

# A Literature Review of the Function of Bats as Disease Vectors Across Fragmented Habitats

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## Abstract

All mammals, including humans, live in an increasingly fragmented habitat. Fragmented habitats are linked to increased concentration of animals, thus, disease. Bats are the most significant vector of disease transmission to humans and other mammals. They are also the second most abundant mammalian group, comprising over 1200 species and inhabiting all land masses aside from Antarctica and some assorted islands. While our understanding of how bats exhibit low virulence while remaining a significant vector is limited, it has been significantly expanded through recent research. Preliminary results show that the deadliest mechanisms of disease transmission evolved alongside these animals' ability to fly. Namely their ability to manage high viral loads but remain asymptomatic. Initial research suggests that bats' viral load increases when combined with fragmentation. Further research is needed to definitively state what mechanisms make bats superior vectors and how fragmentation may continue to affect disease spread across landscapes. A review of the current literature is needed to guide future research. Through this review, I will link the issues of disease across fragmented habitats, bats as superior disease vectors, and bats' increased ability to transmit disease over great distances. The purpose of this review is to provide necessary context for continued research.

## Introduction

Bats belong to the second largest family among mammals (Chiroptera), comprising 20% of mammalian species. They have incredible physical and ecological diversity, with predators eating insects, fish, and other bats, scavengers eating fruit and parasites sucking the blood of sleeping animals. They are widespread, inhabiting all continents besides Antarctica, and can live among a wide variety of habitats, such as forested regions in high latitudes and tropical regions of low latitudes. Throughout these ranges, bats have significant ecological and economic roles in the ecosystem, including pollination, seed dispersal,

and insect control (O'shea and Clark Jr. 2002). However, bats can cause potential health threats for other mammals, including humans, due to their ability to harbor and spread deadly diseases. Although the mechanisms by which they transmit disease are contested, most researchers agree that infected bats can be problematic for other mammalian species (Hanadhita et al. 2017, O'Shea et al. 2014).

This paper will address the hypothesized mechanisms that allow bats to be effective carriers of disease while also examining how they as a group contribute to the spread of diseases within and across fragmented habitats.

For this review, a fragmented landscape is defined as a landscape that has limited connectivity between high-quality habitat patches. This subject is particularly important as diseases harbored by bats can affect nearly all mammalian species, not only the ones specifically examined here (Alexander et al. 2018). Bats are also linked to a multitude of highly lethal disease outbreaks affecting numerous mammalian species worldwide (Wang et al. 2011).

### **Mammals in increasingly fragmented environments**

Humans, like all mammals, live in an increasingly fragmented landscape. Fragmentation has three major components: loss of original habitat; decrease in habitat patch size; increased isolation of habitat patches. Plainly stated, fragmentation occurs when preferred habitat is destroyed, decreased, and separated from other patches of preferred habitat. There are a variety of causes of fragmentation, nearly all of which are anthropogenic, such as deforestation for the purpose of logging and agriculture (Andrén 1994). Fragmentation is linked to negative effects on mammalian population dynamics; namely, the phenomenon that increased habitat fragmentation leads to small habitat patches that need to support higher concentrations of animals. Within high-quality patches, especially those that are highly isolated, animals are not able to disperse across the landscape. As diseases are brought into these patches by vectors such as bats, close inter- and intraspecies interactions through foraging, mating, and fighting result in rampant disease transmission (Seltmann et al. 2017).

Numerous researchers have theorized that bats can adapt to habitat fragmentation more

easily than other mammalian species due to their ability to fly, especially if fragmentation comes with increased urbanization (Hanadhita et al. 2017). This is contested by Gorresen and Willig's 2004 paper which found that the highest level of bat diversity existed in moderately deforested habitats that maintained some remnant habitat patches. However, this study focused only on one family of bats, Phyllostomidae, so the results cannot be generalized for all species across the world. Some bat species, specifically the insectivores, will choose urbanized environments over surrounding habitats to forage and roost, although the fine-scale habitat preferences are still not fully understood (Gehrt and Chelsvig. 2003). Densely urban environments can mimic high-quality habitat attributes, such as roost sites within and among buildings, ample foraging sites where light pollution attracts a variety of insects, and connectivity between necessary landing and takeoff sites (i.e., buildings and other structures). It is also important to note that urban environments are linked to increased disease prevalence and transmission (Avila-Flores and Fenton. 2005) and the bats' ability to travel from one highly isolated patch to another only increases this risk. This intersection of urbanization, fragmentation, and high viral loads results in potentially catastrophic effects on the health of other mammals.

### **Bats as superior disease reservoirs**

Bats are a reservoir of infectious diseases, many of which are highly lethal to humans and other mammals, such as rabies (Kuzmin et al. 2012), coronavirus and astrovirus (Seltmann et al. 2017), Ebola (Leroy et al. 2005), etc. The combination of low virulence paired with bat and viral biological diversities could have deadly results.

As the only true flying mammals, bats can travel hundreds of miles carrying a high viral load, interacting with countless other mammals, and increasing the spread of disease. Although it is well-documented that bats have a superior ability to harbor and spread diseases, the mechanisms for this are still not well-understood (Hanadhita et al. 2017). It is highly likely that bats' ability to retain low virulence while carrying a high viral load evolved through multiple mechanisms over millions of years.

#### *Disease load as a function of geographic extent*

Some researchers suggest that the number of bat species explains the seemingly disproportionate viral loads that they harbor. The Chiroptera family contains over 1200 species, comprising 20% of all mammal species, so this widespread presence may explain their virulence. However, rodents populate 40% of mammalian species, so if this were the case, we would see considerably higher viral loads in rodents, but we do not. Bats act as hosts to more diseases than rodents, with only half the number of species (Luis et al. 2013). Wang et al. (2011) reported that at a single location, 10-50% of bats were infected with coronavirus, astrovirus, or both. Comparatively, none of the rats at this site were infected with coronavirus and only 1.6% were infected with astrovirus. In addition, analyses of the coronaviruses affecting other mammals showed that many of these viruses shared a common ancestor with the coronaviruses infecting bats, suggesting that bats were the source from which many coronaviruses evolved (Wang et al. 2011). Coronavirus, astrovirus, and many other viruses that bats harbor are RNA viruses, which allows

for rapid evolution through high rates of replication, mutations, and recombination (Hanadhita et al. 2017). These virus types offer some explanation as to how bats may be responsible for the spread of disease but provides little-to-no explanation as to how bats harbor high disease loads while remaining asymptomatic.

#### *Disease load as a function of flight and roost behavior*

Bats are unique in that they are the only mammal that exhibits true sustained flight. Adaptations that either evolved with flight or as a consequence of flight have shown promising links that enable a high viral load. During flight, a bat's metabolic rate can increase up to 16 times that of a bat at rest. In contrast, a bird in flight will only increase their rate by two. This increase in metabolic rate is coupled with a rise in core body temperature, or fever (O'Shea et al. 2014). In mammals, fever typically functions as a response to an infection to kill or reduce viral load in the body (Hasday et al. 2000). On average, when experiencing a fever, a mammal's core body temperature will rise to 38-41°C. This increase in body temperature is linked to a variety of immunoresponses such as increased production of antibodies, increased destruction of bacteria within cells, and increased bacterial-killing effects of antimicrobials (O'Shea et al. 2014). This biological process is highly advantageous for bats. Of the bat species that have had their core temperature sampled during sustained flight, nearly all of them exhibited temperatures in the 38°C-41°C range (O'Shea et al. 2014). Thus, these daily fevers are likely integral in bats' ability to carry a high viral load without high virulence. As these fever cycles

are daily when not in hibernation, it is distinctly possible that the short-term fever dramatically reduces the viral load but does not wholly diminish it. Once the bat returns to roost and its metabolism slows, the remaining viruses multiply and mutate within the body. This effect has the potential to be exacerbated by extended hibernation events, where bats have low metabolic and immunoresponse rates for an extended period, allowing diseases to proliferate within the body and spread between hibernating bats (Saltmann et al. 2017). In addition, it is possible that bats' initial response to infectious agents varies from that of other mammals. Zhang et al. (2013) suggested that bats' immunoresponse characteristics evolved alongside flight, and that the loss of specific genes that regulate detection of pathogenic microorganisms may be linked to their inability to extinguish pathogens fully. In general, this loss is not harmful, as the bat can manage virulence through daily metabolic spikes, but it provides further explanation as to the persistence of infection in bat species.

### **How bats act as disease vectors**

Bats carrying high viral loads continue to engage in natural behaviors such as hunting, foraging, mating, and roosting. Many mechanisms of disease transmission have been studied extensively, and the links between bats, intermediate hosts, and other mammals are compelling. In cave-roosting bats, multiple species may choose to inhabit the same cave, which is a common method of disease transmission (Saltmann et al. 2017). Caves provide a landscape similar to that of fragmentation, where high animal populations inhabit a relatively small and isolated habitat. Bats that exhibit high viral loads but low virulence remain in close contact with other bats in their

colony, and so can spread disease both within and among species (Saltmann et al. 2017). In addition, there is evidence that other mammals travelling along cave floors can contract diseases harbored by bats through contact with their infected urine and feces on the cave floor (Hanadhita et al. 2017).

Frugivorous, fruit-eating, and insectivorous, insect-eating, bats in the Rhinolophidae family both exhibit a pattern of eating that has been linked to the spread of disease. These species partially ingest their food, extracting easy to digest nutrients, and then discard the harder-to-digest portions, such as fruit pits (Dobson 2005). Through this process, the discarded pieces become saturated with bat saliva, and in turn any pathogens the bat may be harboring. Intermediate hosts, such as livestock, ingest the discarded portions and become infected with these pathogens. Once infected, they quickly become symptomatic and spread pathogens to other livestock and, potentially, humans. An outbreak of Nipah virus in humans was linked to a pig farm in Malaysia, where pigs had eaten discarded fig pits, contracted Nipah virus, and spread it to human hosts (Dobson 2005). In Bangladesh, Nipah virus has infected humans without an intermediate host. During the fruiting season, children climb trees to collect ripe fruit to sell in their villages. Fruit that has been chewed on by bats is sold to salespeople who mash it into a pulp and produce a drink that they then transport on foot to neighboring villages. Nipah virus outbreaks follow the exact routes taken by these salespeople (Dobson 2005). This effect is mirrored in seasonal disease outbreaks in primates. When trees undergo mast seeding events, where fruit production is significantly increased, primates tend to sit beneath trees and eat fruit that has fallen to the ground, which is interspersed with discarded pits from fruit bats. Disease outbreaks in primates are highly correlated with these mast seeding events, further supporting this

mechanism of disease transmission (Dobson 2005).

### **Bats as disease vectors across landscapes**

The bats' ability of true flight allows for the most obvious mechanism of disease spread. Bats can disperse across the landscape with little-to-no restrictions, up to hundreds of miles from their roosting sites (Hanadhita et al. 2017). This dispersal creates a major opportunity for bats to spread disease both directly and indirectly to other mammalian species across a wide geographic range (Wang et al. 2011). This is potentially exacerbated by the increased fragmentation and habitat loss of the landscapes primarily used by bats (Seltmann et al. 2017). Seltmann et al. (2017) sought to show a correlation between fragmented landscapes and increased coronavirus and astrovirus on the landscape. While their primary results showed that these viruses are distributed evenly across the landscape, they were able to discern that in fragmented habitats, bats infected with one virus were highly likely to be infected with the other, suggesting that fragments may harbor a higher overall viral load. Seltmann et al. (2017) found that bats in disturbed forest patches, experiencing either fragmentation or habitat loss, had a reduced body condition, or body mass, when compared to those living in undisturbed patches. They also found that bats from forest fragments showed higher signs of chronic stress compared to those in undisturbed habitats. Reduced body condition and chronic stress are correlated with increased susceptibility to disease (Seltmann et al. 2017), so bats experiencing the stress of habitat loss and potential relocation may carry additional pathogens. Research on bats to investigate parasite and disease loads in habitat fragments is lacking, however Mbona and McPeck (2009) found that prevalence and richness of

parasites in two species of monkeys was higher in fragmented landscapes when compared to primates in undisturbed habitats. They also found that richness and prevalence was significantly linked to attributes associated with human disturbance, suggesting that fragmentation and habitat loss is a driver for increased disease prevalence in some animals. Countless studies have shown that landscapes are becoming increasingly fragmented, habitat patches are decreasing in size, and undisturbed patches are disappearing (Andr n 1994). As landscapes become more fragmented, it is probable that diseases will concentrate within these fragments, creating additional challenges for the animals living within them.

### **Conclusion**

Bats are the most prevalent carriers of disease. Their ability to inhabit a variety of geographical landscapes and occupy nearly all predatory niches while harboring these diseases has the potential to be catastrophic to other mammalian species. Through flight, they can spread disease across landscapes that are unable to be traversed by terrestrial mammals, potentially infecting isolated patches of animals. By using novel metabolic processes, bats can maintain high concentrations of pathogens in their bodies while remaining asymptomatic. Our understanding of their reduced display of symptoms while remaining a disease vector is limited, though recent research has significantly expanded this, suggesting a combination of metabolic processes and evolution. Further research that examines the effects of fragmentation is still much needed, but preliminary results show that habitat patches have the potential to increase the viral load of Chiropteran species by allowing increased contact between infected species, thus resulting in more severe disease outbreaks. Future researchers should continue to focus on the effects that increased fragmentation

and habitat loss have on increased disease prevalence and spread, with special attention paid to bats, as they have a demonstrated ability to transfer these diseases.



## Literature Cited

- Alexander, K. A., C. J. Carlson, B. L. Lewis, W. M. Getz, M. V. Marathe, S. G. Eubank, C. E. Sanderson, J. K. Blackburn. 2018. The Ecology of Pathogen Spillover and Disease Emergence at the Human-Wildlife-Environment Interface. *Advances in Environmental Microbiology: The Connections Between Ecology and Infectious Disease*:67–298.
- Andrén, H. 1994. Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat: A Review. *Oikos* 71(3):355–366.
- Avila-Flores, R., M. B. Fenton. 2005. Use of Spatial Features by Foraging Insectivorous Bats in a Large Urban Landscape. *Journal of Mammalogy* 86(6):1193–1204.
- Dobson, A.P. 2005. What links bats to emerging infectious diseases? *Science* 310(5748):628-629.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual review of ecology, evolution, and systematics*. 34(1):487-515.
- Gehrt, S. D., J.E. Chelsvig. 2003. Bat activity in an urban landscape: patterns at the landscape and microhabitat scale. *Ecological Applications* 13:939–950.
- Gibbons, R.V. 2002. Cryptogenic rabies, bats, and the question of aerosol transmission. *Annals of Emergency Medicine* 39(5):528-536.
- Gorresen, P.M., M.R. Willig. 2004. Landscape Responses of Bats to Habitat Fragmentation in Atlantic Forest of Paraguay. *Journal of Mammalogy*. 85(4):688–697.
- Hanadhita D., A.S. Satyaningtijas, S.A. Priyono. Bats as A Viral Reservoir: A Short Review of Their Ecological Characters and Immune System. 1st International Conference in One Health.
- Hasday, J. D., K. D. Fairchild, C. Shanholtz. 2000. The role of fever in the infected host. *Microbes Infect* 2(15):1891-904.

- Kuzmin, I.V., M. Shi, L.A. Orciari, P.A. Yager, A. Velasco-Villa, N. A. Kuzmina, D. G. Streicker, D. L. Bergman, C. E. Rupprecht. 2012. Molecular inferences suggest multiple host shifts of rabies viruses from bats to mesocarnivores in Arizona during 2001–2009. *PLoS Pathogens*.
- Leroy, E.M., B. Kumulungui, X. Pourrut, P. Rouquet, A. Hassanin, P. Yaba, A. Délicat, J. T. Paweska, J.P. Gonzalez, and R. Swanepoel. 2005. Fruit bats as reservoirs of Ebola virus. *Nature* 438(7068):575.
- Luis, A. D., D. T. Hayman, T. J. O'Shea, P. M. Cryan, A. T. Gilbert, J. R. Pulliam, J. N. Mills, M. E. Timonin, C. K. Willis, A. A. Cunningham, A. R. Fooks. 2013. A comparison of bats and rodents as reservoirs of zoonotic viruses: Are bats special? *Proceedings of the Royal Society* 280(1756):20122753.
- Mbora, D.N., M.A. McPeck. 2009. Host density and human activities mediate increased parasite prevalence and richness in primates threatened by habitat loss and fragmentation. *Journal of Animal Ecology*. 78(1):210-8.
- O'Shea, T. J., D. R. Clark Jr. 2002. An overview of contaminants and bats, with special reference to insecticides and the Indiana bat. *The Indiana bat: biology and management of an endangered species*. *Bat Conservation International*:237-253.
- Seltmann, A., V. M. Corman, A. Rasche, C. Drosten, G. Á. Czirják, H. Bernard, M. J. Struebig, C. C. Voigt. 2017. Seasonal Fluctuations of Astrovirus, But Not Coronavirus Shedding in Bats Inhabiting Human-Modified Tropical Forests. *EcoHealth* 14(2):272-284.
- Seltmann, A., G. Á. Czirják, A. Courtiol, H. Bernard, M. J. Struebig, C. C. Voigt. 2017. Habitat disturbance results in chronic stress and impaired health status in forest-dwelling paleotropical bats. *Conservation physiology* 5(1).



Wang, L.F., P. J. Walker, L. L. Poon. 2011. Mass extinctions, biodiversity, and mitochondrial function: are bats 'special' as reservoirs for emerging viruses? *Current Opinion in Virology* 1(6):649-57.

Zhang, G., C. Cowled, Z. Sh, Z. Huang, K. A. Bishop-Lilly, X. Fang, J. W. Wynne, Z. Xiong, M. L. Baker, W. Zhao, M. Tachedjian. 2013. Comparative analysis of bat genomes provides insight into the evolution of flight and immunity. *Science* 339(6118):456-460.