



# Adaptability and vulnerability of high flying Neotropical aerial insectivorous bats to urbanization

Kirsten Jung<sup>1\*</sup> and Elisabeth K. V. Kalko<sup>1,2</sup>

<sup>1</sup>Institute of Experimental Ecology, University of Ulm, Albert-Einstein-Allee 11, 89069 Ulm, Germany, <sup>2</sup>Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Balboa, Panamá

## ABSTRACT

**Aim** Urbanization is a dominant demographic trend throughout the world that involves massive habitat alterations. Understanding how urbanization affects biota is a crucial prerequisite for development and application of effective species conservation programmes. Our study focuses on Neotropical high flying aerial insectivorous bats, an ecologically important, but so far seriously understudied group of vertebrates.

**Location** Panama.

**Methods** Using acoustic monitoring, we assessed and compared species occurrence, composition and activity of aerial insectivorous bats at three site categories located on the isthmus in Panama: forest, urban areas and a forest–town interface.

**Results** In 2 years of field work, we recorded 44,744 bat passes over the microphone and identified a total of 25 aerial insectivorous bat species. Species richness was highest in the forest, decreased towards the forest–town interface and was lowest at the urban sites, while dominance (Berger-Parker-Index) increased from the forest to the urban sites. Overall, general bat activity (passes  $\text{min}^{-1}$ ) was highest at the forest–town interface and lowest at the urban sites. Multivariate analysis suggests compositional differences in species occurrence and activity among site categories with mainly molossid species occurring in urban areas.

**Main conclusions** Our results clearly demonstrate species-specific differences between high flying aerial insectivorous bats concerning their adaptability and vulnerability to urban areas. Our results suggest that a suite of morphological traits including species mobility determine persistence of aerial insectivorous species in cities. Our results underline the necessity for detailed assessments of species-specific habitat requirements and dynamics of species occurrence and activity over time to develop meaningful conservation tools targeted at aerial insectivorous bats.

## Keywords

Acoustic monitoring, adaptability, anthropogenic influence, chiroptera, conservation, Panama.

\*Correspondence: Kirsten Jung, Institute of Experimental Ecology, University of Ulm, Albert-Einstein-Allee 11, 89069 Ulm, Germany. E-mail: kirsten.jung@uni-ulm.de

## INTRODUCTION

Worldwide, humans are transforming landscapes and fundamentally alter biodiversity patterns and ecosystem functioning (e.g. Vitousek *et al.*, 1997; Ellis & Ramankutty, 2008). The steady increase in human population puts pressure on areas with pristine habitats, mainly because of agricultural expansion

and urbanization, typically with detrimental effects on the associated wildlife. Urbanization as a dominant demographic trend (Pickett *et al.*, 2001) involves some of the most extreme forms of land use alteration (Shochat *et al.*, 2006). This is particularly true for the species-rich tropics (Myers *et al.*, 2000), including Central and South America, where human population is projected to nearly double by the year 2050

(United Nations, 2008). This underlines the necessity for conservation-related studies in tropical areas where anthropogenic growth directly interacts with the highest levels of biodiversity (Rompré *et al.*, 2008).

Some species of wildlife are capable to adjust to urban conditions as they can exploit refuse as food and man-made structures as roost sites (e.g. Bowers & Breland, 1996; Fedriani *et al.*, 2001; McKinney, 2002; Prange & Gehrt, 2004; Prange *et al.*, 2004; Williams *et al.*, 2006). Other species, however, disappear from urban areas as they depend on food, shelter and habitats that are rarely found in cities. Consequently, only a few species persist in urban environments, and overall local species richness tends to decline with increasing urbanization (McKinney, 2002; Shochat *et al.*, 2006). This also results in altered assemblage structures in urban environments, often with a few highly abundant species, which account for a much higher proportion of the whole community in urban environments compared to the surrounding wildlands (Shochat *et al.*, 2006). Population- and assemblage-level responses to urbanization have been examined most profoundly for the highly diverse and mobile group of birds (McKinney, 2002; McDonnell & Hahs, 2008). This has led to a classification of species into three categories, namely urban avoiders, urban adapters and urban exploiters (e.g. Blair, 2001; McKinney, 2002). In birds, urban avoiders that are not found in anthropogenically modified landscapes or urban environments are typically forest interior species such as tree foraging insectivores and many ground nesting birds (McKinney, 2002). Urban adapters refer to species that can adapt to anthropogenic landscapes, profiting from additional resources provided by humans. Most birds in this category are typical edge species, including ground foragers, seedeaters and aerial sweepers (McKinney, 2002). Finally, urban exploiters are species where populations depend largely on resources provided by humans (Johnston, 2010) including food or habitat structures (Blair, 2001; McKinney, 2002; Shochat *et al.*, 2004). Avian urban exploiters are often species evolutionarily adapted to rocky areas, which permits increased population sizes in urbanized areas (McKinney, 2002; Johnston, 2001).

Bats are the only mammals capable of active flight. Similar to birds, the ability to fly allows bats to move easier between habitat patches compared to non-flying vertebrates. Especially the group of aerial insectivorous bats which forage for insects on the wing includes highly mobile species some of which are able to cover large distances of many kilometres in a single night (Avila-Flores & Fenton, 2005). Individual species of aerial insectivorous bats in temperate and tropical areas take advantage of anthropogenically modified landscapes for example by using roosting sites in houses (Gaisler *et al.*, 1998; Kössl *et al.*, 1999) and by exploiting insects around street lights (Rydell, 1992; Lesiński *et al.*, 2000; Avila-Flores & Fenton, 2005; Jung & Kalko, 2010). However, other aerial insectivorous bat species appear to avoid human-modified landscapes (e.g. Gaisler *et al.*, 1998; Lesiński *et al.*, 2000; Pottie *et al.*, 2005; Jung & Kalko, 2010) and areas with reduced forest cover (Estrada-Villegas *et al.*, 2010). This suggests that, as it has been

shown for birds, the ability of aerial insectivorous bats to persist in anthropogenically transformed landscapes might be highly species-specific. Hence, in-depth knowledge on ecological demands of individual species is required to forecast local extinction risks and to propose adequate conservation strategies in an increasingly urbanized world.

In the Neotropics, aerial insectivorous bats, which provide essential ecosystem services by controlling insect populations (Federico *et al.*, 2008; Kalka *et al.*, 2008; Williams-Guillén *et al.*, 2008), constitute about a third of the local bat assemblages in the lowlands (Kalko *et al.*, 2008). Known to forage primarily along forest edges and in semi-open space within the forest (edge space) or far from vegetation above the canopy (open space) (Schnitzler & Kalko, 2001), they go almost unaccounted in ecological monitoring studies, as they are rarely sampled by harp traps or mist nets (Kalko & Handley, 2001; Hourigan *et al.*, 2008; MacSwiney *et al.*, 2008; Flaquer *et al.*, 2009). As a consequence, local distribution and activity patterns as well as (micro)habitat associations of many Neotropical aerial insectivorous bats remain largely unknown.

Our study focuses on vulnerability and adaptability of Neotropical aerial insectivorous bats flying at and above the canopy level in edge and open space (hereafter: high flying aerial insectivorous bats) by comparing species richness and activity patterns in three habitat categories forest, urban areas and a forest–town interface situated across the isthmus of Panama. With two major cities, Colon and Panama City, at each side of the isthmus, urbanization is one of the most important factors influencing habitat change in this area (Rompré *et al.*, 2008). This situation is similar to many tropical landscapes, where forests and their biota are facing rapid changes because of a multitude of anthropogenic threats (Laurance, 2007).

We expected that species richness of high flying aerial insectivorous bats should be highest at the forest sites because of higher structural diversity (Fischer & Lindenmayer, 2007) associated with a higher variety of roost types (Barclay & Kurta, 2007) and prey diversity (Haddad *et al.*, 2009). We further presumed a subset of species being present in the forest–town interface and even fewer species in the city. In addition, we predicted higher general activity and foraging activity of aerial insectivorous bats at forest sites and at the forest–town interface compared to urban areas, as abundance of potential prey should be higher in natural or semi-natural areas. Finally, we discuss whether high flying aerial insectivorous bats can be classified as urban avoiders, urban adapters and urban exploiters *sensu* Blair (2001) and McKinney (2002) and evaluate morphological traits such as body mass, forearm length, wing morphology and echolocation frequency, which might in part influence whether a species avoids or adjusts to urban environments.

## METHODS

### Study region

We investigated species composition and foraging activity of high flying aerial insectivorous bats in the Panama Canal

corridor, Republic of Panamá. At present, about 50% of the forest in the Panama Canal corridor are included in national parks (Robinson *et al.*, 2004). However, the area is exposed to strong urbanization pressure particularly on the Pacific side of the isthmus (Rompré *et al.*, 2008) where 1.7 million people live in the rapidly growing capital of Panama City and its surroundings [Instituto Nacional de Estadística y Censo (INEC), Panamá, 2010, <http://www.censos2010.gob.pa>].

Annual rainfall varies across the isthmus from the wet Caribbean side (2900 mm rain per year) to the drier Pacific side (1800 mm rain per year). A pronounced dry season starts in mid-December and ends at the beginning of April. Annual daily temperatures average 27°C, and nighttime temperatures account for 23°C throughout the year and region (meteorological and hydrological branch of the Panama Canal Authority, <http://striweb.si.edu/esp/index.php>).

### Recording sites

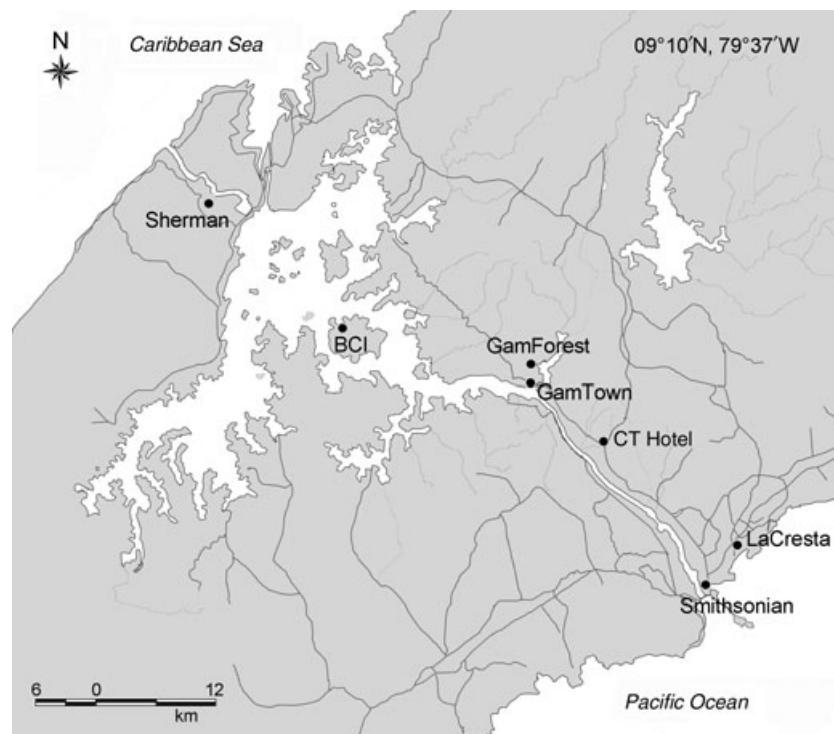
We consistently used high structures for the investigation of high flying aerial insectivorous bats to assure high quality and equal recording conditions (edge to open space above canopy, see Fischer *et al.*, 2009). Acoustic recording sites were located in the three main habitat types (hereafter: site categories) present in the Panama Canal corridor (Fig. 1): forest ( $N = 4$ ), urban areas ( $N = 2$ ) and a forest–town interface ( $N = 1$ ; Fig. 1).

All forest recording sites were located in tropical moist forest (Holdridge, 1967) with rather similar structure and a closed canopy at about 40 m (Condit *et al.*, 2001). We conducted

acoustic monitoring on (1) the platform of a 50-m tall crane operated by the Smithsonian Tropical Research Institute (STRI) in the forest of San Lorenzo, Fort Sherman (9653 ha), (2) a tower (45 m) on the STRI field station, Barro Colorado Island (BCI; 1500 ha), (3) the observation platform (40 m) of the Gamboa Rainforest Resort (hereafter: Gamboa Forest) and (4) the platform of a former radio tower, now the Canopy Tower Hotel (40 m), both located in Soberania National Park (22104 ha). Most of the forest surrounding our recording sites classify as mature secondary forest (approximately 100 years) (Condit *et al.*, 2001; Ibáñez *et al.*, 2002; Rompré *et al.*, 2008). Only a few patches of old growth forest (400–600 years) remain on Barro Colorado Island and in Fort Sherman (Pyke *et al.*, 2001).

The two urban recording sites were located in the centre of Panama City surrounded by densely populated (INEC Panamá, 2010), for the most part degraded and noisy neighbourhoods. We recorded aerial insectivorous bats (1) from the roof-deck of the main building at the campus of STRI in Ancon, Panama City (hereafter: Smithsonian; 50 m, approximately 10,500 residents in the surrounding neighbourhood) and (2) from the third floor of a residential building overlooking the neighbourhood of La Cresta (hereafter: La Cresta, 45 m, approximately 11,000 residents in the surrounding neighbourhood).

Representative for a forest–town interface, we recorded high flying aerial insectivorous bats in Gamboa (hereafter: Gamboa Town), a small town (approximately 500 residents) bordered by extensive tall secondary forest of the Soberania National Park (forest–town interface, for details see Jung & Kalko,



**Figure 1** Map of the study area along the Panama Canal ranging from wet, largely undisturbed forest in Fort Sherman at the Caribbean Sea to the dry and densely populated urban area of Panama City at the Pacific Ocean. Acoustic recording sites represented the three habitat types: mature secondary forest (Sherman, BCI, GamForest and CT Hotel), urban areas (LaCresta and Smithsonian) and a forest–town interface (GamTown). The thin black lines delineate main roads in the area next to the Panama Canal.

**Table 1** Observed species richness ( $S_{obs}$ ), estimated species richness ( $S_{exp}$ ) and percentage of inventory completeness for each recording site and site category in Panama. Species richness and dominance are rarefied to 125 occurrence counts (accumulated number of a species' occurrence at a site). Also listed are mean bat activity (passes  $\text{min}^{-1}$  per night) and mean feeding activity (capture attempt  $\text{min}^{-1}$  per night) of high flying aerial insectivorous bats per recording sites and site categories.

Sites	Site category	$S_{obs}$	$S_{exp}$	% completeness	Species OC	Species richness	Dominance	Activity	Feeding activity	Recording nights
Sherman	Forest	19	22.13	86	73	19	0.09	0.71	0.04	7
BCI	Forest	24	24.70	97	158	23	0.08	1.37	0.06	8
Canopy Tower Hotel	Forest	23	24.54	93	126	21	0.09	1.95	0.09	9
Gamboa Forest	Forest	22	22.93	95	125	21	0.08	1.78	0.15	7
Forest (total)		25	25.28	98		23	0.09			31
Panama City Smithsonian	Urban area	11	10.93	100	87	11	0.15	0.53	0.03	11
Panama City La Cresta	Urban area	16	15.91	94	81	15	0.12	0.94	0.09	9
Urban areas (total)		16	16.16	99		15	0.15			20
Gamboa Town	Forest–town interface	21	22.12	95	136	20	0.09	1.68	0.16	9
Forest–town interface		21	22.12	95		20	0.07			9

BCI, Barro Colorado Island.

2010). Here, we installed our recording device at a hill slope, 20 m above an open area (0.5 ha) enclosed by residential buildings.

### Acoustic monitoring of bats

We conducted acoustic monitoring of high flying aerial insectivorous bats throughout full nights (6:00 PM–6:30 AM) from November 2003 until February 2006. We repeatedly returned every 6–7 weeks to the respective recording sites (Table 2) to account for night-to-night variations in activity or seasonal effects. We only choose nights with good weather conditions, such as low wind speeds ( $< 2 \text{ m s}^{-1}$ ). Recordings were suspended during rainfall.

Sound recordings were made with a custom-made real-time recorder (PC-Tape, Institute of Animal Physiology, University of Tuebingen, Germany) at a sampling rate of 480 kHz and 16 bit, stored on the hard disc of a laptop (Panasonic Toughbook 28). The ultrasound microphone was mounted on a 1.40 m tripod and pointed at an angle of  $45^\circ$  from edge into open space. The microphone had a flat frequency response ( $\pm 3 \text{ dB}$ ) between 30 and 120 kHz. Sensitivity dropped by about  $\pm 6 \text{ dB}$  for frequencies down from 15 and up from 160 kHz.

Recordings were taken in the automated recording mode of the equipment, with individual recordings triggered by sound intensities above  $-12 \text{ dB SPL}$  including a pre-trigger time of 1.5 s. Recording continued as long as a sound intensity remained above the threshold followed by a post-trigger time of 1.5 s. The combination of pre- and post-trigger time assured the recordings of complete passes, facilitating subsequent extraction for assessment of activity (passes  $\text{min}^{-1}$ ; see Jung & Kalko, 2010). The automated recording settings, in combination with the high intensity of the echolocation calls of aerial insectivores (120–140 dB SPL; Surlykke & Kalko, 2008), assured equal detection probabilities at frequencies between 20 and 60 kHz, the main frequency band of aerial insectivorous bats, at each recording site.

### Insect abundance

During acoustic monitoring nights, we assessed relative insect availability with four flight interception traps ( $28 \times 16 \text{ cm}$ , Mini-Eklektor, Bioform, Entomology and Equipment, Nürnberg, Germany) installed next to the microphone at each of the study sites except at La Cresta in Panama City, where it turned out to be unfeasible. Traps were operated from dusk (approximately 6:00–6:30 PM) until dawn (approximately 6:00–6:30 AM) and emptied the next morning. Insect samples were stored in 70% alcohol, and dry mass [g] of trap samples was measured using a Mettler Toledo scale (Type AX 304) to the nearest 0.1 mg.

### Acoustic analysis and species identification

We used Avisoft Saslab Pro, Version 4.34 (Raimund Specht, Avisoft Bioacoustics, Berlin, Germany) for sound analysis. Spectrograms were generated with a Hamming window at 512 FFT. We evaluated the number of bat passes defined as a minimum of two consecutive echolocation calls above a threshold of  $-12 \text{ dB SPL}$ . Two passes were separated by a time interval  $> 1.5 \text{ s}$  below the recording threshold of  $-12 \text{ dB SPL}$  (Jung & Kalko, 2010). We also assessed feeding activity of bats by counting terminal phases (call sequences emitted at a high repetition rate prior to prey capture attempts; Schnitzler & Kalko, 2001) per minute.

Sound sequences were manually identified to species (following the nomenclature of Simmons, 2005) by comparing signal structure and frequency parameters of search phase calls (Schnitzler & Kalko, 2001) with a call library established by E. Kalko and K. Jung at the University of Ulm, Germany (see Fig. S1 and Table S1 in Supporting Information), and previously published echolocation data (e.g. O'Farrell & Miller, 1997; Ochoa *et al.*, 2000; Rydell *et al.*, 2002; Jung *et al.*, 2007). Overall call structure and main frequency including harmonics gave in most cases (approximately 95%) sufficient information for identification of the bats to species level (see Fig. S1 and

**Table 2** Mean bat activity (passes  $\text{min}^{-1}$  per night  $\times 10$ ) and percentage of occurrence counts of high flying aerial insectivorous bats at the site categories forests, urban areas and forest–town interface in Panama, species abbreviations and species groups referring to a species ability to persist in urban areas. Also given are total numbers of passes per species (N). Letters indicate the statistical results based on the post hoc Tukey contrast for differences in bat species activity between sites. Different letters indicate significant differences between recording sites.

Species	Abbr.	Group	Family	Activity mean passes $\text{min}^{-1}$ per night			Differences among categories			Occurrence per recording nights at site categories %			Differences among categories		
				Forest	Urban	Forest–town interface	$F_{(2,45)}$	P	Forest	Urban	Forest–town interface	$F_{(2,45)}$	P	N	
<i>Centronycteris centralis</i>	<i>C. cen</i>	1	EMB	0.75a	0b	0b	11.33	< 0.001	68a	0b	0b	27.48	< 0.001	1465	
<i>Commura brevirostris</i>	<i>C. bre</i>	2	EMB	0.44a	0b	0.15a	13.80	< 0.001	81a	0b	89a	42.63	< 0.001	791	
<i>Cyttarops alecto</i>	<i>C. ale</i>	1	EMB	0.86a	0b	0b	4.5	< 0.01	55a	0b	11b	13.06	< 0.001	1697	
<i>Dididurus albus</i>	<i>D. alb</i>	2	EMB	0.15a	0b	0.08a,b	5.65	< 0.01	65a	10b	78a	10.81	< 0.001	312	
<i>Peropteryx macrotis</i>	<i>P. mac</i>	2	EMB	0.58a	0b	0.06b	15.84	< 0.001	84a	0b	56a	38.31	< 0.001	1068	
<i>Peropteryx kappleri</i>	<i>P. kap</i>	1	EMB	0	0	0			19	0	0		n.s.	34	
<i>Saccopteryx bilineata</i>	<i>S. bil</i>	2	EMB	2.10a	0.03b	2.37a	16.77	< 0.001	94a	40b	100a	15.39	< 0.001	4277	
<i>Saccopteryx leptura</i>	<i>S. lep</i>	2	EMB	0.55a	0b	0.69a	11.92	< 0.001	84a	25b	100a	17.20	< 0.001	1183	
<i>Cynomops greenhalli</i>	<i>C. gre</i>	3	MOL	0.18a	0.82b	0.50a	21.20	< 0.001	84	100	88		n.s.	1691	
<i>Cynomops planirostris</i>	<i>C. pla</i>	3	MOL	0.21a	0.47b	0.20a,b	4.26	< 0.5	81	95	67		n.s.	1183	
<i>Eumops spp.</i>	<i>E. spp</i>	3	MOL	1.06a	1.47a,b	4.35b	10.15	< 0.001	97	100	100		n.s.	6285	
<i>Molossus rufus</i>	<i>M. ruf</i>	–	MOL	0.22	0.05	0.26		n.s.	68	60	100		n.s.	623	
<i>Molossus currentium</i>	<i>M. cur</i>	3	MOL	0.24a	0.93b	0.40a,b	10.03	< 0.001	84	100	100		n.s.	1910	
<i>Molossus molossus</i>	<i>M. mol</i>	3	MOL	0.75a	2.53b	6.33c	25.47	< 0.0001	81a	100b	100b	3.37	< 0.05	8229	
<i>Nyctinomops laticaudatus</i>	<i>N. lat</i>	–	MOL	0.11	0.04	0.03		n.s.	61	45	66		n.s.	301	
<i>Pronops centralis</i>	<i>P. cen</i>	3	MOL	0.40a	0.77b	0.10a	7.49	< 0.001	80	100	100		n.s.	1837	
<i>Pteronotus gymnonotus</i>	<i>P. gym</i>	2	MOR	1.37a	0b	0.01b	7.67	< 0.001	80a	5b	44a	14.67	< 0.001	2291	
<i>Pteronotus parnellii</i>	<i>P. par</i>	1	MOR	0.03a	0b	0b	6.08	< 0.01	25a	0b	0b	7.81	< 0.001	33	
<i>Pteronotus personatus</i>	<i>P. per</i>	1	MOR	0.07a	0b	0b	4.7	< 0.01	48a	0b	0b	12.66	< 0.001	134	
<i>Noctilio albiventris</i>	<i>N. alb</i>	–	NOC	0	0	0		n.s.	7	5	33		n.s.	9	
<i>Noctilio leporinus</i>	<i>N. lep</i>	–	NOC	0	0	0.02		n.s.	3	10	44		n.s.	10	
<i>Lasiurus blossevillii</i>	<i>L. blo</i>	2	VES	0.05a	0b	0.03a,b	3.75	< 0.05	38a	0b	22a,b	6.02	< 0.01	63	
<i>Lasiurus ega</i>	<i>L. ega</i>	2	VES	0.55a	0b	0.04a,b	3.28	< 0.05	52a	20b	78a	8.94	< 0.001	942	
<i>Myotis albescens</i>	<i>M. alb</i>	2	VES	0.37a	0b	0.07a,b	4.8	< 0.05	49a	0b	33a,b	6.25	< 0.01	300	
<i>Myotis nigricans</i>	<i>M. nig</i>	2	VES	3.78a	0b	1.09a,b	12.65	< 0.001	96a	25b	100b	84.95	< 0.001	7848	

Table S1). We were unable to reliably separate echolocation calls of the genus *Eumops* (14–21 kHz) to species level and hence pooled them as *Eumops spp.* Calls recorded at the lower frequency range most likely belonged to *E. perotis* and those at the higher range to *E. auripendulus* or *E. glaucinus*. Furthermore, calls of *E. hansae*, which had been caught by F. Wetterich on BCI in 2000 (unpubl. results), might have been overlooked because we lack reference recordings. In addition, we may have erroneously assigned echolocation calls of *Rhogeessa tumida* to *Myotis nigricans*, because echolocation signals of both species have a similar call structure and overlap in frequencies (Jung, unpublished). However, as *R. tumida* appears to be rather rare in the study area with hardly any captures throughout decades of research on BCI (Kalko *et al.*, 2008), we consider the effect of a possible misidentification as negligible compared to the overall results.

### Data analysis

Acoustic monitoring is a valuable method to assess presence and activity of species which rarely get caught in ground or canopy mist nets (Hourigan *et al.*, 2008; MacSwiney *et al.*, 2008; Flaquer *et al.*, 2009). However, as the number of passes does not necessarily reflect the number of individuals, the actual abundance of a species can not be addressed. We therefore used the occurrence of a species at each site and site category per night and calculated accumulated numbers of species occurrences at a recording site during all recording nights (hereafter: occurrence count) to estimate inventory completeness, species richness and dominance. We evaluated inventory completeness using randomized (1000 times), sample-based species accumulation curves (Gotelli & Entsminger, 2006) and assessed the expected number of species with nonparametric species richness estimators. Based on the iterative estimator choice framework developed by Brose & Martinez (2004) that takes movement heterogeneity of mobile animals, such as bats, into account, we selected the Michaelis–Menten<sub>(mean)</sub> estimator to estimate species richness. The percentage of inventory completeness was calculated by dividing observed species richness (*Sobs*) through estimated species richness (*Sest*)  $\times 100$ . Species accumulation curves and species richness estimators were calculated using Estimate S (Colwell, 2005). We compared species richness and dominance among recording sites and site categories by calculating rarefied models using EcoSim (Gotelli & Entsminger, 2006) with 1000 iterations and independent sampling. Predictions were made at a standardized number of occurrence counts to ensure comparability. Dominance of species was assessed using the Berger–Parker Index (Magurran, 2004). Statistical significance was determined based on the simulated 95% confidence intervals generated by the program EcoSim (Gotelli & Entsminger, 2006).

In addition, we compared distribution of species activity (passes  $\text{min}^{-1}$ ) among site categories with a Kolmogorov–Smirnov two-sample test. *P*-values were determined using Monte–Carlo simulations (1000 bootstraps) to account for ties

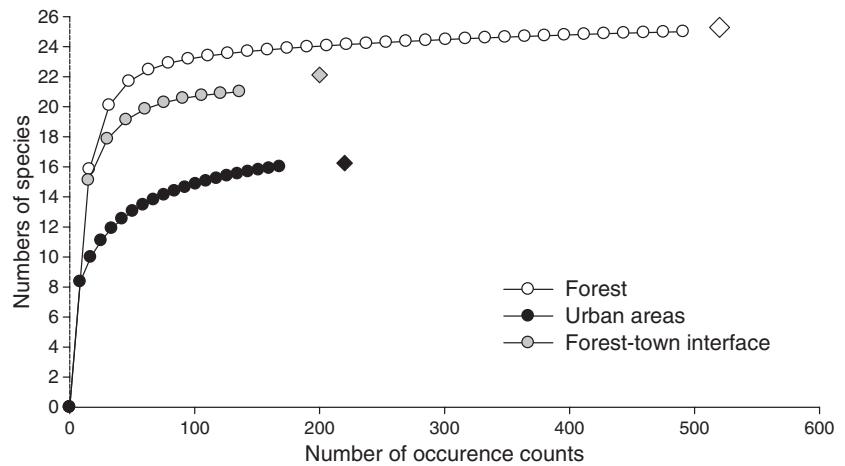
in the distributions. It is important to note that we did not set the number of passes synonymous to the number of individuals. Passes per min rather reflect activity of bats which we consider as an indicator for intensity of habitat use.

To reveal intercategory and inter-site differences in species composition and activity, we used non-metric multidimensional scaling (NMDS) based on the Bray–Curtis dissimilarities (e.g. Magurran, 2004). NMDS is regarded as the most robust unconstrained ordination method in community ecology (McCune & Grace, 2002). To standardize activity of a species between sites, we used mean passes per minute per night at the respective sites as the dependent variable for the NMDS. We excluded both species of *Noctilio* ( $N < 30$  passes, Table 1) from the analysis as both species are known to be strongly associated with water bodies and classify as trawling bats (Schnitzler & Kalko, 2001). We conducted a Mantel test (e.g. Legendre & Legendre, 1998) based on a Pearson's product-moment correlation and 1000 permutations to test for a potential spatial correlation between geographical distance of recording sites (Euclidian distances) and species occurrence and activity (Bray–Curtis dissimilarity) data.

We used linear mixed effect models (Zuur *et al.*, 2009) implemented in the 'nlme' package in 'R' (Pinheiro & Bates, 2000) to investigate differences in general bat activity (total passes  $\text{min}^{-1}$  per night) and general feeding activity (total capture attempt  $\text{min}^{-1}$  per night) between site categories. We also evaluated species-specific differences in occurrence and activity among site categories using linear mixed effect models. For all linear mixed effect models, we square root transformed data to achieve normal distribution. We included season (dry and rainy season) and moon (new moon, half–full moon) as interactive, fixed factors. Sampling nights were included as random factors as we repeatedly collected data at the same recording site (Fox, 2002). Fixed factors and random factors were fit by maximum likelihood (Pinheiro & Bates, 2000), and a stepwise model simplification was conducted based on likelihood ratio tests to the minimum adequate model (Crawley, 2005). Significant responses in models were evaluated by conducting multiple comparison tests using Tukey contrasts implemented in the 'multcomp' package in 'R' (Hothorn *et al.*, 2008).

We assessed differences in insect availability between site categories using a two-way ANOVA and performed a Spearman rank order correlation to reveal possible relationships between general activity and feeding activity of bats with insect dry mass. We also used a Spearman rank order correlation to reveal possible associations between the percentage of a species total activity at site categories with morphological traits including forearm length and body mass as proxies for size, approximate wing loading [body mass (g)  $\times$  gravity/forearm (mm)] for mobility and mean echolocation frequency as an indicator for a species main foraging habitat (edge versus open space). Data of forearm length and body mass were taken from Reid (1997), for mean peak frequency refer to Table S1.

All statistical tests were conducted using 'R' statistical package version 2.6.1 and 2.8.1 (R Development Core Team, 2008).



**Figure 2** Species accumulation curves based on occurrence counts of species at the three site categories forest, urban areas and forest–town interface. The sample order was randomized 1000 times. Estimates of species richness based on the Michaelis–Menten<sub>(means)</sub> estimator are indicated as separate diamonds.

## RESULTS

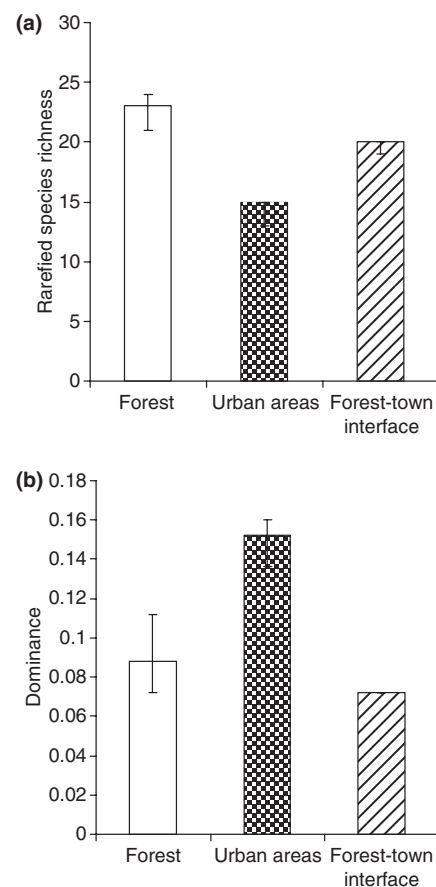
### Species richness and ensemble structure

We recorded a total of 44,744 bat passes over the microphone corresponding to 795 occurrence counts distributed over a 2-year period. We identified 25 aerial insectivorous bats at the seven recording sites (Tables 1 and 2). The number of species detected increased with the number of recording nights and reached an asymptote (Fig. 2) after about 3–4 recording nights at each recording site. We recorded the highest number of species at the forest sites ( $S_{\text{obs}} = 25$ ). The lowest number of species occurred at the urban sites in Panama City ( $S_{\text{obs}} = 16$ ). Species richness was intermediate at the forest–town interface with 21 species. At each site category, the estimate of predicted species richness (Michaelis–Menten<sub>(mean)</sub> estimator) was close to the observed species richness leading to an estimated inventory completeness of more than 95% at each site category (Table 2), indicating that our acoustic monitoring protocol was highly efficient to detect even rare high flying aerial insectivorous bats.

Rarefied species richness, which compares species richness based on a standardized number of occurrence counts, differed among site categories with significantly higher species richness at the forest sites compared to urban areas and the forest–town interface (Fig. 3). Rarefaction results also indicated significantly higher dominance in the occurrence of single species in urban areas compared to the forest sites and the forest–town interface (Table 2).

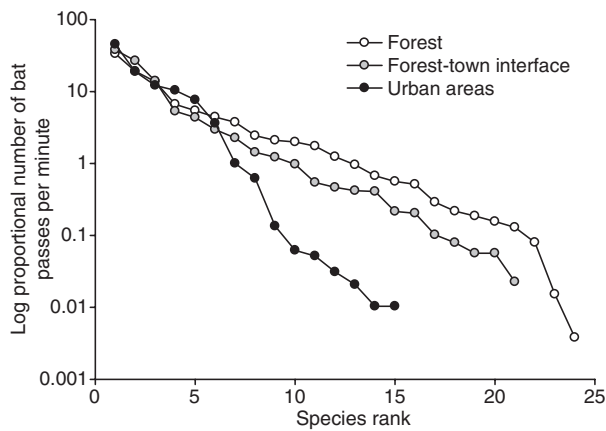
### Habitat use

General bat activity (passes  $\text{min}^{-1}$ ) and feeding activity (capture attempts  $\text{min}^{-1}$ ) differed significantly between the three site categories (bat activity:  $F_{(2,45)} = 9.44$ ,  $P < 0.001$ ; feeding activity:  $F_{(2,45)} = 5.78$ ,  $P < 0.01$ ). While bat activity was significantly higher at the forest sites compared to the forest–town interface ( $P < 0.05$ ) and urban areas ( $P < 0.001$ ), feeding activity was significantly higher at the forest–town interface compared to the forest sites ( $P < 0.01$ ) and the urban



**Figure 3** Rarefied species richness (a) and dominance (b) at the three site categories based on 125 occurrence counts. Error bars indicate the 95% confidence intervals.

areas ( $P < 0.001$ ). Season did not affect general bat activity ( $F_{(1,45)} = 2.24$ ,  $P > 0.05$ ) or feeding activity ( $F_{(1,45)} = 0.06$ ,  $P > 0.05$ ). However, general bat activity ( $F_{(1,45)} = 9.07$ ,  $P < 0.01$ ) and feeding activity ( $F_{(1,45)} = 5.04$ ,  $P < 0.05$ ) at all site categories were significantly lower during nights with moonlight.



**Figure 4** Rank activity plots based on acoustic recordings (passes  $\text{min}^{-1}$ ) of aerial insectivorous bats at the three site categories forest, urban areas and forest–town interface.

Distribution of species activity differed between site categories, with a significantly steeper rank activity curve for the urban areas compared to the forest sites (Fig. 4,  $D = 0.54$ ,  $P < 0.001$ ) and the forest–town interface ( $D = 0.42$ ,  $P < 0.05$ ). This indicates a skewed distribution with a few species dominating the total number of bat passes at the urban recording sites.

Insect availability as assessed with the passive flight interception traps did not differ significantly between the three site categories ( $F_{(2,20)} = 0.33$ ,  $P > 0.5$ ). Further, dry mass of insects did not correlate with bat activity ( $R_s = 0.22$ ,  $P > 0.05$ ) or feeding activity ( $R_s = 0.12$ ,  $P > 0.05$ ).

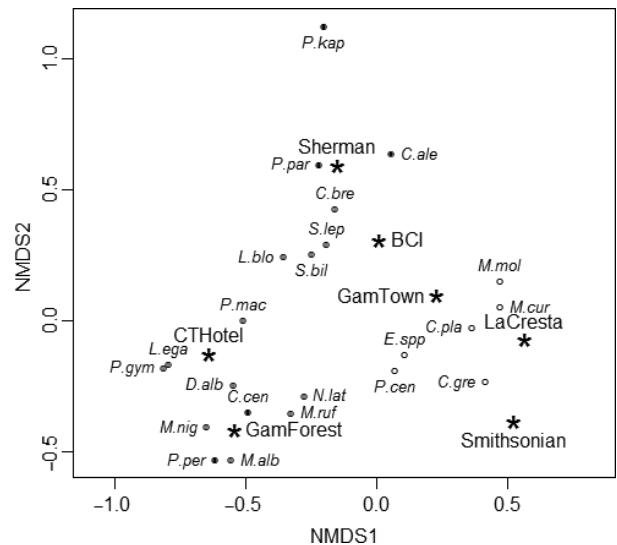
### Species composition

Non-metric multidimensional scaling (NMDS, final stress = 4.85, linear fit of ordination distance and observed dissimilarity  $R^2 = 0.98$ ) separated the ensembles of high flying aerial insectivorous bats between recording sites based on Bray–Curtis dissimilarities in species composition and activity. Although we did not find distinct clusters of sites, two of the forested sites, Gamboa Forest and the Canopy Tower Hotel, as well as BCI and Sherman were grouped more closely together, indicating similar occurrence patterns and habitat use of species. We also observed a higher degree of similarity for the two urban sites Smithsonian and La Cresta. The forest–town interface Gamboa Town had an intermediate position between forest and urban recording sites (Fig. 5).

Both, species occurrence ( $R = 0.31$ ,  $P > 0.05$ ) and activity ( $R = 0.27$ ,  $P > 0.05$ ) at the different recording sites did not correlate with geographical proximity of recording sites, rejecting the possibility for spatial autocorrelation of the species ensemble data.

### Species-specific occurrence patterns and habitat use

Most high flying aerial insectivorous bat species revealed differences in occurrence and activity patterns at the site



**Figure 5** Ordination of different recording sites (forest, urban areas and forest–town interface) based on Bray–Curtis dissimilarity of occurrence and activity of high flying aerial insectivorous bats. Asterisks represent the placement of recording sites and circles represent the placement of a species within multidimensional space. Black circles indicate species classified as ‘urban avoiders’, grey circles indicate ‘urban adapters’ and white circle indicate ‘urban exploiters’. Abbreviations: CTHotel = Canopy Tower Hotel, GamTown = Gamboa Town, GamForest = Gamboa Forest; for species abbreviations see Table 2.

categories (Table 2). Five species from two families, *Centronycteris centralis*, *Cyttarops alecto* and *Pteronotus kappleri* (Emballonuridae) as well as *Pteronotus parnellii* and *Pteronotus personatus* (Mormoopidae) occurred exclusively at the forest sites. Twelve species were regularly recorded at the forest sites as well as at the forest–town interface. Of those, four species (*Pteronotus macrotis*, *Cormura brevirostris*, *Lasiurus blossevillii* and *Myotis albescens*) were not recorded at the urban sites in Panama City during the whole study period. Six species (*Didelidurus albus*, *Lasiurus ega*, *Myotis nigricans*, *Pteronotus gymnotus*, *Saccopteryx bilineata* and *Saccopteryx leptura*) were occasionally documented at the recording sites in Panama City. However, their occurrence counts and activity levels were significantly higher at the forest sites and the forest–town interface compared to the urban sites (Table 2). In contrast, six free-tailed bats, *Molossus molossus*, *Molossus currentium*, *Cynomops greenhalli*, *Cynomops planirostris*, *Promops centralis* and *Eumops spp.*, occurred frequently (> 95% of recording nights) in urban areas and showed significantly higher activity compared to forest sites (Table 2). Only two species *Nyctinomops laticaudatus* and *Molossus rufus* did not differ significantly in occurrence and activity between the three site categories.

While occurrence and activity of aerial insectivorous bats at forest sites was negatively associated with body mass (occurrence:  $R_s = -0.64$ ,  $P < 0.05$ ; activity:  $R_s = -0.57$ ,  $P < 0.05$ ) and wing loading (occurrence:  $R_s = -0.79$ ,



$P < 0.05$ , activity:  $R_s = -0.75$ ,  $P < 0.05$ ), the opposite was true for species which were mainly occurring and active at urban recording sites (body mass  $R_s = 0.63$ ,  $P < 0.05$  activity  $R_s = 0.70$ ,  $P < 0.05$ ; approximate wing loading (occurrence:  $R_s = 0.75$ ,  $P < 0.05$ ; activity:  $R_s = 0.79$ ,  $P < 0.05$ ). In contrast, echolocation frequency was positively associated with occurrence ( $R_s = 0.58$ ,  $P < 0.05$ ) and activity ( $R_s = 0.51$ ,  $P < 0.05$ ) at forest sites and negatively associated with occurrence ( $R_s = -0.48$ ,  $P < 0.05$ ) and activity at urban sites ( $R_s = -0.56$ ,  $P < 0.05$ ). At neither site category did occurrence and activity of bats correlate with forearm length. In addition, we did not find any significant association of the selected species-specific traits with occurrence and activity at the forest–town interface.

## DISCUSSION

### Species richness and ensemble structure

We investigated occurrence and activity patterns of high flying aerial insectivorous bats in the Panama Canal corridor to identify species that rely on forested areas and those that are capable to adjust to anthropogenically modified landscapes (urban areas, forest–town interface). As expected, our results showed that only a subset of a few species persisted in urban areas and accounted for a higher proportion of the whole ensemble in urban environments compared to the forest sites. This pattern is similar to previous results for Neotropical aerial insectivorous bats in the large urban environment of Mexico City (Avila-Flores & Fenton, 2005) and in fragmented landscapes in Panama (Estrada-Villegas *et al.*, 2010), where overall species richness decreased and dominance of a few species increased with increasing human impact. It also corroborates responses of New World leaf-nosed bats (Phyllostomidae; Fenton *et al.*, 1992; Medellín *et al.*, 2000; Meyer & Kalko, 2008) towards forest disturbance, fragmentation and urbanization.

### Habitat use

Bat activity was significantly lower in urban areas compared to forest sites and at the forest–town interface. However, feeding activity was highest at the forest–town interface. This suggests that Gamboa is a very profitable foraging ground for high flying aerial insectivorous bat. This conclusion is supported by results of a parallel study where we demonstrated, using passive insect traps mounted at the street lights, that the lights of Gamboa are attracting large numbers of insects (Jung & Kalko, 2010). Although in this study acoustic recordings were conducted away from street lights, it is likely that the bats profited from higher insect abundance in the small town as a spill-over effect from the attraction of the insects by artificial lights.

In contrast, overall low activity and feeding activity of aerial insectivorous bats in Panama City hint towards a less profitable habitat. Although Panama City harbours high numbers and a range of different artificial lights which could potentially

attract insects, extensive green areas that are an important source for a diverse and abundant insect fauna (Avila-Flores & Fenton, 2005; Haddad *et al.*, 2009) are for most parts missing. Contrary to our expectations, our data on insect abundance did not reveal any differences between the three site categories. This might be caused in part by the generally low numbers of insects caught in passive flight interception traps.

### Species composition, occurrence and activity patterns

As expected, the ensemble of high flying aerial insectivorous bats differed between the three site categories forest, urban areas and forest–town interface. While we recorded 25 species of high flying aerial insectivorous bats of five families at forest sites and the forest–town interface, urban areas yielded almost exclusively molossid bats (Table 2). These results clearly demonstrate species-specific differences between high flying aerial insectivorous bats with regard to adaptability towards urban areas. *C. centralis*, for example, seems particularly vulnerable to urbanization as it only occurred at forest sites, although potential roost sites, i.e. palm trees, (Starett, 1972; Simmons & Handley, 1998) are present along roads at the forest–town interface in Gamboa and in urban areas of Panama City. This finding is in accordance with the results of (Estrada-Villegas *et al.*, 2010), where the occurrence of *C. centralis* was strongly associated with forest cover. In addition, the three species, *P. parnellii*, *P. personatus* (Mormoopidae) and *P. kappleri* (Emballonuridae), occurred exclusively at forest sites as well, suggesting similar sensitivity to anthropogenic habitat alterations. In contrast, a subset of six species of molossids dominated the urban areas with significantly higher activity (except *Eumops spp.*) compared to forest sites (Table 2).

Species occurrence and activity at the three site categories correlated with species-specific morphological traits. Bats that occurred mostly or exclusively at forest sites were for the most part smaller, slow-flying, highly manoeuvrable (Norberg & Rayner, 1987) and used higher echolocation frequencies. In contrast, urban areas mainly harboured bats with higher body mass, higher wing loading and aspect ratio. These morphological traits allow high flight speeds, high mobility and the potential to commute long distance per night (Norberg & Rayner, 1987). While the ensemble of high flying aerial insectivorous bats at forest sites included edge foragers as well as open space bats (Schnitzler & Kalko, 2001), edge foragers were mostly missing from urbanized areas and mainly open space bats remained in Panama City.

We argue that the observed species distribution pattern can be explained by a combination of habitat characteristics and species-specific traits. Many buildings in cities provide potential roost sites that resemble natural crevices (Burnett *et al.*, 2001; Avila-Flores & Fenton, 2005) and are known to be readily taken by molossid bats (Gaisler *et al.*, 1998; Keeley & Keeley, 2004). In contrast, roosting sites such as cavities of larger trees which are preferred roosts by many emballonurids (Yancey *et al.*, 1998) and vespertilionids (Kurta & Lehr, 1995)

are rather scarce in cities or non-existent because of the lack of vegetation. Furthermore, previous studies (Blair & Launer, 1997; McIntyre, 2000) revealed lower insect abundance and diversity in the city compared to forest habitats and parklands. Thus, in urban areas, foraging sites with sufficient food resources for bats are most likely more scattered, mainly limited to urban parks (Avila-Flores & Fenton, 2005) or possibly outside the city and thus require longer commutes or longer foraging activity per night. The group of bats least affected by these unfavourable conditions in urban areas are molossids, as they are characterized by high wing loading and aspect ratio, which implies relatively high flight speeds at energetically low costs (Norberg & Rayner, 1987). Consequently, molossids have the potential for longer and larger commutes to suitable foraging grounds (e.g. Cleveland *et al.*, 2006), while they still can take advantage of higher roost site availability in urban areas. In contrast, species with lower wing loading, aspect ratio and smaller home ranges such as *S. bilineata* (8–40 ha, Hoffmann *et al.*, 2007) are less likely to or will not be able to persist in a city. We thus propose that mobility is one of the most important factors influencing the persistence of aerial insectivorous species in urban areas. This corroborates similar results in the large Neotropical family of Phyllostomid bats, where low mobility is associated with higher fragmentation sensitivity (Meyer *et al.*, 2008).

We conclude that similarly to birds, all bat species in our study except the two molossids, *M. rufus* and *N. laticaudatus*, can be classified into three groups. The first group contains species exclusively recorded in forested areas. Similar to birds, all of them, except *P. kappleri*, are known to be forest interior species (Schnitzler & Kalko, 2001; Jung *et al.*, 2007; Estrada-Villegas *et al.*, 2010). The second group encompasses bats that regularly foraged at forest sites and the forest–town interface but only rarely at urban sites. Similar to avian urban adapters, these bat species forage mainly along forest edges and adjacent open areas; they also readily take advantage of favourable conditions provided by humans (e.g. foraging sites at street lights, roosting sites in man-made structures). However, they do not depend on those resources for survival. The third group includes species frequently recorded in urban areas with significantly higher activity at urban sites and the forest–town interface compared to forest sites. Interestingly, most of them are rock and crevice-roosting species similar to most avian urban exploiters (McKinney, 2002).

The first two groups of bats are synonymous to the categories of ‘urban avoiders’ and ‘urban adapters’ proposed by McKinney (2002) and Blair (2001). Assuming that roost sites can be limited resources in natural areas, the third group, molossids, might come close to the category of ‘urban exploiter’ as they depend to a certain degree on urban resources such as houses that provide suitable roosting sites and sustain large colonies of molossids (Gaisler *et al.*, 1998; Keeley & Keeley, 2004).

We deduce from our results that the categorization of bats into three groups is a crucial prerequisite for species conservation in an increasingly urbanized world. Particularly, this classification allows using the proportion of the three groups

within an ensemble of aerial insectivorous bats as an indicator for habitat disturbance. This potentially permits to identify areas which need conservation management attention at an early stage of disturbance.

## CONCLUSION

About half of the forest in the Panama Canal corridor is currently protected in national parks. Because of two growing cities at both sides of the isthmus anthropogenic growth in Central Panama directly interacts with the highest levels of biodiversity (Myers *et al.*, 2000; Rompré *et al.*, 2008). This is similar to many rapidly changing tropical landscapes, where forests and their biota are facing an enormous array of anthropogenic threats (Laurance, 2007). Although many aerial insectivorous bats are considered at lower risk and least concern by the IUCN red list, our results clearly demonstrate that especially less mobile species, such as f. ex. *C. centralis* are negatively affected by anthropogenically altered environments. We argue that these species need special attention concerning their conservation needs and IUCN status, because their local risk for extinction is most likely underestimated.

Here, we provide the first assessment of adaptability and vulnerability of high flying aerial insectivorous bats to urbanization in the Neotropics. It encompasses comprehensive data sets from several carefully selected sites throughout 2 years. Our results clearly demonstrate species-specific differences between high flying aerial insectivorous bats concerning their adaptability and vulnerability to urban areas and suggest that a suite of morphological traits including species mobility determine persistence of aerial insectivorous species in cities. We thus consider our results to provide a first step for recommendations towards conservation management actions targeted at aerial insectivorous bats.

## ACKNOWLEDGEMENTS

We cordially thank Y. Basset, N. Gomez, R. Arias (Canopy Tower Hotel) and the Gamboa Resort Hotel; all who provided excellent acoustic monitoring sites. We thank the Environmental Sciences Program of the Smithsonian Tropical Research Institute (STRI); C. Meyer for all the discussions and statistical advice; we kindly thank K. Rex and T. Czaczes for revising our English. We acknowledge the valuable input of four anonymous reviewers. We thank STRI in Panama, especially O. Acevedo, for excellent logistic support and the German Academic Exchange Program (DAAD) for financial support to the first author.

## REFERENCES

- Avila-Flores, R. & Fenton, M.B. (2005) Use of spatial features by foraging insectivorous bats in a large urban landscape. *Journal of Mammalogy*, **86**, 1193–1204.
- Barclay, R.M.R. & Kurta, A. (2007) Ecology and Behaviour of bats roosting in tree cavities and under bark. *Bats in forests: conservation and management* (ed. by M.J. Lacki, J.P. Hayes

- and A. Kurta), pp. 17–37, John Hopkins University Press, Baltimore Maryland.
- Blair, R.B. (2001) Birds and butterflies along urban gradients in two ecoregions of the U.S. *Biotic homogenizati* (ed. by J.L. Lockwood and M.L. McKinney), pp. 33–56, Kluwer, New York.
- Blair, R.B. & Launer, A.E. (1997) Butterfly diversity and human land use: species assemblages along an urban gradient. *Biological Conservation*, **80**, 113–125.
- Bowers, M.A. & Breland, B. (1996) Foraging of gray squirrels on an urban-rural gradient: use of the GUD to assess anthropogenic impact. *Ecological Applications*, **6**, 1135–1142.
- Brose, U. & Martinez, N.D. (2004) Estimating the richness of species with variable mobility. *Oikos*, **105**, 292–300.
- Burnett, S.E., Jennings, J.B., Rainey, J.C. & Best, T.L. (2001) *Molossus bondae*. *Mammalian Species*, **668**, 1–5.
- Cleveland, C.J., Betke, M., Federico, P., Frank, J.D., Hallam, T.G., Horn, J., Lopez, J.D., McCracken, G.F., Medellin, R.A., Moreno-Valdez, A., Sansone, C.G., Westbrook, J.K. & Kunz, T.H. (2006) Economic value of the pest control service provided by Brazilian Free-tailed bats in south-central Texas. *Frontiers in Ecology and the Environment*, **4**, 238–243.
- Colwell, R.K. (2005) *EstimateS: statistical estimation of species richness and shared species from samples*. <http://viceroy.eeb.uconn.edu/EstimateS>.
- Condit, R., Robinson, W.D., Ibáñez, R., Aguilar, S., Sanjur, A., Martinez, R., Stallard, R.F., Garcia, T., Angehr, G.R., Petit, L., Wright, S.J., Robinson, T.R. & Heckadon, S. (2001) The status of the Panama Canal watershed and its biodiversity at the beginning of the 21st century. *BioScience*, **51**, 389–398.
- Crawley, M. (2005) *Statistics: an introduction using R*. Wiley, Chichester.
- Ellis, E.C. & Ramankutty, N. (2008) Putting people in the map: anthropogenic biomes of the world. *Frontiers in Ecology and the Environment*, **6**, 439–447.
- Estrada-Villegas, S., Meyer, C.F.J. & Kalko, E.K.V. (2010) Effects of tropical forest fragmentation on aerial insectivorous bats in a land-bridge island system. *Conservation Biology*, **143**, 597–608.
- Federico, P., Hallam, T.G., McCracken, G.F., Puruckers, S.T., Grant, W.E., Correa-Sandoval, A.N., Westbrook, J.K., Medellín, R.A., Cleveland, C.J., Sansone, C.G., López, J., Juan, D., Betke, M., Moreno-Valdez, A. & Kunz, T.H. (2008) Brazilian Free-tailed bats as insect pest regulators in transgenic and conventional cotton crops. *Ecological Applications*, **18**, 826–837.
- Fedriani, J.M., Fuller, T.K. & Sauvajot, R.M. (2001) Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with Coyotes in southern California *Ecography*, **24**, 325–331.
- Fenton, M.B., Acharya, L., Audet, D., Hickey, M.B.C., Merri-man, C., Obrist, M.K. & Syme, D.M. (1992) Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics. *Biotropica*, **24**, 440–446.
- Fischer, J. & Lindenmayer, D.B. (2007) Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography*, **16**, 265–280.
- Fischer, J., Stott, J., Law, B.S., Adams, M.D. & Forrester, R.I. (2009) Designing effective habitat studies: quantifying multiple sources of variability in bat activity. *Acta Chiropterologica*, **11**, 127–137.
- Flaquer, C., Torre, I. & Arrizabalaga, A. (2009) Comparison of sampling methods for inventory of bat communities. *Journal of Mammalogy*, **88**, 526–533.
- Fox, J. (2002) *Linear mixed models. Appendix to an R and S-PLUS Companion to Applied Regression*, Sage Publications Inc., Thousand Oaks, CA.
- Gaisler, J., Zukal, J., Rehak, Z. & Homolka, M. (1998) Habitat preference and flight activity of bats in a city. *Journal of Zoology*, **244**, 439–445.
- Gotelli, N.J. & Entsminger, G.L. (2006) *EcoSim: null models software for ecology*. Acquired Intelligence Inc. & Kesey-Bear, Jericho, VT 05465. <http://garyentsminger.com/ecosim.htm>.
- Haddad, N.M., Crutsinger, G.M., Gross, K., Haarstad, J., Knops, J.M. & Tilman, D. (2009) Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters*, **12**, 1029–1039.
- Hoffmann, F.F., Hedjuk, J., Caspers, B., Siemers, B.M. & Voigt, C.C. (2007) In the mating system of *Saccopteryx bilineata*, bioacoustic constraints impede male eavesdropping on female echolocation calls for their surveillance. *Canadian Journal of Zoology*, **85**, 863–872.
- Holdridge, L.R. (1967) *Life zone ecology*, Occasional Papers of the Tropical Science Center, San José, Costa Rica.
- Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous inference in general parametric models. *Biometrical Journal*, **50**, 346–363.
- Hourigan, C.L., Catterall, C.P., Jones, D. & Rhodes, M. (2008) A comparison of the effectiveness of bat detectors and harp traps for surveying bats in an urban landscape. *Wildlife Research*, **35**, 768–774.
- Ibáñez, R., Condit, R., Angher, G., Aguilar, S., Garcia, T., Martinez, R., Sanjur, A., Stallard, B., Wright, S.J., Rand, A.S. & Heckadon, S. (2002) An ecosystem report on the Panama Canal: monitoring the status of the forest communities and the watershed. *Environmental Monitoring and Assessment*, **80**, 65–95.
- Johnston, R.F. (2001) Synanthropic birds of North America. *Avian Ecology in an Urbanizing World* (ed. by J.M. Marzluff, R. Bowman and R. Donnelly), pp. 49–67, Kluwer Academic, Norwell, MA.
- Jung, K. & Kalko, E.K.V. (2010) Where forest meets urbanization: foraging plasticity of aerial insectivorous bats in an anthropogenically altered environment. *Journal of Mammalogy*, **91**, 144–153.
- Jung, K., Kalko, E.K.V. & Helversen, V.O. (2007) Echolocation calls in Central American emballonurid bats: signal design and call frequency alternation. *Journal of Zoology*, **272**, 125–137.
- Kalka, M.B., Smith, A.R. & Kalko, E.K.V. (2008) Bats limit arthropods and herbivory in a tropical forest. *Science*, **320**, 71.

- Kalko, E.K.V. & Handley, C.O.J. (2001) Neotropical bats in the canopy: diversity, community structure, and implications for conservation. *Plant Ecology*, **153**, 319–333.
- Kalko, E.K.V., Estrada Villegas, S., Schmidt, M., Wegmann, M. & Meyer, C. (2008) Assessing and evaluating the use of atmosphere by bats. *Integrative and Comparative Biology*, **48**, 60–73.
- Keeley, A.T.H. & Keeley, B.W. (2004) The mating system of *Tadarida brasiliensis* (Chiroptera, Molossidae) in a large highway bridge colony. *Journal of Mammalogy*, **85**, 113–119.
- Kössl, M., Mora, E., Coro, F. & Vater, M. (1999) Two-toned echolocation calls from *Molossus molossus* in Cuba. *Journal of Mammalogy*, **80**, 929–932.
- Kurta, A. & Lehr, G. (1995) *Lasiurus ega*. *Mammalian Species*, **515**, 1–5.
- Laurance, W.F. (2007) Have we overstated the tropical biodiversity crisis? *Trends in Ecology and Evolution*, **22**, 65–70.
- Legendre, P. & Legendre, L. (1998). *Numerical ecology*, 2nd English Edn, Elsevier, Amsterdam.
- Lesiński, G., Fuszara, E.B. & Kowalski, M. (2000) Foraging areas and relative density of bats (Chiroptera) in differently human transformed landscapes. *Zeitschrift für Säugetierkunde*, **65**, 129–137.
- MacSwiney, C.G.M., Clarke, F.M. & Racey, P.A. (2008) What you see is not what you get: the role of ultrasonic detectors in increasing inventory completeness in Neotropical bat assemblages. *Journal of Applied Ecology*, **45**, 1364–1371.
- Magurran, A.E. (2004) *Measuring biological diversity*, Blackwell Publishing, Oxford, UK.
- McCune, B. & Grace, J.B. (2002) *Analysis of ecological communities*, MjM Software, Gleneden.
- McDonnell, M.J. & Hahs, A.K. (2008) The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions. *Landscape Ecology*, **23**, 1143–1155.
- McIntyre, N.E. (2000) Ecology of urban arthropods: a review and a call to action. *Annals of the Entomological Society of America*, **93**, 825–835.
- McKinney, M.L. (2002) Urbanization, biodiversity, and conservation. *BioScience*, **52**, 883–890.
- Medellin, R.A., Equihua, M. & Amin, M.A. (2000) Bat diversity and abundance as indicators of disturbance in Neotropical rainforests. *Conservation Biology*, **14**, 1666–1675.
- Meyer, C.F.J. & Kalko, E.K.V. (2008) Assemblage-level responses of phyllostomid bats to tropical forest fragmentation: land-bridge islands as a model system. *Journal of Biogeography*, **35**, 1711–1726.
- Meyer, C.F.J., Fründ, J., Pineda Lizano, W. & Kalko, E.K.V. (2008) Ecological correlates of vulnerability to fragmentation in Neotropical bats. *Journal of Applied Ecology*, **45**, 381–391.
- Myers, N., Mittermeier, R.A.M., Cristina, G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.
- Norberg, U.M. & Rayner, J.M.V. (1987) Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society B*, **316**, 335–427.
- Ochoa, J., O'Farrell, M.J. & Miller, B.W. (2000) Contribution of acoustic methods to the study of insectivorous bat diversity in protected areas from northern Venezuela. *Acta Chiropterologica*, **2**, 171–183.
- O'Farrell, M.J. & Miller, B.W. (1997) A new examination of echolocation calls of some neotropical bats (Emballonuridae and Mormoopidae). *Journal of Mammalogy*, **78**, 954–963.
- Pickett, S.T.A., Cadenasso, M.L., Grove, J.M., Nilon, C.H., Pouyat, R.V., Zipperer, W.C. & Costanza, R. (2001) Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. *Annual Review of Ecology and Systematics*, **32**, 127–157.
- Pinheiro, J.C. & Bates, D.M. (2000) *Mixed-effect models in S and S plus*. Springer, London.
- Pottie, S.A., Lane, D.J.W., Kingston, T. & Lee, B.P.Y.-H. (2005) The microchiropteran bat fauna of Singapore. *Acta Chiropterologica*, **7**, 237–247.
- Prange, S. & Gehrt, S.D. (2004) Changes in mesopredator-community structure in response to urbanization. *Canadian Journal of Zoology*, **82**, 1804–1817.
- Prange, S., Gehrt, S.D. & Wiggers, E.P. (2004) Influences of anthropogenic resources on racoon (*Procyon lotor*) movements and spatial distribution. *Journal of Mammalogy*, **85**, 483–490.
- Pyke, C.R., Condit, R., Aguilar, S. & Lao, S. (2001) Floristic composition across a climatic gradient in a neotropical lowland forest. *Journal of Vegetation Science*, **12**, 553–566.
- R Development Core Team (2008) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Reid, F.A. (1997) *A field guide to the mammals of Central America and southeast Mexico*. Oxford University Press, Oxford.
- Robinson, W.D., Angehr, G.R., Robinson, T.R., Petit, L.J., Petit, D.R. & Brawn, J.D. (2004) Distribution of bird diversity in a vulnerable neotropical landscape. *Conservation Biology*, **18**, 510–518.
- Rompré, G., Robinson, W.D. & Desrochers, A. (2008) Causes of habitat loss in a neotropical landscape: the Panama Canal corridor. *Landscape and Urban Planning*, **87**, 129–139.
- Rydell, J. (1992) Exploitation of insects around streetlamps by bats in Sweden. *Functional Ecology*, **6**, 744–750.
- Rydell, J., Arita, H.T., Santos, M. & Granados, J. (2002) Acoustic identification of insectivorous bats (order Chiroptera) of Yucatan, Mexico. *Journal of Zoology*, **257**, 27–36.
- Schnitzler, H.-U. & Kalko, E.K.V. (2001) Echolocation by insect eating bats. *BioScience*, **51**, 557–569.
- Shochat, E., Lerman, S.B., Madhusudan, K. & David, L.B. (2004) Linking optimal foraging behavior to bird community structure in an urban-desert landscape: field experiments with artificial food patches. *The American Naturalist*, **164**, 232–243.
- Shochat, E., Warren, P.S., Faeth, S.H., McIntyre, N.E. & Hope, D. (2006) From patterns to emerging processes in

- mechanistic urban ecology. *Trends in Ecology and Evolution*, **21**, 186–191.
- Simmons, N.B. (2005) Order Chiroptera. *Mammal species of the world* (ed. by D.E. Wilson and D.M. Reeder), pp. 312–529, John Hopkins University Press, Baltimore.
- Simmons, N. & Handley, C. Jr (1998) A revision of *Centronycteris gray* (Chiroptera: Emballonuridae) with notes on natural history. *American Museum Novitates*, **3239**, 2–28.
- Starett, A. (1972) *Cyttarops alecto*. *Mammalian Species*, **13**, 1–4.
- Surlykke, A. & Kalko, E.K.V. (2008) Echolocating bats cry out loud to detect their prey. *PLoS ONE*, **3**, 1–10.
- United Nations (2008) *World population prospects*. Available at: <http://esa.un.org/unpp> (accessed September 2010).
- Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997) Human domination of earth's ecosystems. *Science*, **277**, 494–499.
- Williams, N.S.G., McDonnell, M.J., Phelan, G.K., Keim, L.D. & Van der Ree, R. (2006) Range expansion due to urbanization: increased food resources attract Grey-headed flying-foxes (*Pteropus poliocephalus*) to Melbourne. *Austral Ecology*, **31**, 190–198.
- Williams-Guillén, K., Perfecto, I. & Vandermeer, J. (2008) Bats limit insects in a neotropical agroforestry aystem. *Science*, **320**, 70.
- Yancey, F.D., Goetze, J.R. & Jones, C. (1998) *Saccopteryx leptura*. *Mammalian Species*, **582**, 1–3.
- Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York.

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

**Figure S1** Overview of basic echolocation call structures within and across families of Neotropical aerial insectivorous bats.

**Table S1** Search flight call parameters including call structure, harmonics and peak frequency that have been used to identify freely flying aerial insectivorous bats in Panama.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be reorganized for online delivery, but are not copy edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

## BIOSKETCHES

**Kirsten Jung** conducted this work as part of her PhD at the Institute of Experimental Ecology, University Ulm. Her interest lies in sensory ecology, biodiversity and conservation ecology with emphasis on anthropogenically modified landscapes and urban areas in temperate and tropical regions.

**Elisabeth K.V. Kalko** is director of the Institute of Experimental Ecology at the University Ulm. Her expertise reaches from biodiversity and community ecology to sensory ecology and bioacoustics with particular emphasis on vertebrates in tropical and temperate regions.

Author contributions: K.J. and E.K. conceived the ideas, K.J. and E.K. designed the research, K.J. collected and analysed the data, and K.J. and E.K. led the writing.

---

Editor: George Stevens