

Mobility explains the response of aerial insectivorous bats to anthropogenic habitat change in the Neotropics



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ABSTRACT

Habitat loss due to anthropogenic activities is a critical threat to biodiversity. Understanding which factors determine species persistence in degraded environments is essential for conservation management. Here, we investigated how aerial insectivorous bats in the Neotropics, an ecologically important, but understudied group of vertebrates, are affected by deforestation and urbanization. We conducted a standardized acoustic survey in four habitat types in 14 areas across Panama (500 km × 260 km), a scale hitherto unprecedented for the Neotropics, and assessed occupancy in 13 aerial insectivorous bat species, accounting for species- and habitat-specific detectability. In addition, we used wing measures to derive a proxy for flight efficiency and flight speed, as an indication of species-specific mobility. Results show that detectability does not only vary strongly among species but also, within a species, depending on the habitat: for nine species intra-specific detectability varied >10%. Model estimates for occupancy revealed that aerial insectivorous bats are highly heterogeneous in their response to deforestation and urbanization. Canopy height and canopy cover predicted occupancy best for most species. Relating occupancy to mobility we found that less mobile species with broad wings (high wing loading and low aspect ratio) decrease occupancy in deforested and urban areas, while more mobile species with narrow wings increase in these habitats. We suggest that this pattern applies also to species not analyzed in this study. Our study exemplifies how morphological information can help define conservation priorities when information on occurrence and distribution is limited.

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1. Introduction

Deterioration and fragmentation of original forest through deforestation and urbanization represents one of the most important threats to biodiversity, especially in the tropics (e.g. Barlow et al., 2007). Over the last decades, many studies have revealed species loss and altered community composition in response to tropical forest degradation (Hill and Curran, 2003; Turner, 1996). Type and intensity of land degradation has an effect on habitat quality and structure, which in turn impacts species populations, often in a negative way. At highly altered sites, tropical mammal

communities are characterized by decreased species richness and diversity as well as by higher dominance compared to less disturbed habitats (Ahumada et al., 2011). Urbanization affects community composition drastically (Jung and Kalko, 2011; Sattler et al., 2010; Threlfall et al., 2011) and may lead to homogenization of urban species assemblages worldwide (McKinney, 2006). Loss of biodiversity often results in a loss of ecosystem functions and services (Foley et al., 2007; Klein et al., 2002; Maas et al., 2013). Bats as the second largest mammalian order provide essential ecosystem functions and services including pollination, seed dispersal and insect control (Castro-Arellano et al., 2007; Kunz et al., 2011). Tropical bat studies have revealed that some assemblages, such as gleaning animalivorous bat species, are negatively affected by deforestation and urbanization, while large frugivorous bats profit from such changes (Williams-Guillen and Perfecto, 2010) and have higher diversity in areas with human impact than in areas without (Garcia-Morales et al., 2013).

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Aerial insectivorous bats (AIB) emit ultrasonic calls for orientation, foraging and communication. This species group has been largely omitted from Neotropical community analysis because the sophisticated echolocation skills of these bats allow them to detect and avoid mist nets, and thus evade capture, identification and quantification (Kalko et al., 2008). As a result, knowledge on the distribution and susceptibility to deforestation and urbanization in AIB is scarce (but see Estrada and Coates-Estrada, 2002; Jung and Kalko, 2011), resulting in weak baseline information for conservation threat status. The description of new, usually cryptic, species (Baird et al., 2012; Baker et al., 2009; Clare et al., 2013) further complicates the identification of AIB threat status (Sattler et al., 2007). AIB constitute 30–50% of local bat species assemblages (Kalko et al., 2008), so omitting this group from bat community analysis is a major drawback of many studies. Additionally, AIB are of great value in multiple aspects of conservation: AIB are good bioindicators as their position on a high trophic level makes them sensitive to pesticides as well as to general changes in prey abundance (Jones et al., 2009), and they are known to be of important economic value, consuming pest insects (Boyles et al., 2011).

Most AIB can be recognized by their species-specific echolocation calls, i.e., ultrasonic vocalizations emitted for orientation, communication and foraging (Parsons and Szewczak, 2009). Recent advances in acoustic survey techniques and continuously growing libraries of reference calls for acoustic identification to the level of species (e.g. Jung et al., 2007, 2014; Obrist et al., 2004; Rydell et al., 2002; Walters et al., 2012) now allow the inclusion of this group in bat community studies (Avila-Flores and Fenton, 2005; Estrada-Villegas et al., 2012; Jung and Kalko, 2011). Acoustic surveys have helped to increase knowledge on the distribution and ecology of AIB in temperate and tropical areas. In temperate areas, AIB activity was shown to increase with structural connectivity in farmlands, but optimum connectivity varied for short- and long-range echolocating bats (Frey-Ehrenbold et al., 2013). Ethier and Fahrig (2011) found positive effects of forest fragmentation on relative abundance of various AIB species. Jung et al. (2012) found that bat occurrence and activity was correlated to structural forest heterogeneity. Studies on the isthmus of Panama have shown that AIB react in more diverse ways to habitat patch isolation than other bat trophic guilds (Estrada-Villegas et al., 2010). While some AIB species disappear with urbanization (urban avoiders), others seem rather unaffected (urban adapters) or might even profit from human settlements, where they find high numbers of roosting sites (urban exploiters, Jung and Kalko, 2011). Most studies on AIB in the Neotropics, however, have focused on geographically restricted areas like national parks or cenotes (Delgado-Jaramillo et al., 2011; MacSwiney et al., 2008; Rydell et al., 2002) or the canal area in Panama (Estrada-Villegas et al., 2012; Jung and Kalko, 2010, 2011). Working across broader geographical scales is important to reveal broad scale patterns and to test the validity of ecological hypotheses in multiple habitat contexts. Here we investigated whether and how aerial insectivorous bats respond to different land use types on a large scale in Panama by sampling nationwide in different locations and multiple landscape contexts.

Detectability, the likelihood of detecting a given species in a survey with a given method, may vary significantly depending on species, habitat, weather conditions, field method, observer, and survey effort (e.g. Gorresen et al., 2008; Royle et al., 2005). Ignoring the odds of detectability often leads to an underestimation of site occupancy, which is the fraction of an area that is inhabited by a given species. This can lead to erroneous estimations of species richness, extinction rates, or modeled species distributions (Kéry, 2011; MacKenzie et al., 2006). AIB use different, species-specific call frequencies, call structures and call intensities

(Kalko et al., 2008), all of which affect the ability of ultrasound microphones to record them, which in turn affects detectability in acoustic surveys (Adams et al., 2012). Hence, to calculate species-specific detectability and occupancy, repeated surveys are necessary (MacKenzie et al., 2006). The only acoustic sampling study to date to calculate detectability for Neotropical AIBs found an average detectability of 0.71 (i.e., given its presence, a species is detected in 71% of all sampling events), a value considerably higher than the detectability ranging from 0.25 to 0.58 calculated for other bat trophic guilds through mist netting (Meyer et al., 2011). Thus including detectability can be crucial when estimating the effects of anthropogenic processes on species.

Mobility is a key trait affecting susceptibility to habitat change in many species (Henle et al., 2004), including bats (Meyer et al., 2008). Typically bat mobility is assessed using wing shape, described as a function of aspect ratio (wing length to width) and wing loading (body mass per wing area, Norberg and Rayner, 1987). More mobile bat species with small-surfaced and narrow wings are able to fly fast, cover long distances between roosts and foraging sites, and predominantly hunt in open space (Norberg and Rayner, 1987). Less mobile species with large-surfaced and broad wings fly more slowly but have greater maneuverability and rather hunt in habitats of high structural complexity such as forests (Estrada-Villegas et al., 2010; Kalko, 1998).

In this study, we estimated occupancy by explicitly considering species- and site-specific detectability of AIBs. We tested the hypothesis that more mobile bat species are more common in anthropogenically altered habitats than in primary habitats (forests), and that less mobile species are more common in primary than in anthropogenically altered habitats. By measuring the relationship between occupancy and wing indices across different habitats, we quantified the degree to which mobility explains susceptibility to deforestation and urbanization in AIBs. To test the general validity of this hypothesis, we collected data across the entire country of Panama (500 km × 260 km), a scale hitherto unprecedented for the Neotropics.

2. Material and methods

2.1. Study area and study design

Panama is dominated by a tropical climate with average temperatures around 27 °C and annual precipitation from 1600 mm to over 3020 mm per year (Condit et al., 2000). The meteorological divide follows the central cordillera, splitting the country into a wetter Caribbean and a drier Pacific region.

To study the effects of anthropogenic habitat change on AIBs, we chose a space-for-time substitution (Pickett, 1989). Studies using space-for-time substitutions assume that, in species diversity, what drives spatial variation also drives temporal changes. Thus variation in one can be used as a proxy for variation in the other. For site selection in the field, we first chose four habitat types that span a gradient of anthropogenic disturbance: mature forest, disturbed forest, pasture, and human settlement. Then, we measured and analyzed the same environmental covariates in all habitat types to know the effects on a continuous scale, rather than in discrete units (see 2.3. and 2.6 for details). To study AIBs on a broad scale, we replicated the sampling in the four habitat types in 14 areas in a spatially stratified design throughout Panama (Fig. 1). Site selection was influenced by availability of appropriate habitat type, permissions for land use, and accessibility with field equipment. Each habitat type in a given area contained one sampling point, summing to a total of $14 \times 4 = 56$ points. As small altitudinal differences can change the composition of tropical vertebrate species communities (McCain, 2009), we restricted

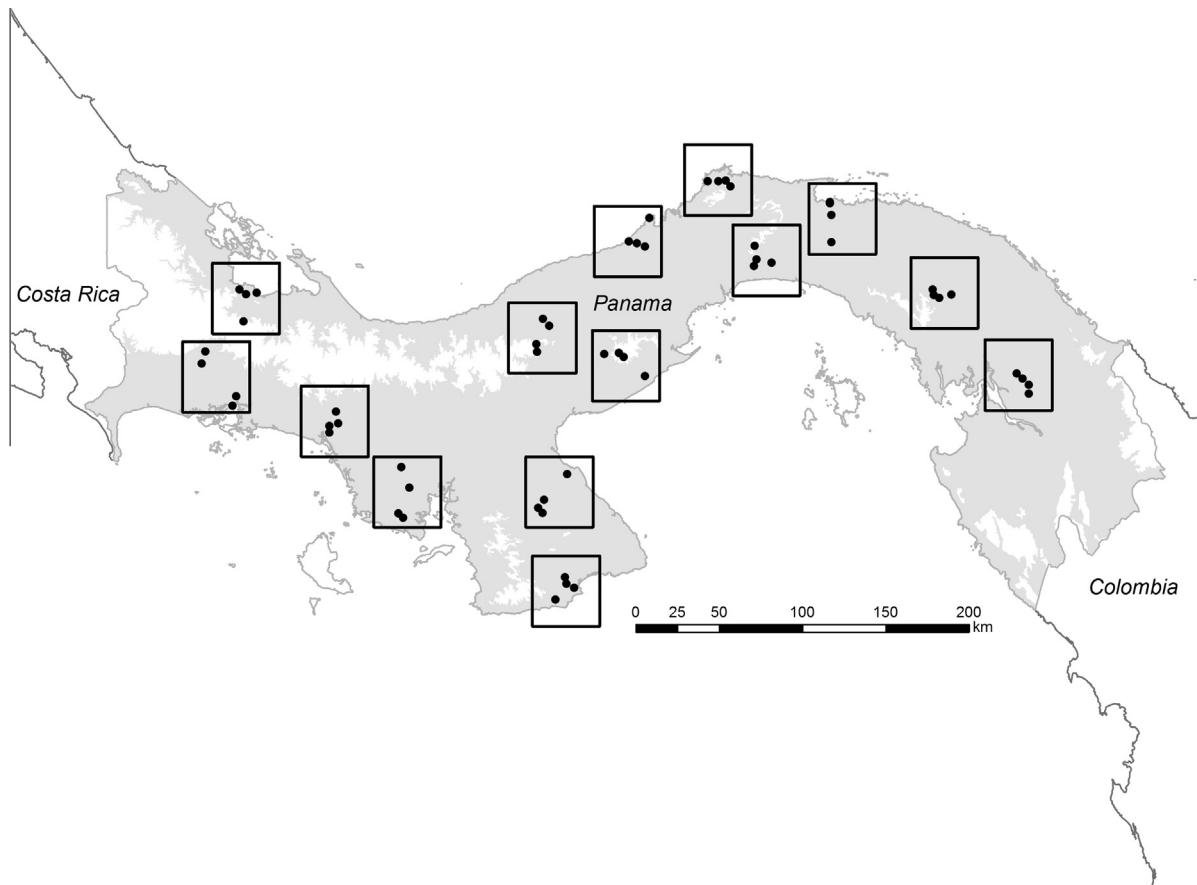


Fig. 1. Map of the study area in Panama. Each square represents a sampling area of the spatially stratified design ($n = 14$). Each dot represents a sampling point ($n = 56$). Minimum distance between sampling points was 4 km.

sampling to lowlands <700 m above sea level. Sampling points were positioned within habitat patches such that they met our distance criteria: we required that sampling points be a minimum of 400 m from the edge of the habitat type in mature forest, disturbed forest, and pasture, and 100 m from the edge in settlement. Additionally, sampling points were separated by a minimum distance of four kilometers to minimize the possibility of recording an individual bat at multiple sampling points in one night, avoiding spatial dependence of sampling points.

2.2. Field sampling

From 3 June to 14 September 2012, we sampled the four habitat types of each area simultaneously (168 sample nights). Simultaneous sampling in one area avoids possibly strong effects of climatic variation on bat activity between sampling nights (Fischer et al., 2009). Points were sampled in three non-consecutive nights for three hours each, starting at sunset. This sampling regime has been shown to yield >90% of all local AIB species (Estrada-Villegas et al., 2010; Meyer et al., 2011). We restricted sampling to nights with no or very limited rainfall (<20 mm). Bat calls were recorded with Batloggers (Elekon AG, Lucerne, Switzerland), which allow autonomous real-time recording. An electret condenser microphone was connected to the Batlogger, positioned 120 cm above ground at an angle of 45° above the horizontal, and protected against humidity by a layer of tightly sealed cellophane. The single microphone was faced in the direction where we expected AIB to pass with highest probability. Usually, this was the direction least obscured with obstacles in the forest (trees and branches) and in settlements (buildings) or along a fence or close to a tree in pastures. All

fieldwork was conducted according to regulations of the Smithsonian Tropical Research Institute and Panama's Autoridad Nacional del Ambiente (permit SE/A-54-12).

2.3. Habitat types and environmental covariates

For each sampling point in all habitat types, we recorded three structural covariates and one climatic covariate, all known to affect detectability and occupancy (Patriquin et al., 2003). In addition to relevant habitat covariates, the structural covariates included vegetation clutter, which is known to attenuate bat calls before they reach the microphone and thus affect species detectability (Kalounis et al., 1999). (1) We calculated canopy cover from 180° fisheye lens photos, taken 50 cm above ground, aimed toward the sky (Canon EOS Digital Rebel with Sigma 4.5 mm F 2.8 EX DC HSM Circular Fisheye Lens), and analyzed with software ImageJ64 1.46r (Rasband, 2012). (2) We assessed canopy height by visual estimation, taking the average of estimates of three observers. (3) We calculated tree distance as the average distance from our sampling point to the four nearest trees (more than 10 cm diameter at breast height) in four opposite directions, using the same method of visual estimation. (4) As proxy for climate we included orientation to the ocean (categorizing each sampling point as either Atlantic or Pacific, with the central cordillera as the dividing line), as Estrada-Villegas et al. (2012) found precipitation-dependent distribution patterns in AIB in the Panama Canal area. These measurements helped us to characterize the four habitat types used for site selection in the field: (1) Mature forest, the habitat type with least anthropogenic influence, was characterized by extensive canopy cover, a high canopy and reduced distance

between trees (see [Table A1](#) and [Fig. A1 in the online appendix](#) for examples and values). We did not distinguish between pristine and old-grown secondary forest, as distinction is difficult, habitat structure (e.g. tree height, canopy cover) has a greater impact on bat diversity than other characteristics typical for pristine forests ([Jung et al., 2012](#); [Mueller et al., 2012](#)), and animal species richness resembles that of mature forests only 20–40 years after farmed land is abandoned ([Dunn, 2004](#)). Here we selected sampling points in relatively open areas such as tree-fall gaps or forests with scanty understory, so that bat calls were less attenuated by foliage, resulting in higher detectability. (2) Disturbed forest was characterized by intermediate canopy coverage, low canopy and intermediate tree distance. Tall trees were scarce. Disturbed forest may have been impacted by substantial timber extraction or was regrowing after land abandonment. (3) Pasture, usually grazed by cattle, was habitat that had been cleared, did not have a forest canopy and thus showed very low crown coverage. (4) Settlement was the habitat of highest anthropogenic influence, where vegetation was greatly reduced. Canopy coverage contained buildings and was therefore intermediate. We avoided small settlements <200 m in diameter and centers of large cities.

2.4. Call analysis

We selected ten species (*Centronycteris centralis*, *Cormura brevirostris*, *Peropteryx macrotis*, *Saccopteryx bilineata*, *Saccopteryx leptura*, *Noctilio albiventris*, *Pteronotus parnellii*, *Pteronotus gymnonotus*, *Myotis nigricans* and *Molossus molossus*) and three sonotypes (groups of species with similar calls) for call and occupancy analysis. Sonotypes were defined as follows: *Vespertilionid* > 56 (frequency modulated – constant–frequent calls of the *Vespertilionidae* family with an end frequency >56 kHz, stemming from *Myotis riparius* or *Myotis keaysi*); *Molossus* < 35 (the large *Molossus* species *M. bondae*, *M. rufus* and *M. sinaloae*, whose calls predominantly are below 35 kHz); and *Cynomops* sp. (in Panama probably *C. cf. mexicanus* and *C. planirostris*). To simplify the text, the term ‘species’ henceforth includes sonotypes. All focal species were common enough for statistical analysis and could be identified to their respective taxonomic level with high confidence.

Bat calls were analyzed with Raven Pro 1.4 ([Bioacoustics Research Program, 2011](#)) and Batscope 3.1.6 ([Boesch and Obrist, 2013](#)), which is both a database of reference calls and a software program used to automatically measure echolocation call characteristics. To ensure consistent species determination, criteria for the different species were established based on call characteristics (e.g. shape, duration, maximum, minimum and peak frequency) taken from existing literature ([Jung et al., 2007, 2009, 2014](#); [Rydell et al., 2002](#)) and from our own reference calls. Species-specific calls are shown in [Fig. A2](#). To obtain presence or absence of a species at a given location during a specific sampling night, we manually screened all sequences potentially corresponding to the species of interest until either the species was found or all sequences in question within the range of the possible call characteristics for this species had been checked.

2.5. Mobility estimation

Wing morphology was measured with ImageJ64 ([Rasband, 2012](#)) from photos of the opened wing, positioned on 1 mm² graph paper. Photos for morphological data were obtained from our own captures, as well as from the University of Ulm (Elisabeth Kalko and Hans Dietrich von Staaden, unpublished data). For *C. centralis*, no photos were available, so measurements were taken from [Sanborn \(1937\)](#). For specimens for which no body mass measurements were available, we used average body masses from [Reid \(2009\)](#). The measurements of two species, *M. riparius* and *M. keaysi*,

were averaged for the sonotype *Vespertilionid* > 56, while *M. bondae* was used for *Molossus* < 35 and *Cynomops cf. mexicanus* for *Cynomops* sp. Due to the lack of data, we could not include all possible species for the latter two sonotypes. However, we consider our approximation acceptable because there is little variation in wing shape among Molossids.

Aspect ratio and wing loading, metrics derived from wing morphology, are widely used calculations for estimating bat mobility ([Norberg and Rayner, 1987](#)). Despite their frequent application, cross-author comparisons are problematic because researchers vary considerably in their measurements, due to individual differences in the position in which they position the wing when measuring. In our study, in addition to taking our own measurements, we used pictures from different authors with different wing positions, and were thus confronted with the challenge of integrating potentially differing measurement techniques. To circumvent this difficulty, we used the following bone-based measurements – instead of measures of wing area – as proxies for mobility.

Aspect ratio is based on wing length, which depends on how much the wing is stretched open for measurement ([Norberg and Rayner, 1987](#)). To circumvent inconsistencies associated with standard measurements for aspect ratios, [Findley et al. \(1972\)](#) introduced a method that relied on bone measurements: Aspect Ratio Index ARI = ((d3 + FA)/d5), where FA = forearm, d3 = third digit and d5 = fifth digit.

Wing loading is defined as body weight divided by wing area ([Norberg and Rayner, 1987; Winkler and Leisler, 1992](#)). The values for wing loading depend not only on the position of the wing (which varies by researcher) but also on a researcher's definition of 'wing'. Researchers vary in their delineations of the membranes that compose the wing, for example, differing in the amount of tail membrane that is included. To circumvent these inconsistencies, we replaced the traditional Wing Loading with a more robust index: we defined the Wing Loading Index WLI = $m/((FA + d3) \times d5 \times 2)$, with m = body mass. A Pearson Correlation between WLI and Wing Loading based on our own pictures (angle between humerus and forearm kept at 90°) was 0.972 with $p < 0.001$ ($n = 102$). We thus conclude that WLI, which is based on absolute bone-based measures, is well suited to replace the original wing loading measurements.

2.6. Statistical analysis

Presence-absence data derived from call analysis and summed as detection histories (detections and non-detections for the three sampling nights per site) served as baseline data to calculate detectability and occupancy. Data was analyzed for each species with the software PRESENCE 5.5 ([Hines, 2006](#)). We assumed closed populations, meaning that a site remained either occupied or unoccupied for the entire study duration, a justifiable assumption since we sampled over a rather short period (three months during wet season). We further assumed detectability to be constant for a species at a sampling point during the three survey repetitions. We then assessed how environmental covariates affect occupancy of different bat species by using an information-theory approach based on maximum likelihood models ([Burnham and Anderson, 2002](#)). To identify the relevant environmental covariate sets, we chose a two-step approach: first we calculated occupancy combining all different sets of the four covariates (orientation, tree distance, canopy cover and canopy height) obtaining 16 candidate models for each species ([Table A2](#)). Occupancy models were ranked by the Akaike Information Criterion corrected for small sample size, AICc ([Hurvich and Tsai, 1989](#)). In a second step and to the plausible models only (AICc weight >10%), we added habitat as an additional covariate. This way, we tested the relevance of the covariates included in the first step on occupancy of a certain

habitat type by a given bat species. If these habitat models were selected, then additional covariates not explicitly measured but consisting of habitat were considered relevant for occupancy. We then obtained species-specific detectability and occupancy for each location from the most plausible model of this second step. Location-specific values were then summarized by habitat, which allowed us to calculate the mean and the variation of detectability and occupancy per habitat.

In a further analysis, we related each species' occupancy to its wing morphology. We used the difference in mean occupancy of the respective habitat to the mean of all habitats, as we were interested in the relative change of occupancy among habitats and not in the absolute occupancy per se. Each species represented one data point ($n = 13$). We studied the dependency of the difference in occupancy to median wing indices with linear and quadratic least square regressions. This analysis was performed with SPSS 20 (IBM, 2011).

3. Results

3.1. Occupancy and detectability modeling

Field surveys at 56 locations sampled three times each (total of 504 h) resulted in 54,226 call sequences, from which we obtained 900 detections and 1284 non-detections for the detection histories of the 13 selected species (for species-specific information, see Table 1).

Selection of models with AICc weight >10% resulted in one to four plausible models per species, which revealed species-specific differences in the importance of environmental covariates (Table 2). Environmental covariates explained the occupancy of all species well, with the exception of *M. molossus* and *S. leptura*, suggesting that the selected covariates indeed are crucial for AIB. The covariates that best predicted the occupancy of most species were canopy height and canopy cover, both present in plausible models of 11 species. Five out of the 34 plausible models included habitat as a covariate (Table 2). For just one species, *M. molossus*, the most plausible model was a model including only habitat as covariate. This means that additional factors not reflected by the covariates we included into

the analysis, explained *M. molossus* occupancy in the different habitats. For two species, *P. gymnonotus* and *S. leptura*, the null models without covariates were the most plausible, suggesting indifference to habitat and the environmental covariates included in this study. In five species, orientation was included in the most plausible model. Three species showed considerable differences in occupancy on the two slopes with *M. nigricans* being more common on the Pacific slope and *Vespertilionid* > 56 and *S. bilineata* being more common on the Caribbean slope.

Species- and habitat-specific detectability varied greatly (Fig. A3) from $4.2\% \pm SD 3.7$ (*Vespertilionid* > 56 in pastures) to $100\% \pm 0.0$ (*M. molossus* in settlement, meaning *M. molossus* was detected in every survey in this habitat type). For nine species detectability among habitat types varied more than 10%, while for four species this value varied less than 10% (Table 1). This means that for most species, ignoring detectability in a cross-habitat study would seriously affect results. Mean detectability for all species in a single survey was $65.2\% \pm 22.1$ and ranged from 31% (*Vespertilionid* > 56) to 91% (*M. molossus*).

3.2. Occupancy and mobility

The study species varied greatly in their occupancies in the different habitat types (Fig. 2). Within species, the difference between the habitat types with highest and lowest occupancy, based on the most plausible model was on average 39.5%. For mobility estimation, we obtained wing measurements of 132 individuals representing 14 species (Fig. A4).

Relating occupancy and mobility, we identified four main occupancy patterns among the 13 species when summarized to the four habitat types (Fig. 2): (1) Less mobile species such as *P. parnellii* and *C. centralis* were most common in mature forest and decreased in anthropogenically altered habitats. *C. centralis* was never observed in pastures and settlements (Table 1), the species' occupancy estimates >0 in those habitat types (Fig. 2) are a consequence of the covariates included in the most plausible model (Table 2). (2) Mobile species such as the molossids *M. molossus*, *Molossus* < 35 and *Cynomops* sp. showed lowest occupancy in mature forest and increased in the other habitats, often with

Table 1

Overview of field data and model results for detectability and occupancy. The field data consists of the number of surveys with detections (n_{max} per species: 56 sites \times 3 surveys = 168) and the number of sampling points with detections (n_{max} per habitat = 14, n_{max} total = 56) for all 13 species. Max. change in mean detectability (%) shows the difference in detectability between the habitats with highest and lowest detectability per species. Max. change in mean occupancy (%) shows the difference in occupancy between the habitats with highest and lowest occupancy per species.

Species	Field data					Model results		
	No. surveys with detections	No. sampling points with detections					Max. change per species in	
		Mature forest	Disturbed forest	Pasture	Settlement	Total	Mean detectability (%)	Mean occupancy (%)
<i>Centronycteris centralis</i>	21	5	4	0	0	9	70	23
<i>Cormura brevirostris</i>	31	4	6	7	2	19	12	12
<i>Peropteryx macrotis</i>	43	2	7	11	4	24	7	64
<i>Saccopteryx bilineata</i>	107	9	12	13	9	43	17	31
<i>Saccopteryx leptura</i>	95	9	12	12	7	40	8	29
<i>Pteronotus gymnonotus</i>	70	6	8	12	7	33	23	4
<i>Pteronotus parnellii</i>	84	13	9	11	5	38	9	44
<i>Cynomops</i> sp. ^a	83	3	13	13	14	43	23	71
<i>Molossus molossus</i>	66	1	10	12	14	37	20	93
<i>Molossus</i> < 35 ^b	118	3	13	14	14	44	9	71
<i>Noctilio albiventris</i>	30	0	7	7	3	17	33	33
<i>Myotis nigricans</i>	130	9	13	14	13	49	8	29
<i>Vespertilionid</i> > 56 ^c	22	6	5	2	2	15	29	9
Total	900	70	119	133	94	411	20.6	39.5

^a *Cynomops cf. mexicanus* and *C. planirostris*.

^b *Molossus bondae*, *M. rufus* and *M. sinaloae*.

^c *Myotis riparius* and *M. keaysi*.

Table 2

Plausible occupancy models for 13 aerial insectivorous bat species. A maximum likelihood model was considered plausible when its AICc weight > 10%. Model no. refers to full list of a-priori models in Table A2; X indicates that this covariate was included in this model (Model no. 1 has no X which indicates the selection of the null model, i.e., the model without any covariates); k is the number of parameters per model.

Species	Model no.	Orientation	Tree distance	Canopy cover	Canopy height	Habitat	k	Delta AICc	AICc weight (%)
<i>Centronycteris centralis</i>	9		X	X			4	0	24.53
	10		X		X		4	0.69	17.25
	3		X				2	1.19	13.42
<i>Cormura brevirostris</i>	4			X			2	0	35.48
	5				X		2	0.71	24.88
	1						2	2.24	10.58
<i>Peropteryx macrotis</i>	10		X		X		4	0	57.42
	9		X	X			4	2.82	14.02
<i>Saccopteryx bilineata</i>	7	X		X			6	0	33.96
	14	X		X	X		8	1.74	14.23
<i>Saccopteryx leptura</i>	1						2	0	65.15
<i>Noctilio albiventris</i>	5				X		2	0	31.48
	–					X	8	0.28	27.37
	10		X		X		4	1.89	12.23
	11			X	X		4	2.26	10.17
<i>Pteronotus parnellii</i>	15		X	X	X		6	0	30.19
	10		X		X		4	1.48	14.40
	–					X	8	1.8	12.27
<i>Pteronotus gymnonotus</i>	1						2	0	32.06
	11			X	X		4	1.8	13.03
	13	X	X		X		8	1.82	12.90
	2	X					4	2.22	10.56
<i>Vespertilionid > 56^a</i>	7	X		X			6	0	31.99
	13	X	X		X		8	0.37	26.59
	3		X				2	1.45	15.50
<i>Myotis nigricans</i>	7	X		X			6	0	34.90
	8	X			X		6	0.25	30.80
	–					X	8	1.31	18.13
	1						2	2.08	12.34
<i>Cynomops sp.^b</i>	8	X			X		6	0	46.20
	13	X	X		X		8	1.68	19.94
	11			X	X		4	1.92	17.69
<i>Molossus molossus</i>	–					X	8	0	99.95
<i>Molossus < 35^c</i>	8	X			X		6	0	48.41
	–					X	8	0.84	31.81

^a *Myotis riparius* and *M. keaysi*.

^b *Cynomops cf. mexicanus* and *C. planirostris*.

^c *Molossus bondae*, *M. rufus* and *M. sinaloae*.

highest values in settlements suggesting that these species may profit from anthropogenically altered conditions such as artificial roosting sites and increased food accessibility at artificial lights. Species included in occupancy pattern categories 3 and 4 are of intermediate mobility. (3) *M. nigricans*, *S. bilineata*, *P. macrotis*, *N. albiventris* and *C. brevirostris* had lowest occupancy values in mature forests and highest in pastures with intermediate values in the two other habitat types. Based on this study they preferably forage in open spaces and are able to utilize those habitats created by deforestation. (4) *S. leptura*, *P. gymnonotus* and *Vespertilionid > 56* exhibit no or very limited variation in occupancy among the different habitat types, at least with the covariates included in this study.

In summary, these findings suggest that among AIB in the Neotropics, species with an ARI of less than 2.1 or a WLI of less than 0.4 should be classified as less mobile and thus as susceptible to habitat change reducing mature forest coverage. Species with an ARI greater than 2.8 or a WLI greater than 1.3 are classified as mobile and thus seem to profit from human induced habitat change.

Differences in occupancy among habitats correlated well with wing morphology (Fig. 3). Simple linear regressions were significant for all habitats but pasture (marginally significant for WLI in settlements, $p = 0.062$) and explained around 70% of the variation between species in ARI and between 28% and 60% in WLI (exact

values in Fig. 3). Occupancy increased positively with increasing wing indices in settlements ($y = 0.34x - 0.77$) and in disturbed forest ($y = 0.16x - 0.38$), which contrasted strongly with mature forest where occupancy showed a strong negative correlation ($y = -0.70x + 1.52$).

4. Discussion

In this study, we used an approach involving space-for-time substitution in different habitat types to assess the impact of anthropogenic habitat change on AIB on a broad spatial scale across the country of Panama. By correcting occurrence for the detectability of bats we obtained true occupancy (sensu Kéry, 2011) which we related to mobility. We found that less mobile species with large-surfaced, broad wings are more widely distributed in forests and decrease in occupancy in more open and anthropogenically altered habitats like pastures and settlements. Conversely, more mobile species with small-surfaced, narrow wings show the opposite pattern. Mobility, therefore, has a high impact on occupancy in a given habitat type, and as such can be used as a predictor of susceptibility to habitat change. In general, less mobile species forage in dense vegetation clutter where broad wings enable for high maneuverability. Broad wings have been identified as a factor contributing to higher extinction risk and thus

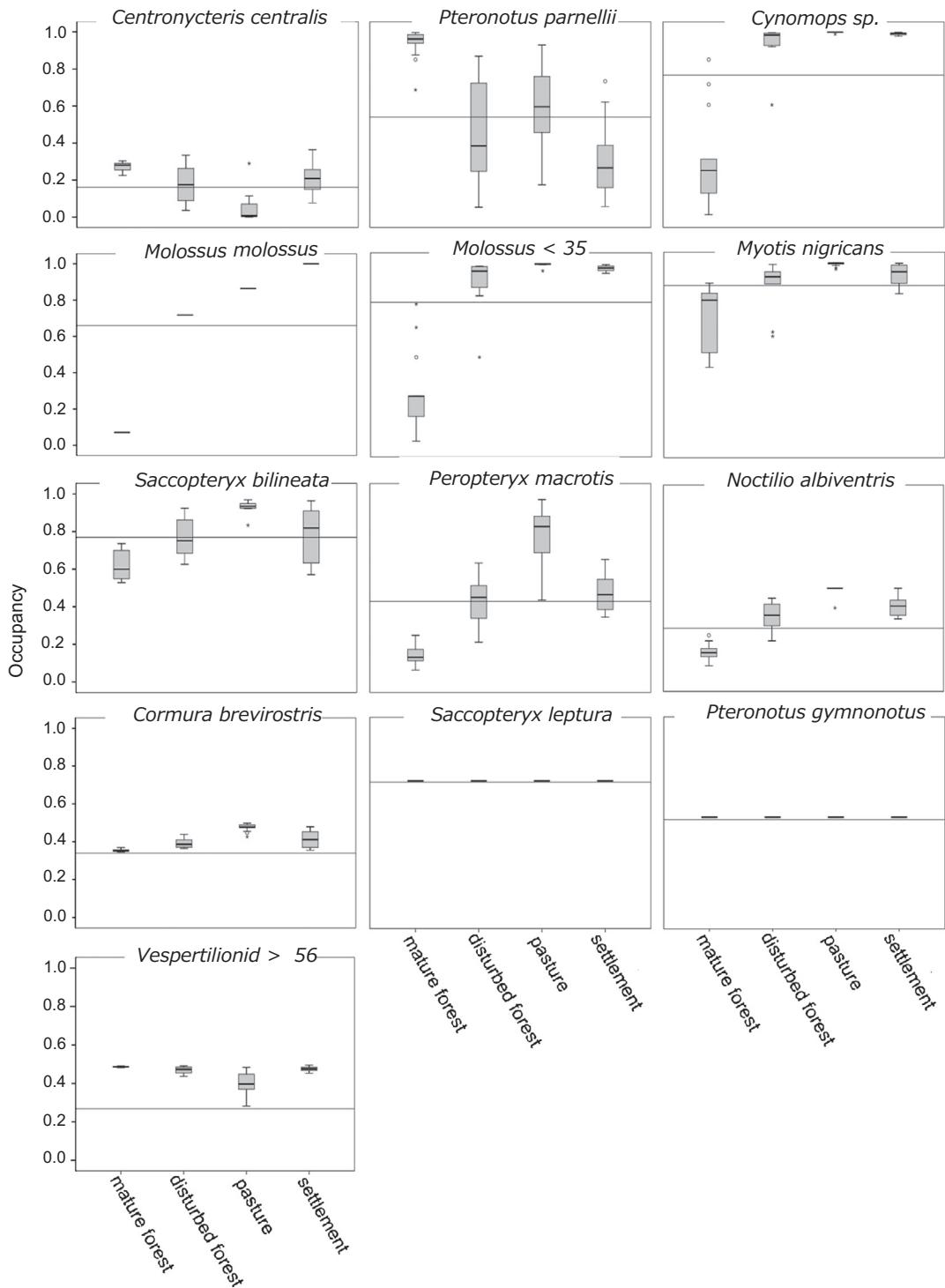


Fig. 2. Boxplots of the occupancy by species summarized by habitat type. Each boxplot shows median, second and third quartile and 95% – CI of the values obtained by the best model (Table 2); n per habitat = 14; 1 signifies a species occupies every sampling point of a certain habitat type; 0 signifies a species does not occupy any sampling point of a certain habitat type. The horizontal line represents the naive occupancy estimate for each species without accounting for habitat-specific detectability.

increased conservation concern in temperate zone bats (Safi and Kerth, 2004) as well as in bats worldwide (Jones et al., 2003).

4.1. Differences in detectability affect occupancy

Naive occupancy estimates, i.e. those not corrected for detectability, often deviate substantially from the estimates corrected for detectability (here between 36% underestimation and 59% overestimation), indicating that environmental covariates are

important factors in determining whether a bat is detected or not. This finding highlights the need to take habitat- and species-specific detectability into account when studying occupancy or distribution. Otherwise, the variation in detectability biases occupancy results, possibly leading to erroneous conclusions.

Our results showed, that inter-specific detectability varied from 31% to 91% and intra-specific detectability varied up to 70% among different habitat types (Table 1). This is very likely due to the fact that detectability in bats is affected by several factors, including

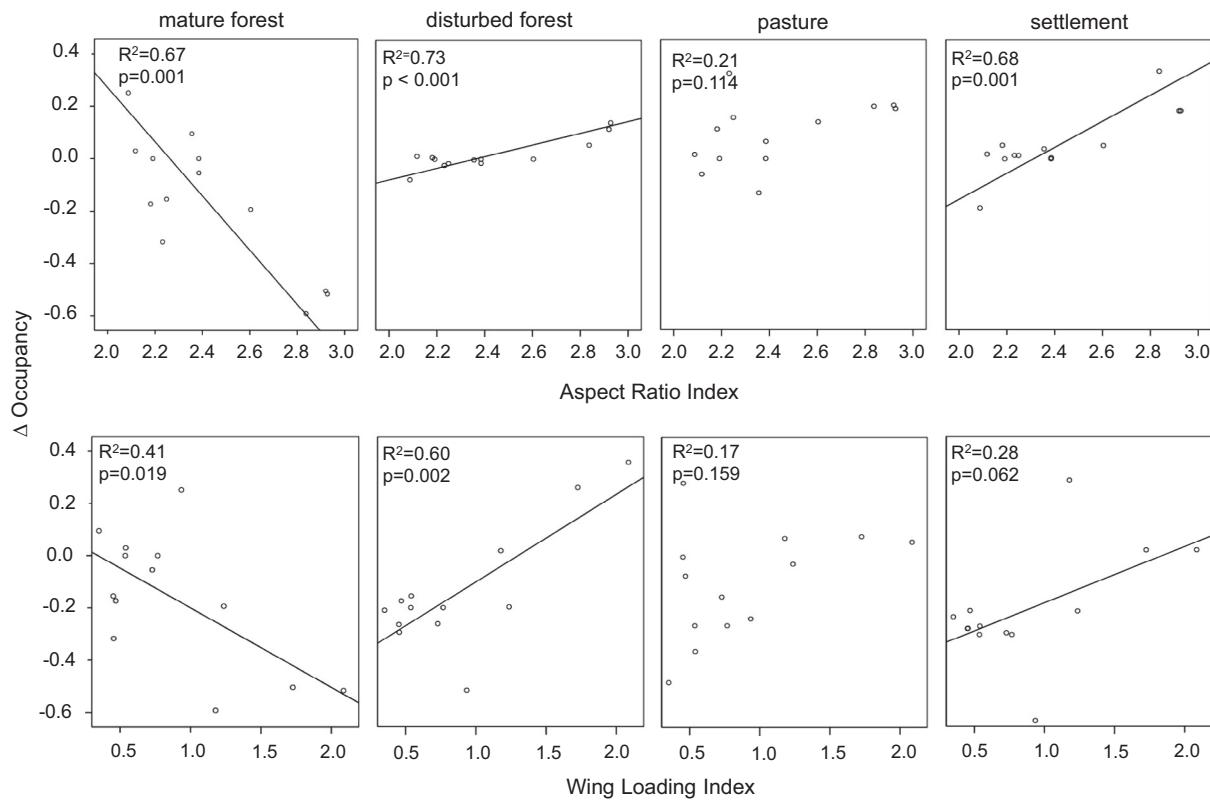


Fig. 3. Linear regression of wing indices and occupancy. Δ occupancy is the difference between the species' value and the mean occupancy of all species in a certain habitat. Each point represents a species ($n = 13$).

characteristics of echolocation calls such as intensity and frequency (Patriquin et al., 2003); species' activity, the assessment of which is in turn affected by the overall abundance; climate and time of recording (McCarthy et al., 2013); and habitat characteristics such as vegetation structure (e.g. canopy height, and canopy closure), which can absorb echolocation calls of lower frequencies that are not already attenuated by air (Kalounis et al., 1999; Patriquin et al., 2003). All of these factors contribute to the detectability of species. Thus it is essential to standardize recording equipment, recording situations and include habitat characteristics when evaluating species- and habitat-specific occupancy patterns correctly.

Our overall detectability of 65% in a single survey agrees well with observations from Meyer et al. (2011), who found average detectability with acoustic sampling to be 71% for Neotropical AIB. Both values are substantially higher than the 36–40% observed by Duchamp et al. (2006) for temperate North America, which could be related to lower overall bat abundance in higher latitudes or to methodological differences, e.g. in recording devices or survey effort. This finding underlines the importance of considering detectability not only as species-, but also as habitat-specific.

4.2. Wing measures as proxies for mobility

Our findings underline the usefulness of wing measurements to assess the mobility of bats, corroborating former studies (Duchamp and Swihart, 2008; Findley, 1993; Norberg and Rayner, 1987). Additionally, our study highlights the importance and practicality of wing measurements that rely on bone lengths instead of wing area and wingspan. In line with the well-established Aspect Ratio Index ARI describing energy efficiency (Findley et al., 1972), we hereby introduce another bone-based Wing Loading Index WLI, which is related to flight speed. Mobility is determined by both energy efficiency and flight speed, but the two indices do not

necessarily coincide. While the two indices showed quite consistent ranking among the more mobile species, rankings varied considerably among the less mobile species (Fig. A4). Thus, for species that can clearly be classified into distinct categories, the assessment of the susceptibility to habitat change is quite straightforward (less mobile, negatively affected vs. mobile, positively affected, Section 3.2, Fig. 2). For species in between, a prediction of their response to anthropogenic habitat change is more complex. In such cases it is useful to assess mobility from several perspectives, e.g. with both, ARI and WLI, to better relate these traits to susceptibility to habitat change. These indices are not independent across species, however, because a species' mobility is not independent from phylogeny. This is most apparent in molossids, where nearly all species are highly mobile (Vaughan, 1966). However, this objection does not limit the utility of wing indices, as used in this applied context. Also, the presence of a species or its abundance in a certain habitat does not only depend on its mobility. Other relevant factors may include abundance of preferred prey items (e.g. Gonsalves et al., 2013) or climatic preferences (Estrada-Villegas et al., 2012).

4.3. Conclusions and Implications for conservation

Our study underlies the importance of explicitly modeling detectability when studying the occurrence or distribution of bats with acoustic methods, concurring with results from previous studies (Duchamp et al., 2006; Kéry, 2011; MacKenzie et al., 2006). The great variation we found in detectability was not limited to different AIB species but was also found across different habitat types within the same species. This finding is of crucial importance when comparing different habitat types. Conservation studies ignoring this variation risk either over- or underestimating species' occurrence

in one habitat type relative to another, potentially leading to erroneous conclusions.

We found habitat-specific occupancies of AIB species. Some species, such as *C. centralis*, *M. molossus*, *Cynomops* sp. and *N. albiventris*, clearly preferred or avoided certain habitat types. In general, our findings, covering a very large geographic scale, confirm habitat preferences identified on geographically more restricted scales (Estrada-Villegas et al., 2012; Jung and Kalko, 2010, 2011). In order to sustain a species-rich AIB community, which will provide crucial ecosystem functions and services including insect control on a regional scale, it is critical to secure a diversity of different habitat types. For AIB, important habitat types are not limited to pristine, intact forest but also include anthropogenically altered habitats, where we show several species increase their occupancy.

By studying the habitat-specific occupancy values of AIB species, we identified a general pattern linking a species' mobility and its susceptibility to habitat change. The broader and larger-surfaced the wings, the less mobile the species and the more likely it will disappear with deforestation and urbanization. Bats with small-surfaced and narrow wings are more mobile and can profit from anthropogenic habitat changes. Based on our quantitative results on wing shape, we can go beyond these qualitative statements and predict the vulnerability to habitat change even for species not included in the analysis. As long as its wing shape measures are known, one can predict the degree to which a species will be impacted by deforestation and urbanization. Such a prediction is especially valuable for species for which little or nothing is known about ecology or natural history, e.g. newly described species. There is evidence that in addition to wing morphology (Jones et al., 2003), characteristics such as distribution range, habitat specialization and, to a certain degree, food preferences, predict extinction risk in bats (Boyles and Storm, 2007). For 22% of all mammals, there is no data on these predictive factors other than morphology; small species such as bats are overrepresented in this fraction (Gonzalez-Suarez et al., 2012). For AIB in the tropics, the absence of such information is the norm (Kalko et al., 2008), thus alternative approaches estimating vulnerability, such as the one presented here, may be critical to guide conservation efforts. Conservation agencies could use mobility, as predicted from wing morphology, possibly together with additional information, such as the extent of occurrence (IUCN, 2012), to prioritize conservation actions. Our study contributes to a growing body of literature investigating how trait information can be used to assess species' susceptibility to habitat change and extinction risk (e.g. Jennings and Pocock, 2009; Meyer et al., 2008). The inclusion of the type and extent of expected future habitat change, as well as additional traits, would further improve the assessment of vulnerability and thus extinction risk for many species, including the elusive AIB in the tropics.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2015.02.028>.

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