk of avian influenza transmission though the region. However, the study did not investigate live bird contact but rather assessed the risk associated with secondary modes of influenza transmission via contact surfaces (ie. vehicles or machinery), workers moving between locations and geographic proximity of farms. Though these modes of transmission pose a potential transmission risk, studies have shown that it is the movement of individuals which present the greatest transmission potential, due to the high rates of transmission associated with contact between susceptible and infected individuals (Shirley & Rushton 2005). Understanding how avian influenza disseminates though a domestic system in which substantial movements of animals occurs, thus requires a movement network, similar to those which have aided in understanding FMD epizootics.

A recent outbreak of avian influenza in the Western Cape region of South Africa represents an opportunity to study how a movement network may have contributed to an outbreak of the disease. The production system of the ostrich industry lends itself well to network analysis, with batch movements of birds occurring at multiple times during the ostrich production cycle. The South African ostrich industry contributes 65% of global ostrich production, and generates an annual export income in excess of R1.2 billion. There are currently over 550 ostrich farms in South Africa, of which 80% are located within the Western Cape (SAOBC 2011). In April 2011 the highly pathogenic avian flu virus (HPAI) H5N2 was discovered on five ostrich farms, near Oudtshoorn, Western Cape (Western Cape Department of Agriculture 2011). It was initially believed that the flu had been contained, but as of January 2012, 42 farms have tested positive for the virus. This has resulted in the full eradication of all positive farms, substantial economic losses within the region, and government payouts in excess of R23’000’000.

There are few datasets that include contact structure data that are both relevant to disease transmission in large populations and sufficiently detailed to test the relevance of the network based approach (Kao et al. 2007). One such dataset is the network of livestock movements in the U.K. This dataset has been used extensively to understand epizootics and disease dynamics in networks (Shirley & Rushton 2005; Kiss et al. 2006; Robinson et al. 2007).

Here I explore a rich and detailed dataset which includes all movements of domestic ostriches between farms within the Western Cape over five years based on permit records. The goal of the study is to identify aspects of the ostrich industry that increase its vulnerability to disease epizootics, as well as making recommendations aimed at reducing this vulnerability. In particular, I posed three questions: i) Do the infected farms display properties that one would anticipate makes them more vulnerable to contracting and/or transmitting the disease? ii) Does the ostrich farm industry in South Africa exhibit properties that indicate vulnerability to disease outbreak? iii) Is there evidence that vulnerability increased leading up to the epizootic and/or varied depending on the time of year?

Answering these questions represents a first step towards understanding avian influenza via the movement of ostriches within South Africa. Studying disease transmission in agricultural systems is of benefit for conservation efforts because it facilitates the development of recommendations for agricultural controls and practices that may curtail the spread of disease and subsequent spillover into wild populations.

Network Vulnerability

Past research has revealed how a number of network indicies can be used to understand the vulnerability of a network to the spread of disease (Table 1: Shirley & Rushton 2005; Jeger et al. 2007; Danon et al. 2011).

Table 1. Definitions of network parameters calculated for the Ostrich Movement Network. (OMN)

Network Level Indices	***Definition***
Network Size (Vertex Count)	Number of nodes or vertices in a network
Number of Edges	Number of edges or links in a network
Density	The number of realized edges in a network as a proportion of all possible edges.
Diameter	The length of the longest path (number of linking edges) between connected nodes
Average Path Length	The mean of all shortest path lengths between every node pair in a network
Number of Components	Number of connected components (aka isolated groups within a network)
Degree Distribution [P(k)]*	The probability that a selected node has exactly k links in the studied network. It is obtained by counting the number of nodes N(k) with k= 1,2… links and dividing by the total number of nodes
Node Level Indices	
Degree	The number of edges a node has
Out Degree	The number of outgoing edges of a node (directed network)
In Degree	The number of incoming edges of a node (directed network)
Betweenness**	The number of shortest paths between any two nodes in a network that pass through a given node

Source: Hanneman & Riddle 2005, * Barabasi et al. 2009, **Opsahl et al. 2010

Initial insights into the vulnerability of the Ostrich Movement Network (OMN) can be gained by investigating attributes of farms, specifically those which contracted disease during the 2011 HPAI epizootic. Node level investigations typically focus on connectivity, which is revealed by the degree of a node, and centrality, which is measured by its betweenness (Table 1). Nodes with higher values for these indices would be expected to contract disease earlier during an epizootic or epidemic (Barabasi et al. 2000; Danon et al. 2011).

Heterogeneous patterns observed at the node level have provided large amounts of insight in determining the transmission dynamics of contact networks (Colizza et al. 2006). In addition, many contact networks have revealed the presence of super-connected nodes, known as hubs. These hubs can often increase variability in transmission which contributes to the heterogeneous topology of a disease network (Paull et al. 2012). In addtion, these nodes exert a large amount of influence on network topology, and are of specific concern during disease epizootics as they tend to contract disease early in an epizootic, and redistribute the disease to a disproportionally high number of other nodes (Shirley & Rushton 2005).

While node level indices can provide insight into network features such as connectivity and centrality, investigations at the network level can reveal traits which further inform on the vulnerability of a network to a disease epizootic. The first of these features is network size, which can be described simply as the number of nodes in a network (Table 1). A larger network would contain a greater number of susceptible nodes, though in order to gain a clear understanding of the impact of network size, the frequency of relations between these nodes must be considered. Edges in a network provide the scaffold upon which disease can move, with larger numbers of edges providing more opportunities for the disease dissemination (Table 1). When applying network analysis to a contact network in a disease study, it is important to note that even if an edge exists between an infected and susceptible node, transmission may not occur. The edges indicate contact, and the probability of transmission is dependent on the factors such as the frequency of contact or the number of entities being transferred (in this case the number of ostriches) or attributes of the nodes, or farms involved. Within a directed contact network, density has been used to understand the frequency of interactions, which in turn informs on transmission potential of a disease due to the density-dependant nature of epizootic spread (Wilcox & Gubler 2005; Smith et al. 2006; Ferrari et al. 2011).

Generally, networks are not fully connected, often being composed of a number of isolated components. If the majority of nodes within a network are in a certain component, this component is labeled the Giant Component. Since the extent of an epizootic is limited to the number of nodes present in the component it begins in, a large Giant Component has an increased probability of contracting a disease randomly introduced to the network. If this large size is coupled with a low number of components within the network, the epizootic potential of a virulent disease increases (Jeger et al. 2007).

The length or distance of a network indicates the number of steps a disease must take in order to reach the every other node in the network. The average path length and the diameter of movement networks provide information about the speed an epizootic can spread though a network. Specifically, a shorter average path length of a network indicates greater likelihood that subsequent nodes connected to an infected node will become infected, while a shorter diameter indicates that the number of generations for a disease to spread throughout a movement network is reduced (Kiss et al. 2006).

The final network feature investigated during this study was determining whether the OMN displayed traits of a particular network type. There are a number of idealized network types which have been described in the literature, though three types consistently emerge and are commonly cited and studied in the literature (Barabasi et al. 2000; Danon et al. 2011). Each of these network types displays distinct trends in both network and node indices, while also significantly impacting the epizootic potential of disease within each system (Jeger et al. 2007). The network index most commonly used to diagnose network types is the degree distribution. This is defined as the set of probabilities, $P(k)$, that a node chosen at random will have degree k. The first of these networks is a random or Erdos-Renyi network which is typified by a degree distribution which follows a binomial distribution (Danon et al. 2011). The second type of network is a small-world or Watts-Strogatz network which are described as a having high levels of local connectivity, while also including some nodes which have links which provide shortcuts between the distinct clusters of nodes. (Jeger et al. 2007). The degrees for nodes in these networks is relatively homogeneous, thus the degree distribution is similar to a random graph, but a distinct peak at the mean degree value (Barrat & Weigt 2000). The final network type is known as scale-free or Barabasi-Albert network. Within this network, the probability that a node is highly connected is significantly different to random networks. Thus, the network is typified by the presence of hub nodes, and the degree distribution follows a power-law distribution. This power-law distribution is described as the probability that a node has k links follows $P(k) \sim k^{-\gamma}$, where γ is the degree exponent. In real world networks the degree exponent is typically between two and three (Barabási & Oltvai 2004). For further description and representation of each network type in a figure see Barabasi & Oltavi (2004) for random and scale free networks and Watts & Strogatz (1998) for small world networks. Disease spread through these three types of networks is drastically different, with the transmission in random networks being the slowest.

While transmission in small world networks is at a moderate rate, and transmission within scale-free networks is typically highly rapid (Barabási 2009).

2. Methods

2.1 Study Site and Farming Practices

The region of study includes farms within the Western Cape, South Africa which are known to have moved one or more ostrich(s) between September 2005 and March 2011. Many of these are located in the Little Karoo region, with particularly high densities of farms around the town of Oudtshoorn (33°58'S, 22°20'E). The region is semi-arid with sparse natural grazing and highly seasonal, unreliable rainfall averaging 228mm per year (Sinclair et al. 2005).

The system of Ostrich production in South Africa incorporates a number of different farm types that are specialized to manage different stages of the ostrich life-cycle, and thus relies on frequent movement of ostrich individuals between locations (Figure 1). Typically, when birds are moved between locations they are integrated into enclosures with the standing populations of birds already on the target farm. The resulting interaction and contact between new individuals and standing populations on farms highlights a probable mechanism for disease transmission. Accordingly, this movement network potentially represents the central route of transmission in this epizootic because the disease is most commonly spread by direct contact between infected and susceptible birds.

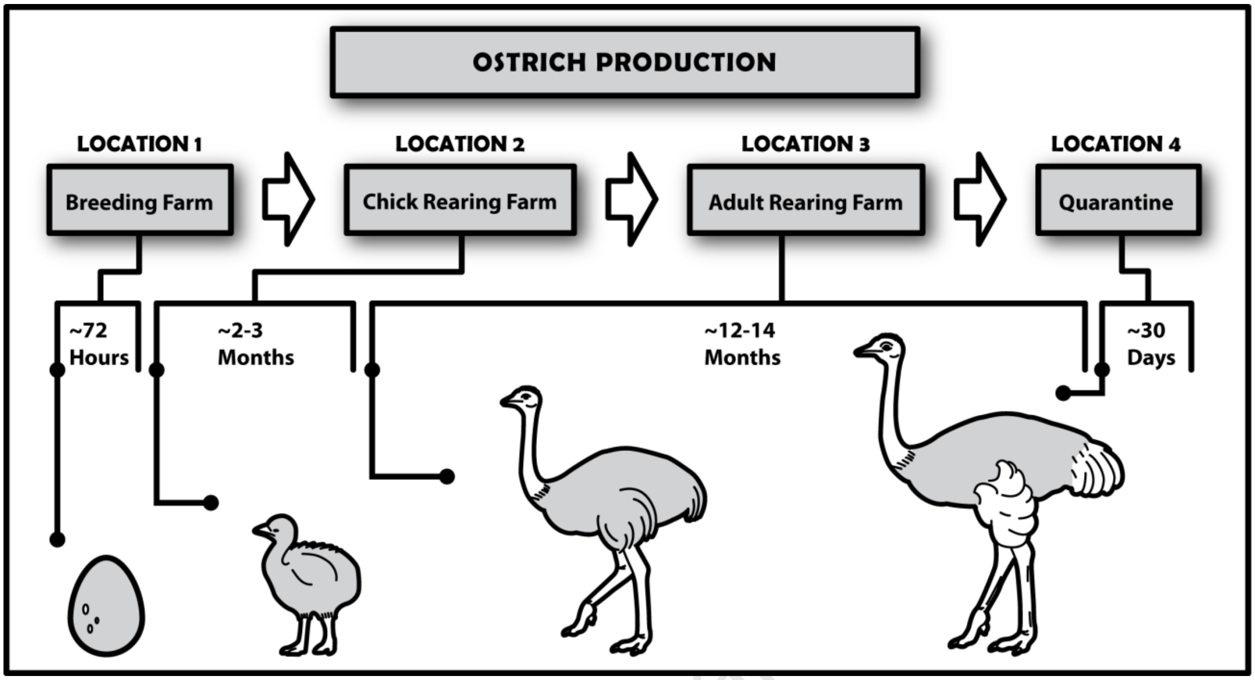

Figure 1. Ostrich production in South Africa incorporates the movement of birds between a number of different types of farms before they are sent to the abattoir to be slaughtered. The process begins at hatcheries where eggs are incubated and, once hatched, chicks are moved to chick rearing farms within 72 hours. This most frequently occurs between September and February each year. The birds remain at these rearing farms for 2-3 months, when they are moved to adult rearing farms. They remain at these locations until they reach 70-90kg (for approx. 12-14 months) when they are moved to quarantine farms. They remain at these farms for ~30 days, and once deemed disease free they are transferred to an abattoir for slaughter. These last two steps of the production cycle occur primarily between September and February.

2.2 Dataset & Network Construction

Ostrich movements were recorded via permits issued by the Department of Agriculture of the Western Cape. This database of records contains the date, source, destination, batch size, as well as farmer specific information for each movement. The system has been in operation since 2005, when it was established following an outbreak of Highly Pathogenic Avian Influenza (HPAI) in 2004. The data available prior to September 2005 and after March 2011 were deemed incomplete and thus excluded from all analyses. Cleaning of the dataset involved assigning unique farm ID numbers to each farm in the network. This was accomplished using farmer demographic information and farm name. Due to the high replication of surnames as well as farm names in the region this process proved extremely arduous and the dataset used in this analysis is estimated to be 85-90% accurate (pers. comm.., Dr. John Grewar). In addition, the data only account for movements between farms which are registered to export ostrich products. For the analysis it was assumed that all movements of Ostrich movements within the system were accounted for in the dataset and unregulated movement of birds between export and/or non-export farms did not take place

The movement database was used to construct an Ostrich Movement Networks (OMN), which included directed ostrich movements (edges) between source and destination farms (nodes). The weight of each edge reflected the number of birds moved between nodes in each time period. These were constructed for each month, indicating seasonal variation in the data; for each year, indicating changes through time; and for the dataset as a whole. Seasonal fluctuations are commonly observed in movement networks of livestock (Kiss et al. 2006, Robinson et al. 2007). The ostrich production system within the Western Cape is coupled to seasonal variation in the ostrich life-cycle and climatic conditions in the region, resulting in seasonal fluctuation in bird movements. Movements of chicks between sites, as well as adult birds to the abattoir occur most frequently between September and February (pers. comm.. Dr. John Grewar). Monthly and annual sub-networks allow investigation of dynamic changes in network properties. Any pair of nodes is considered connected by a directional link if there is at least one movement of ostriches between them during any month or year. These networks are static, containing all the movements that happened within a particular time period, irrespective of their relative timing within that period. All network indices were measured across all monthly (n=67) and annual (n=5) sub-networks as well as for the entire dataset (n=1). Seasonal profiles were generated to explore general seasonal trends incorporating all years (n=12) by averaging measures by month across all years. An autocorrelation function (acf) was used to test for seasonal autocorrelation in the measures of network size and number edges (see Figure 4).

2.3 Data Analysis

2.3.1 Network Description

All network indices (Table 1) were calculated from directed networks for the full dataset and for monthly and annual subsets of the data using the package *igraph* 0.5.5-3 (Csardi & Nepusz 2006) in the R statistical computing environment version 2.14.1 (R Development Core Team, 2011). The network and node level indices calculated during this analysis are listed and defined in Table 1.

The standard practice for understanding the structure of real world networks is to compare them to randomly generated networks with the same number of nodes and edges. Discrepancies between the random network and the OMN provide insight into non-random network features, which may be indicative of disease vulnerability. Random networks were generated at each time step (n=67) as well as for monthly (n=12) and annual (n=5) sub-networks as well as for the network as a whole (n=1).

2.3.2 Network Vulnerability

The relevance of each network feature as well as what to expect for network indices in a vulnerable network are summarized in Table 2.

In order to determine if nodes which became infected during the 2011 HPAI epizootic were more connected (degree) or central (betweenness), Wilcoxon sign rank tests were used to test if the infected farms display higher values in one or both of these node indices relative to the set of uninfected farms. In addition, to determine whether hub nodes were present in the OMN, as well as whether these nodes became infected, betweenness and degree for each node in the network were determined. These were then used to rank the centrality and the connectivity of each node and determine if any hubs are present in the OMN, and to see if these hubs were infected with HPAI. All network visualizations were generated using Gephi 0.8 (Bastian et al. 2009).

Table 2. Network features which affect disease transmission potential within a network, as well as how these features are measured using specific network indices. In addition, the behavior or traits of these indices within a network which is vulnerable to disease spread is listed.

Network Feature	**Relevance to Disease Transmission**	**Network Index (What to expect if vulnerable)**
Network Size	Larger networks contain greater numbers of susceptible nodes, while increasing numbers of edges increases possible routes a disease could take through the network.	• Number of nodes • Number of edges (High) • Density (High)
Components	The extent of an epizootic is limited to the number of nodes in the component it begins in.	• Number of components (Low) • Giant Component (High proportion)
Distance	If it only takes a short number of steps to reach every node in the network, diseases are able to spread much more rapidly	• Average path length (Low) • Diameter (Low) • Giant Component (High proportion)
Connectivity	The higher the number of edges a node has, the more likely it is to be a neighbour of an already infected node.	• Number of edges (High) • Density (High) • Node degree (High)
Centrality	Nodes which are central to the network lie on the shortest path through the network and are more likely to become infected early in an epizootic.	• Betweenness (High)
Network Type	Disease transmission differs between type: Lowest rates in random networks, moderate rates in small world networks and highest rates in scale-free networks	• Average path length (Low) • Degree distribution (Power law) • Node degree (High)

2.3.4 Time-series analysis

To detect temporal changes in the monthly network indices, and thus in the vulnerability of the network, the strong seasonality of the movement network was controlled for using time-series analysis in the the R package *bfast* 2.1-1 (Verbesselt et al. 2009) . Originally developed for use with remotely sensed data, BFAST uses a generic change detection approach which relies on a piecewise linear model to decompose a time-series into its trend, seasonal and remainder components.

3. Results

3.1 Network Description

A total of 1617 farms (nodes) participated in the Ostrich Movement Network (OMN), with 17 955 movement events (edges) moving 2 677 478 bird individuals over the entire time series. Nine strong components for the full network were identified. Of these, eight ranged from two to five nodes, while the Giant Component contained 1596 nodes. The density of the full network was 0.0069, indicating that even when all nodes are considered, irrespective of time, the network itself displays low density. The diameter was 11 edges, while the average path length was 4.57 edges.

3.2 Network Vulnerability

Wilcoxon signed rank tests for differences in betweenness and degree between infected and uninfected farms revealed that infected farms were significantly more connected ($p<0.001$) and more central ($p<0.001$) than the rest of the network (Figure 2. Note that the sample sizes for the tests of degree and betweenness differed due to the high number of null betweenness values for many nodes which were excluded from the analysis (Figure 2).

Visualization of the OMN (Figure 3) provides some indication of its architecture or topology. Farms 490 and 342 could be identified as the prominent hubs in the OMN due to high out-degree, while the disproportionally high in-degree of farm 64 lead to it also being labeled a hub. The high betweenness values of these nodes (1st, 2nd & 7th highest values) further confirm the high level of influence these farms have on the functioning of the network.

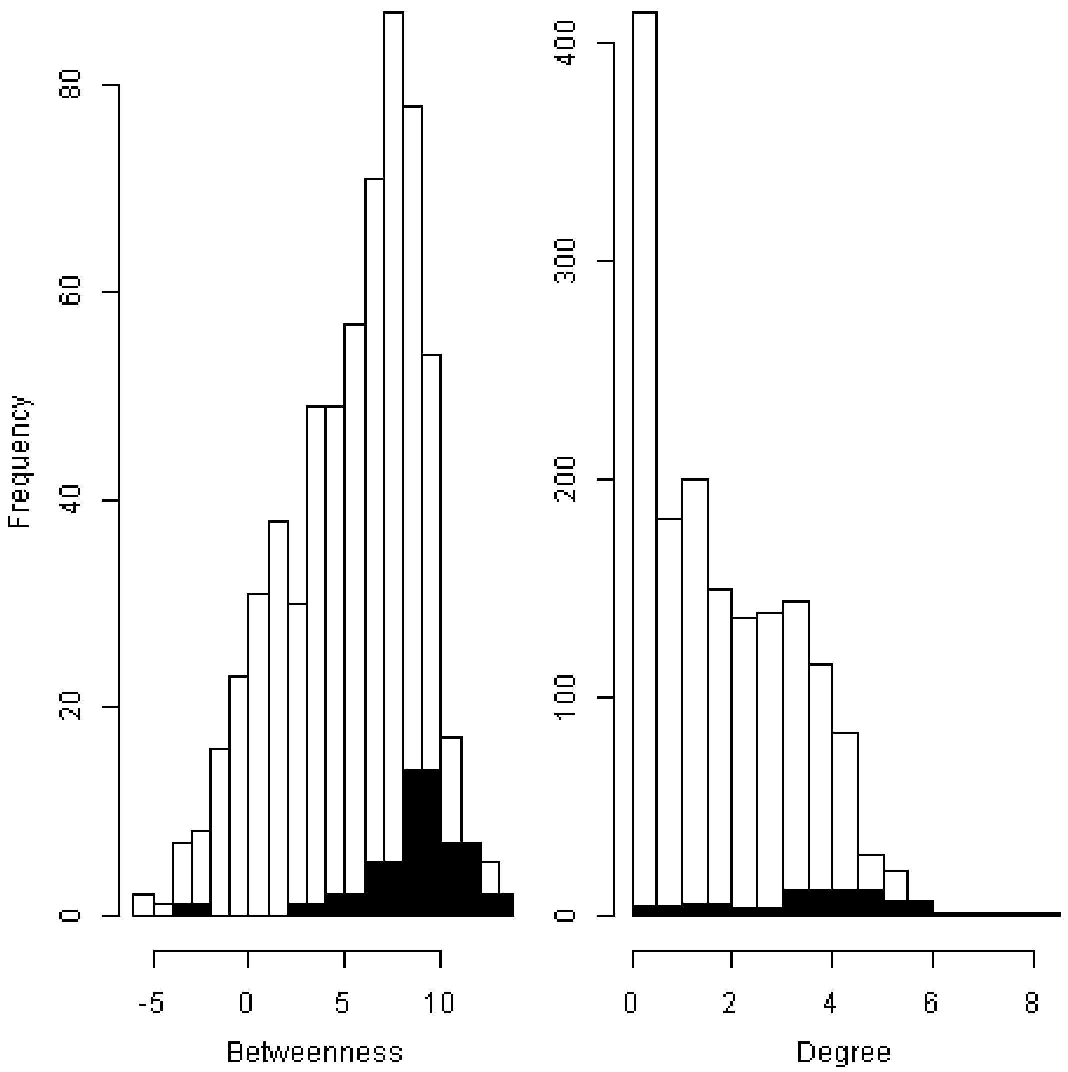

Figure 2. The distribution of logged betweenness ($n_{Infected}$=23, $n_{Non\_Infected}$ = 324) and degree ($n_{Infected}$=42, $n_{Non\_Infected}$ = 1575 scores for all farms (white) as well as the farms which tested positive for HPAI (black). A Wilcoxon sign rank test revealed that the infected farms are significantly different from infected farms in the network in both betweenness (p<0.001) and degree (p<0.001).

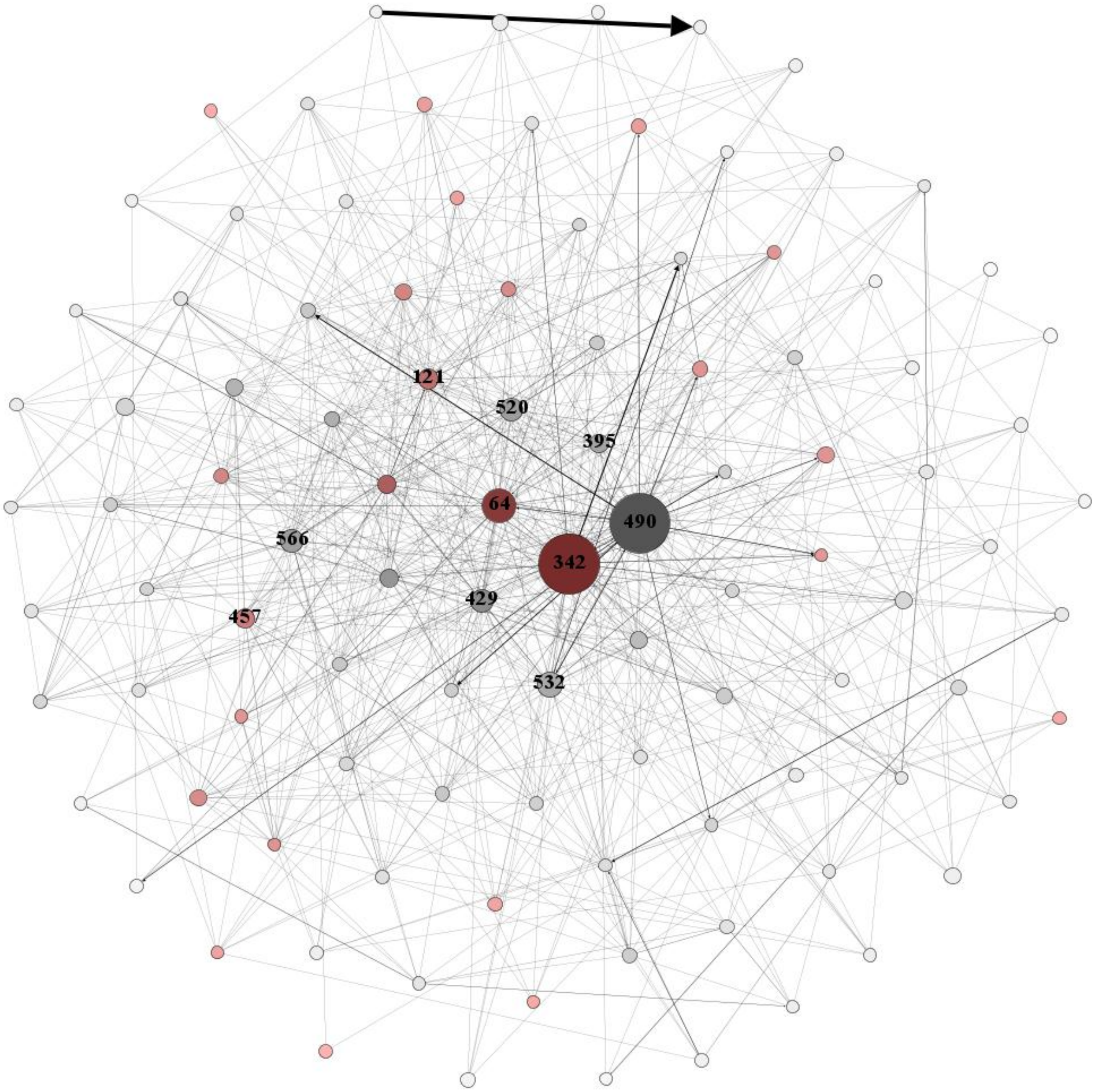

Figure 3. Full ostrich movement network visualization with the least connected nodes (degree < 20) not shown. Node size indicates the degree of each node with the most connected nodes appearing as the largest nodes. The intensity links indicates the frequency of interaction (a notably strong relationship can be seen at the top of the figure between two otherwise minimally connected nodes). The farm ID numbers for the 10 most connected nodes are displayed, and the farms which contracted HPAI are shaded red, though only 27 of the total 42 infected farms are displayed (due the lower degree values of the remaining 15).

Seasonal Variation in Vulnerability

The dynamic nature of the OMN revealed strong seasonality for many network indices. This was confirmed for network size by the autocorrelation function (acf), which revealed strong autocorrelation at 2, 6 and 12 months. Network size fluctuated seasonally as both the number of nodes and edges ranged from 111 to 331 interacting farms and 82 to 444 bird movements in any given month, respectively (Figure 4). This seasonality was mirrored in the connectivity and centrality of nodes in the network (Figure 5). The topology of the network remained relatively constant with a small fraction of nodes maintaining higher than average levels of connectivity, however the relative centrality and connectivity of the three hubs (64, 342 & 490) changed seasonally. These changes highlighted the heterogeneity of the network.

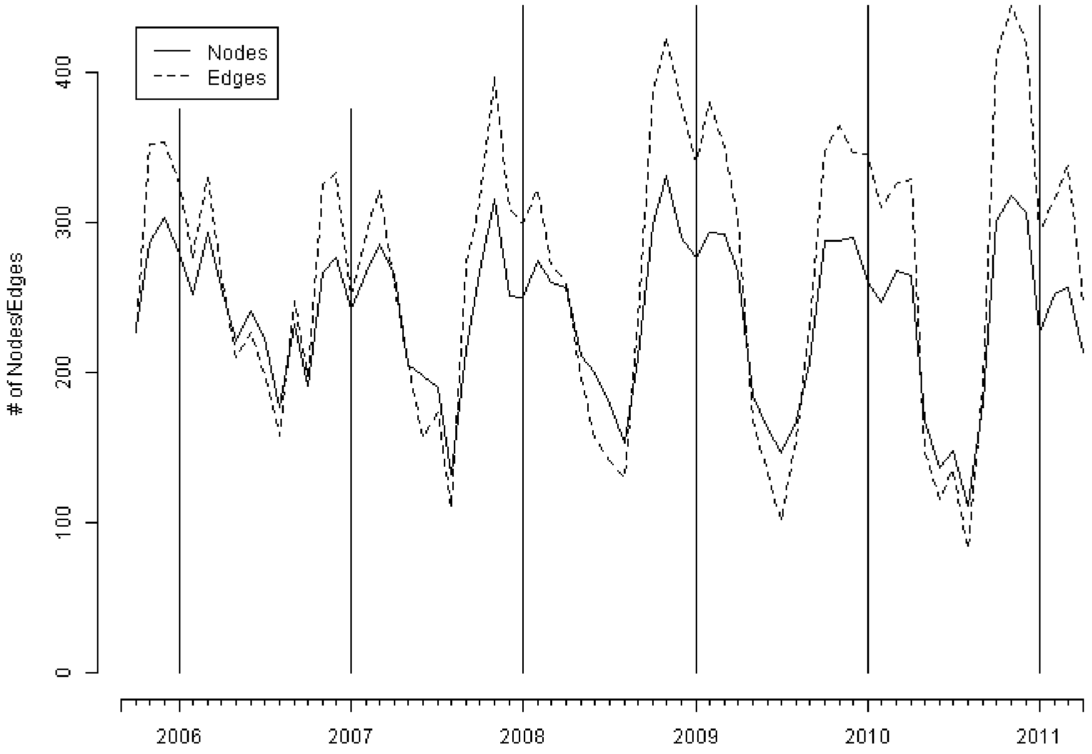

Figure 4. The monthly number of nodes (farms) and edges (ostrich movement events) occurring in the Western Cape, between September 2005 and March 2011. The vertical lines occur mark December of every year.

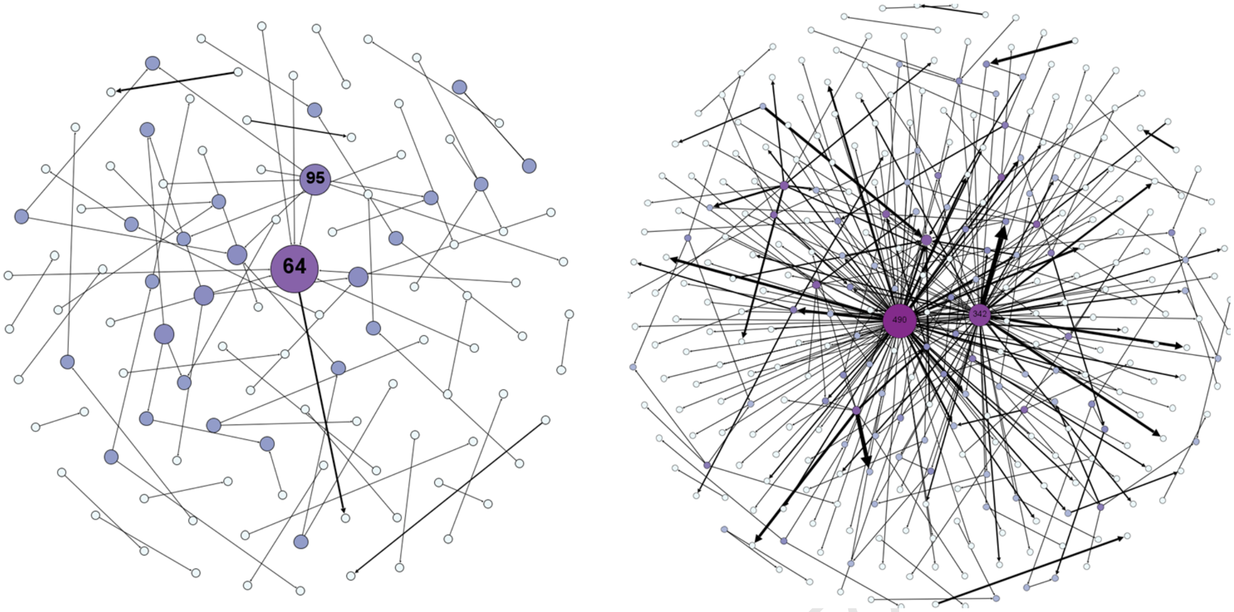

Figure 5. Network visualizations of the ostrich movement network for July 2010 (left) and October 2010 (right). These were the least and most connected months in the dataset, respectively. Node size and colour indicates the degree of each node, while the edge size and colour depict the strength of the tie, i.e. the frequency of movement between nodes. The node degree scores for July 2010 range from 1 to 10 (farm 64), while the node degree scores for October 2010 range from 1 to 143 (farm 490).

The number of components and Giant Component size of the OMN showed no difference from the randomly generated networks. Both the average path length and diameter of the OMN were, however, consistently lower than those for the random network implying greater vulnerability to the spread of disease (Figure 6). In addition, average path length and diameter showed dampened seasonal variability, though they typically displayed peaks at the same time step as the node and edge peaks.

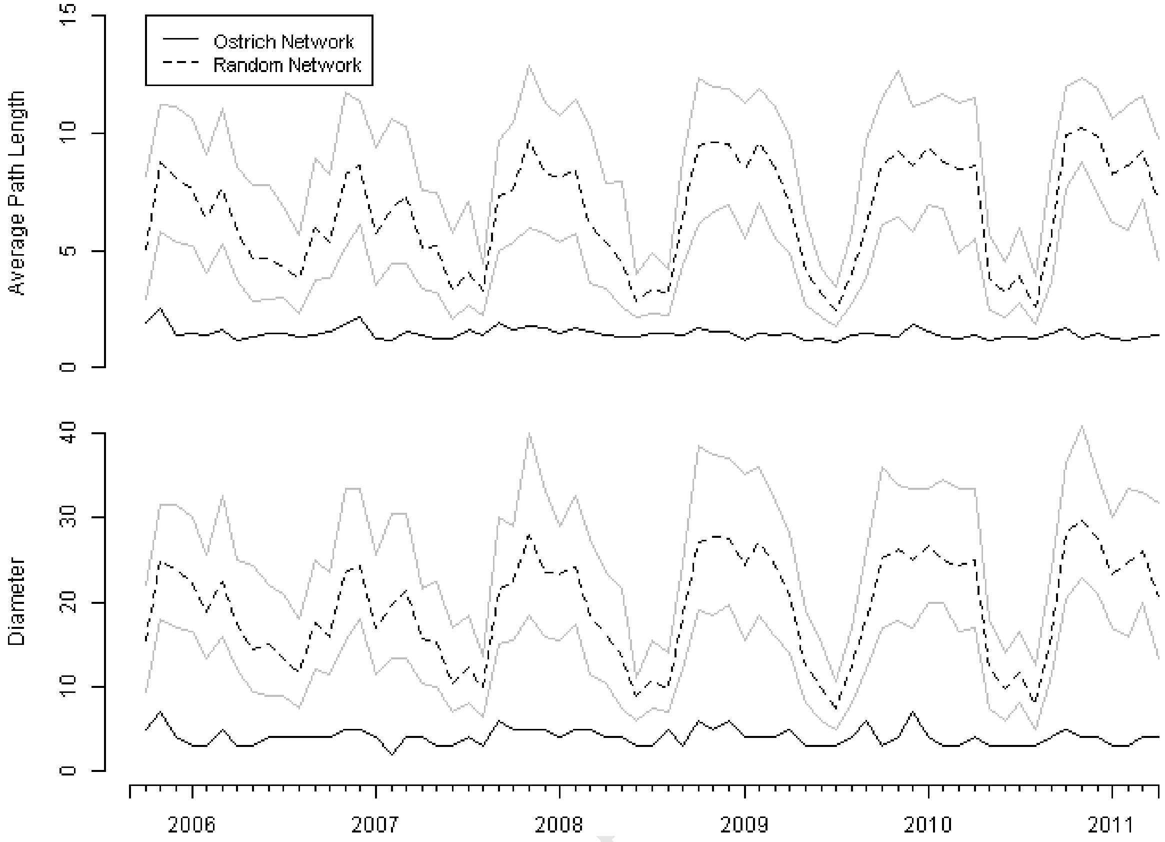

Figure 6. The average path length and diameter of the ostrich movement network as well as a random network for each month between September 2005 and March 2011. The random network scores were generated over 50 iterations, with the upper (0.95) and lower (0.05) quantiles displayed (grey).

The degree distribution of the OMN differed greatly from the random network (Figure 7). Once normalized, the random network displayed a Gaussian distribution, while the normalized trend of the OMN was linear. The degree exponent of the OMN degree distribution is γ=1.36, however the degree exponents for each monthly sub-network ranged from γ=2.12 to γ=2.46. The linearity of the normalized degree distribution, along with the very low average path length and diameter of the network through time, indicate that the OMN displays the characteristics of a scale-free network (Jerger et al. 2007).

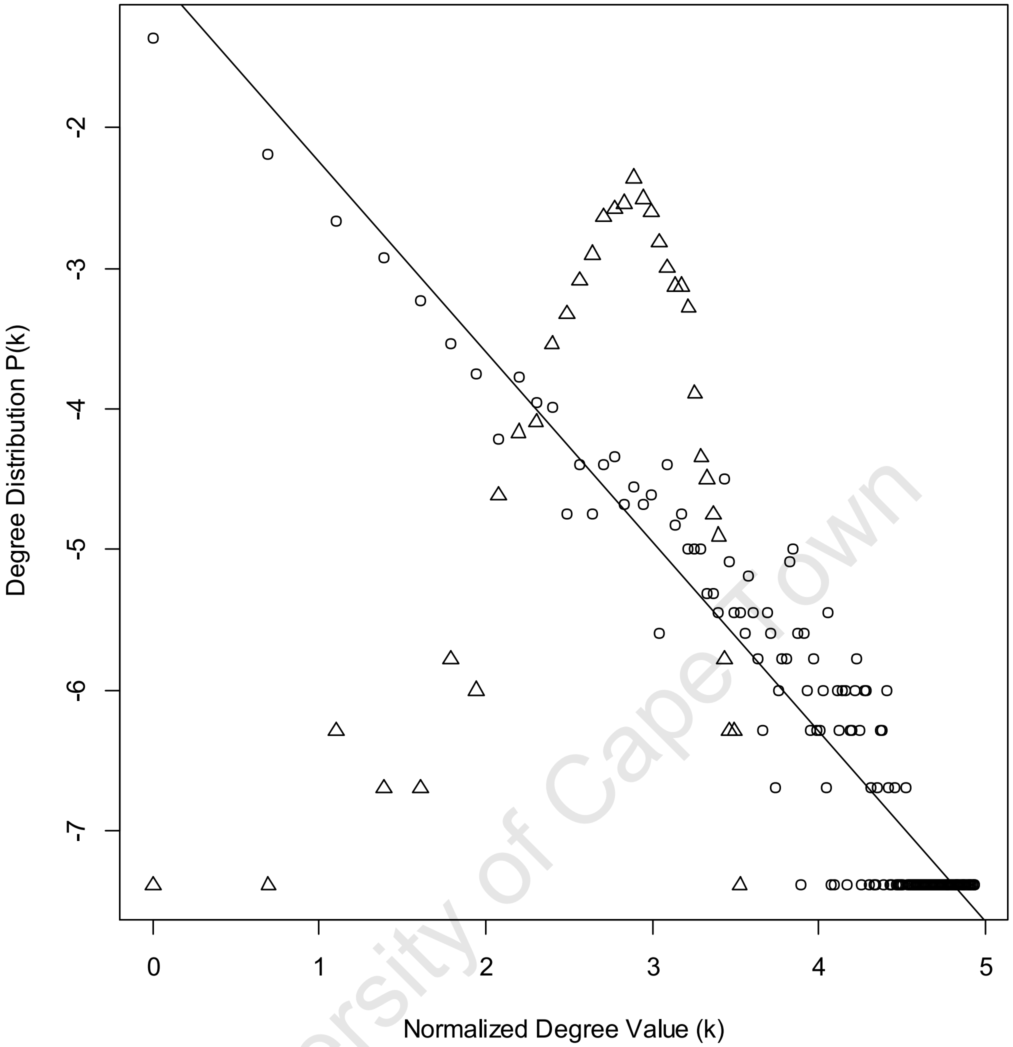

Figure 7 The degree distribution of the total ostrich movement network (OMN) (○) as well as a random network (Δ) with the same number of nodes and edges.

3.3 Time-series analysis

The decoupling of the node and edge counts became increasingly prominent with time (Figure 4). The BFAST analysis showed a decrease in the number of components coupled with greater numbers of birds being moved, as well as increasing network density and a larger Giant Component, indicated that the OMN was becoming more vulnerable to disease spread over time (Figure 8).

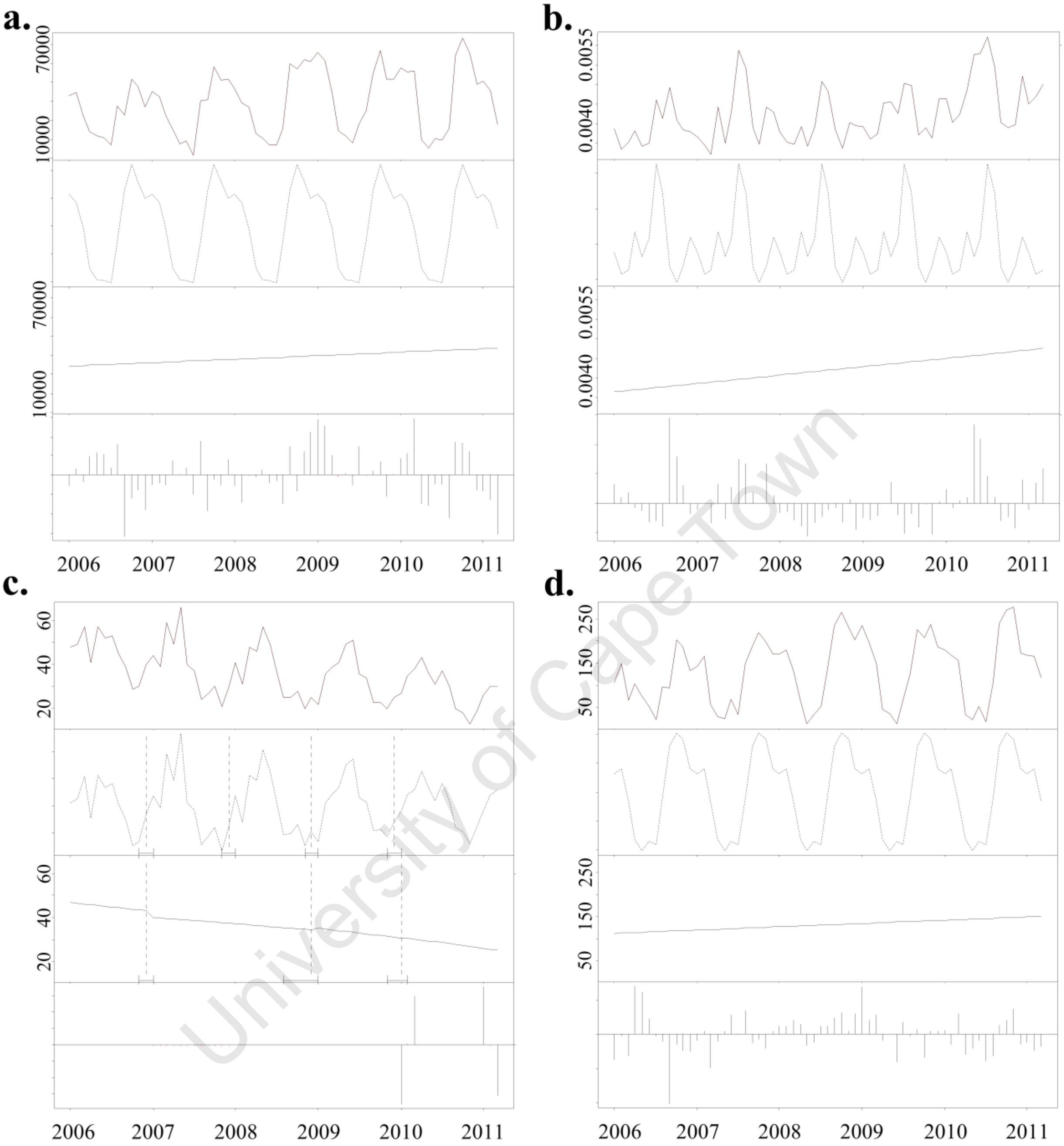

Figure 8. The results of a BFAST analysis of (a) the number of birds moved, (b) network density, (c) number of components and (d) Giant Component size. The first frame of each panel displays the network index at each time step, while the second panel depicts seasonal variation detected in the measure over time. This variation is then removed and the resulting trend is displayed in panel three. The fourth panel depicts residual variation which cannot be accounted for in the seasonal variation or trend. The vertical lines in the second panel of image c indicate shifts in the season trends, while the vertical lines in the 3rd panel signify an abrupt change in the trend component of the time series. The corresponding confidence interval of each shift or change is depicted by horizontal lines below each.

4. Discussion

The analysis of the ostrich movement data using a network approach revealed several findings consistent with the hypotheses that the infected farms imbued properties that predisposed them to contracting disease, and that the system as a whole was becoming increasingly vulnerable to disease outbreak through time. These findings highlight the value of using network analysis to uncover the dynamics of disease transmission, and exploring the drivers behind the emergent patterns in the network allows key issues and potential management interventions to be identified.

Farms which tested positive for HPAI had above average centrality and connectivity scores, indicating that the movement of ostriches between these locations provided a pathway of transmission for disease in this system. This finding indicates that the connectivity and centrality of farms is non-random and this heterogeneity is known to impact disease spread in transmission networks (Barabasi et al. 2000). For example farms 64, 342 and 490 were identified as hubs. Due to their high connectivity and centrality, there is a disproportionately high chance that if disease is introduced to this system, these farms will quickly contract the disease, as well as facilitate its rapid dissemination throughout the rest of the network (Jeger et al. 2007). The fact that two of the three hubs, farms 64 and 342, tested positive for HPAI provides further insight into how production practices predisposed this network to a disease epizootic. While farm 490 not contracting disease provides evidence that contact between farms does not necessarily mean that every movement will result in further transmission. This indicates that the transmission potential of each edge is not solely dependent on the degree or centrality of each node involved in each interaction. The transmission potential of each edge is likely depends on other factors such as node attributes (e.g. geographic location, farm type or rearing practices) of the source and/or target nodes.

In fact, Barthélemy et al. (2004) found that once a hub has contracted disease, transmission pervades the network in a progressive cascade from the most connected nodes towards lesser connected nodes. However, the activity of farms also proved highly variable based on network size, which itself highlights the seasonal fluctuation in activity of the industry.

Seasonal variation in the size of livestock movement networks is commonly observed (Kiss et al. 2006, Robinson et al. 2007). The size of the OMN varied predictably each year with peak activity in October as well as secondary peaks in January or February; the lowest levels of activity were observed in July. Though these changes in network size were coupled with reduced connectivity and centrality of nodes, the actual network structure was surprisingly consistent, with a few nodes often monopolizing ostrich movements. From a disease perspective this indicates that although the actual number of farms that are susceptible varies throughout the year, the potential for transmission to farms involved in movements during any month does not vary greatly. An additional network feature which did not follow the variation were average path length and diameter, measures of network distance. The very short distance of the network indicates that disease introduced in any random farm can disseminate to most other farms in a small number of steps. The consistently low average path lengths and diameters across months further highlight the perpetual vulnerability of the OMN.

Trends in the degree distribution of the complete network provided further insights into the vulnerability of the OMN. This network was found to be scale-free, primarily due to the negative linear relationship observed when the degree distribution was normalized. Scale-free networks are further characterized by the value of their degree exponent. Typically scale-free networks have degree exponent values between two and three, which essentially indicate how easy it is to traverse the network. Higher values are associated with maximum efficiency, and increasing reliance on hub nodes for system functioning. The degree exponent for each month was above two, which not only affirms the influence of farms 64, 342 and 490, but also indicates that the network is consistently scale-free, regardless of seasonal variation observed in other measures. The scale-free nature of a network has a large impact on disease transmission dynamics within the system, specifically impacting on the epizootic threshold of a disease. Within scale-free networks this threshold converges on zero, allowing disease to spread through network virtually unencumbered (Pastor-Satorras & Vespignani 2001). The scale-free nature of the OMN not only relates to its vulnerability to disease, but also provides a basis for intervention to prevent future epizootics.

Scale-free networks are notoriously tolerant to random node and link removal. When considering the OMN, this means that randomly removing farms or blocking specific movements will do little to stem an epizootic. However, targeted attacks on specific nodes can cripple transmission within a network, and thus halt disease spread before the extent or scope of infections are known. Implementing an optimized surveillance system whereby sampling is proportional based on farm movement activity could increase early detection of viruses in the system. Shirley & Rushton (2005) demonstrated that the 2001 Food and Mouth Disease (FMD) outbreak could have been reduced by 80% had any one of three specific farms been removed from network at the time of disease detection. These farms were hubs, and this represents just one example of how targeted removal of hubs has the potential to largely disable disease spread within a network (Jeong et al. 2000; Dezső & Barabási 2002; Butts 2009). The current strategy of disease containment in the Western Cape Ostrich industry involves establishing geographic buffers around each of the infected farms. The findings of this study indicate that rather than establishing geographic buffers, a more suitable intervention technique would be to establish ‘network buffer zones’. This strategy would involve investigating farms which have received or sent ostriches to the infected farm within the previous 30 days. In addition, the proven influence of hubs should require that movement activity to and from these locations be suspended until intense sampling reveals the site to be free of disease. Additionally, due to the highly influential nature of these nodes, it would be advisable to suspend all movements to and from these locations (even if they are found to be disease free) until the system is found to be disease free. It is also important note the possibility of illegal movements of birds and the potential impact of this activity on the spread of disease. This would be especially pertinent during times of disease outbreak when farmers are struggling financially and the opportunity to move birds they suspect to be healthy exists. However, if any infected birds are moved without record the ability to diagnose possibility infected farms using this method becomes problematic. This represents an area of possible future investigation.

The scale-free properties of the OMN coupled with other indicators of vulnerability should be particularly concerning to the stakeholders involved in the South African ostrich industry. However, a potentially more concerning finding of this study concerns the network evolution which took place during the time-series of the OMN analysis. The ostrich industry has been steadily growing over the last two decades to meet the demand for ostrich meat in the European Union (EU) (Mather & Marshall 2010). This increase in production fostered not only network growth, but also network evolution, resulting in a system which was becoming increasingly vulnerable every year. The number of birds moved during the last 5 years increased, while the number of farms in the network did not. This indicates that the number of susceptible birds in the network is increased and that at least some farms were stocking larger numbers of birds. The network density also increased, indicating that more movements between farms were taking place. Furthermore, the decrease in number of components in the network coupled with the greater size of the Giant Component indicates that nodes are preferentially attaching to the Giant Component in greater numbers every year. This finding is consistent with Robinson et al. (2007), who concluded that changes in the network properties of the British cattle industry between 2002 and 2005 were increasing the potential for large epizootics. The authors similarly reported an increase in the size of the Giant Component and a decrease in the number of components.

The evolution of network properties which have increased the vulnerability of the system likely occurred due to changing drivers within the industry itself. There are a number of possible ‘real world’ factors which may have contributed to this network evolution. The first relates to a large scale outbreak of HPAI in South Africa in 2004. The outbreak had a large economic impact, with over 35’000 birds culled from more than 100 confirmed infected farms, some of which did not recover financially and closed down (Mather & Marshall 2010). Of the remaining farms, the desire to enter into secure contracts with ostrich processers resulted in many increasing stocking densities. This implies that not only are there a larger number of susceptible ostrich individuals within the system, but a large proportion of these are being kept at densities which increase disease risk. The economic downturn also limited the number of ‘closed system’ farms in the network. These are farms which engage in every step of the production process themselves, negating the need to move birds to and from other farms. This practice requires a large amount of standing capital, and ties up this capital for long periods of time. Few farms that were capable of this remained after the 2004 epizootic.

The vulnerability of the OMN may have been further affected by management changes and biosecurity measures implemented following the 2004 outbreak (Mather & Marshall 2010). A month before HPAI was detected the ostrich industry in 2004, a strain of Low Pathogenic Avian Influenza (LPAI) was isolated from a wild bird in the Western Cape. When this virus was compared with a virus isolated from an infected ostrich, the two were found to be virtually identical. This finding lead to the industry fully implicating wild birds in the transmission of avian influenza, and further disease management strategies focused on minimizing the contact between domestic ostrich and wild birds. As a result, there was little emphasis on regulating production practices or the flows of ostriches between farms (Mather & Marshall 2010). The interactions between farms during the period investigated by this study were thus largely unencumbered by disease management regulations on ostrich movement, allowing the OMN to self-organize. The current management system focuses on minimizing inter-specific transmission of disease into the domestic system from wild birds and though necessary, should not be the central tenant of the management protocols in the ostrich industry. This study highlights the role and importance of intra-specific transmission between ostriches within the domestic production system. An effective management and disease surveillance system must be one that focuses on both inter and intra-specific processes which impact disease transmission and dissemination within the Western Cape ostrich industry.

Conservation implications

The potential for disease spillover from the ostrich industry to wild birds and people during a time of epizootic disease outbreak is substantial. Furthermore, actions taken by the governing bodies of this industry towards implementing short-sighted disease management regimes indicated that they have failed to accept the role of the social aspect of this social-ecological system. With at least three HPAI outbreaks within the ostrich system in the last 10 years, current management strategies are obviously inadequate for controlling the disease. This has implications for wild populations of birds in the region for two reasons. The first is that while the isolation of avian influenza from a wild bird was used as evidence that wild birds were acting as disease vectors, it is plausible for the infection to ‘spill-back’ into the wild system (Daszak et al. 2000). Southern Africa is globally recognized for its avian diversity (Sinclair et al. 2011) and has substantial connectivity to Europe though migrating birds (Gaidet et al. 2011). Should a highly virulent strain of avian influenza be introduced from a domestic ostrich to a rare or vulnerable wild species, or make its way through southern African wetlands to populations of Eurasian migrants, the consequences could be dire. The second implication for wild bird conservation emerges from the implication of wild birds in the HPAI epizootics in the ostrich industry and how resulting biases could lead to human wildlife conflict. Biosecurity measures taken by authorities heavily implicated wild birds as being the source of HPAI in the 2004 outbreak (Mathers & Marshall 2010). This could lead to farmers as poisoning or shooting ‘pest’ wild birds (as is currently the case for Egyptian Geese, *Alopochen aeqyptiaca*) with inevitable side-effects on other species in the area.

Chapter 3. Synthesis, Management Recommendations and Future Research

Synthesis

The network analysis conducted in this study indicates that the contact structure of the ostrich movement network within the Western Cape lends itself to vulnerability to disease outbreaks. The current ostrich production system fosters a large number of livestock movements annually, which provides a large potential for disease transmission. The scale-free nature of the network identified in this study highlight how the non-random structure of connections between farms has resulted in a system which can be quickly and easily traversed by a virulent pathogen. Though a high level of seasonality was observed in network size, the vulnerability of the network remained relatively consistent, though the scope of a potential epidemic was maximized in October and January. The influence of small number of hyper-connected farms, not only predisposes these farms to early disease transmission during a disease outbreak, but also greatly increases the scope of epizootics in the system. Additionally, analysis of network evolution over the past six years indicated that the movement network was becoming increasingly vulnerable to disease outbreak.

Management Recommendations

Network traits identified in this study can be used to inform on how changes in management protocols and production practices could greatly reduce the severity of disease epizootics within the Western Cape ostrich industry. The first recommendation involves reducing the influence of the hubs identified in this analysis. This can be achieved by controlling production levels of hubs, restricting the number of movements each farm is allowed each month, or separating the hubs in network space thereby creating neighborhoods within the network with higher proportions of local ‘neighbourhood’ movements and little interaction between neighborhoods. An additional strategy could involve partitioning hubs into subsections, essentially creating a number of entities which could function as independent farms. Implementing constraints on the movement of ostrich within these subsections could reduce transmission potential of disease within hubs. Contingency plans for detecting future outbreaks should focus on shutting down highly connected farms immediately due to their propensity to contract disease early in an epizootic, as well as their ability to directly infect a large proportion of the network.

This study also highlights how undertaking particular surveillance strategies will maximize the efficiency of sampling. Targeted surveillance of farms with high numbers of connections, such as hubs, will lead to early disease detection. Since these farms are so influential, it is the recommendation of this study these be included in every surveillance event. Additionally, surveillance efforts must be increased in months when the network size is the largest, such as in October and January.

The network evolution towards a more vulnerable system could possibly have been facilitated by the change of disease management strategies adopted in the region following an HPAI outbreak in 2004. The primary strategies currently focus on minimizing the contact between wild and domestic birds, while virtually disregarding the impact of ostrich movements. Not only does this create a large potential to exacerbate human wildlife conflict in the region, it is also disregarding a system which has proven to be the primary transmission pathway of disease in other systems (Kiss et al. 2006; Mather & Marshall 2010).

Future Research

The large amount of research conducted on the movement database of livestock in the U.K. highlights the diverse utility of a well recorded, detailed, long-term dataset (Kao et al. 2007). The database used for this study is similarly structured and detailed, creating a good opportunity for future study of the disease dynamics within the ostrich industry in the Western Cape.

Subsequent research efforts should initially focus on adding geographic information to the relational data. Information regarding farm proximity to other farms as well as landscape features (such as water bodies) could begin to provide information on the relative influence of different transmission pathways on epizootics in the region. An additional pathway which should be studied should incorporate other types of farm contact via interaction of humans, or movement of vehicles, equipment, feed or other goods or domestic species between farms. A study by Leibler et al. (2010) found that the movement of part time workers between farms contributing to significant increases in transmission risk. Additionally, the potential for disease spread via wild birds must also remain a consideration. There are large communities of birds which interact with ostriches within this system, particularly Egyptian Geese. Understanding how interactions between ostriches and wild birds may impact disease dynamics in both domestic and wild systems is of vital importance. Increased study of social interactions and testing for disease within wild populations would greatly improve our understanding of the dynamics of the disease and levels of interaction and transmission between wild and domestic populations. It would also be interesting to test whether seasonal or annual trends are common in both the domestic and wild systems, indicating possible peak seasons of vulnerability to spillover and disease outbreak. In addition, this system could greatly benefit from the use of molecular methods to track disease transmission between wild and domestic populations by identifying common strains as well as monitoring of the introduction of new strains introduced to the system.

Farm attributes considered in conjunction with this network could inform on specific farming practices which could dispose farms to higher disease vulnerability. These actions include farm type, stocking densities, chlorination of water troughs, feed quality and other factors which have been shown to affect ostrich health and reduce the incidence of disease (Mather & Marshall 2010). In addition, assessing more specific network properties of farms such as indegree and outdegree. Depending on the dominant degree, farms could be found to be superspreaders (sends out a large number of ostriches) or sentinel nodes (receives a large number of ostriches) and thereby adding a finer level of analysis. Finally, modeling and network simulations have proven extremely informative when considering disease dynamics in domestic systems, and could inform on the potential success of different management strategies.

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