## THESIS INTRODUCTION

TIM LUCAS. JANUARY 13, 2016

## 1. Abstract

ABSTRACT. Pathogens make up a huge proportion of global diversity and their role in disease strongly affects human disease, economics and development as well as having an important ecological role. However, the factors that control the number of pathogen species are poorly understood.

The patterns of contacts between individuals — in both human and animal populations — are nonrandom and depend on the density of individuals. Population structure and density have important epidemiological consequences, but their role in the control of pathogen richness is unknown.

It is still unknown whether population structure and density controls pathogen richness in bats. Furthermore, the specific mechanisms by which structure might influence pathogen richness have not been studied.

In this thesis I have studied how population structure and density control pathogen richness using bats as a case study. I have used epidemiological simulations and comparative analyses of data from wild bat populations to show that population structure does not have a strong affect on pathogen richness. Using further simulations I have shown that the interaction between population density and population structure is an important consideration. Finally, I have created a model for estimating bat densities — previously an incredibly challenging task — using acoustic data. Together, these studies clarify the relative roles of population density and structure and facilitate further study of population density in bats as a driver of pathogen richness.

While theory previously predicted that population structure should increase pathogen richness, the expectation in the ecological literature was that population structure would decrease pathogen richness. My studies support neither of these views, instead suggesting that population structure does not have a strong affect in either direction.

## 2. Introduction

The diversity of pathogens is huge and largely unknown (poulin2014parasite ). Recent large studies have found tens (Anthony et al. 2013) or even hundreds of virus species in a single host species (Anthony et al. 2015). This suggests the number of mammalian viruses globally is of the order of hundreds of thousands of virus species (Anthony et al. 2013) while only three thousand species of virus, across all host groups, are currently described (ICTV 2014). Recent large databases include nearly 2,000 pathogens from approximately 400 wild animal hosts (wardeh2015database). Given that there are nearly 4,000 named mammal species (wilson2005mammal), the undiscovered diversity of pathogens is likely huge.

This diversity of pathogens presents a risk to human health. 60% of newly emerged disease are zoonotic (acquired from animals) with wild animals being the predominant source (jones2008global; woolhouse2006host; taylor2001risk). Zoonotic diseases can be extremely virulent: viruses such as Nipah (luby2009recurrent), Ebola (lefebvre2014case) having case fatality rates over 50%. Furthermore these pathogens can have large economic costs (e.g. SARS is estimated to have cost \$40 billion (knobler2004learning)). In particular these impacts can have huge affects on developing economies. For example the 2014 ebola epidemic caused both Liberia and Guinea to fall from positive to negative per capita growth rates (ebolaWorldbank; ebola2015worldbank). In general we can expect competition between pathogens.

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Competition between pathogens can occur by different mechanisms: immunological mechanisms such as cross-immunity or shared immune respone (fenton2010applying) and ecological mechanisms such as removal of susceptable hosts by death (rohani2003ecological) or competition for internal host resources (griffiths2014analysis). Like ecological systems this competition leads us to expect competitive exclusions (bremermann1989competitive; martcheva2013competitive; ackleh2003competitive; ackleh2014robust; turner2002impact) so the diversity of parasites needs an explanation.

Surveillance of zoonotic diseases is crucial. In particular we want to categorise diseases before they spillover into humans (SARS was not identified until months into the pandemic for example (drosten2003identification)) and we want to anticipate outbreaks. If we know there is an increased number of infections in host species, increased numbers of a species that is a known reservoir of a high risk zoonotic disease, or increased contacts between humans and a pathogen reservoir, we can prepare for a potential outbreak in that area. However, funds for zoonotic surveillance are limited and so efforts must be optimised. Knowing which species are likely to have many pathogens allows us to sample and identify potentially zoonotic viruses efficiently. Many factors have been suggested in having a role in controlling pathogen richness including body mass (kamiya2014determines; arneberg2002host; poulin1995phylogeny), animal density (kamiya2014determines; nunn2003comparative; arneberg2002host) and species range size (kamiya2014determines; nunn2003comparative). This understanding provides a basis for predicting which species will have high pathogen richness and should be prioritised for sampling and surveillance.

In recent decades bats have been implicated in a number of high profile zoonotic outbreaks including Nipah (field2001natural), Ebola (leroy2005fruit), SARS (li2005bats) and Hendra (field2001natural). This has lead to much research on whether bats are a particular source of zoonotic disease (Luis et al. 2013; Olival et al. 2015; Wang et al. 2011) and examinations of factors, such as flight, social living and longevity, that might predispose them to being reservoires of zoonotic viruses (calisher2006bats; O'Shea et al. 2014; Dobson 2005). Given that bats are the second largest order of mammals (wilson2005mammal), we may expect them to be the source of many viruses simply through weight of numbers (Luis et al. 2013). The broad conclusions are that while bat do host more zoonotic viruses than other groups (Luis et al. 2013) they do not host more virus species in general (Olival et al. 2015). Questions remain as to why bat viruses have a tendancy to have such high zoonotic potential.

Define. Simple count of pathogens across whole species. Ignores heterogeneity in prevalence, across space and time.

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