

**THE ROLE OF POPULATION STRUCTURE IN PATHOGEN DIVERSITY IN WILD  
BAT POPULATIONS**

TIM LUCAS. DECEMBER 12, 2015

## 1. Abstract

1.0.1. *One or two sentences providing a basic introduction to the field.* It is still unclear what factors determine the number of pathogens a wild species carries. But once understood, these factors could provide a way to prioritise surveillance of wild populations for zoonotic disease.

1.0.2. *Two to three sentences of more detailed background.* The pattern of contacts between individuals (i.e. population structure) has long been known to strongly affect epidemic processes. Theory suggests that population structure can promote pathogen richness while the ecological literature generally assumes it will decrease richness. Previous studies in wild populations have had contradictory results and the different measures of population structure have different shortcomings.

1.0.3. *One sentence clearly stating the general problem (the gap).* Here I use comparative data to test whether population structure influences pathogen richness in bats as they have been associated with a number of important, recent zoonotic outbreaks. Unlike previous studies I use two measures of population structure: a novel measure, number of subspecies, and a more careful application of genetic measures which have been used previously.

1.0.4. *One sentence summarising the main result.* I find that both of these measures are associated with pathogen richness but with effects in opposite directions suggesting that population structure has no clear effect.

1.0.5. *Two or three sentences explaining what the main result reveals in direct comparison to what was thought to be the case previously.* The results conflict with each other and with other studies which suggests that tests of population structure are sensitive to the exact measurements and data used. Given the conflicting results in the literature and unclear results here, it seems likely that population structure does not strongly affect pathogen richness in bats.

1.0.6. *One or two sentences to put the results into a more general context.* The use of larger datasets and multiple measurements of population structure is therefore important to ensure the robustness of results. Given the weakness of any association between population structure and pathogen richness in bats, this is not a useful metric for prioritising zoonotic disease surveillance.

1.0.7. *Two or three sentences to provide a broader perspective,*

## 2. Introduction

**2.1. General Intro.** The number of pathogen species carried by a host species has important consequences for the ecology of the host and the probability that the host will be a reservoir of a zoonotic pathogen. However, the factors that affect pathogen richness are poorly understood.

### 2.2. Specific Intro.

**2.3. Theoretical background.** Single pathogen models show that increasing population structure simply slows disease spread and makes establishment less likely (). In the ecological literature this is often taken as predicting that increased population structure will decrease pathogen richness (). However, models of competition between multiple pathogens show that in unstructured populations a competitive exclusion process occurs but that splitting the population into two patches allows coexistence ().

**2.4. Previous Studies.** Three studies have used comparative data to test for an association between population structure and viral richness. A study on 15 African bats found a positive relationship between distribution fragmentation and viral richness (Maganga et al. 2014) while a study on 20 South-East Asian bats found the opposite relationship (Gay et al. 2014). A global study on 33 bats found a positive relationship between  $F_{ST}$  — a measure of genetic structure — and viral richness (Turmelle and Olival 2009). However, this study included measures using mtDNA which only measures female dispersal which may have biased the results many bat species show female philopatry (Kerth et al. 2002; Hulva et al. 2010). Furthermore, this study used measures of  $F_{ST}$  irrespective of the study scale with studies covering from tens (McCracken and Bradbury 1981) to thousands (Petit and Mayer 1999) of kilometers. As isolation by distance has been shown in a number of bat species (Burland et al. 1999; Hulva et al. 2010; O'Donnell et al. 2015; Vonhof et al. 2015) this could bias results further. Finally, when a global  $F_{ST}$  value is not given they use the mean of all pairwise  $F_{ST}$  between sites. It is not clear that this is correct as from global  $F_{ST}$  we expect migration rates of  $M = \frac{1-F_{ST}}{8F_{ST}}$  while from  $F_{ST}$  between pairs of populations we expect migration rates of  $M = \frac{1-F_{ST}}{8F_{ST}}$  where  $M$  is the absolute number of diploid individuals dispersing per generation (Slatkin 1995). As it is in fact the movement of individuals that is epidemiologically relevant, using these studies is probably not correct without attempting to correct for these difference.

Studies on single pathogens, notably rabies, have also shown that for virulent pathogens, space can allow persistence where a well mixed population could experience a single, large epidemic then pathogen extinction (**rabiespaper**; **colizza**; Pons-Salort et al. 2014).

### 2.5. Rates.

**2.6. Choice of measure of population structure.** A number of measurements of population structure have been used and each has its own shortcomings. In particular, the better, more direct measurements tend to be very work intensive which consequently means data is available for few species.

**2.6.1. Direct dispersal measurements.** The ideal measurement of population structure is direct measurement of dispersal rates and distance. These are incredibly difficult to obtain, especially over large scales. Due to white nose syndrome, some very large mark-recapture studies have been conducted, but recapture rates are low. Further, these large studies have been in species that live in a few large colonies, so recapture rates should be higher than in less social species.

2.6.2. *Genetic measures.* As direct measurement of dispersal are difficult, genetic data is often used. Measurement such as  $F_{ST}$  are used to calculate migration. There are strong model assumptions under the conversion from  $F_{ST}$  to migration. However, the main issue with this measure is the effort required for each study and the subsequent low number of measurements. Further, there are differences in the scales of the studies and the genetic regions being sequenced. This differences should not be ignored.

2.6.3. *Number of Subspecies.* For a population to evolve distinct phenotypic or genetic traits, such that they can be classed as a subspecies, there must be limited migration between populations. The number of subspecies a species has therefore reflects the level of population structure in that species. The value of this measurement is available for every bat species. However, it is likely biased, with well studied species being likely to have more recognised subspecies. Further, this is a very coarse measure and it is important to consider whether it is measuring migration at a timescale and rate that is epidemiologically relevant.

2.6.4. *Measures from range.* The final measurement that has been used is derived from the shape of the species' range, typically from IUCN (**iucn**) maps. The ratio between the perimeter of the range and the area (or similar values) are calculated. Range maps are very coarse for many species. Furthermore there is a potential bias with island living species being given sea based edges where continental species might be assumed to live everywhere in between locations where it is known to live, without considering the different terrestrial habitats in these areas.

2.7. **The gap.** There is a lack of studies using multiple measures of population structure and larger datasets to robustly estimate the importance of population structure. Furthermore, the

2.8. **What I did.** Here I use two measures of population structure — the number of subspecies and gene flow — to robustly test for an association between population structure and pathogen richness. Furthermore, I use a much larger dataset for one of these analyses, further promoting robustness of results.

2.9. **What I found.**

### 3. Methods

#### References

- Maganga, G. D. et al. (2014). "Bat distribution size or shape as determinant of viral richness in african bats". In: *PloS one* 9.6, e100172.
- Gay, N. et al. (2014). "Parasite and viral species richness of Southeast Asian bats: Fragmentation of area distribution matters". In: *International Journal for Parasitology: Parasites and Wildlife* 3.2, pp. 161–170. doi: [doi:10.1016/j.ijppaw.2014.06.003](https://doi.org/10.1016/j.ijppaw.2014.06.003).
- Turmelle, A. S. and K. J. Olival (2009). "Correlates of viral richness in bats (order Chiroptera)". In: *EcoHealth* 6.4, pp. 522–539.
- Kerth, G., F. Mayer, and E. Petit (2002). "Extreme sex-biased dispersal in the communally breeding, nonmigratory Bechstein's bat (*Myotis bechsteinii*)". In: *Molecular Ecology* 11.8, pp. 1491–1498.
- Hulva, P. et al. (2010). "Mechanisms of radiation in a bat group from the genus *Pipistrellus* inferred by phylogeography, demography and population genetics". In: *Molecular ecology* 19.24, pp. 5417–5431.
- McCracken, G. F. and J. W. Bradbury (1981). "Social organization and kinship in the polygynous bat *Phyllostomus hastatus*". In: *Behavioral Ecology and Sociobiology* 8.1, pp. 11–34.

- Petit, E. and F. Mayer (1999). “Male dispersal in the noctule bat (*Nyctalus noctula*): where are the limits?” In: *Proceedings of the Royal Society of London B: Biological Sciences* 266.1430, pp. 1717–1722.
- Burland, T. et al. (1999). “Population genetic structure and gene flow in a gleaning bat, *Plecotus auritus*”. In: *Proceedings of the Royal Society of London B: Biological Sciences* 266.1422, pp. 975–980.
- O’Donnell, C. F. et al. (2015). “Genetic diversity is maintained in the endangered New Zealand long-tailed bat (*Chalinolobus tuberculatus*) despite a closed social structure and regular population crashes”. In: *Conservation Genetics*, pp. 1–12.
- Vonhof, M. J., A. L. Russell, and C. M. Miller-Butterworth (2015). “Range-Wide Genetic Analysis of Little Brown Bat (*Myotis lucifugus*) Populations: Estimating the Risk of Spread of White-Nose Syndrome”. In: *PloS one* 10.7.
- Slatkin, M. (1995). “A measure of population subdivision based on microsatellite allele frequencies.” In: *Genetics* 139.1, pp. 457–462.
- Pons-Salort, M. et al. (2014). “Insights into persistence mechanisms of a zoonotic virus in bat colonies using a multispecies metapopulation model”. In: *PloS one* 9.4, e95610.
- Luis, A. D. et al. (2013). “A comparison of bats and rodents as reservoirs of zoonotic viruses: are bats special?” In: *Proceedings of the Royal Society B: Biological Sciences* 280.1756, p. 20122753.
- ICTV (2014). *International Committee on Taxonomy of Viruses Master Species List*. url: [http://talk.ictvonline.org/files/ictv\\_documents/m/msl/5208/download.aspx](http://talk.ictvonline.org/files/ictv_documents/m/msl/5208/download.aspx).
- Wilson, D. E. and D. M. Reeder (2005). *Mammal species of the world: a taxonomic and geographic reference*. Vol. 12. JHU Press.
- Integrated Taxonomic Information System (ITIS)*. <http://www.itis.gov>.
- Chamberlain, S. A. and E. Szöcs (2013). “taxize: taxonomic search and retrieval in R”. In: *F1000Research* 2.
- Wickham, H. (2015). *rvest: Easily Harvest (Scrape) Web Pages*. R package version 0.2.0. url: <http://CRAN.R-project.org/package=rvest>.
- Jones, K. E., J. Bielby, et al. (2009). “PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090-184”. In: *Ecology* 90.9, pp. 2648–2648.
- Canals, M. et al. (2005). “Relative size of hearts and lungs of small bats”. In: *Acta Chiropterologica* 7.1, pp. 65–72.
- Arita, H. T. (1993). “Rarity in Neotropical bats: correlations with phylogeny, diet, and body mass”. In: *Ecological Applications*, pp. 506–517.
- López-Baucells, A. et al. (2014). “Echolocation of the big red bat *Lasiurus egregius* (Chiroptera: Vespertilionidae) and first record from the Central Brazilian Amazon”. In: *Studies on Neotropical Fauna and Environment* 49.1, pp. 18–25.
- Orr, T. J. and M. Zuk (2013). “Does delayed fertilization facilitate sperm competition in bats?” In: *Behavioral Ecology and Sociobiology* 67.12, pp. 1903–1913.
- Lim, B. K. and M. D. Engstrom (2001). “Bat community structure at Iwokrama forest, Guyana”. In: *Journal of Tropical Ecology* 17.05, pp. 647–665.
- Aldridge, H. (1987). “Turning flight of bats”. In: *Journal of Experimental Biology* 128.1, pp. 419–425.
- Ma, J. et al. (2003). “Dietary analysis confirms that Rickett’s big-footed bat (*Myotis ricketti*) is a piscivore”. In: *Journal of Zoology* 261.03, pp. 245–248.
- Owen, S. F. et al. (2003). “Home-range size and habitat used by the northern myotis (*Myotis septentrionalis*)”. In: *The American midland naturalist* 150.2, pp. 352–359.

- Henderson, L. E. and H. G. Broders (2008). “Movements and resource selection of the Northern Long-Eared Myotis (*Myotis septentrionalis*) in a forest-agriculture landscape”. In: *Journal of Mammalogy* 89.4, pp. 952–963.
- Heaney, L. R. et al. (2012). “*Nyctalus plancyi* and *Falsistrellus petersi* (Chiroptera: Vespertilionidae) from northern Luzon, Philippines: ecology, phylogeny, and biogeographic implications”. In: *Acta Chiropterologica* 14.2, pp. 265–278.
- Oleksy, R., P. A. Racey, and G. Jones (2015). “High-resolution GPS tracking reveals habitat selection and the potential for long-distance seed dispersal by Madagascan flying foxes *Pteropus rufus*”. In: *Global Ecology and Conservation* 3, pp. 678–692.
- Zhang, L. et al. (2009). “Recent surveys of bats (Mammalia: Chiroptera) from China. I. Rhinolophidae and Hipposideridae”. In: *Acta Chiropterologica* 11.1, pp. 71–88.
- Fritz, S. A., O. R. Bininda-Emonds, and A. Purvis (2009). “Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics”. In: *Ecology letters* 12.6, pp. 538–549.
- Bininda-Emonds, O. R. et al. (2007). “The delayed rise of present-day mammals”. In: *Nature* 446.7135, pp. 507–512.
- Paradis, E., J. Claude, and K. Strimmer (2004). “APE: analyses of phylogenetics and evolution in R language”. In: *Bioinformatics* 20, pp. 289–290.
- Revell, L. J. (2012). “phytools: An R package for phylogenetic comparative biology (and other things)”. In: *Methods in Ecology and Evolution* 3, pp. 217–223.
- Burnham, K. P. and D. R. Anderson (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. Springer Science & Business Media.
- Whittingham, M. J., R. D. Swetnam, et al. (2005). “Habitat selection by yellowhammers *Emberiza citrinella* on lowland farmland at two spatial scales: implications for conservation management”. In: *Journal of applied ecology* 42.2, pp. 270–280.
- Whittingham, M. J., P. A. Stephens, et al. (2006). “Why do we still use stepwise modelling in ecology and behaviour?” In: *Journal of animal ecology* 75.5, pp. 1182–1189.
- Pinheiro, J. et al. (2015). *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-122. url: <http://CRAN.R-project.org/package=nlme>.
- Revell, L. J. (2010). “Phylogenetic signal and linear regression on species data”. In: *Methods in Ecology and Evolution* 1.4, pp. 319–329.
- Wickham, H. (2009). *ggplot2: elegant graphics for data analysis*. Springer New York. isbn: 978-0-387-98140-6. url: <http://had.co.nz/ggplot2/book>.
- Lucas, T. (2015). *palettetown: Use Pokemon Inspired Colour Palettes*. R package version 0.1.0. url: <http://CRAN.R-project.org/package=palettetown>.
- Solt, F. and Y. Hu (2015). *dotwhisker: Dot-and-Whisker Plots of Regression Coefficients from Tidy Data Frames*. Available at The Comprehensive R Archive Network (CRAN). url: <http://CRAN.R-project.org/package=dotwhisker>.
- Yu, G. (2015). “ggtree: an R package for versatile annotation and visualization of phylogenetic tree”. In:
- Jones, K. E., O. R. Bininda-Emonds, and J. L. Gittleman (2005). “Bats, clocks, and rocks: diversification patterns in Chiroptera”. In: *Evolution* 59.10, pp. 2243–2255.