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Human-bat Interactions in a Disease Emergence Hotspot: Implications for Human Health and
Bat Conservation

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in Biology

by

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December 2023
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ABSTRACT

Bats are an ecologically important taxon that can host zoonotic pathogens. Globally, many bat species are synanthropic and live closely with humans, often roosting in man-made structures. The spatial overlap between humans and bats creates opportunities for human-bat contact, which can lead to human exposure to bat-borne pathogens and conflicts that cause bat mortality. Despite this risk, little is known about the drivers and characteristics of these human-bat interactions in buildings and work is needed to understand this aspect of the wildlife-urban interface.

In Chapter I, I present a literature review that identifies the geographic and taxonomic trends in reported interactions between wildlife, humans, and domestic animals in areas of land-use change. From 529 included articles, I found that reports of human-wildlife interactions are greatest in areas of Africa, Asia, and South America undergoing agriculturalization. Additionally, I saw high reporting of indirect human interactions with birds and mammals in Europe. Interactions with mammals were reported most often, however important gaps in knowledge were identified, including human-bat interactions in areas of land-use change.

In Chapter II, I conducted a study to identify building features that attract and repel bats in a rural region of southeastern Kenya. I surveyed 257 buildings, both used and unused by bats, to identify roost selection parameters. Bats selected taller cement-walled buildings with higher water vapor pressure and lower presence of permanent human occupants. However, roost selection criteria differed across the most common bat species: molossids, selected structures consistent with these same overall attributes whereas *Cardioderma cor* selected buildings with lower presence of permanent human occupants. My results show that roost selection of

synanthropic bat species is based on specific buildings attributes, which, when altered, may reduce bat use of these structures and subsequent opportunities for human-bat interactions.

In Chapter III, I present a human behavior study to characterize and quantify human-bat interactions in buildings. To this end, I surveyed 102 people living and working in buildings used by bats in rural Kenya. Bats usually occupied buildings for at least 5-10 years, during which human and domestic animal contact with bats was common. People frequently mentioned the presence of dead bats, often because of lethal removal efforts. These interactions support pathways that could expose humans to bat-borne pathogens. Measures to prevent human-bat interactions, such as adjusting building attributes, can reduce these contacts, subsequently reducing opportunities for human exposure to pathogens and bat mortality.

In Chapter IV, I present the results of a pathogen screening study to identify paramyxoviruses in synanthropic bats using human buildings in rural Kenya. Of the 297 samples screened, 4.04% were positive for a jeilongvirus, with 4.43% prevalence in *Mops condylurus* and 3.95% prevalence in *Mops pumilus*. Positive samples were collected at multiple sites and time points, suggesting that this virus may be endemic to this system. This jeilongvirus is present at the wildlife-urban interface, where humans may be exposed to it; however, the zoonotic potential of this virus is unknown, although it is related to viruses that cause severe human disease.

ACKNOWLEDGEMENTS

Much of the data for this dissertation was collected from the homelands of the Taita people in southeastern Kenya. I am indebted to the community and the land for allowing me to collect this data that will benefit myself, the Taita people, and the bats of Taita-Taveta county. Specifically, I wish to thank Benson Lombo, Peter Mwasi, Darius Kimuzi, Miltone Kimori, Ken Gicheru, Jonathan Mbinga, and Phenna Flavour for their assistance and friendship during my time in Taita. Peter and Ben, I am especially appreciative of your time, knowledge, patience, and passion for wildlife conservation over the last few years. Chawucha sana.

So many people have helped me in this process. First, I would like to thank my advisor, Kristian Forbes, for all his guidance during my degree. Kris, I am incredibly grateful for all the time and effort you have spent helping me become a better researcher and scientific writer, which has been one of the most rewarding parts of this process. I would also like to thank our Kenya bat project team, including Tamika Lunn, Paul Webala, Joseph Ogola, Tarja Sironen, Essi Korhonen, Lauri Kareinen, Simo Miettinen, Moses Masika, and Ruut Uusitalo. Tamika, I am so appreciative of the time and effort you put in to helping me gain confidence in my statistical analysis abilities and for working with me to craft the narratives in the chapters of this dissertation. Paul, I am so grateful to you for all your knowledge about Kenyan bats, their conservation, and your insight into conducting fieldwork with Kenyan communities. Joseph, your way with people and helping spread our message of bat conservation is inspiring and I am so glad to have had your help through this process. And to Tarja and the University of Helsinki team, thank you for the times in the field and for your guidance and assistance with lab work in Helsinki.

I am incredibly appreciative of my friends and colleagues at the University of Arkansas. The community at the University of Arkansas has been so supportive, and I am so thankful for the support and friendship of Nathaniel Mull, Ellery Lassiter, Elliot Lassiter, John Veon, Leah Bayer, Mike Shaw, Isabella DeAnglis, Brent Newman, and Sarah Chewning. I am also grateful for the help from my committee members, Don Catanzaro, Brett DeGregorio, and, again, Tarja Sironen. Additionally, I appreciate the financial support from the University of Arkansas' Sturgis International Fellowship that partially supported my time in Kenya and Finland.

The people from the University of Tennessee helped get me to this point, and I am still incredibly thankful for their continued guidance, friendship, and support. Namely, Riley Bernard, Devin Jones, Mallory Tate, and Emma Willcox – I am so lucky to have all your help and support for so many years now.

Lastly, I want to thank my partner, Gabriel Gutierrez, for his support during this whole process and being so cool while I was in Kenya and Finland for so long. I'd also like to thank my mom, Keri Jackson, and my friends Kelsey Trisler, Margaret O'Leary, and Carson Lillard for a steady stream of adventures to help me stay motivated and take a break. Of course, my dog, Juno, is amazing and has been the absolute best support anyone could have.

TABLE OF CONTENTS

INTRODUCTION	1
LITERATURE CITED	5
CHAPTER I: GLOBAL PATTERNS OF REPORTED HUMAN-WILDLIFE INTERACTIONS IN AREAS OF LAND-USE CHANGE	8
ABSTRACT	9
INTRODUCTION.....	10
METHODS.....	12
RESULTS.....	14
DISCUSSION	16
REFERENCES.....	19
TABLES	25
FIGURES	26
APPENDIX	31
CHAPTER II: ROOST SELECTION BY SYNANTHROPIC BATS IN RURAL KENYA AND IMPLICATIONS FOR HUMAN-WILDLIFE CONFLICT.....	86
ABSTRACT	87
INTRODUCTION.....	87
METHODS.....	90

STUDY AREA.....	90
DATA COLLECTION.....	91
STATISTICAL ANALYSES.....	93
RESULTS.....	95
BUILDINGS USED BY ANY BAT SPECIES	95
BUILDINGS USED BY MOLOSSID BATS.....	96
BUILDINGS USED BY CARDIODERMA COR	96
DISCUSSION	97
REFERENCES	100
TABLES.....	107
FIGURES	109
APPENDIX	114
CHAPTER III: BUILDINGS PROMOTE FREQUENT AND INTENSE CONTACT	
BETWEEN HUMANS AND BATS IN RURAL KENYA	122
ABSTRACT	123
INTRODUCTION.....	123
METHODS.....	125
RESULTS.....	127
DISCUSSION	129
REFERENCES	131

TABLES.....	136
FIGURES	137
APPENDIX	139
CHAPTER IV: IDENTIFICATION OF PARAMYXOVIRUSES IN SYNANTHROPIC FREE- TAILED BATS IN KENYA.....	
ABSTRACT	144
INTRODUCTION.....	144
METHODS.....	146
RESULTS.....	148
DISCUSSION	148
REFERENCES.....	150
TABLES.....	154
FIGURES	155
APPENDIX	156
CONCLUSION.....	157
LITERATURE CITED	160
APPENDIX.....	163

LIST OF PUBLISHED PAPERS

- Jackson, R.T., Lunn, T.J., Mull, N., McClung, M.R., & Forbes, K.M. Global patterns of reported human-wildlife interactions in areas of land-use change. *Prepared for submission to People and Nature* (CHAPTER I)
- Jackson, R.T., Webala, P.W., Ogola, J.G., Lunn, T.L., & Forbes, K.F. (2023) Roost selection by synanthropic bats in rural Kenya and implications for human-wildlife conflict. *Royal Society Open Science* 10(9): 230578. (CHAPTER II)
- Jackson, R.T., Lunn, T.J., DeAnglis, I.K., Ogola, J.G., Webala, P.W., & Forbes, K.M. Buildings promote frequent and intense contact between humans and bats in rural Kenya. *In review at PLOS Neglected Tropical Diseases* (CHAPTER III)
- Jackson, R., Pulkkinen, E., Lunn, T., DeAnglis, I., Erdin, M., Jasskelainen, A., Uusitalo, R., Masika, M.M., Miettinen, S., Korhonen, E., Webala, P., Ogola, J., Sironen, T., & Forbes, K. Identification of paramyxoviruses in synanthropic free-tailed bats in Kenya. *Prepared for submission to Journal of Virology* (CHAPTER IV)

INTRODUCTION

Emerging infectious diseases are a major concern given their potential impacts on human health, society, and economies (Morens and Fauci 2013). Many of the pathogens causing these diseases have spilled over into people from animals, including many wildlife species (Jones et al. 2008). However, the risk of emergence of these zoonotic pathogens is spatially aggregated around the world (Allen et al. 2017). High-risk regions are partially determined by high levels of mammalian diversity, land-use changes, and growing human populations (Han et al. 2016, Allen et al. 2017, Olival et al. 2017). When viewed holistically, these characteristics often define the likelihood of a human contacting wild animals, some of which may carry zoonoses.

Human exposure to parasites is one of the necessary steps in zoonotic pathogen spillover, and these exposure opportunities can stem from humans and our domestic animals contacting wildlife (Plowright et al. 2017). Areas with growing human populations often change landscapes to accommodate their needs, and these land-use changes can alter the composition, behavior, and distribution of wildlife species (Plowright et al. 2021). These changes can ultimately lead to increased contact and conflict between humans and wildlife, especially as humans encroach on wildlife habitat and as wildlife enter anthropogenic spaces after habitat loss (Soulsbury and White 2015). Wildlife may also be stressed by such land-use changes, which can alter infection dynamics within hosts and increase rates of pathogen shedding (Eby et al. 2023). Wildlife using human-dominated habitats are often generalist species that can cope with urbanization, and their presence can increase pathogen prevalence in areas simultaneously occupied by humans (Schmidt and Ostfeld 2001, Reusken and Heymann 2013, Hough 2014, Hassell et al. 2017).

Bats are a highly diverse and ecologically important taxon that use a variety of ecosystems across the globe. With almost 1,500 species, they are the second most species-rich mammalian taxon, with many species that regularly interact with one another and with humans

(Geiselman & Younger 2020, Simmons & Ciranello 2023). Interactions between humans and bats can be common, in part due to many bat species adapting to urban environments and exploiting them in some cases (Jung and Threlfall 2016). Numerous bat species have been documented using human structures globally, and the continued or increased use of these buildings can facilitate human-bat contact that can negatively affect both taxa (Russo and Ancillotto 2015, Voigt et al. 2016). Bats may experience heightened stress and mortality while using buildings, often due to human actions to remove their roosts (Russo and Ancillotto 2015). Stress can alter infection dynamics within hosts and increase the shedding of pathogens into the environment where humans may contact them (Streicker et al. 2013). High mortality in bat populations can impact their ability to provide important ecosystem services, including pest suppression, pollination, and seed dispersal of fruiting plants (Kunz et al. 2011).

A potential, albeit severe, consequence of human-bat contact is human and domestic animal exposure to bat-borne pathogens. Bats host a wide diversity of viruses, thought to be linked to the high diversity within their taxon (Mollentze and Streicker 2020). Many significant zoonoses that have emerged in humans in the last 50 years are due to (or are closely related to) viruses hosted by bats, including several coronaviruses (SARS-like coronaviruses and MERS), filoviruses (such as Marburg virus), and paramyxoviruses (Nipah and Hendra virus; Letko et al. 2020). The close association of bats and humans throughout the world, either through interactions in buildings, human consumption of bats, or sharing of resources and exposure to bat excreta, is thought play a major role in the spillover of these viruses from bats to domestic animals and humans (Plowright et al. 2015). Practices that increase this spatial overlap in bats and humans, like land-use change, are associated with the emergence of these pathogens in

humans, mostly because they alter bat behavior and habitats in ways that create interfaces for human exposure (McKee et al. 2021, Faust et al. 2023, Eby et al. 2023).

Paramyxoviruses hosted by bats have recently spilled over into human populations, with the most well-known spillover events involving Hendra virus in Australia and Nipah virus in Bangladesh and Malaysia (Thibault et al. 2017). These viruses can have high human mortality during outbreaks and human infections are characterized by encephalitis and occasionally respiratory distress (Eaton et al. 2006). At least eight paramyxoviruses have spilled over from bats into humans, with several other paramyxoviruses described that may be capable of zoonotic transmission (Thibault et al. 2017). This viral family is found worldwide, and work across Africa has shown that paramyxoviruses are present in many bat species, but little is known about their ecology or infection dynamics within hosts (Hayman et al. 2008, Amman et al. 2015, Waruhiu et al. 2017). Many parts of sub-Saharan Africa have large and diverse bat populations that exist within or on the periphery of human-dominated areas. Further work is needed to explore paramyxovirus diversity within these synanthropic bat populations, and to understand human-bat contacts in the region and their ramifications for human and bat health.

This dissertation characterizes the human-bat interface in southeastern Kenya, a potential hotspot for the emergence of zoonotic diseases (Allen et al. 2017). In this region, human occupancy and land-use changes are increasing, putting additional pressure on land, water, and wildlife. In Chapter I, a review prepared for submission to *People and Nature*, I conducted a systematic review of the literature to identify global trends in human-wildlife interactions in areas of land-use change, characterizing these interactions and understanding where knowledge gaps exist. Chapter II, an empirical study published in *Royal Society Open Science*, explores bat selection of human structures as roosts based on their microclimatic and structural features and

demonstrates that building selection criteria varies among synanthropic bat species. Chapter III, an empirical study submitted to *PLOS Neglected Tropical Diseases*, characterizes and quantifies the human-bat interface that exists in buildings where bats cohabitate with people and shows that human-bat interactions are frequent, prolonged, and intense and may have negative impacts on both humans and bats. Chapter IV, a viral surveillance study prepared for submission to *Journal of Virology*, reports the presence and initial identification of a paramyxovirus in bats living in buildings and anthropogenic areas in rural Kenya, where humans may be exposed to bat-borne pathogens.

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CHAPTER I

GLOBAL PATTERNS OF REPORTED HUMAN-WILDLIFE INTERACTIONS IN AREAS OF LAND-USE CHANGE

Reilly Jackson, Tamika Lunn, Nathaniel Mull, Maureen McClung, Kristian Forbes

ABSTRACT

Emerging infectious diseases are one of the greatest and most pertinent threats to human health and security. Land-use changes, which are increasing globally, are a key driver of emerging infectious disease outbreaks; they increase contact between wildlife and humans and create opportunities for transmission of pathogens between them. While there is great emphasis on characterizing the circumstances underlying disease outbreaks in search of mitigation strategies, a global synthesis of documented human-wildlife interactions in the context of land-use change has not been previously done. We conducted a systematic literature review to identify the geographic, taxonomic, and land-use change focus of reported interactions between wildlife, humans, and domestic animals, and discuss the implications of our results in the context of understanding high-risk settings for zoonotic pathogen exposure. From 529 included articles, we show that reports of exposure opportunities are elevated in areas of Africa and Asia experiencing land use changes related to agricultural practices. Humans and domestic animals interacted with 1021 species of wildlife, including various amphibians, birds, mammals, and reptiles. Interactions with mammals were reported most often, mostly with species in the orders Artiodactyla, Carnivora, Primates, and Rodentia. The intensity of contact, and thus potential for cross-species pathogen transmission, varied; specifically, there was high reporting of indirect contacts between humans and wildlife in Europe, which may contribute to the risk of environmentally transmitted pathogens in the region. Findings from our review highlight the geographic, taxonomic, and land-use contexts at highest documented risk for pathogen exposure opportunity. Further, we identified important gaps in knowledge, such as a surprising lack of documented human interactions with bats globally, despite their high number of synanthropic species and role as hosts of zoonotic pathogens.

INTRODUCTION

Emerging infectious diseases (EIDs) are an increasing threat to global human health and security, as evidenced by the recent Mpox outbreak and COVID-19 pandemic (Daszak et al. 2000, Morens and Fauci 2013, Wang et al. 2022, Zumla et al. 2022). Most EIDs are zoonotic in origin, reaching human populations via transmission from animal host species (spillover), with the majority initiating in wildlife hosts (Jones et al. 2008). Once in human populations, some zoonotic diseases have the potential to spread efficiently due to high population densities and connectedness in contemporary globalized societies, hindering the ease and potential efficacy of downstream mitigation efforts (Coltart et al. 2017).

A major research priority is to understand the circumstances by which wildlife pathogens are transmitted to humans (Plowright and Hudson 2021). Exposure to pathogens at the human-wildlife interface is a crucial step in zoonotic spillover and is driven by multiple ecological mechanisms, including the distribution and abundance of reservoir host species, the prevalence and intensity of infection within reservoir hosts, and the persistence of pathogens once outside the host (Plowright et al. 2017, Wilkinson et al. 2018). Human exposure to wildlife pathogens can occur via direct (e.g., contact with wildlife through butchering and consumption) and indirect mechanisms (e.g., contact with excreted pathogens in environments where human and wildlife activities overlap) (Wolfe et al. 2005, Magouras et al. 2020). Additionally, domestic animals, including pets and livestock, can serve as intermediate (bridging) hosts between wildlife and humans, as occurred with several high-profile disease outbreaks (e.g., pigs and horses for Nipah and Hendra viruses, respectively; Chua et al. 2000, Playford et al. 2010).

One of the principal drivers of human exposure to wildlife pathogens is land-use change (LUC), also known as anthropogenically induced environmental change (Foley et al. 2005,

Woolhouse and Gowtage-Sequeria 2005, Jones et al. 2008, Gottdenker et al. 2014). Land-use change can impact the abundance and distribution of wildlife and shape wildlife-pathogen interactions, collectively increasing pathogen shedding by reservoir hosts and creating new contact opportunities that facilitate intra- and interspecies pathogen spread (Patz et al. 2004, Keesing et al. 2010, Jones et al. 2013, Faust et al. 2018, Mendoza et al. 2019, Carlson et al. 2022). For example, Nipah virus emergence in Malaysia is believed to have occurred due to *Pteropus* bats moving to roost and feed in orchards surrounding pig farms following deforestation and El Niño-induced drought in their habitat (Chua et al. 2002); Nipah virus was shed in bat saliva and excreta, infecting pigs below, who in turn transmitted the virus to humans. Land-use change has also been associated with spillover of *Borrelia burgdorferi* (the causative agent of Lyme disease), hantaviruses, ebolaviruses, and Hendra virus through effects on pathogen exposure (Allan et al. 2003, Wolfe et al. 2007, Prist et al. 2017, Rulli et al. 2017, Eby et al. 2023).

Existing review articles have evaluated links between LUC and pathogen spillover and emergence (Jones et al. 2013, Gottdenker et al. 2014, Johnson et al. 2015). These reviews focus on zoonotic disease outbreaks as a measure of spillover risk but do not evaluate exposure risk specifically. This nuance is crucial because documented disease outbreaks only capture a small fraction of total disease outbreaks (e.g., Glennon et al. 2019), and miss the many exposure opportunities that could have – but did not – lead to disease outbreaks (Plowright et al. 2017). Given that LUC primarily increases pathogen spillover and disease emergence in humans through effects on pathogen exposure risk, mechanistic insights into how LUC has influenced zoonotic spillover can be gained through evaluation of studies that link LUC with opportunities for wildlife exposure. To this end, we conducted a systematic, quantitative literature review that

characterizes the global breadth of studies that document human exposure to wildlife in the context of LUC to: 1) identify the geographic, taxonomic, and LUC focus of reported interactions; and 2) discuss and compare our results with previously identified geographic and taxonomic hotspots for spillover and emergence risk to highlight the most at risk settings and identify research needs.

METHODS

We conducted a systematic literature search in Web of Science in May 2022 to identify empirical articles that report on wildlife interactions with humans and domestic animals in areas of LUC (Figure 1; a full description of the search strategy is available in the Supplementary Materials). To ensure that articles contained relevant information, we applied the following criteria. First, studies had to report human-wildlife interactions within the context of human-induced LUC that is occurring or has occurred in the study area and describe the type of modification. Second, studies had to identify the type of wildlife involved to at least order level. Third, studies had to report the type of human-wildlife interaction (direct, indirect, or domestic animal contact, see below). Fourth, studies must have been based on empirical data. We limited our scope to terrestrial and arboreal vertebrates since they are the overwhelming reservoir source of zoonotic disease outbreaks (Han et al. 2016, Olival et al. 2017).

For each included article, we extracted the following information: the country where the interaction occurred, type of LUC, wildlife taxa involved, domestic animals involved, type of interaction, and standard journal article details (publication date, publishing journal). Land-use change was categorized into five types (Foley et al. 2005): (1) agriculturalization, (2) energy development, (3) land restoration, (4) resource extraction, and (5) urbanization (full definitions

of each category are provided in the Supplementary Materials). Contacts between humans and wildlife were categorized into three types: (1) direct physical contact, such as humans touching or consuming wildlife, (2) indirect contact, such as when humans and wildlife occupy the same areas but not necessarily simultaneously (e.g., humans observing wildlife on their property or contacting wildlife effluent), or (3) domestic animal-mediated contact, as a way of quantifying the potential for human pathogen exposure via intermediate domestic animals that also have contact with wildlife (Table S1). Lastly, we collected information on the type of study (before-after comparison, cross-sectional, experimental, and longitudinal) and on techniques of data collection to understand methods applied within included studies.

To investigate how the total number of publications reporting human-wildlife interactions varied by continent, taxa, contact intensity, and LUC type, we used generalized linear models with publication count as the response variable (Poisson error distribution; R base package); continent, taxonomic group, contact intensity, and LUC type were set as explanatory variables. Due to a small number of studies on energy development ($n = 12$) this LUC type was not included in analyses. Due to lack of studies reporting human interactions with amphibians ($n=2$), we removed these records from analyses. For studies mentioning multiple continents, wildlife taxa, contact intensity levels, or LUC types, we counted the study for multiple categories (Gottdenker et al. 2014).

A candidate set of models was generated to explore the potential two-level interactive effects of continent, wildlife taxon, contact intensity, and LUC type. Model fit was assessed using diagnostic plots of residuals (R base package). Model selection was then conducted by comparing Akaike's Information Criterion corrected for small sample size (AICc) scores of models fit with all combinations of explanatory factors (package "AICmodavg"; Mazerolle

2023). To identify differences within our interactions of categorical variables in our final model, we performed post-hoc testing with a Tukey's HSD test (package "emmeans"; Lenth et al. 2023). Lastly, to assess disparity and biases in reported interactions, we used a chi-square analysis to compare publication count among orders within each class. Due to the large number of orders involved in interactions, we included orders documented in 10 or more publications.

RESULTS

A total of 529 articles were identified that met our inclusion criteria (Figure 1; a full list of included articles and their citations are provided in the Appendix). Articles were published from 1994-2022 in 172 different journals and two pre-print servers. Over 85% of included articles were published since 2012 ($n = 462$), demonstrating a strong recent increase in relevant literature. Almost 70% of articles included cross-sectional data ($n = 357$), followed by longitudinal ($n = 231$), experimental ($n = 15$), and before-after comparisons ($n = 8$). There were 13 main types of data collection techniques, with the most common methods including human interviews ($n = 298$), structured observation ($n = 137$), and analysis of government, non-governmental organization, or public records ($n = 121$; Table S2).

We identified differences in reporting of human-wildlife interactions within all four categories (Table 1). Human-wildlife interactions in areas experiencing LUC were reported in 96 countries, including all continents except Antarctica. Human and domestic animals interacted with wildlife belonging to 50 distinct orders and 1,021 species, all of which fall into amphibians, birds, mammals, and reptiles (Classes: Amphibia, Aves, Mammalia, and Reptilia, respectively). Wildlife was documented to interact with 20 different species of domestic animal, with cows ($n = 99$), goats ($n = 71$), and sheep ($n = 63$) most reported.

The interactive effects of continent by LUC, by wildlife taxon, and by contact intensity, as well as the interaction of contact intensity by wildlife taxon were included in our top model. The number of human-wildlife interactions reported varied across LUC types on all continents except Oceania (Figs. 2–3; $P \geq 0.499$). In Africa, reports of human-wildlife interactions were more common in areas of agriculturalization and restoration than in other LUC types ($P \leq 0.009$). In Asia, reports from areas of agriculturalization were more common than in any other LUC type ($P \leq 0.006$). In South America, reports of interactions in agriculturalized areas were more common than reports from areas of resource extraction and urbanization ($P < 0.045$). Contrastingly, in Europe and North America, only human-wildlife interactions in areas of resource extraction were the least reported ($P \leq 0.017$).

Our best model included the interactive effects of contact intensity and continent (Fig. 4). Intensity of reported interactions did not differ significantly in Africa, Asia, North America, Oceania, or South America ($P \geq 0.089$). In Europe, indirect contacts (i.e., human spatial proximity to wildlife without physical contact) were more commonly reported than direct interactions (i.e., physical contact between a human and wildlife or their effluent; $P < 0.001$) but no more than domestic-animal mediated interactions (i.e., interactions between wildlife and domestic animals; $P = 0.862$).

The location and intensity of reported human-wildlife interactions in areas experiencing LUC varied by taxa. Interactions with mammals were more commonly reported than with birds or reptiles across Africa, Asia, Europe, and North America ($P < 0.001$). In Oceania and South America, human-wildlife interactions involving mammals were more commonly reported than with birds ($P \leq 0.048$) and were no different than interactions between humans and reptiles ($P \geq 0.663$). Contact intensity also varied across taxa: indirect contacts with birds and mammals

were reported more than direct or domestic-animal mediated contacts ($P < 0.001$). There was no difference in the contact intensity levels of human-reptile interactions ($P \geq 0.788$).

Order diversity within taxa also varied considerably. Humans and domestic animals interacted with one amphibian, 27 avian, 19 mammalian, and three reptilian orders (Figure 3). Our analysis reporting interactions with different taxa varied among avian ($\chi^2 = 14.44$, $df = 6$, $P = 0.025$), mammalian ($\chi^2 = 829.45$, $df = 10$, $P < 0.001$) and reptilian ($\chi^2 = 17.10$, $df = 2$, $P < 0.001$) orders. Across avian orders, only Galliformes were reported more often than expected, with all other orders (Accipitriformes, Anseriformes, Charadriiformes, Columbiformes, Passeriformes, and Psittaciformes) reported as often as expected ($P = 0.025$). Within Mammalia, the orders Artiodactyla, Carnivora, Primates, and Rodentia were reported more often than expected; the orders Chiroptera, Cingulata, Didelphimorphia, Lagomorpha, Perissodactyla, and Pholidota were reported less often than expected; and the order Proboscidea was reported as often as expected ($P < 0.001$). Within Reptilia, the order Crocodilia was reported more often than expected, the order Testudines was reported less often than expected, and the order Squamata was reported as expected ($P = 0.002$).

DISCUSSION

This study is the first to characterize global publication trends documenting human and domestic animal exposure to wildlife in the context of LUC. Findings from our review highlight the contexts at highest documented risk for wildlife contact, with subsequent opportunities for pathogen exposure. Our results suggest that reports of human-wildlife interactions are highest in areas of Africa and Asia experiencing LUC related to agricultural practices, and for indirect interactions with birds and mammals that could facilitate contact with environmentally

transmitted pathogens in Europe. These settings align with previously identified global hotspots of emerging zoonotic diseases, and documented panzootics of environmentally transmitted pathogens (e.g., avian influenza in Europe; Kilpatrick et al. 2006, Will and Barre 2022). This concordance highlights exposure to wildlife under LUC as a key but underexplored driver of global disease patterns and emphasizes the importance of information reporting exposure to wildlife.

To explain the likelihood of zoonotic disease emergence in humans, past work has largely focused on land cover change, human population size and growth, socioeconomic traits of communities, and the species richness of wild mammals as significant predictors (Jones et al. 2008, Grace et al. 2012, Allen et al. 2017, Jagadesh et al. 2022). While such correlates are important, they can fit EID emergence data poorly, hinting that additional explanatory covariates are needed to fully characterize drivers of pathogen emergence (Allen et al. 2017). The nexus of these focal predictors are important factors that are missing from previous models and could provide additional power to accurately predict EID hotspots. Further, there is evidence that some explanatory variables currently used singularly, like land cover change and human density, cannot accurately predict human-wildlife interactions, reducing their ability to account for these contacts despite their importance to the EID emergence process (Buchholtz et al. 2020, Nickel et al. 2020). Therefore, a landscape metric that can estimate the likelihood of human-wildlife interactions is needed for future EID predictions and may benefit other disciplines as well.

Pathogen persistence in the environment and subsequent transmission is predicted to be an important driver of pathogen dynamics in wildlife (Plowright et al. 2017). Our results suggest that frequency of indirect contacts, which provide opportunities for environmental transmission, may be an important correlate of spillover, especially in higher latitudes like Europe, a hotspot

for past EID emergence (Jones et al. 2008). This is exemplified most recently by the ongoing avian influenza epizootic in Europe where wild birds have recurrently shed highly pathogenic avian influenza into the environment, causing massive outbreaks in domestic animal production, including poultry and mink operations (Rohani et al. 2009, Agüero et al. 2022, EFSA 2023, Lindh et al. 2023). These pathogens have subsequently spilled over into humans multiple times (Phillipon et al. 2020). Environmentally transmitted pathogens, particularly those from birds and mammals, may be a relevant priority in Europe going forward, especially as such pathogens are expected to increase in the frequency of their emergence with changing climates and land use regimes (Rees et al. 2021).

Globally, human-wildlife contacts likely occur daily for most people, especially those living in areas of LUC (Soulsbury and White 2019). Such changes can impact the movement patterns of wildlife species, forcing contact between wildlife and humans inhabiting these shifting regions (Doherty et al. 2021). Despite this frequency, we only identified 529 articles that reported human-wildlife interactions and provided context of landscape change occurring in these studies. Given the evidence for altered likelihood of human-wildlife interactions in response to LUC, future research is needed to better identify the diversity of these interactions and provide better context for opportunities for human exposure to wildlife and their pathogens. For example, of the many wildlife orders reported to interact with humans and domesticated animals that are focal taxa for zoonotic disease research (Olival et al. 2017), bats (order: Chiroptera), which carry numerous zoonotic pathogens, are infrequently reported in the literature compared to other mammalian orders. This trend likely demonstrates a reporting bias and highlights the need for hypothesis-driven research to understand the nuances of interactions between bats, humans, and domestic animals, especially within a disease transmission and LUC

framework. Understanding the frequency, types of interactions, and location of these interactions is integral to developing zoonotic disease transmission models for numerous bat-borne zoonotic pathogens, as well as mitigating human-bat conflict and cross species pathogen transmission (Plowright et al. 2017, Plowright and Hudson 2021).

The information from this systematic review provides a synopsis, and an important baseline, of reports of human-wildlife interactions in areas of LUC, with evidence showing that these contacts vary wildly depending on continent, intensity, LUC type, and wildlife taxon involved. However, the inference of our results is limited by the literature and, specifically, the lack of context of many publications. Reports of human-wildlife contacts stemming from wildlife trade or human consumption are important to understanding the drivers of interactions (Shivakaprash et al. 2021). Many of these studies often do not provide details on LUCs occurring in areas where traded wildlife originated, reducing our ability to incorporate and evaluate the role these interactions may play in exposing humans to wildlife-borne pathogens. We therefore suggest that future studies on these systems include details of geographic changes occurring in these regions to better contextualize these interactions. In conjunction with future focus on the taxonomic gaps in the literature, the information provided will inevitably benefit efforts to predict and mitigate the emergence of zoonotic diseases in human populations.

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TABLES

Table 1. The number of publications documenting human-wildlife interactions differed by continent where interactions occurred, contact intensity, land-use change type, and wildlife taxon involved.

Variable	Number of publications
<hr/> Continent <hr/>	
Africa	142
Asia	194
Europe	52
North America	70
Oceania	14
South America	62
<hr/> Contact intensity <hr/>	
Direct	219
Domestic-animal mediated	223
Indirect	400
<hr/> Land-use change type <hr/>	
Agriculturalization	407
Resource extraction	73
Restoration	263
Urbanization	223
<hr/> Wildlife taxon <hr/>	
Aves	74
Mammalia	493
Reptilia	45

FIGURES

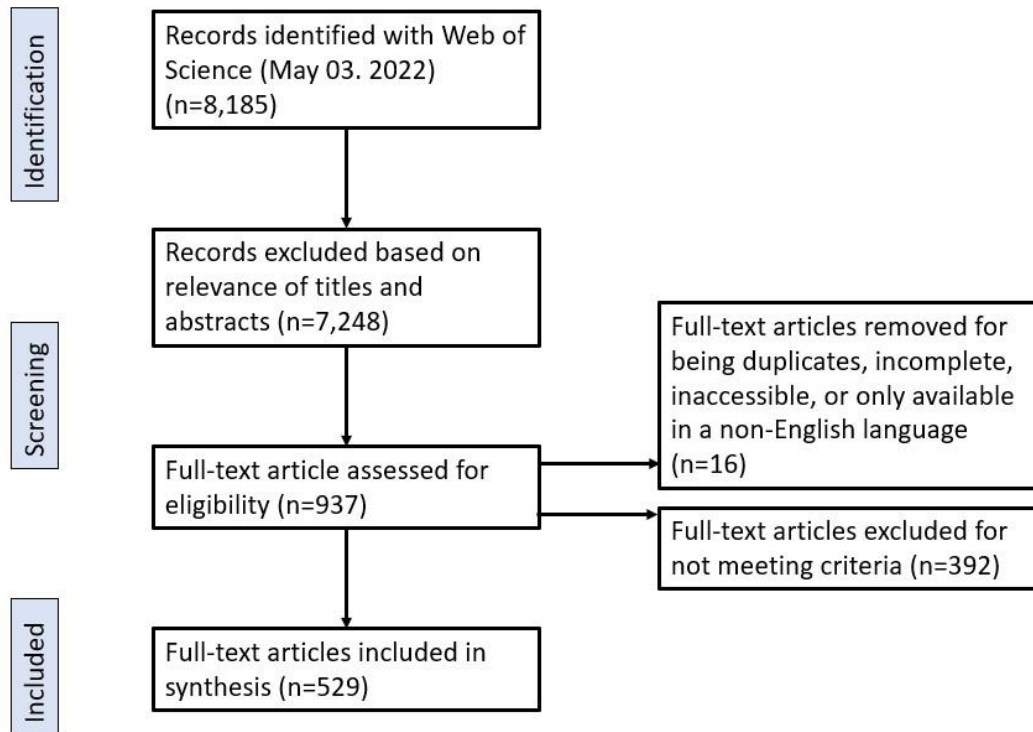


Figure 1. PRISMA style workflow of the systematic literature search and article inclusion process. We performed a Boolean search in Web of Science on May 3, 2022, for articles published since 1970.

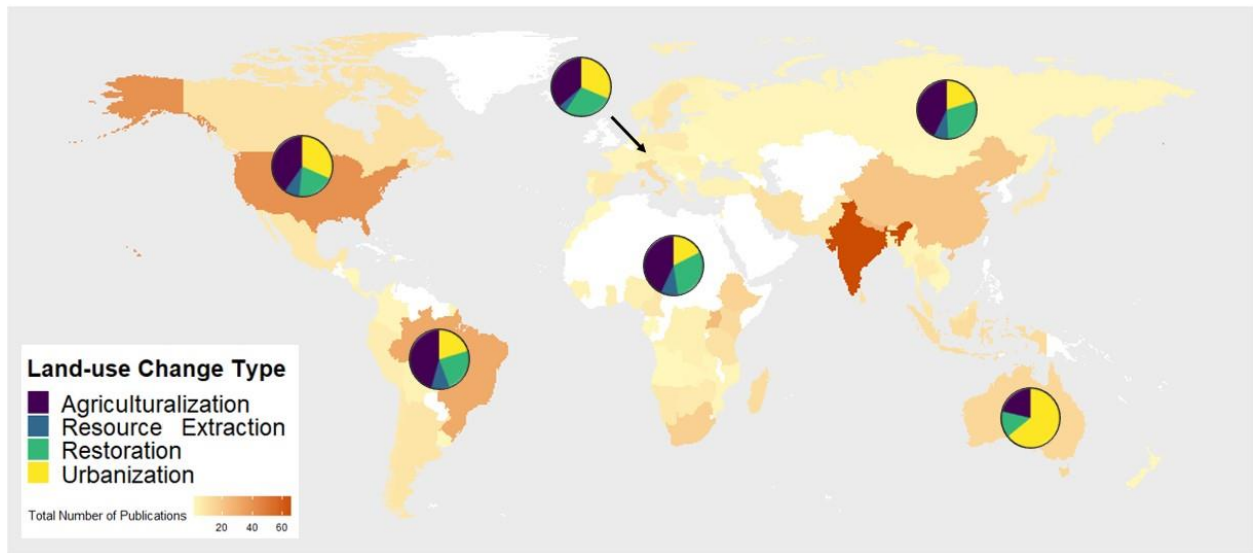


Figure 2. Geographic distribution of reported human-wildlife interactions and the type of land-use changes (LUC) involved. Studies were selected during a systematic review process based on their inclusion of data on human-wildlife interactions in areas of land-use change. Map lines delineate assumed country boundaries and do not necessarily depict accepted national boundaries.

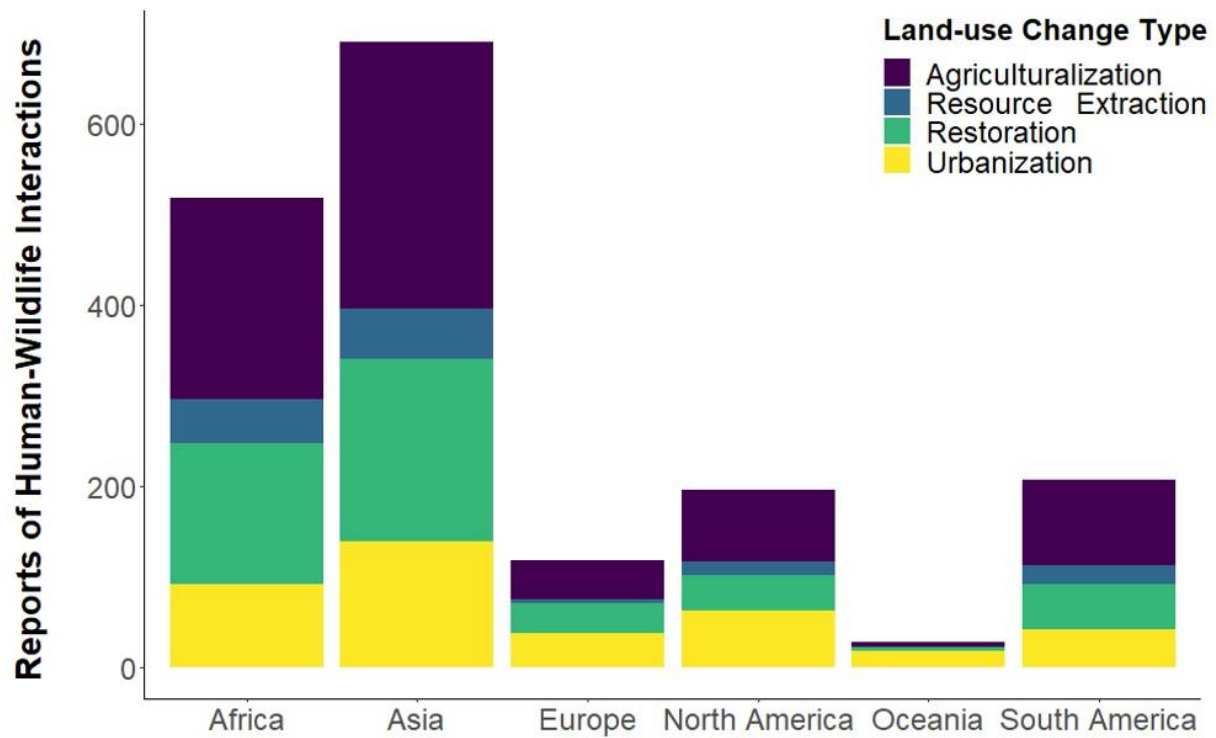


Figure 3. Total number of studies reporting human-wildlife interactions based on continent and land-use change type. Studies were selected during a systematic review process based on their inclusion of data on human-wildlife interactions in areas of land-use change.

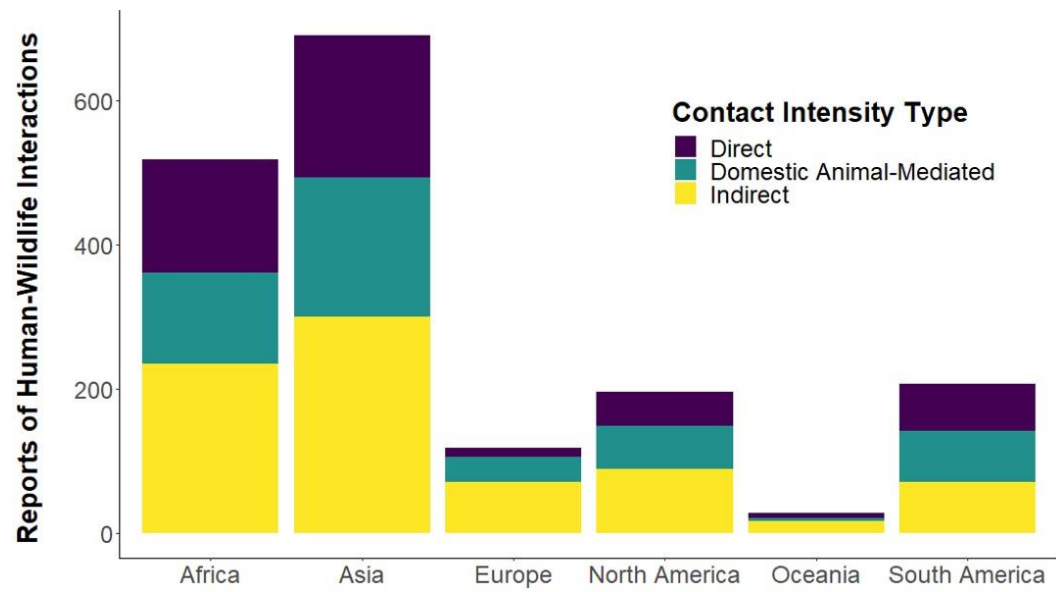


Figure 4. Total number of studies reporting human-wildlife interactions based on continent and contact intensity type. Studies were selected during a systematic review process based on their inclusion of data on human-wildlife interactions in areas of land-use change.

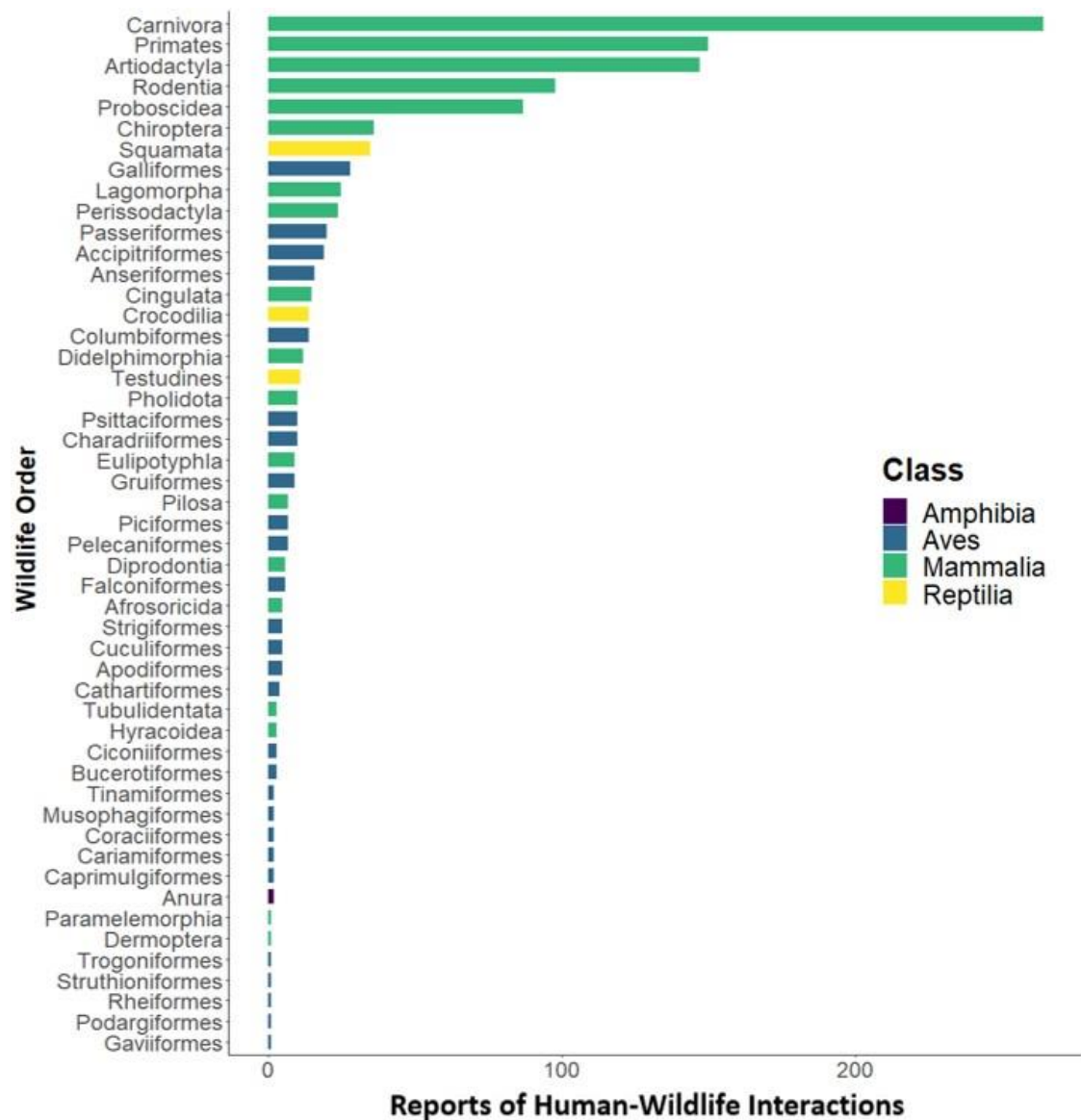


Figure 5. Total number of studies that reported human-wildlife interactions involving an identifiable order of wildlife. Studies were selected during a systematic review process based on their inclusion of data on human-wildlife interactions in areas of land-use change. Interactions with mammals were most documented (19 orders, 493 unique studies), followed by birds (27 orders; 74 unique studies), reptiles (3 orders, 45 unique studies), and amphibians (1 order, 2 unique studies).

APPENDIX

Search Terms:

A Boolean search was performed in Web of Science on May 03, 2022 using the search terms: ('interaction' OR 'conflict' OR 'exposure' OR 'interface' OR 'contact') AND ('wildlife' OR 'wild*' OR pest) AND ('land-use change' OR 'habitat fragmentation' OR 'logging' OR 'habitat modification' OR 'habitat restoration' OR 'deforestation' OR 'urbanization' OR 'agricultur*' OR 'energy development' OR 'habitat degradation' OR 'resource extraction' OR 'forest*' OR 'habitat conversion') NOT ('insect*' OR 'arthropod*' OR 'invertebrate' OR 'aqua*' OR 'fish*' OR 'marine' OR 'wildfire*' OR 'wild-type').

Definitions of included types of land use change:

Land-use change was categorized into five types: agriculturalization (areas with farming, grazing, or ranching), energy development (fossil fuel prospecting and drilling, dam building, solar or wind energy development), restoration (areas with conversion from human-modified areas to a natural status, including human-induced reforestation, protection of areas to allow plant regeneration moderated by humans, habitat management for wildlife, or removal of humans and their activities to allow land restoration), resource extraction (logging or mining), or urbanization (urban/suburban areas and infrastructure).

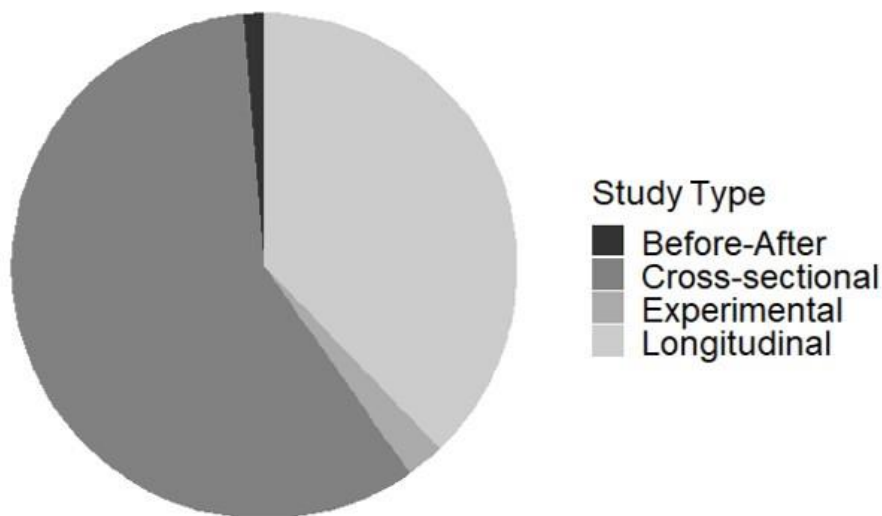


Figure S1. The proportion of four types of studies across 529 included articles reporting human-wildlife interactions in areas of land-use change.

Table S1. Different examples of interactions documented during a scoping review of 529 articles recording human-wildlife interactions in areas of land-use change. These interaction types were analyzed with other categorical variables to understand geospatial and taxonomic trends in risk of exposure to zoonotic pathogens.

Interaction Type	Interaction Examples
Direct contact	<ul style="list-style-type: none"> • Animal attacked/killed human • Animal shared provisions with human • Human consumed animal • Human killed animal • Human fed animal • Human cared for animal/kept as pet
Domestic animal-mediated contact	<ul style="list-style-type: none"> • Domestic animal attacked/killed/consumed wild animal • Wild animal attacked/killed/consumed domestic animal • Wild animal shared provisions with domestic animal • Wild animal shared space with domestic animal • Wild animal physically contacted domestic animal (i.e., reproduction, non-aggressive contact, etc.)
Indirect contact	<ul style="list-style-type: none"> • Human interacted with animal effluent • Human contacted/killed wild animal via locomotive (car, train, etc.) • Human observed animal in close proximity • Wild animal chased human (and vice versa) • Wild animal damaged human property • Wild animal raided human areas (i.e., crops, homes, kitchen, stores, etc.)

Table S2. We documented four main study types and 13 main data collection methods. Many articles contained multiple types of studies (n=86) and multiple data collection methods (n=275).

Study Type	Data Collection Methods
Before and after (including BACI)	<ul style="list-style-type: none"> • Analysis of records • Diet analysis • Experiment • Human interviews • Radio collars • Structured observation
Cross-sectional	<ul style="list-style-type: none"> • Acoustic detectors • Analysis of government/NGO/public records • Animal capture • Camera traps • Damage assessment • Diet analysis • Health analysis • Human interviews • Radio collars • Structured observation • Track plots
Experimental	<ul style="list-style-type: none"> • Damage assessment • Diet analysis • Experiment • Health analysis • Human interviews • Radio collars • Structured observation
Longitudinal	<ul style="list-style-type: none"> • Acoustic detectors • Analysis of government/NGO/public records • Animal capture • Camera traps • Damage assessment • Diet analysis • Health analysis • Human interviews • Radio collars • Structured observation • Track plots

Citations for all empirical articles and manuscripts included in primary analyses:

Abdullah, A., Sayuti, A., Hasanuddin, H., Affan, M., & Wilson, G. (2019). People's perceptions of elephant conservation and the human-elephant conflict in Aceh Jaya, Sumatra, Indonesia. *European Journal of Wildlife Research*, 65(5), 1-8. <https://doi.org/10.1007/s10344-019-1307-1>

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CHAPTER II

ROOST SELECTION BY SYNANTHROPIC BATS IN RURAL KENYA: IMPLICATIONS FOR HUMAN-WILDLIFE CONFLICT AND ZOOBOTIC PATHOGEN SPILLOVER

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ABSTRACT

Many wildlife species are synanthropic and use structures built by humans, creating a high-risk interface for human-wildlife conflict and zoonotic pathogen spillover. However, studies that investigate features of urbanizing areas that attract or repel wildlife are currently lacking. We surveyed 85 buildings used by bats and 172 neighboring buildings unused by bats (controls) in southeastern Kenya during 2021 and 2022 and evaluated the role of microclimate and structural attributes in building selection. We identified eight bat species using buildings, with over 25% of building roosts used concurrently by multiple species. Bats selected taller cement-walled buildings with higher water vapor pressure and lower presence of permanent human occupants. However, roost selection criteria differed across the most common bat species: molossids selected structures like those identified by our main dataset whereas *Cardioderma cor* selected buildings with lower presence of permanent human occupants. Our results show that roost selection of synanthropic bat species is based on specific buildings attributes. Further, selection criteria that facilitate bat use of buildings are not homogenous across species. These results provide information on the general mechanisms of bat-human contact in rural settings, as well as specific information on roost selection for synanthropic bats in urbanizing Africa.

INTRODUCTION

Urbanization has a pervasive and continuing impact on wildlife species. While urbanization has led to habitat loss for wildlife, some species utilize environmental conditions and structures that are products of human presence (Constanza et al., 2001, Baker and Harris 2007, Magle et al. 2012, Neate-Clegg et al. 2023). Many wildlife species within the urban human-wildlife interface are known to harbor zoonotic pathogens, and this close connectivity

can facilitate pathogen spread (spillover) and spillback of these pathogens between wildlife and humans (Schmidt and Ostfeld 2001, Hough 2014, Fagre et al. 2022). Close interactions often also cause human-wildlife conflict which can lead to human-induced wildlife mortality (Dickman 2010). Information to inform contact- and conflict-mitigation strategies is needed to improve outcomes for both groups and is a key priority in the growing field of urban ecology.

Model systems that identify and characterize regions of high-risk human-wildlife interfaces will be critical to efforts to reduce human-wildlife conflict and pathogen spillover. Bats are progressively inhabiting urbanizing landscapes, with some species increasingly adapting and exploiting resources in these regions, while others may be moving into those areas due to anthropogenic land-use changes that destroy native habitat (Russo and Ancilloto 2015, Schoeman 2016, Voigt and Kingston 2016, Eby et al. 2023). Some species are known to harbor pathogens, especially viruses, that can spill over into humans and domestic animals (Olival et al. 2017, Letko et al. 2020). Bats are also increasingly imperiled, with 15% of bat species considered endangered or threatened, primarily due to anthropogenic actions such as land-use change, hunting, persecution, and urbanization (Voigt and Kingston 2016). They provide several critical ecosystem services, including insect suppression, seed dispersal, and pollination of many tropical plants, and addressing their conservation needs is important to environmental function (Kunz et al. 2011, Voigt et al. 2016). The increasing use of human areas, such as buildings, connects bats to people and domestic animals intimately, thus creating opportunities for pathogen spillover, spillback, and bat mortality at this cross-section of the human-wildlife interface (Voigt et al. 2016, Plowright et al. 2017).

Bats have been recorded in urban areas on all human-inhabited continents, and often roost in human structures such as houses, schools, offices, abandoned buildings, and bridges

(Voigt et al. 2016, Monadjem et al. 2020). For bats, human structures can provide stable shelter, breeding sites, and safety from predators (Entwistle et al. 1997, Jenkins et al. 1998). Structural attributes of buildings, such as their height, age, complexity, and composition have been reported as important for determining bat roost suitability (Entwistle et al. 1997, O'Malley et al. 2020). However, studies on this topic usually suffer from key limitations, often due to practical necessities while conducting research on bats in difficult environments, including low roost sample numbers, missing or inadequate controls, and statistical approaches that fail to account for interactions among relevant covariates (e.g., Moussy 2011, Kubista and Bruckner 2015). These limitations ultimately impair the ability to draw inferences that can inform strategies to mitigate human contact with wildlife. Further, the global ubiquity of synanthropic bats, their potential to host zoonotic pathogens, and their conservation importance make them key systems to understand how human-wildlife contact occurs and can be mitigated in rural and urbanizing settings (Kunz et al. 2011, Han et al. 2016, Olival et al. 2017, Letko et al. 2020).

Accounting for interactions among relevant covariates and the mediated effect of variables is necessary for understanding nuances of habitat selection by wildlife. Structural equation modelling (SEMs) is a method that allows for comparison of multiple covariates, but also can identify both direct and indirect interactions among variables (Kline 2011). This method allows for the *a priori* formulation of hypothesized causal models based on previous empirical research and calculates partial regression coefficients corresponding to predicted causal effects. By developing models using the existing literature on roost selection, SEMs can identify covariates with direct effects on roost selection, as well as variables that may indirectly impact (but are still important) selection criteria through their impact on direct effects. Fine-scale

identification of these features can provide a comprehensive characterization of structures facilitating human-wildlife contact.

We investigated the features of buildings that contribute to bat roost use in rural southeastern Kenya to identify the traits of anthropogenic structures that bats select. This region has several bat species known to host a variety of pathogens and that roost in buildings with humans and domestic animals (Kading et al. 2015, Schoeman 2016, Waruhiu et al. 2017, Forbes et al. 2018). By understanding building characteristics key for bat roost selection, we can better characterize hotspots of human-wildlife contact in urbanizing areas and provide information to help target measures that mitigate contact between bats and humans. We applied SEMs to represent the direct and indirect interactions among building features, microclimate, and bat use. These data contribute important information in an area of the Global South where human contact with bats and disease risks are high, but where data are scarce. More broadly, we fill a need for information on bat roost selection globally and provide a model system for understanding human-wildlife contact in progressively urbanizing areas.

METHODS

Study area

This study was conducted in Taita-Taveta County, in rural Kenya, during August – October 2021 and January – April 2022 (Figure S1). The region covers an approximate area of 17,000 km² and is characterized by high diversity of wildlife, with patches of isolated cloud forest between 1400 to 2200 m above sea level surrounded by lower-elevation (400 to 1400 m above sea level) grasslands and woodlands, all distributed amongst rural villages and smallholder farms (Platts et al. 2011, Abera et al. 2022). The climate is semi-arid and has an average annual

temperature of 23 °C (Ogallo et al. 2019, Autio et al. 2021). Typically, there have been two rainy seasons, March to May/June and October to December, with an average yearly rainfall of 150 to 600 mm in the lowlands and 800 to 1200 mm in the highlands (Ogallo et al. 2019, Autio et al. 2021). However, an ongoing drought has reduced the rains since 2019 (Musyimi et al. 2023). Urbanization has dramatically increased over recent decades in Taita-Taveta county, with over 95% of original forest cover cleared and a 700% increase in development landcover (Newmark 2002, Nyongesa et al. 2022). Bat diversity is high here, with over 30 species recorded in the county (Lopez-Baucells et al. 2016) and humans often have bats living in their buildings (Figure S2). The region has also been identified as a hotspot for zoonotic disease emergence and numerous bat species in the area are known to host a diversity of pathogens (Allen et al. 2017, Waruhiu et al. 2017, Forbes et al. 2019).

Data collection

We identified buildings used by bats via word-of-mouth conversations with community members throughout the study area. Roost coordinates and elevation were recorded using a handheld GPS unit (Model: GPSMAP 64sx; Garmin International Ltd., Olathe, KS, US), and upon permission from homeowners and care takers, we entered buildings to confirm active bat presence and species identity. Bats were captured from buildings using hand nets at roosts or mist nets placed at exit points and identified to species level based on Patterson and Webala (2012). We identified slit-faced bats (Family: Nycteridae) to genus only because the taxonomy of this genus is complicated and requires revision, reducing our ability to correctly identify to species (Demos et al. 2019, Monadjem et al. 2020).

For every bat-occupied building, we selected at least two of the closest accessible buildings that had both no sustained (>1 night/day) bat use within the homeowner's memory and

no physical evidence of bat use (e.g., guano deposits, urine staining, bat-associated smells), as controls for microclimate and structural attribute comparison. We collected the following information from each roost type (used and unused by bats): 1) maximum daily light (lux), maximum daily temperature (°C), and maximum daily relative humidity (rH) (measured with an Enviro-Meter, ThermoFisher Scientific, Watham, MA); 2) building height from base to peak of the structure (m); 3) building aspect (cardinal direction of bat entry into building); 4) roof material; 5) wall material (categorized as cement, mud, or other (metal, stone, unknown brick type)); 6) presence or absence of compartment above ceiling of the main living area (i.e., attic); and 7) presence/absence of permanent human occupants in the building (Supplementary Materials 2). Microclimate data were collected between 11:00 and 17:00 hours based on preliminary data collection showing the highest daily temperatures during this period (Table S1). Microclimate characteristics and building aspect were measured at the roost in bat-occupied buildings; in control buildings, these characteristics were measured at equivalent roost positions (i.e., where bats were roosting in similar structures; Fagan et al. 2018).

Building variables were assessed for collinearity using Spearman's Correlation coefficient, although we detected no correlation amongst numeric variables ("corr" in "survival" R package; Therneau et al. 2023). Two variables, roof material and ceiling presence, showed no variation among surveyed buildings (>80% of surveyed buildings had the same characteristic) and were dropped from analyses (Table S2). Aspect was not included in analyses due to most buildings having multiple entry points used by bats (Table S2). Instead of using raw relative humidity levels, due to the inherent relationship with temperature (Kurta et al. 2014), we used humidity and temperature data collected at buildings to calculate water vapor pressure (WVP;

kPa) and used this as a measurement for moisture content at roosts (Campbell and Norman 1998, Haase et al. 2019).

Statistical analyses

Prior to analysis we tested whether the grouping of sites (i.e., selection of one occupied building and the two closest non-occupied buildings as controls) had any effect on building selection (“lme4” R package; Bates et al. 2023). Groupings did not have a significant effect on results, and so were not included in model structures (Table S3). We used structural equation models (SEMs) to evaluate direct and indirect effects of building features on bat roost selection (“lavaan” R package; Rosseel et al. 2012). Direct effects are covariates with an unmediated impact on response variables whereas indirect effects are covariates mediated through another covariate. Model structure was guided by a pre-conceived conceptual model containing all measured building features (Figure 1). To understand the importance of different factors to bat species, we further divided our main dataset into two groups: buildings used by co-roosting molossid bats (*Mops condylurus* and *M. pumilus*, formerly *Chaerephon pumilus*) and those used by the regionally endemic megadermatid, *Cardioderma cor*. We used SEMs to evaluate buildings used by molossids, however due to fewer data points, we used different methods to analyze building roost selection by *C. cor* (described below).

For our all species and molossid datasets, analyzed via SEMs, we used diagonally weighted least squares (DWLS) estimation, with a Bollen-stine bootstrap resampling procedure to estimate standard errors (1000 bootstrap samples). This approach is robust to non-continuous response variables (Mîndrilă et al. 2010, Kline 2011). Model fit was evaluated using the χ^2 statistic, comparative fit index (CFI), and the root mean square error of approximation (RMSEA) (Kline 2011). Both the χ^2 statistic and RMSEA values are absolute fit indices which determine

how well the *a priori* model structure fits the data. A non-significant ($P > 0.05$) χ^2 statistic and significant RMSEA ($P \leq 0.05$) indicate good model fit. CFI is a relative fit index, which assesses the relative improvement in fit of the *a priori* model structure compared to a baseline model, with $CFI \geq 0.9$ indicating acceptable fit. Only models that fit sufficiently proceeded to further interpretation. The final SEM models for our main dataset included direct effects on bat roost selection from peak light, WVP, temperature, the presence or absence of permanent human occupants, and building height, and indirect effects from wall material moderated through its influence on building height (Figure 2).

As a general guide, an SEM requires at least five rows of data per path coefficient (Wolf et al. 2013), meaning at least 40 buildings were required per species for our model structure. We identified fewer buildings used by *C. cor* ($n = 18$ used buildings, 36 associated control buildings), which prohibited the use of SEMs. Therefore, for this species we used generalized linear models (GLMs) with a binomial error structure and logit link function to assess the role of microclimate and structural attributes on building selection (“glm” in R base package). The GLM structures were guided by the pre-conceived conceptual model, as in SEMs, with a stepwise regression approach to identify important variables from the main covariates: building height, human occupancy, lux, temperature, WVP, and wall material. Model fit of GLMs was checked with χ^2 goodness-of-fit tests (Hosmer et al. 1997). We identified the best performing model(s) with Akaike Information Criterion corrected for small sample size (AICc) scores. Models within 2 AICc units were considered competitive, and the weighted averages of coefficients were calculated for equally competitive models (R package “MuMIn”; Symonds and Moussalli 2011). All analyses were conducted in RStudio version 2022.7.1+554.

RESULTS

We identified 85 buildings used by bats and 172 nearby control buildings. Bats inhabited homes with humans ($n = 31$), abandoned buildings ($n = 15$), schools ($n = 11$), offices ($n = 6$), storage buildings ($n = 5$), staff lodging buildings ($n = 5$), isolated kitchen buildings ($n = 3$), medical dispensaries ($n = 2$), guest houses ($n = 2$), and conference buildings ($n = 2$). We also found bats roosting in one boma (a fortified livestock enclosure), one church, and one shop. Bats roosted inside buildings, mostly at the junction of the walls and roof ($n = 37$), the seam of the roof ($n = 30$), along roof structural support beams ($n = 23$), or under furniture ($n = 2$). Roost elevation ranged from 536 m a.s.l to 1439 m a.s.l ($\bar{x} = 952.42 \pm 20.09$ m a.s.l) and we present the first records of *C. cor* presence above 940 m a.s.l (902.72 ± 52.24 m a.s.l; range: 536 – 1135 m a.s.l).

Eight bat species were found roosting inside human structures (Table 1). Over 25% of bat-occupied buildings contained more than one bat species roosting within the building ($n = 22$, Table 1). *Mops pumilus*, the most frequently encountered species (n roosts = 65), co-roosted with six different species including *Epomophorus wahlbergi* ($n = 1$); *C. cor* ($n = 2$); *M. condylurus* ($n = 13$); *Nycteris* sp. ($n = 1$), *Rhinolophus cf. lobatus* ($n = 2$); and *Scotophilus andrewreborii* ($n = 2$) (Table 1). One building contained three species co-roosting together (*C. cor*, *M. pumilus*, and *R. landeri*). Nonvolant young of *C. cor* were observed in roosts in October and March – April, whereas young of *M. pumilus* and *M. condylurus* were observed during February – April. Nonvolant young of a slit-faced bat (*Nycteris* sp.) were observed in February. Nonvolant young of the other species were not observed.

Buildings used by any bat species

In our all-species SEM, model fit was validated by all but one metric ($\chi^2 = 0.06$, CFI = 0.99, RMSEA = 0.06, $R^2 = 0.99$). The model showed that height and WVP had significant, direct positive effects on bat selection of buildings, with bats selecting taller buildings with higher WVP compared to controls ($P < 0.01$). The presence of permanent human occupants had a significant, direct negative effect, with bats selecting buildings without permanent human occupants compared to controls ($P \leq 0.03$, Figs. 2A & 3, Table S4 & S5). Wall material had a significant indirect effect mediated through building height ($P < 0.01$, Fig. 2A), with cement-walled buildings being taller (mean = 4.79 ± 0.09 meters) than mud (mean = 3.67 ± 0.18 meters) or other material buildings (mean = 4.25 ± 0.45 meters), having a positive impact on bat presence.

Buildings used by molossid bats

We identified 65 buildings used by molossids and surveyed 130 associated control buildings. For our molossid-only SEM ($\chi^2 = 0.29$, CFI = 0.99, RMSEA = 0.04, $R^2 = 0.98$), building height and WVP had similarly significant direct positive effects on bat use of buildings, whereas presence of permanent human occupants had a significant direct negative effect ($P \leq 0.03$; Fig. 2B & 4, Table S6 & S7). Wall material had a significant indirect effect, mediated through building height ($P < 0.01$, Fig. 2B & Table S6), with cement-walled buildings being taller (mean = 4.71 ± 0.18 meters) than mud (mean = 3.87 ± 0.31 meters) or other material buildings (mean = 4.25 ± 0.46 meters), having a positive impact on bat presence.

Buildings used by Cardioderma cor

We identified 18 buildings used by *Cardioderma cor* and surveyed 36 associated control buildings. We derived six equally ranked GLMs explaining building roost selection by *C. cor* (Table 2). Averaged models showed *C. cor* selected buildings that were less likely to have

permanent human occupants ($\beta = -2.80$; $P < 0.01$) when compared to control buildings (Fig. 5, Table S8).

DISCUSSION

We use bats, a highly pervasive taxa in anthropogenic environments, as a model system to understand features of urban settings that do and do not attract wildlife species. Our study demonstrates that building roosts of synanthropic bats in rural East Africa are associated with specific microclimate and structural attributes. Bats in general selected buildings that were taller, had higher WVP, and had lower presence of permanent human occupants compared to control buildings. Building roost selection was moderated by the effect of wall material on building height, with cement-walled buildings being taller than buildings made with other materials. However, our models had trouble incorporating data from the two disparate taxa into one model. When separated by taxonomic group, molossids selected building roosts based on reduced presence of permanent human occupants, building height, WVP, and wall material moderated by building height. In contrast, although our *Cardioderma cor* sample size was smaller than ideal, we found that this species focused on the absence of permanent human occupants in their selection criteria. These results provide valuable general information on synanthropic bat roost selection and help characterize contact between humans and bats in an urbanizing region of the Global South.

Building features that increase the likelihood of bat use can have major ramifications for human-wildlife contact and conflict. We identified direct and indirect pathways influencing bat building use, with models showing direct positive effects of building height and WVP and direct negative effects of presence of human occupants on bat use of buildings. Height is important for

wildlife to avoid ground-based predators and also bat species that must take-off from tall roosts to become airborne (Vaughan 1966, Lausen and Barclay 2006). Avoidance of buildings with permanent human occupants is a likely result of reduced disturbance and predation risk since many homeowners in this region have reported killing bats in their residence (Webala et al. 2014). We also identified a significant indirect effect of wall material on bat use of buildings, mediated through the significant effect of building height. Although this has not been cited previously as an important characteristic in building roost selection by bats, wall material is a crucial factor in building height as certain materials, like cement, provide structural integrity or increase building height. While previous studies may have missed the effects of wall material due to counteracting impacts, SEMs have the power to identify these intricacies and will be important for future research on similar questions (Kline 2011).

Our large dataset enabled us to compare building preferences between taxa, whereas previous investigations of building roost selection by bats have only focused on a single species or have grouped multiple species together (Entwistle et al. 1997, Fagan et al. 2018). Our results highlight the limitation of combining disparate bat species in analyses, showing that not all synanthropic species are homogenous in their roost preferences and that they may present different risks for contact with humans. For example, within our dataset most buildings selected by *C. cor* had no permanent human occupants. In comparison, almost half of buildings selected by molossids had permanent human occupants, which could put them at higher risk for contact with humans. Moreover, given that bats are present on all human-inhabited continents and have been recorded roosting in buildings throughout the world (Voigt et al. 2016), this principle is likely to be relevant in other settings.

We observed numerous cases of roost sharing by multiple bat species. While roost use by multiple species is not uncommon in bats, large multi-species aggregations may play an important role in viral evolution and diversity within bat populations (Luis et al. 2013, Furey et al. 2016, Phelps et al. 2016, Willoughby et al. 2017, Ntumvi et al. 2021). Currently, bat species documented to roost in multi-species assemblages have largely been described to co-roost with 2-3 other bat species (Geiselman & Younger 2020, Salinas-Ramos et al. 2020). We found that *M. pumilus* roosted with at least six other bat species in anthropogenic roosts, indicating great potential for multi-species interactions. In this region, *M. pumilus* hosts a high diversity of viruses, including coronaviruses, flaviviruses, adenoviruses, and potentially filoviruses (Kading et al. 2015, Forbes et al. 2019, Nziza et al. 2020, Ntumvi et al. 2021). Several of these viral families are highly capable of recombination, meaning that these diverse roosts may facilitate viral evolution in anthropogenic environments (Chan et al. 2013). Given that *M. pumilus* regularly roosts with other species in buildings, including bat genera like *Rhinolophus*, which are also known to host high-risk pathogens, these areas may be important hotspots within the wildlife-human urban interface for human exposure to viruses with zoonotic potential (Tao et al. 2017).

Understanding features of the urban-wildland interface that attract and repel wildlife is important for mitigating human-wildlife conflict that can lead to wildlife mortality. Mass mortality events of bats are generally human-caused, and most species are unable to recover quickly due to low reproductive output (O'Shea et al. 2015). Risk of spillback of zoonotic pathogens from humans to synanthropic bat populations may also exist, with additional negative ramifications for bat health (Olival et al. 2020). Bats provide critical ecosystem services, ranging from insect suppression that benefits local agriculture and forestry, to seed dispersal and

pollination of many tropical plants, and reducing their mortality directly benefits humans on many levels (Kunz et al. 2011, Voigt et al. 2016) Thus, our results can help inform the development of methods to reduce bat use of buildings. For example, our study indicates that construction of buildings under four meters in height and with venting to decrease water vapor pressure are likely to reduce bat use. Further, while structural changes are not possible for many existing buildings, emphasis can be placed on sealing entry points so that bats are unable to enter (Barclay et al. 1980); such actions are especially important for existing tall cement structures.

Ultimately, our results help characterize environmental conditions that can lead to human-bat contact. By identifying microclimate and structural attributes important to building roost selection, we can better understand characteristics that may increase the chance of human-bat interactions, with implications for human-wildlife conflict, pathogen transmission within synanthropic wildlife communities, and potential exposure risk for humans. Efforts to mitigate these interactions are useful in reducing human exposure to pathogens and anthropogenic mortality of bats. Our results show that it can be possible to identify hotspots of human-wildlife interactions in the human-wildland interface, which can help target where measures mitigating contact in urbanizing areas should be applied, especially in the Global South where resources are patchily distributed and limited.

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TABLES

Table 1. Eight bat species were found roosting in human buildings during surveys throughout communities in Taita-Taveta County, Kenya, 2021–2022. The number of other species sharing roosts refers to the number of other bat species a focal species was found roosting with across all shared buildings. All species except *Hipposideros caffer* were documented sharing buildings with at least one other bat species.

Species	Total no. of building roosts	No. roosts shared with other species	No. of other species sharing roosts
<i>Cardioderma cor</i>	18	4	2
<i>Epomophorus wahlbergi</i>	1	1	1
<i>Hipposideros caffer</i>	1	0	0
<i>Mops condylurus</i>	13	13	1
<i>Mops pumilus</i>	65	21	6
<i>Nycteris</i> sp.	4	1	1
<i>Rhinolophus cf. lobatus</i>	3	3	2
<i>Scotophilus andrewrebori</i>	3	2	1

Table 2. Rank of generalized linear models used to investigate the impacts of six covariates on roost selection of buildings by *Cardioderma cor*. Models were selected for comparison based on Aikake's Information Criterion corrected for small sample sizes (AICc) score and models within 2 Δ AICc units were considered competitive, with the weighted averages (W_i) of coefficients calculated for equally competitive models. We present the number of coefficients in each model (k) and results from chi-square goodness-of-fit-tests (χ^2).

Model	AICc	Δ AICc	W_i	k	χ^2
Building height + Human occupancy + Lux	48.78	0	0.30	4	0.84
Human occupancy + Lux	49.72	0.94	0.19	3	0.92
Building height + Human occupancy + Lux + Temperature + Water vapor pressure + Wall Material	50.34	1.55	0.14	7	0.83
Building height + Lux + Human occupancy + Water vapor pressure	50.47	1.68	0.13	5	0.84
Building height + Human occupancy + Wall Material	50.57	1.78	0.12	4	0.84
Building height + Human occupancy + Lux + Temperature	50.78	2.00	0.11	5	0.77

FIGURES

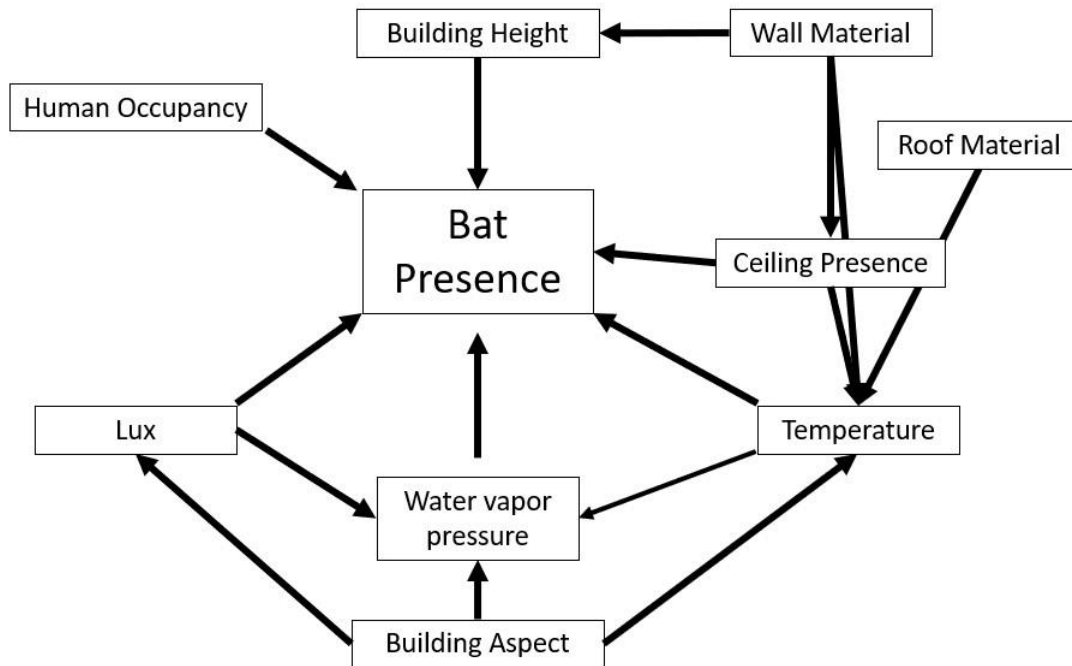


Fig. 1. We used a pre-conceived conceptual model containing all measured structural and microclimate features to guide structural equation model (SEM) development for assessing variables important to building roost selection by bats. Pathways were conceived based on knowledge of bat ecology, the impacts of different structural features on microclimate, and building construction limitations.

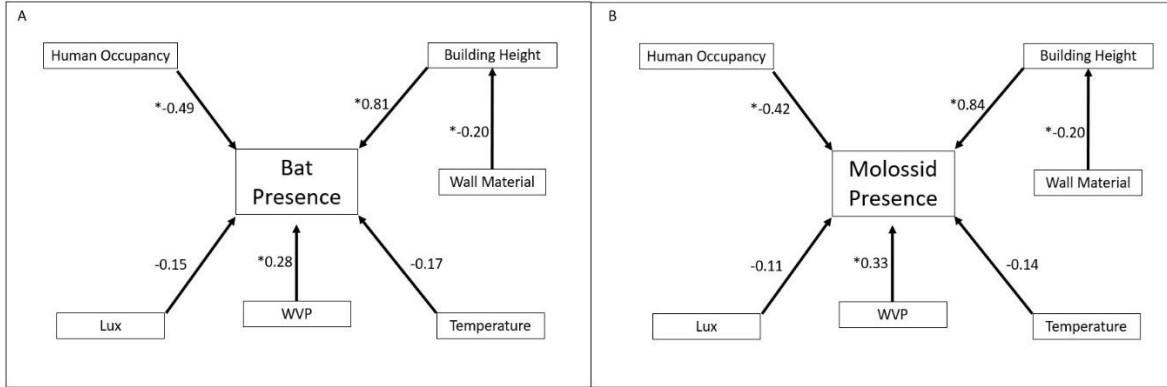


Fig. 2. Relationships of microclimate and structural attributes on bat selection of building roosts for A) buildings used by all bat species, and B) buildings used only by molossid bats (*Mops condylurus* and *M. pumilus*) analyzed with structural equation models. Numbers adjacent to arrows are the total path regression coefficients for each variable's effect on bat presence. The greater the absolute value of the number, the larger the impact on bat presence. Asterisks after each parameter estimate represent statistically significant relationships between variables ($P \leq 0.05$).

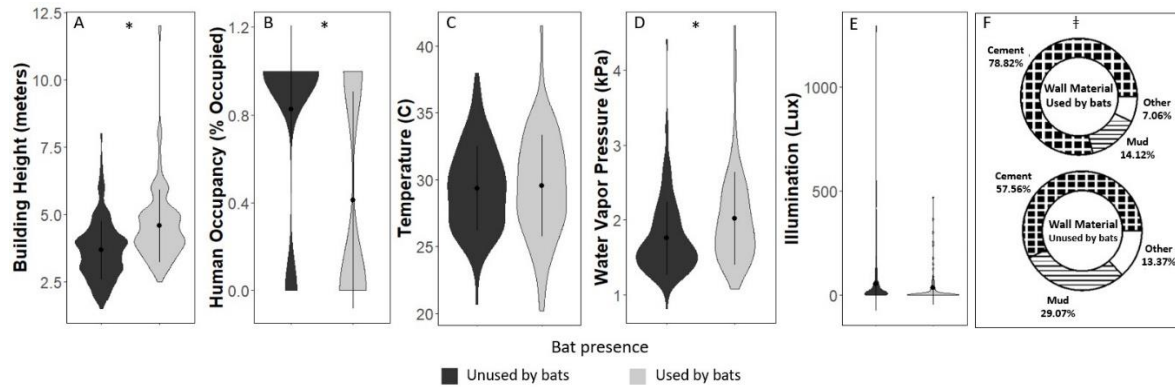


Fig. 3. Comparison of microclimate and structural attributes that contributed to selection of buildings as roosts by any bat species (A: building height; B: human occupancy; C: building temperature; D: building water vapor pressure; E: illumination; F: wall material). Asterisk (*) and alveolar clicks (‡) denote statistically significant (i.e., $P \leq 0.05$) direct and indirect effects, respectively, of covariates on bat roost selection identified via structural equation models. Dots and bars inside violins represent mean and standard deviation of the raw data, respectively.

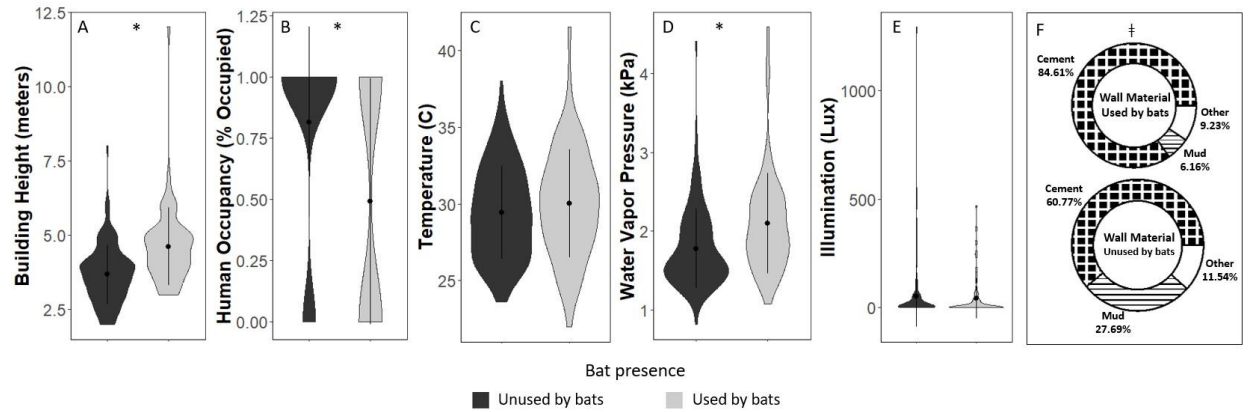


Fig. 4. Comparison of microclimate and structural attributes that contributed to selection of buildings as roosts by molossid bat species (A: building height; B: human occupancy; C: building temperature; D: building water vapor pressure; E: illumination; F: wall material). Asterisk (*) and alveolar clicks (‡) denote statistically significant (i.e., $P \leq 0.05$) direct and indirect effects, respectively, of covariates on bat roost selection identified via structural equation models. Dots and bars inside violins represent mean and standard deviation of the raw data, respectively.

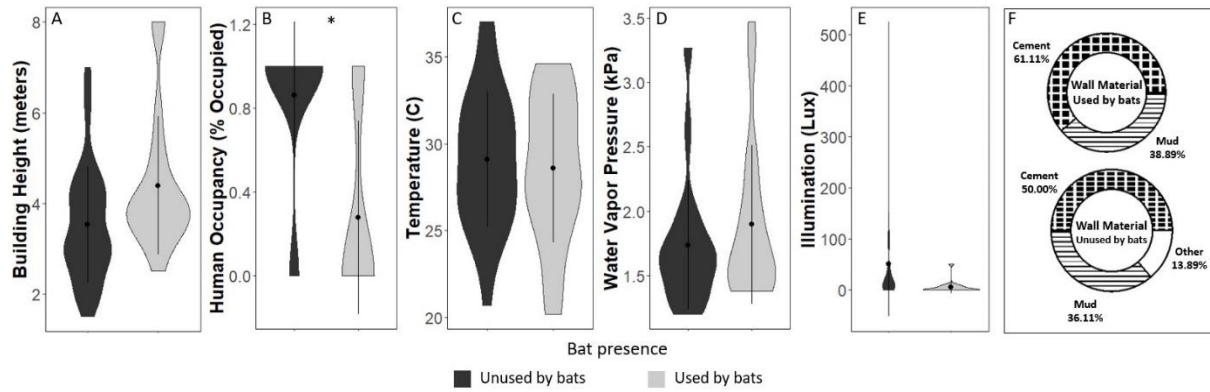


Fig. 5. Comparison of microclimate and structural attributes that contributed to selection of buildings as roosts by *Cardioderma cor* (A: building height; B: human occupancy; C: building temperature; D: building water vapor pressure; E: illumination; F: wall material). Asterisk (*) denotes statistically significant differences (i.e., $P \leq 0.05$) based on generalized linear models used to analyze data. Dots and bars inside violins represent mean and standard deviation of the raw data, respectively.

APPENDIX

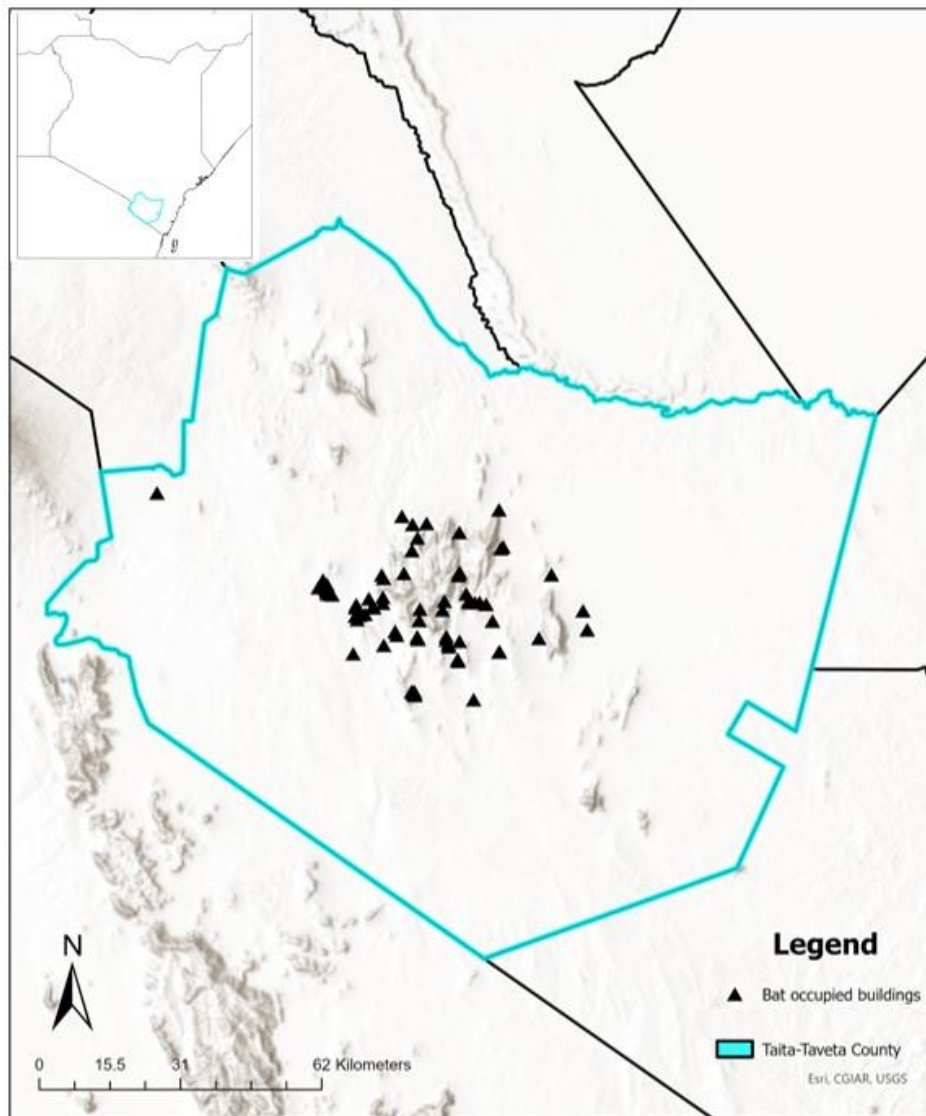


Figure S1. We investigated building roost selection by bats in Taita-Taveta county, Kenya, during 2021 – 2022. Taita-Taveta county is in southeastern Kenya and is characterized by lowland savanna surrounding remnant cloud forest patches of the Eastern Arc Mountains.



Figure S2. Synanthropic bats roosting in buildings often deposit feces that accumulates over time. Feces is frequently present in areas used by humans, catalyzing human-wildlife conflicts that can lead to public health risks and bat mortality.

Table S1. We removed two variables (roof material and attic presence) from analyses due to low variation within our dataset. Variables with >80% similarity were excluded from analyses (i.e., 97% of data points had metal walls, only 1.17% were thatch, 0.78% were wood, 0.39% were tile, and 0.39% were cement). We removed a third variable (building aspect) from analyses due to building having numerous entrances, which reduced our ability to confirm where bats entered buildings.

Variable	Reason for exclusion
Roof material	97% ($n = 250$) of surveyed buildings had metal roofs
Aspect	>80% ($n = 207$) of surveyed buildings had multiple access points
Attic presence	>80% ($n = 210$) of surveyed buildings did not have an attic

Table S2. We placed iButtons (Thermocron iButtons, Model DS1921, Maxim Integrated, San Jose, CA, USA) at a subset of buildings used by bats ($n=18$) and associated controls ($n=18$) for one week. Due to monetary and time constraints, as well as iButtons being removed from buildings by unknown people, we were unable to place iButtons at every building. Using this data, we based our building sampling during the hottest time of the day (11:00 – 17:00) to record peak daily temperature, humidity, and light at sampled building roosts and controls.

	Daily maximum	Daily minimum	Average variance between 11:00-17:00
Temperature (°C; $X \pm SE$)	34.88 ± 1.06	19.38 ± 0.53	3.99 ± 0.36
Time of occurrence (range)	14:09 (12:00 – 16:22)	6:15 (3:30 – 7:33)	

Table S3. Variance of grouping of sites (i.e., one occupied building and the two closest non-occupied buildings as controls) based on generalized linear mixed effect models (“lme4” R package). We tested the significance of grouping prior to analyses to determine if the non-random collection of buildings used by bats and associated controls had any impact on building roost selection. Our model structure for all datasets was the same: Building status (used or unused by bats) ~ Building height + Human occupancy + Lux + Temp + WVP + (1| Group). The ‘lme4’ R package uses constrained optimization to report variance of effects and returns values of exactly 0.

Dataset	Number of groupings	Variance
Main	85	0
Molossid-only	65	0
<i>Cardioderma cor</i> -only	18	0

Table S4. The direct and indirect pathway coefficients for structural equation models (SEMs) for all bats. Indirect effects (covariates mediated through another variable) can be calculated as the product of the coefficients along the path. The total effect one variable has on another can also be calculated as the sum of its direct and indirect effect. Asterisks denote significant direct and indirect effects.

Bat use of buildings				Building Height	
Variable	Direct	Indirect	Total	Variable	Direct
Building Age	0.15		0.15*	Wall Material	-0.21*
Building Height	0.80		0.80*		
Human Occupancy	-0.47		-0.47*		
WVP	0.26		0.26*		
Lux	-0.15		-0.15		
Temperature	-0.16		-0.16		

Table S5. Summary statistics of the covariates included in structural equation models used to analyze factors important in building roost selection by bats in Kenya, based on 85 buildings used by bats and 172 associated controls. Wall material is a categorical factor; therefore, we have presented the percent of surveyed buildings that had walls made with each material. ‘Other’ incorporates buildings with walls made of stone, metal, or unknown brick type.

		Bat-occupied buildings		Unoccupied buildings	
Variable	Description	X	SE	X	SE
Microclimate					
Water vapor pressure	kPa	2.02	0.07	1.75	0.03
Illumination	Lux	118	9.97	171	7.63
Temperature	°C	29.69	0.33	29.36	0.24
Structure					
Age	Years	20.51	2.03	15.14	1.12
Height	Meters	4.57	0.15	3.67	0.08
Occupancy	Percent occupied	41.17	5.37	82.55	2.90
Wall Material	Percent of buildings				
Cement		78.82		57.56	
Mud		14.12		29.07	
Other		7.06		13.37	

Table S6. The direct and indirect pathway coefficients for structural equation models (SEMs) for molossids. Indirect effects (covariates mediated through another variable) can be calculated as the product of the coefficients along the path. The total effect one variable has on another can also be calculated as the sum of its direct and indirect effect. Asterisks denote significant direct and indirect effects.

Variable	Bat use of buildings			Building Height	
	Direct	Indirect	Total	Variable	Direct
Building Height	0.84		0.84*	Wall Material	-0.20*
Human Occupancy	-0.42		-0.42*		
WVP	0.33		0.33*		
Lux	-0.11		-0.11		
Temperature	-0.14		-0.14		

Table S7. Summary statistics of the covariates included in structural equation models used to analyze factors important in building roost selection by molossids in Kenya. Wall material is a categorical factor; therefore, we have presented the percent of surveyed buildings that had walls made with each material. ‘Other’ incorporates buildings with walls made of stone, metal, or unknown brick type.

		Bat-occupied buildings		Unoccupied buildings	
Variable	Description	X	SE	X	SE
Microclimate					
Water vapor pressure	kPa	2.09	0.08	1.78	0.04
Illumination	Lux	45.02	11.46	53.43	12.28
Temperature	°C	30.13	0.40	29.45	0.26
Structure					
Age	Years	16.42	1.92	14.75	1.31
Height	Meters	4.62	0.16	3.67	0.08
Occupancy	Percent occupied	49.23	6.24	81.53	3.42
Wall Material	Percent of buildings				
Cement		84.61		60.77	
Mud		6.16		27.69	
Other		9.23		11.54	

Table S8. Summary statistics of the covariates included in generalized linear models used to analyze factors important in building roost selection by *Cardioderma cor* in Kenya. Wall material is a categorical factor; therefore, we have presented the percent of surveyed buildings that had walls made with each material. ‘Other’ incorporates buildings with walls made of stone, metal, or unknown brick type.

		Bat-occupied buildings		Unoccupied buildings	
Variable	Description	X	SE	X	SE
Microclimate					
Water vapor pressure	kPa	1.89	0.15	1.73	0.08
Illumination	Lux	5.67	2.81	50.17	17.02
Temperature	°C	28.57	1.00	29.11	0.64
Structure					
Age	Years	33.71	4.35	13.79	2.07
Height	Meters	4.38	0.36	3.53	0.21
Occupancy	Percent occupied	27.77	10.86	86.11	5.85
Wall Material	Percent of buildings	61.11		50.00	
Cement		38.89		36.11	
Mud		0.00		13.89	
Other					

CHAPTER III

BUILDINGS PROMOTE FREQUENT AND INTENSE CONTACT BETWEEN HUMANS AND BATS IN RURAL KENYA

Reilly Jackson, Tamika Lunn, Isabella DeAnglis, Joseph Ogola, Paul Webala, Kristian Forbes

ABSTRACT

Simultaneous use of domestic spaces by humans and wildlife is little understood, despite global ubiquity, and can create an interface for human exposure to wildlife pathogens. Bats are associated with several pathogens that can spillover and cause disease in humans and, due to loss of natural habitat and urbanization, increasingly use anthropogenic structures for roosting. The purpose of this study was to characterize human interactions with bats in shared buildings to assess potential for human exposure to and spillover of bat pathogens. We surveyed 102 people living and working in buildings used as bat roosts in rural Kenya between 2021 and 2023. Based on responses, we characterized and quantified the duration, intensity, and frequency of human-bat interactions occurring in this common domestic setting. Survey respondents reported living with bats in buildings year-round, with cohabitation occurring consistently for at least 10 years in 38% of cases. Human contact with bats occurred through direct and indirect routes, including exposure to excrement (90% of respondents), and direct touching of bats (39% of respondents). Indirect contacts most often occurred daily, and direct contacts most often occurred yearly. Domestic animal consumption of bats was also reported (16% of respondents). We demonstrate that shared building use by bats and humans in rural Kenya leads to prolonged, frequent, and sometimes intense interactions between bats and humans, consistent with exposure interfaces that can facilitate pathogen exposure and spillover. Identifying and understanding the settings and practices that may lead to zoonotic pathogen spillover is of great global importance for developing countermeasures, and this study establishes bat roosts in buildings as such a setting.

INTRODUCTION

Emerging infectious diseases (EIDs) are a significant threat to global health and security, as demonstrated by the recent COVID-19 pandemic and Mpox disease outbreak [1-3]. Most EIDs have zoonotic origins and emerge in humans via spillover of pathogens from animals, often wildlife [4]. These risks are exacerbated by growing human populations and conversion of natural lands to anthropogenic regions, which can increase human contacts with wildlife and exposure to their pathogens [4-6].

Settings and practices that lead to pathogen spillover are little understood but of great importance for informing outbreak mitigation strategies. In lieu of direct knowledge on pathogen exposure, which is extremely difficult to identify from wild animals, characterization of human-wildlife contact can be used to infer exposure risk. Identifying exposure settings has primarily focused on direct contact between humans and wildlife, largely in the form of wildlife hunting and markets for the sale of live animals [7-10]. For example, wildlife consumption and associated handling and butchering creates human contact with wildlife viscera and bodily fluids, which can facilitate spillover of their pathogens [11]. However, contacts between humans and wildlife occur across numerous settings outside of wildlife trade and consumption and can result in human exposure to wildlife pathogens [12]. Other settings and practices that promote contact between wildlife and humans have received far less focus despite the importance of their characterization to mitigating zoonotic pathogen spillover.

Wildlife often share spaces with humans and domestic animals, especially in the Global South, where humans and wildlife coexist closely in developing landscapes and EID risk is high [13-14]. Studies have reported many communities struggling to manage small mammal incursion into buildings [15-17]. The presence of mammals in these spaces can create opportunities for human and domestic animal contact with wildlife and their excreta, potentially exposing them to

wildlife-borne pathogens [18]. Despite the risk, characterization and quantification of contacts within buildings, where people may spend significant portions of their lives, is lacking.

Bats can harbor zoonotic pathogens that may be shed in excreta and bodily fluids (eg., feces, urine, saliva, blood, etc.) [19-20]. Several bat-borne viruses have emerged in humans after transmission from bats via indirect contact with bat excreta or direct contact with bat bodily fluids [21-24]. Domestic animals can also be exposed to these pathogens after contact with bats excreta and fluids [25]. In developing settings, anthropogenic structures, like family homes, places of worship, and schools, can be highly permeable to bats, and with ongoing habitat loss bats are increasingly using these buildings as roosts [26-27]. Few options exist for people to safely manage bat use of their buildings, and this provides numerous opportunities for human-bat contact and conflict. However, detailed characterization of how humans contact bats and their excreta in relation to pathogen exposure risk in shared spaces is lacking and requires attention.

We investigated human-bat interactions in anthropogenic structures in rural south-eastern Kenya to characterize and quantify forms of contact that could lead to human exposure to bat pathogens. Bats are known to roost frequently in buildings simultaneously used by humans across Africa [28-31], including the focus area [32], and this region of Kenya has been forecasted as a hotspot for zoonotic pathogen emergence where surveillance and mitigation efforts are needed [14]. By understanding interactions between humans and bats and their potential to facilitate pathogen exposure and spillover, we can better identify human health risks and develop evidence-based strategies towards mitigation.

METHODS

This study was conducted in Taita-Taveta County, Kenya. The most recent 2019 population estimate of Taita-Taveta County was 340,671 people in 2019 [33], with a 1.8% annual increase in population over the preceding 10 years. Almost three-quarters of the population is considered rural, although urbanization and deforestation are increasing substantially in the region [34-35]. This area is characterized by remnant patches of high-elevation cloud forest surrounded by low-elevation grasslands, woodlands, and agriculture [36].

We surveyed people in Taita-Taveta County during 2021 (August – October), 2022 (January – April), and 2023 (May – June) to understand and characterize human and domestic animal interactions with bats living in buildings. Participants were identified via word-of-mouth conversations with community members throughout the study area. We sought out adults who had bats in their homes (permanent and rental properties) or workplaces at the time of the survey, or who had evidence of recent sustained bat use (i.e., urine staining, fecal deposits, dead bats, etc.). Surveys were directed to one individual per property, however additional family members were sometimes present during questioning. Participants were informed about the study and verbal consent was obtained prior to conducting surveys. This research was approved by the Kenyan National Commission for Science, Technology and Innovation (#NACOSTI/P/21/9267) and University of Arkansas Institutional Review Board (Protocol #2103320918).

Surveys were conducted in the local Taita language, Swahili, or English by local Taita assistants and at least one of the authors. Questions were read to respondents by the research team and answers were transcribed by the team. Our survey consisted of short-answer, dichotomous, and categorical questions to characterize resident human and domestic animal demographics of the property, the duration of bat use of the property and its buildings, and human and domestic animal interactions with bats and their excreta (see Supplementary

Materials for detailed information on survey questions). Surveys from 2021 ($n = 23$) included 23 multi-part questions. After this initial data collection, we added one additional question to characterize human and domestic animal contact with dead bats on the property. Therefore, surveys conducted in 2022 and 2023 ($n = 79$) included 24 multi-part questions.

To explore the effect of the number of residents on the property, length of bat building use, and respondent demographics (gender, education, and age) on direct (e.g., touching, scratches, bites, etc.) and indirect (e.g., contact with bat excrement) interactions with bats, we used univariate generalized linear models with a binomial error distribution and logit link function. We used chi-square tests to compare the frequencies of bat interactions, duration of bat occupation of buildings, bat exclusion methods employed by inhabitants, and reasons for exclusion. All analyses were conducted in R (Version 2023.06.2+561) using the stats package (v4.1.3).

RESULTS

We surveyed 102 people who lived or worked in buildings used by bats (Table S1). Over 70% of people reported bat use of their buildings for >5 years ($n = 72$), with bat presence for 5-10 years most commonly reported ($\chi^2 = 36.52$, $P < 0.01$, Fig. 1). Most properties (88%) had bat presence year-round ($n = 90$). Survey participants described frequent exposure to bats that would support pathogen transmission through two main routes: direct and indirect (fecal/oral) contact, with indirect contact between bats and humans reported more frequently than direct contacts ($\chi^2 = 24.77$, $P < 0.01$, Fig. 2A).

Close to half of participants (39%) reported direct contact with bats, including people touching bats ($n = 40$) and one report of being bitten. People on the property (children, spouses,

custodians) other than the respondent engaged in these interactions as well. Direct interactions occurred with varying frequencies over time according to respondents (Fig. 2B). Reports of direct contact did not differ significantly based on the number of residents on the property, length of time of bat use, or respondent demographics (gender, education, and age; $P > 0.06$).

Over 90% of respondents reported indirect contact with bats, mostly through interactions with their feces and urine ($n = 98$). Daily occurrences of indirect contact were reported by most participants (78%, $\chi^2 = 285.06$, $P < 0.01$, Fig. 2B) and children, spouses, house guests, and custodians were also involved in these interactions. Reports of indirect contact did not differ significantly among the number of residents on the property, length of time of bat use, or respondent demographics (gender, education, and age; $P > 0.13$).

Attempts to remove bats from buildings create opportunities for direct human-bat contact and were reported by almost 80% of participants ($n = 81$). Of those reporting removal efforts, almost half reported direct contact with bats ($n = 34$). Numerous removal methods were reported, with fumigation via pesticide, blocking access to building entry points, and scaring bats from buildings reported more than other methods ($\chi^2 = 107.37$, $P < 0.01$; Table 1). Bats returned to the property after removals in over 90% of cases ($n = 76$). Bad smells ($n = 39$), noise ($n = 39$), dirt from feces and urine ($n = 36$), and damage to property ($n = 21$) were the most common reasons reported for removing bats. Significantly fewer respondents mentioned worries about witchcraft ($n = 15$), that bats were a general nuisance ($n = 12$) or posed health risks to people ($n = 8$) compared to more common removal reasons ($\chi^2 = 123.47$, $P < 0.01$).

We asked a subset of participants about the presence of dead bats on their properties ($n = 79$). Nearly 65% reported dead bats on properties ($n = 51$). Most removed dead bats, usually by throwing them over property lines ($n = 30$) or swept them outside ($n = 7$). Some also reported

burning ($n = 6$), feeding to domestic cats ($n = 2$), and burying bat carcasses ($n = 1$). Interestingly, 13 respondents reported seeing domestic animals (dogs, cats, and chickens) consume dead bats on their property, most often their own animals.

DISCUSSION

We establish that buildings are a common interface for human-bat contact in rural Africa and that these interactions can be intense, frequent, and occur consistently over long periods of time. Our survey respondents had exposure to bats in ways that can promote pathogen transmission through direct or indirect pathways, as well as via domestic animals as intermediate hosts. Much attention has focused on bushmeat hunting and wet markets as high-risk practices and settings for wildlife pathogen exposure risk. Given the increasing rate of urbanization and subsequent habitat loss bats are experiencing, anthropogenic structure sharing by humans and bats is likely to become more common across the globe and a greater risk setting for zoonotic spillover.

Our results show that bats and humans contacted each other directly (e.g., touching, scratches, bites, etc.) and indirectly (e.g., contact with bat excrement). Direct contacts can expose humans to lethal viruses hosted by bats, with various lyssaviruses (including rabies virus) being the most well-known bat-borne pathogens transmitted in this manner [37]. Indirect contacts were frequently reported in our study and are also common pathways for zoonotic pathogen spillover [38]. Bat excreta reported in these indirect interactions, mostly feces, can contain pathogens shed by bats in this region, including coronaviruses, rotaviruses, and paramyxoviruses that are viral families of concern [20]. Fungal pathogens, like *Histoplasma capsulatum*, the causative agent of

histoplasmosis, may also be inhaled from bat fecal dust and have infected people living in buildings with bat roosts in Africa [39].

Multiple respondents reported observing domestic animals – mainly cats, dogs, and chickens – consuming bats. Predation and consumption of bats can facilitate transmission of zoonotic parasites into consumers, including domestic animals [40], which can also serve as bridge or intermediate hosts for onward transmission to humans [41]. Furthermore, bats often roost in livestock enclosures in this region and may deposit feces or bodily fluids in spaces frequently used by domestic animals [42]. Many frugivorous bat species chew and eject saliva-covered fruit pulp below their roosts, which domestic animals may also then consume and become exposed to shed pathogens [43]. Indeed, it is thought that Nipah and Hendra virus, both paramyxoviruses with high human mortality, emerged in pigs and horses in this fashion, respectively [25].

Our results show that community members attempted to remove bats from their buildings, mostly via fumigation with pesticides, blocking bat entrance points, and direct killing of bats. Paradoxically, these activities often led to direct human contact with bats, creating additional opportunities for pathogen exposure. Stress to bats caused by removal attempts can also increase pathogen transmission risk by altering bat behavior and immune function, which collectively drive contact rates and pathogen susceptibility and shedding [44-46]. Furthermore, high bat mortality can negatively impact the critical ecosystem services that bats provide by reducing their ability to consume insect pests, pollinate fruit trees, and disperse seeds [47].

It is worth noting that this study employed a survey, which required respondents to opt in for participation. In this region, there is negative cultural stigma associated with people interacting with bats, as bats are often maligned as witches, bad omens, or general harbingers of

malaise [29, 48]. Therefore, it is possible that our respondents were biased towards people with strong opinions or greater interactions with bats that were willing to share more of their experiences, or that did not care or were unaffected by regional customs about bats [49]. Nevertheless, the identification and characterization of these interactions demonstrates relevant pathways for zoonotic pathogen exposure and spillover.

The presence of bats in buildings is common in developing settings and our findings establish that there are frequent and prolonged interactions between humans and bats in these areas, consistent with interactions that can facilitate pathogen spillover. Bat mortality is also frequent in these settings, with further ramifications for facilitating bat-human contact and wildlife and ecosystem health. Given the increasing rate of urbanization and subsequent habitat loss bats are experiencing, anthropogenic structure sharing by humans and bats is likely to become more common across the globe and a greater risk setting for zoonotic pathogen spillover. [26-27].

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TABLES

Table 1. Methods used by people to remove bats from buildings. Attempts to remove bats were common and frequently led to direct contact with bats that could facilitate pathogen exposure.

Type of removal effort	Number of responses (%)
Fumigation via pesticide	36 (44.44)
Blocking access to buildings	25 (30.86)
Scaring bats	22 (27.16)
Killing individual bats	19 (23.46)
Smoking bats out	5 (6.17)
Application of holy water	2 (2.47)
Removal of ceiling	2 (2.47)
Application of salt	2 (2.47)
Killing via domestic animal	1 (1.23)

FIGURES

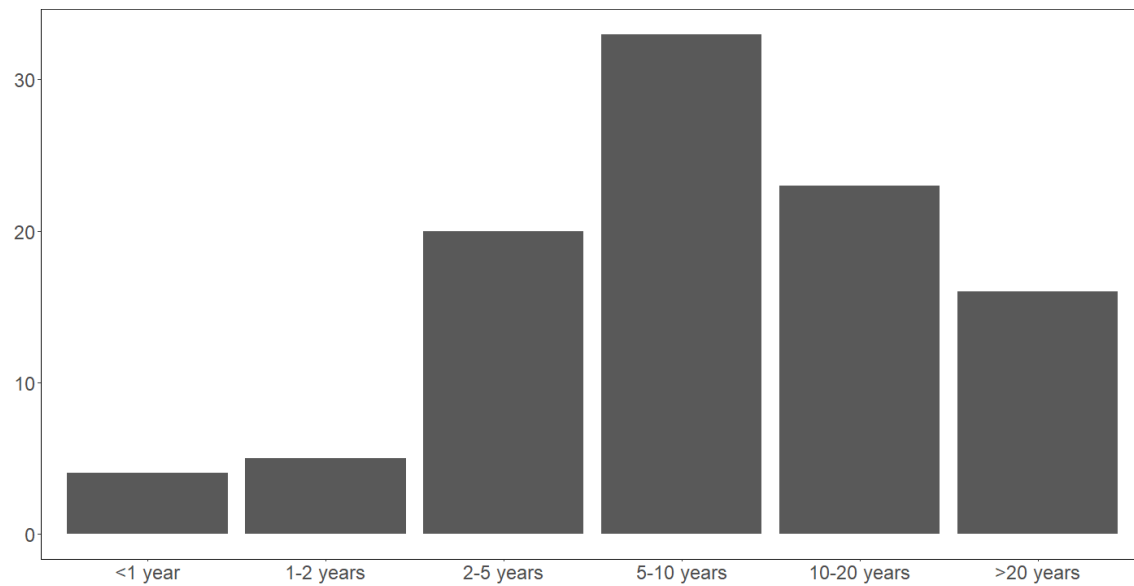


Figure 1. The number of respondents reporting the length of time bats had been present in their buildings. All but one participant answered this question.

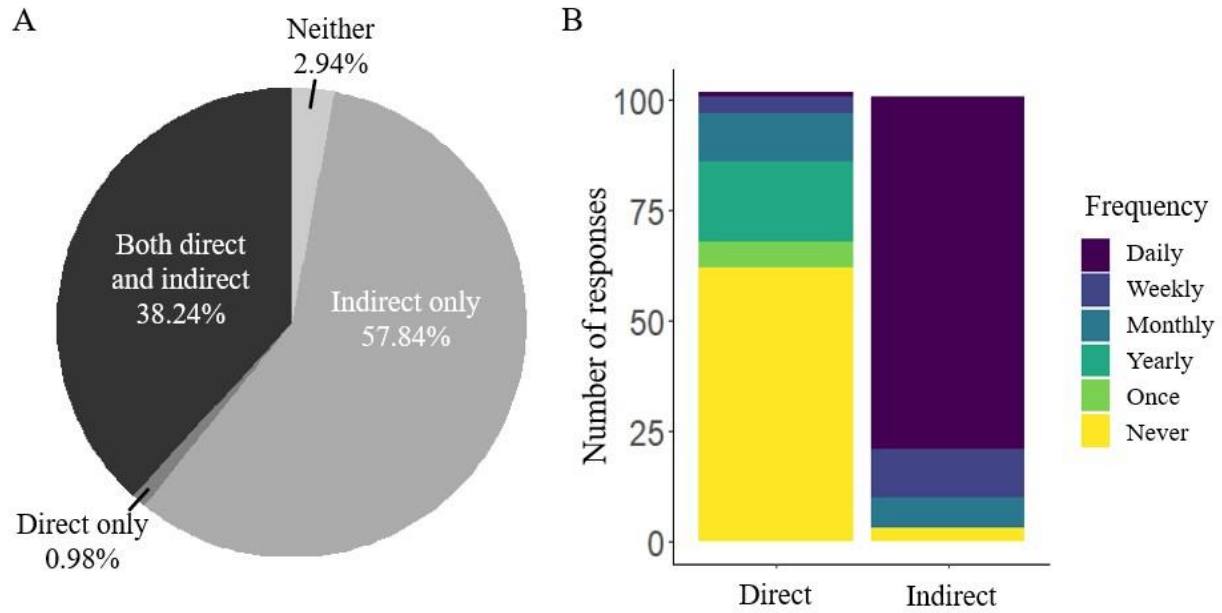


Figure 2. People surveyed about human-bat interactions in their buildings reported both direct (e.g., touching, scratches, bites, etc.) and indirect (e.g., contact with bat excrement) contacts between humans and bats. (A) Indirect interactions were the most reported of the two interaction types; (B) Frequency of these contacts varied from daily interactions to never having these interactions.

APPENDIX

Appendix S1. The survey used to characterize and quantify human-bat interactions in buildings in rural Kenya. This survey was directly translated from English into Swahili and Taita for interviews requiring use of these languages.

50. Who lives on the property?

1a. Respondent demographic data (Age: ____/Prefer not to say, Sex: Male/Female/Other/Prefer not to say, Occupation:_____/Prefer not to say, Education level:_____/Prefer not to say)

1b. Number of people: _____

1c. Number of men (age): _____

1d. Number of women (age): _____

1e. Number of children: _____

51. Structure of the property:

2a. Is there a ceiling in the main building? (Yes/No/I do not know)

2a.i. If yes, how large is the ceiling? (1-3 meters, 3.1-5 meters, 5.1-7 meters long)

2b. How many rooms does the main building? (1-3, 4-6, 7+)

2c. How many levels is the house? (1, 2, 3, 4+)

2d. What are the walls of the home made from: (Brick/stone, wood, vinyl, metal, thatch, mud brick, mud plaster, other:_____)

2e. What is the roof of the home made from: (Brick/stone, wood, vinyl, metal, thatch, mud brick, mud plaster, other:_____)

2f. Is the home occupied during the night? (Yes/No/I do not know)

2g. Are there animals kept on the property? (Yes/No/I do not know)

2f.i. If so, what animal species are present and how many? Cow (), pig (), horse (), camel (), sheep (), goat (), chicken (), dog (), cat (), other:_____

2h. Is there an open water source on the property? (pond, animal trough, other:_____, none)

2i. Are there other structures on the property aside from the main home? (Yes/No/I do not know)

2i.i. Please list: (Barn/livestock building, shed, old unused houses, latrine, kitchen, other:_____)

52. Bats on property:

3a. If bats are on your property, where do they roost? Main home, stores, old unused houses, livestock building, toilet, kitchen, trees, other:_____

3a.i. If in a building, what part of the building do the bats live in? Roof, ceiling, walls, other:_____

3a.ii. If in a tree, what type (or species) of tree do they live in on the property? Fruit tree (species (if known):_____) or other:_____

3.a.iii. Are the bats on the property year-round? (Yes/No/I do not know)

3.a.iii.1 If not year-round, what time of year are bats present? _____

- 3.a.iv. How many bats are present? _____
- 3b. How long have you had bats on the property? (1-4 weeks, 1-12 months, 1-2 years, 2-5 years, 5-10 years, 10-20 years, >20 years)
- 3c. Do all of the bats on the property look the same? (Yes/No/I do not know)
- 3c.i. If no, how many different types of bats live on the property: _____
- 3c.ii. If no, do all of the different bats live in the same area?: _____
- 3d. Do you see bats drinking water on the property? (Yes/No/I do not know)
- 3d.i If yes, where do the bats drink from? _____
- 3d.ii If yes, is this the same water source used by livestock or humans? (Yes/No/I do not know)
- 3e. How many times in the past have you or a household member touched bats on the property? (Every day, every week, every month, every year, never) _____
- 3e.i. If not you, has someone in your household touched bats on the property (Yes/No/I do not know)
- Who: _____
- 3f. Have you or a family member received bites from bats on the property? (Yes/No/I do not know)
- 3f.i. If yes, when have you or a family member ever been bitten by a bat on the property previously? (Within a year, over a year ago, never)
- 3f.ii. If yes, how many bat bites have you and your family received since you have lived on the property? (1-3, 4-7, 7+) ex: _____
- 3f.iii. If yes, who on the property has received bat bites previously?
- _____
- 3g. If you or a family member have interacted with bats on the property, what were they doing during these interactions? (flying, roosting/sleeping, biting, crawling, dying, _____)
- 3h. How many times in the last year have you or a family member interacted with bat urine/feces on the property: (Every day, every week, every month, every year, never, unknown)
- 3h.i. If not you, has anyone in your family interacts with bat urine/feces on the property: (Yes/No/I do not know)
- 3h.ii. Who else besides you interacts with feces/urine on the property? _____
- 3h.iii. How many times a year do you or a family member clean bat urine/feces from the property: (Every day, every week, every month, every year, never)
- 3h.iv. If not you, has anyone in your family cleaned bat urine/feces from the property: (Yes/No/I do not know)
- 3h.v. Who else besides you cleans urine/feces property? _____
- 3i. Do you or a family member ever try to remove the bats from the property: (Yes/No/I do not know) Who removes bats from the property? _____
- 3i.i. If yes, what method(s) do you use to remove bats from the property: (Killing bats, poisoning, scaring bats, blocking access, other: _____)

3i.ii. If yes, do the bats return to the property: (Yes/No/I do not know)

3i.iii If yes, why do you choose to remove the bats from the property:

(
_____)

3i.iv. If no, why do you choose not to remove the bats from the property:

(
_____)

3j. Do you or anyone in your family find dead/dying bats on the property: (Yes/No/I do not know)

3j.i. If yes, are dead bats removed from the property: (Yes/No/I do not know)

3j.ii. If yes, how are dead bats removed from the property:

3j.iii. If yes, do livestock (i.e., cats, dogs, pigs, etc.) ever contact or consume dead bats found on the property: (Yes/No/I do not know) Which livestock animals?

Table S1. Demographics of respondents asked about their interactions with bats living in their buildings in rural Kenya. Data from these demographics were incorporated into analyses to understand risk factors for direct and indirect interactions between humans and bats in anthropogenic structures.

Demographic	Number of people	Mean (Range)
Gender:		
Female	50	
Male	52	
Non-binary/Other	0	
Age (years)		51.88 (21-92)
Education Level:		
None	2	
Primary	41	
Secondary	17	
Post-secondary	19	
Property residents (number of people)*		3.89 (0-13)

*Two properties contained large unknown numbers of residents and were not incorporated in analysis of resident population size.

CHAPTER IV

IDENTIFICATION OF PARAMYXOVIRUSES IN SYNANTHROPIC FREE-TAILED BATS IN KENYA

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ABSTRACT

Several paramyxoviruses have recently emerged in humans and domestic animals after exposure to infected bats and their excreta. The proximity of synanthropic bats to humans may create opportunities for human exposure to bat viruses and pose a risk to human health. To identify paramyxoviruses present at the human-bat interface, we screened feces of synanthropic *Mops condylurus* and *Mops pumilus* bats captured in rural Kenya during 2021 and 2023. Bats were infected with a jeilongvirus within the paramyxovirus family and sequencing results indicated this virus was related to jeilongviruses found in bats in North America, Asia, and other regions of Africa. Of 297 fecal samples, 4.04% were positive for this jeilongvirus, with 4.43% prevalence in *M. condylurus* and 3.95% prevalence in *M. pumilus*. The paramyxovirus was detected in adult bats, both males and females, and across all reproductive classes. The zoonotic potential of jeilongviruses is currently unknown, however host-switching capacity and prevalence in bats living with humans necessitate further investigation.

INTRODUCTION

Wildlife-borne pathogens are a major source of emerging infectious diseases for humans, and these diseases can have large, negative impacts on global human health and security (Daszak et al. 2000, Jones et al. 2008, Madhav et al. 2018). Humans may be exposed to synanthropic wildlife and their zoonotic parasites, many of which have spilled over to people and domestic animals in the past (Jones et al. 2013, Hassell et al. 2017). The identification of zoonotic pathogens present in synanthropic wildlife is therefore important to mitigate risks and prepare for future outbreaks.

Synanthropic bats exist worldwide, and many species are increasing their use of anthropogenic spaces shared by humans (Russo and Ancillotto 2015, Voigt et al. 2016). This overlap in space use by humans and bats regularly leads to interactions between taxa, for example through consumption of bats by humans and domestic animals, bats preying on livestock, and bats roosting in human buildings (Voigt et al. 2016, Openshaw et al. 2017, Mendoza-Saenz et al. 2021). These interactions between humans and bats can create opportunities for human exposure to bat-borne zoonoses, which is a critical step in zoonotic pathogen spillover (Plowright et al. 2017).

Paramyxoviruses are a viral family with multiple members that have spilled over from wildlife into humans, with bats as key reservoir hosts (Thibault et al. 2017). They are highly diverse and many viruses in this family are known to cause severe human disease (Drexler et al. 2012). For example, Nipah and Hendra viruses are paramyxoviruses that emerged in humans and domestic animals after exposure to the contaminated bodily fluids of fruit bats (Daszak et al. 2006). These viruses have had major effects on human and domestic animal health, with human case fatality up to 75% in some outbreaks (Epstein et al. 2006). Several less pathogenic paramyxoviruses of bat origin have also spilled over into humans, often with a single human case documented and no onward transmission (Thibault et al. 2017). Given the broad diversity of this family and demonstrated record of spill over events, additional work is needed to identify bat-borne paramyxoviruses in anthropogenic areas.

Identification and characterization of paramyxoviruses in synanthropic bats is necessary because of the risk for human exposure during interactions with bats. We sampled bats in rural southeastern Kenya, which is an estimated hotspot for zoonotic disease emergence (Allen et al. 2017). Bats and humans share buildings in this region of Kenya and interactions that can expose

humans to bat pathogens occur frequently in these spaces (Jackson et al. 2023a, 2023b).

Therefore, we screened common bat species living in and around domestic spaces to identify paramyxoviruses present at this wildlife-urban interface.

METHODS

We captured bats in Taita-Taveta county in southwestern Kenya during August-October 2021 and May 2023. This region is largely rural; lowland areas (<1400 m.a.s.l) are dominated by savanna-scrub, agriculture, and two growing urban centers that have high population growth rates (Abera et al. 2022, Nyongesa et al. 2023). In this area, bats commonly roost in buildings coinhabited by humans, creating an interface for potential human exposure to bat-borne pathogens (Jackson et al. 2023a, Lunn et al. 2023a).

Bats were captured via mist-nets in flyways, building roosts, and by hand inside building roosts (see Jackson et al. 2023a). Upon capture, bats were placed into individual cotton bags and were stored in a cool, humid location overnight prior to processing to allow for fecal deposition in bags (Forbes et al. 2019, Lunn et al. 2023b). During processing, bats were identified to species level (based on Patterson and Webala 2012), sexed (male or female), and aged based on fusion of the phalangeal epiphysis (adult or juvenile). We assigned adults to various reproductive classes: for males, we noted the presence or absence of enlarged testicles and for females we classified individuals as non-reproductive, pregnant, lactating, and post-lactating (see Lunn et al. 2023b). We collected feces from bags or any fresh feces a bat produced during processing. Bats were released at their point of origin at dusk the evening following capture. We placed fecal pellets in 2 ml tubes containing 0.5 ml of RNAShield or RNALater (VWR International, Radnor,

Pennsylvania, USA). After collection, samples were stored at -20°C for a short initial period, after which they were stored in -80°C freezers until RNA extraction.

We screened bat fecal samples for paramyxoviruses. RNA was extracted using Invitrogen TRIzol (Thermo Fisher Scientific, Waltham, Massachusetts, USA), following the manufacturer guidelines. We used a conventional PCR protocol targeting the partial RdRp nucleotide sequences of paramyxoviruses, which consisted of the conversion of RNA to cDNA via two rounds of nested traditional PCR (Supplementary Materials). The first round of PCR (forward primer: 5'-GAA GGN TAT TGT CAN AAR NTN TGG AC-3'; reverse primer: 5'-GCT GAA GTT CAN GGN TCN CCD ATR TTN C-3') included SuperScript™ III One-Step RT-PCR (Thermo Fisher Scientific), and we used AllTaq polymerase (Qiagen, Hilden, Germany) in the secondary touchdown PCR (forward primer: 5'-GTT GCT TCA ATG GTT CAR GGN GAY AA-3'; reverse primer: 5'-GCT GAA GTT CAN GGN TCN CCD ATR TTN C-3'). We used gel electrophoresis in 2% agars to verify amplification of paramyxovirus in PCR products. Lastly, positive samples were sent for Sanger sequencing to identify detected paramyxoviruses.

To characterize detected paramyxoviruses, we ran amplified partial RdRp nucleotide sequences from Sanger sequencing results in BLASTn. Based on BLASTn results, the paramyxovirus present was a jeilongvirus, in the family Orthoparamyxoviridae. A phylogenetic tree was constructed with previously identified bat and rodent-borne paramyxoviruses and used henipaviruses, a closely related paramyxovirus genus, as the out-group for rooting the tree. We used a maximum likelihood tree structure fitted in ModelFinder with 1000 bootstrap computations and used Bayesian information criterion (BIC) scores to select the best fit model (Minh et al. 2020). A general time reversible model with empirical base frequencies and

invariable sites with a gamma distribution in rate category 4 (GTR+F+I+G4) was used to generate the final phylogenetic tree. We performed all consensus tree editing in iTOL.

RESULTS

We screened 297 fecal samples collected from *Mops condylurus* and *M. pumilus* bats in 2021 and 2023. We detected paramyxovirus RNA in 12 individuals across both species. We successfully sequenced amplified products from two *M. condylurus* captured from buildings in 2023 (Table 1). Phylogenetic analyses showed that both individuals were infected with a jeilongvirus (Figure 1). Sequencing results indicated this virus is related to jeilongviruses found in bats in North America, Asia, and other regions of Africa.

Paramyxoviruses were present in fecal samples in August and October of 2021, and May of 2023. Positive samples were from bats captured from one bridge and five buildings; three of the buildings are used daily by homeowners and workers, while two are used intermittently by building owners. Infection prevalence in *M. condylurus* was 4.34% and prevalence in *M. pumilus* was 3.95% (Table 1). All positive bats were adults. Most positive bats were female (n = 8; 66.67%), while four were male. Of the females, three individuals were non-reproductive, three had evidence of recent nursing, and three were pregnant. Most positive males had descended testes when captured (n = 3; 75%).

DISCUSSION

Our results show that bats infected with a jeilongvirus – a type of paramyxovirus – are present at the wildlife-urban interface in rural Kenya, a predicted hotspot for zoonotic pathogen emergence. This jeilongvirus was present throughout the year in adults of the two bat species

commonly found in anthropogenic areas. Little is currently known about the zoonotic potential of jeilongviruses. However, as our work shows, this genus of paramyxoviruses is present in bats near humans and further research is warranted to understand bat-borne jeilongvirus prevalence and capacity for spilling over into humans and domestic animals.

Bats harbored a jeilongvirus, which belongs to a recently recognized genera of Paramyxoviruses that have a global distribution in bats, rodents, and other small mammals (Rima et al. 2019, Su et al. 2023). Recent paramyxovirus surveillance has shown this genus to be highly diverse, with many viruses described but information lacking on their interactions with bats, such as host range and infection dynamics (Wells et al. 2022). Despite being closely related to henipaviruses, the genus hosting the lethal Hendra and Nipah viruses, the zoonotic potential of jeilongviruses is currently unknown and no cases of spillover into humans or domestic animals have been documented (Haas and Lee 2023). Significantly, however, this genus has host-switching potential, and it is theorized that jeilongviruses originated in rodents before becoming globally distributed in bats (Zhu et al. 2022, Su et al. 2023). Host-switching capacity is an important characteristic of zoonotic pathogens and paramyxoviruses with this trait, especially those of bat origin, may be a cause for concern (Johnson et al. 2015).

Our results show that jeilongvirus infection occurred in molossid bats captured in multiple sites and sampling periods, and in individuals of two species, both sexes, and various reproductive classes, suggesting that this virus may be endemic to the molossids of this system. Although the prevalence of paramyxoviruses was low across both bat species tested, our results mirror prevalence rates documented in bats previously (Conrardy et al. 2014, Waruhiu et al. 2017, Hoarau et al. 2023). Various life history characteristics, including gregariousness, small intervals between the birth of young, and mixing of species within roosts may all contribute to

paramyxovirus prevalence found in this family across geographies (Luis et al. 2013, Willoughby et al. 2017, Jackson et al. 2023, Lunn et al. 2023b). Many species of molossid are synanthropic and their active use of anthropogenic spaces can facilitate human and domestic animal exposure to molossid-borne paramyxoviruses circulating in these areas (Plowright et al. 2017, Lunn et al. 2023a).

In sum, we identified a jeilongvirus that is present in bat species that commonly share space with humans and domestic animals in Kenya. While the zoonotic capability of this virus is unknown, additional efforts to understand the ecology and zoonotic potential of jeilongviruses may be warranted given their close relatedness to zoonotic henipaviruses, the capacity for host-switching of jeilongviruses, and their presence in multiple synanthropic bat species at the wildlife-urban interface. Future studies with larger sample sizes will increase our understanding of paramyxovirus infection trends across additional synanthropic bat species, sexes, ages, and reproductive stages, which will be necessary to reduce human exposure to bat-borne paramyxoviruses at this intersection of humans and bats.

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TABLES

Table 1. Summary of fecal samples screened and positive samples for paramyxoviruses based on bat species, year of sampling, population prevalence, and sequencing.

Species	Number positive/Number screened		Total prevalence (%)	Sequenced
	2021	2023		
<i>Mops condylurus</i>	0/42	5/75	4.34	2
<i>Mops pumilus</i>	4/60	3/120	3.95	0

FIGURES

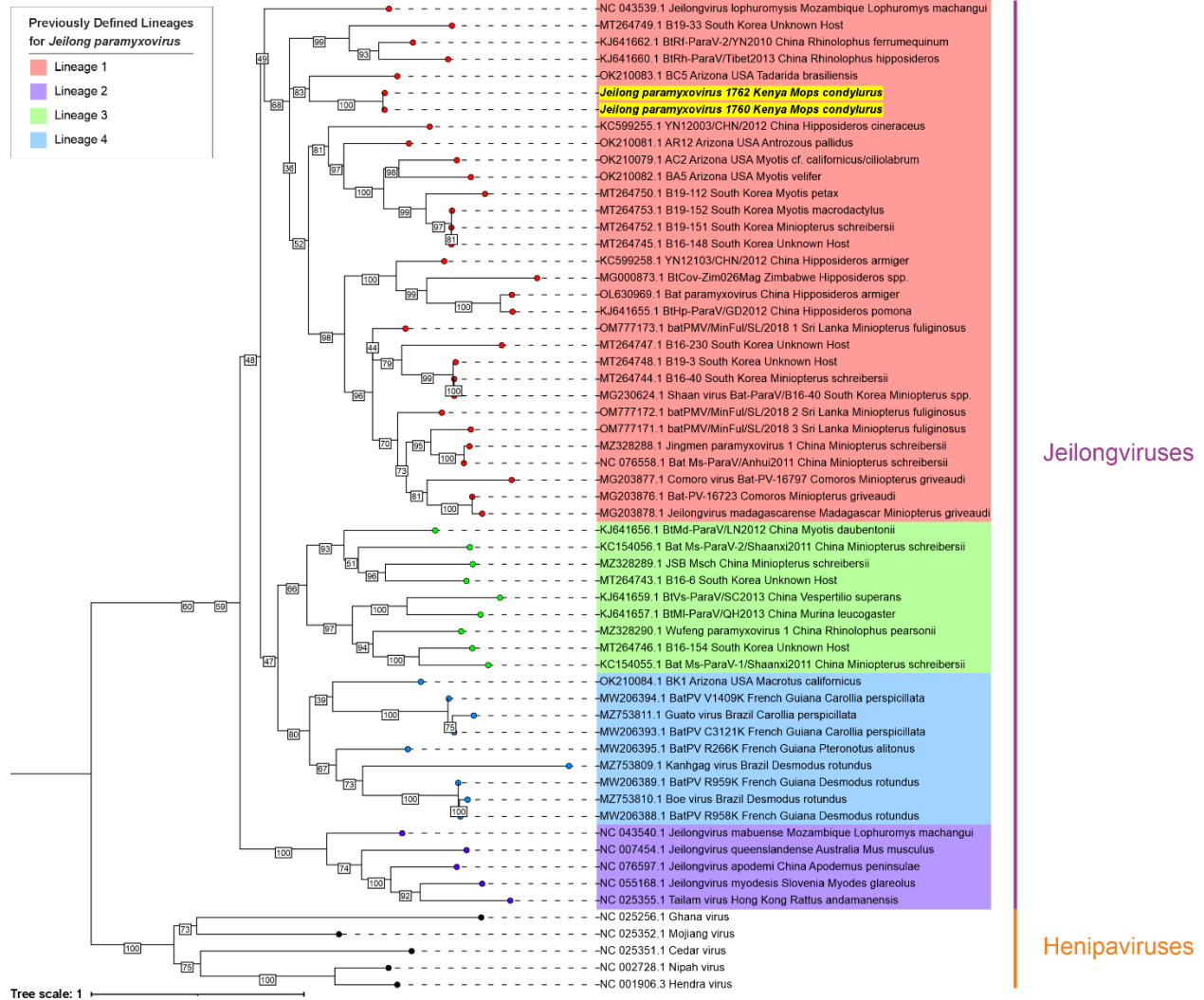


Figure 1. Phylogeny of a paramyxovirus detected in *Mops condylurus* bats from Kenya. Our virus sequences (highlighted in yellow) cluster within one of four Jeilongvirus lineages (in red), which like henipaviruses, are genera of the paramyxovirus family.

APPENDIX

Appendix S1. We screened bat fecal samples using two rounds of nested, conventional PCR.

Round 1 consisted of 1) 30 minutes at 50°C, 2) 2 minutes at 94 °C, 3) 45 cycles of: 94°C for 20 seconds, 50°C for 30 seconds, 72°C for 60 seconds, and 4) a final extension of 72°C for 5 minutes. The product from Round 1 was then prepared for the nested Round 2, consisting of: 1) 95°C for 2 minutes, 2) 5 cycles of: 94°C for 15 seconds, 61°C for 30 seconds, 72°C for 30 seconds, 3) 20 cycles of: 94°C for 15 seconds, 61°C for 30 seconds with a decrease of -0.5°C per cycle, 72°C for 30 seconds, 4) 15 cycles of: 94°C for 15 seconds, 50°C for 30 seconds, 72°C for 30 seconds, and 5) a final extension of 72°C for 5 minutes. All products were held at 4°C after the PCR was completed.

CONCLUSION

In this dissertation, I sought to understand and characterize a part of the wildlife-urban interface undergoing land-use changes. This work started by determining general trends through reports of human-wildlife interactions in areas of land-use change. Upon identifying gaps in the literature related to human-wildlife interactions, I used a study system in rural Kenya to target these gaps and better understand the risks human-bat interactions pose to both human health and bat conservation. Thus, my focus included understanding environmental drivers of human-wildlife interactions, human and bat behaviors (i.e., the building roosts they selection) that may facilitate pathogen exposure and bat mortality, and paramyxoviruses present at this interface.

In Chapter I, I performed a literature review of human-wildlife interactions in areas of documented land-use change, where I show that publication trends mirror identified hotspots of zoonoses emergence but there are critical gaps in knowledge. The literature shows that reports of human-wildlife interactions are heightened in areas of Africa, Asia, and South America undergoing agriculturalization, a process that can catalyze the spillover of zoonotic pathogens (Jones et al. 2013, Allen et al. 2017). Our results also indicated that indirect human contact with birds and mammals is high in Europe, which has important implications for human exposure to environmentally transmitted pathogens like avian influenza (Rohani et al. 2009). One of the starkest knowledge gaps, however, is human-bat contacts in areas of land-use change, despite their reputation as hosts for zoonotic pathogens (Olival et al. 2017, Letko et al. 2020). The number of publications documenting human-bat contacts was much fewer than expected, and this knowledge is important for understanding mechanisms that can facilitate the spillover of bat-borne pathogens into humans and our domestic animals.

In Chapter II, I explored the environmental drivers of bat selection of building roosts in rural Kenya, an estimated hotspot for zoonotic pathogen emergence (Allen et al. 2017). This

region has undergone large changes in land-use as human populations grow and the climate changes (Platts et al. 2011). We found that overall, bats selected tall, humid, cement-walled structures with low human occupancy. However, these preferences were not consistent across species. The common synanthropic molossids *Mops condylurus* and *Mops pumilus* showed these same building preferences; in contrast, the regional endemic *Cardioderma cor* solely focused on human occupancy as a selection factor, preferring buildings with less human presence. Our results show that selection of roosts varies across species, which has important ramifications for determining the bat species humans may interact with in this region.

In Chapter III, I continued my work in buildings used by humans and bats and used a survey to quantify and characterize human-bat interactions at this interface and evaluate their potential for facilitating human exposure to bat-borne pathogens. Our results show that humans and domestic animals are interacting with bats in three ways that could lead to exposure of bat pathogens: daily human contact with bat feces and occasional handling and domestic animal consumption of bats. Efforts to remove bats, mostly through killing, were commonly reported in our study. Removal efforts may stress surviving bats, which can alter infection dynamics within hosts and increase the shedding of pathogens into the environment where humans may contact them (Streicker et al. 2013, Eby et al. 2023). High bat mortality in these systems may also depress the critical ecosystem services these bats provide, namely as major pest suppressors in urban and agricultural ecosystems (Noer et al. 2012, Nsengimana et al. 2023). Efforts to prevent human-bat contact will benefit bats, humans, and domestic animals by reducing opportunities for pathogen exposure and bat mortality.

Lastly, in Chapter IV, I report the findings of a paramyxovirus surveillance study using feces collected from synanthropic bats that commonly live in buildings with people in this region

of Kenya. From 297 screened samples, we detected a jeilongvirus within the paramyxovirus family Orthoparamyxoviridae. Total paramyxovirus prevalence was 4.04%, which is similar to previous work on bats and paramyxoviruses (Conrardy et al. 2014, Waruhiu et al. 2017, Hoarau et al. 2023). Currently, the zoonotic potential of jeilongviruses is unknown and no human disease cases have been documented (Haas and Lee 2023). However, jeilongviruses are closely related to henipaviruses, members of which have spilled over and caused human mortality. Jeilongviruses also have the capacity to switch hosts and have done this in past, including their initial spillover from rodents into bats (Zhu et al. 2023). This host switching capacity is an important characteristic of zoonotic pathogens and, coupled with the presence of jeilongviruses at this wildlife-urban interface and their close relationship to henipaviruses, provides evidence that future scrutiny and research efforts into this viral genus is warranted.

Together my dissertation shows that the wildlife-urban interface in rural Kenya is a setting where humans and domestic animals are regularly interacting with bats. These contacts can have ramifications for both human and bat health; bats in this region can carry viruses that are closely related to known zoonotic pathogens that have spilled over into humans. However, bats inhabiting buildings at this interface must cope with human-induced mortality that can reduce populations and induce stress, both of which may alter the critical ecosystem services provided by bats. Prevention of these human-bat interactions is needed to reduce both the risk of human exposure to bat-borne pathogens and bat mortality, for the benefit of humans and bats in this region.

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APPENDIX



Office of Research Compliance

To: Kristian Forbes
Fr: Craig Coon
Date: December 18th, 2018
Subject: IACUC Approval
Expiration Date: December 13th, 2021

The Institutional Animal Care and Use Committee (IACUC) has APPROVED your protocol # **19043**: *Emerging zoonotic infections in wild small mammals of Kenya*.

In granting its approval, the IACUC has approved only the information provided. Should there be any further changes to the protocol during the research, please notify the IACUC in writing (via the Modification form) prior to initiating the changes. If the study period is expected to extend beyond December 13th, 2021 you must submit a newly drafted protocol prior to that date to avoid any interruption. By policy the IACUC cannot approve a study for more than 3 years at a time.

The following individuals are approved to work on this study: and Kristian Forbes. Please submit personnel additions to this protocol via the modification form prior to their start of work.

The IACUC appreciates your cooperation in complying with University and Federal guidelines involving animal subjects.

CNC/tmp



UNIVERSITY OF ARKANSAS

Office of Research Compliance

To: Kristian Forbes
From: Jeff Wolchok
Date: December 21, 2021
Subject: IACUC Approval
Expiration Date: December 20, 2024

The Institutional Animal Care and Use Committee (IACUC) has APPROVED your protocol #22012, *Emerging zoonotic infections in wild small mammals of east Africa*.

In granting its approval, the IACUC has approved only the information provided. Should there be any further changes to the protocol during the research, you must notify the IACUC in writing (via the Modification form) and receive approval prior to initiating the changes. If the study period is expected to extend beyond the above expiration date, you must submit a new protocol. The IACUC may not approve a study for more than three years at a time.

The following individuals are approved to work on this study: Kristian Forbes, Reilly Jackson, and Tamika Lunn. You must submit personnel additions to this protocol via the modification form prior to their starting work.

The IACUC appreciates your cooperation in complying with University and federal guidelines involving the care and use of animals.

JCW/rek

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