Bats and their bat flies: community composition and host specificity on a Pacific island archipelago

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Bats and their ectoparasites are excellent model organisms to assess the conservation status of protected areas because both groups are speciose, and bats can be particularly affected by land use changes. The majority of bat studies conducted in Panama are clustered in protected areas around the Isthmus of Panama, while protected areas outside the Isthmus have not been studied in depth or remain largely unexplored. Coiba National Park is located on the Pacific coast of the country and is the fourth largest national park in Panama. Despite its distinct isolation from the mainland and the periodic dry spells it has undergone during the last 25,000 years, Coiba National Park has highly preserved forests. We provide the first study that assesses the structure of the bat assemblage of Coiba National Park, describe echolocation calls of some of its aerial insectivorous species, and contribute the first species list of ectoparasitic bat flies (Diptera: Streblidae). Using mist nets and acoustic monitoring techniques, we identified 30 bat species from 904 captures and 751 recordings. *Artibeus jamaicensis* and *Carollia perspicillata* were the most abundant species captured, while *Myotis nigricans*, *Saccopteryx leptura* and *Molossus bondae* were the most frequently recorded aerial insectivores. Associated with the bats we also identified 22 species of streblid flies, all representing new records for Coiba National Park. The host specificity was 98.2%, a high value compared to studies in other areas of Latin America. In total, we found eight new bat species for Coiba National Park, increasing the species list to 39, making it, with a rather limited study effort, the National Park with the fourth highest bat species richness recorded in Panama. We reckon that such levels of richness are correlated with the highly preserved forests of Coiba National Park.

Key words: biodiversity monitoring, national parks, Central America, protected areas

INTRODUCTION

Monitoring bat assemblages through space and time is an ideal approach to assess the conservation status of protected areas (Kalko, 1998; Rex *et al*., 2008). Bats are a suitable proxy to evaluate overall conservation status because bats are highly speciose (Kalko *et al*., 1996), show a widely differentiated sensitivity to habitat transformation (Fenton *et al*., 1992; Meyer and Kalko, 2008), and provide important ecosystem services (e.g. insect predation or seed dispersal, Kunz, 2011). In the Neotropics, bat monitoring depends largely on the use of mist nets because the speciose New World leaf-nosed bat family (Phyllostomidae) is easily captured with this method, and captures can provide direct information

on species' relative abundances and general bat biology (Kalko *et al*., 1996; Kunz *et al*., 2009). Despite the importance and widespread use of mist nests to assess bat assemblages, aerial insectivorous bats, another diverse and important group of bats, are rarely captured with this technique (O'Farrell and Gannon, 1999; Barnett *et al*., 2006; MacSwiney *et al*., 2008). Additionally, most bat surveys fail to assess bat ectoparasites, an understudied, yet crucial aspect of bat ecology (Wibbelt *et al*., 2009). Sampling bat ectoparasites, along with other information from captures (e.g., body mass), can provide information on animal health (Linhares and Komeno, 2000), and offers insight whether host specificity changes between protected and unprotected areas (Bruyndonckx *et al*., 2009). Therefore,

robust bat monitoring programs should combine complementary methodologies that sample across bat guilds, including acoustic methods to detect aerial insectivorous bats, and assess the specific relationships between bat species and their ectoparasites (Wibbelt *et al.*, 2009; Meyer *et al.*, 2015). Even though ultrasonic bat detectors have facilitated acoustic monitoring, and despite the fact that parasites are usually collected from captured bats, very few studies simultaneously report capture, acoustic and ectoparasite data from protected areas.

Bat sampling has a long history in Panama, but sampling has not been evenly distributed across the country. The bat assemblage of the Barro Colorado Nature Monument, in the Lake Gatún area of Panama, is one of the most studied bat assemblages in the world. Bat studies at the Barro Colorado Nature Monument began in the 1950s, and intensive and consecutive surveys started in 1975 (Kalko *et al.*, 1996). The latest account tallies 76 species on just 5,400 hectares (Kalko *et al.*, 2008). At a larger spatial scale, bat inventories employing mist nets and acoustic surveys have been conducted in other protected areas along the Isthmus of Panama. There have been inventories in San Lorenzo National Park, on the northern portion of the Isthmus (Weise, 2007), on the smaller islands and peninsulas around Barro Colorado Island (Meyer and Kalko, 2008), in Soberanía National Park (Samudio and Carrion de Samudio, 1989), in Chagres National Park (Samudio, personal communication), and in Metropolitano Natural Park, on the southern side of the Isthmus (Samudio *et al.*, 1998). Acoustic monitoring of aerial insectivorous bats has also been conducted across the Isthmus (Jung and Kalko, 2011; Estrada-Villegas *et al.*, 2012), and a recent study by Bader *et al.* (2015) assessed aerial insectivorous bats in 14 areas across the country. Despite these studies, much less is known about the bat diversity of other protected areas in Panama. This omission needs to be remedied because Panama, with approximately 9% of all bat species in the world (119 bat species in Panama — Moras *et al.*, 2018; Samudio and Pino, 2018; 1,364 bat species in the world — Tsang *et al.*, 2015) within 0.05% of the world's land area, bridges Mesoamerican ecosystems with South American ecosystems, and much of the Panamanian bat diversity outside of the Isthmus of Panama remains largely unexplored.

Research on bat ectoparasites in Panama mirrors the uneven distribution of bat inventories across the country. The only extensive investigation on bat ectoparasites from Panama was conducted by Wenzel *et al.* (1966) in a large scale survey of vertebrate ectoparasites across the country. Bat flies (Nycteribiidae and Streblidae) are the most conspicuous bat ectoparasites (Dick and Patterson, 2007). They are obligate blood feeders and usually associated with a single bat host species, or primary host (Dick and Gettinger, 2005; Dick, 2007). After Wenzel's research in the 1960s, there were only two studies on bat ectoparasites in Panama; one described the life history of *Megistopoda aranea,* a bat fly of the Jamaican fruit-eating bat, *Artibeus jamaicensis* (Overal, 1980), and the other showed that higher ectoparasite load was associated with the expression level of some alleles of the Major Histocompatibility Complex (MHC) genes in the lesser bulldog bat, *Noctilio albiventris* (Schad *et al.*, 2012). The study of bat ectoparasites in Panama is limited and much remains to be researched.

The bats of Coiba National Park (CNP), the fourth largest national park in Panama, were initially inventoried by Ibáñez *et al.* (1997). Using both mist nets and acoustic sampling, they recorded 30 species comprising seven families, but did not provide information on species' relative abundances. At that time, Coiba was both a national park and a large penitentiary facility with several inmate camps throughout the island. Since the closure and abandonment of the penitentiary facilities in 2004, there has not been any comprehensive bat sampling in CNP. Therefore, the purpose of this study was to provide a baseline dataset on the structure of the bat assemblage and provide the first list of bat flies (Streblidae) in CNP. We describe the echolocation calls of new species found in CNP, and compare our results with those from Ibáñez *et al.* (1997) and other bat studies across Panama.

MATERIALS AND METHODS

Study Site

Coiba National Park (CNP) is located on the Pacific coast of the Veraguas province, on the south-eastern border of the Gulf of Chiriquí, Republic of Panama. It became a protected area in 1991, while Coiba Island was still used as a penitentiary. All Coiba penitentiaries were finally shut down in 2004. In 2002 the CNP became part of the 'Pacific Biological Corridor' that spans from Galapagos (Ecuador) to Cocos Island (Costa Rica) (Guzman *et al.*, 2004). The CNP has 270,125 ha, of which 53,582 ha are distributed among 30 islets and nine main islands of which Coiba is the largest (50,314 ha), followed by Jicarón (1,868 ha). Isla Ranchería (also known as Isla Coibita) has 222 ha (Ibáñez, 2011). The CNP receives an average rainfall of 3,403 mm yr⁻¹, and as such is classified as tropical wet forest, according to the Holdridge life zone classification (Holdridge, 1967). The CNP has a biotemperature of 25.1ºC, and shows

a marked dry season from December to April (Ibáñez, 2011). The western portion of the island can receive up to 6,000 mm rainfall per year, making it a tropical wet premontane forest (Ibáñez, 2011). The topography of Coiba is heavily influenced by the Central Fault of Coiba, which runs north-west to southeast (Kolarsky and Mann, 1995). This creates two mountain ridges parallel to the fault, with the highest point of the island (416 m) located two kilometers north of the fault. The CNP was part of the continent when sea levels were 100 to 120 m below current levels in the late Pleistocene (15,000–18,000 yr) (Cardiel *et al*., 1997). The physiognomy of the forest has been affected not only by the isolation from the continent, but also by strong dry spells in Central Panama (25,000–10,000 yr and 8,200–5,500 yr — Bush *et al*., 1992). For example, plant diversity is on average 30% lower on Coiba than on the mainland, which is just 25 km away (Ibáñez, 2011). During the 20ᵗʰ century, various areas of Coiba were used by inmates to raise cattle and for sustainable agriculture, especially on the eastern side of the island between Punta Esquina and Punta Damas, along the Bahia Damas, and along Ensenada de María. In these areas, the forest was completely cleared for cattle ranching, and horses, along with water buffalos, were introduced. In Playa Hermosa there was also forest clearing for agriculture. We would expect that the bat assemblage in these areas, which are the ones easily accessible by boat, reflect the type of forest where we were able to sample. Nonetheless, more than 80% of the island has not experienced any recent human intervention, and thus it is highly conserved (Ibáñez, 2011).

Surveys

Our surveys were part of a three-week intensive biodiversity survey on the islands of Coiba, Jicarón and Ranchería from 2 February to 23 February 2015 (Fig. 1). We sampled the first two islands because they are the largest islands in the park and the third island because it was easily accessible. These three islands were also sampled by Ibáñez *et al*. (1997). We sampled during 14 nights at 13 sites, with a total netting effort of 527 mist net hours (mnh), and 38 hours of acoustic sampling (Table 1). One mnh was defined as one 6-m long and 2.5-m height mist net open for 1 h (Meyer and Kalko, 2008). We calculated the capture rate as a standard measure of relative abundance by dividing the number of bats captured by the number of mnh. Relative abundance is then provided as number of bats per 100 mnh (Meyer and Kalko, 2008). Recaptures were identified by their wing membrane samples (see below) and recaptures of the same night were excluded from data analysis.

We sampled a variety of habitat types including forested areas that were anthropogenically modified (e.g., secondary forests), beach shores, and pristine forested areas within a few hundred meters from the shore. We were limited in our ability to access the interior of the island, as most of the trails and roads that once provided access to the central portion of the island are now covered by thick regrowth. However, one access trail was cut to access the highest point of the island and allowed us to sample four kilometers inland. Five of our sampling sites overlapped with those from Ibáñez *et al*. (1997): Santa Cruz trail, Playa Blanca, Playa Hermosa, Jicaron north 1, and Rancheria. For each mist netting night, we deployed between four and nine mist nets and located them ad libitum and over streams to maximize capture success. Even though canopy mist nets can sample a complementary set of species (Kalko and Handley, 2001),

we did not employ them due to logistical constraints of the rapid biodiversity assessment.

Captured bats were weighed, measured and handled following standardized protocols (Handley *et al*., 1991). All capture and sampling procedures were licensed and approved by the Smithsonian Tropical Research Institute (IACUC protocol: 2015-0206-2018) and the government of Panama (Autoridad Nacional del Ambiente de Panamá: SE/APH-1-15). Wing membrane samples and ectoparasites were collected and stored for each bat individually in separate vials with 96% ethanol. We identified bats with two dichotomous keys (Timm and LaVal, 1998; Handley *et al*., unpublished). Bat taxonomy followed Simmons (2005), with the following exceptions: (i) we used *Dermanura* for the smaller *Artibeus*, as suggested by Hoofer *et al*. (2008), (ii) we used *Uroderma convexum* instead of *U. bilobatum* following Cuadrado-Ríos and Mantilla-Meluk (2016), (iii) we follow the distribution of *Cynomops greenhalli* as provided by Gardner (2007), (iv) and we follow Baird *et al*. (2008) for the distribution of *Rhogeessa tumida* for western Panama. Finally, Ibáñez *et al*. (1997) reported *Micronycteris megalotis* for the CNP but we follow Simmons (2005) and treat *M. megalotis* as *Micronycteris microtis,* given its current geographical distribution. We also used *Lampronycteris brachyotis* and *Vampyressa thyone* instead of *Micronycteris brachyotis* and *Vampyressa pusilla* (Simmons, 2005).

We acoustically sampled aerial insectivorous bats during 12 out of the 14 capture nights. To do so, we created a sampling transect with 4–8 recording stations, usually 50 m apart from each other. Recording stations did not overlap with the location of the mist nets. On each recording station, we recorded all bats heard during five-minute intervals. We started sampling between 18:00 and 18:30, and did between 2 to 6 rounds throughout the transects except in Boca Grande and Jicarón north 1, where we sampled from a boat and because of battery failure, respectively. In some cases, we extended the five-minute interval if there was particularly high bat activity. Because different sampling intervals can produce a sampling bias, we kept a detailed record of the recording time at each recording station to accurately calculate bat activity. We used a Pettersson-D1000x bat detector (sample rate: 384 kHz, 16 bit — Pettersson Electronic AG, Uppsala, Sweden;), and recorded all the bats we heard through the heterodyne system while scanning frequencies between 20–100 kHz. We set the pre-trigger time and post-trigger time for three and five seconds, respectively.

Data Analysis

We compared our pooled capture and acoustic sampling data (see below for acoustic data analysis) with the species accumulation curves published by Ibáñez *et al*. (1997). To do so, we first extracted the data points from Ibáñez *et al*. (1997) by digitizing the accumulation curve (see Fig. 3 in Ibáñez *et al*., 1997) using Plot Digitizer v2.6.8 (Huwaldt, 2015). Second, we calculated our species accumulation curves with presence/absence data for Phyllostomidae, non-Phyllostomidae and all species combined, using the function specaccum as implemented in the package vegan (Oksanen *et al*., 2011) for R ver. 3.3.1 (R Core Team, 2016). We acknowledge that accumulation curves should be scaled in terms of individuals (Gotelli and Colwell, 2001). However, we refrained from doing so to simplify comparisons with Ibáñez *et al*. (1997). Sampling effort in their curves is represented as sampling days not sampled individuals. Finally, we joined the digitized data from Ibáñez *et al*.
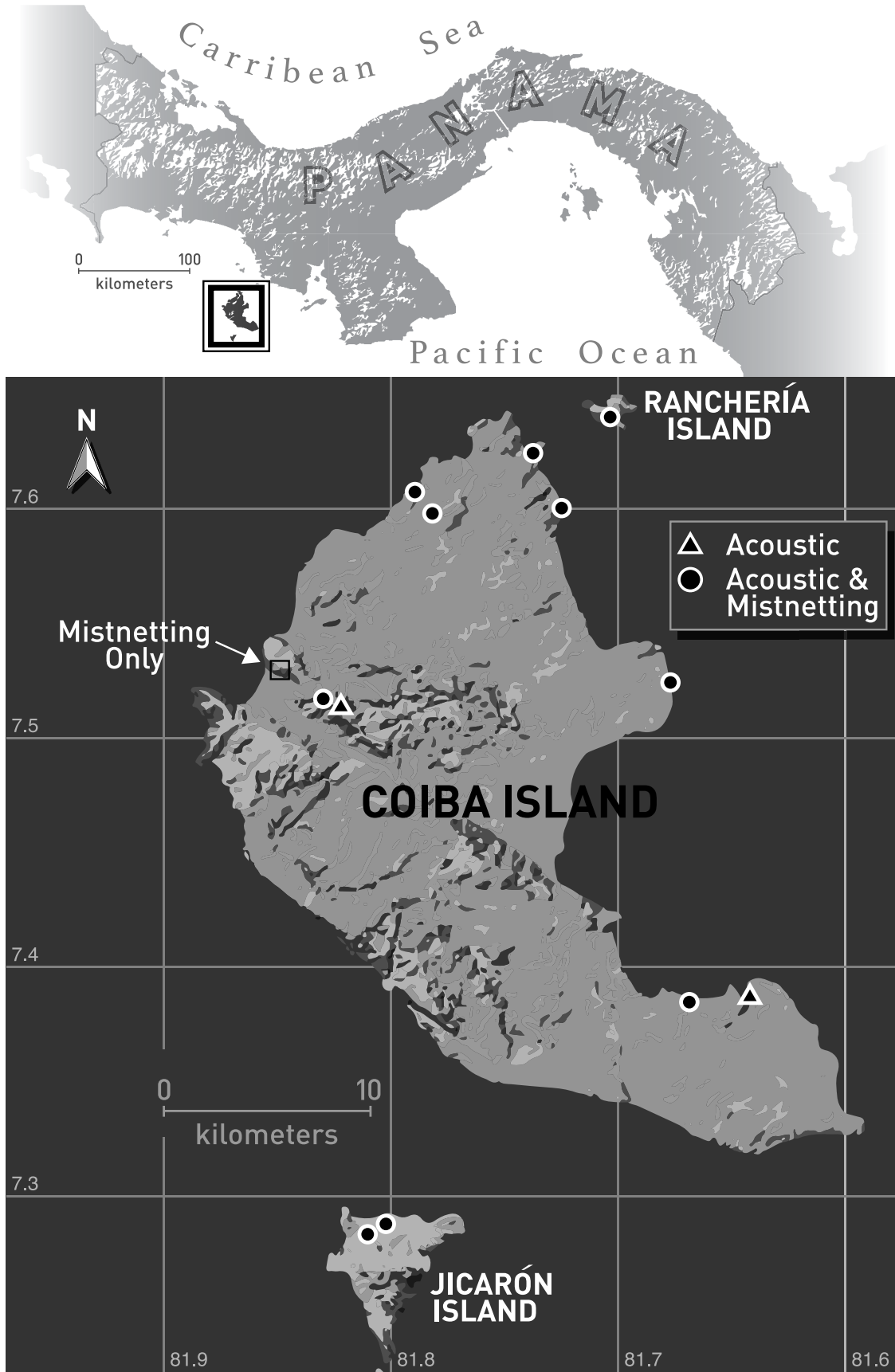
F<small>IG</small>. 1. Map of sampling locations across Coiba National Park

TABLE 1. Sampling locations and sampling efforts of bat mist netting and acoustic monitoring across 13 sites in Coiba National Park. The ratio between total number of recordings and recordings used to identify bats is a measure of how many recordings had to be excluded from our analysis. mnh — mist net hour

Island	Netting/Recording location	Coordinates		Mist net sampling effort (mnh)	Number of captures	Acoustic sampling effort (hours)	Number of recordings (total/with ID bats)
		°N	°W				
Coiba	Santa Cruz trail	7.624398	-81.737643	88	68	6.0	102/43
	Los Monos trail	7.600682	-81.725021	77	42	3.5	42/21
	Punta Damas north	7.524141	-81.676925	50	27	3.5	203/178
	Playa Blanca	7.385387	-81.668725	112	174	3.5	138/125
	Boca Grande	7.386439	-81.642327	NA	NA	1.0	25/20
	Playa Hermosa	7.529695	-81.848931	29	113	NA	NA
	Cerro La Torre	7.517062	-81.829515	23	105	4.0	113/101
	Cerro La Torre 2[a]	7.607517	-81.789221	NA	NA	3.0	98/70
	Rio Escondido 1	7.513904	-81.822612	27	29	4.0	38/30
	Rio Escondido 2	7.607517	-81.789220	33	65	4.5	53/39
Jicarón	Jicarón north 1	7.284681	-81.809462	38	42	0.5	27/13
	Jicarón north 2	7.288421	-81.804065	25	42	3.0	100/92
Ranchería	Ranchería	7.639958	-81.703645	27	198	1.5	14/9

[a] — Sampling conducted from the top of an abandoned communication tower on the highest point of the island

(1997) and our accumulation curve. For the Phyllostomidae curve we used all 14 capture nights, but for the all species' curve, we used 12 nights to harmonize the presence/absence data of aerial insectivorous bats with the capture data. We took care that during the harmonization we did not lose any of the new records for CNP. We also used the first order jackknife estimator for presence/absence data to calculate the expected number of species according to our sample. This estimator is commonly used in bat assemblage studies (Meyer *et al.*, 2015). As a proxy for the relative abundance of the species we captured bats in CNP, we summed the relative abundance per species across all sites, and plotted the relative abundance for all bats. Statistical comparisons between sites were not possible due to lack of replicas.

To identify aerial insectivorous species and calculate their relative activity, we analyzed sound recordings with Avisoft SASLab Pro, version 5.2.10 (Raimund Specht, Avisoft, Germany). We followed four steps to identify species. First, we generated spectrograms using a Flat Top window with a 512 FFT, a 100% frame size and an overlap of 75%. These features gave us a frequency resolution of 750 Hz and a temporal resolution of 0.01667 ms. Second, we used the spectrograms to determine the number of bat passes, which are defined as a succession of more than two echolocation pulses emitted by a bat as it flies near the observer (Fenton, 2004). We excluded recordings with very faint bat passes or passes with undistinguishable call shape (Table 1). Third, we manually assigned species identification to each bat pass by measuring pulse duration, pulse interval, peak frequency and terminal frequency. We also typified the shape of the call and identified the harmonic with the highest energy. Measurements were generally made on the calls with the lowest amount of background noise and echo and on the strongest harmonic. For species identification, we used a reference library created for the bats of Barro Colorado Nature Monument (E. K. V. Kalko, unpublished and used in Estrada-Villegas *et al.*, 2010) and additional echolocation call literature on species from Central America and northern South America (Ibáñez *et al.*, 1997; O'Farrell and Miller, 1997, 1999; Ochoa *et al.*, 2000, Ibáñez *et al.*, 2002; Rydell *et al.*, 2002; Jung *et al.*, 2007; MacSwiney *et al.*, 2008; Surlykke and Kalko, 2008;

Kraker-Castañeda *et al.*, 2013; Jung *et al.*, 2014; Bader *et al.*, 2015). We acknowledge that some recordings of *Rhogeessa tumida* could have been erroneously identified as *Myotis nigricans* because their echolocation calls are likely to be similar in shape and peak frequency (Estrada-Villegas *et al.*, 2012). Then, we calculated spectral and temporal parameters for those aerial insectivorous bats that were not acoustically sampled or were not recorded by Ibáñez *et al.* (1997). We used the aforementioned spectral and temporal parameters and used the Automatic Parameter Measurement tool from Avisoft SASLab Pro, to calculate call duration, call interval, minimum frequency at the start of the call, minimum frequency at the end of the call, and peak frequency. Finally, we calculated an index of relative activity for aerial insectivorous bats by dividing the number of bat passes per species by the number of hours sampled per sampling site (Law *et al.*, 1999). The index of relative activity allowed us to quantify which species were recorded more often than others, which can be a descriptive measure for relative abundance. As a proxy for the structure of the aerial insectivorous bats in CNP, we summed the indices of relative activity per species across all sites, and plotted the relative indices for all aerial insectivorous bats.

Finally, we identified all collected bat flies to species level based on published keys (Wenzel *et al.*, 1966; Wenzel, 1976; Guerrero, 1993, 1994*a*, 1994*b*, 1995*a*, 1995*b*, 1996, 1997, 1998). Despite the age of publication, these keys are the conventional standard to identify bat flies because they provide detailed and extensive morphological descriptions. We also used other sources to complement species identification (e.g. Miller and Tschapka, 2001; Dick, 2013). We omitted sampled bat flies from our analysis if they were collected from bat hosts not identified to species level. Based on all collected streblid bat flies, we calculated a specificity index (SI) taking the percentage of total bat fly individuals of a single species found on each bat host (Dick and Gettinger, 2005). We then built an interaction web of all bat hosts with their corresponding bat flies using the function plotweb as implemented in the bipartite package (Dormann *et al.*, 2009) for R v3.3.1 (R Core Team, 2016). The datasets analyzed in the current study are available in the figshare repository (10.6084/m9.figshare.5033468).

RESULTS

We captured 904 bats and recorded 751 bat passes, tallying 30 species from five families across the CNP. Twenty-eight species were identified for the island of Coiba, and 13 for both the islands of Jicarón and Ranchería (Table 2). *Artibeus jamaicensis*, *Carollia perspicillata*, *Glossophaga soricina* and *Phyllostomus discolor* were captured on all three islands. *Saccopteryx leptura*, *Myotis nigricans* and *Lasiurus blossevilli* were detected acoustically on all the islands. Only *Pteronotus parnellii* was captured and recorded on Coiba and Jicarón, but not on Ranchería. Several species are new records for CNP and for specific islands. From the capture data, and based on the size and shape of the upper incisors, we identified a *Glossophaga* cf. *commissarisi* as a new record for CNP and for Coiba. An upcoming study will allow us to corroborate our field identification of *G.* cf. *commissarisi*. *Micronycteris hirsuta* is a new record for Jicarón and *Platyrrhinus helleri* is a new record for Ranchería. From the species that were detected acoustically, *Balantiopteryx* cf. *plicata*, *Diclidurus albus*, *Pteropteryx macrotis*

TABLE 2. List of bat species of Coiba National Park broken down by island. We compare our results (2015) with those from Ibáñez *et al.* (1997). C — captures, A — acoustically detected, ? — possible detection. New species for the Park in bold

Family	Species	Coiba		Jicarón		Ranchería	
		1997	2015	1997	2015	1997	2015
Emballonuridae	**Balantiopteryx cf. plicata**		A				
	Diclidurus albus	?	A				
	Peropteryx macrotis		A				
	Saccopteryx bilineata	CA	A			A	
	S. leptura	CA	A	A	A	A	A
Noctilionidae	*Noctilio albiventris*	CA	A				
	N. leporinus	CA	CA	CA	A	CA	
Mormoopidae	*Pteronotus davyi*	CA	A	A	A	A	
	P. parnellii	CA	CA	CA	CA	CA	
Phyllostomidae	*Artibeus jamaicensis*	C	C	C	C	C	C
	A. lituratus	C	C			C	C
	Carollia perspicillata	C	C	C	C	C	C
	Centurio senex					C	
	Chiroderma villosum	C	C	C		C	
	Dermanura cinerea[a]	?					
	Desmodus rotundus	C					
	Glossophaga cf. commissarisi		C				
	G. soricina	C	C	C	C	C	C
	Lichonycteris obscura	C					
	Lonchophylla robusta	C	C	C			
	Lampronycteris brachyotis	C					
	Micronycteris hirsuta	C			C		
	M. microtis	C	C	C			
	Phyllostomus discolor	C	C	C	C	C	C
	Platyrrhinus helleri	C	C	C			C
	Tonatia saurophila	C	C	C	C	C	
	Uroderma convexum	C	C	C		C	C
	Vampyressa thyone	C	C				
	Vampyrum spectrum	C				C	
Natalidae	*Natalus stramineus*	C					
Vespertilionidae	*Lasiurus blossevillii*		A		A	C	A
	Myotis nigricans	C?	A	C?	A		A
	Rhogeessa tumida	C?				C?	
Molossidae	**Cynomops cf. greenhalli**		A				
	Eumops cf. glaucinus		A		A		A
	Molossus coibensis	CA	A	A		CA	
	M. cf. bondae		A				A
	M. cf. rufus		A				A
Total		28	28	16	13	18	13

[a] — *Dermanura cinerea* was captured on another island of CNP and may be expected to occur also on Coiba Island

and *Cynomops* cf. *greenhalli* are new records for CNP and for Coiba. *Eumops* cf. *glaucinus* is also a new record for the Park and found on all the islands. Likewise, *Molossus* cf. *bondae* and *Molossus* cf. *rufus* represent new records for CNP but were detected only in Coiba and Ranchería. Overall, we report nine new bat species for CNP (Table 2). According to the jackknife richness estimator, CNP should have 38.42 species (SD = 3.37). We complement these new records of aerial insectivorous bats not previously recorded in CNP with the spectral and temporal parameters of their echolocation calls (Table 3 and Fig. 2).

The most abundant species captured in CNP were *A. jamaicensis* (80.5 captures per 100 mnh) and *C. perspicillata* (54.0), followed by *P. discolor* (8.2) and *G. soricina* (4.4). The remaining 12 species displayed relative abundances lower than 4.2 captures per 100 mnh (Fig. 3). The most active aerial insectivorous bat was *M. nigricans*, with 42.5 passes per hour, followed by *S. leptura* and *M. bondae* with 32.2 and 26.9 passes per hour respectively. *Noctilio leporinus*, *P. parnellii*, *M.* cf. *rufus*, *Pteronotus davyi* and *M. coibensis* ranged from 18.8 to 13.4 passes per hour (Fig. 4). Please note that the relative activity of *M. nigricans* may be confounded with calls from *R. tumida*. Our species accumulation curves did not reach the asymptote (Fig. 5), and the Phyllostomidae curve overlapped with the non-

Phyllostomidae because we identified 16 species for both groups.

Finally, we collected 514 streblid bat flies, comprising 22 species, from 141 individual bats (13 species). All 22 species of streblid bat flies are new records for CNP. Ninety-eight point two percent of all collected bat flies were associated with their primary host species, which indicates high host specificity. In four cases a single bat fly was collected from a non-primary associated bat species (Fig. 6 and Appendix). We tentatively assigned a single bat fly collected from *Tonatia saurophila* to an undescribed species following the recommendations of Miller and Tschapka (2001) and Dick (2013) for Costa Rica and Honduras, respectively. Furthermore, we tentatively assigned two morpho-species to five individuals of the *Paratrichobius salvini* species complex; four individuals to morphospecies A (collected from *Chiroderma villosum*), and one distinctly smaller individual to morphospecies B (collected from *P. helleri*) following the characteristics and bat host species associations given in Wenzel *et al.* (1966) for Panama.

DISCUSSION

Our study increases the number of bat species known from Coiba National Park from 30 to 39, making it the fourth highest bat species richness

TABLE 3. Search call echolocation parameters ($\bar{x} \pm$ SD) of a subset of aerial insectivorous bats in Coiba National Park. This list complements the list provided by Ibáñez *et al.* (1997). 'Type' refers to changes in call frequency whereas Structure refers to modulation in frequency of different components of the call. 'Type' and 'Structure' for Emballonuridae and Molossidae taken from Jung *et al.* (2007) and Jung *et al.* (2014), respectively. QCF — quasi-constant frequency (change in the frequency of the echolocation call < 400 Hz ms⁻¹), FM — frequency modulated (change in the frequency of the echolocation call > 400 Hz ms⁻¹) (Jung *et al.*, 2007)

Species	Type	Structure	Duration (ms)	Interval (ms)	Start freq. (kHz)	End freq. (kHz)	Peak freq. (kHz)	Calls	Seq.
B. cf. *plicata*		QCF-straight	7.3 ± 1.4	99.6 ± 11.2	37.9 ± 1.9	34.1 ± 1.4	40.6 ± 1.2	65	3
D. albus	Low	QCF-straight	14.6 ± 2.1	185.6 ± 55.2	20.6 ± 1.8	20.4 ± 1.3	23.7 ± 0.8	14	1
	High	QCF-straight	14.7 ± 2.3	NA	22.9 ± 3.7	23.6 ± 0.6	27 ± 0.0	2	1
P. macrotis		QCF-straight	9.3 ± 2.8	144.7 ± 21.2	35.7 ± 2.7	34.6 ± 4.7	39.6 ± 2.1	289	17
L. blossevilli[a]		FM down QCF	4.5 ± 1.2	102.3 ± 31.2	50.6 ± 7.2	42.1 ± 5.7	48 ± 5.3	117	9
C. cf. *greenhalli*	Low[b]	QCF-down	13.9 ± 1.8	164.6 ± 50.9	19.3 ± 3.7	10.9 ± 3.8	16.7 ± 3.9	37	3
E. cf. *glaucinus*	Low	QCF-down	14.5 ± 3.3	147.9 ± 59.7	19.7 ± 3.3	16 ± 2.3	21.2 ± 2.2	245	25
	High	QCF-down	13.7 ± 2.0	378.6 ± 130.6	24 ± 3.5	20.6 ± 2.7	25.6 ± 2.2	97	25
M. coibensis[c]	Low	QCF-down	7.9 ± 1.7	80.8 ± 47.1	32.1 ± 3.3	28.8 ± 2.8	34.3 ± 2.4	52	12
	Middle	QCF-down	7.2 ± 2.0	80.6 ± 33.2	35.6 ± 3.0	32.4 ± 2.5	38 ± 2.0	70	12
	High	QCF-down	7.2 ± 2.3	124.5 ± 50.7	39.9 ± 2.7	35.2 ± 2.9	41.9 ± 2.2	62	12
M. cf. *bondae*	Low	QCF-down	12.1 ± 1.8	97.6 ± 33.8	28.5 ± 2.6	25.4 ± 2.5	30.3 ± 2.0	197	12
	High	QCF-down	12.3 ± 1.9	178.1 ± 64.1	33.6 ± 3.2	30.4 ± 2.4	32.3 ± 2.2	134	12
M. cf. *rufus*	Low	QCF-down	10.4 ± 2.3	106.4 ± 34.5	23 ± 3.1	23.2 ± 3.0	27.2 ± 2.3	148	20
	High	QCF-down	11.1 ± 2.8	237.2 ± 92.6	27.6 ± 2.1	27 ± 3.3	31.9 ± 1.2	23	20

a — Ibáñez *et al* (1997) captured *L. blossevilli* but did not describe its spectral parameters
b — We were unable to record high calls
c — Ibáñez *et al.* (1997) captured and recorded this species, but we include its spectral and temporal parameters for comparison with other molossids
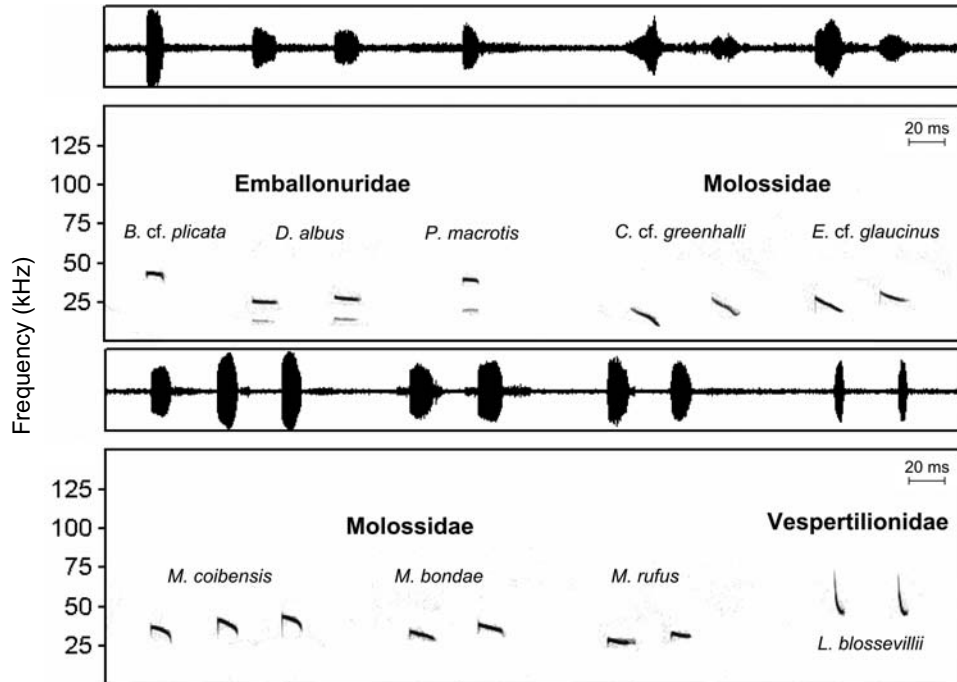
FIG. 2. Echolocation calls of a subset of aerial insectivores bats in Coiba National Park. Spectrograms (below) and oscillograms (above) of typical search calls. Pulse intervals are not to scale. These calls complement the list provided by Ibañez *et al.* (1997)

within all the protected areas surveyed in Panama. After 40 years of monitoring, Barro Colorado Nature Monument has the highest species richness for all Panamanian national parks (76 species — Kalko *et al.*, 2008), followed by Chagres National Park (62 species — R. Samudio, personal communication) and San Lorenzo National Park (42 species — Weise, 2007; Estrada-Villegas *et al.*, 2012). Our results alone, compared to the long history of monitoring around the Isthmus of Panama, highlights the importance of CNP among protected areas in Panama and underlines its high conservation value.

The combined sampling effort of Ibáñez *et al.* (1997) and our study totals 24 days, therefore the species list for CNP can only be considered provisional. Our sampling protocol precluded us from surveying more mature forests in the center of the island, where additional species that depend on old growth forests might be found [e.g., *Vampyrum spectrum* (Ibañez *et al.*, 1997), or *Phylloderma stenops* (Meyer and Kalko, 2008)]. Second, additional acoustic sampling needs to be conducted in other areas of the park to confirm our new records, especially the presence of *Balantiopteryx* cf. *plicata.* Although our recordings match the temporal and spectral measurements reported by Jung *et al.* (2007), our new records represent a ca. 400 km

range extension to the south from its southernmost locality at northern dry coast of Costa Rica for *B.* cf. *plicata.* It is plausible that Coiba might harbor a relict population of this species after the island underwent several dry spells. Nonetheless, other identifications of our list have higher support; the presence of *C.* cf. *greenhalli*, *E.* cf. *glaucinus* and *M.* cf. *bondae* as new species for CNP is supported by a clear overlap between our spectral and temporal parameters with the values reported by Jung *et al.* (2014). Our values for *M.* cf. *coibensis* also match the values reported by Gager *et al.* (2016) for this species. The identification of *C.* cf. *greenhalli* is also well supported given its distinctive call structure at the frequency range in which it emits (Jung *et al.*, 2014). Likewise, we are confident the identification of *E.* cf. *glaucinus* is correct because it has a distinctive call shape and the longest pulse interval at the frequency range in which it emits (Jung *et al.*, 2014). With respect to *M.* cf. *bondae,* we followed the classification provided by Simmons (2005), the most recent analysis by Gager *et al.* (2016), and the most current distribution of this species with respect to *Molossus currentium* (Gardner, 2007, but see Estrada-Villegas *et al.*, 2010, and Jung and Kalko, 2011). Finally, we are cautious with our estimation of richness species; when adding our new findings to the list from
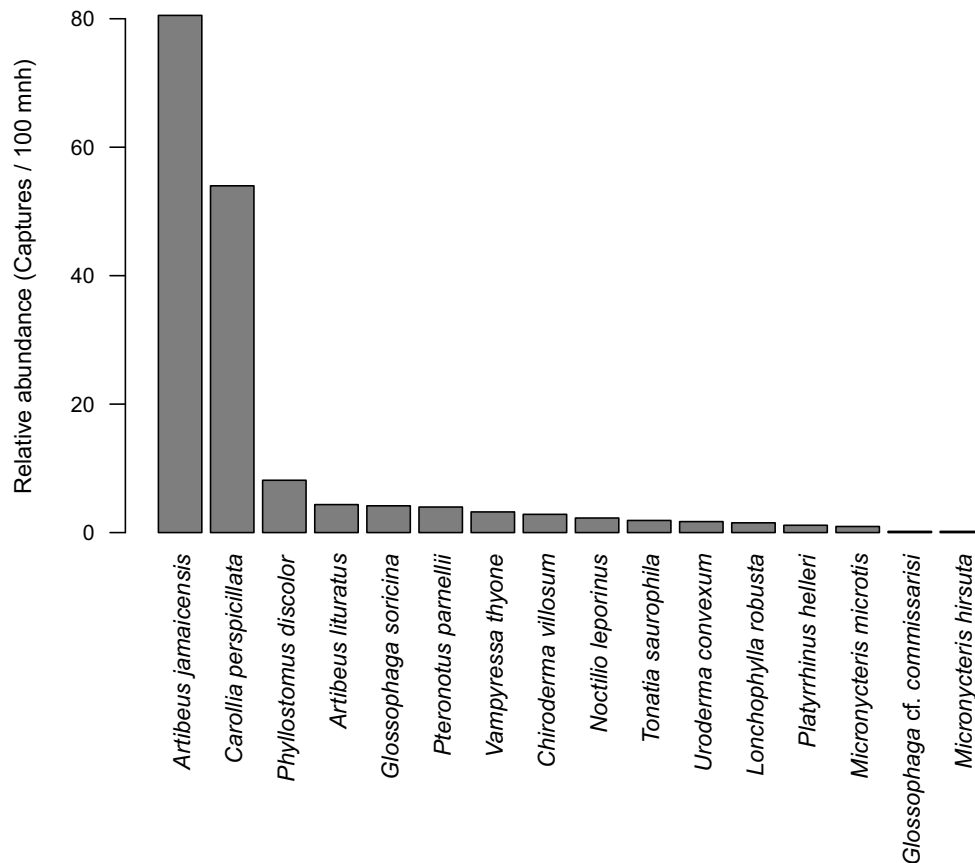
FIG. 3. Distribution of relative abundance of bats captured in mist nets in Coiba National Park, Panama. Please note that *P. parnellii* and *N. leporinus* were also detected acoustically

Ibáñez *et al.* (1997), the total number of species in CNP is within the range of the estimated species richness. We expect that estimations should be much higher if abundance data from captures or from pooled observations (e.g., Estrada-Villegas *et al.*, 2010) were to be used. In sum, we consider our species list provisional due to our limited sampling period and the regular corrections in bat taxonomy.

The wide differences in sampling protocols between our study and Ibáñez *et al.* (1997), and the limited sampling effort in both studies, precludes us from assessing fluctuations in populations over time. On the one hand, Ibáñez *et al.* (1997) did not provide a detailed account of sampling effort and capture success per site, and they were able to use the extensive trail system while the CNP was a penitentiary facility. On the other hand, Ibáñez *et al.* (1997) were able to sample for 11 nights in Coiba, four in Ranchería, and three in Jicarón, whereas we were only able to sample eight nights in Coiba, one in Ranchería and two in Jicarón. The lack of information that Ibáñez *et al.* (1997) provided regarding sampling effort and capture success, combined

with poor accessibility to the same sampling sites, prevented us from more detailed comparison between the two sampling events. Nonetheless, comparing the species occurrences of Ibáñez *et al.* (1997) with our results on species' relative abundances, it comes as no surprise that the most abundant and active species, such as *A. jamaicensis*, *C. perspicillata, G. soricina* and *S. leptura*, were found in both studies and on all the islands. Compared to other bat assemblages from the region (e.g., Meyer and Kalko, 2008; Rex *et al.*, 2008), it is somewhat surprising that *Dermanura watsoni* and *D. phaeotis*, two small frugivorous bat species that are abundant in other localities, are apparently absent in CNP. Isolation of CNP could have probably led to a local extinction of these two species, but further sampling needs to be conducted to confirm this assertion. However, the much smaller frugivorous bat *Vampyressa thyone* is present in CNP, which could indicate that body size and feeding guild alone do not explain the local extinction of the two aforementioned species. Finally, our species accumulation curves show that we were able to detect more
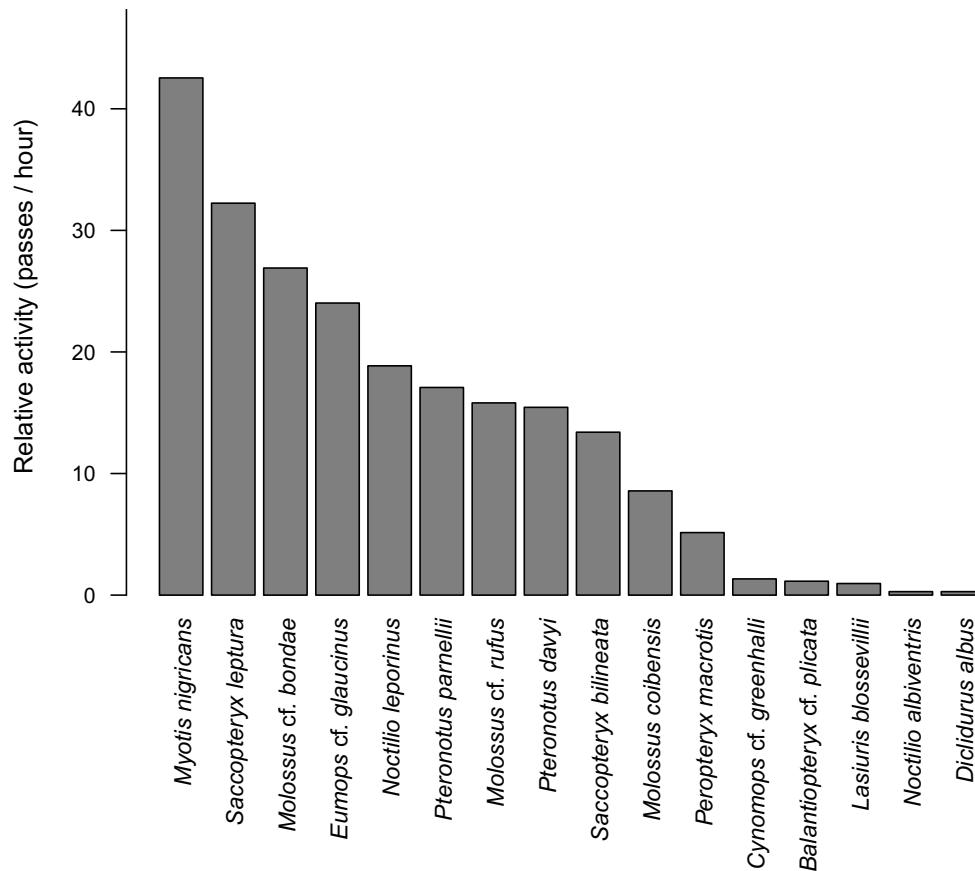
FIG. 4. Distribution of relative activity of all aerial insectivorous bats identified acoustically in Coiba National Park, Panama. Please note that *P. parnellii* and *N. leporinus* were also captured in mist nets

aerial insectivores than Ibáñez *et al*. (1997), likely because there are more complete call libraries now, better equipment is available today, and more studies describing echolocation calls have been published since 1997. The higher number of aerial insectivores detected is also the reason why we accumulated more species with comparable sampling effort than Ibáñez *et al*. (1997). Again, more work is needed to fully describe the bat assemblage of CNP given that we were not able to verify the presence of species like *Natalus stramineus* or *Vampyrum spectrum,* which were reported by Ibáñez *et al*. (1997). Future studies may use our baseline data to establish a larger study with more intense sampling effort detect temporal fluctuations of the bat assemblage in the park.

Three factors may have affected the bat assemblage in CNP: strong dry spells in the last 25,000 years, isolation due to the increase in ocean levels, and habitat transformation in some areas of the park in the last century (Bush *et al*., 1992; Ibáñez *et al*., 1997; Ibáñez, 2011). The first two factors probably contracted bat populations and filtered out some

species while making conditions more amenable for species typical of drier areas. For example, *M. nigricans*, *S. leptura* and *E. glaucinus*, which are the most active aerial insectivorous bats in Coiba, are also frequently recorded in the drier portion of the Isthmus of Panama (Jung and Kalko, 2011; Estrada-Villegas *et al*., 2012). The last factor probably allowed generalist species such as *A. jamaicensis, C. perspicillata* or *P. discolor* to increase in abundance. Particularly the first two have been shown to be among the most abundant species in many Central and South American lowland bat assemblages (Estrada *et al*., 1993; Kalko *et al*., 1996; Meyer and Kalko, 2008).

Our study not only provides species' relative abundances and relative activity for the bat assemblage, it also provides the first record of ectoparasites from Coiba. Although Wenzel *et al*. (1966) mentioned two bat species from Coiba island (*N. stramineus* and *M. coibensis*), they did not report the ectoparasites associated with these bat species. We identified 22 streblid bat fly species parasitizing 13 bat species. Nonetheless, we are confident
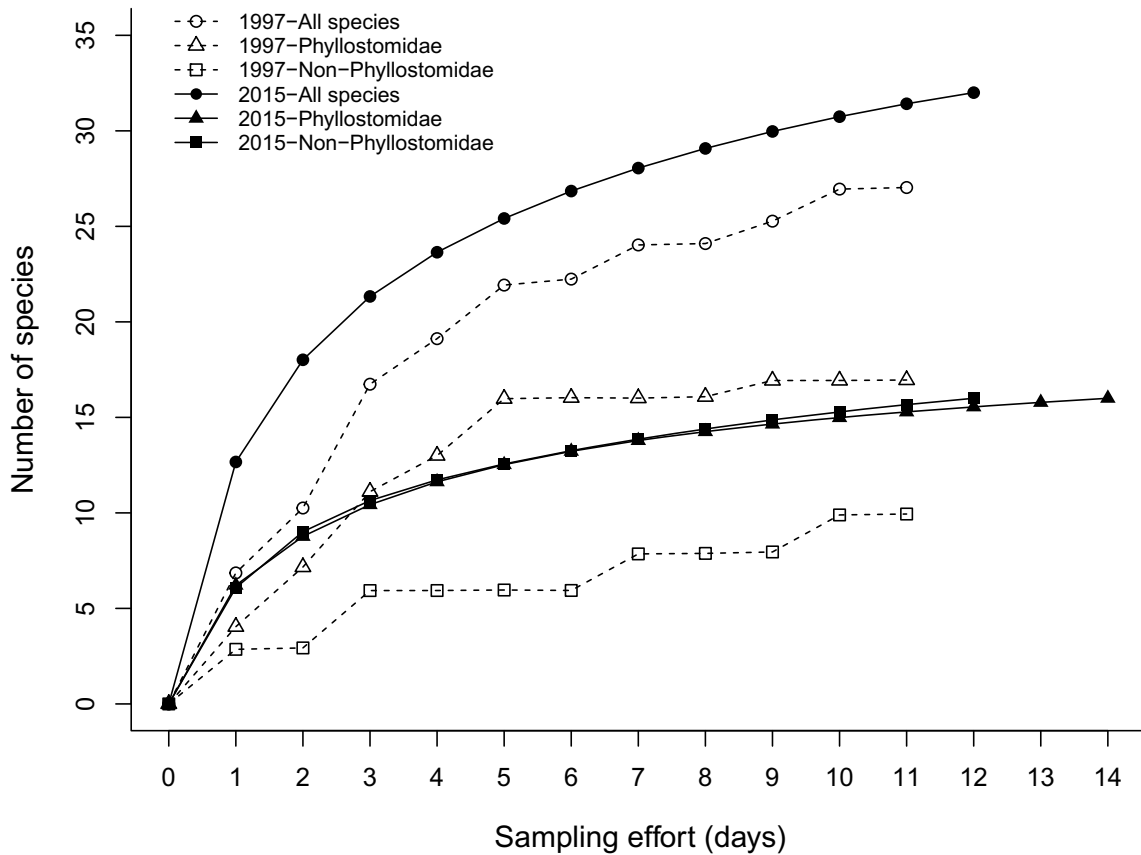
FIG. 5. Species accumulation curves for Coiba National Park, graphed as Phyllostomidae, non-Phyllostomidae, and all species combined. The Phyllostomidae curve included all 14 sampling nights, the number of nights we sampled using mist nets. For the curve where all species are combined, we harmonized the data to 12 nights, the number of nights we conducted acoustic monitoring. We digitized the accumulation curves provided by Ibáñez *et al*. (1997) for comparison

that more bat fly species should be present in CNP because our sample sizes for some bat species was small, and we missed some of the species reported by Ibañez *et al*. (1997). The discovery of three possibly undescribed bat fly species (following Wenzel *et al*., 1966; Wenzel, 1976; Dick, 2013) highlights the need of more ecological and taxonomical studies on host–parasite interactions in Panama.

The bat fly-host associations we found are highly specific; 98.2% of all the bat flies collected were associated with their primary host. This result is comparable to studies from other sites in Panama, Venezuela and Paraguay (Wenzel *et al*., 1966; Wenzel, 1976; Dick and Gettinger, 2005; Dick and Patterson, 2007). The occasional occurrence of single bat flies on non-primary hosts are most likely due to contamination in the net or while handling the bat (Dick, 2007). In most of these cases the primary host was captured with non-primary hosts during the same sampling night, or the specific parasite is very abundant on their primary host. For example, *Trichobius joblingi* is the most abundant bat fly collected in our

study and its primary host, *C. perspicillata*, was abundant at every capture site. Therefore, the single individual of *T. joblingi* collected from *P. parnellii* is very likely just an accidental occurrence of an individual leaving its original host during handling. The same applies to *Noctiliostrebla traubi* from *A. jamaicensis* and *Trichobius costalimai* from *C. villosum*. Interestingly, the host association of *Speiseria ambigua* do not conform with previous studies: while the single individual on *P. discolor* could be accidental, as this streblid flies off easily when the host bat is in distress (Dick and Gettinger, 2005), the remaining five individuals were all found on *Lonchophylla robusta,* which is not its reported primary host. Moreover, we did not record any other bat fly species from *L. robusta* (*n* = 7). This association differs from Wenzel (1976), who found that 96% of all *S. ambigua* were collected from *C. perspicillata* in Venezuela. In comparison, we did not collect a single individual of *S. ambigua* on *C. perspicillata* (*n* = 54). The unexpected association between *S. ambigua* and *L. robusta* may indicate a host
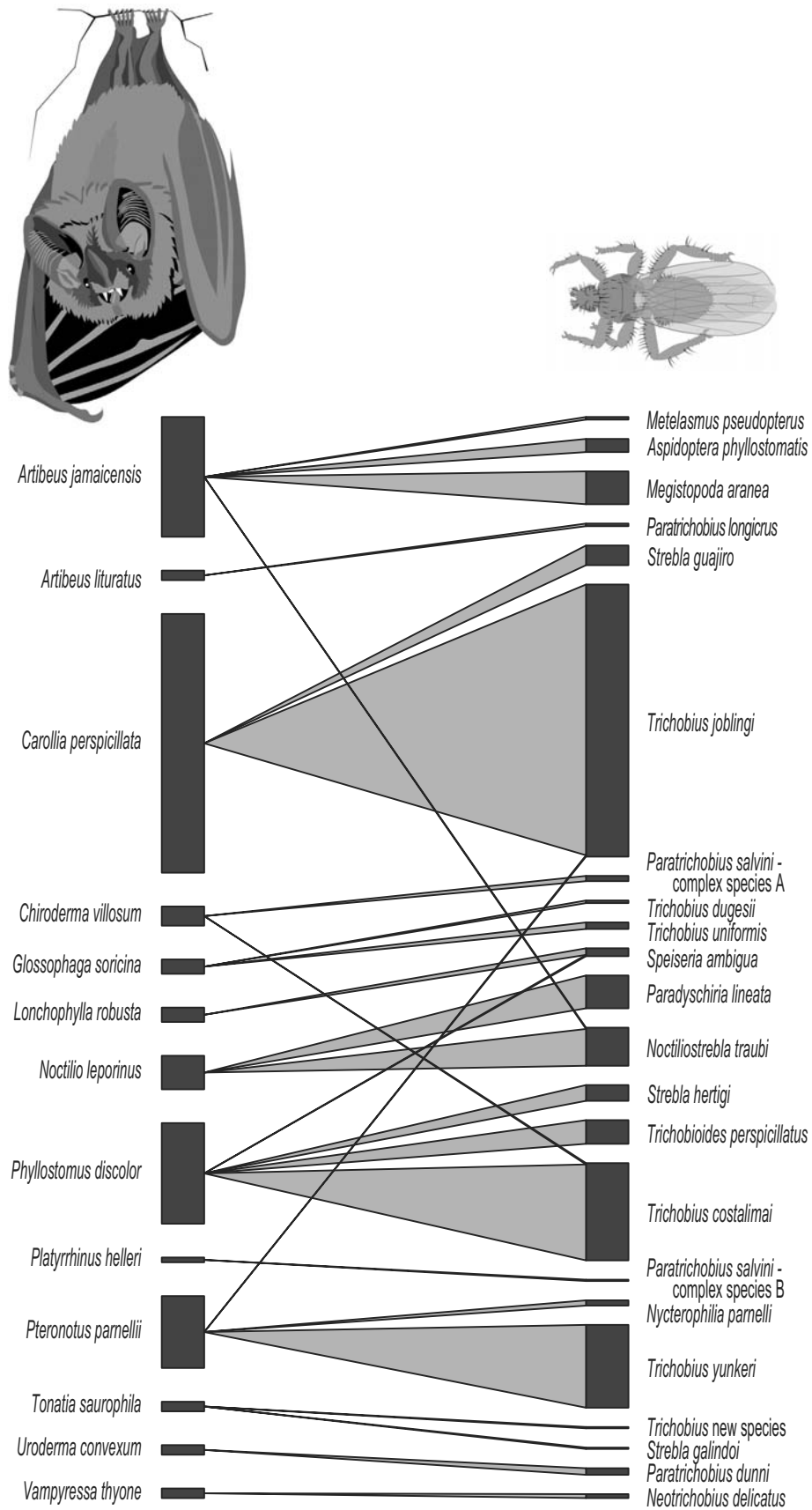
FIG. 6. Interaction web between bat species and bat ectoparasites (strelibid flies) from Coiba National Park. The width of the bars is proportional to the number of individuals in each network level

switch, possibly promoted by a reduction in roost availability, prompted by a reduction in habitat size. Further studies are necessary to clarify the host-parasite relationship of *L. robusta* and *S. ambigua* in Coiba.

In conclusion, climatic fluctuations and changes in habitat structure due to anthropogenic activities might have had a strong effect on the community structure of the bats of CNP. In spite of a relatively low sampling effort, we have shown that CNP is currently the protected area with the fourth richest bat assemblage in Panama. Our results reflect the high conservation status of the Park and we expect many more species to be found in mature forests farther from the shore. We describe the spectral and temporal parameters of nine aerial insectivorous bats, contributing to the growing literature on tropical bat echolocation. Finally, we provide the first list of streblid bat ectoparasites for CNP, the first detailed list of this kind for any protected area in Panama. Comprehensive surveys that combine bat capture data, echolocation monitoring, supplemented by ectoparasite sampling, provide essential baseline data for monitoring how assemblages change through time after modifications in landscape management.

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APPENDIX

List of streblid fly species collected during this study. *n* — number of samples of host species harboring parasites; int. max — maximum intensity of parasitation; sp. max — maximum number of bat fly species on a single host individual; *N* — number of collected bat flies; SI — specificity index (ratio of total bat flies of a single species found on one host species); * — non-primary host

Bat species (*n,* int. max, sp. max)	Bat fly species	*N*	SI	Coiba	Jicarón	Ranchería
Artibeus jamaicensis (*27*, 4, 3)	*Aspidoptera phyllostomatis*	10	1.00	X	X	
	Megistopoda aranea	27	1.00	X	X	X
	Metelasmus pseudopterus	3	1.00	X	X	
	Noctiliostrebla traubi	1	0.03	X*		
Artibeus lituratus (*2*, 1, 1)	*Paratrichobius longicrus*	2	1.00	X		
Carollia perspicillata (*48*, 17, 2)	*Strebla guajiro*	13	1.00	X		
	Trichobius joblingi	175	0.99	X	X	X
Chiroderma villosum (*4*, 2, 2)	*Paratrichobius salvini* complex species A (Wenzel 1966)	4	1.00	X		
	Trichobius costalimai	1	0.01	X*		
Glossophaga soricina (*3*, 4, 1)	*Trichobius dugesii*	2	1.00	X		
	Trichobius uniformis	5	1.00	X		X
Lonchophylla robusta (*3*, 3, 1)	*Speiseria ambigua*	5	0.83	X		
Noctilio leporinus (*7*, 18, 2)	*Noctiliostrebla traubi*	28	0.97	X		
	Paradyschiria lineata	25	1.00	X		
Phyllostomus discolor (*21*, 13, 3)	*Speiseria ambigua*	1	0.17		X*	
	Strebla hertigi	12	1.00	X		X
	Trichobius costalimai	73	0.99	X	X	X
	Trichobioides perspicillatus	18	1.00	X	X	X
Platyrrhinus helleri (*1*, 1, 1)	*Paratrichobius salvini* complex species B (Wenzel, 1966)	1	1.00	X		
Pteronous parnellii (*15*, 10, 2)	*Nycterophilia parnelli*	4	1.00	X		
	Trichobius joblingi	1	0.01	X*		
	Trichobius yunkeri	63	1.00	X	X	
Tonatia saurophila (*2*, 1, 1)	*Strebla galindoi*	1	1.00	X		
	Trichobius new species (Miller and Tschapka, 2009)	1	1.00		X	
Uroderma convexum (*2*, 4, 1)	*Paratrichobius dunni*	5	1.00			X
Vampyressa thyone (*2*, 2, 1)	*Neotrichobius delicatus*	3	1.00	X		