

**Distribution of Aerial Insectivorous Bats in Panama Using Site-Occupancy Models**

**Raul Andres Rodriguez Moreno**

**Trabajo de grado como requisito para optar el título de Magister en Biología**

**Director**

**Victor Hugo Serrano Cardozo**

**Universidad Industrial de Santander**

**Codirector**

**Thomas Sattler**

**Swiss Ornithological Institute**

**Universidad Industrial de Santander**

**Facultad de Ciencias**

**Escuela de Biología**

**Maestría en Biología**

**Bucaramanga**

**2017**

**Dedication**

A mi familia y Eli Kalko; en especial, a mi madre, mi esposa y a Martincito.....

### **Acknowledgements**

A mi familia, y en especial a mi madre por su paciencia y empuje.

A mi esposa y a Martincito quienes siempre estuvieron allí.

Agradezco infinitamente a mis asesores, Victor y Thomas, grandes amigos que siempre estuvieron pendientes de mis avances; muchas gracias por sus consejos en lo académico, profesional y personal.

A Elias B., quien acompañó en Panama esta aventura en campo. A M. Kery, M. K. Obrist, M. Gumprich, M. Tschapka, S. Estrada-Villegas, F. Delgado, M. Miller, R. Samudio, J. Samudio, R. Arias, R. Page, K. Jung por todo su apoyo durante la logística y ejecución proyecto.

Expreso mi gratitud a todas las personas que permitieron el acceso a sus propiedades durante el trabajo de campo.

A todos los profesores de la Escuela de Biología, al Grupo de Estudios en Biodiversidad, en especial a Martha Patricia Ramírez quien estuvo muy pendiente de mis avances.

Agradecimientos especiales a todas las entidades financiadoras de la presente investigación: Smithsonian Tropical Research Institute, Swiss Federal Research Institute WSL, Elekon AG, University of Ulm y Universidad Industrial de Santander.

A los jurados del presente documento por sus valiosos aportes.

## Contents

|                                        |    |
|----------------------------------------|----|
| Introduction.....                      | 13 |
| 1. Objectives .....                    | 17 |
| 2. Hypotheses.....                     | 17 |
| 3. Methods.....                        | 18 |
| 3.1. Study area and survey design..... | 18 |
| 3.2. Field sampling.....               | 20 |
| 3.3. Call analysis .....               | 21 |
| 3.4. Environmental covariates.....     | 22 |
| 3.5. Statistical analyses .....        | 24 |
| 4. Results.....                        | 26 |
| 5. Discussion.....                     | 33 |
| 6. Conclusions.....                    | 38 |
| References.....                        | 39 |
| Appendix.....                          | 49 |

### List of figures

|                                                                                                                                                                                                                                                                                      |    |
|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----|
| <i>Figure 1.</i> Study area (shaded) depicting the fifteen study areas in Panama. Each dot represents a sampling point (n = 64).....                                                                                                                                                 | 20 |
| <i>Figure 2.</i> Importance of each covariate type (land use, topographic and climate) on occupancy of eleven aerial insectivorous bats. Label on bars correspond to covariates included in the best models and bold letters show covariates with $>\sum wAIC$ (see Appendix C)..... | 30 |
| <i>Figure 3.</i> Occupancy maps and richness map of eleven aerial insectivorous bats in Panama. Each dot represents a presence point each species. ....                                                                                                                              | 32 |

### List of tables

*Table 1.* Covariates used for modeling the occupancy and detection modeling of aerial insectivorous bats in Panama. .... 23

*Table 2.* Detectability, occupancy and area of occupancy for eleven aerial insectivorous bats in Panama in taxonomic order. Detectability  $p$  indicates the probability of finding the species when surveying once with the described method; the naïve occupancy  $\psi$  is the simple fraction of  $n$  sites detected/ $n$  sites sampled) without considering detectability;  $\psi_i$  is the detection-corrected estimate of occupancy probability; the area of occupancy (AOO) is the sum of all occupancy probabilities of the study area. .... 27

### List of appendix

|                                                                                                                                                                                                                                                                                                                                                                                         |    |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----|
| <i>Appendix A.</i> Example of the a-priori models calculated for aerial insectivores bats from Panama, <i>Peropteryx macrotis</i> in this case. Abbreviations in Table 1 .....                                                                                                                                                                                                          | 49 |
| <i>Appendix B.</i> Final top ranked model(s) ( $\Delta AIC < 2$ ) for predicting occupancy of aerial insectivores bats in Panama. $wAIC$ is the AIC model weight, $nPars$ is the number of parameters in the model, $\Delta AIC$ is the difference in values between lowest AIC model and each model, and $c\text{-hat}$ is a variance inflation factor. Abbreviations in Table 1. .... | 54 |
| <i>Appendix C.</i> Parameter from the final top models for aerial insectivores bats from Panama. Abbreviations in Table 1.....                                                                                                                                                                                                                                                          | 57 |
| <i>Appendix D.</i> Expected site occupancy of AIB in Panama, as a function of annual mean temperature ( $^{\circ}C$ ) for those species in which this variable was in the top-ranked model set. Gray lines represent the 95% confidence interval around these estimates. ....                                                                                                           | 59 |



### Resumen

**Título:** Distribución de murciélagos insectívoros aéreos en Panamá, usando modelos de sitio ocupación\*

**Autor:** Raul Andres Rodriguez Moreno\*\*

**Palabra claves:** Ocupacion, detectabilidad, chiroptera, clima, uso de suelo, Panama

### Descripción:

Los modelos de distribución de especies son una importante herramienta en estudios de distribución, riqueza de especies y potencial de especies invasivas. A pesar de su importancia, los estudios de modelado de distribución usualmente ignoran que la detección es imperfecta. Los murciélagos insectívoros aéreos representan más de un tercio de las comunidades locales de murciélagos neotropicales y cumplen importantes servicios ecosistémicos. La detección de murciélagos insectívoros aéreos es afectada por la intensidad de las llamadas y las condiciones del entorno. Nosotros modelamos la ocupación de los murciélagos insectívoros aéreos, considerando la detectabilidad en combinación con co-variables, para construir mapas de ocupación. Este estudio es el primero de este tipo en el neotrópico. Nosotros realizamos un muestreo acústico estandarizado en 64 sitios a lo largo de Panamá. Subsecuentemente, evaluamos la asociación de 12 co-variables de clima, topografía y hábitat con la ocupación de once especies de murciélagos. La detectabilidad en los murciélagos insectívoros aéreos varió de manera especie-específica desde 0.32 a 0.83. Los modelos de ocupación para las especies de murciélagos fueron principalmente explicados por co-variables climáticas, especialmente por la temperatura promedio anual que se correlaciono positivamente con cuatro especies y negativamente con dos especies. La mayoría de los modelos de distribución fueron afectados por la actividad humana, especialmente por hábitats perturbados. Especies de bosque tales como *Centronyterix centralis* dependen del bosque maduro, mientras que especies tales como *Peropteryx macrotis* y *Cormura brevirostris* prefieren áreas agrícolas evitando zonas densamente pobladas. Los molosidos están distribuidos en áreas abiertas y semi-abiertas, incluyendo asentamientos. La consideración explícita del proceso de observación, cuando se tiene interés en modelar el proceso ecológico es especialmente importante para especies que son fuertemente afectadas por la probabilidad de detección. La detección de los murciélagos insectívoros aéreos por registros acústicos es afectada tanto por factores intrínsecos como extrínsecos.

---

\* Tesis de maestría

\*\*Facultad de Ciencias, Escuela de Biología, Maestría en Biología Director: Victor Hugo Serrano. Codirector: Thomas Sattler

### Abstract

**Title:** Distribution of Aerial Insectivorous Bats in Panama Using Site-Occupancy Models\*

**Author:** Raul Andres Rodriguez Moreno\*\*

**Keywords:** occupancy, detectability, chiroptera, climate, land use, Panama

### Description:

Species distribution modeling is an important tool in studies of distribution, species richness and invasive species potential. Despite its importance, studies involving distribution modeling usually ignore that detection is imperfect. Aerial insectivorous bat species represent up to one third of local Neotropical bat communities and fulfill important ecosystem functions. The detection of aerial insectivorous bats is heavily affected by call intensity of the bats as well as by the environment. We modeled aerial insectivorous bats occupancy considering detectability in combination with covariates to build area of occupancy maps. The present study is the first of its kind for the Neotropics. We conducted a standardized acoustic survey at 64 sites across Panama. Subsequently, we assessed the association of twelve covariates according to climate, topography and habitat to occupancy of eleven bat species. Detectability in aerial insectivorous bats varied species-specific from 0.32 to 0.83. Occupancy models of the bats species were mainly explained by climatic covariates, especially by the annual mean temperature that correlated positively with four species and negatively with two species. Most distribution models are affected by human activity. Forest species such as *Centronyterix centralis* are limited to mature forests, while species such as *Peropteryx macrotis* and *Cormura brevirostris* prefer semi-open landscapes as represented by agricultural areas but avoid densely built areas. Other species groups such as molossids are distributed in any semi-open and open areas including settlements. The explicit consideration of the observer process when one is interested in the underlying ecological process (e.g. species – environmental relationship) is especially important for species that are heavily affected by the detection probability. Detection of aerial insectivorous bats by acoustical recordings are affected by both intrinsic (e.g. call intensity) and extrinsic (e.g. vegetation) factors. Thus, the approach presented here is applicable for similar studies for the Neotropics and beyond.

---

\* Master Thesis

\*\*Faculty of Sciences, School of Biology, Masters in Biology. Director: Victor Hugo Serrano. Codirector: Thomas Sattler

### Introduction

Species distribution models (SDMs) have become an increasingly important research tool, providing relevant information that can be used to respond a wide array of questions in ecological and conservation studies (Angelieri, Adams-Hosking, Ferraz, de Souza, & McAlpine, 2016; Gutiérrez-Tapia & Palma, 2016; Russo, Maiorano, Rebelo, & Preatoni, 2016). Despite the fact that SDM experienced a rapid theoretical and development in recent years, some problems remain unsolved in most studies. A critical issue for the utility and validity of any SDM is the reliability of the data used to build it (Kéry, 2011). Distribution data is crucial for quantify the species geographic ranges by using Extent of Occurrence (EOO) and Area of Occupancy (AOO), which are globally accepted as surrogates of extinction risk under IUCN Red List Criteria (Jiménez-Alfaro, Draper, & Nogués-Bravo, 2012; Miller et al., 2007). The EOO is defined by the area which encompasses all localities where a species has been recorded (e.g. a minimum convex polygon defined by the most extreme locations). The AOO usually is based on a grid-map of the EOO for which cells with a record of the species are considered as occupied and cells with no record or clearly unsuitable habitats (e.g. water bodies for terrestrial species) as unoccupied (Gaston, 1994). However, these estimates are commonly built at coarse grain resolution (>1 km of resolution) and species ranges are expected to be overestimated at habitat level (IUCN, 2001).

In the absence of misidentification, the presence of a species is confirmed by simply detecting it at a given site. In contrast, it is usually not possible to confirm if an animal was truly absent or if the species was present but not detected during the survey, hence, the detection probability (= detectability) of any species at any place and time, arguably, is less than 1 (MacKenzie, 2006).

This results in under - estimation of species occurrence, obtain only the apparent distribution and possibly erroneous conclusions about species and covariates relationships (Kéry, 2011; Lahoz-Monfort, Guillera-Arroita, & Wintle, 2014; MacKenzie, 2006). Site - occupancy models explicitly deal with this source of error by estimating detection probability as a parameter next to occurrence probability. Importantly, both parameters can be modelled by covariates, which may be identical or different among the two model parts. Hence, these models enable the evaluation of species – covariates relationships while correcting for the probability of detecting the species when present that may be less than one and may depend on the very environmental factors that may also affect the presence/absence of a species (MacKenzie, 2006). When species detection is imperfect, these site-occupancy models may be more powerful for predicting species occurrence than more traditional regression analyses (Kéry, Gardner, & Monnerat, 2010; Rota, Fletcher, Evans, & Hutto, 2011). Only few studies have investigated the effect of detectability in SDMs (Comte & Grenouillet, 2013; Karanth, Nichols, & Hines, 2010; Kéry et al., 2010; Mendes, With, Signorelli, & De Marco, 2017). The main reason for the comparatively rare application of this rigid modeling approach to model occurrence in space is that it requires temporal replication at sampling sites (i.e., detection histories) and hence it is an intensive and time-consuming field labour (Koshkina et al., 2017; MacKenzie, 2006). SDM studies that rely on presence, including or excluding (assumed or inferred pseudo-) absence data, often use data that originally were collected for other reasons or that stem from multiple sources (e.g., Hughes, 2017).

Bats are the second largest mammalian order and they provide essential ecosystem services including pollination, seed dispersal and insect control (Jones, Jacobs, Kunz, Willig, & Racey,

2009; Kunz, Braun de Torrez, Bauer, Lobova, & Fleming, 2011). Neotropical bats do not only stand out due to their abundance and species richness, but also for their multiple functional groups (Denzinger & Schnitzler, 2013; Kalko, Villegas, Schmidt, Wegmann, & Meyer, 2008; Schnitzler & Kalko, 2001). Aerial insectivorous bat species (AIBs) form one functional group that has in common to capture insects during flight, both in the open space and in the vegetation. Although Neotropical bat assemblages are dominated by frugivores, aerial insectivorous bats may represent up to 39% of the local bat community (Kalko et al., 2008). Despite this high fraction and their ecological importance, the presence of aerial insectivorous bats is frequently underestimated, mainly due to the outstanding ability of these bats to detect and avoid mist nets, the traditional method to study bats. In this way, they avoid their capture, identification and quantification (Kalko et al., 2008). Advances in bioacoustics now allow to record and identify many AIBs by their species - specific echolocation calls also in the Neotropical region (Bader et al., 2015; K. Jung, Kalko, & von Helversen, 2007; Kirsten Jung & Kalko, 2011). The few studies that have analyzed detectability for this species group have obtained species - specific values between 0.7 and 100% per survey (Bader et al., 2015; Gorresen, Miles, Todd, Bonaccorso, & Weller, 2008; Meyer et al., 2011).

Given their high importance as ecosystem service providers especially in tropical ecosystems bat conservation is an important task (Bader et al., 2015; Kirsten Jung & Kalko, 2010; Kunz et al., 2011). The identification of essential environmental covariates is fundamental for effective species protection and management (e.g., Karanth et al., 2010). While SDMs for bats have become a widely used tool for endeavors such as identifying discriminant environmental covariates at broad scales in the temperate zone over the past decade (Razgour, Rebelo, Di

Febbraro, & Russo, 2016; e.g., Sattler, Bontadina, Hirzel, & Arlettaz, 2007), there is only a limited number of such studies with bats in the Neotropical region (e.g., Mendes et al., 2017). Additional studies covariates related to climate (temperature and precipitation) and habitat (land use) have been identified as essential for the distribution of bats both at regional and global scale (Bader et al., 2015; Estrada-Villegas, McGill, & Kalko, 2012; Patten, 2004; Rodríguez-Aguilar, Orozco-Lugo, Vleut, & Vazquez, 2017; Wang, Owen, Sánchez-Hernández, & De Lourdes Romero-Almaraz, 2003; Weber & Grelle, 2012). Detectability in bats may be affected by habitat covariates such as vegetation structure (Bader et al., 2015; e.g., clutter, canopy height and canopy closure; Patriquin, Hogberg, Chruszcz, & Barclay, 2003; Yates & Muzika, 2006).

We conducted a country-wide survey based on a spatially and altitudinal stratified random sampling design of acoustic surveys in the Neotropics (Panama) and analyzed these data using occupancy species distribution models to estimate the area of occupancy of eleven aerial insectivores bats. We modeled AIBs occurrence in relation to climate, topographic and land use covariates to understand the factors associated with species occurrence. Specifically, we examined which land use type, climate and topographic covariate influences the occupancy of which species. We expected that climatic and topographic covariates would primarily influence species distributions on studied both scale and extend. For each species, we estimated occupancy probability while explicitly accounting for the detection process and produced occupancy maps at a 1km<sup>2</sup> resolution to calculate Areas of Occupancy (AOO).

## 1. Objectives

The major aim of my Master thesis was establish the area of occupancy of eleven species of aerial insectivorous bats in Panama, performing an acoustic survey throughout the entire country and accounting for imperfect detection. In order to achieve this general objective, I had the following specific goals:

1. To identify environmental variables that determines the occupancy of eleven aerial insectivorous bat species in Panama considering the best models in function of detectability.
2. To determine the area de occupancy of eleven aerial insectivorous bat species in Panama considering the best models identified in Objective 1.

## 2. Hypotheses

*Hypothesis 1:*

*Ho.* The occupancy of bats is mainly determined by broad scale variables (e.g., temperature and precipitation) and not by fine scale variables (e.g., land use) in selected models.

*Ha.* The occupancy of bats is mainly determined by fine scale variables (e.g., land use) and not by broad scale variables (e.g., temperature and precipitation) in selected models.

*Hypothesis 2:*

*Ho.* Occupancy for aerial insectivorous bats do not differ from random distributions.

*Ha.* Occupancy for aerial insectivorous bats do differ from random distributions.

### 3. Methods

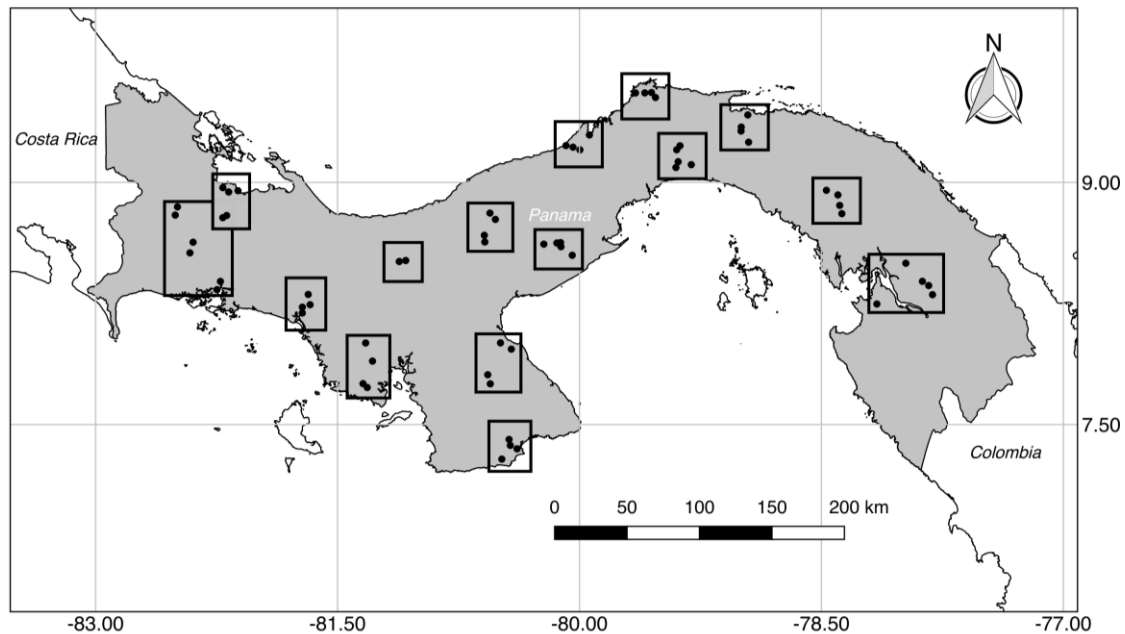
#### 3.1. Study area and survey design

Panama is located in Central America covering approximately 76,433 km<sup>2</sup> and an range of elevation from sea level to 3,475 m a.s.l (ANAM, 2010). The climate is warm with average temperatures around 27 °C and annual precipitation from 1600 mm to over 3020 mm per year. The annual rainfall pattern divides the year into two seasons: an approximately 4-month dry season January–April and a wet season lasting May into December (Milton & Giacalone, 2014). The central cordillera mountains split the county into a wet Caribbean (1600 per year) and a drier Pacific (4000 per year) regions (Condit, 1998). Primeval and generally mature forest areas still are under pressure by human exploitation and land use changes (ANAM, 2014), however an approximate 32,305 ha of reforested area has been reported between 2001 and 2012 (Hansen et al., 2013).

In order to obtain detection/non-detection information for aerial insectivorous bat species in



Panama, we acoustically sampled 64 sites ( $n$ ) located in 15 areas, which were stratified to cover broadly the geographic extent of Panama (Figure 1) as well as its altitudinal range (sampling sites from 12 m to 2,312 m a.s.l.). Sampling sites were chosen to reflect the environmental gradients in each area, including anthropogenic disturbance. In this way an area usually contained four (60 % of the areas) or five sites (26.7 % areas). Exceptionally, one area consisted of six sites while another one contained only two sites. As 54 of the 64 sites had already been included in the study of Bader et al. (2015), we applied their description of habitat types also to the new sites: mature forests ( $n= 20$ ), disturbed forests ( $n= 14$ ), pastures ( $n= 14$ ) and settlements ( $n= 16$ ). For a detailed description of the habitat types see Bader et al. (2015). To obtain detection histories, i.e., detection/non-detection data of sampled bat species, we replicated sampling in non-consecutive nights (usually a minimum of three weeks between sampling replicates) in 61 sites: 59 sites were sampled three times and one site each was sampled two and four times. Three sites were surveyed only once, yielding in a total of 186 surveys. On average, there was a lag time of 33 days between replicates at any given site. Therefore, we consider the basic assumption of a closed population for this type of occupancy analysis to be met. To minimize edge effects, sampling points were positioned within habitat patches with 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, sites were separated by a minimum distance of two kilometers to minimize the spatial dependence of sampling points.



*Figure 1.* Study area (shaded) depicting the fifteen study areas in Panama. Each dot represents a sampling point (n = 64).

### 3.2. Field sampling

96.8% of acoustic surveys took place from 3 June 2012 to 14 September 2012 while a complementary 3.2% of surveys were realized between 11 October 2012 and 17 February 2013. We recorded AIB starting at sunset for three hours simultaneously in all its sites in each area, which was shown to yield >90% of all local AIB species (Estrada-Villegas, Meyer, & Kalko, 2010; Meyer et al., 2011). 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 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. This

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

### 3.3. Call analysis

We selected eleven bat species from the families of Emballonuridae (*Centronycteris centralis*, *Cormura brevirostris*, *Saccopteryx bilineata*, *Saccopteryx leptura*, *Peropteryx macrotis*), Noctilionidae (*Noctilio albiventris*), Mormopidae (*Pteronotus parnellii*, *Pteronotus gymnonotus*) and Molossidae (*Molossus bondae*, *Molossus molossus*) and one sonotype. A sonotype groups two or more species (here *Cynomops* sp., in Panama probably encompassing *C. freemani* and *C. planirostris*) which call very similarly and therefore are supposed to have similar ecological requirements. To simplify the text, the term 'species' henceforth includes also this sonotype. All focal species were common enough for occupancy analysis (presences in at least 18% of the sites) and could be identified to their respective taxonomic level with high confidence. Initially we had also included seven additional species into the analysis (*Peropteryx kappleri*, *Rhynchonycteris naso*, *Noctilio leprinus*, *Pteronotus personatus*, *Promops centralis*, *Rhogeessa io*, and *Myotis nigricans*) but they were excluded from further analysis due to little occurrence, taxonomic insecurity and lack of model convergence.

Bat calls were analyzed with Raven Pro 1.4 (Bioacoustics Research Program, 2011) and Batscope 3.1.6 (Boesch & 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 (K. Jung et al., 2007; Kirsten Jung, 2009; Kirsten Jung, Molinari, & Kalko, 2014; Rydell, Arita, Santos, & Granados, 2002) and from our own reference calls. Species-specific calls are shown in Bader et al. (2015). To obtain presence 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.

### 3.4. Environmental covariates

We selected twelve covariates that are ecologically relevant and most likely to influence the occupancy of AIBs, focusing on climate, topographic and land use covariates (Table 1; Estrada-Villegas et al., 2012; Mendes et al., 2017; Patten, 2004; Wang et al., 2003; Weber & Grelle, 2012). These three types of covariates reflect gradients that are supposed to influence species distribution on broad (climate), regional (topography) and local scale (habitat) (McGill, 2010; Patten, 2004; Pearson & Dawson, 2003; Wang et al., 2003). We used bioclimatic covariates obtained from the Worldclim database (30 arc-sec, [www.worldclim.org](http://www.worldclim.org)), i.e, annual mean temperature, mean diurnal range, annual precipitation and precipitation of the coldest quarter. Topographic covariates derived from the SRTM database (30 arc-sec, [www2.jpl.nasa.gov/srtm](http://www2.jpl.nasa.gov/srtm)), included slope and aspect ratio, but this latter was transformed to continuous values of northness (cosine [aspect]) and eastness (sine [aspect]). We did not include elevation as a covariate, as this variable is highly correlated with temperature covariates. The latter affects bats more directly through physiological constraints. Data on land use was obtained from the Panama's Autoridad Nacional del Ambiente for the year 2000 (ANAM) (30 arc min, [mapserver.strsi.edu/](http://mapserver.strsi.edu/)). Fifteen land use categories were summarized to four categories (mature forest, disturbed forest, pasture

and settlements), and we derived land use cover (%) considering a 3 km radius (circular analysis). We considered human population density (Gridded Population of the World, GPW, 1 km resolution), datasets from (beta.sedac.ciesin.columbia.edu) as a proxy for anthropogenic influence and therefore included it into the category as “land use”. Colinearity between covariates was low ( $r^2 < 0.4$ ) as revealed by Pearson correlation analysis which meant we did not have to exclude any of them based on this criteria. All covariates were processed in QGIS and raster (Hijmans & van Etten, 2014), rgdal (Bivand, Keitt, & Rowlingson, 2014), dismo (Hijmans, Phillips, Leathwick, & Elith, 2015), maptools (Bivand & Lewin-Koh, 2013) packages in R version 3.3 and analyzed using an 1 km spatial resolution.

*Table 1.* Covariates used for modeling the occupancy and detection modeling of aerial insectivorous bats in Panama.

| Model                | Type        | Covariates                            | Abbreviations | min. - max.   |
|----------------------|-------------|---------------------------------------|---------------|---------------|
| <b>Detectability</b> |             | Canopy cover proportion (%)           | cc            | 0.01 to 0.96  |
|                      |             | Rainfall (mm)                         | rf            | 0 to 280      |
| <b>Occupancy</b>     | Climate     | Annual Mean Temperature (°C)          | b1            | 14.30 to 27.4 |
|                      |             | Mean Diurnal Range (°C)               | b2            | 6.1 to 10.20  |
|                      |             | Annual Precipitation (mm)             | b12           | 1117 to 3676  |
|                      |             | Precipitation of Coldest Quarter (mm) | b19           | 254 to 1336   |
|                      |             |                                       |               |               |
|                      | Topographic | Slope (degrees)                       | slp           | 0 to 17.20    |
|                      |             | Eastness                              | east          | -1 to 1       |
|                      |             | Northness                             | north         | -1 to 1       |

| Model | Type     | Covariates                     | Abbreviations | min. - max. |
|-------|----------|--------------------------------|---------------|-------------|
|       |          | Mature forest (%)              | mf            | 0 to 100    |
|       |          | Disturbed forest (%)           | df            | 0 to 100    |
|       | Land use | Pasture (%)                    | pa            | 0 to 100    |
|       |          | Settlement (%)                 | se            | 0 to 70.59  |
|       |          | Number persons/km <sup>2</sup> | pd            | 4 to 1953   |

Not only species characteristics such as call intensity and flight height but also varying conditions at each site may affect detectability. Detectability is affected by vegetation clutter which attenuates echolocation calls (Patriquin et al., 2003) and also rainfall is known to affect bat activity (Erickson & West, 2002). Thus we recorded canopy cover as a surrogate for vegetation clutter at each site by taking 180° fisheye lens photos 50 cm above ground (Canon EOS Digital Rebel with Sigma 4.5 mm F2.8 EX DC HSM Circular Fisheye Lens), and analyzed them with software ImageJ64 1.46r (Rasband, 2012). While we did not survey with heavy rain, we recorded rainfall for each survey (mm).

### 3.5. Statistical analyses

We used single-season, single-species occupancy models to estimate the occupancy  $\psi$  (the probability that a site is occupied by the target species) and detection probability  $p_j$  (the probability of detecting the species during the  $j$ th survey, given it is present). Occupancy models are hierarchical; the ecological process that influences occupancy is modeled separately from the observation process. This model type assumes closed populations, meaning that a site remains either occupied or unoccupied for the entire study duration, a justifiable assumption since we sampled over a rather short period. As dependent variables we used the detection – non-detection

information obtained at each site which is summarized as species' detection histories (MacKenzie, 2006). We evaluated whether the covariates canopy cover and rainfall really had an influence on the detection process. We included covariates from the three categories climate, topography and land use as explanatory covariates of occupancy. Since the original covariates had distinct numerical ranges, all covariates included in the modeling were centered to a mean of zero and scaled by their respective standard deviations prior to model fitting. We fit occupancy models using the “unmarked” package in program R (Fiske & Chandler, 2011), and compared models using AIC scores and AIC weights to determine the best supported models for each species (lowest AIC score and highest  $w_{AIC}$ ) (Burnham & Anderson, 2002). We examined the relative importance of covariates by summing the AIC weights for each covariate across all models that it occurred. We tested whether the data for best selected models were overdispersed by calculating the  $c\text{-hat}$ , obtained by MacKenzie and Bailey goodness-of-fit test (1,000 times) (MacKenzie & Bailey, 2004). Models with  $c\text{-hat} > 5$  were overdispersed (Kéry, *pers. comm.*). Occupancy analysis excluded islands, so only continental territory was included (74,952.3 km<sup>2</sup>). We discarded models was not reached numerical convergence, and so parameter estimation was not reliable.

The detailed steps were: 1) we calculated occupancy and detectability without any covariates obtaining a null (or constant) model consisting of an intercept only. This model served as a basis for comparison in the modeling process; 2) we modeled the detection process ( $p$ ) using six models including all combinations of observation-specific covariates in linear and quadratic forms with constant occupancy; to model  $\psi$ , we opted for an additional three step approach summarizing 147 basic models with linear and quadratic terms (Appendix A in supporting

information): 3) we first selected the most important covariates for category climate in addition to the most plausible detection model of step No. 2, in this way we obtained 28 basic models; 4) after kept the model structure that was best in the step No. 3 to model topographic covariates, thus we obtained 18 basic models. 5) Finally, we used the best models of step No. 4 to model land use covariates, in this way we obtained 101 basic models. In addition to the basic models in each step (linear and quadratic forms), we considered interactions between variables in the most parsimonious models ( $<2 \Delta AIC$ ), varied the number of final models evaluated for each species (Appendix C). Our inferences and posterior analysis are based on a single final model, to estimate parameters and coefficients of occupancy models. This framework consists of specifying, a priori, potential models explaining the process of interest and selecting models that fit the data well with a minimum number of covariates (i.e., a trade-off between bias and variance).

The area (or number of sites) occupied by a species, i.e., area of occupancy (AOO) derived from best model selected to each species by summing the site occupancy probabilities obtained over the studied area (Kéry & Royle, 2015). We stacked separate AOO maps for each aerial insectivorous bats to derive predictions of species richness ((Guillera-Arroita et al., 2015), following a ‘predict first, assemble later’ strategy (Ferrier & Guisan, 2006). The sum of species occupancy probabilities at a site is equal to the expected number of species present, and hence is a good estimator of species richness (Calabrese, Certain, Kraan, & Dormann, 2014).

#### 4. Results



Field surveys at 64 locations resulted in 186 site-sampling nights (58,474 call sequences) of which we obtained 687 detections and 369 non-detections from eleven species. All selected species recordings gave a naïve detection-estimate of occupancy (meaning without considering detection probability) ranging from 0.19 (*C. centralis*) to 0.69 (*S. bilineata*, Table 2).

*Table 2.* Detectability, occupancy and area of occupancy for eleven aerial insectivorous bats in Panama in taxonomic order. Detectability  $p$  indicates the probability of finding the species when surveying once with the described method; the naïve occupancy  $\psi$  is the simple fraction of  $n$  sites detected/ $n$  sites sampled) without considering detectability;  $\hat{\psi}_i$  is the detection-corrected estimate of occupancy probability; the area of occupancy (AOO) is the sum of all occupancy probabilities of the study area.

|                                 | $p$ [SE]    | Naïve $\psi$ | $\hat{\psi}_i$ | AOO (km <sup>2</sup> ) |
|---------------------------------|-------------|--------------|----------------|------------------------|
| <i>Centronycteris centralis</i> | 0.62 [0.11] | 0.19         | 0.25           | 24,890                 |
| <i>Cormura brevirostris</i>     | 0.55 [0.09] | 0.31         | 0.35           | 31,019                 |
| <i>Peropteryx macrotis</i>      | 0.49 [0.10] | 0.38         | 0.48           | 29,395                 |
| <i>Saccopteryx bilineata</i>    | 0.83 [0.04] | 0.69         | 0.69           | 53,001                 |
| <i>Saccopteryx leptura</i>      | 0.73 [0.07] | 0.67         | 0.67           | 56,045                 |
| <i>Noctilio albiventris</i>     | 0.54 [0.11] | 0.27         | 0.32           | 21,515                 |
| <i>Pteronotus parnellii</i>     | 0.66 [0.04] | 0.66         | 0.73           | 64,803                 |
| <i>Pteronotus gymnonotus</i>    | 0.65 [0.05] | 0.56         | 0.60           | 47,864                 |
| <i>Cynomops</i> sp              | 0.71 [0.06] | 0.66         | 0.78           | 56,869                 |
| <i>Molossus molossus</i>        | 0.73 [0.06] | 0.52         | 0.78           | 71,478                 |
| <i>Molossus bondae</i>          | 0.32 [0.09] | 0.34         | 0.48           | 33,280                 |

Differences in detection among species in function of covariates were strongly supported, models that suggested constant detection received support for two species (Appendix B). *S. bilineata* had the highest predicted detection probability at a given site ( $p = 0.83$ ) while *M. bondae* had the lowest ( $p = 0.32$ ). The most supported model for each species indicated that the probability of detection varied as a function canopy cover or rainfall (Appendix B and Appendix C). The exception were family Mormoopidae, *Pteronotus parnelli* and *P. gymnonotus* where  $p$  when modelled as constant had a better fit. Models where  $p$  varied as a function of rainfall were only supported for two species (*C. brevirostris* and *S. leptura*). Increasing canopy cover was negatively related to detection of six species, while detectability of *C. centralis* was positively associated with canopy cover.

As the most important covariates categories, climatic and land use covariates were included in the best models of ten species, while topography was included in six species (Appendix C and Figure 2). Annual mean temperature (b1) was the most important climatic covariate and exerted positive effect on the occupancy of *P. macrotis*, *S. bilineata*, *N. albiventris*, *Cynomops* sp, while in *C. brevirostris*, *S. leptura* and *P. gymnonotus* had quadratic form with an apparent peak of occupancy from 24 - 27°C (Appendix D). Probability of occupancy modelled as a function of mean diurnal range (b2) was strongly supported for *C. centralis*, *C. brevirostris*, *S. bilineata*, *S. leptura*, *P. gymnonotus* and *M. molossus*. Occupancy models from *P. parnellii* and *P. gymnonotus* included positive effects of precipitation of the coldest quarter (b19). Almost all best models included some land use covariates, except the number persons for area that was unranked in the top models. Mature forest cover had positive effect on occupancy of three aerial insectivorous bats (*C. centralis*, *C. brevirostris* and *N. albiventris*). A decreased of forest cover

(mature and perturbed forest) was associated with an increased occupancy in *S. bilineata*, *S. leptura*, *Cynomops* sp and *M. bondae*, such as mature forest percentage was very important in it latter species. The proportion of pastures had a positive effect on occupancy in *P. macrotis*. The occupancy models for two aerial insectivores bats included the proportion of settlements as an important covariate, one of them with a positive (*M. molossus*) and the other (*P. parnellii*) with a negative sign. The AIC-best model for *P. gymnonotus* did not include any land use covariates, such this covariate type had low relevance for it species. Topographic covariates had an effect in six of eleven species such as second covariate type ranked for explained the occupancy. Slope showed a positive effect on two species (*C. brevirostris* and *P. macrotis*) and negative on *S. leptura*, thus this latter specie is more likely to occupy sites with a gentle topography. Aspect on the landscape, east–west gradient mainly, had effect on occupancy of *P. parnellii* (+), *P. gymnonotus* (-) and *M. molossus* (-).

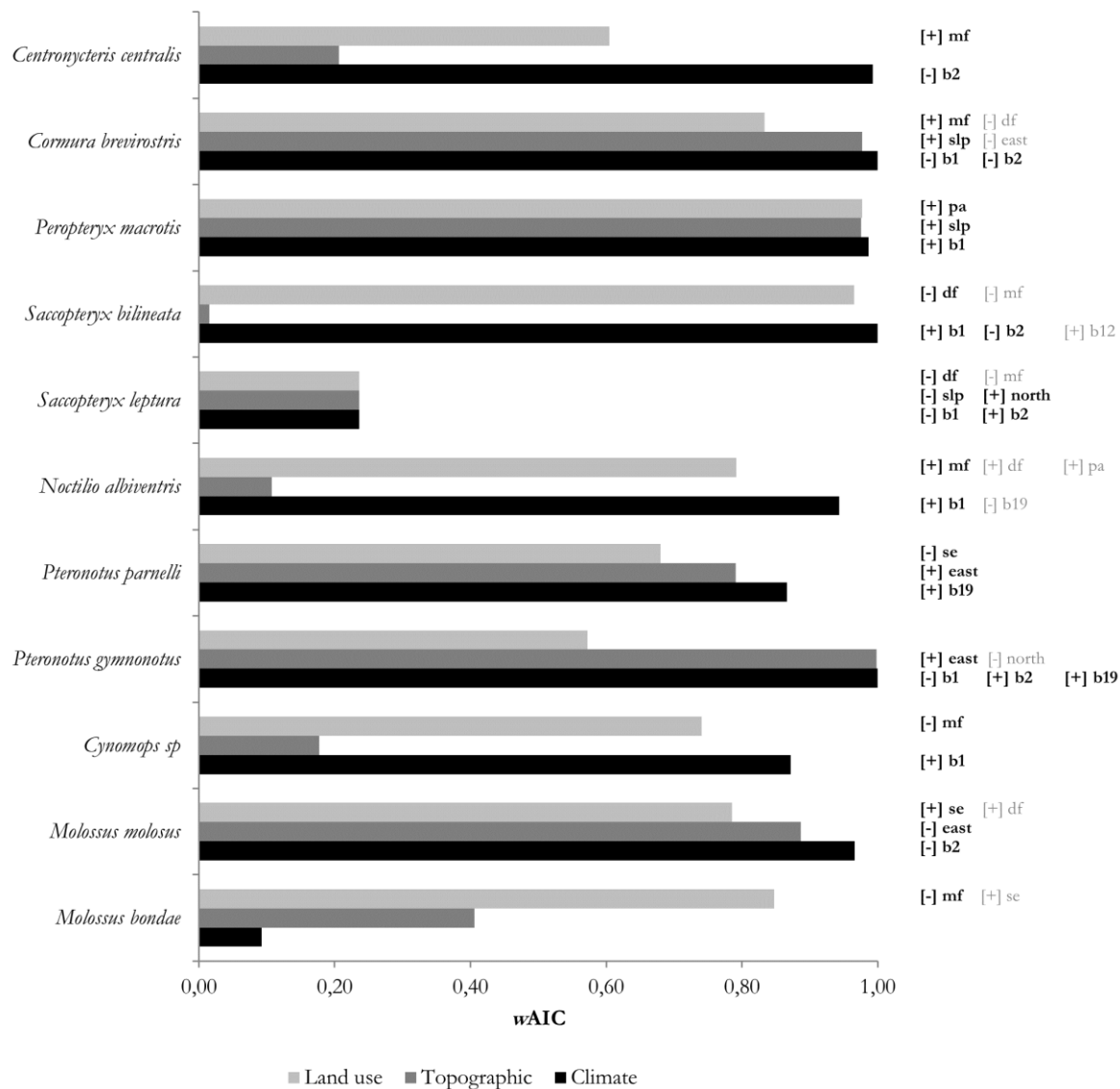


Figure 2. Importance of each covariate type (land use, topographic and climate) on occupancy of eleven aerial insectivorous bats. Label on bars correspond to covariates included in the best models and bold letters show covariates with  $>\sum wAIC$  (see Appendix C).

The estimates of occupancy probability were slightly higher than the detection-naïve estimates of occupancy for nine aerial insectivorous bats species, with values for all species from 0.25 to 0.78 (Table 2). Molossids was family with greater increased in model estimated

occupancy. Thus, the naïve vs. estimated site occupancies were 0.52 vs. 0.78 in the case of *M. molossus* ( $p = 0.73$ ), 0.34 vs. 0.48 ( $p = 0.32$ ) for *M. bondae* and 0.66 vs. 0.78 ( $p = 0.71$ ) for *Cynomops* sp. The main patterns of predicted  $\psi$  and the relationships of  $\psi$  with the dominant covariates were represented in occupancy maps for eleven aerial insectivorous bats shown in Figure 3. According to the occupancy model, the most widespread species in Panama were *M. molossus* and *P. parnellii*, showed a continue distributions which occurred in 95% and 86% of the country, respectively. Two species shown the smaller area of occupancy, *N. albiventris* (mainly distributed on Pacific region) and *C. centralis* (mainly distributed on Caribbean region), those recorded 29% and 33% of Panama area. Areas of predicted *M. bondae* occurrence was main in lowland of the Pacific region, consisting largely of scattered “islands” of high predicted value. The occupancy maps indicates that the probability of presence of *C. brevirostris*, *C. centralis*, *S. bilineata* and *P. gymnonotus* increases in the east and central parts of the study area. Aerial insectivorous bats showed occupancy in almost all country, lowland mainly, except some highland areas to the west of Panama. Only two species, *P. parnellii* and *M. molossus* were predicted distributed in both high and lowlands. “Hotspots” of species richness were located mainly in the center of country on Panama provinces (e.g. Panama Canal Zone), which was predicted as suitable for at least 10 taxa. According to the combined map, 82% of Panama area support a 67% of richness of studied AIBs.

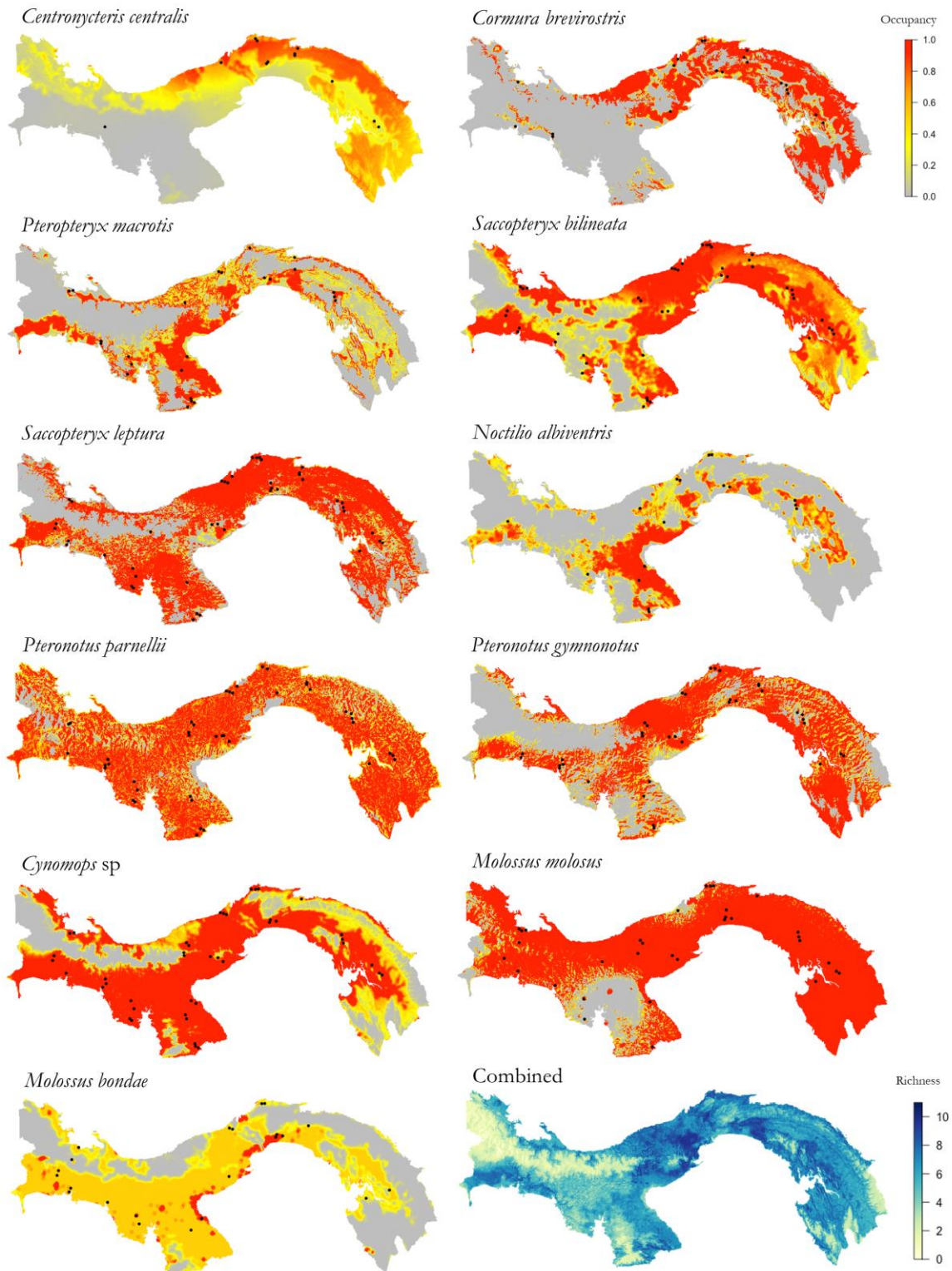


Figure 3. Occupancy maps and richness map of eleven aerial insectivorous bats in Panama. Each dot represents a presence point each species.

## 5. Discussion

Our study shows how acoustic data collected using a spatially and altitudinal stratified random sampling design, and analyzed with statistical approaches that account for imperfect detection next to environmental covariates, provide a robust distributional assessment of aerial insectivorous bats in the Neotropics. The incorporation of detection probability into the modeling procedure acknowledges the fact that hardly any survey detects a species when it is present (Royle, Nichols, & Kéry, 2005). We also determined how ecological covariates such as annual mean temperature, mature forest and exposition explain the occupancy of most AIB species. Finally, we derive spatially-explicit, occupancy models based on covariates, which gives important baseline information for the ecology of the species that possibly be used in conservation, especially of poorly known species such as aerial insectivorous bats (AIB) in the Neotropics.

The species-specific occupancy analysis revealed the need to include corrections for imperfect detection in the modelling process. This need is clearly shown by the remarkable variation of detection probability between different AIB species (range 0.32 – 0.83). Because of this variation in detection probability, the difference between naïve and estimated occupancy also changes substantially for almost all species, with an increment of 7.1 to 50% from naïve to estimated occupancy in nine AIB species. For two species (both Mormoopids) detection probability was

not affected by the covariates used in this study. Possibly, additional fine scale habitat characteristics, which are not available at the national scale, may influence detection probabilities of bats (e.g., percent vegetation clutter at sampling point; Bender, Castleberry, Miller, & Bently Wigley, 2015). Therefore, the opposing result for these two species does not hamper the general finding that not accounting for imperfect detection may yield biased or even incorrect results. Six of eleven species showed negative relation between detectability and canopy cover, corroborating previous studies which showed that bats were not equally detectable in habitat with different vegetation structure, that can be related to echolocation call intensity or habitat use by foraging bats (Bader et al., 2015; Patriquin et al., 2003).

The null model was the least supported for any AIB species so the importance of allowing occupancy and detectability to vary with covariates. Previous studies investigated covariates associations from bioacoustics data in occupancy models for bats (Bader et al., 2015; Bender et al., 2015; Gorresen et al., 2008; Hein, Castleberry, & Miller, 2009). We find evidence that climate, topographic, and land use covariates were important to predict site occupancy of aerial insectivores bats species. Pearson & Dawson (2003) proposed a useful hierarchy framework for show how covariates may affect the distribution of species at different scales. Thus, at the continental scale, climate can be considered the dominant factor, while at more local scales factors including topography and land-cover type become increasingly important for bats (Estrada-Villegas et al., 2012; Gutiérrez-Tapia & Palma, 2016). Even though working only at a regional scale, climate covariates were selected by almost all of our study species. Possibly, the inclusion of a broad elevation gradient (2300 m) partially compensates for the limited spatial extent of our study in relation to climate variables. Climate, in the form of temperature,



precipitation and humidity, can directly impact the mammals metabolic rate, thus influencing its resource requirements and survival (Letcher, 2009). This influence becomes evident in insectivorous bats, because they have low metabolic rate and weight, that have poor thermoregulation, such that some bats can suffer hypo or hyper-thermia when subjected to change drastic than normal temperatures (McCain, 2007; McNab, 1969). Next to these direct consequences, climate exerts additional, indirect effect on mammals by affecting their resources (Letcher, 2009), for instance low temperatures reduce insect abundance and activity (Wolda, 1988). We found occupancy of *P. macrotis*, *S. bilineata*, *N. albiventris* y *Cynomops* sp were highest in areas with highest temperatures, while *P. gymnonotus* and *C. brevirostris* occupied areas mainly with temperatures between 24°C and 28°C, possibly hinting at a narrow physiological comfort zone (Appendix D).

Based on theoretical reflections, land use, reflecting habitat, should be an important covariate category at the regional scale (Pearson & Dawson, 2003). This was supported by our regional (i.e. national) study as land use covariates were included in the top ranked models of most species. In this way our results corroborate the study by Jung & Kalko (2011) who split aerial insectivores bat communities between forest, forest–town interface and urban species, reflecting a gradient of anthropogenic disturbance. The “forest” group contains species exclusively recorded in forested areas, such as *C. centralis* and *P. parnellii*. The second group included bats (*P. macrotis*, *C. brevirostris*, *S. bilineata*, *N. albiventris* and *S. leptura*) that foraged mainly along forest edges and adjacent open areas taking advantage of favorable conditions provided by humans (e.g. street lights). The “urban” group (*Molossus molossus*, *M. bondae* and *Cynomops* sp.) includes species frequently recorded in urban areas with significantly higher activity at urban

sites. Mehr et al. (2011) found that land use is more important to predict assemblages of insectivores bats than climate. He concluded that urban areas were mainly responsible for this pattern, as this land use type affected bat communities most in temperate zones. We showed that *M. bondae* occupancy is negatively related to mature forest percentage and positive related to settlement percentage. Several studies have noted that human settlements and other areas dominated by human activities provide roosts and foraging possibilities for fast-flying bats (Avila-Flores & Fenton, 2005; Bader et al., 2015; Gehrt & Chelsvig, 2004; Hourigan, Johnson, & Robson, 2006; Kirsten Jung & Kalko, 2011).

The final distribution maps obtained through modeling can also be used to apply to the red list criteria where distribution area (criteria B; IUCN, 2001) is often one of the principle criteria to evaluate species (Gärdenfors, Hilton-Taylor, Mace, & Rodríguez, 2001; IUCN, 2001). These distribution models are an advanced type of an area of occupancy (AOO). Our AOO maps reveals those areas with relative high occurrence for a number of species that are poorly known, and poorly detected using traditional methods (e.g., mist nets). For example, *P. parnellii* is a forest-dependent AIB species distributed in 86% the Panama area. This is of potential conservation concern as Panama reported an average annual of 21,491 ha of forest cover loss between 2001 and 2013 (Hansen et al., 2013). Estrada & Coates-Estrada (2002; 2001) suggested that *P. parnellii* traverse long distances through open areas in the landscape, taking advantage of isolated forest fragments and those man-made habitats that most closely resemble the forest in vertical and horizontal complexity. Two species shown a relatively restricted distribution to warm lowland in Panama, *N. albiventris* and *C. centralis*. The latter occupied areas mainly distributed on wet Caribbean region in provinces with highest forest cover percentage (e.g.,

Comarca Emberá-Wounaan, Comarca Kuna Yala, and Darien; ANAM, 2010), it suggested the importance of climate and land use covariates on occupancy for this bat. On the other hand, *N. albiventris*, preferred occupied mainly anthropogenically altered habitats on drier Pacific zone, with lowest forest cover percentage, dominated for towns, pastures and disturbed forests (e.g., Herrera, Los Santos and Coclé; ANAM, 2010).

Conservation efforts require distribution maps that are robust and unbiased (Guillera-Aroita et al., 2015). Many regional and global surveys overlook and fail to incorporate non-detection (MacKenzie, 2006). In Neotropical, distribution maps for most mammals are outdated, collected from a variety of sources and accumulated over time, rendering them inadequate for current conservation efforts. We used random sampling design of acoustic surveys and occupancy modeling to update these maps and investigated some determinants of AIBs occupancy in Panama. We find that failure to incorporate detection probability substantially bias (underestimate) overall area of occupancy. Arroyo-Cabrales *et. al.* (2015) showed to *Centronycteris centralis* as a wide distribution species IUNC-listed as Least Concern, however we evidenced that on considerate scale and extent, this species no was very wide distribute, occupying the 33% area continental of Panama in lowland associated to mature forest. We know that AOO is an important criterion for assigning threatened and endangered status for species globally; although many aerial insectivorous bats are considered at lower risk and Least Concern by the IUCN red list, our result invited evaluated the correct classification of IUCN maps that showed large differences from occupancy maps for some species, such as *Centronycteris centralis* or *Noctilio albiventris*.

## 6. Conclusions

We improved existing knowledge about AIBs distributions while explicitly accounting the detection process, and we showed the influence of climate, topographic and land use covariates in relation to species occurrence. This study suggests that detection probability should be included and considered as a determinant in the distribution of AIBs, in function of covariates which are likely to either be directly physiologically limiting, or to change access to important resources. Climatic was an important factor in limited the distribution AIBs on the scale and extend studied, thus warm lowland increased the occupancy of almost all species. Land use covariates explained the AIBs occupancy, although the strength and direction of those relationships vary among species. Although the occupancy maps (AOO) represent potential distributions, they provide important insights on areas that merit more effective monitoring and conservation concern, and highlight as well, low elevation regions with warm temperatures and anthropogenically altered habitats that likely provide important food and roost to AIBs. For future investigations, we suggest include models of dynamics where temporal variation is incorporated in the modelling of occurrence (e.g., Kéry et al., 2009) for long-term conservation status assessments.

### References

- ANAM. (2010). *Atlas Ambiental de la República de Panamá* (Primera). Editora Novo Art, S.A.
- ANAM. (2014). GEO Panamá 2014, Informe del Estado del Ambiente. *Autoridad Nacional del Ambiente*.
- Angelieri, C. C. S., Adams-Hosking, C., Ferraz, K. M. P. M. de B., de Souza, M. P., & McAlpine, C. A. (2016). Using Species Distribution Models to Predict Potential Landscape Restoration Effects on Puma Conservation. *PLOS ONE*, 11(1), e0145232. <https://doi.org/10.1371/journal.pone.0145232>
- Arroyo-Cabral, J., Miller, B., Reid, F., Cuarón, A. D., & de Grammont, P. C. (2015). *Centronycteris centralis*: The IUCN Red List of Threatened Species 2015: e.T136350A22023809. <https://doi.org/10.2305/IUCN.UK.2015-4.RLTS.T136350A22023809.en>
- Avila-Flores, R., & Fenton, M. B. (2005). Use of spatial features by foraging insectivorous bats in a large urban landscape. *Journal of Mammalogy*, 86(6), 1193-1204. <https://doi.org/10.1644/04-MAMM-A-085R1.1>
- Bader, E., Jung, K., Kalko, E. K. V., Page, R. A., Rodriguez, R., & Sattler, T. (2015). Mobility explains the response of aerial insectivorous bats to anthropogenic habitat change in the Neotropics. *Biological Conservation*, 186, 97-106. <https://doi.org/10.1016/j.biocon.2015.02.028>
- Bender, M. J., Castleberry, S. B., Miller, D. A., & Bently Wigley, T. (2015). Site occupancy of foraging bats on landscapes of managed pine forest. *Forest Ecology and Management*, 336(Supplement C), 1-10. <https://doi.org/10.1016/j.foreco.2014.10.004>

- Bioacoustics Research Program. (2011). Raven Pro: interactive sound analysis software. Version 1.4.
- Bivand, R., Keitt, T., & Rowlingson, B. (2014). rgdal: Bindings for the geospatial data abstraction library. *R package version 0.8-16*.
- Bivand, R., & Lewin-Koh, N. (2013). maptools: Tools for reading and handling spatial objects. *R package version 0.8*, 27.
- Boesch, R., & Obrist, M. (2013). *BatScope - Implementation of a BioAcoustic Taxon Identification Tool*. Birmensdorf, Switzerland: Swiss Federal Research Institute WSL.  
Recuperado a partir de <http://www.batscope.ch>.
- Burnham, K. P., & Anderson, D. (2002). *Model Selection and Multi-Model Inference* (2nd ed.). Springer.
- Calabrese, J. M., Certain, G., Kraan, C., & Dormann, C. F. (2014). Stacking species distribution models and adjusting bias by linking them to macroecological models: Stacking species distribution models. *Global Ecology and Biogeography*, 23(1), 99-112.  
<https://doi.org/10.1111/geb.12102>
- Comte, L., & Grenouillet, G. (2013). Species distribution modelling and imperfect detection: comparing occupancy versus consensus methods. *Diversity and Distributions*, 19(8), 996-1007. <https://doi.org/10.1111/ddi.12078>
- Condit, R. (1998). Ecological implications of changes in drought patterns: shifts in forest composition in Panama. *Climatic Change*, 39(2-3), 413-427.
- Denzinger, A., & Schnitzler, H.-U. (2013). Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Frontiers in Physiology*, 4.  
<https://doi.org/10.3389/fphys.2013.00164>

- Erickson, J. L., & West, S. D. (2002). The Influence of Regional Climate and Nightly Weather Conditions on Activity Patterns of Insectivorous Bats. *Acta Chiropterologica*, 4(1), 17-24. <https://doi.org/10.3161/001.004.0103>
- Estrada, A., & Coates-Estrada, R. (2001). Bat species richness in live fences and in corridors of residual rain forest vegetation at Los Tuxtlas, Mexico. *Ecography*, 24(1), 94-102. <https://doi.org/10.1034/j.1600-0587.2001.240111.x>
- Estrada, A., & Coates-Estrada, R. (2002). Bats in continuous forest, forest fragments and in an agricultural mosaic habitat-island at Los Tuxtlas, Mexico. *Biological Conservation*, 103(2), 237–245.
- Estrada-Villegas, S., McGill, B. J., & Kalko, E. K. (2012). Climate, habitat, and species interactions at different scales determine the structure of a Neotropical bat community. *Ecology*, 93(5), 1183-1193.
- 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. *Biological Conservation*, 143(3), 597-608. <https://doi.org/10.1016/j.biocon.2009.11.009>
- Ferrier, S., & Guisan, A. (2006). Spatial modelling of biodiversity at the community level. *Journal of Applied Ecology*, 43(3), 393-404. <https://doi.org/10.1111/j.1365-2664.2006.01149.x>
- Fiske, I., & Chandler, R. (2011). unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, 43(10), 1-23.
- Gärdenfors, U., Hilton-Taylor, C., Mace, G. M., & Rodríguez, J. P. (2001). The Application of IUCN Red List Criteria at Regional Levels. *Conservation Biology*, 15(5), 1206-1212. <https://doi.org/10.1111/j.1523-1739.2001.00112.x>

- Gaston, K. (1994). *Rarity*. UK: *Chapman & Hall*.
- Gehrt, S. D., & Chelsvig, J. E. (2004). Species-specific patterns of bat activity in an urban landscape. *Ecological Applications*, 14(2), 625–635.
- Gorresen, P. M., Miles, A. C., Todd, C. M., Bonaccorso, F. J., & Weller, T. J. (2008). Assessing bat detectability and occupancy with multiple automated echolocation detectors. *Journal of Mammalogy*, 89(1), 11–17.
- Guillera-Aroita, G., Lahoz-Monfort, J. J., Elith, J., Gordon, A., Kujala, H., Lentini, P. E., ... Wintle, B. A. (2015). Is my species distribution model fit for purpose? Matching data and models to applications: Matching distribution models to applications. *Global Ecology and Biogeography*, 24(3), 276-292. <https://doi.org/10.1111/geb.12268>
- Gutiérrez-Tapia, P., & Palma, R. E. (2016). Integrating phylogeography and species distribution models: cryptic distributional responses to past climate change in an endemic rodent from the central Chile hotspot. *Diversity and Distributions*, 22(6), 638-650. <https://doi.org/10.1111/ddi.12433>
- Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., ... Townshend, J. R. G. (2013). High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science*, 342(6160), 850–853. <https://doi.org/10.1126/science.1244693>
- Hein, C. D., Castleberry, S. B., & Miller, K. V. (2009). Site-occupancy of bats in relation to forested corridors. *Forest Ecology and Management*, 257(4), 1200-1207. <https://doi.org/10.1016/j.foreco.2008.09.054>
- Hijmans, R. J., Phillips, S., Leathwick, J., & Elith, J. (2015). dismo: Species distribution modeling. R package version 1.0-12. *The R Foundation for Statistical Computing, Vienna* <http://cran.r-project.org>.



- Hijmans, R. J., & van Etten, J. (2014). raster: Geographic data analysis and modeling. *R package version*, 2, 15.
- Hourigan, C. L., Johnson, C., & Robson, S. K. A. (2006). The structure of a micro-bat community in relation to gradients of environmental variation in a tropical urban area. *Urban Ecosystems*, 9(2), 67–82.
- Hughes, A. C. (2017). Mapping priorities for conservation in Southeast Asia. *Biological Conservation*, 209, 395-405. <https://doi.org/10.1016/j.biocon.2017.03.007>
- IUCN. (2001). *IUCN Red List Categories and Criteria, Version 3.1. Prepared by the IUCN Species Survival Commission*. IUCN Gland, Switzerland, and Cambridge, United Kingdom.
- Jiménez-Alfaro, B., Draper, D., & Nogués-Bravo, D. (2012). Modeling the potential area of occupancy at fine resolution may reduce uncertainty in species range estimates. *Biological Conservation*, 147(1), 190-196. <https://doi.org/10.1016/j.biocon.2011.12.030>
- Jones, G., Jacobs, D., Kunz, T., Willig, M., & Racey, P. (2009). Carpe noctem: the importance of bats as bioindicators. *Endangered Species Research*, 8, 93-115. <https://doi.org/10.3354/esr00182>
- Jung, K. (2009). *Effects of urbanization on neotropical aerial insectivorous bats*. University of Ulm, Germany, Ulm.
- 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(1), 144-153. <https://doi.org/10.1644/08-MAMM-A-313R.1>
- Jung, K., & Kalko, E. K. V. (2011). Adaptability and vulnerability of high flying Neotropical aerial insectivorous bats to urbanization: Responses of insectivorous bats to urbanization.

- Diversity and Distributions*, 17(2), 262-274. <https://doi.org/10.1111/j.1472-4642.2010.00738.x>
- Jung, K., Kalko, E. K. V., & von Helversen, O. (2007). Echolocation calls in Central American emballonurid bats: signal design and call frequency alternation. *Journal of Zoology*, 272(2), 125-137. <https://doi.org/10.1111/j.1469-7998.2006.00250.x>
- Jung, K., Molinari, J., & Kalko, E. K. V. (2014). Driving Factors for the Evolution of Species-Specific Echolocation Call Design in New World Free-Tailed Bats (Molossidae). *PLoS ONE*, 9(1), e85279. <https://doi.org/10.1371/journal.pone.0085279>
- Kalko, E. K. V., Villegas, S. E., Schmidt, M., Wegmann, M., & Meyer, C. F. J. (2008). Flying high—assessing the use of the aerosphere by bats. *Integrative and Comparative Biology*, 48(1), 60-73. <https://doi.org/10.1093/icb/icn030>
- Karanth, K. K., Nichols, J. D., & Hines, J. E. (2010). Occurrence and distribution of Indian primates. *Biological Conservation*, 143(12), 2891-2899. <https://doi.org/10.1016/j.biocon.2010.02.011>
- Kéry, M. (2011). Towards the modelling of true species distributions: Commentary. *Journal of Biogeography*, 38(4), 617-618. <https://doi.org/10.1111/j.1365-2699.2011.02487.x>
- Kéry, M., Dorazio, R. M., Soldaat, L., Van Strien, A., Zuiderwijk, A., & Royle, J. A. (2009). Trend estimation in populations with imperfect detection. *Journal of Applied Ecology*, 46(6), 1163-1172. <https://doi.org/10.1111/j.1365-2664.2009.01724.x>
- Kéry, M., Gardner, B., & Monnerat, C. (2010). Predicting species distributions from checklist data using site-occupancy models: Distribution modelling from checklists. *Journal of Biogeography*, no-no. <https://doi.org/10.1111/j.1365-2699.2010.02345.x>

- Kéry, M., & Royle, J. A. (2015). *Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 1: Prelude and Static Models*. Academic Press.
- Koshkina, V., Wang, Y., Gordon, A., Dorazio, R. M., White, M., & Stone, L. (2017). Integrated species distribution models: combining presence-background data and site-occupancy data with imperfect detection. *Methods in Ecology and Evolution*, 8(4), 420-430.  
<https://doi.org/10.1111/2041-210X.12738>
- Kunz, T. H., Braun de Torrez, E., Bauer, D., Lobova, T., & Fleming, T. H. (2011). Ecosystem services provided by bats. *Annals of the New York Academy of Sciences*, 1223(1), 1–38.  
<https://doi.org/10.1111/j.1749-6632.2011.06004.x>
- Lahoz-Monfort, J. J., Guillera-Arroita, G., & Wintle, B. A. (2014). Imperfect detection impacts the performance of species distribution models. *Global Ecology and Biogeography*, 23(4), 504-515. <https://doi.org/10.1111/geb.12138>
- Letcher, T. M. (2009). *Climate change: observed impacts on planet Earth* (1st ed). Amsterdam ; Boston: Elsevier.
- MacKenzie, D. I. (2006). *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Access Online via Elsevier.
- MacKenzie, D. I., & Bailey, L. L. (2004). Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics*, 9(3), 300-318.
- McCain, C. M. (2007). Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and Biogeography*, 16(1), 1–13.
- McGill, B. J. (2010). Matters of scale. *Science*, 328(5978), 575–576.

- McNab, B. K. (1969). The economics of temperature regulation in neotropical bats. *Comparative biochemistry and physiology*, 31(2), 227–268.
- Mehr, M., Brandl, R., Hothorn, T., Dziok, F., Förster, B., & Müller, J. (2011). Land use is more important than climate for species richness and composition of bat assemblages on a regional scale. *Mammalian Biology - Zeitschrift Für Säugetierkunde*, 76(4), 451-460.  
<https://doi.org/10.1016/j.mambio.2010.09.004>
- Mendes, P., With, K. A., Signorelli, L., & De Marco, P. (2017). The relative importance of local versus landscape variables on site occupancy in bats of the Brazilian Cerrado. *Landscape Ecology*, 32(4), 745-762. <https://doi.org/10.1007/s10980-016-0483-6>
- Meyer, C. F. J., Aguiar, L., Aguirre, L. F., Baumgarten, J., Clarke, F. M., Cosson, J. F., ... others. (2011). Accounting for detectability improves estimates of species richness in tropical bat surveys. *Journal of Applied Ecology*.
- Miller, R. M., Rodríguez, J. P., Aniskowicz-fowler, T., Bambaradeniya, C., Boles, R., Eaton, M. A., ... Walker, S. (2007). National Threatened Species Listing Based on Iucn Criteria and Regional Guidelines. *Conservation Biology*, 21(3), 684-696.
- Milton, K., & Giacalone, J. (2014). Differential effects of unusual climatic stress on capuchin (*Cebus capucinus*) and howler monkey (*Alouatta palliata*) populations on Barro Colorado Island, Panama. *American Journal of Primatology*, 76(3), 249-261.  
<https://doi.org/10.1002/ajp.22229>
- Patriquin, K. J., Hogberg, L. K., Chruszcz, B. J., & Barclay, R. M. (2003). The influence of habitat structure on the ability to detect ultrasound using bat detectors. *Wildlife Society Bulletin*, 475-481.

- Patten, M. A. (2004). Correlates of species richness in North American bat families. *Journal of Biogeography*, 31(6), 975–985.
- Pearson, R. G., & Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global ecology and biogeography*, 12(5), 361–371.
- Rasband, W. (2012). ImageJ: Image processing and analysis in Java. *Astrophysics Source Code Library*, 1, 06013.
- Razgour, O., Rebelo, H., Di Febbraro, M., & Russo, D. (2016). Painting maps with bats: species distribution modelling in bat research and conservation. *Hystrix, the Italian Journal of Mammalogy*; Vol 27, No 1 (2016): *Species Distribution Models: exploring patterns and processes in mammal ecology* DO - 10.4404/hystrix-27.1-11753. Recuperado a partir de <http://www.italian-journal-of-mammalogy.it/article/view/11753>
- Rodríguez-Aguilar, G., Orozco-Lugo, C. L., Vleut, I., & Vazquez, L.-B. (2017). Influence of urbanization on the occurrence and activity of aerial insectivorous bats. *Urban Ecosystems*, 20(2), 477-488. <https://doi.org/10.1007/s11252-016-0608-3>
- Rota, C. T., Fletcher, R. J., Evans, J. M., & Hutto, R. L. (2011). Does accounting for imperfect detection improve species distribution models? *Ecography*, 34(4), 659-670. <https://doi.org/10.1111/j.1600-0587.2010.06433.x>
- Royle, J. A., Nichols, J. D., & Kéry, M. (2005). Modelling occurrence and abundance of species when detection is imperfect. *Oikos*, 110(2), 353-359. <https://doi.org/10.1111/j.0030-1299.2005.13534.x>
- Russo, D., Maiorano, L., Rebelo, H., & Preatoni, D. G. (2016). Distribution Models: exploring patterns and processes in mammal ecology. *Hystrix, the Italian Journal of Mammalogy*,

- 27(1). Recuperado a partir de <http://www.italian-journal-of-mammalogy.it/article/view/12101>
- Rydell, J., Arita, H. T., Santos, M., & Granados, J. (2002). Acoustic identification of insectivorous bats (order Chiroptera) of Yucatan, Mexico. *Journal of Zoology*, 257(1), 27-36. <https://doi.org/10.1017/S0952836902000626>
- Sattler, T., Bontadina, F., Hirzel, A. H., & Arlettaz, R. (2007). Ecological niche modelling of two cryptic bat species calls for a reassessment of their conservation status. *Journal of Applied Ecology*, 44(6), 1188-1199.
- Schnitzler, H.-U., & Kalko, E. K. V. (2001). Echolocation by Insect-Eating Bats. *BioScience*, 51(7), 557-569. [https://doi.org/10.1641/0006-3568\(2001\)051\[0557:EBIEB\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0557:EBIEB]2.0.CO;2)
- Wang, H. G., Owen, R. D., Sánchez-Hernández, C., & De Lourdes Romero-Almaraz, M. (2003). Ecological characterization of bat species distributions in Michoacán, México, using a geographic information system. *Global Ecology and Biogeography*, 12(1), 65–85.
- Weber, M. de M., & Grelle, C. E. V. (2012). Does environmental suitability explain the relative abundance of the tailed tailless bat, *Anoura caudifer*? *Natureza & Conservação*, 10(2), 221-227. <https://doi.org/10.4322/natcon.2012.035>
- Wolda, H. (1988). Insect seasonality: why? *Annual review of ecology and systematics*, 19(1), 1-18.
- Yates, M. D., & Muzika, R. M. (2006). Effect of Forest Structure and Fragmentation on Site Occupancy of Bat Species in Missouri Ozark Forests. *Journal of Wildlife Management*, 70(5), 1238-1248. [https://doi.org/10.2193/0022-541X\(2006\)70\[1238:EOFSAF\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2006)70[1238:EOFSAF]2.0.CO;2)

## Appendix

Appendix A. Example of the a-priori models calculated for aerial insectivores bats from Panama,

*Peropteryx macrotis* in this case. Abbreviations in Table 1

| No.        | Candidates models ( $\sim p$ covariates $\sim \psi$ covariates) | Comments                       |
|------------|-----------------------------------------------------------------|--------------------------------|
| Step No. 1 |                                                                 |                                |
| 1          | $p(.)\Psi(.)$                                                   | Model null                     |
| Step No. 2 |                                                                 |                                |
| 2          | $p(rf)\Psi(.)$                                                  |                                |
| 3          | $p(cc)\Psi(.)$                                                  |                                |
| 4          | $p(rf+cc)\Psi(.)$                                               |                                |
| 5          | $p(rf^2)\Psi(.)$                                                |                                |
| 6          | $p(cc^2)\Psi(.)$                                                | Best model selected step No. 2 |
| 7          | $p(rf^2+cc^2)\Psi(.)$                                           |                                |
| Step No. 3 |                                                                 |                                |
| 8          | $p(cc^2)\Psi(b1)$                                               | Best model selected step No. 3 |
| 9          | $p(cc^2)\Psi(b2)$                                               |                                |
| 10         | $p(cc^2)\Psi(b12)$                                              |                                |
| 11         | $p(cc^2)\Psi(b19)$                                              |                                |
| 12         | $p(cc^2)\Psi(b1+b2)$                                            |                                |
| 13         | $p(cc^2)\Psi(b1+b12)$                                           |                                |
| 14         | $p(cc^2)\Psi(b1+b19)$                                           |                                |
| 15         | $p(cc^2)\Psi(b2+b12)$                                           |                                |
| 16         | $p(cc^2)\Psi(b2+b19)$                                           |                                |
| 17         | $p(cc^2)\Psi(b12+b19)$                                          |                                |
| 18         | $p(cc^2)\Psi(b1+b2+b12)$                                        |                                |
| 19         | $p(cc^2)\Psi(b1+b2+b19)$                                        |                                |
| 20         | $p(cc^2)\Psi(b1+b12+b19)$                                       |                                |
| 21         | $p(cc^2)\Psi(b2+b12+b19)$                                       |                                |
| 22         | $p(cc^2)\Psi(b1^2)$                                             |                                |
| 23         | $p(cc^2)\Psi(b2^2)$                                             |                                |
| 24         | $p(cc^2)\Psi(b12^2)$                                            |                                |
| 25         | $p(cc^2)\Psi(b19^2)$                                            |                                |
| 26         | $p(cc^2)\Psi(b1^2+b2^2)$                                        |                                |
| 27         | $p(cc^2)\Psi(b1^2+b12^2)$                                       |                                |
| 28         | $p(cc^2)\Psi(b1^2+b19^2)$                                       |                                |
| 29         | $p(cc^2)\Psi(b2^2+b12^2)$                                       |                                |
| 30         | $p(cc^2)\Psi(b2^2+b19^2)$                                       |                                |
| 31         | $p(cc^2)\Psi(b12^2+b19^2)$                                      |                                |

| No.        | Candidates models ( $\sim p$ covariates $\sim \psi$ covariates) | Comments                       |
|------------|-----------------------------------------------------------------|--------------------------------|
| 32         | $p(cc^2)\Psi(b1^2 + b2^2 + b12^2)$                              |                                |
| 33         | $p(cc^2)\Psi(b1^2 + b2^2 + b19^2)$                              |                                |
| 34         | $p(cc^2)\Psi(b1^2 + b12^2 + b19^2)$                             |                                |
| 35         | $p(cc^2)\Psi(b2^2 + b12^2 + b19^2)$                             |                                |
| 36         | $p(cc^2)\Psi(b1 * b2)$                                          |                                |
| Step No. 4 |                                                                 |                                |
| 37         | $p(cc^2)\Psi(slp)$                                              |                                |
| 38         | $p(cc^2)\Psi(east)$                                             |                                |
| 39         | $p(cc^2)\Psi(north)$                                            |                                |
| 40         | $p(cc^2)\Psi(slp + east)$                                       |                                |
| 41         | $p(cc^2)\Psi(slp + north)$                                      |                                |
| 42         | $p(cc^2)\Psi(east + north)$                                     |                                |
| 43         | $p(cc^2)\Psi(b1 + slp)$                                         |                                |
| 44         | $p(cc^2)\Psi(b1 + east)$                                        |                                |
| 45         | $p(cc^2)\Psi(b1 + north)$                                       |                                |
| 46         | $p(cc^2)\Psi(b1 + slp + east)$                                  |                                |
| 47         | $p(cc^2)\Psi(b1 + slp + north)$                                 |                                |
| 48         | $p(cc^2)\Psi(b1 + east + north)$                                |                                |
| 49         | $p(cc^2)\Psi(b1 + slp^2)$                                       |                                |
| 50         | $p(cc^2)\Psi(b1 + east^2)$                                      |                                |
| 51         | $p(cc^2)\Psi(b1 + north^2)$                                     |                                |
| 52         | $p(cc^2)\Psi(b1 + slp^2 + east^2)$                              |                                |
| 53         | $p(cc^2)\Psi(b1 + slp^2 + north^2)$                             |                                |
| 54         | $p(cc^2)\Psi(b1 + east^2 + north^2)$                            |                                |
| 55         | $p(cc^2)\Psi(b1 * slp)$                                         | Best model selected step No. 4 |
| Step No. 5 |                                                                 |                                |
| 56         | $p(cc^2)\Psi(df)$                                               |                                |
| 57         | $p(cc^2)\Psi(mf)$                                               |                                |
| 58         | $p(cc^2)\Psi(pa)$                                               |                                |
| 59         | $p(cc^2)\Psi(se)$                                               |                                |
| 60         | $p(cc^2)\Psi(pd)$                                               |                                |
| 61         | $p(cc^2)\Psi(df + mf)$                                          |                                |
| 62         | $p(cc^2)\Psi(df + pa)$                                          |                                |
| 63         | $p(cc^2)\Psi(df + se)$                                          |                                |
| 64         | $p(cc^2)\Psi(df + pd)$                                          |                                |
| 65         | $p(cc^2)\Psi(mf + pa)$                                          |                                |
| 66         | $p(cc^2)\Psi(mf + se)$                                          |                                |
| 67         | $p(cc^2)\Psi(mf + pd)$                                          |                                |
| 68         | $p(cc^2)\Psi(pa + se)$                                          |                                |
| 69         | $p(cc^2)\Psi(pa + pd)$                                          |                                |
| 70         | $p(cc^2)\Psi(se + pd)$                                          |                                |



| No. | Candidates models ( $\sim p$ covariates $\sim \psi$ covariates) | Comments |
|-----|-----------------------------------------------------------------|----------|
| 71  | $p(cc^2)\Psi(df + mf + pa)$                                     |          |
| 72  | $p(cc^2)\Psi(df + mf + se)$                                     |          |
| 73  | $p(cc^2)\Psi(df + mf + pd)$                                     |          |
| 74  | $p(cc^2)\Psi(df + pa + se)$                                     |          |
| 75  | $p(cc^2)\Psi(df + pa + pd)$                                     |          |
| 76  | $p(cc^2)\Psi(df + se + pd)$                                     |          |
| 77  | $p(cc^2)\Psi(mf + pa + se)$                                     |          |
| 78  | $p(cc^2)\Psi(mf + pa + pd)$                                     |          |
| 79  | $p(cc^2)\Psi(mf + se + pd)$                                     |          |
| 80  | $p(cc^2)\Psi(pa + se + pd)$                                     |          |
| 81  | $p(cc^2)\Psi(df^2)$                                             |          |
| 82  | $p(cc^2)\Psi(mf^2)$                                             |          |
| 83  | $p(cc^2)\Psi(pa^2)$                                             |          |
| 84  | $p(cc^2)\Psi(se^2)$                                             |          |
| 85  | $p(cc^2)\Psi(pd^2)$                                             |          |
| 86  | $p(cc^2)\Psi(df^2 + mf^2)$                                      |          |
| 87  | $p(cc^2)\Psi(df^2 + pa^2)$                                      |          |
| 88  | $p(cc^2)\Psi(df^2 + se^2)$                                      |          |
| 89  | $p(cc^2)\Psi(df^2 + pd^2)$                                      |          |
| 90  | $p(cc^2)\Psi(mf^2 + pa^2)$                                      |          |
| 91  | $p(cc^2)\Psi(mf^2 + se^2)$                                      |          |
| 92  | $p(cc^2)\Psi(mf^2 + pd^2)$                                      |          |
| 93  | $p(cc^2)\Psi(pa^2 + se^2)$                                      |          |
| 94  | $p(cc^2)\Psi(pa^2 + pd^2)$                                      |          |
| 95  | $p(cc^2)\Psi(se^2 + pd^2)$                                      |          |
| 96  | $p(cc^2)\Psi(df^2 + mf^2 + pa^2)$                               |          |
| 97  | $p(cc^2)\Psi(df^2 + mf^2 + se^2)$                               |          |
| 98  | $p(cc^2)\Psi(df^2 + mf^2 + pd^2)$                               |          |
| 99  | $p(cc^2)\Psi(df^2 + pa^2 + se^2)$                               |          |
| 100 | $p(cc^2)\Psi(df^2 + pa^2 + pd^2)$                               |          |
| 101 | $p(cc^2)\Psi(df^2 + se^2 + pd^2)$                               |          |
| 102 | $p(cc^2)\Psi(mf^2 + pa^2 + se^2)$                               |          |
| 103 | $p(cc^2)\Psi(mf^2 + pa^2 + pd^2)$                               |          |
| 104 | $p(cc^2)\Psi(mf^2 + se^2 + pd^2)$                               |          |
| 105 | $p(cc^2)\Psi(pa^2 + se^2 + pd^2)$                               |          |
| 106 | $p(cc^2)\Psi(b1 * slp + df)$                                    |          |
| 107 | $p(cc^2)\Psi(b1 * slp + mf)$                                    |          |
| 108 | $p(cc^2)\Psi(b1 * slp + pa)$                                    |          |
| 109 | $p(cc^2)\Psi(b1 * slp + se)$                                    |          |
| 110 | $p(cc^2)\Psi(b1 * slp + pd)$                                    |          |
| 111 | $p(cc^2)\Psi(b1 * slp + df + mf)$                               |          |
| 112 | $p(cc^2)\Psi(b1 * slp + df + pa)$                               |          |

| No. | Candidates models ( $\sim p$ covariates $\sim \psi$ covariates) | Comments                      |
|-----|-----------------------------------------------------------------|-------------------------------|
| 113 | $p(cc^2)\Psi(b1 * slp + df + se)$                               |                               |
| 114 | $p(cc^2)\Psi(b1 * slp + df + pd)$                               |                               |
| 115 | $p(cc^2)\Psi(b1 * slp + mf + pa)$                               |                               |
| 116 | $p(cc^2)\Psi(b1 * slp + mf + se)$                               |                               |
| 117 | $p(cc^2)\Psi(b1 * slp + mf + pd)$                               |                               |
| 118 | $p(cc^2)\Psi(b1 * slp + pa + se)$                               |                               |
| 119 | $p(cc^2)\Psi(b1 * slp + pa + pd)$                               |                               |
| 120 | $p(cc^2)\Psi(b1 * slp + se + pd)$                               |                               |
| 121 | $p(cc^2)\Psi(b1 * slp + df + mf + pa)$                          |                               |
| 122 | $p(cc^2)\Psi(b1 * slp + df + mf + se)$                          |                               |
| 123 | $p(cc^2)\Psi(b1 * slp + df + mf + pd)$                          |                               |
| 124 | $p(cc^2)\Psi(b1 * slp + df + pa + se)$                          |                               |
| 125 | $p(cc^2)\Psi(b1 * slp + df + pa + pd)$                          |                               |
| 126 | $p(cc^2)\Psi(b1 * slp + df + se + pd)$                          |                               |
| 127 | $p(cc^2)\Psi(b1 * slp + mf + pa + se)$                          |                               |
| 128 | $p(cc^2)\Psi(b1 * slp + mf + pa + pd)$                          |                               |
| 129 | $p(cc^2)\Psi(b1 * slp + mf + se + pd)$                          |                               |
| 130 | $p(cc^2)\Psi(b1 * slp + pa + se + pd)$                          |                               |
| 131 | $p(cc^2)\Psi(b1 * slp + df^2)$                                  |                               |
| 132 | $p(cc^2)\Psi(b1 * slp + mf^2)$                                  |                               |
| 133 | $p(cc^2)\Psi(b1 * slp + pa^2)$                                  | Best final model (step No. 5) |
| 134 | $p(cc^2)\Psi(b1 * slp + se^2)$                                  |                               |
| 135 | $p(cc^2)\Psi(b1 * slp + pd^2)$                                  |                               |
| 136 | $p(cc^2)\Psi(b1 * slp + df^2 + mf^2)$                           |                               |
| 137 | $p(cc^2)\Psi(b1 * slp + df^2 + pa^2)$                           |                               |
| 138 | $p(cc^2)\Psi(b1 * slp + df^2 + se^2)$                           |                               |
| 139 | $p(cc^2)\Psi(b1 * slp + df^2 + pd^2)$                           |                               |
| 140 | $p(cc^2)\Psi(b1 * slp + mf^2 + pa^2)$                           |                               |
| 141 | $p(cc^2)\Psi(b1 * slp + mf^2 + se^2)$                           |                               |
| 142 | $p(cc^2)\Psi(b1 * slp + mf^2 + pd^2)$                           |                               |
| 143 | $p(cc^2)\Psi(b1 * slp + pa^2 + se^2)$                           |                               |
| 144 | $p(cc^2)\Psi(b1 * slp + pa^2 + pd^2)$                           |                               |
| 145 | $p(cc^2)\Psi(b1 * slp + se^2 + pd^2)$                           |                               |
| 146 | $p(cc^2)\Psi(b1 * slp + df^2 + mf^2 + pa^2)$                    |                               |
| 147 | $p(cc^2)\Psi(b1 * slp + df^2 + mf^2 + se^2)$                    |                               |
| 148 | $p(cc^2)\Psi(b1 * slp + df^2 + mf^2 + pd^2)$                    |                               |
| 149 | $p(cc^2)\Psi(b1 * slp + df^2 + pa^2 + se^2)$                    |                               |
| 150 | $p(cc^2)\Psi(b1 * slp + df^2 + pa^2 + pd^2)$                    |                               |
| 151 | $p(cc^2)\Psi(b1 * slp + df^2 + se^2 + pd^2)$                    |                               |
| 152 | $p(cc^2)\Psi(b1 * slp + mf^2 + pa^2 + se^2)$                    |                               |
| 153 | $p(cc^2)\Psi(b1 * slp + mf^2 + pa^2 + pd^2)$                    |                               |

| No. | Candidates models ( $\sim p$ covariates $\sim \psi$ covariates) | Comments |
|-----|-----------------------------------------------------------------|----------|
| 154 | $p(cc^2)\Psi(b1 * slp + mf^2 + se^2 + pd^2)$                    |          |
| 155 | $p(cc^2)\Psi(b1 * slp + pa^2 + se^2 + pd^2)$                    |          |
| 156 | $p(cc^2)\Psi(b1 * slp * pa^2)$                                  |          |
| 157 | $p(cc^2)\Psi(b1 + slp * pa^2)$                                  |          |
| 158 | $p(cc^2)\Psi(b1 * slp * pa)$                                    |          |
| 159 | $p(cc^2)\Psi(b1 + slp * pa)$                                    |          |

Appendix B. Final top ranked model(s) ( $\Delta AIC < 2$ ) for predicting occupancy of aerial insectivores bats in Panama.  $wAIC$  is the AIC model weight,  $nPars$  is the number of parameters in the model,  $\Delta AIC$  is the difference in values between lowest AIC model and each model, and  $c-hat$  is a variance inflation factor. Abbreviations in Table 1.

| Species                         | Top ranked model(s)                              | wAIC | Model AIC | nPars | $\Delta AIC$ | c-hat |
|---------------------------------|--------------------------------------------------|------|-----------|-------|--------------|-------|
| <i>Centronycteris centralis</i> | $p(cc)\Psi(b2+mf)$                               | 0.07 | 81.48     | 5     | 0.00         | 0.3   |
|                                 | $p(cc)\Psi(b2+df+mf+pa)$                         | 0.06 | 81.80     | 7     | 0.32         |       |
|                                 | $p(cc)\Psi(b2+df+mf)$                            | 0.06 | 81.85     | 6     | 0.36         |       |
|                                 | $p(cc)\Psi(b2+pa)$                               | 0.05 | 82.10     | 5     | 0.61         |       |
|                                 | $p(cc)\Psi(b2)$                                  | 0.04 | 82.81     | 4     | 1.33         |       |
|                                 | $p(cc)\Psi(b2+mf+pa)$                            | 0.04 | 82.96     | 6     | 1.47         |       |
|                                 | $p(cc)\Psi(b2+north)$                            | 0.03 | 83.18     | 5     | 1.69         |       |
|                                 | $p(cc)\Psi(b2+mf^2)$                             | 0.03 | 83.24     | 6     | 1.75         |       |
|                                 | $p(cc)\Psi(b2+pa^2)$                             | 0.03 | 83.29     | 6     | 1.81         |       |
|                                 | $p(cc)\Psi(b2+mf+pd)$                            | 0.03 | 83.45     | 6     | 1.96         |       |
|                                 | $p(cc)\Psi(b2^2+b19^2)$                          | 0.03 | 83.46     | 7     | 1.98         |       |
| <i>Cormura brevirostris</i>     | $p(rf^2)\Psi(b1^2+b2^2*slp+east+df^2+mf^2)$      | 0.12 | 133.58    | 15    | 0.00         | 0.95  |
|                                 | $p(rf^2)\Psi(b1^2+b2^2+slp+east+df^2+mf^2)$      | 0.11 | 133.65    | 14    | 0.07         |       |
|                                 | $p(rf^2)\Psi(b1^2*b2^2+slp+east+df^2+mf^2)$      | 0.09 | 134.06    | 15    | 0.48         |       |
|                                 | $p(rf^2)\Psi(b1^2*b2^2*slp+east+df^2*mf^2)$      | 0.09 | 134.15    | 16    | 0.57         |       |
|                                 | $p(rf^2)\Psi(b1^2+b2^2+slp+east+df^2+mf^2+se^2)$ | 0.07 | 134.74    | 16    | 1.16         |       |
| <i>Peropteryx macrotis</i>      | $p(cc^2)\Psi(b1*slp+pa^2)$                       | 0.43 | 155.60    | 9     | 0.00         | 1.58  |
|                                 | $p(cc^2)\Psi(b1*slp+pa)$                         | 0.22 | 156.95    | 8     | 1.35         |       |
| <i>Saccapteryx bilineata</i>    | $p(cc)\Psi(b1+b2+b12+df+mf+se)$                  | 0.23 | 170.48    | 9     | 0            | 2.09  |
|                                 | $p(cc)\Psi(b1+b2+b12+df+mf+pd)$                  | 0.11 | 172.02    | 9     | 1.54         |       |
| <i>Saccopteryx leptura</i>      | $p(rf^2)\Psi(b1^2+b2^2+slp^2+north^2+df+mf)$     | 0.23 | 172.60    | 14    | 0            | 1.18  |
|                                 | $p(rf^2)\Psi(b1^2+b2^2+slp^2+north^2+df+mf+se)$  | 0.10 | 174.24    | 15    | 1.65         |       |
|                                 | $p(rf^2)\Psi(b1^2+b2^2+slp^2+north^2+df+mf+pd)$  | 0.09 | 174.36    | 15    | 1.76         |       |
|                                 | $p(rf^2)\Psi(b1^2+b2^2+slp^2+north^2+df+mf+pa)$  | 0.09 | 174.51    | 15    | 1.92         |       |
| <i>Noctilio albiventris</i>     | $p(cc^2)\Psi(b1+b19+df*mf+pa)$                   | 0.07 | 124.65    | 10    | 0.00         | 1.23  |
|                                 | $p(cc^2)\Psi(b1+b19+df+mf+pa)$                   | 0.04 | 125.51    | 9     | 0.85         |       |

| Species                      | Top ranked model(s)                             | wAIC | Model AIC | nPars | ΔAIC | c-hat |
|------------------------------|-------------------------------------------------|------|-----------|-------|------|-------|
| <i>Pteronotus parnelli</i>   | $p(cc^2)\Psi(b1+b19+df^2+mf^2+pa^2)$            | 0.04 | 125.72    | 12    | 1.06 | 2.06  |
|                              | $p(cc^2)\Psi(b1+b19+mf^2)$                      | 0.03 | 126.13    | 8     | 1.47 |       |
|                              | $p(cc^2)\Psi(b1+b19+df^2*mf^2+pa^2)$            | 0.03 | 126.23    | 13    | 1.58 |       |
|                              | $p(cc^2)\Psi(b1*b19+df*mf+pa)$                  | 0.03 | 126.30    | 11    | 1.64 |       |
|                              | $p(cc^2)\Psi(b1+b19+df+mf*pa)$                  | 0.03 | 126.59    | 10    | 1.93 |       |
|                              | $p(.)\Psi(b19*east^2+se)$                       | 0.11 | 210.76    | 7     | 0.00 | 2.06  |
|                              | $p(.)\Psi(b19*east^2+se+pd)$                    | 0.07 | 211.76    | 8     | 0.99 |       |
|                              | $p(.)\Psi(b19*east^2)$                          | 0.05 | 212.15    | 6     | 1.39 |       |
|                              | $p(.)\Psi(b19*east^2+pa+se)$                    | 0.05 | 212.24    | 8     | 1.48 |       |
|                              | $p(.)\Psi(b19*east^2+mf+se)$                    | 0.05 | 212.27    | 8     | 1.51 |       |
|                              | $p(.)\Psi(b19*east^2*se)$                       | 0.05 | 212.33    | 8     | 1.57 |       |
|                              | $p(.)\Psi(b19*east^2+df+se)$                    | 0.04 | 212.66    | 8     | 1.90 |       |
|                              | $p(.)\Psi(b19*east^2+se^2)$                     | 0.04 | 212.76    | 8     | 2.00 |       |
| <i>Pteronotus gymnonotus</i> | $p(.)\Psi(b1^2*b2^2*b19^2+east+north)$          | 0.19 | 192.32    | 12    | 0.00 | 3.01  |
|                              | $p(.)\Psi(b1^2*b2^2*b19^2+east*north)$          | 0.13 | 192.98    | 13    | 0.66 |       |
|                              | $p(.)\Psi(b1^2*b2^2*b19^2+east+north+pd^2)$     | 0.10 | 193.48    | 14    | 1.17 |       |
|                              | $p(.)\Psi(b1^2*b2^2*b19^2*east+north)$          | 0.10 | 193.54    | 13    | 1.22 |       |
|                              | $p(.)\Psi(b1^2*b2^2*b19^2+east+north+pa+se+pd)$ | 0.09 | 193.79    | 15    | 1.47 |       |
|                              | $p(.)\Psi(b1^2*b2^2*b19^2+east+north+mf^2)$     | 0.08 | 193.94    | 14    | 1.63 |       |
|                              | $p(.)\Psi(b1^2*b2^2*b19^2+east+north+pd)$       | 0.08 | 194.10    | 13    | 1.79 |       |
|                              | $p(.)\Psi(b1^2*b2^2*b19^2+east+north+mf)$       | 0.07 | 194.14    | 13    | 1.83 |       |
|                              | $p(.)\Psi(b1^2*b2^2*b19^2+east+north+se)$       | 0.07 | 194.28    | 13    | 1.96 |       |
| <i>Cynomops sp</i>           | $p(cc^2)\Psi(b1+mf)$                            | 0.10 | 208.48    | 6     | 0.00 | 0.7   |
|                              | $p(cc^2)\Psi(b1+df)$                            | 0.06 | 209.51    | 6     | 1.03 |       |
|                              | $p(cc^2)\Psi(b1)$                               | 0.05 | 209.88    | 5     | 1.40 |       |
|                              | $p(cc^2)\Psi(b1+df+mf)$                         | 0.05 | 209.99    | 7     | 1.52 |       |
|                              | $p(cc^2)\Psi(b1+mf^2)$                          | 0.05 | 210.06    | 7     | 1.58 |       |
|                              | $p(cc^2)\Psi(b1+df+pa)$                         | 0.04 | 210.13    | 7     | 1.65 |       |
|                              | $p(cc^2)\Psi(b1*df)$                            | 0.04 | 210.16    | 7     | 1.68 |       |
|                              | $p(cc^2)\Psi(b1+mf+pa)$                         | 0.04 | 210.18    | 7     | 1.70 |       |
|                              | $p(cc^2)\Psi(b1+north)$                         | 0.04 | 210.36    | 6     | 1.88 |       |
|                              | $p(cc^2)\Psi(b1*mf)$                            | 0.04 | 210.44    | 7     | 1.97 |       |
|                              | $p(cc^2)\Psi(b1+mf+pd)$                         | 0.04 | 210.48    | 7     | 2.00 |       |

| Species                  | Top ranked model(s)                                             | wAIC | Model AIC | nPars | ΔAIC | c-hat |
|--------------------------|-----------------------------------------------------------------|------|-----------|-------|------|-------|
| <i>Molossus molossus</i> | p(cc <sup>2</sup> )Ψ(b2 <sup>2</sup> +east <sup>2</sup> +df+se) | 0.23 | 186.42    | 10    | 0.00 | 0.68  |
|                          | p(cc <sup>2</sup> )Ψ(b2 <sup>2</sup> +east <sup>2</sup> +se)    | 0.20 | 186.73    | 9     | 0.31 |       |
|                          | p(cc <sup>2</sup> )Ψ(b2 <sup>2</sup> +east <sup>2</sup> +se+pd) | 0.10 | 188.10    | 10    | 1.68 |       |
| <i>Molossus bondae</i>   | p(cc)Ψ(mf+se)                                                   | 0.05 | 158.04    | 5     | 0.00 | 0.42  |
|                          | p(cc)Ψ(df+mf+pa)                                                | 0.05 | 158.10    | 6     | 0.07 |       |
|                          | p(cc)Ψ(mf+se+pd)                                                | 0.04 | 158.69    | 6     | 0.65 |       |
|                          | p(cc)Ψ(slp+se+pd)                                               | 0.03 | 158.96    | 6     | 0.92 |       |
|                          | p(cc)Ψ(mf+se*pd)                                                | 0.03 | 159.03    | 7     | 0.99 |       |
|                          | p(cc)Ψ(slp+se)                                                  | 0.03 | 159.11    | 5     | 1.07 |       |
|                          | p(cc)Ψ(se+pd)                                                   | 0.03 | 159.23    | 5     | 1.19 |       |
|                          | p(cc)Ψ(se)                                                      | 0.03 | 159.32    | 4     | 1.28 |       |
|                          | p(cc)Ψ(slp+mf+se)                                               | 0.03 | 159.45    | 6     | 1.41 |       |
|                          | p(cc)Ψ(mf*se)                                                   | 0.03 | 159.52    | 6     | 1.48 |       |
|                          | p(cc)Ψ(slp+df+mf+pa)                                            | 0.02 | 159.64    | 7     | 1.60 |       |
|                          | p(cc)Ψ(mf)                                                      | 0.02 | 159.65    | 4     | 1.61 |       |
|                          | p(cc)Ψ(df+mf*pa)                                                | 0.02 | 159.68    | 7     | 1.64 |       |
|                          | p(cc)Ψ(slp+mf+se+pd)                                            | 0.02 | 159.91    | 7     | 1.87 |       |
|                          | p(cc)Ψ(mf+pa+se)                                                | 0.02 | 159.99    | 6     | 1.95 |       |
|                          | p(cc)Ψ(df+mf+se)                                                | 0.02 | 159.99    | 6     | 1.95 |       |

Appendix C. Parameter from the final top models for aerial insectivores bats from Panama. Abbreviations in Table 1.

| Species                         | Parameters | Detectability |       | Occupancy |       |      |       |             |       |       |              |       |       | No. models evaluated |       |     |
|---------------------------------|------------|---------------|-------|-----------|-------|------|-------|-------------|-------|-------|--------------|-------|-------|----------------------|-------|-----|
|                                 |            | cc            | rf    | Climate   |       |      |       | Topographic |       |       | Land use (%) |       |       |                      |       |     |
|                                 |            |               |       | b1        | b2    | b12  | b19   | slp         | east  | north | mf           | df    | pa    |                      | se    |     |
| <i>Centronycteris centralis</i> | β          | 1.94          |       |           | -1.67 |      |       |             |       |       |              | 0.72  |       |                      | 169   |     |
|                                 | SE         | 0.59          |       |           | 0.63  |      |       |             |       |       |              | 0.40  |       |                      |       |     |
|                                 | ΣwAIC      |               |       |           | 0.99  |      |       |             |       |       |              | 0.40  |       |                      |       |     |
| <i>Cormura brevirostris</i>     | β          |               | -0.29 | -28.96    | -2.18 |      |       | 7.98        | -0.06 |       |              | 9.85  | -4.86 |                      | 204   |     |
|                                 | SE         |               | 0.17  | 21.94     | 1.56  |      |       | 4.89        | 0.78  |       |              | 5.64  | 2.79  |                      |       |     |
|                                 | ΣwAIC      |               |       | 1.00      | 1.00  |      |       | 0.97        | 0.93  |       |              | 0.71  | 0.68  |                      |       |     |
| <i>Peropteryx macrotis</i>      | β          | -0.31         |       | 18.24     |       |      |       | 0.76        |       |       |              |       |       | 1.63                 | 161   |     |
|                                 | SE         | 0.30          |       | 10.07     |       |      |       | 1.57        |       |       |              |       |       | 1.10                 |       |     |
|                                 | ΣwAIC      |               |       | 0.99      |       |      |       | 0.97        |       |       |              |       |       | 0.90                 |       |     |
| <i>Saccopteryx bilineata</i>    | β          | -0.30         |       | 0.90      | -2.40 | 0.67 |       |             |       |       |              | -2.64 | -2.07 |                      | -1.30 | 157 |
|                                 | SE         | 0.26          |       | 0.97      | 0.82  | 0.53 |       |             |       |       |              | 1.22  | 0.91  |                      | 0.60  |     |
|                                 | ΣwAIC      |               |       | 1.00      | 1.00  | 0.99 |       |             |       |       |              | 0.56  | 0.63  |                      | 0.59  |     |
| <i>Saccopteryx leptura</i>      | β          |               | 0.59  | -8.00     | 6.10  |      |       | -5.08       |       | 3.87  |              | -3.27 | -3.28 |                      |       | 161 |
|                                 | SE         |               | 0.54  | 3.87      | 2.74  |      |       | 2.26        |       | 1.84  |              | 1.80  | 1.34  |                      |       |     |
|                                 | ΣwAIC      |               |       | 1.00      | 1.00  |      |       | 1.00        |       | 1.00  |              | 0.57  | 0.78  |                      |       |     |
| <i>Noctilio albiventris</i>     | β          | -0.75         |       | 5.91      |       |      | -0.93 |             |       |       |              | 5.36  | 5.66  | 4.61                 |       | 187 |
|                                 | SE         | 0.46          |       | 2.50      |       |      | 0.68  |             |       |       |              | 2.50  | 2.43  | 2.11                 |       |     |
|                                 | ΣwAIC      |               |       | 0.93      |       |      | 0.89  |             |       |       |              | 0.64  | 0.58  | 0.59                 |       |     |
| <i>Pteronotus parnelli</i>      | β          |               |       |           |       | 2.82 |       |             | 5.28  |       |              |       |       |                      | -5.26 | 162 |
|                                 | SE         |               |       |           |       | 1.83 |       |             | 3.21  |       |              |       |       |                      | 4.47  |     |
|                                 | ΣwAIC      |               |       |           |       | 0.97 |       |             | 0.88  |       |              |       |       |                      | 0.56  |     |
| <i>Pteronotus</i>               | β          |               |       | -6.56     | 0.34  |      | 0.34  |             | 2.12  | -2.40 |              |       |       |                      |       | 160 |

| Species                                                                                                        | Parameters | Detectability |    | Occupancy |       |     |      |             |       |       |              |       |    | No. models evaluated |     |
|----------------------------------------------------------------------------------------------------------------|------------|---------------|----|-----------|-------|-----|------|-------------|-------|-------|--------------|-------|----|----------------------|-----|
|                                                                                                                |            | cc            | rf | Climate   |       |     |      | Topographic |       |       | Land use (%) |       |    |                      |     |
|                                                                                                                |            |               |    | b1        | b2    | b12 | b19  | slp         | east  | north | mf           | df    | pa |                      | se  |
| gymnonotus                                                                                                     | SE         |               |    | 4.56      | 1.14  |     | 0.77 |             | 0.97  | 1.34  |              |       |    |                      |     |
|                                                                                                                | ΣwAIC      |               |    | 1.00      | 1.00  |     | 1.00 |             | 1.00  | 0.99  |              |       |    |                      |     |
| Cynomops<br>sp                                                                                                 | β          | -0.81         |    | 2.82      |       |     |      |             |       |       |              | -1.57 |    |                      | 156 |
|                                                                                                                | SE         | 0.26          |    | 1.44      |       |     |      |             |       |       |              | 0.77  |    |                      |     |
|                                                                                                                | ΣwAIC      |               |    | 0.86      |       |     |      |             |       |       |              | 0.47  |    |                      |     |
| Molossus<br>molossus                                                                                           | β          | -1.06         |    |           | -6.77 |     |      |             | -3.97 |       |              | 1.46  |    | 19.23                | 168 |
|                                                                                                                | SE         | 0.27          |    |           | 5.01  |     |      |             | 2.89  |       |              | 1.17  |    | 15.48                |     |
|                                                                                                                | ΣwAIC      |               |    |           | 0.95  |     |      |             | 0.83  |       |              | 0.30  |    | 0.66                 |     |
| Molossus<br>bondae                                                                                             | β          | -0.33         |    |           |       |     |      |             |       |       |              | -0.78 |    | 2.40                 | 161 |
|                                                                                                                | SE         | 0.27          |    |           |       |     |      |             |       |       |              | 0.46  |    | 2.41                 |     |
|                                                                                                                | ΣwAIC      |               |    |           |       |     |      |             |       |       |              | 0.53  |    | 0.51                 |     |
| Standard errors (SE) for final top models and the sum of weights AIC for all models evaluated for each species |            |               |    |           |       |     |      |             |       |       |              |       |    |                      |     |

Standard errors (SE) for final top models and the sum of weights AIC for all models evaluated for each species



*Appendix D.* Expected site occupancy of AIB in Panama, as a function of annual mean temperature (°C) for those species in which this variable was in the top-ranked model set. Gray lines represent the 95% confidence interval around these estimates.

