

Modern building structures are a landscape-level driver of bat-human exposure risk in Kenya

Tamika J. Lunn¹, Reilly T. Jackson¹, Paul W. Webala¹, Joseph Ogola¹, and Kristian M. Forbes¹

¹Affiliation not available

July 25, 2023

Abstract

Identifying the areas and drivers of high-risk interfaces for human-wildlife interaction is crucial for managing and reversing human zoonotic disease risk. We suggest that continent-wide improvement to African housing is inadvertently creating roosting habitat for synanthropic free-tailed bats (family Molossidae), and opportunity for human exposure to bat-associated pathogens. We mapped building use by free-tailed bats from 1,109 buildings along a residential gradient in rural south-eastern Kenya where viruses of concern have been detected. We show that bats frequently roost in human-occupied buildings; almost one-in-ten buildings showed evidence of bat occupation (9.2%), and one-in-13 were active roosts (7.6%). We identified modern-build style and triangular roofing as building-level predictors of bat occupation, and the proportion of modern buildings as a landscape-level predictor of bat occupancy. Given the international focus on building improvement in Africa, and the increasing access to improved housing already reported in the literature, we suggest that this is a rapidly accelerating exposure interface that needs urgent attention and investment. Ethical pre-emptive exclusion of bats (by sealing bat entrance points) and restoration of natural roosting habitats should be prioritized as One Health land-use planning strategies in rural Africa.

Introduction

The emergence and re-emergence of zoonotic disease is driven by ecosystem changes at the landscape level ¹. Ecosystem disturbances through anthropogenic land use changes have been key drivers of emerging infectious diseases over the last century ². Changes to ecosystem features – such as wildlife abundance, community composition, demography, behaviour, movement, contact patterns, and pathogen susceptibility – directly and indirectly alter the risk of pathogen transmission from wildlife to humans, through modifying disease dynamics within wildlife hosts and contact between wildlife and humans¹. Because spatial overlap between wildlife reservoirs and humans is a key requirement for cross-species transmission (spillover), studies that investigate how human activities increase exposure to wildlife are critical for mitigating the transmission and emergence of zoonoses ³.

Urbanisation commonly results in destruction and fragmentation of wildlife habitat, with ensuing encroachment creating human-wildlife interfaces at the edges of anthropogenic areas. For synanthropic wildlife, urbanisation can additionally create habitat and increase key resources, creating mosaics of human-wildlife interfaces within anthropogenic areas. Human pathogen exposure from synanthropic wildlife has been observed for various zoonoses, including tick-borne bacterial pathogens and viral infections (e.g., McFarlane et al. 2012; Bermúdez et al. 2016; Bermúdez et al. 2017). Identifying the specific drivers of these high-risk interfaces is especially important in global hotspots for emerging infectious diseases ^{7,8}, countries with limited resources for disease surveillance, prevention and control⁷, and for taxonomic groups identified to harbour zoonotic pathogens ⁹. However, information on wildlife-human exposure remains limited for many

under-resourced disease hotspots, particularly in sub-Saharan Africa and parts of Asia, as well as for many host taxa, including bats. These deficiencies are exacerbated by limited understanding of basic bat ecology in remote parts of Africa and Asia ¹⁰.

African molossid bats, or free-tailed bats, are some of the most widely distributed and abundant bats on the African continent¹¹. Several Molossid species host zoonoses-associated viral families, including corona-, filo-, paramyxo-, rota-, astro-, flavi-, and lyssaviruses^{12–17}. Two Molossid species (*Mops condylurus* and *Mops pumilus*) are also putative ebolavirus hosts, both showing evidence of infection in the wild, and the ability to replicate ebolaviruses without morbidity following experimental inoculation^{18–20}.

Synanthropic free-tailed bat species are increasingly using human-built structures as roosts, instead of natural roosts in tree hollows and rock crevasses ²¹. Continent-wide changes to African housing have seen human dwellings change from traditional buildings with natural materials (e.g., mud walls and thatch roofs), to modern-style buildings with finished materials and modern design elements, including structural beams and ceilings²². Spaces in ceilings, and between beams and walls, create roosting habitat for free-tailed bats, and appear to sustain larger colonies than natural roosts and traditional buildings (up to thousands in modern housing) ²³. Changing patterns of bat-bat and bat-human contact through the use of these anthropogenic structures creates an exposure interface that may increase pathogen transmission, both among bat species and from bats to humans.

Given the limited information available on basic bat ecology and wildlife-human exposure in remote parts of Africa, particularly at landscape scales, this study aimed to: 1) map high-risk interfaces of bat-human exposure along a residential gradient in rural south-eastern Kenya, and 2) to identify building- and landscape-level attributes of bat-human exposure risk. This study provides empirical information on the roosting of anthropogenic free-tailed bats in south-eastern Kenya, and describes the conditions in which housing improvement (without proper consideration of local bat ecology) could facilitate the emergence of zoonotic disease in remote parts of Africa. This information is critical to better understand bat-virus exposure interfaces that drive disease risk, and to inform strategies for One Health land-use planning in changing landscapes.

Results

We directly assessed occupation by synanthropic free-tailed bats for 1,014 buildings (checked for signs, sighting and/or audio confirmation, or discussed occupation with owner) (Figure 1). Of these 1,014 buildings, 93 showed evidence of free-tailed bat occupation and were included in building- and landscape-level analyses of bat building use. We recorded the building and roof structure for an additional 95 buildings which could not be accessed directly (1,109 buildings total) (Figure 2). With evidence weighted to better reflect active roosts (Appendix S1), 84 out of the total 1,109 buildings surveyed were considered presently active (occupation category ≥ 4) and included in landscape-level analyses of bat-human exposure risk. Lines of evidence for free-tailed and other bat occupation are given in Appendix S2.

Modern-build style and triangular roofing were identified as building-level attributes of synanthropic free-tailed bat occupancy (modern build style: $\text{coef} = 1.36 \pm 0.29$, $p < 0.0001$; triangular roofing: $\text{coef} = 2.17 \pm 0.37$, $p < 0.0001$). At the landscape level, building availability and the proportion that were of modern-build – but not the proportion with triangular roofing – drove the number of buildings occupied by free-tailed bats (total number of buildings: $\text{coef} = 0.007 \pm 0.002$, $p = 0.0008$; proportion of modern-builds: $\text{coef} = 0.012 \pm 0.006$, $p = 0.030$; proportion with triangular roofing: $\text{coef} = -0.004 \pm 0.007$, $p = 0.540$).

This positive association remained when the more stringent assessment of building occupancy was applied to capture roosts very likely to be actively occupied (occupation category ≥ 4) (total number of buildings: $\text{coef} = 0.005 \pm 0.002$, $p = 0.001$; proportion of modern-builds: $\text{coef} = 0.015 \pm 0.006$, $p = 0.017$; proportion with triangular roofing: $\text{coef} = -0.005 \pm 0.008$, $p = 0.521$, Figure 3). In both datasets, the effect of building number was less than half of the effect from the availability of modern buildings.

The average building-roost density of roosts considered to be actively occupied, was 8.4 occupied buildings per km^2 (range 2–24 per km^2), estimated using a traditional measure of density, or 8.2 occupied buildings

per km² (range 2-21.7 per km²) estimated as a kernel density (Figure 4).

Given specific interest in the transition from traditional- to modern-style housing, all analyses were repeated on a subset of data that included traditional- and modern-style houses only, and houses with triangle and flat roofing only (i.e., with structures including latrines, livestock coupes, and greenhouses removed, leaving 806 buildings total). Model results were not substantially or directionally different in the sensitivity analysis (Appendix S3), though proportionally more houses were occupied (one-in-seven with evidence of occupation, 13.1%, and with nearly one-in-ten being active roosts, 10.4%).

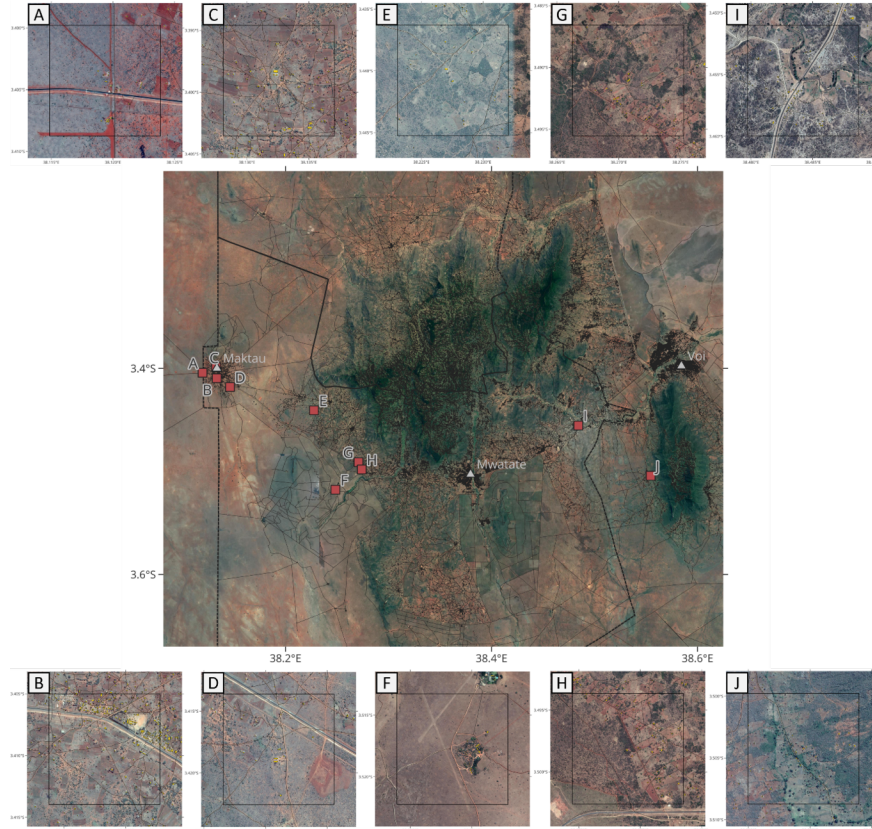


Figure 1: Map of study sites. Central panel shows the distribution of study sites in the Taita-Taveta county, south-eastern Kenya. Note that sites were distributed across low-lying areas only, as synanthropic free-tailed bats do not occur at higher elevations of the county (observable as green cover in the centre, centre-bottom, and right areas of the satellite image). Small panels show the ten, 1x1 km sites with roads (black lines) and building footprints (yellow). Building footprints were obtained from Microsoft (2022), and are based on satellite imagery collected in 2020 and 2021. Human land-use in this county spans a gradient of development, from rural areas with predominantly traditional building practices, to more urbanised areas in the townships of Mwatate, Maktau and Voi (labelled), with predominantly modern building practices.

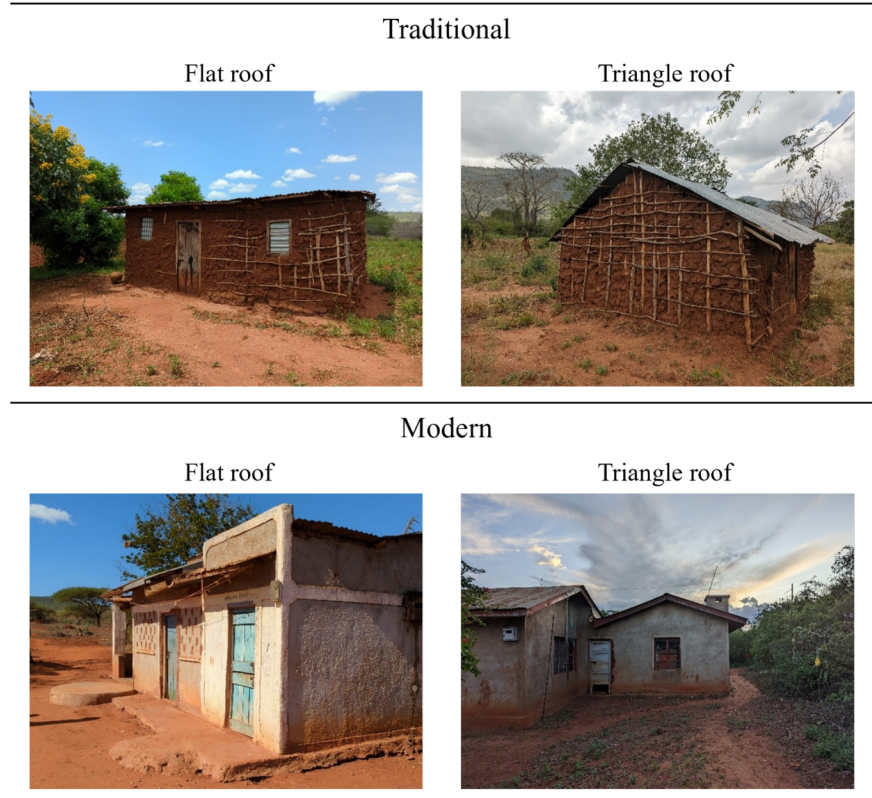


Figure 2: Building type and roof design of buildings evaluated in the survey. We classified modern buildings as those with walls and flooring built from finished materials (e.g., cement and tiles), and traditional as those with walls and flooring built from unfinished materials (e.g., compacted earth). Modern-style designs often have exposed structural beams and ceilings, whose spaces create roosting habitat for synanthropic free-tailed bats. Triangular roofs provide a taller apex for bat emergence, needed for molossid bats to take flight due to their wing morphology²⁵. The added height from triangular roofs also keeps roosting bats out-of-easy-reach from people, and makes disturbance more difficult.

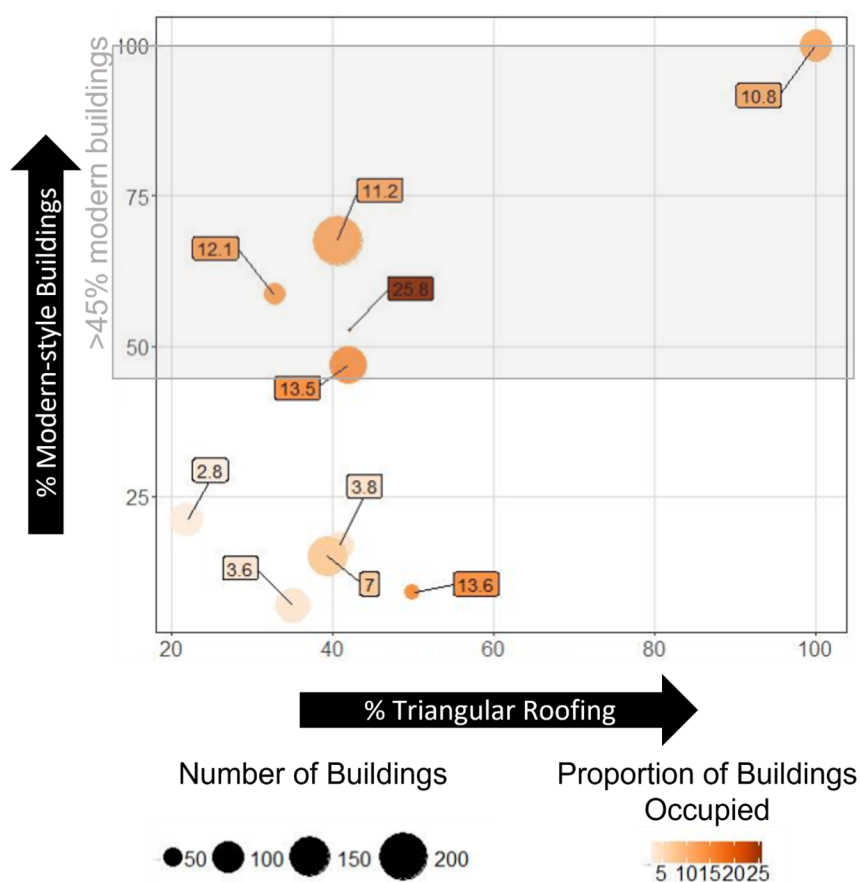


Figure 3: Proportion of occupied buildings relative to the number of buildings available, and the proportion of buildings that were of modern build with triangular roofing. Figure shows that sites with higher proportions of modern buildings have higher occupancy, regardless of number of available buildings or triangular roofing. Occupancy was determined using a threshold score of four or more (occupancy is very likely).

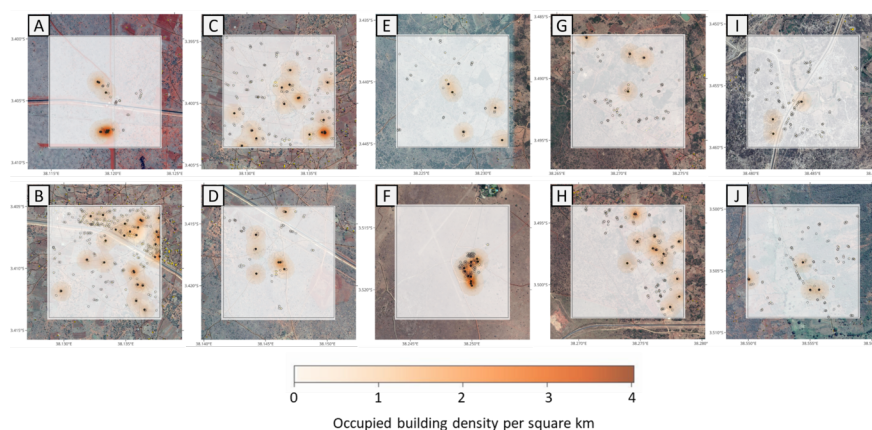


Figure 4: Building occupation by bats across the landscape. Distribution of occupied buildings are shown as filled circles, and unoccupied buildings as unfilled circles. Occupied building density per km^2 is indicated

with orange shading. Occupied building density is estimated as a fixed-bandwidth kernel estimate from an occupation index of [?]4 (occupation very likely).

Discussion

Continent-wide improvements to African housing have precipitated a myriad of positive human health outcomes, including reductions in soil-transmitted helminths, diarrhoeal disease, leishmaniasis, malaria, and respiratory disease, and improved mental wellbeing^{22,26}. In this way, house design is integral to the United Nations Sustainable Development Goal 3: ‘*ensure healthy lives and promote well-being for all at all ages*’. We report an inadvertent and so-far undocumented outcome of housing improvement in sub-Saharan and rural Africa; that changes to building practices are simultaneously creating habitat for bats, and potentially increasing human exposure risk to bat-associated pathogens. Of the 1,109 buildings surveyed in our study, almost one-in-ten showed evidence of bat occupation (9.2%), and one-in-13 were active roosts (7.6%). We identified modern-build style and triangular roofing as building-level predictors of bat occupation, and the proportion of modern buildings as a landscape-level predictor of bat occupancy. Given the international focus on building improvement in Africa, and the increasing access to improved housing already reported in literature²², we suggest that this is a rapidly accelerating exposure interface that needs urgent attention and investment.

Synanthropic free-tailed bat species are highly aggregative and use social cues to locate existing roosts²⁷. Modern-build structures typically have more spaces for bats to roost and can support higher densities of individuals. The reported occupation of modern-build houses possibly reflects a preference in habitat by these bats; roosting with conspecifics in large roosts, as opposed to roosting separately in smaller roosts, has several advantages including reduced risk of predation²⁸, and access to mates during the breeding season²⁹. It is possible that the removal of natural habitat, particularly large hollow-bearing trees, could be contributing to the use of anthropogenic structures, similar to other bat systems^{30,31}. However, there is insufficient data on historical and current vegetation in this area to investigate. Practically, large roosts likely pose a greater risk of exposure to humans, and a greater burden to residents. Ceiling collapse due to the weight of accumulated faeces was frequently reported by owners of modern buildings with ceilings containing large numbers of bats, for instance.

Not all modern structures that were available were occupied. This may be partly associated with building-level nuances not captured in this dataset, such as successful blockage of roost access points by owners, or recent bat eviction efforts. Alternatively, this may indicate that availability of ideal refugia is not a limiting factor in bat occupation, and instead, that landscape patterns in building use are driven by the presence of at least a few ideal habitats in which animals can aggregate. Speculatively, this could indicate that synanthropic free-tailed bat occupation is unlikely to saturate available buildings beyond a certain threshold of availability. Baseline information and continued monitoring of bat roosting would be needed to investigate this, though the positive association between landscape-level occupancy and the proportion of modern-style buildings suggests that this threshold (if it exists) has not been reached.

We caution that bat occupation of housing may be an accelerating exposure interface. The African continent’s population is the fastest growing in the world, with an estimated increase of 1.3 billion people expected between 2015 and 2050³². This growth will necessitate hundreds of millions of new homes. In addition, shifting economic and demographic profiles in the continent will continue to promote access to improved housing. The proportion of houses built with finished materials increased from 32% in 2000 to 51% in 2015, with hundreds of millions of Africans accessing improved housing²². These changes present a powerful opportunity to improve human wellbeing, but only with proper consideration of local ecological context. Investment in bat- and human-friendly housing infrastructure is needed to ensure that vulnerable populations are not left exposed to bats and bat-associated pathogens. Investment in key areas will also contribute to the global effort in preventing emerging infectious diseases. African countries are hotspots for bat species diversity and disease spillover, yet rural and remote regions of Africa often have limited resources to detect or combat the first stages of disease emergence after exposure and spillover^{7,8}. Intervention at exposure interfaces will help pre-empt spillover of potentially new emerging infectious diseases, and prevent large-scale

emergence in-country or globally.

Housing improvement initiatives should include proper consideration of local bat ecology to reduce human-bat exposure risk. Individual risk can be immediately reduced by pre-emptively and thoroughly sealing access points to bats. This a highly successful mitigation strategy but can be prohibitively expensive in rural areas³³. Depending on availability and affordability of materials, sealing access points can also leave design features unfunctional (e.g., sealing ventilation points and chimneys with wire mesh vs with cement or clay). Improvements to the availability and affordability of suitable and bat-safe materials should be made a priority. In addition, the restoration of natural roosting habitats should be considered as a long-term mechanism for reversing building use³⁴. This could be achieved by providing support to existing environmental stewardship programs involving tree planting (e.g., local groups like the Taita Taveta WCK Action Group, and broader ACK initiatives)³⁵.

The removal of bats using pesticides or chemicals was frequently reported by building owners, and/or by blocking entrance points with thorny plants that get caught in bat wings and cause death. These approaches are both non-ethical and not effective for long-term exclusion of bats, as killing bats does not prevent roost repopulation^{36,37}. Extermination attempts have also been linked with increased pathogen shedding by bats, and transmission to humans^{38,39}. Pre-emptive exclusion is the safest and most ethical approach for limiting bat-human exposure in the immediate term.

This is the first study to provide empirical estimation on building roost density of synanthropic free-tailed bats, and describes the conditions facilitating human-bat exposure in remote parts of Africa. These results set the foundation for additional research and management actions to alleviate the risks posed by identified bat-human exposure interfaces. Surveillance for priority zoonotic pathogens at interfaces where transmission risks are identified, and the development of culturally appropriate and locally feasible interventions that can be used to reduce the risk of contact and transmission at these high-risk interfaces, should be prioritized for future research and management action. Analysis of temporal patterns in occupation and/or within-roost density could also be used to highlight variation in bat exposure risk within and between years, and prioritise educational efforts on disease risk and mitigation. Empirical information provided by this study, on the building-roost density of anthropogenic free-tailed bats, will be crucial for understanding baseline ecological states for these species, and could be used for future management efforts for these species. This information could also be utilised to develop host-virus models to examine spillover risk now, and under conditions of anthropogenic change.

Methods

We collected data on synanthropic free-tailed bat building use in the Taita-Taveta county of south-eastern Kenya (East Africa), between February and April 2022 (Figure 1). Topography of the county spans low-lying savannah plains to mountain ranges, with elevations between 700 m (in the plains), up to 2200 m (highest peak of the Taita Hills)⁴⁰. Human land-use in this county spans a gradient of development, from rural areas with predominantly traditional building practices, to more urbanised areas in the townships of Mwatate, Maktau, Voi, and Wundanyi, with predominantly modern building practices. Bat-borne viruses of zoonotic interest have been detected from free-tailed bats in this area, including coronaviruses and Bombali virus (genus: *ebolavirus*)^{41–43}.

We assessed buildings for synanthropic free-tailed bat occupancy within ten, 1x1 km sites (Figure 1). Sites were chosen to represent the gradient of human landscapes utilised by free-tailed bats (traditional-style housing to modern-style housing, Figure 2), and each was centred on a single building roost identified to contain synanthropic free-tailed bats. Building footprint maps, derived from satellite imagery collected in 2020 and 2021, were used to identify all buildings within sites²⁴. As public attitude towards bats is negative in this region – being associated with witchcraft and witch doctors (Mwasi & Mwakachola pers. comm.) – we endeavoured to become familiarised and trusted by the community prior to surveying sites and conducted all surveys with a local field assistant.

We individually evaluated each building within our 1 km² sites for occupation by synanthropic free-tailed

bats. To do this, we (1) asked building owners whether they had recently seen or heard bats inside the building during the day, (2) assessed the building for signs of bat use (e.g., bat faeces on the ground, stained ceiling, staining around external roost entrance points, and smell, Appendix S1), and where possible (3) assessed the building for physical presence of bats, for sighting and/or auditory confirmation. We noted features of each building that could impact roosting suitability for synanthropic free-tailed bats (building type, roof design, and, where possible, presence of a ceiling) (Figure 2). We classified modern buildings as those with walls and flooring built from finished materials (e.g., cement and tiles), and traditional as those built from unfinished materials (e.g., compacted earth). Buildings were considered occupied if: the building owners confirmed bat occupation, the building had signs of bat occupation, or bats were seen or heard inside the building. While multiple bat species can occupy buildings in this region, synanthropic free-tailed bats are the most common and are distinctive in their building use (Appendix S1). Buildings that were occupied by species other than free-tailed bats were noted, but not included in analyses of bat building use.

To identify building-level attributes of bat building use, we modelled the response in building occupation relative to 1) building type (modern or other), and 2) roof structure (triangular or other). Models were generalized linear models (GLMs) with maximum likelihood (ML) estimation and a binomial distribution with a logit-link, fit using the `mgcv` package in R. We performed checks of standardised residuals to evaluate model fit, as per Wood (2017)⁴⁴. Note that these indicators of occupation may reflect past or current occupation by synanthropic free-tailed bats, but nevertheless provide an indication of building suitability.

To identify landscape-level attributes of bat-human exposure risk, we modelled response in the number of occupied buildings per site, relative to 1) the total number of buildings available, 2) the proportion of those buildings that were a modern-build style, and 3) the proportion of those buildings with a triangular roof style. To better reflect the landscape of active roosts (and therefore, the landscape of human exposure risk), we ran models on an additional dataset where building occupation was rated based on the collective weight of evidence indicating current free-tailed bat occupation; 0=very unlikely; 1-2=possible; 3=likely; 4=very likely; 5=certain (Appendix S1). Highly weighted evidence for occupation included sighting and/or auditory confirmation of free-tailed bats by the authors (inclusion into category 5, certain of occupation). Moderately weighted evidence for occupation included owner confirmation of occupation, and signs of occupation. Low-weighted evidence included building suitability, as per findings relating to building-level attributes, described above. Buildings were considered presently occupied if they were categorised as four or greater (occupation very likely). All levels of evidence were evaluated in addition to knowledge on where and how many bats were roosting, to indicate synanthropic free-tailed bats, as detailed in Appendix S1. Models were fitted as above, but with a Poisson distribution and log link.

To provide an empirical estimate on landscape-scale building-roost density, we calculated density as: 1) the total number of occupied buildings (occupation category ≥ 4) divided by the total site area, and 2) the average of fixed-bandwidth kernel estimates, estimated using the `spatstat` package in R⁴⁵. Kernel estimates have the advantage of explicitly incorporating the distribution of buildings into the density estimate, and can therefore account for spatial heterogeneity in building aggregation⁴⁶. Kernel values were estimated using roost building location with Gaussian kernel smoothing and a smoothing bandwidth of 0.3⁴⁷. Bandwidth was selected by comparing projected kernel density values to expected density values based on building distances and survey area. Kernel averages were calculated per site (pixel size = 0.008969 x 0.00896 meters).

Given the specific interest in the transition from traditional- to modern-style housing, all analyses were repeated on a subset of data that included traditional- and modern-style houses only, and houses with triangle and flat roofing only (Appendix S3).

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Acknowledgements : We thank Peter Mwasi for his assistance in data collection. We also thank the Taita Environmental Research and Resource Arc for their logistical assistance, especially Miltone Kimori and Ken Gicheru. We also acknowledge and thank the Taita people of Taita-Taveta County for their enthusiasm and participation with this research.

Author Contributions:

TJL and RTJ conceived the research; TJL designed the research methodology, led project administration, collected the data, curated the data, analysed and visualised the data, and drafted the manuscript; PWW and JO provided resources; KMF acquired funding for the research and provided supervision; and all authors participated in review and editing of the manuscript. All authors have read the manuscript, agree that the work is ready for submission to a journal, and accept responsibility for the manuscript’s contents.

Competing Interests statement : The authors declare that they have no conflict of interest.

Funding : This study was supported by funding by the Arkansas Biosciences Institute.

Ethical approval : All applicable institutional and/or national guidelines for the care and use of animals were followed. Bat fieldwork was conducted under permits from the National Commission for Science, Technology and Innovation (#NACOSTI/P/21/9267), and the Kenya Wildlife Service (#KWS/BRM/500 and WRTI/RP/118.6). Ethics approval was granted by the University of Nairobi Biosafety, Animal use and Ethics committee (H84/53146/2018), and under Institutional Animal Care and Use Committee (IACUC) protocol #22012, granted by the University of Arkansas Institutional Animal Care and Use Committee. Human ethics approval was conducted under the University of Arkansas Institutional Review Board protocol number 2103320918.