Published by Associazione Teriologica Italiana
Online first – 2017
OPEN ACCESS
Hystrix, the Italian Journal of Mammalogy
Available online at:
http://www.italian-journal-of-mammalogy.it/article/view/12046/pdf
doi:10.4404/hystrix-28.1-12046

Research Article

Roost selection by synanthropic bats in rural Madagascar: what makes non-traditional structures so tempting?

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Keywords:
Chiroptera
conservation
East Africa
human-wildlife conflict
Molossidae
synanthropy

Article history:
Received: 14 August 2016
Accepted: 28 October 2016

Acknowledgements
We thank Georges Razafindrakoto and Eric Marcel Temba for fieldwork and logistical assistance, and MICET and Centre ValBio staff for their hospitality and logistical support. Christoph F.J. Meyer and Kati Suominen collaborated on the project idea and carried out the first pilot expedition in 2014. We also thank the Department of Biosciences, University of Helsinki for supporting the RESPECT field course and Johannes Nyman for preparing the map figure. Madagascar National Parks and the "Ministere de l'Environnement de l'ecologie et des forests" (Département de Biologie Animale, DBA) provided the research permits to capture and collect bat specimens within the study area (293/15/MEEMF/SG/DGF/DAPT/SCBT). This work was supported by the Portuguese Foundation for Science and Technology under Grant PD/BD/52597/2014 to ALB, SFRH/BD/80488/2011 to RR and PD BD 114363 2016 to JK. KMF is financially supported by the Finnish Cultural Foundation and MC by the Academy of Finland (grant #257686). Finally, we thank the anonymous reviewers for their constructive comments.

Abstract

Humanised landscapes are causing population declines and even extinctions of wildlife, whereas a limited number of species are adapting to the new niches and resources within these modified habitats. Synanthropy is widespread among many vertebrates and often causes co-habitation conflicts between humans and wildlife species. Bats often roost in anthropogenic structures, and especially in the tropics, mitigation of human-bat conflicts arising from co-habitation is hampered by a paucity of research focusing on roost preferences. We assessed roost selection by bats in villages around Ranomafana National Park, eastern Madagascar. Ten villages were surveyed, with bats occupying 21 of the 180 evaluated buildings. Of those, 17 were public buildings harbouring large molossid colonies. Although beneficial ecosystem services provided by bats are well-known, several cases of colony eviction were noted, mostly due to unwanted co-habitation. Bat preference was driven by the type of building, its height and a lack of fire use by the inhabitants. Colonies were mainly found under metal sheets within large empty chambers, whereas only isolated bats were detected in the roofs of traditional cabins. Temperatures up to 50 °C were recorded inside a roost, representing one of the highest temperatures recorded for an African maternity roost. Molossidae bats appear to have found a suitable alternative to their native roosts in hollow, old and tall trees in pristine forests, which are becoming rare in Madagascar. This suggests that human-bat interactions in Madagascar will likely increase alongside rural development and the loss of primary forest habitats. Shifting to modern construction methods while combining traditional techniques with proper roof sealing could prevent the establishment of bat colonies in undesired locations, whereas co-habitation conflicts could alternatively be minimised by reducing direct interaction with humans. In light of our results, we urge caution with bat evictions, and greater attention when introducing modern building practices, often supported by foreign initiatives, to poor rural communities in developing countries.

Introduction

Anthropogenic landscape modification is driving changes in wildlife foraging, nesting, roosting and breeding behaviour across a range of taxa (Collen et al., 2011; Dirzo et al., 2014). While the proliferation of humanised landscapes is causing population declines and even extinctions for some species (Dirzo et al., 2014), others are adapting to the availability of new habitat niches and resources (Oro et al., 2013; Vasconcelos et al., 2015). This brings wildlife in close contact to human populations, potentially resulting in human-wildlife conflict. A key challenge for conservation biologists is to understand the causes and patterns of synanthropy, and when appropriate, provide amicable solutions which allow for the long-term viability of wildlife populations.

Synanthropy is widespread among some bat groups, with several species often found to roost in human-made structures such as dwellings, schools, offices and bridges (Adam and Hayes, 2000; Jung and Kalko, 2011; Amorim et al., 2013; Jung and Threlfall, 2015; Russo and Ancillotto, 2015). The abundance of human-associated species in some cases tends to increase proportionally with construction rate and settlement expansions (Voight et al., 2015). These associations are often viewed negatively due to the noise, smell and perceived risk of pathogen transmission conferred by close association with bats (Calisher et al., 2006; Voight et al., 2015). However, bats also have positive local impacts on livelihoods due to the ecosystem services they provide, such as insect crop pest control, which can help reduce pesticide use and increase crop yields (Kunz et al., 2011; Boyles et al., 2013; Puig-Montserrat et al., 2015). It is also likely that bats reduce disease risk by foraging on pathogen vectors (Reiskind and Wund, 2009).

Wildlife-human interactions are common among commensal species in rural areas of developing African countries. The few studies to have investigated bat roost selection have found that molossid bats tend to select large, public buildings (Ratrimomanarivo and Goodman, 2005; Randrianandrianina et al., 2006; Razafindrakoto et al., 2010). Molossids are especially well adapted to human environments due to a suite of morphological traits, such as high wing loading and aspect ratio, which enables rapid flight and the potential to travel long distance per night (Jung and Kalko, 2011). However, building attributes, which

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doi:10.4404/hystrix-28.1-12046

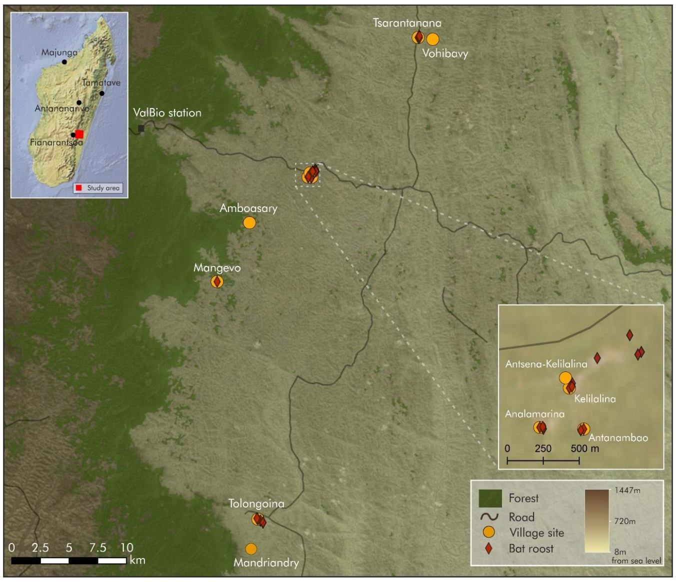

Figure 1 – Study area in Ranomafana National Park and surroundings. Sampled villages and roosts with bat colonies are indicated with orange and red circles and rhombus respectively. Green areas correspond to the National Park.

facilitate and discourage bat roosting, have scarcely been investigated in these rural regions. This information is essential to enable evidence-based construction practices that minimise human-bat conflicts.

To address this lack of knowledge, here we report on a study investigating bat roosting behaviour in human-modified landscapes in Madagascar. Madagascar is one of the poorest countries in the world (Horning, 2008; WorldBank, 2010). It has an increasing population size and is experiencing large-scale landscape changes, mostly driven by deforestation and agricultural expansion (Allnutt et al., 2013; Rocha et al., 2015). While extensive research has been carried out in Madagascar on endemic taxa - lemurs, rodents and tenrecs (Goodman and Benstead, 2003; Amori et al., 2015) - in-depth ecological research on bats lags behind (Eger and Mitchell, 2003; Racey et al., 2010). The limited available literature regarding bat ecology (Ratrimomanarivo and Goodman, 2005) is mainly focused on forest and cave-dwelling species (Bambini et al., 2010; Andrianaivoarivelo et al., 2011).

Providing building guidance on bat colony management is paramount, especially when cohabitation conflicts are present, and remedial and preventative actions should incorporate bat conservation priorities and recommendations. In this study, we aim to evaluate roost selection by bats in rural towns and villages around Ranomafana National Park in eastern Madagascar. This area is characterised by high biodiversity, and an expanding network of villages and their associated farming practices encroaching into the park. We focus in particular on comparing bat roost selection between private residences and public buildings, delineating structural features of colonised buildings that facilitate their suitability, and measuring environmental conditions (temperature and humidity) within roosts.

Material and Methods

Study area

Bat surveys were conducted between November and December 2015, in the rural landscape surrounding Ranomafana National Park (RNP) (21°16′ S, 47°20′ E, Fig. 1) in eastern Madagascar. The park, founded in 1991 (Wright, 1995), holds more than 42000 ha of continuous humid forest and ranges in altitude from 500 to 1500 m (Wright, 1995). The forest is classified as submontane rainforest, with canopies ranging from 20 to 25 m in height. Rainfall oscillates between 2300 and 4000 mm, with a rainy season between December and March (Overdorff, 1993; Hemingway, 1996). RNP has its lowest temperature recordings from June to September (4 to 6 °C) and the highest between December and March (28 to 30 °C) (Andreone, 1994).

The region is located between the central highlands and eastern lowlands, and is of particular ecological and economic interest due to its high biodiversity and watershed protection role. It is considered one of the richest areas in the world in terms of primate, small mammal, bird and plant diversity (Duke, 1990). However, before it was demarcated as a national park, the area was selectively logged during the 1980s (Wright, 1995). It is currently surrounded by over 160 villages of different sizes, with a combined population of 27000 people over an area of approximately 500 km^2. Although recent infrastructure improvements have resulted in increased tourism around RNP (the second most visited park in Madagascar), the local economy is still dominated by irrigated rice cultivation, slash-and-burn agriculture and animal husbandry, with limited hunting and gathering (Peters, 1998; Brooks et al., 2009; Kari and Korhonen-Kurki, 2013).

Roost surveys

A total of 10 separate villages were visited during the study period, and 180 buildings surveyed for bat occupancy. In small villages all buildings were surveyed, while in large towns a subset (32 on average) representing different buildings types (private houses, schools, churches, offices, public toilets, markets, hospitals and libraries) were randomly selected. For each building, a total of 17 variables were collected via interview and direct measurements, these included: 1) total height; 2) building type (private house, school, offices, markets, hospitals or churches); 3) building age; 4) wall material; 5) presence of potential roost sites (such as empty cavities below the roof, or elongated and deep cracks on the walls); 6) number of bat emergence points; 7) maximum width of emergence points; 8) roost height (from the ground); 9) internal cavity height; 10) cardinal orientation of the roost within the building; 11) roof material; 12) number of human inhabitants (only for houses); 13) presence/absence of cooking/fire inside the house; 14) presence/absence of bat faeces or bat carcasses; 15) past and present problems with bats as determined by the inhabitants/custodians; 16) number of cats living in the house (as domestic cats are known bat predators (Ancillotto et al., 2013; Rocha, 2015), and 17) reports of bat predation by cats.

Temperature and humidity inside the roost were recorded for a subset of roosts using IButton DS1922L (Measurement Systems Ltd., Berkshire, United Kingdom) and Lascar EL-USB-2 data loggers (Farnell, Leeds, United Kingdom). These were placed at the entrance (in the shade) of both occupied and unoccupied roosts for three consecutive days. Data loggers were programmed to record temperature every 10 minutes throughout the period. Humidity data loggers were added to some roosts to provide supplementary information. These variables were measured in each village, with buildings selected to include the different building types.

In order to obtain additional information on human-bat conflicts, inhabitants of houses and building custodians were interviewed regarding occasional, current or previous presence of bats in the buildings, actions carried out to exclude bat colonies (such as roof changes), their attitudes toward co-habitation with bats, as well as a brief history of the building.

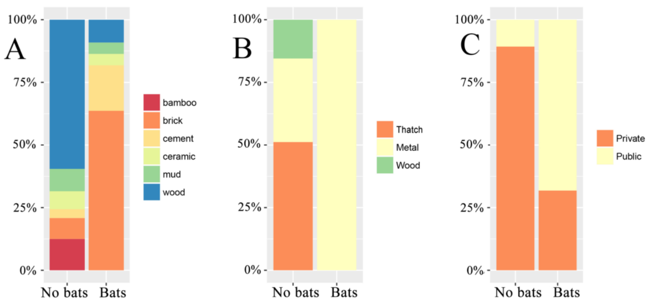

Figure 2 – Proportion of available and occupied buildings by A) wall type, B) roof type and C) building ownership.

Bat mist-netting

When clear emergence points could be identified from buildings with bat roosts, mist-netting was conducted to confirm the species identity of the roosting bats. Mist nets (12×2.5 m, 16 mm mesh, 0.16 mm netting and 6×2.5 m, 14 mm mesh, 0.08 mm netting, ECOTONE, Poland) were set in front of a total of 7 buildings, usually 1–2 m from exterior walls. Additionally, mist-netting was opportunistically conducted in different habitats such as in the rice paddies, forest fragments, caves and within open areas of the villages (see Tab. S1). All nets were continuously monitored, and captured bats removed. A maximum of 50 individuals were captured per night. Captured bats were identified using keys (Peterson et al., 1995; Russ et al., 2001; Monadjem et al., 2010), weighed (nearest 0.25 g), and morphological features were measured (nearest 0.1 mm). They were classified as juvenile or adult based on bone ossification, and the reproductive status of females (non-reproductive / pregnant / lactating) was assessed visually and by palpation.

Statistical analyses

Roost selection was evaluated using compositional analysis (e.g. Aebischer et al., 1993; Kauhala and Auttila, 2010) and preference indexes, including selection ratios (% buildings used / % buildings available) and Jacobs index (index D in Jacobs, 1974). Jacobs index was calculated according to the formula: $D = \frac{(r-p)}{(r+p-2rp)}$, where r is the proportion of used buildings and p the proportion of available buildings. D varies from -1 (strong avoidance) to +1 (strong preference), with values close to zero indicating that a certain building type is occupied proportionally to its availability. This approach was used to test for preferences between public and private buildings. Then, using the residuals of a Chi-square goodness of fit test, with p values corrected with Bonferroni confidence intervals, all building types were ranked and the significance of bat selection tested. Analysis was conducted at the family level, as occupied roosts primarily harboured mixed species colonies of molossid bats (Andrianaivoarivelo et al., 2006) and it was often not possible to confirm species identity.

Logistic regression was used to evaluate the influence of building attributes on the likelihood of bat occupancy. We first checked which variables had a significant effect on roost selection, considering both private and public constructions. Since public buildings were usually the only constructions occupied, using a second model, we assessed the effects of structural attributes on molossid bat occupancy. The reason we used two models with the same variables is because we first wanted to check which factors influenced roost selection in general. However, once we realised that they positively select public buildings, we removed personal houses from the model, and evaluated which factors influenced roost selection in public buildings only. Following Burnham and Anderson (2002) the most parsimonious models were selected using Akaike's Information Criterion corrected for small samples sizes (AICc). A set of suitable models were obtained selecting those models with an AICc difference from the best model (Δi)<2, using the R package `bestglm` v. 0.34 (McLeod and Xu, 2014). To avoid possible multicollinearity issues we: 1) calculated autocorrelation between model predictors, using the `Corrplot` package (Wei, 2013), and excluded all predictors with r>0.6; and 2) calculated each predictor variance inflation factor (VIF) and excluded all predictors with VIFs$\geqslant$3 (Neter et al., 1990).

All analyses were conducted using R software, version 3.2.4 (R Core Team, 2016). Plots were built with the `ggplot2`, `effects` (Fox and Hong, 2009; Wickham, 2009) and `gridExtra` (Auguie, 2012) statistical packages.

Results

Of the 180 buildings surveyed in the RNP area, bats were found roosting in 21 buildings (Tab. 1); either forming large colonies with several hundred individuals, or small groups made up of tens of individuals. Both females and males were present in each roost for most of the species. Six different species were identified (*Mops leucostigma*, *Chaerephon atsinanana*, *Mormopterus jugularis*, *Myotis goudoti*, *Paremballonura atrata* and *Neoromicia matroka*), with bats belonging to the Molossidae family forming the largest colonies and by far the most abundant.

Figure 3 – Types of buildings surveyed during the study. A) Mud house from Antanambao without bats; B) Mud/wood house from Amboasary without bats; C) Wood house with *ravinala* roof from Mangevo with small colony of bats; D) Wooden common house with metal roof, with a bat colony inside; E) Library built from wood in Kelilalina with one of the largest bat colonies; F & G) Cement primary school from Kelilalina with a bat colony; H) Cement hospital with metal roof in Tolongoina with a bat colony; I) Cement church with ceramic roof with a bat colony in Tolongoina; J) Cement personal house from Kelilalina harbouring a bat colony; K) Cement offices from school with metal roof with a bat colony from Kelilalina; L & M) Modern catholic church from Kelilalina with one of the largest bat colonies and a woody under-roof; N & O) Different structures of emerging points from occupied bat colonies.

Bat species identity was confirmed for many of the occupied buildings by mist-netting. A total of 372 bats were captured across the 10 villages. Pregnant females of most species and lactating females of *M. goudoti* and *N. matroka* were captured in several buildings. However, no juveniles or reproductively active males were encountered across the different species and villages (Tab. S1).

Of the 21 identified buildings with bat roosts, 17 were public institutions without permanent human occupancy, but frequented daily by a large number of people. The remaining four buildings were private houses, which generally had small colonies (Tab. 1). Large colonies of bats were mainly detected in large, modern, public buildings, built with cement and bricks rather than small traditional private houses, constructed with mud and wood (Fig. 2). Although small colonies were also found in the latter, no bats were identified in small traditional cabins (Fig. 2, Fig. 3). Colonies were mainly found under sheet metal roofs, within large empty cavities. These chambers were closed spaces between the roof of the house and the internal roof of the living quarters (usually wooden frames). Conversely, only single bats or small groups were found to roost in the traditional cabins without large cavities under the roof (between the dry leaves and branches) (Fig. 2, Fig. 3). Emergence points were at the eaves of buildings, where the roof materials join the walls (Fig. 3). When these spaces were properly sealed, bats used broken roof sections to emerge and return to the roost.

Synanthropic bats were found most commonly in public buildings (Tab. 2a). Of these, schools, offices and libraries were most likely to house bat colonies (Tab. 2b). Molossid bats were found in large public buildings, while small colonies of vespertilionids were only found in private houses with roofs made from leaves. Of the studied building attributes, the presence of ground fires, building size and the wall mater-

Table 1 – Summary of the 21 buildings where bat colonies were found in Ranomafana National Park surroundings.

Village	Building age	Height (m)	Area (m^2)	Orient.	Roost material	House type	Wall/roof	Occupants	Bat species*	Estimated n°bats	Emerg.**	Colony in the past?
Analamarina	2009	4	50	All	Metal/wood	Secondary school	Brick/wood	380+	Mop leu	100	2/5	Colony
	2012	4	50	NW	Metal/wood	Secondary school	Brick/wood	200+	0	50	1/2	No
	2012	8	84	SE	Metal/wood	Library	Wood/wood	200+	Mor jug	50	3/5	No
Antanambao	2003	2	24	S	Metal/wood	Personal house	Brick/wood	4	0	10	3/10	No
	2005	2	24	S	Metal	Common house	Ceramic/ceramic	200+	0	50	2/4	No
Kelilanina	1998	2	216	N/S	Metal/wood	Primary school	Brick/wood	200+	0	300	3/10	Colony
	2002	3	225	W	Metal	Shop	Brick/wood	4	0	100	2/2	No
	2003	3	150	NE	Metal	Personal house	Cement/wood	4	0	100	1/2	No
	2003	3.5	84	All	Metal/wood	Gendarmerie office	Brick/wood	2	Cha ats	200	13/15	Colony
	2005	2.5	75	E/W	Metal/wood	Shop	Brick/wood	4	Cha ats, Mor jug	200	4/6	Colony
	2005	2.5	75	E/W	Metal/wood	Shop	Brick/wood	60+	Cha ats, Mor jug	200	4/6	Colony
	?	7	660	All	Metal/wood	Church	Brick/wood	60+	Cha ats, Mor jug, Mop leu	100	3/15	No
Mangevo	?	3.5	240	All	Metal/wood	Secondary school	Cement/wood	100+	0	10	All/3	Colony
Tolongoina	1935	7	180	All	Metal	Church	Cement/wood	200+	Mor jug	200	All/3	No
	1960	5	60	W	Metal/wood	Primary school	Mud/wood	50+	Mor jug, Neo mat, Par atr	200	All/3	No
	1985	4.5	60	All	Metal/wood	Hospital	Brick/wood	15+	Cha ats, Mop leu	200	All/3	No
Tsarantanana	<1960	4	200	All	Metal/wood	Common house***	Brick/wood	0	0	50	All/3	Colony
	1963	4	100	W	Metal/wood	Personal house	Brick/wood	6	0	20	All/3	Colony
	1990	3	48	All	Metal	Administrative office	Wood/wood	10	0	10	All/3	?
	1920	4	48	All	Metal/ceramic	Primary school	Brick/wood	80+	Mor jug	50	6/20	No
	2008	3	40	E/W	Metal	Mayor office	Brick/wood	10	0	10	2/2	Colony

* Mop leu (*Mops leucostigma*), Mor jug (*Mormopterus jugularis*), Cha ats (*Chaerephon atsinanana*), Neo mat (*Neoromicia matroka*), Par atr (*Paremballonura atrata*).
** Emergence points (number/size in cm^2).
*** Common houses remain unoccupied for most of the time as they are reserved to community meetings.

Table 2a – Building selection by synanthropic bats in rural areas surrounding the Ranomafana National Park in Madagascar (public vs private).

	r	*p*	Jacob's index	Selection
Public buildings	0.4545	0.1737	0.5971	+
Private houses	0.0446	0.8263	−0.9806	-

Table 2b – Building selection by synanthropic bats in rural areas surrounding the Ranomafana National Park in Madagascar (considering all types of buildings surveyed).

Type of building	Expected		Observed		Residuals		*p* value	*p* value
	Colony absent	Colony present	Colony absent	Colony present	Colony absent	Colony present	(single step adj.)	(single step adj.)
Private house	137.937	18.063	149	7	0.942	−2.603	<0.05	0.0569*
Common house*	0.884	0.116	1	0	0.123	−0.340	0.999	1
Toilet	0.884	0.116	1	0	0.123	−0.340	0.999	1
Market	3.537	0.463	3	1	−0.285	0.788	0.992	1
Church	5.305	0.695	4	2	−0.567	1.566	0.850	1
Hospital	1.768	0.232	1	1	−0.578	1.597	1.000	1
Library	0.884	0.116	0	1	−0.940	2.598	0.999	1
Office	6.189	0.811	3	4	−1.282	3.543	1.000	1
School	10.611	1.390	6	6	−1.415	3.911	1.000	1

* * Common houses remain unoccupied for most of the time as they are reserved to community meetings.

ial (specifically brick and cement) significantly influenced bat presence (Fig. 4, Tab. 3). When the analysis was restricted to public buildings, only roost height influenced molossid bat presence.

Temperatures over 50 °C were recorded in bat roosts, and ranged from 54.5 to 13.6 °C. Roost temperatures started increasing from 06:00 until midday, reached maximum values between 11:00 and 13:00, and then decreased up until 21:00, when they became moderately stable throughout the night, with minimum temperature at around 05:00 (Fig. 5). Unoccupied roosts tended to have slightly higher and more variable temperatures than roosts with bat colonies, although this difference was not statistically significant. No significant differences in relative humidity were detected among the different types of constructions (Fig. S1-S7).

The local communities reported being aware of bat colonies in their villages, and when public or private buildings were occupied, discomfort or complaints were clearly expressed. Several cases of colony removal were noted but major actions were limited by financial and technical constraints. Methods of removal included upgrading and/or replacing traditional roofs with corrugated iron; using cats as domestic animals; and using smoke/fumigation to expel roosting bats by house owners. We recorded two cases where home owners removed the entire structure underneath the roof and sealed any potential emergence points in order to successfully rid their house of bats.

Discussion

We identified a systematic preference of synanthropic bats for public buildings, especially by large colonies of the Molossidae family. These bats appear to have found a suitable alternative to their native roosts in the hollow, old and tall trees of pristine forests (Rhodes and Catterall, 2008; Breviglieri and Uieda, 2014), which are becoming rare in Madagascar due to deforestation and selective logging (Eklund et al., 2016). The implications of our findings are manifold, from human-wildlife conflict avoidance, to the conservation of bats and the promotion of health and agricultural ecosystem services.

Roost selection

Of the five different bat species we identified to be roosting synanthropically, the most common bats were those of the Molossidae family, consistent with previous reports for other worldwide regions (Razafindrakoto et al., 2010; Jung and Kalko, 2011; Jung and Threlfall, 2015; Voight et al., 2015). As reported for the eastern town of Moramanga where 46 out of the 50 occupied roosts were found in schools (Razafindrakoto et al., 2010), most of the colonies found around the RNP were also in public buildings such as schools or churches, predominantly modern structures built with bricks, cement and metal roofs with large chambers to roost. This suggests that human-bat interactions are likely to have steeply risen in Central Madagascar in line with rural development and the destruction of the primary natural roosts available for bats. However, in contrast to findings from the east coast of Madagascar where only buildings aged over 10 years were occupied (Razafindrakoto et al., 2010), we report colonies in newly built constructions. This indicates that bat colonies can establish in new buildings that offer suitable roosts, regardless of their age. However, further research is required to investigate the effects of synanthropic roost selection on bat fitness, and determine the extent to which synanthropic roost selection is driven by a loss of natural habitat (Ancillotto et al., 2013; Threlfall et al., 2013).

Key building variables affecting roost choice include "type of building/wall", "lack of fire use" and "height of the building". Maternity colonies were found in large cavities under the roofs, with warm stable temperatures that can speed up gestation and reduce predation pressure (Voight et al., 2015). A lack of fire use was a crucial factor in roost choice. Bats have been previously shown to actively avoid smoke (Phillips et al., 2007), which may explain why we did not find bats when fire was used inside buildings. High buildings were positively selected as molossid bats require high and clear spaces for take-off (due to the long and narrow wings that allow fast flight but poor manoeuvrability). Although no temperature differences were recorded between occupied and non-occupied buildings, further research is required to determine if temperature affects roost choice for molossids. The lack of temperature differences could be due to measurement biases as we placed temperature loggers at easily retrievable places at roost entrances where airflow might be greater and temperatures may thereby differ from large chambers. Nonetheless we found breeding colonies in roosts where temperatures exceeded 50 °C. This data represents one of the few published temperature recordings from maternity roosts in the African continent (Bronrier et al., 1998). With rising temperatures and heatwaves associated with the changing climate, roosts, especially those with metal sheets, may overheat and become unsuitable places to shelter (Flaquer et al., 2014).

Human-bat conflicts

Bats are often repelled by local inhabitants and can suffer from direct persecution, chemical contamination or fumigation (Mühldorfer, 2013). Unsustainable eradication and eviction practices from an increased fear of zoonoses (Laidlaw and Fenton, 1971), and unwanted cohabitation (Randrianandrianina et al., 2006; Andriafidison et al., 2008,

2014) has led to much research focusing on evaluating methods to eradicate bats from buildings (Silver, 1935; Kunz et al., 1977; Barclay et al., 1980; Neilson and Fenton, 1994). However, few studies of human-bat roost co-existence have been conducted from an ecological perspective.

Although there are no published occurrences of disease transmission from bats to humans in Madagascar, our interviews indicated that bats were often noticed by villagers, and sometimes disliked or feared. Attempts to remove bats from buildings were reported, with some successful and others not. In our study area, as described for other countries, the most common problem was the accumulation of guano and the smell associated with bats (Voight et al., 2015). This could be resolved with better cleaning of the properties, and by repairing broken ceilings, roofs, or windows. There is neither a clear procedure nor appropriate legislation to deal with synanthropic bat colonies in Madagascar, and thus most cases of bat evictions from human-made structures remain unnoticed by the responsible authorities and researchers. Displacement of any bat colonies, with no risk assessment or advice from specialists, can be highly damaging to bat populations (Neilson and Fenton, 1994), and may only provide short term solutions (Voight et al., 2015), with probable displacements within the same village.

The presence of bats in anthropogenic areas, especially in agroforestry systems, provides benefits to communities, such as the control of disease vectors (Andrianaivoarivelo et al., 2006; Goodman et al., 2008) and crop insect pests (Jones et al., 2009; Kunz et al., 2011; Puig-Montserrat et al., 2015). Thus, the eradication of synanthropic bat colonies might increase pest damage to crops, and have subsequent negative consequences on yields and the local economy (Maas et al., 2013; Puig-Montserrat et al., 2015).

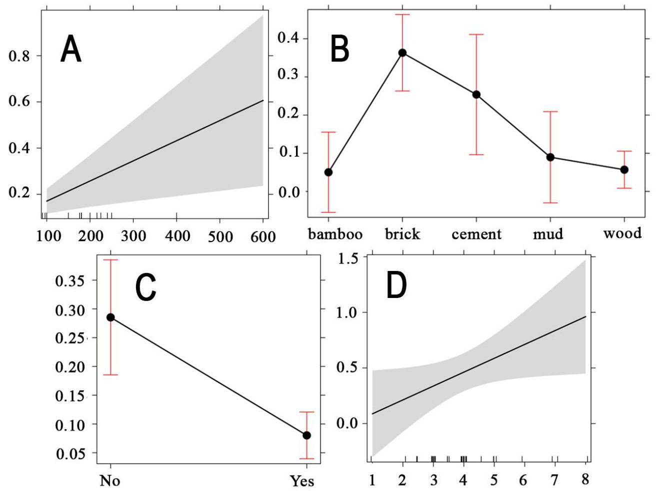

Figure 4 – Effect of the A) building area, B) wall material and C) the presence/absence of fire upon the probability of bat colonies occurring (modelled considering all sampled houses); and D) effect of the height of the roost (modelled considering only public buildings). The vertical axis is labelled on the probability scale, and a 95-percent pointwise confidence interval is drawn around the estimated effect in shaded areas (A, D) and stands (B, C).

Table 3 – Summary of the logistic linear models to predict bat colony occupation probabilities within A) all buildings and B) only public buildings. Odd-ratios and confidence intervals are provided.

A) Model: $Bats\ Fire + Area + Wall$, binomial

Residuals

Min	1Q	Median	3Q	Max
-0.8984	−0.0225	0.0049	0.0093	0.7180

Coefficients	Estimate	Std. Error	z value	p>|z|)
(Intercept)	0.2330	0.0784	2.973	**<0.01**
House Area	0.0009	0.0003	2.704	**<0.01**
Presence of Fire	−0.2579	0.0590	−4.372	**<0.01**
Wall brick	0.3131	0.0760	4.122	**<0.01**
Wall cement	0.2036	0.0979	2.080	**<0.05**
Wall mud	0.0394	0.0802	0.491	0.6239
Wall wood	0.0067	0.0578	0.116	0.9080

Residual standard error: 0.2412 on 170 degrees of freedom
Multiple R^2: 0.4654 Adjusted R^2: 0.4466
F-statistic: 24.67 on 6 and 170 DF p-value: <0.001

	OR	2.5%	97.5%
(Intercept)	1.2624	1.0814	1.4737
House Area	1.0009	1.0002	1.0015
Presence of Fire	0.7727	0.6878	0.8681
Wall brick	1.3676	1.1772	1.5889
Wall cement	1.2258	1.0105	1.4870
Wall mud	1.0402	0.8880	1.2185
Wall wood	1.0068	0.8981	1.1285

B) Model: $Bats\ Height$, binomial

Residuals

Min	1Q	Median	3Q	Max
-0.5869	−0.4621	−0.2749	0.5379	0.7875

Coefficients	Estimate	Std. Error	z value	p(>|z|)
(Intercept)	−0.0371	0.2449	−0.152	0.8805
Roost Height	0.1248	0.0584	2.136	**<0.05**

Residual standard error: 0.4797 on 31 degrees of freedom
Multiple R^2: 0.1283 Adjusted R^2: 0.1001
F-statistic: 4.561 on 1 and 31 DF p-value: 0.0407

	OR	2.5%	97.5%
(Intercept)	0.9636	0.5848	1.5877
House Area	1.1330	1.0057	1.2763

Conservation implications

The bat species identified in this study are mostly endemic (except *Chaerephon atsinanana*) and comprised several families. Most of the known forest and cave dwelling specialists were not captured in villages, being only captured either in caves, forest or open habitats (*Miniopterus manavi*, *Miniopterus majori* and *Myotis goudoti*). Although these species are not of conservation concern, the lack of encounters in anthropogenic landscapes combined with decreasing forest habitats, highlights the importance of conserving the remaining forests of Madagascar. We only captured 1 of the 5 bat species listed as threatened in Madagascar (*Hipposideros commersoni*), and this occurred within a forest site. We provide the second account of a building roost for *Paremballonura atrata* (Goodman et al., 2014). However, this is based on a single individual that was captured in a school in Tolongoina, and the species is thought to be fully dependent on forest habitats (Goodman et al., 2006). Like other emballonurids in the Neotropics, this species might be well adapted to foraging in open spaces and therefore, more common in synanthropic settings than expected (Goodman et al., 2005). Regarding molossids, despite no current conservation concern, they include island endemics, for which there are increasing threats, especially due to their synanthropic habits. For instance, bushmeat hunting is a common practice in Madagascar, and the ease of capture from colonies in human settlements makes these species vulnerable to overexploitation (Goodman et al., 2008). At least *Mormopterus jugularis* and *Mops leucostigma* are known to be hunted for food in Madagascar (Goodman et al., 2008; Jenkins and Racey, 2008; Andriafidison et al., 2014).

Conclusions

Shifting to modern construction methods, in a manner that minimises disturbances, while combining old techniques with improved roof sealing (Voight et al., 2015), could prevent the establishment of bat colonies in undesired locations. Less detrimental alternatives to current eradication methods exist, such as placing bat box stations near rice fields, far from human populations (Agnelli et al., 2011). Such practices may reduce the unwanted aspects of bat synanthropy while preserving the

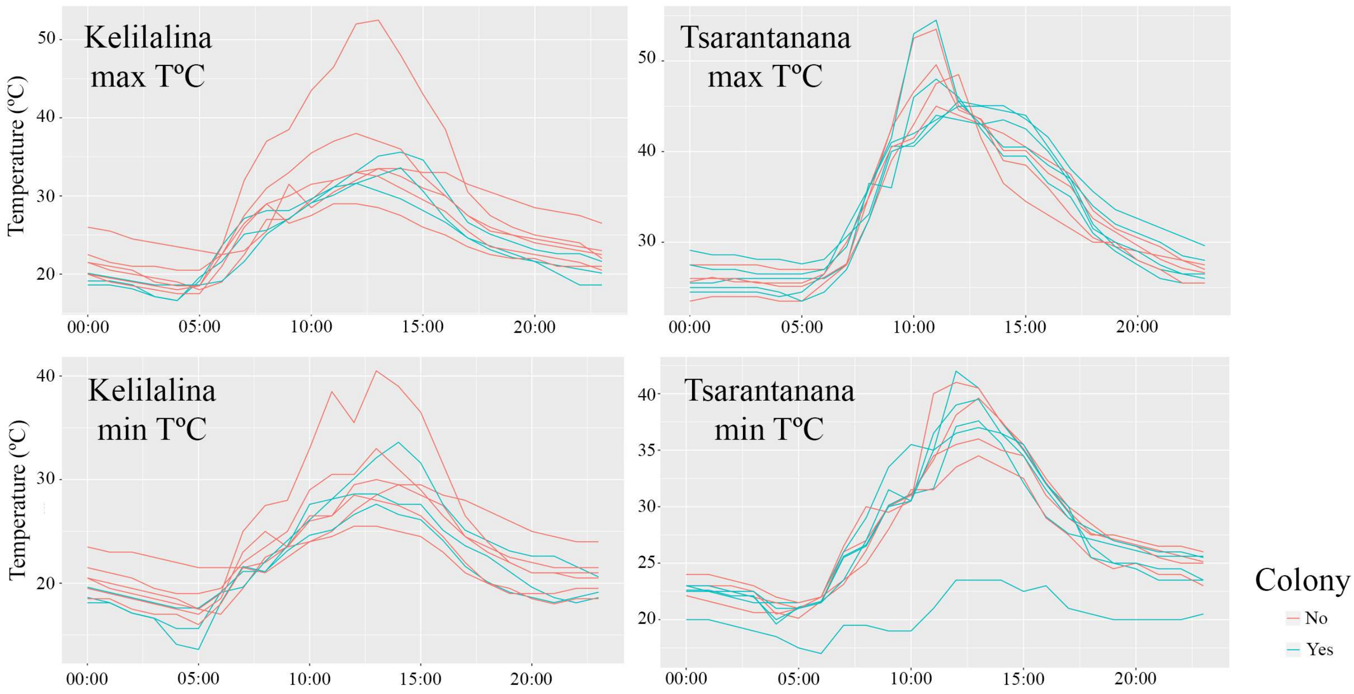

Figure 5 – Maximum (upper panels) and minimum (lower panels) daily cycle temperatures recorded in both the available non-occupied roosts and the occupied bat roosts in Kelilalina and Tsaratanana towns.

ecosystem services bats provide for local communities. However, further research is required to determine the extent to which the occupation of urban roosts is driven by a loss of natural forest roosts, as opposed to preference selections of anthropogenic roosts due to perhaps their more favourable conditions. While reducing direct interactions and contact with humans, bats could sometimes be allowed to remain in human-made structures. We urge caution in evicting bat colonies from public buildings, and show that a greater focus on construction design is likely to minimise human-bat conflicts in rural communities of developing countries.

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Associate Editor: D. Russo

Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1 Bat captures summary by sampled village.

Figure S2 Differences in temperature recorded across four daily periods between both available non-occupied and occupied roosts.

Figure S3 Temperatures recorded in all construction types.

Figure S4 Temperatures recorded in houses with and without a ground fire inside.

Figure S5 Temperatures recorded in both constructions with metal roofs and roofs made of *ravinala* leaves.

Figure S6 Relative humidity recorded in all construction types.

Figure S7 Relative humidity recorded in houses with and without a ground fire inside.

Figure S8 Relative humidity recorded in both constructions with and without bat colonies.