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Records of the cave-dwelling bats (Mammalia: Chiroptera) of Hispaniola with an examination of seasonal variation in diversity

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Despite a long history of scientific collection of bats, Hispaniola remains the least studied island of the Greater Antilles. Using standardized trapping methods during the wet and dry season at four major caves — Honda de Julián, La Chepa, Los Patos, and Pomier #4, we sampled a total of 1,472 individuals in four families, 11 genera and 12 species (of 18 recorded for the island). We report significantly fewer captures on the second night of sampling. We document seasonal variation in abundance of *Macrotus waterhousii*, *Monophyllus redmani*, and *Artibeus jamaicensis*, that results in 1–4 more species captured in the wet season. Additionally, singleton captures at all caves except for Honda de Julian produced wide confidence intervals in estimates of richness. Finally, we highlight the role of caves as major ecosystems for maintaining Hispaniolan mammal biodiversity. The high diversity recorded at La Chepa, together with possible declines at the historically very diverse Los Patos, highlight the conservation importance of all surveyed caves.

Key words: Chiroptera, harp trap, Natalidae, Phyllostomidae, wet and dry season

INTRODUCTION

The Hispaniolan bat fauna is understudied compared to the fauna of other Greater Antilles (Silva-Taboada, 1979; Gannon *et al*., 2005; Genoways *et al*., 2005). Unlike Cuba or Puerto Rico, no long-standing monitoring of bats has taken place to provide island-wide systematic records (Silva-Taboada, 1979; Gannon *et al*., 2005). Most sampling on Hispaniola has been opportunistic and instrumental to other goals such as sampling for phylogenetics (Tejedor *et al*., 2005*a*, 2005*b*), molecular ecology in general (Corthals *et al*., 2015), or more recently focused on fossil communities (Velazco *et al*., 2013). Only recently have extant records in museum collections been harnessed to provide an overview of the bat fauna, as previously done for Jamaica (Genoways *et al*., 2005). That review found records for 18 species in six families, comprising 90% of the native extant mammals of the Dominican Republic (Núñez-Novas and León, 2011). Of these, 16 species, or 89% of the total recorded, use caves as diurnal refuges. Lacking any systematic sampling, however, the composition, richness and relative abundance of bat communities in Hispaniolan caves remains unknown.

To address the lack of systematic sampling at Hispaniolan caves, our goal was to survey the bat communities of four caves in the Dominican Republic in a standardized manner for the first time. Additionally, we compared the current species composition with historical records for all caves using specimens from museum collections in the Dominican Republic and continental North America. Standardized and repeated sampling enabled us to compare captures between nights, caves and, crucially, seasons. Sampling hundreds of individuals each night made it possible to estimate species richness using rarefaction. Since historical records suggested the target caves had at least one hot chamber, these surveys are the first to systematically sample bat communities in Hispaniolan hot caves.

Materials and Methods

Sampling Locations

To identify suitable caves, we reviewed the bat collections of the National Museum of Natural History of Santo Domingo (MNHNSD), as well as online databases collections from the American Museum of Natural History (AMNH) and collections with databases online in the Mammal Networked Information System (MaNIS). These records were then used to identify historically sampled caves that could be surveyed at present. Four caves were selected based on the availability of historical information in collections and collection databases (Fig. 1).

Honda de Julián

Cueva Honda de Julián Cáceres is located in the area of Don Miguel, Platanal, Cotuí municipality in the Sánchez Ramírez province (19°7’56.60”N, 70°4’46.20”W). The cave is located in the north zone of a karst valley. The valley vegetation comprises grassland and mixed crops (Tejedor *et al*., 2005*a*). There are disturbed forests and extensive cattle pastures surrounding the entrance of the cave. The length of the cave is more than 100 m, and it has eight chambers and three entrances, two of which measure approximately one meter in diameter. The ground around the largest cave entrance is moist and the interior of the cave shows evidence of episodic flooding (Tejedor *et al*., 2005*a*). This is supported by observations within the cave, where soil is covered with mollusk shells, fish can be seen inside the cave, and there are reports of fishing by locals. The cave entrance is occasionally used as a water trough for cattle.

La Chepa

Cueva La Chepa or Chepe is located in the Valle Grande area, at the headwaters of the Comate river, Bayaguana province (18°52’8.80”N, 69°34’34.70”W). The cave is located in the source of the Comate river and since 2009 is part of the protected area called Monumento Natural de Salto Grande (category II of IUCN). There are extensive forests near the cave.

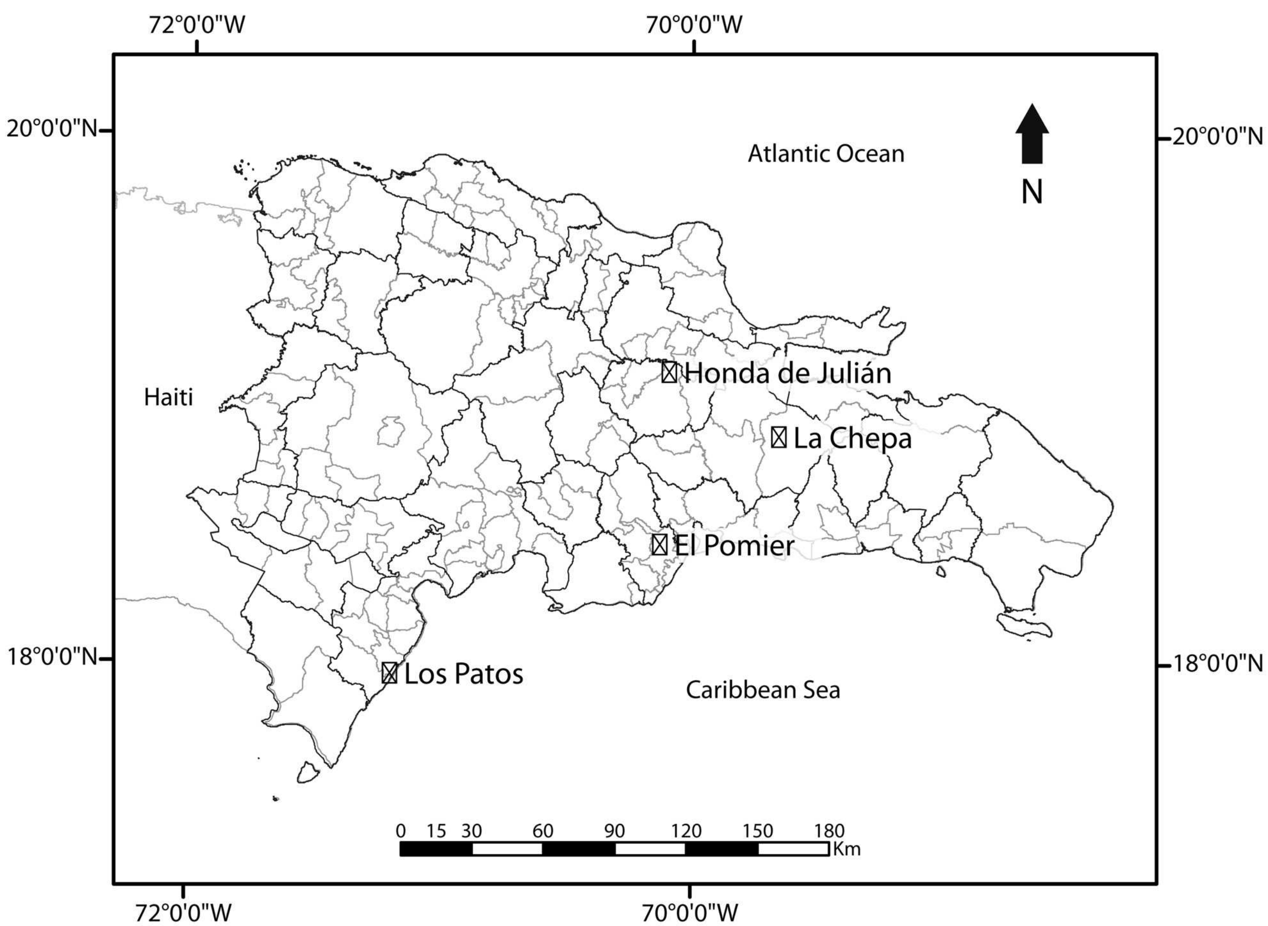

Fig. 1. Province and county map of the Dominican Republic, showing the four caves selected for this study

Despite disturbance, a verified record of the critically endangered *Buteo ridgwayi* was made in June 2009 right outside the cave entrance.

La Chepa cave is 500 m long, with ceilings up to 25 m tall. The cave entrance leads to a huge chamber roofed with a colossal dome; this chamber is round with a diameter of ca. 60 meters. After this chamber, there is a network of interconnected tunnels, some of them large but unmeasured. All are flooded with clay soils, in some cases covered by guano layers. A second narrow pathway leads to another tunnels network with similar characteristics. In some cases, tunnels are divided by enormous formations from the ground to the roof of the cave (Abréu Collado, 2007).

Los Patos

Cueva Los Patos is located near the Los Patos resort, town of Los Patos, Barahona Province (17°57’35.05”N, 71°10’59.80”W). The cave is located on a mountain near the road to the town of Los Patos. Los Patos cave is about 290 m long; it has three entrances and eight chambers, 3–15-m wide. Los Patos River emerges from the flooding part of the cave and this river passes immediately below a bridge and forms a reservoir (Los Patos resort) and flows into the sea (D. Abréu Collado, personal communication). There is a disturbed forest around the cave.

El Pomier #4

Cueva No. 4, also known as Ricardo Ramírez No. 4, or Borbón del Monumento Natural Cuevas del Pomier, is located in the Reserva Antropólogica Monumento Natural Cuevas del Pomier of San Cristóbal province (18°28’0.90”N, 70°8’9.60”W). The cave is surrounded by secondary forest and there is a baseball field in front of its entrance. Visitors can visit the cave with guides from the parks system.

The cave has two 258-m-long chambers (Ottenwalder, 1995). The main entrance shows rockslides because of mining in the 1970’s (D. Abréu Collado, personal communication) and is ca. 20 m long. The chamber then descends abruptly, leading to a lower, shorter chamber, this cave has approximately five chambers and one of them could be considered a hot cave (Ottenwalder, 1995).

Capture Methods

A harp trap (1.83 m wide × 1.27–2.29 m height, G5 Bat Trap, Bat Conservation and Management, Inc., Carlisle, PA) was used as the single method of capture. The harp trap was placed in the entrance of each cave and opened for five hours, beginning at 18:00 h. Branches and large leaves were used to block most of the entrance surrounding the harp trap. A total of 16 nights of surveying were conducted: four for each cave divided into two in August–September 2009 (wet season) and two in February–March 2010 (dry season). The sampling effort totaled 80 hours for all caves and both seasons.

Data Collection

The time of capture was documented for each bat that fell into the trap and recorded at 15-min intervals. Individuals were identified to species using field guides by Baker *et al*. (1984) and Silva-Taboada (1979). Each individual captured was identified, examined to determine sex and sexual maturity, and subsequently marked using punches. These consisted of punching small holes in the form of numbers through the outstretched wing membrane (Bonaccorso and Smythe, 1972). The right wing area close to the inferior margin of the patagium was marked using a tattoo for pets (Stone Manufacturing Co. No. 300, Kansas City, MO), corresponding to a unique combination of 2–4 digits, depending of the species. At least one individual of each species was photographed at each cave (head and complete ventral view) to be used as reference electronic voucher.

Data Analysis

All data were analyzed using the Statistical Package for the Social Sciences (SPSS version 17.0), and the package ggplot2 (Wickham, 2009) in the R statistical language v.3.1.2 (R Core Team, 2013). For each cave, we calculated the Shannon-Wiener diversity index (H’), Pielou equity index (J’), and Simpson’s dominance index (λ). To estimate the species richness of the caves, we calculated species accumulation curves using EstimateS v.9.0.1, and randomizing the observed data 100 times (Colwell *et al*., 2012). The resulting curve is a prediction of the expected number species and its error as a function of the sampling effort.

Ethics Statement

Field sampling was authorized by permit number: 060079 from the Ministry of the Envrionment and Natural Resources (Ministerio de Medio Ambiente y Recursos Naturales) of the Dominican Republic. No animals were euthanized for this study, as all of the individuals were released at the capture location.

Results

Sampling and Captures

Each cave was sampled a total of 20 hours over two nights in each of two seasons in this first standardized sampling of the bat fauna of Hispaniola. A total of 1,482 individuals were captured, including 10 individuals recaptured the same night. Honda de Julian and La Chepa were the caves with the greatest number of individuals collected, adding up to 72% of total captures. The average catch per unit effort (CPUE) for samples of all caves at all times was ca. 18 bats/hour, with important variation between seasons and among caves (Fig. 2). The greatest number of captures was recorded during the dry season at Honda de Julián. In every case there was a consistent decrease the second night of capture in both seasons. This effect could not be measured at Los Patos because sampling was not conducted in consecutive nights, but 28 days after the first sampling.

Cave Community Composition and Diversity

Twelve species were recorded in 11 genera and four families (Table 1). This represents 67% of all

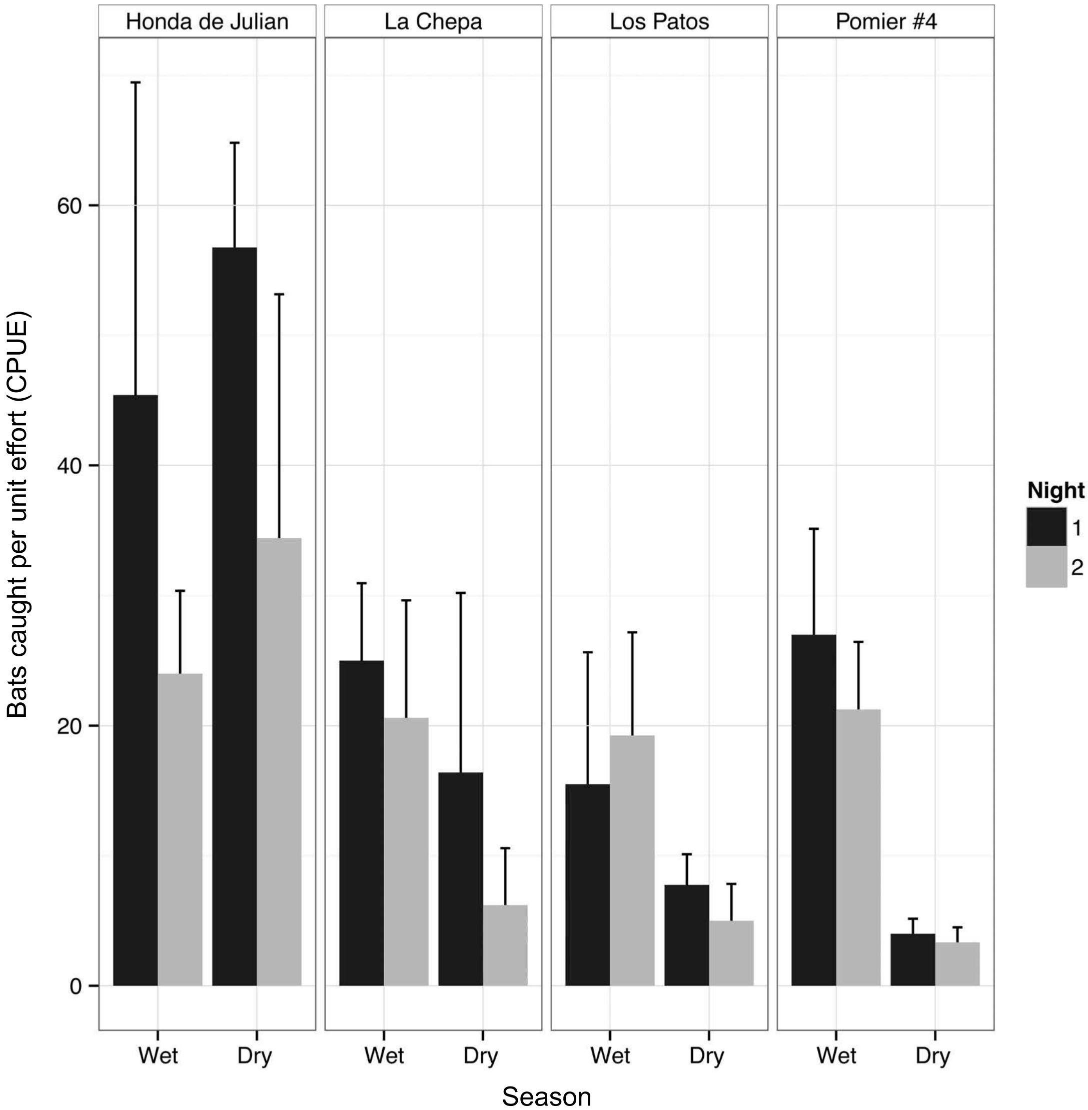

FIG. 2. Seasonal catch per unit effort (CPUE) by night of sampling. Note that wet-season sampling at La Chepa took place in non-consecutive nights

the species reported for Hispaniola. Mormoopids made up 54% the total of captures, followed by phyllostomids (45.6%), natalids (0.3%) and one vespertilionid (0.1%). The most common species were mormoopids (*Pternotus parnellii*, *P. quadridens* and *Mormoops blainvillei* — Fig. 3). Three rarely sampled species were uncommon in the total sample: the natalids *Natalus major* and *Chilonatalus micropus* (captured only twice each), and *Eptesicus fuscus* (captured only once). Both natalid species were found at La Chepa, and one *C. micropus* individual was also sampled at Los Patos cave. *Eptesicus fuscus* was only found at El Pomier #4 (Fig. 3).

La Chepa had the highest diversity as measured using the Shannon-Wiener index (1.62), and the lowest was recorded at Pomier #4 (1.12). These differences in sampling uncertainty and relative diversity were also reflected in the total captures (Fig. 3). With the exception of Los Patos, diversity was always higher during the dry season, corresponding to higher evenness as measured using Pielou's equity (Table 2). Conversely, Simpson's dominance index was highest during the wet season,

TABLE 1. Comparison in the number of species recorded in this study and found in museum collections

Caves	Species recorded in collections	Sampled here	Total species
Honda de Julián	7	6	9
La Chepa	10	10	12
Los Patos	11	8	12
Pomier #4	3	6	7

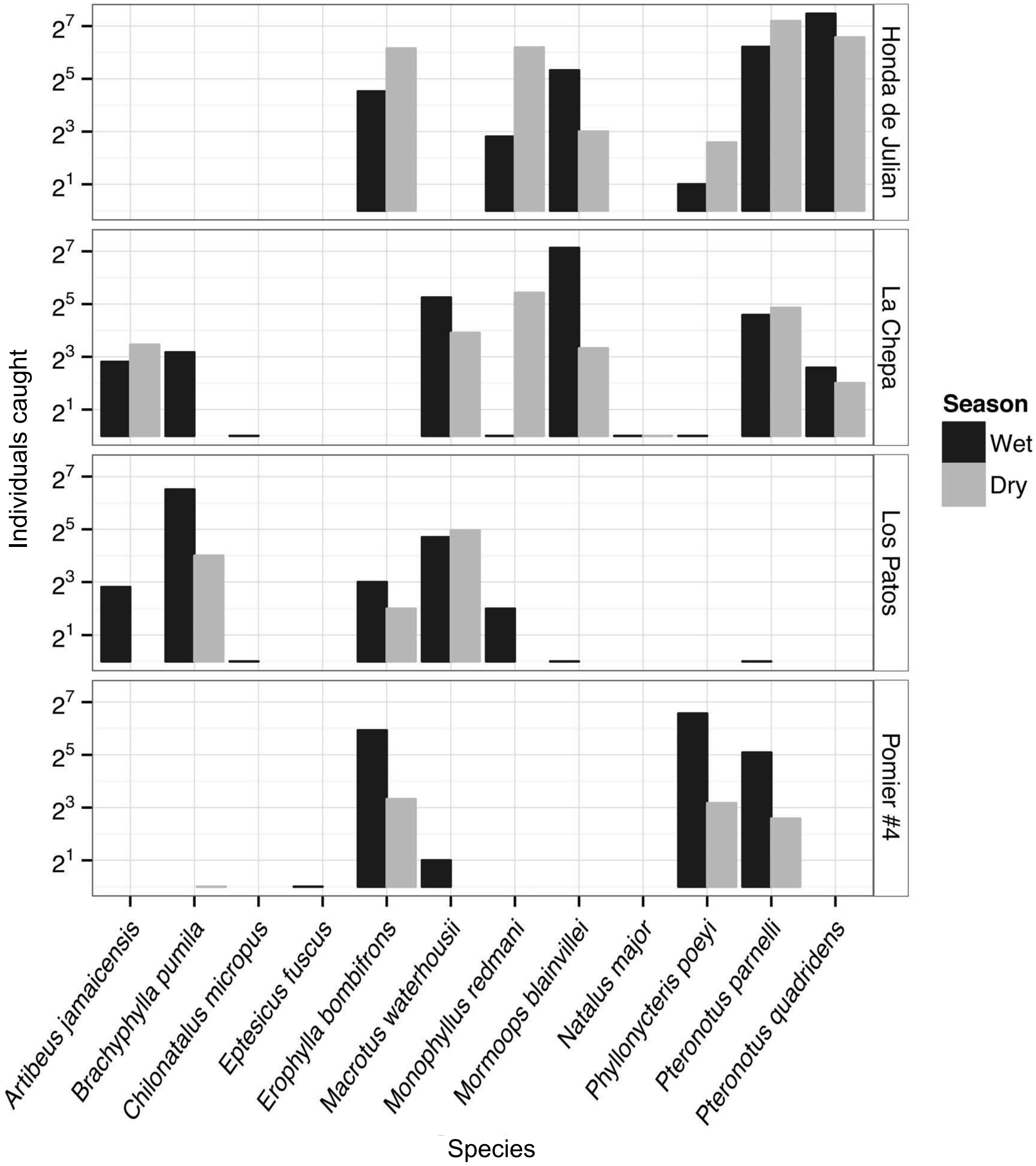

FIG. 3. Total captures per cave for individual species by season

and at Los Patos cave. Two species; *Brachyphylla pumila* and *Macrotus waterhousii,* strongly dominated captures in both seasons at Los Patos (Table 2 and Fig. 3).

Species Richness

The rarefaction curves revealed plateaus in species accumulation in both seasons for Honda

TABLE 2. Biodiversity indices for the caves studied. W = wet season, D = dry season

Caves	Shannon's diversity (H')			Pielou's equity (J')			Simpson's dominance (λ)		
	W	D	Total	W	D	Total	W	D	Total
Honda de Julián	1.22	1.46	1.46	0.69	0.82	0.81	0.37	0.19	0.27
La Chepa	1.26	1.58	1.62	0.55	0.82	0.70	0.42	0.25	0.26
Los Patos	1.11	0.86	1.14	0.54	0.79	0.55	0.47	0.45	0.41
Pomier #4	1.09	1.19	1.12	0.68	0.87	0.62	0.38	0.32	0.36

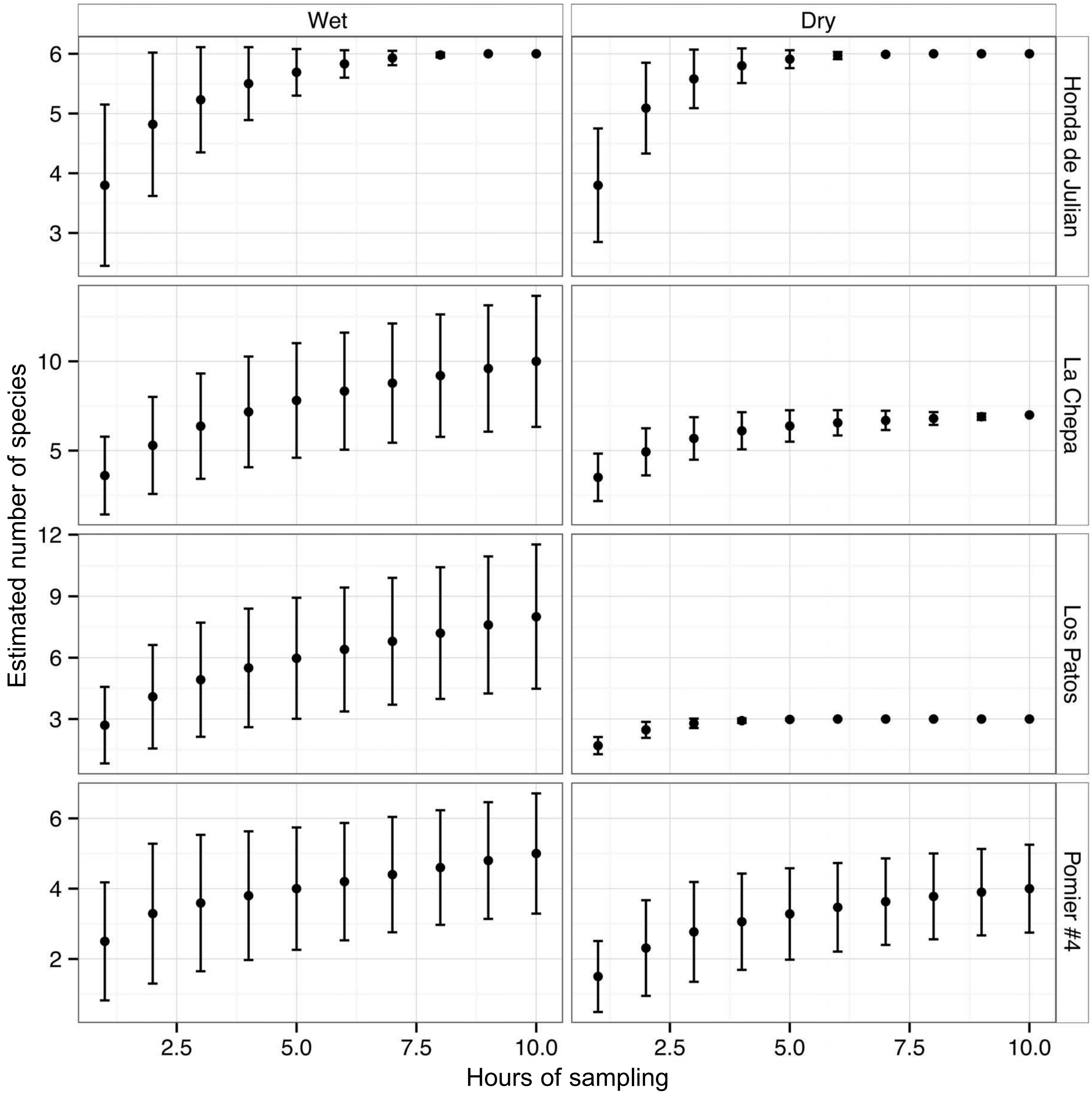

FIG. 4. Seasonal species accumulation curves by cave with 95% confidence calculated by rarefaction

de Julián, suggesting the bat community of the cave is well represented by these samples (Fig. 4). Stable plateaus were not reached at any other cave during the wet season, although the number of species yet to be sampled was not great. During the dry season, curves plateaued between the 3–8 hours of sampling at La Chepa and Los Patos, suggesting the number of sampled hours was enough to uncover bat species richness at this time (Fig. 4).

Comparison to Historical Records

Based on data from museum collections, this study added new records for all caves and confirmed the presence of species previously reported (Supplementary Table S1). The main discrepancy between the historical record and current sampling was recorded at Los Patos, where 12 species had been previously recorded and only eight species were found. At the other three caves there was little difference between presently sampled and previously recorded species. Noteworthy differences in species composition include not sampling the endemic *N. major* at Honda de Julián or Los Patos, where it was previously reported. The previous *N. major* record at Honda de Julián involved sampling within the cave using hand nets (Tejedor *et al*., 2005*a*), a method we did not pursue here, and which may account for this discrepancy.

Discussion

This first systematic cave survey in the Dominican Republic reveals three unambiguous patterns for understanding bat diversity on Hispaniola. The first is the steep drop in individual captures from one night to the next (Fig. 2). Second, is strong seasonality in some bat populations (Fig. 3), which translates into different seasonal estimates of diversity (Table 2). Finally, the proportion of singleton captures at most caves results in wide confidence intervals for local richness and implies that continued sampling is needed at most of these sites (Fig. 4).

Trap Avoidance and Individual Captures

Previous studies have shown the number of individuals, species captured when sampling bats, and capture condition depends mostly of the collection technique (Tidemann and Woodside, 1978; Simmons and Voss, 1998). The harp trap is one of the most efficient capture methods for bats, and is better than mist nets when capturing bats at cave exits (Tidemann and Woodside, 1978; Francis, 1989). There are, however, limitations with all sampling methods. The combination of high-intensity calls that enable some species to detect the trap, and possibly learned avoidance (see below) leads to less than perfect sampling. Nonetheless, the efficiency of this method was corroborated in our study, in which we captured almost 1,500 bats in only 16 nights, sampling a substantial portion of the island's richness, and many individuals despite using only one capture method.

We consistently found a decrease in captures on the second consecutive night, and we hypothesize this drop was caused by bats learned how to avoid the trap. We observed some individuals avoiding the trap by flying above or besides the trap, or even fleeing, and others have reported this behavior as well (Torres-Flores, 2005). Trapping on consecutive nights is thought to cause a behavioral response in bats, to minimize the risk of predation (Torres-Flores, 2005) Our results suggest trapping on two consecutive days is not recommended for future studies surveying diversity or relative abundance.

Trap avoidance may also play a role in preventing recaptures between nights. Some captured individuals may have learned to avoid the trap altogether. Additionally, sampling may have been too limited to obtain recaptures, or cave populations may be much larger than the number of bats marked in this study. Finally, it is possible that some marked individuals used a different exit, relocated to another cave, or died during the study. The multiple documented exits of each cave, coupled with spatial learning (Safi and Dechmann, 2005), may enable bats to avoid the trap in consecutive nights.

Seasonality in Abundance and its Influence on Diversity

All samples were dominated by the cave-dwelling mormoopid and phyllostomid species (Fig. 3). The presence of *P. parnellii* in every sample indicates that all caves had 'hot-cave' chambers (Silva-Taboada, 1979; Herd, 1983). These caves are therefore critical to species that depend on this specialized refuge such as *P. parnellii*. There were strong cave-specific seasonal changes in the captures of the mormoopids *M. blainvillei* and *P. parnellii*, as well as the phyllostomids *Macrotus waterhousii*, *Phyllonycteris poeyi* and *Artibeus jamaicensis* Leach (1821) (Fig. 3). These mormoopids were found at all caves, although with marked seasonal changes at Honda de Julian, La Chepa, and Pomier #4.

Among phyllostomids, *A. jamaicensis* and *M. waterhousii* are usually found solitary or forming colonies of dozens to hundreds of individuals (Anderson, 1969; Silva-Taboada, 1979). Smaller colonies are subject to greater stochasticity and this may explain at least part of the seasonal variation. In contrast, *P. poeyi* is gregarious and forms colonies of thousands of individuals (Silva-Taboada, 1979; Swanepoel and Genoways, 1983; Gannon *et al.*, 2005). This makes the sharp variation in captures between seasons, particularly at Pomier #4, more difficult to explain.

In general, such dramatic changes in abundance correspond to bat populations tracking food resources, changes in reproductive status, or large disturbances such as hurricanes (Jones *et al.*, 2001; Fleming and Eby, 2003; Fleming and Murray, 2009). Given that there were no catastrophic hurricane events affecting relevant localities between sampling seasons, tracking of insect (mormoopids) and plant (*Phyllonycteris*) resources may influence differences observed. At present, there is no ongoing monitoring of cave populations to examine if these changes correspond to reproductive status, or whether they relate to phenological shifts in the abundance of insects and plan resources. Nevertheless, this study provides baseline information on the populations and sites that might be most relevant for this kind of monitoring.

Singleton Captures and Rare Species

Singleton captures greatly increase the sampling variance and therefore have a disproportionate impact on estimates of richness (Colwell and Coddington, 1994). The singleton captures of natalids (*N. major* and *C. micropus*) as well as *Eptesicus* and *Phyllonycteris* (Fig. 3), explain the wide confidence intervals in estimates of species richness at all caves except Honda de Julian (Fig. 4). Natalids are uncommon even with opportunistic sampling. The MNHNSD collection, for example, houses only seven specimens of *N. major* (one specimen from 1967, two from 1968 and four from 1975). Only three specimens of *C. micropus*, collected in 1968, have been deposited.

This paucity of natalid records likely reflects their natural abundance, tendency to live in small isolated groups, and sampling bias. In the West Indies, natalids form groups of few to 100 individuals that maintain distance between each other and remain alert Silva-Taboada (1979) and Hoyt and Baker (1980). Tejedor *et al*. (2005*b*) also found that individuals could be alert or quiet within the caves, and if those individuals perceived perturbation, they responded by flying away immediately. In addition to being rare within their roost, natalids fly slowly and close to the ground, making their capture difficult even with a harp trap.

Implications for Conservation

Historical records combined with our results suggest Los Patos and La Chepa have the highest known species richness in Hispaniola, totaling 12 species each (Table 1), and La Chepa may harbor > 12 species (Fig. 4). This richness is comparable to the highest species richness in the Caribbean, found at La Barca and Cueva del Indio with 13 species each (Silva-Taboada, 1979; Tejedor *et al*., 2005*a*). Cuba is a larger island than Hispaniola, with more species, and these two Cuban caves have experienced greater sampling effort than any Hispaniolan site. That the richness of La Chepa and Los Patos is comparable to that of La Barca highlights the conservation importance of the Hispaniolan caves.

The species accumulation curves suggest La Chepa and El Pomier require more sampling hours to achieve a complete sample during the wet season. La Chepa recorded the highest species richness in our study. Twelve of 18 bat species reported for the island were found at this site. Documenting 10 species in one Hispaniolan cave, using only one sampling method (harp trap) suggests the possibility of finding more species by using other methods of capture and extending sampling. *Natalus major* has previously been recorded at Honda de Julián and Los Patos, but in these surveys it was only sampled at La Chepa. Our results suggest La Chepa is a cave of current importance to natalid populations and deserves further sampling using alternative methods of capture as well as longer surveys using a harp trap.

Only eight species were found at Los Patos in this study, including new records for *M. blainvillei* and *E. fuscus* (Supplementary Table S1). Historically, collection effort at Los Patos has been higher in comparison with other caves, and this may explain discrepancy between the previously recorded 11 species and our new records. The majority of the populations at Los Patos might comprise few individuals, so that the high richness could not be detected with four nights of sampling. Finally, Los Patos is located near to a highway and a natural public pool and visual and olfactory evidence show that the cave entrance is commonly used as a toilet. This anthropogenic perturbation might affect the bats and may also contribute to the fewer species detected when compared to the historical sample. We propose that Los Patos is a valuable refuge whose continued use by bats merits a longer-term assessment for conservation and restricted access to the resort-visiting public.

We recorded six species at El Pomier and La Cueva Honda de Julián. At El Pomier we sampled three previously unsampled species: *P. parnellii*, *B. pumila*, and *P. poeyi*, all indicators of hot caves. Honda de Julián had by far the highest abundance of bat captures and was dominated by large moormopid populations. This cave was the one located in the most disturbed area, as cattle paddocks and pastures replace the forest that once surrounded it. Despite the environmental perturbation, two newly sampled species were found: *M. blainvillei* and *P. poeyi*. Numerous local reports suggest other caves in the vicinity of Honda de Julián also house large bat populations, and future work should focus on surveying other sites and assessing priorities for potential conservation in this transformed landscape.

Conclusion

This first systematic survey of bat populations at four Hispaniolan caves has revealed strong seasonality in a small number of bat populations, as well as the need for continued monitoring to adequately estimate richness at most sites. We also found evidence of changes in species composition through time, with possible declines in richness at Los Patos probably related to human disturbance. Seasonal variation in relative abundance results in declines in estimates of richness during the dry season, and monitoring of bats and their foraging resources is needed to understand this pattern. La Chepa was found to have the highest species richness of the caves sampled, including the rare species *N. major* and *C. micropus*, highlighting the conservation importance of this refuge.

Supplementary Information

Table S1. Species and number of individuals captured by cave. Supplementary Information is available exclusively on BioOne.

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SUPPLEMENTARY INFORMATION

Table S1. Species and number of individuals captured by cave. W = wet season, D = dry season

Taxonomy	**Honda de Julián**		**La Chepa**		**Los Patos**		**Pomier #4**		**Total**
	W	D	W	D	W	D	W	D	
Mormoopidae									
Mormoops blainvillei	40	8	1		140	10			199
Pteronotus parnellii	74	146	1		24	29	34	6	314
Pteronotus quadridens	177	95			6	4			282
Natalidae									
Chilonatalus micropus			1		1				2
Natalus major					1	1			2
Phyllostomidae									
Artibeus jamaicensis			7		7	11			25
Brachyphylla pumila			91	16	9			1	117
Erophylla bombifrons	23	71	8	4			61	10	177
Macrotus waterhousii			26	31	38	15	2		112
Monophyllus redmani	7	73	4		1	43			128
Phyllonycteris poeyi	2	6			1		95	9	113
Vespertilionidae									
Eptesicus fuscus							1		1
Total	323	399	139	51	228	113	193	26	1,472