

Response of Bat Activity to Land Cover and Land Use in Savannas is Scale-, Season-, and Guild-Specific

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Highlights

- The features and spatial scales that savanna bats respond to vary by guild and season
 - Responses are stronger in the dry season than the wet season for all three foraging guilds
 - Maintaining water sources promotes bat activity
- Shrub encroachment negatively affects edge bats.

Abstract

Tropical savannas are biomes of global importance under severe pressure from anthropogenic change, including land-cover and land-use change. Bats, the second-most diverse group of mammals, are critical to ecosystem functioning, but vulnerable to such anthropogenic stresses. There is little information on how savanna bats respond to land cover and land use, especially in Africa, limiting our ability to develop conservation strategies for bats and maintain the ecosystem functions and services they provide in this biome. Using acoustic monitoring, we measured guild-specific (aerial, edge, and clutter forager) responses of bat activity to both fine-scale vegetation structure and landscape-scale land-cover composition and configuration across the wet and dry seasons in a southern African savanna undergoing rapid land-cover and land-use change. Responses were guild- and season-specific but generally stronger in the dry season. Aerial and clutter bats responded most strongly to landscape metrics in the dry season (positive responses to savanna fragmentation and water cover, respectively) but fine-scale metrics in the

wet season (positive responses to water cover and grass cover, respectively). Edge bats responded most strongly (negatively) to the distance to water in the dry season and fine-scale shrub cover in the wet season. Our results show it is possible to maintain high levels of bat activity in savanna mosaics comprised of different land covers and land uses. Bats, and the ecosystem services they provide, can be conserved in these changing landscapes, but strategies to do so must consider foraging guild, spatial scale, and seasonal variation in bat activity.

Key words: Agriculture, Chiroptera, landscape ecology, savanna

1. Introduction

Tropical savannas are biomes of global importance for people and wildlife (Bond and Parr, 2010; Murphy et al., 2016; Parr et al., 2014). They contain high levels of biodiversity, provide essential habitat for endemic and endangered species (Murphy et al., 2016), account for a large amount of terrestrial net primary productivity, and store carbon (Parr et al., 2014). Savannas also provide essential resources to people, such as pasture for livestock, firewood, thatching materials, and medicinal plants (Egoh et al., 2009; Fensham et al., 2005; Hoffmann et al., 2012; Parr et al., 2014; van der Werf et al., 2010).

Despite their importance, tropical savannas are generally underappreciated, understudied and under-protected (Laurance et al., 2014; Parr et al., 2014), with less than 13% under any kind of official protection (Jenkins and Joppa, 2009). Globally, one of the principal threats to tropical savannas is land-cover change, particularly the conversion of savanna to agriculture, including both low-intensity croplands and high intensity commercial production (Aleman et al., 2016; Laurance et al., 2014).

Land-cover change has profound, often negative impacts on wildlife (Foord et al., 2018; Reynolds et al., 2018; Sala et al., 2000). At fine spatial scales, land-cover change alters the type and structure of vegetation, eliminating foraging habitat or shelter (Fahrig et al., 2011; Goodwin et al., 2002; Tschardt et al., 2012). On larger scales, landscape composition (the different types of land cover) and configuration (the spatial pattern of land cover) affect wildlife through different mechanisms: changes in landscape composition typically lead to reductions in native vegetation or other habitats and the loss of resources located in them (Fischer and Lindenmayer, 2006; Tschardt et al., 2012), while changes in landscape configuration, regardless of the amount of cover, affect wildlife through edge effects, patch isolation, and loss of connectivity across the landscape (Fahrig, 2003).

Bats are the second most diverse order of mammals (Burgin et al., 2018) and provide important ecosystem services such as pest control, pollination, and seed dispersal (Boyles et al., 2011; Kunz et al., 2011; Maas et al., 2013; Taylor et al., 2017; Williams-Guillén et al., 2008). They may also serve as bioindicators (Jones et al., 2009). There is growing evidence that in savannas

in particular, some bat species exhibit strong preferences for agricultural landscapes (Noer et al., 2012; Toffoli and Rughetti, 2017) where they play an important role in consuming pest insects (Bohmann et al., 2011; Puig-Montserrat et al., 2015; Taylor et al., 2013, 2018, 2017).

The role of the entire landscape mosaic is increasingly recognized as essential for effective species conservation (Hansson and Angelstam, 1991; Hobbs, 1994; Wiens, 2009). Conserving bats, and thus maintaining the ecosystem services and functions that they provide therefore requires an understanding how they use the mosaics of various land covers and land uses increasing found in modified landscapes. Understanding how bats respond to the composition and configuration of these different land covers can then inform conservation planning by indicating key elements (e.g. size or shape of native vegetation patches) in the landscape necessary for maintaining or promoting bat activity. Without this understanding, conservation planning may be ineffective due to missing key elements of the landscape or preserving habitat at the wrong spatial scale (Hansson and Angelstam, 1991; Hobbs, 1994; Wiens, 2009).

Bats can respond to variation in both fine-scale vegetation structure and landscape-scale composition and configuration (Brigham et al., 1997; Fuentes-Montemayor et al., 2013; Gehrt and Chelsvig, 2003; P. Mendes et al., 2017; Monadjem and Reside, 2008). Their response to land cover varies greatly between regions, biomes, seasons (Ferreira et al., 2017; Klingbeil and Willig, 2010; Mendes et al., 2014; Monadjem et al., 2018a), and species or guilds (Gorresen et al., 2005; Klingbeil and Willig, 2009; E. S. Mendes et al., 2017; Müller et al., 2012).

To date, most research on the impacts of land-cover change on bats has been conducted in forest biomes (Estrada-Villegas et al., 2010; Ferreira et al., 2017; Pinto and Keitt, 2008; Williams-Guillén and Perfecto, 2011), limiting our ability to generalize patterns. Our understanding of how land-cover change affects bats in savannas, particularly in Africa, is far more limited (Meyer et al., 2016; Monadjem and Reside, 2008; Mtsetfwa et al., 2018; Weier et al., 2018). Studies from North American pine savannas and South America Cerrado savannas show land cover modification and reduced canopy cover (land cover composition) not configuration reduce bat diversity metrics (Bailey et al., 2019; Pereira Ramos et al., 2018). However, these responses are often species-specific, varying by foraging guild or other traits (Bailey et al., 2019; P. Mendes et al., 2017; Muylaert et al., 2016; Pereira Ramos et al., 2018).

In southern African savannas, changes in land cover and land use may impact bats by eliminating their foraging habitat, destroying their roosts, or reducing populations of their insect prey. This could be an especially grave threat to clutter foraging bats, which rely on dense vegetation for foraging, and edge foraging bats, which use edge habitats between dense and open vegetation (Cooper-Bohannon et al., 2016; Monadjem et al., 2010). There is evidence that high intensity agriculture can negatively affect some bat species (Mtsetfwa et al., 2018), but remnant natural and semi-natural vegetation (Mtsetfwa et al., 2018; Weier et al., 2018) and wetlands (Sirami et

al., 2013) in such landscapes may promote bat activity. However, the role of landscape configuration has not been considered. In addition, the relative effects of fine-scale vegetation compared to landscape composition and configuration have not been directly compared. Finally, studies in this region have only compared the effects of savanna and commercial agriculture on bats (Mtsetfwa et al., 2018; Sirami et al., 2013; Weier et al., 2018), while the role of rural areas and villages has been largely neglected, despite comprising a large, and growing component of the landscape (Bailey et al., 2015).

In order to understand the effects of land cover and land use on bats in tropical savannas, we measured guild-level responses in bat activity across the wet and dry seasons to both vegetation structure and land cover composition and configuration across northeastern Eswatini (formerly Swaziland). This region is part of the Maputaland-Albany-Pondoland biodiversity hotspot (Steenkamp et al., 2005) and undergoing rapid land-cover change, primarily as a result of agricultural expansion and intensification (Bailey et al., 2015). Our objectives were to: 1) quantify the response of bats to variation in fine-scale vegetation structure and landscape-scale land-cover composition and configuration; 2) compare the variation in responses by foraging guild; 3) determine the most relevant spatial scale of the response for each guild; and 4) ascertain how responses vary by season.

We expected to see guild-specific responses to both fine- and landscape-scale characteristics. Previous studies have found that guilds respond to different characteristics at different spatial scales depending on their ecology (Ferreira et al., 2017; Fuentes-Montemayor et al., 2013; Pereira Ramos et al., 2018; Pinto and Keitt, 2008). We expected clutter bats that use denser vegetation and fly shorter distances to respond more strongly to fine-scale vegetation structure because they rely on dense vegetation immediately around them for foraging, while edge and aerial bats that forage in open areas and fly longer distances were expected to respond more strongly to landscape-scale characteristics since they fly and forage above vegetation (Cooper-Bohannon et al., 2016; Monadjem et al., 2010). In general, we expected to see a greater effect of landscape composition than configuration on bats, as has been reported in previous studies (Arroyo-Rodríguez et al., 2016; Meyer and Kalko, 2008). We also expected to see strong seasonal variation in response from all guilds, because this has been observed in previous studies in the region (Monadjem and Reside, 2008; Mtsetfwa et al., 2018; Taylor et al., 2013), likely due to the scarcity of resources, such as water or insect prey in the dry season (Fukui et al., 2006; Hagen and Sabo, 2012; Salsamendi et al., 2012).

2. Materials and Methods

2.1 Study Area

This study was conducted across an area of approximately 2,300 km² in the eastern low-lying region of Eswatini referred to as the “Lowveld,” which is bordered by the Drakensberg Mountains in the west and the Lubombo Mountains in the east (Figure 1). The area is a part of

the Maputaland-Pondoland-Albany biodiversity hotspot (Steenkamp et al., 2005), which stretches from southern Mozambique, through eastern Eswatini, and into South Africa. This region has been subject to rapid land-cover change, mainly from expansion of commercial and small-holder croplands (Bailey et al., 2015). Elevation ranges from approximately 150 m to 600 m above sea level. The Lowveld is characterized by a warm, semi-arid subtropical climate (Matondo et al. 2004). The annual mean temperature is 20-22°C, with a mean monthly temperature of 26° C in January and 18° C in July (Monadjem and Garcelon, 2005). Annual rainfall is 500-700 mm per year, concentrated in the summer months of October to March (Matondo et al. 2004; Monadjem and Reside 2008; Knox et al. 2010).

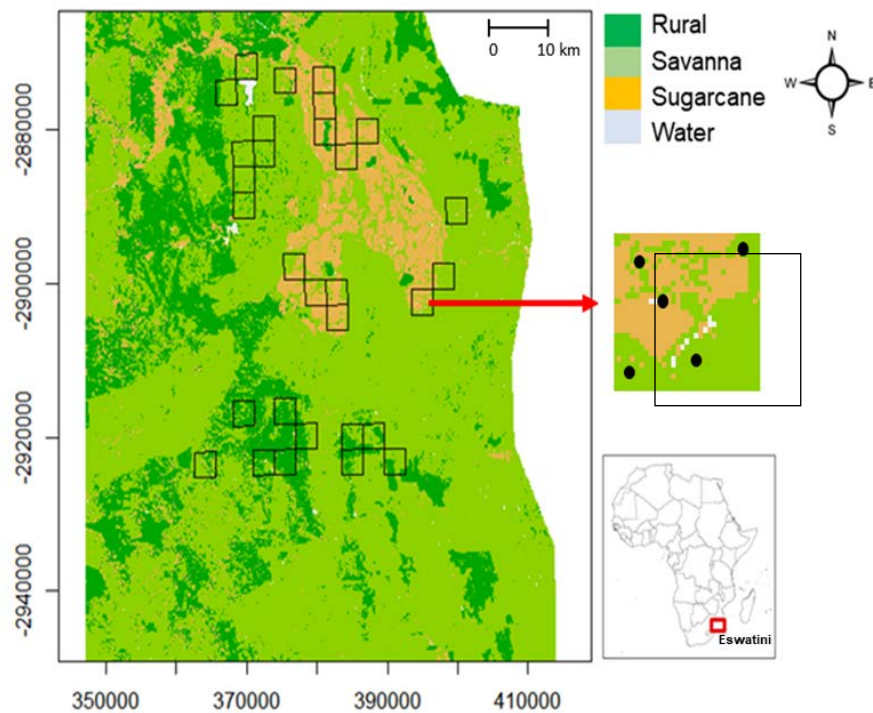


Figure 1. Map of the study region with sampling blocks outlined in black. The inset shows a close-up of one block, with Anabat points indicated by the black circles.

2.2 Land-Cover Classification

Land cover at our site is made up of savanna vegetation (open savanna and woodland), commercial sugarcane plantations, and rural settlements, which are comprised of buildings, subsistence crops (primarily maize), pasture for domestic livestock, and remnant savanna vegetation (Bailey et al., 2015; Monadjem and Reside, 2008) (Figure 2). Several perennial rivers run through the study area and a number of dams occur here, mostly acting as reservoirs for the commercial plantations. Therefore, we classified land cover across the study region into four categories: rural settlements (hereafter “rural”), savannas, sugarcane plantations (hereafter “sugarcane”), and water. We used these four categories to create a classified raster of the region. First we carried out supervised classification in Google Earth Engine

(www.earthengine.google.com) using a cloud-free Landsat 8 8-day raw composite image from March 21 – 29, 2016 at 30 m resolution. We then trained a voting support vector machine (voting SVM) classifier using 193 manually drawn polygons including each of the four land-cover categories. Resampling of the classified raster yielded an overall validity of 99.97%.



Figure 2. Land uses and land covers in northeast Eswatini: A. Savanna; B. Rural settlements; C. Sugarcane plantations. Savannas are a mix of open, grassier areas with some trees and shrubby thickets with higher canopy cover.

Because the rural land-cover class included crops and pasture that may have a similar spectral signature to savanna vegetation (Prestele et al., 2016), we incorporated population density to further distinguish rural areas from savanna. We used the population count raster for Eswatini from WorldPop projected for 2015 (WorldPop, 2013) to identify rural areas (Linard et al., 2012). We resampled this population count raster to the resolution of the classified raster using the nearest-neighbor algorithm. We overlaid the population raster on the classified raster and reclassified any cells with population count >1 as rural (Figure 1).

2.3 Acoustic Sampling

To capture variation in landscape cover across our study site we created a grid of 3 km^2 ($\sim 1.73 \text{ km} \times \sim 1.73 \text{ km}$) blocks (hereafter “block”). We then overlaid this grid on the classified raster. We randomly selected 30 blocks (out of a possible 780) for acoustic surveys. These blocks were stratified between the three land-cover categories, with ten blocks for each type (10 rural, 10 savanna, 10 sugarcane). Sampling 30 blocks allowed us to capture the variation across the landscape and obtain a suitable sample size for statistical analyses at the landscape scale. Within each block, we deployed five Anabat Express detectors (Titley, Inc., Ballina, Australia) at randomly placed points (hereafter “points”). These five points served as spatial replicates within each block for fine scale models (Figure 1). Detectors were generally placed 200 m from each other, with a minimum distance of 100 m. As the maximum distance at which any bat species in Eswatini can be detected is 30 m (Monadjem et al., 2017), the call of an individual bat could not be recorded by more than one detector at a given time. Each detector was attached to a tree trunk or electric pole at 1.5 m above the ground. Anabat detectors were set to record starting half an

hour before sunset and continued recording for six hours. Each block was surveyed twice per season (wet: November – March; dry: May – July) for a total of four survey nights.

2.4 Classification of Bat Calls

We first trained a support vector machine (SVM) algorithm to classify bat calls based on calls from hand-released bats in the region (Monadjem et al., 2017). Five bat species (*Mops midas*, *Neoromicia nana*, *Scotophilus dinganii*, *Miniopterus natalensis*, and *Hipposideros caffer*) have calls that are distinctive and do not overlap in parameters with other species in the region. These species could be individually identified by the SVM algorithm. Several other species exhibit varying amounts of overlap in their call parameters (Monadjem et al., 2017) and were therefore grouped together into the following three “sono-species” during classification:

1. *Chaerephon pumilus* – *Mops condylurus* – *Taphozous mauritanus*
2. *Neoromicia zuluensis* – *Nycticeinops schlieffeni* – *Pipstrellus hesperidus* – *Scotophilus viridis*
3. *Rhinolophus blasii* – *R. darlingi* – *R. simulator*

In addition, we manually searched through bat files to identify calls from the two *Myotis* species from the region (*Myotis bocagii* and *M. tricolor*), which are acoustically distinctive from other bat species in the region, but have highly variable call parameters (Monadjem et al., 2017).

We examined the echolocation calls recorded at each point with the program ANALOOK (Chris Corben, version 4.8, <http://www.hoarybat.com>). Calls were first filtered to remove files with only noise and no bat calls. We then extracted the call parameters from those Anabat files that passed the noise filter. These parameters describe each bat pulse within a pass, a sequence of pulses from a single bat (Miller, 2001). The SVM algorithm classified bat calls at the level of the bat pulse within a pass. In order to be counted, four consecutive pulses had to be classified as the same sono-species. We validated the classifier by comparing a manual identification to the SVM classifier for 639 calls. SVM classification and manual identification were in agreement for 98.3% of the 639 validation calls.

We standardized the number of calls per sono-species by counting each species a maximum of once per minute (Miller, 2001). Finally, we grouped classified calls from each species or species group into three foraging guilds based on their wing morphology, echolocation, and foraging ecology: aerial foragers, edge foragers, and clutter foragers (Arita and Fenton, 1997; Meyer et al., 2004; Monadjem et al., 2010; Monadjem and Reside, 2008; Schnitzler and Kalko, 2001). Aerial foragers are adapted to fast, less maneuverable flight in open areas, while clutter foragers are adapted to slower, more maneuverable flight within dense vegetation; edge foragers are intermediate in terms of flight speed and maneuverability and often use vegetation at the edge of more open areas (Arita and Fenton, 1997; Meyer et al., 2004; Monadjem et al., 2010; Monadjem and Reside, 2008; Schnitzler and Kalko, 2001) (Table 1).

Table 1. Definition of foraging guilds and classification of bat species by foraging guild.

Foraging guild	Wing morphology	Echolocation	Foraging ecology	Species / Species Group
Aerial	Long and narrow, high wing-loading	Low duty-cycle - Quasi-constant frequency	Open spaces, high altitudes	<i>Chaerephon pumilus</i> – <i>Mops condylurus</i> – <i>Taphozous mauritanus</i> group <i>Mops midas</i>
Edge	Intermediate length, width, and wing loading	Low duty-cycle frequency-modulated or frequency-modulated-quasi-constant frequency	Edges between open areas and dense vegetation	<i>Neoromicia nana</i> <i>Scotophilus dinganii</i> <i>Neoromicia zuluensis</i> – <i>Nycticeinops schlieffeni</i> – <i>Pipstrellus hesperidus</i> – <i>Scotophilus viridis</i> group <i>Myotis bocagii</i> – <i>Myotis tricolor</i> group <i>Miniopterus natalensis</i>
Clutter	Short and broad, low wing-loading	Constant frequency	Dense, cluttered vegetation	<i>Rhinolophus blasii</i> – <i>R. darlingi</i> – <i>R. simulator</i> group

2.5 Fine- and Landscape-Scale Metrics

We quantified the environment at two spatial scales: a fine scale around each sampling point and the landscape scale within each sampling block. At the fine scale, we measured vegetation cover and structure. In order to do so, we established a 30 m transect in each of the cardinal directions from the sampling point. We evaluated canopy and ground cover at the sampling point where the Anabat detector was placed and at points at 10 m intervals along each 30 m transect (total of thirteen measurements) while shrub cover was measured along the length of each 10 m interval within each transect (total of twelve measures). We measured the canopy cover using a spherical densiometer (Forestry Suppliers, Inc., Jackson MS) (Lemmon, 1956). We visually estimated ground cover in 1×1 m quadrats. We classified ground cover as: sugarcane, crop (all crops other than sugarcane), grass, bare ground, and water. We measured shrub cover, woody vegetation < 2 m in height (Edwards, 1983), using the line intercept method (Canfield, 1941). For each sampling point, we took the mean canopy cover and ground cover from the thirteen points where we took these measures and the mean shrub cover from the twelve transects around the sampling point. We also measured the distance from each Anabat sampling point to the nearest water source because bats are known to use and forage around water bodies and riparian corridors (Monadjem and Reside, 2008; Pinto and Keitt, 2008; Sirami et al., 2013), using the function “gDistance” in the package rgeos (Bivand et al., 2017).

We calculated a variety of land-cover composition and configuration metrics within each sampling block (Gustafson, 1998). To account for land-cover composition, we measured the percent cover of savanna, rural, sugarcane, and water. For configuration metrics, we used savanna edge density because many bats use edges of natural vegetation (Chambers et al., 2016; Ethier and Fahrig, 2011; E. S. Mendes et al., 2017; Müller et al., 2012) and the savanna splitting index (hereafter “savanna splitting”), to account for the connectivity of savanna land cover, which may also be important for bats (Frey-Ehrenbold et al., 2013). We calculated all land-cover

composition and configuration metrics using the “ClassStat” function in the SDMTools package (VanDerWal et al., 2014) in R version 3.3.3 (R Core Team, 2013).

We calculated pairwise correlations between all fine-scale metrics and all landscape-scale metrics using the function “rcorr” in the package Hmisc (Harrell, 2006). We found no correlations >0.7 among either the fine- or landscape-scale metrics that we used in our models.

2.6 Statistical Analysis

2.6.1 Bat activity

We measured the response of aerial, edge, and clutter foragers’ activity at two scales: fine scale and landscape scale. At the fine scale, we summed the total number of calls at each Anabat point over all the sampling nights per season. For the landscape scale, we summed the number of bat calls per season from all Anabat detectors within the block. We measured bat response separately for each season (wet vs. dry) at both spatial scales because levels of bat activity are known to vary between seasons due to changes in temperature, precipitation, prey abundance and water availability (Cisneros et al., 2015; Ferreira et al., 2017; Klingbeil and Willig, 2010; Mendes et al., 2014).

We evaluated *a priori* suites of models to explain bat activity at both the fine and landscape scales. Each fine scale model included one of the fine-scale measures of vegetation structure: canopy cover, shrub cover, sugarcane cover, bare ground cover, water cover, and distance to water. We also included a null model (Table 2). To evaluate these models, we used generalized linear mixed models with the function “glmer” in the package lme4 (Bates et al., 2015), with a Poisson distribution to measure the response to fine-scale covariates. We used an offset term to account for the different number of sampling nights per point (Kotze et al., 2012; Warton et al., 2015), due to occasional equipment failure. For fine scale models, each individual point was treated as a spatial replicate. We therefore used “block” as a random effect in order to account for spatial autocorrelation between points within the same block (Bailey et al., 2017). We checked for overdispersion using the functions “simulateResiduals” and “testDispersion” in the R package DHARMA (Hartig, 2019) and found no evidence of overdispersion in the fine-scale models.

Landscape-scale models included one measure of landscape composition or configuration: rural, sugarcane, savanna, and water cover, edge density of savanna, or savanna splitting index. We also included two models with interactive effects between savanna composition and configuration: savanna cover \times savanna edge density and savanna cover \times savanna splitting (Table 2). We included interaction terms in order to determine whether savanna configuration may exacerbate or mitigate the effects of reduced savanna cover (composition). Using the functions “simulateResiduals” and “testDispersion” in the R package DHARMA (Hartig, 2019) we found evidence of overdispersion with generalized linear models fit to a Poisson distribution

and therefore analyzed the data using with a quasi-Poisson distribution (Kotze et al., 2012; O’Hara and Kotze, 2010). Because the landscape response was aggregated at the block level, we did not include a random term to account for block. We used an offset term that was the sum of the number of sampling nights from all detectors within the block (Kotze et al., 2012; Warton et al., 2015).

Table 2. List of models used for each spatial scale. “×” indicates interactive term in models.

Scale of bat response	Spatial scale of model covariates	Model covariates
Fine	30 m	Canopy cover (percent) Shrub cover (percent) Bare ground cover (percent) Grass cover (percent) Sugarcane cover (percent) Water cover (percent) Distance to water (m) Null
Landscape	3 km ²	Rural cover (percent) Savanna cover (percent) Sugarcane cover (percent) Water cover (percent) Savanna edge density Savanna splitting Savanna cover × Savanna edge density Savanna cover × Savanna splitting Null

¹See Methods section 2.5 - Fine- and Landscape-Scale Metrics for detailed definitions of covariates.

For each season, we compared the fine-scale models using Akaike Information Criterion corrected for small sample size (AICc) and compared the landscape-scale models using quasi-Akaike Information Criterion corrected for small sample size (QAICc) (Burnham and Anderson, 2002). QAICc is an approximation of AICc for models with quasi-distributions (Burnham and Anderson, 2002). We calculated AICc using the function “model.sel” for fine-scale models and calculated QAICc with the function “QAICc” for landscape-scale models. Both functions are in the package MuMIn (Barton, 2017). We considered models within 2 AICc or QAICc units to be competing models. We evaluated the parameters of the top models and any competing models by examining their 95% Confidence Intervals (CIs) and considered those that did not cross 0 to be relevant. We then graphed relevant parameters to understand how bat activity changes across variables of interest.

Finally, we measured the fit of the best models containing relevant predictors for each season at each scale using Pseudo R^2 . We calculated Pseudo R^2 for the fine-scale (generalized linear mixed) models using the function “r.squaredGLMM” in the package MuMIn (Barton, 2017; Johnson, 2014; Nakagawa and Schielzeth, 2013) and using the function “rsq.kl” in the package rsq for landscape-scale (generalized linear) models (Zhang, 2018, 2017).

3. Results

We recorded acoustic data for a total of 3,408 hours during 120 sampling nights across the 30 sampling blocks. During this period, we identified a total of 69,011 bat calls. There were more calls in the wet season (n=56,062) than the dry season (n=12,949). Calls were predominantly from aerial bats (n=47,645), followed by edge bats (n=21,296), while the number of calls of clutter bats were orders of magnitude lower (n=70). Activity was higher for aerial and edge bats in the wet season, but for clutter bats, activity was higher in the dry season (Table 3).

Table 3. Summary of bat activity at the fine- and landscape-scale for each foraging guild and season.

Guild	Scale	Season	Mean Calls	Minimum Calls	Maximum Calls
Aerial	Fine	Wet	261	12	627
		Dry	60	0	376
	Landscape	Wet	1,295	386	2,446
		Dry	293	8	758
Edge	Fine	Wet	115	0	849
		Dry	28	0	217
	Landscape	Wet	573	58	2,282
		Dry	136	8	379
Clutter	Fine	Wet	0.1	0	2
		Dry	0.4	0	28
	Landscape	Wet	0.4	0	2
		Dry	2	0	39

Table 4. Top model and any competing models for each guild at each spatial scale in each season. See Supplemental Information for full model selection tables. We do not include Pseudo R^2 for top models in which the predictors were not significant (95% confidence intervals of β coefficients did not include 0).

Guild	Scale	Season	Top Model	Pseudo R^2	Competing models
Aerial	Fine	Wet	Water cover*	0.04	None
		Dry	Water cover*	0.03	None
	Landscape	Wet	Savanna splitting	-	Water cover Null Sugarcane cover
		Dry	Savanna splitting*	0.22	Water cover
Edge	Fine	Wet	Shrub cover*	0.05	None
		Dry	Distance to water*	0.30	None
	Landscape	Wet	Sugarcane cover	-	Null Water cover Savanna cover
		Dry	Water cover	-	Savanna splitting
Clutter	Fine	Wet	Grass cover*	0.02	Bare ground cover Null model
		Dry	Sugarcane cover*	0.02	Water cover
	Landscape	Wet	Rural cover	-	None
		Dry	Water cover*	0.46	None

*Indicates that variables in top model were significant (95% confidence intervals of β coefficients did not include 0).

3.1 Aerial foraging guild

At the fine scale, water cover explained the activity of aerial foragers. Activity increased with increasing water cover during both seasons, although the magnitude was greater in the dry season ($\beta = 0.14$ [95% confidence interval: 0.13, 0.16]) than the wet ($\beta = 0.09$, [0.09, 0.10]) (Figure 3). There were no other competing models (Table 4, Table S1). The Pseudo R^2 for top models in both seasons was relatively low, though slightly higher in the wet season than the dry (0.04 vs. 0.03) (Table 4).

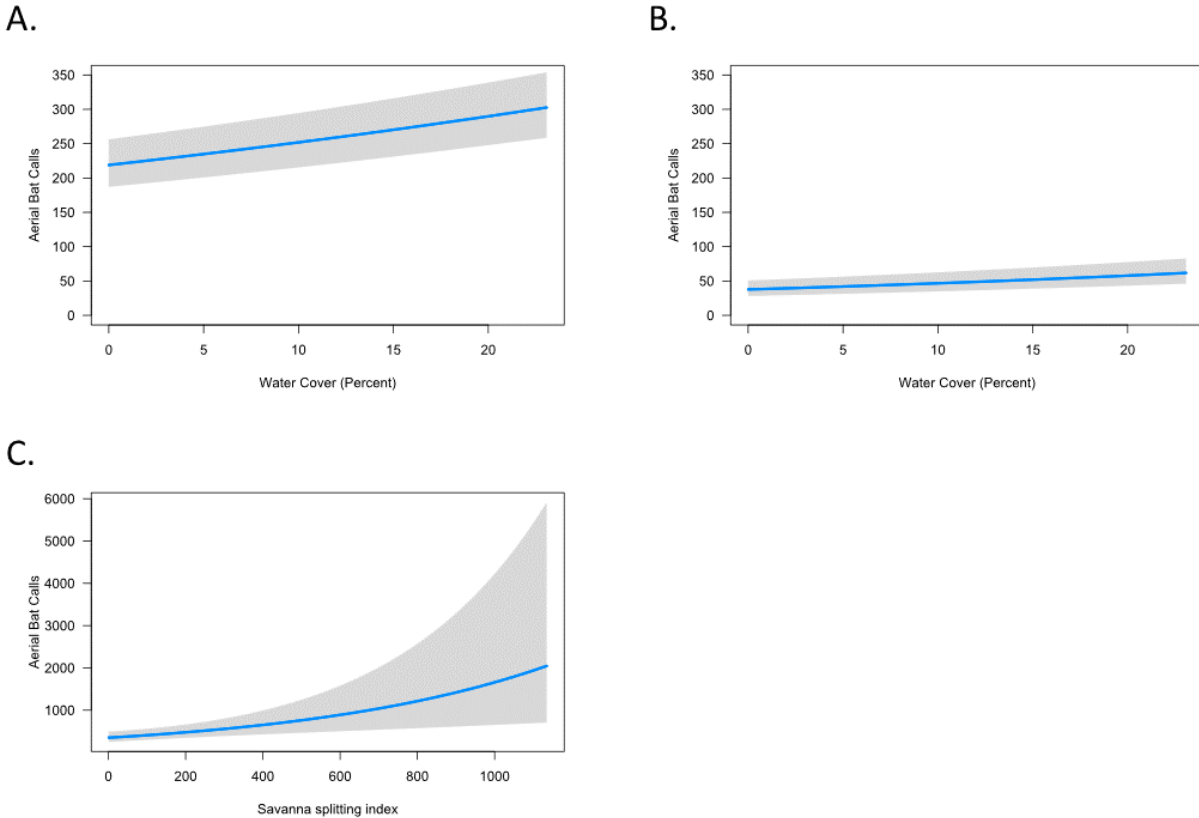


Figure 3. Response of aerial foraging guild bats at the fine scale in the A. wet season, B. dry season and at the landscape scale in the C. dry season.

Landscape metrics were relevant predictors of aerial bat activity only in the dry season. While the best model to explain activity at the landscape scale in the wet season was savanna splitting, this was not a relevant predictor since the confidence interval of its coefficient included 0 ($\beta = 0.32$ [-0.17, 0.59]). There were several competing models including the null model, water cover, and sugarcane cover. Neither water cover nor sugarcane cover were relevant variables as the confidence intervals for all of them included 0 (Table 4, Table S2). In the dry season, there was a positive relationship between activity and savanna splitting ($\beta = 0.32$ [0.08, 0.49]) (Figure 3). There were no competing models. The Pseudo R^2 for the dry season model containing savanna splitting was 0.22 (Table 4, Table S2).

3.2 Edge foraging guild

Fine scale metrics could explain variation in edge bat activity in both the wet and dry seasons. The best model explaining activity of edge bats during the wet season included percent shrub cover. Shrub cover was a relevant predictor of bat activity, which decreased with increasing cover ($\beta = -0.20$ [-0.22, -0.17]) (Figure 4). The best model to explain bat activity in the dry season included distance to water. Bat activity increased with decreasing distance from water ($\beta = -0.78$ [-0.88, -0.68]) (Figure 4). There were no other competing models to explain edge bat activity during either season (Table 4, Table S3). Pseudo R^2 was much higher in the dry season models than the wet (0.30 vs. 0.05) (Table 4).

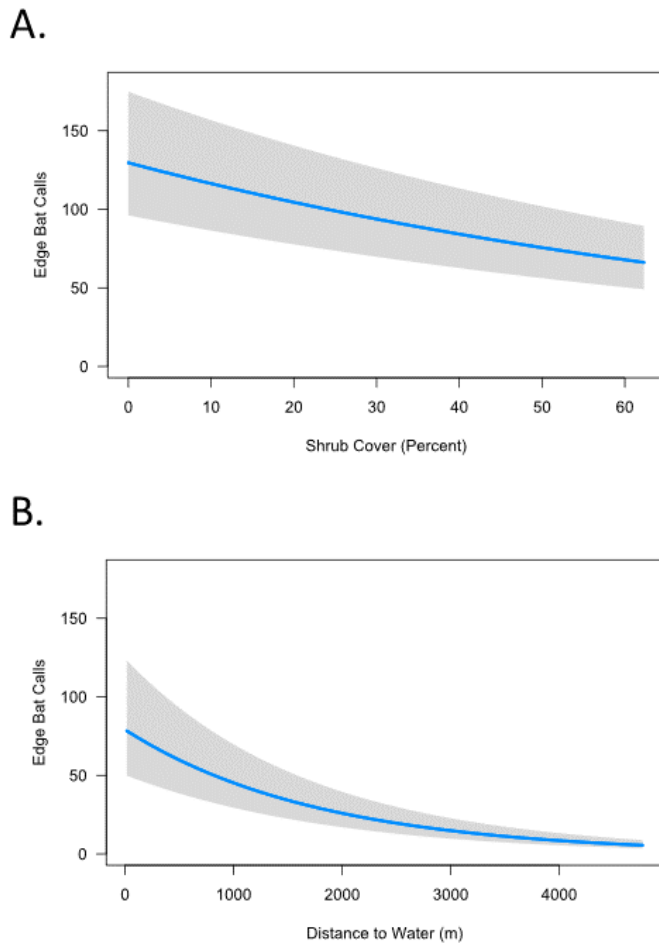


Figure 4. Response of edge foraging guild bats at the fine scale in the A. wet season, B. dry.

Landscape metrics did not explain variation in edge bat activity in either season. The best model to explain the activity of edge bats in the wet season was sugarcane cover, but with confidence intervals including 0, this was not a relevant predictor ($\beta = 0.33$ [-0.11, 0.74]). The null model and models containing water cover and savanna cover were competing models, but neither variable was relevant. In the dry season, the best model contained the variable water cover, but this was not a relevant predictor as the confidence interval of its coefficient included 0 ($\beta = 0.34$

[-0.03, 0.67]). The model containing savanna splitting was a competing model, but this was also not a relevant predictor ($\beta = 0.28$ [-0.10, 0.51]) (Table 4, Table S4).

3.3 Clutter foraging guild

Fine scale metrics explained clutter bat activity only in both the wet and dry seasons. In the wet season, the best model of activity of clutter bats included the variable grass cover; bat activity increased with grass cover ($\beta = 0.56$ [0.005, 1.2]), but the magnitude of this increase was small (<1 call) (Figure S1). The null model and a model with bare ground cover were competing models but bare ground was not a relevant predictor ($\beta = -0.55$ [-1.40, 0.12]). In the dry season the best model included the variable sugarcane cover, which was a relevant predictor ($\beta = 0.36$ [0.09, 0.61]); bat activity increased with increasing sugarcane cover, although the magnitude of this increase was small (<1 call) (Figure S2). A model including the variable water cover was a competing model ($\beta = -0.53$ [-1.1, -0.09]) (Table 4, Table S5, Figure S3). Pseudo R^2 for the top models in both seasons was 0.02.

Landscape metrics better explained clutter bat activity in the dry season. While the best model to explain the activity of clutter bats during the wet season was the amount of rural land cover, with a 95% CI that included 0 there was only evidence of a weak relationship ($\beta = -1.55$ [-5.8, 0.05]). During the dry season the best model explaining bat activity was water cover, with activity increasing with increasing water ($\beta = 1.02$ [0.58, 1.5]) (Figure 5). There were no competing models in either season. The dry season model containing water cover fit the data especially well with Pseudo $R^2=0.46$ (Table 4, Table S6).

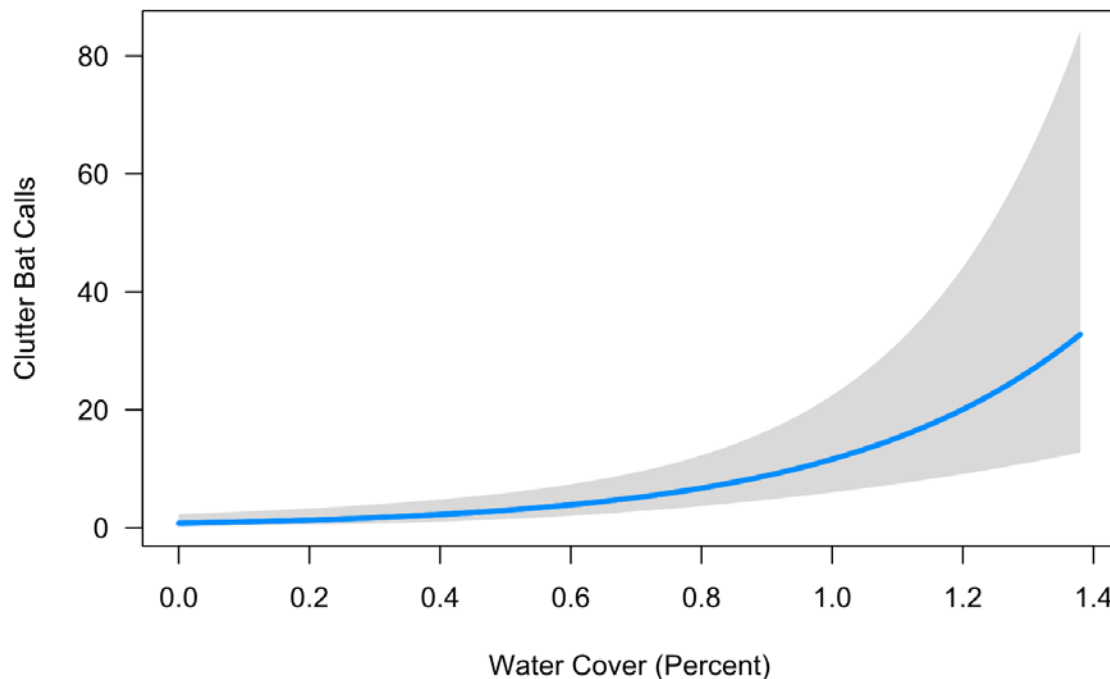


Figure 5. Response of clutter foraging guild bats in the dry season at the landscape scale. See Figure S1-S3 for clutter foraging guild responses at the fine scale.

4. Discussion

This study demonstrates the relative role of both fine-scale vegetation structure and landscape-scale composition and configuration in shaping bat activity within a savanna undergoing rapid land-use and land-cover change (Bailey et al., 2015). Previous studies have reported that bats with larger home ranges respond more strongly to broad-scale features of the landscape, while bats with smaller home ranges respond more to fine-scale vegetation structure (Ferreira et al., 2017; Fuentes-Montemayor et al., 2013; Klingbeil and Willig, 2010; Pinto and Keitt, 2008). Although clutter bats have much smaller home ranges than edge or aerial bats, they may still fly up to 2 km per night, which may explain the relevance of broader scale landscape features as reported here and elsewhere (Fenton, 1990; Fenton and Rautenbach, 1986; Monadjem et al., 2009). Most species in the aerial and edge guild have even larger home ranges than clutter foragers (Monadjem et al., 2010; Noer et al., 2012). We may not have detected a response at the landscape scale for edge bats in either season or aerial bats in the wet season because the spatial scale we examined was too small. Alternatively, the activity of these bats may be responding to variables that we did not measure, such as insect availability (Weier et al., 2018).

We found that activity for all three foraging guilds was generally better explained by our models at both the fine and landscape scales in the dry season than the wet season. Seasonal responses in bat activity are common and have been found in tropical savannas of this region (Monadjem and Reside, 2008; Mtsetfwa et al., 2018; Taylor et al., 2013) as well as other parts of the world (Cisneros et al., 2015; Ferreira et al., 2017; Klingbeil and Willig, 2010; Mendes et al., 2014). During the wet season, essential resources, such as insect prey and water, are more abundant (Fukui et al., 2006; Hagen and Sabo, 2012; Salsamendi et al., 2012) and therefore bats might be less constrained or affected by landscape composition and configuration. The effect of landscape may be more pronounced in the dry season because resources, particularly water, become scarce (Korine et al., 2016).

We predicted that bats should respond more strongly to landscape composition than configuration. We found that these responses varied by guild. Edge bats did not respond to composition or configuration, while clutter bats responded to composition only. In contrast, aerial bats responded to configuration, in particular savanna fragmentation, but only in the dry season. Other studies have reported both negative and positive responses to fragmentation; these responses often being species- or guild-specific (Cosson et al., 1999; Estrada-Villegas et al., 2010; Ethier and Fahrig, 2011; Meyer et al., 2016), as we have shown in this study. Within our study area, the highest levels of savanna fragmentation were found in blocks dominated by sugarcane. In this region, aerial foragers prefer to forage over sugarcane plantations than savanna (Noer et al., 2012), however the presence of savanna fragments within a matrix of sugarcane may provide complementary resources that are lacking in the monocultures, such as particular prey species or roosting sites. Therefore, without these savanna fragments, we suggest that this guild of bats may be greatly reduced, depriving local farmers of their important ecosystem services.

Bat activity tends to increase in lower-intensity agricultural systems, such as agroforestry and organic farms compared with more intense, commercial forms of agriculture (Cleary et al., 2016; Park, 2015; Wickramasinghe et al., 2003). However, we found that intense sugarcane farming had a significant, positive effect on clutter bats at the fine scale. This means that sugarcane plantations, despite being highly modified, may provide important habitat for this guild, at least seasonally. During the dry season these plantations may offer resources, such as water from dams or irrigation canals and associated insect communities that are scarce in savannas or rural areas at this time of the year. In addition, sugarcane is densely planted and may reach 3 m in height and may thus provide suitable foraging habitat for clutter bats. Therefore, we suggest that the structural similarity of agricultural fields to native vegetation is a more important consideration for maintaining bat activity than the intensity of crop production. However, sugarcane is not always tall and dense; prior to harvest the field is burned, often at night, leaving bare ground in its wake. The influence of this practice has not yet been studied on clutter bats.

We found that water was an important variable for all three bat foraging guilds, especially (but not exclusively) in the dry season, although there was variation in the spatial scale at which water drove activity. Water availability is important for bats in general, providing both water for drinking and insect foraging (Adams, 2010; Adams and Hayes, 2008; Monadjem and Reside, 2008; Sherwin et al., 2013; Sirami et al., 2013). Water may play an even more important role in savannas, where availability might be lower than other tropical biomes, particularly during dry seasons (Korine et al., 2016), and may drive bat movement and activity across the landscape (Geluso and Geluso, 2012; Rainho and Palmeirim, 2011). Since savannas, especially in arid and semi-arid areas, are at risk of future droughts and desertification (Engelbrecht et al., 2015; Monadjem et al., 2018b; Stringer et al., 2009), water will likely become increasingly scarce for bats. Artificial water sources which are available year-round, such as the dams and canals within commercial agriculture areas and some villages, may provide an especially important resource for bats in this human-altered landscape (Sirami et al., 2013).

Savannas the world over are threatened by shrub encroachment, which is seen as an increase in woody vegetation (Roques et al., 2001) leading in the extreme case to impenetrable thickets. Shrub encroachment may reduce species richness and abundance of mammals, especially in Africa (McCleery et al., 2018; Stanton et al., 2018), although the effects on bats in particular have not been studied. In this study, we found evidence that shrub encroachment negatively impacts at least one foraging guild, edge bats. Efforts to limit or reverse shrub encroachment may aid in the conservation of this guild.

There are some limitations to the use of acoustic monitoring in this study. A number of echolocating species found in the region, such as *Nycteris thebaica* and *Kerivoula lanosa* cannot be detected by our acoustic detectors (Monadjem et al., 2017). Similarly, non-echolocating species such as the fruit bat *Epomophorus wahlbergi* (Shapiro and Monadjem, 2016) could also

not be included. In addition, many species in the region cannot be distinguished from acoustic calls alone due to similarity in call parameters (Monadjem et al., 2017). While we see clear patterns by foraging guild, there could also be species-specific responses within guilds (Ethier and Fahrig, 2011; Fuentes-Montemayor et al., 2011; Gorresen et al., 2005; Gorresen and Willig, 2004; Pinto and Keitt, 2008), which we were unable to take into account.

Increasing levels of anthropogenic land-cover change around the world are cause for concern for many wildlife species and biodiversity as a whole (Foley et al., 2005; Jetz et al., 2007; Venter et al., 2016), including those in savannas (Laurance et al., 2014; Parr et al., 2014). However, despite the pressures of land-cover and land-use change, it is possible to conserve bats, and the ecosystem services they provide (Kunz et al., 2011; Taylor et al., 2018), in these changing savanna landscapes by preserving the features and resources they utilize.

Bats in savannas have a complex relationship with the landscape that varies by guild, season, and spatial scale. Conservation or management strategies for bats in tropical savannas can maximize their benefits by focusing on the number of remnant savanna fragments in anthropogenic land covers, reducing shrub encroachment, and preserving water sources, both natural and artificial. Doing so not only promotes the activity of aerial, edge, and clutter foragers across spatial and temporal scales, but may also bolster the conservation of a wide range of vertebrate species, such as birds, ungulates, carnivores, and herpetofauna, which benefit from low or intermediate shrub cover (Blaum et al., 2007; McCleery et al., 2018; Sirami and Monadjem, 2012; Soto-Shoender et al., 2018; Stanton et al., 2018) and access to water resources (Maritz and Alexander, 2007; Ogutu et al., 2014; Redfern et al., 2003; Valeix et al., 2010). Maintaining savanna fragments in anthropogenic land covers may also provide habitat and shelter for a range of species, retain connectivity across the landscape, and increase biodiversity (Manning et al., 2006). Thus, management to benefit bats can potentially conserve biodiversity of a wide range of species and possibly improve ecosystem functioning (Manning et al., 2006) across savanna landscapes undergoing anthropogenic land-use change.

Acknowledgements

We thank Hervé Echechoune for assistance in the field; Mandla Motsa, Smart Shabangu, Tal Fineberg, Isaac Magagula, Mduduzi Ngwenya, Letta Dlamini, Thea Litschka-Koen, Clifton Koen, Nick Jackson, Stephen Potts, Alan Howland, Kim Roques, All Out Africa, and The Savana Research Center for help with logistics; and all the residents who generously allowed us to place Anabat detectors in their villages.

Funding: This material is based upon work supported by the National Science Foundation Graduate Research Fellowship under Grant No. DGE-1315138, a Student Research Grant from Bat Conservation International, a National Geographic Young Explorer's Grant 9635-14, and The Explorers Club Exploration Fund – Mamont Scholars Program.

No funding sources played any role in study design; collection, analysis, and interpretation of data; in the writing of the report; or in the decision to submit the paper for publication.

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