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ORIGINAL ARTICLE

Spatio-temporal distribution and reproductive phenology of Neotropical bat species in an altitudinal gradient in Costa Rica

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Abstract

We studied the altitudinal and temporal patterns of species abundance and reproductive status for 18 Neotropical bat species during 17 continuous months in four ranges (low 50, mid–low 500, mid–high 1000, and high 2000 m a.s.l.) in an altitudinal gradient in Costa Rica. We found an effect of elevation on the abundance on ten species. We also found a combined effect of altitude and precipitation in two species; for example, *Carollia castanea* was more abundant at the low altitudinal range and during the high precipitation period, while *Sturnira hondurensis* was more abundant at the high altitudinal range and during the low precipitation period. We also found an effect of altitude and precipitation on the reproductive status of five bat species. *Carollia sowellii* and *C. castanea* showed higher number of reproductive males in the low range and reproductive females in the low altitudinal range during the high precipitation period. We also found a larger number of reproductive males of *Sturnira mordax* in the mid–high range, while pregnant females were more abundant during the low precipitation period. Our results show altitudinal and temporal patterns of abundance and reproductive phenology that highlight the need for long-term studies of species assemblages along altitudinal gradients. This information is crucial to implement conservation strategies that are species-orientated, promoting habitat protection for a large number of species in altitudinal ranges involved at the specific periods when bat abundance or reproduction is higher.

Keywords Altitudinal gradients · Bats · Reproduction · Spatio-temporal patterns

Introduction

One of the most fundamentals goals in ecology is to determine the spatio-temporal distribution of life (Gaston 2000), and how abiotic factors influence the abundance and distribution of species and populations (Sutherland et al. 2013). Spatially, the distribution of organisms has been traditionally studied either from a latitudinal or altitudinal dimension. Of these, the altitudinal distribution of biodiversity has become a major current focus on ecology and biogeography (Manga Mongombe et al. 2019) because it provides clues about the presence, absence or preferences of species to particular habitats or microclimates, and therefore it provides information of potential altitudinal range shifts of species due to changing ecological or climatic conditions (Manga Mongombe et al. 2019). In addition to the altitudinal distribution of species, the temporal dimension has also become an important topic in ecology and conservation, because even though we know that temporal variation occurs in all communities (Magurran and Henderson 2010), it is seldom recorded and thus poorly understood. The temporal

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dimension is linked to the seasonal variation of abiotic conditions and its repercussion on ecosystemic functioning, for example, through predictable changes in temperature and precipitation which affect net primary productivity (Knapp and Smith 2001; Wang et al. 2013). As a consequence, the temporal dimension affects the altitudinal distribution of biodiversity in multiple ways, most notably for species that rely on specific food sources that change over time (Aguirre et al. 2003).

Mountain environments represent ideal model systems to investigate the interrelation of altitudinal and temporal variation on biodiversity (Willig and Presley 2016) because there is a suite of factors that affect the composition of species in space and time (Stegen et al. 2013). From the lowlands to the highlands, tropical mountains contain multiple habitats (Martins et al. 2015) that result from the large variation in climatic variables with altitude. For example, temperature is known to decrease from 0.4 to 0.6 °C with an increase of 100 m in elevation, whereas precipitation follows four patterns depending on latitude, prevailing winds, and slope: (1) an increase of precipitation with an increase in altitude, (2) a decrease of precipitation with an increase in altitude, (3) low- and mid-elevations peaks in precipitation or (4) a mid-elevation peak (McCain and Grytnes 2010). The variation in climatic conditions makes montane ecosystems ideal systems to study the processes that determine species assemblages along environmental gradients (Bateman et al. 2010).

Tropical montane landscapes harbor high diversity of species, usually with many co-existing species within climatic zones or habitat types (Jankowski et al. 2009). They are also considered as areas of high endemism, and thus of high relevance for conservation efforts (Foster 2001; McCain and Colwell 2011). The full set of interactions among climatic variables with elevation is predicted to allow climate change to impact mountain ecosystems in multiple ways, including range shifts, range contractions and extinctions (Bonebrake et al. 2018). Tropical mountains are also important areas for human populations given they provide between 60 and 80% of the fresh water of the planet and more than 900 million people live in mountains (90% of them in developing countries and 40% vulnerable to food insecurity) (Romeo et al. 2015). As a result of the human pressure for natural resources, mountain ecosystems have been converted into grasslands, cattle areas, agriculture and plantations (Foster 2001).

Tropical mountains ecosystems are under the influence of multiple threats, making them important areas for studies that would allow us to properly guide conservation efforts, especially for taxa that may be considered vulnerable. Bats are an example of a group of organisms that may be of great concern, as their high metabolic rates and longevity make them highly vulnerable to anthropogenic changes (Voigt and Kingston 2016). Another important trait that makes bats highly vulnerable is their reproductive biology; bats have low reproductive rates, with small litter sizes (one pup is the most common), large pups in comparison with equally sized terrestrial mammals, coupled with long gestation and lactation periods (Racey and Entwistle 2000). These features make reproduction a highly demanding energetic period (especially lactation) for bats (Kunz and Wood 2000); thus, resource availability and its allocation are critical, especially because reproductive phenology of bat populations (e.g., pregnancy, birth, lactation) are deeply influenced by climatic variables (Durant et al. 2013). Montane bats have also been poorly studied compared to lowland species (Rodríguez-Herrera 2004), and it may even be possible that some highly specialized and spatially restricted montane species have yet to be discovered (Chaverri et al. 2016). Given that abiotic conditions vary widely even among short distances in altitudinal gradients, the study of the effect of climate on reproductive patterns is important for designing adequate conservation efforts and policies, especially if altitudinal movements are involved and the protection of altitudinal ranges that harbor the best reproductive habitats for different bat species is required (De Carvalho et al. 2019a, b).

The understanding of the spatial and temporal distribution and reproduction of bat species in altitudinal gradients is important given the current loss of species caused by the widely recognized, diverse, synergic and complex group of drivers of extinction (climate change, habitat loss, species range shifts, and invasive species) (Heaney 2001). This understanding has become probably one the most important challenges in current conservation science, especially because effective conservation management, strategies and prioritization require knowledge about organism distribution and density (Johnston et al. 2015). In consequence, the aims of this study were (1) to analyze the spatio-temporal distribution and reproductive phenology of bat species in a Neotropical altitudinal gradient, and (2) to investigate how climatic variables are related to the altitudinal and temporal distribution of reproductive events. We expect to observe a similar distribution of altitudinal ranges described for Neotropical species in previous studies (Arias-Aguilar et al. 2020; Bejarano-Bonilla et al. 2007; Coelho et al. 2018; Echeverria 2013; Martins et al. 2015; Navarro and León-Paniagua 1995; Patterson et al. 1996; Rodriguez-Rocha 2017; Timm et al. 1989). Within a species' altitudinal range, we also expect to find temporal differences in abundance according to the availability of food, which is often associated with more precipitation (Fleming 1982; Grindal et al. 1992; Ramos Pereira et al. 2010). Finally, since lactation is known to be the most energetically demanding reproductive stage (Kurta et al. 1989; Racey and Entwistle 2000), we expect to find the majority of lactating females during periods of highest known food availability.

Materials and methods

Study site

Our study site corresponded to the altitudinal gradient of Braulio Carrillo National Park (BCNP) and private reserves located in Área de Conservación Cordillera Volcánica Central, in the northeast part of the Caribbean slope of Costa Rica (Fig. 1). With its 47 689 hectares, the Braulio Carrillo National Park (BCNP) is one of the biggest protected areas in the country, and covers four provinces (SINAC 2005). The altitudinal gradient studied spans a continuous forest track from 30 m a.s.l. in the lowlands to 2906 m a.s.l. at Barva Volcano (Timm et al. 1989). According to Clark et al. (2015), the annual rainfall in the highlands is about 3000 mm, around 4000 mm in the lowlands and as much as 9000 mm at middle elevations, whereas temperature averages 25 °C in the lowlands and 10 °C at the mountaintop (Clark et al. 2015; SINAC 2005). In the altitudinal gradient, there are four life zones and two transition zones represented (Timm et al. 1989) (Fig. 1).

We established four altitudinal ranges along the gradient: the low range with altitudes from 50 to 150 m a.s.l., the mid–low range with altitudes from 375 to 500 m in elevation, the mid–high range from 975 to 1050 m a.s.l., and the high range with altitudes from 1950 to 2050 m in elevation (Table 1). Each range is located in a different life zone (Fig. 1); the low range represents Tropical Wet Forest, the mid–low range is covered by Tropical Wet Forest Premontane belt Transition, the mid–high range represents Premontane Rain Forest, and the high range is covered by Lower Montane Rain Forest. At each altitudinal transect, we established two or three study sites (Table 1), and in each site, we used from 2 to 4 sampling locations depending on topographic conditions. This allowed us to sample the spatial heterogeneity of the altitudinal ranges and to decrease oversampling at the same location (Marques et al. 2013).

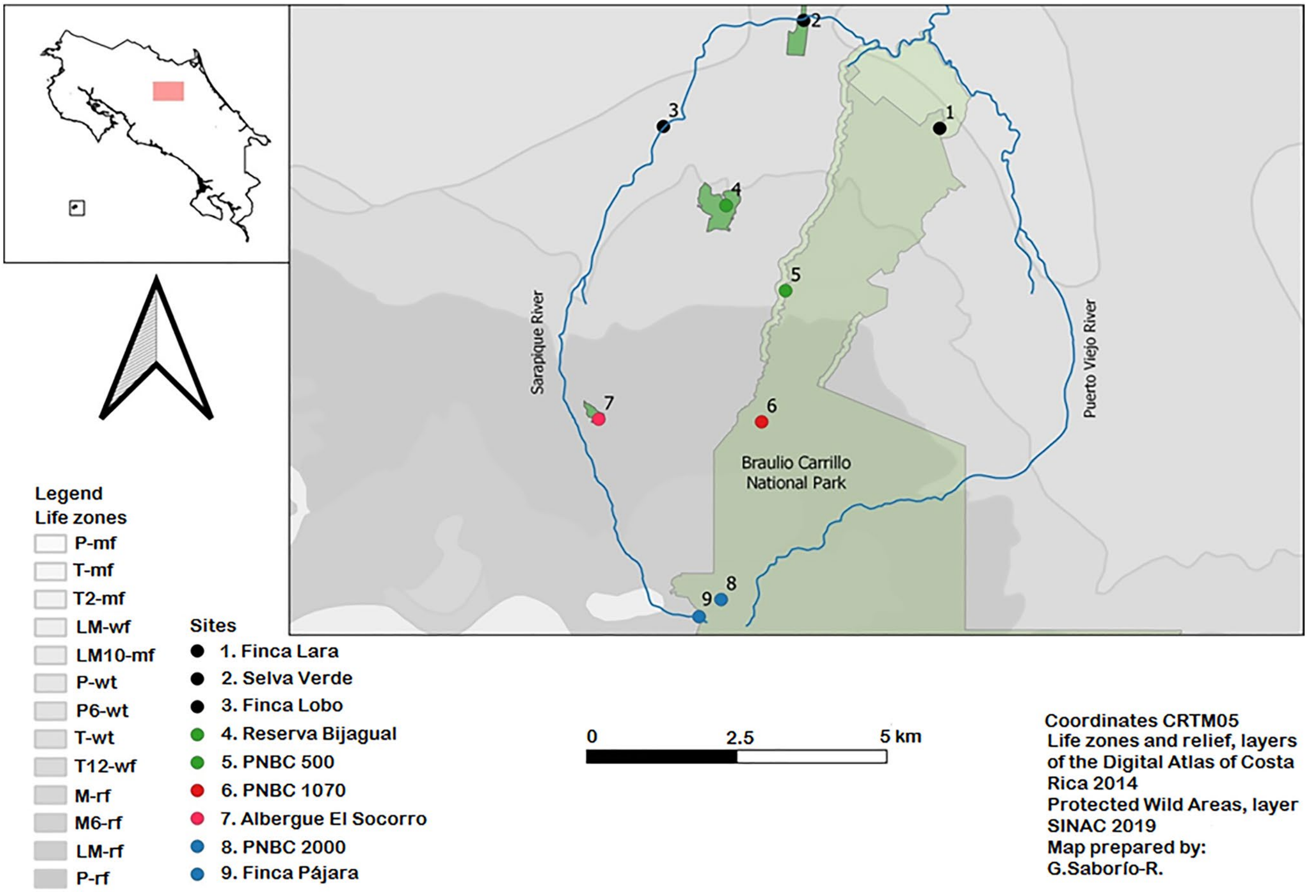


Fig. 1 Sampling sites for altitudinal ranges (black = low range, green = mid–low range, red = mid–high range, and blue = high range), and life zones in the study site of Braulio Carrillo National Park, and private reserves, Costa Rica

Table 1 Range name, life zone, study site, and altitude (m a.s.l.) of the BCNP and private reserves of the study area

Altitudinal range name and range (m a.s.l.)	Life zone	Study sites	Altitude (m a.s.l.)
Low (50–150)	Tropical Wet Forest	Finca Lara	50
		Finca Lobo	80
		Selva Verde Reserve	73
Mid–low (375–500)	Tropical Wet Forest transition to Premontane	Bijagual Reserve	375
		PNBC 500	500
Mid–high (975–1050)	Tropical Premontane Rain Forest	PNBC 1070	1070
		El Socorro Reserve	975
High (1950–2050)	Tropical Lower Montane Rain Forest	PNBC 2000	2000
		Pájara Reserve	1950

Field work

We sampled bats monthly with 8–10 mist-nets (12 m × 2.5 m; mesh 40 mm, Avinet Ltd.) at the four altitudinal ranges from August 2013 to December 2014. Each month, we randomly selected the order in which each site was sampled. All sites were sampled once per month, but sampling was not possible in the mid–low range in June 2014 given the high precipitations that prevented us from accessing the site. Mist-nets were positioned at ground level along trails, forest gaps, and streams from 17:30 to 05:00 h in one night or from 17:30 to 23:00 h in two consecutive nights, depending on weather conditions, storms, or for security reasons. The sample effort per range per month was calculated by multiplying the number of mist-nets used by the number of hours they were opened for and by the length of the mist-net, following Medellín (1993). After capture, each bat was placed in an individual cloth bag and later processed. We identified species based on Timm et al. (1999); sex and reproductive status (scrotal males, pregnant females, lactating females) were determined by external genitalia inspection. After processing, bats were released near the capture site. All research permits (ACCVCR-R-INV-0013, 060-2012-ACCVCR-PI, and 021-2013- ACCVCR-PI) were obtained at Ministerio de Ambiente y Energía (MINAET), Sistema de Áreas de Conservación (SINAC), Área de Conservación Cordillera Volcánica Central (ACCVC), Costa Rica. Finally, we followed the guidelines of animal care and live capture for bats of Sikes and Gannon (2011).

Climatic variables

For each altitudinal range, we obtained monthly precipitation (mm) and temperature (°C) data from meteorological stations of the Organization for Tropical Studies (OTS) for low and mid–low ranges, Instituto Costarricense de Electricidad (ICE), Rara Avis EcoLodge and La Paz Waterfall Lodge for the mid–high and high altitudinal ranges. All measurements were averaged daily, and monthly average was used in all analyses. We assumed temperature is implicitly included in the altitudinal dimension given the high correlation between these variables ($r = -0.97$). Based on the precipitation data, we established three periods: low precipitation from January to April, high precipitation from May to July, and mid-precipitation from August to December (Supplementary Material 1).

Data analysis

We estimated species abundance per month at each altitudinal range for 18 bat species with $n > 20$ individuals registered during the entire study period. These 18 species belong to different feeding guilds (two aerial insectivorous species, two nectarivorous species, 13 frugivorous species, and one hematophagous species). Monthly abundance data were divided by the sample effort of that month. We also estimated the abundance of three reproductive stages, scrotal males, pregnant females, and lactating females, per month at each altitudinal range of the six species with the highest abundance ($n > 99$). We fitted generalized linear models to test the effect of altitude and precipitation period in the abundance of species and reproductive stages of all species used. We fitted all models with the interaction terms between altitude and precipitation. All analyses were performed in InfoStat (Di Rienzo et al. 2020).

Results

We captured a total of 1834 bats belonging to 54 species representing five families (Phyllostomidae, Vespertilionidae, Emballonuridae, Thyropteridae and Mormoopidae). We selected 18 species (1667 individuals representing 90.9% of the individuals captured) for the analysis (species with $n > 20$ individuals). The species with the highest abundance recorded in the gradient was *Sturnira hondurensis* with 450 individuals and the species with the lowest abundance was *Artibeus lituratus* with 24 individuals (Table 2). Frugivorous

Table 2 Number of individuals captured of the 18 species with the highest abundance ($n > 20$) at our study site

Species	Altitudinal range			
	Low	Mid–low	Mid–high	High
Pteronotus mesoamericanus	1	21	2	0
Myotis pilosatibialis	0	0	17	14
Anoura cultrata	0	0	20	10
Hylonycteris underwoodi	3	2	15	17
Carollia castanea	55	38	34	0
Carollia perspicillata	51	135	25	0
Carollia sowellii	33	55	60	0
Artibeus jamaicensis	68	26	5	0
Artibeus lituratus	16	7	0	0
Dermanura azteca	0	0	1	23
Dermanura phaeotis	21	6	8	0
Dermanura tolteca	0	0	42	60
Dermanura watsoni	30	34	16	0
Ectophylla alba	29	0	0	0
Uroderma convexum	54	0	0	0
Sturnira hondurensis	0	1	72	377
Sturnira mordax	0	6	82	45
Desmodus rotundus	6	17	5	1

bats represent the majority of the bats captured (90.8%), followed by nectarivorous bats with 4%, then insectivorous bats with 3.3%, and finally hematophagous bats represent the remaining 1.9% of the individuals captured.

We found an effect of altitude on the abundance of ten species (Table 3). Two species showed higher abundance in the low range: *Ectophylla alba* (Fig. 2a) and *D. watsoni* (Fig. 2b). Two species were more abundant in the mid–low range, *Carollia perspicillata* (Fig. 2c) and *P. mesoamericanus* (Fig. 2d). One species, *S. mordax*, showed higher abundance in the mid–high range than at any other range (Fig. 2e). The nectarivorous bats *A. cultrata* (Fig. 2f) and *H. underwoodi* showed higher abundance both in the mid–high and high ranges (Fig. 2g). Finally, *D. azteca* showed a higher abundance in the high range than at any other range (Fig. 2h).

We also found an effect of altitude and its interaction with precipitation period on the abundance of *Carollia castanea* and *Sturnira hondurensis*. *Carollia castanea* showed the highest abundance at the low and mid–high altitudinal range during the high precipitation period as well at the mid–low altitudinal range during the mid-precipitation period and at the low altitudinal range at the low precipitation period (Fig. 3a). *Sturnira hondurensis* showed the highest abundance at the high altitudinal range and low precipitation period than any other altitudinal range and period (Fig. 3b). We did not find an effect of elevation, precipitation period or their interaction on the species *M. pilosatibalis*, *C. sowellii*, *A. jamaicensis*, *A. lituratus*, *D. phaeotis*, *D. tolteca*, *U. convexum* and *D. rotundus* (Supplementary Material 2).

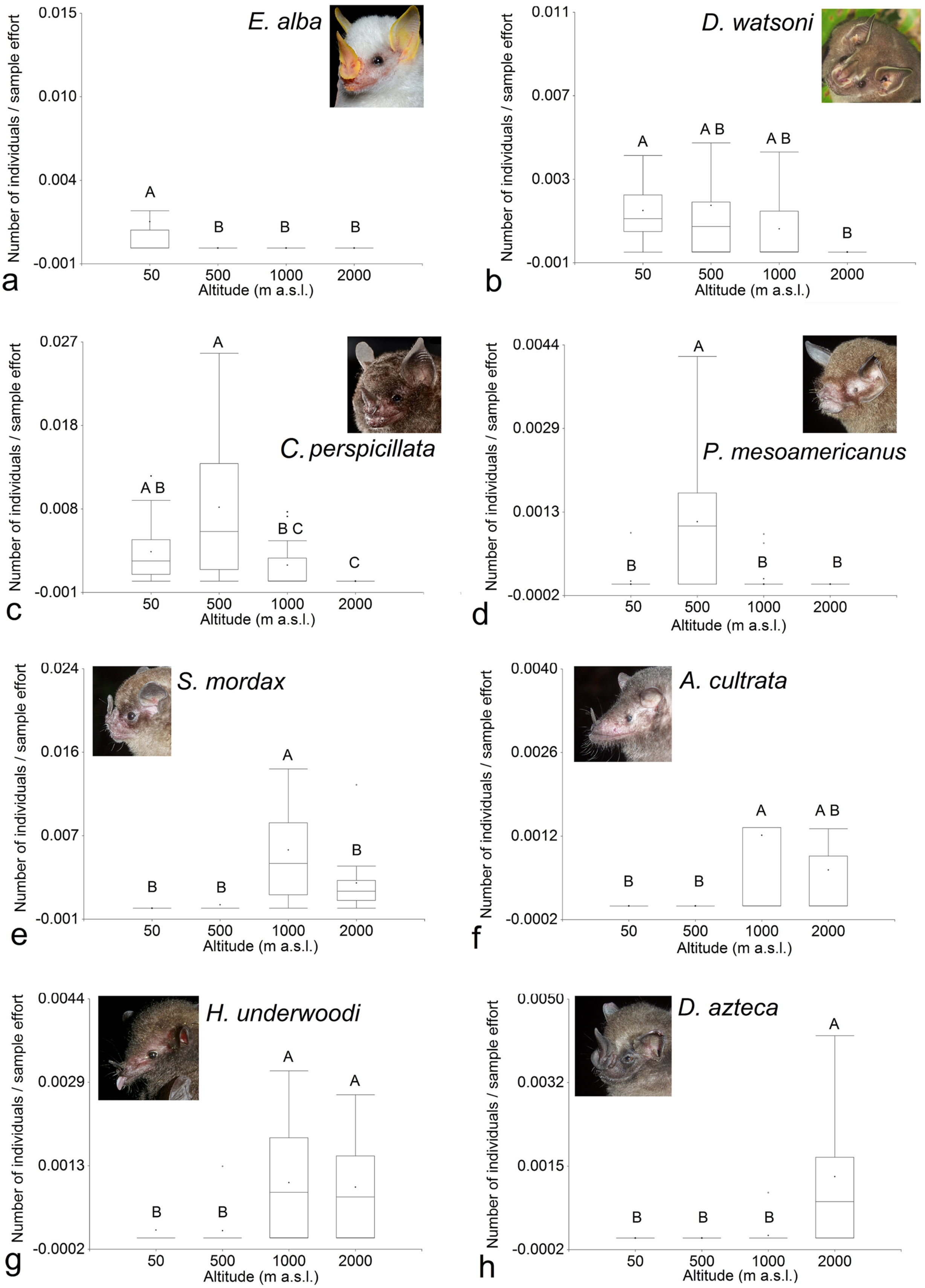
Table 3 Results of generalized linear models testing the effects of altitude and precipitation, and their interaction, on the abundance of ten species of Neotropical bats

Species	Predictive variable	*d.f*	*F*	*p*
P. mesoamericanus	Altitude	3,55	5.14	**0.0033**
	Precipitation period	2,55	0.68	0.5110
	Interaction	6,55	0.36	0.8999
A. cultrata	Altitude	3,55	2.87	**0.0493**
	Precipitation period	2,55	0.90	0.4143
	Interaction	6,55	0.40	0.8746
H. underwoodi	Altitude	3,55	4.49	**0.0068**
	Precipitation period	2,55	0.33	0.7196
	Interaction	6,55	0.36	0.9013
C. castanea	Altitude	3,55	6.96	**0.0005**
	Precipitation period	2,55	2.25	0.1152
	Interaction	6,55	3.07	**0.0116**
C. perspicillata	Altitude	3,55	4.80	**0.0048**
	Precipitation period	2,55	1.75	0.1839
	Interaction	6,55	2.04	0.0756
D. azteca	Altitude	3,55	4.27	**0.0088**
	Precipitation period	2,55	0.14	0.8704
	Interaction	6,55	0.36	0.9030
D. watsoni	Altitude	3,55	3.42	**0.0233**
	Precipitation period	2,55	2.93	0.0616
	Interaction	6,55	1.62	0.1579
E. alba	Altitude	3,55	2.92	**0.0422**
	Precipitation period	2,55	1.43	0.2491
	Interaction	6,55	1.43	0.2199
S. hondurensis	Altitude	3,55	22.52	**0.0001**
	Precipitation period	2,55	0.57	0.5700
	Interaction	6,55	2.32	**0.0453**
S. mordax	Altitude	3,55	6.77	**0.0006**
	Precipitation period	2,55	0.32	0.7275
	Interaction	6,55	0.19	0.9792

Significant effects after Bonferroni correction ($p < 0.05$) are printed in bold. The table only includes results for species in which a significant effect was observed (see Supplementary Material 2 for results on other species)

There was an effect of altitude on the abundance of scrotal males in two of the six most common species (Table 4). Specifically, we found a higher number of scrotal males of *Carollia sowellii* in the low and mid–high ranges (Fig. 4), whereas the number of scrotal males of *Sturnira mordax* was higher at the mid–high elevation than any other altitudinal range (Fig. 4). We also detected an effect of precipitation period on the abundance of scrotal males of *A. jamaicensis*, where the highest number was found in the high precipitation period more than at any other period. We did not find an effect of altitude, precipitation period or its interaction on the abundance of scrotal males of *C. castanea*, *C. perspicillata*, and *S. hondurensis* (Supplementary Material 3).

There was an effect of altitude, precipitation period and their interaction on the abundance of lactating females of


a
E. alba
Number of individuals / sample effort
0.015
0.010
0.004
-0.001
A
B
B
B
50
500
1000
2000
Altitude (m a.s.l.)
b
D. watsoni
Number of individuals / sample effort
0.011
0.007
0.003
-0.001
A
A B
A B
B
50
500
1000
2000
Altitude (m a.s.l.)
c
C. perspicillata
Number of individuals / sample effort
0.027
0.018
0.008
-0.001
A B
A
B C
C
50
500
1000
2000
Altitude (m a.s.l.)
d
P. mesoamericanus
Number of individuals / sample effort
0.0044
0.0029
0.0013
-0.0002
B
A
B
B
50
500
1000
2000
Altitude (m a.s.l.)
e
S. mordax
Number of individuals / sample effort
0.024
0.016
0.007
-0.001
B
B
A
B
50
500
1000
2000
Altitude (m a.s.l.)
f
A. cultrata
Number of individuals / sample effort
0.0040
0.0026
0.0012
-0.0002
B
B
A
A B
50
500
1000
2000
Altitude (m a.s.l.)
g
H. underwoodi
Number of individuals / sample effort
0.0044
0.0029
0.0013
-0.0002
B
B
A
A
50
500
1000
2000
Altitude (m a.s.l.)
h
D. azteca
Number of individuals / sample effort
0.0050
0.0032
0.0015
-0.0002
B
B
B
A
50
500
1000
2000
Altitude (m a.s.l.)

◂**Fig. 2** Altitudinal abundance of 8 bat species in the study site: **a** *Ectophylla alba*, **b** *Dermanura watsoni*, **c** *Carollia perspicillata*, **d** *Pteronotus mesoamericanus*, **e** *Sturnira mordax*, **f** *Anoura cultrata*, **g** *Hylonycteris underwoodi*, and **h** *Dermanura azteca*. Different letters denote significant differences among ranges based on a posteriori Tukey–Kramer test

C. castanea (Table 4). We found a higher number of lactating females in the low altitudinal range and high precipitation period than at any other combination of elevation and precipitation periods (Fig. 5a). We did not find an effect of altitude, precipitation period or their interaction on the abundance of lactating females of *C. perspicillata*, *C. sowellii*, *A. jamaicensis*, *S. hondurensis*, *and S. mordax* (Supplementary Material 3).

Finally, we found an effect of altitude, precipitation period and their interaction on the abundance of pregnant females of *C. sowellii* (Table 4). The highest abundance was registered on the low altitudinal range and high precipitation period than at any other elevation and precipitation period (Fig. 5b). We also detected an effect of the precipitation period on the abundance of pregnant females of *S. hondurensis* and *S. mordax* (Table 4), where the number of pregnant females for both *S. hondurensis* and *S. mordax* was higher in the low precipitation period. We did not find an effect of altitude, precipitation period or their interaction on the abundance of pregnant females of *C. castanea*, *C. perspicillata*, and *A. jamaicensis* (Supplementary Material 3).

Discussion

We found a correlation between altitude and climatic variables with the abundance and reproduction of the most common bat species in a tropical altitudinal gradient. According to our prediction, the altitudinal range of the species studied coincides with their known altitudinal distribution (Baker et al. 2002; Cloutier and Thomas 1992; LaVal 2004; LaVal and Rodríguez-Herrera 2002; Matson and McCarthy 2004; Reid 1997; Tamsitt and Nagorsen 1982; Timm 1982; Torres-Morales 2019; Webster and Knox Jones 1982) and follows a clear segregation pattern. We found, for example, that *Ectophylla alba* and *D. watsoni* were most abundant at the low range, *Carollia perspicillata* and *P. mesoamericanus* at the mid–low range, *S. mordax* at the mid–high range, *A. cultrata* and *H. underwoodi* at both the mid–high and high ranges, and *D. azteca* was most abundant at the high range.

The effect of altitude on species abundance in phyllostomid assemblages has been characterized in other Neotropical sites (Bejarano-Bonilla et al. 2007; De Carvalho et al. 2019a, b; Estrada-Villegas et al. 2010; Estrada and Coates-Estrada 2001; Martins et al. 2015; Patterson et al. 1996), where the common pattern consists of some species that are mostly found at lower altitudes (e.g., species of *Carollia*), and other species mostly found at higher altitudes (e.g., some species of *Sturnira*). However, the altitudinal patterns observed in our study showed that even if species have been recorded by different authors in a wide altitudinal distribution, the bats species of our study site showed specific responses to particular altitudes in this gradient. For example, even if *S. mordax* has been recorded from sea level to 3000 m a.s.l. in its geographic distribution (Matson and McCarthy 2004), in this study, it was more abundant at 1000 m a.s.l. than at any other altitude, which is opposite to the altitudinal pattern found in other regions of the country as in Monteverde´s Premontane Tropical Forest where it is usually found at higher altitudes (LaVal 2004; LaVal and Rodríguez-Herrera 2002).

Differences in the altitudinal distribution of species within a taxon have been explained by a suite of factors, including food availability (Fleming and Eby 2003; Hernindez-Conrique et al. 1997; Nobre et al. 2013), competition (Jankowski et al. 2010), physiological limitations (Castaño et al. 2018; Soriano et al. 2002), evolutionary history (Giannini 1999; Sánchez and Giannini 2014), or abiotic conditions (Coelho et al. 2018; De Carvalho, et al. 2019a, b; McCain 2006; Sánchez-Cordero 2001; Willig and Presley 2016). In the latter case, we found a combined effect of altitude and precipitation in the distribution of two species: *Carollia castanea* and *Sturnira hondurensis*. In support of our prediction, we found that *Carollia castanea* was more abundant at the low altitudinal range during the high precipitation period, while in contrast to our prediction, *Sturnira hondurensis* showed higher abundance at the high altitudinal range and low precipitation period. Temperature and precipitation are the two abiotic variables most often associated with species range limits (McCain and Colwell 2011). Precipitation is known to affect species distribution in multiple ways, either indirectly by, for example, influencing food production (Estrada and Coates-Estrada 2001; Fleming 1982; Mello and Fernandez 2000; Mello et al. 2004, 2009; Racey 1979; Racey and Entwistle 2000; Ramos Pereira et al. 2010) or directly by affecting foraging efficiency. In the latter case, Boyle et al. (2010) found that high precipitation produced by severe tropical storms reduce foraging opportunities in a tropical bird species (*Corapipo alterra*), restricting the number of hours available for foraging and thus energy intake, which might drive altitudinal movements from mid to low elevations in search of better climatic conditions.

Because reproduction represents costs both in the short (energetic expense) and long term (body condition), it is expected that bat species make decisions about where and when to reproduce in relation to body condition, food availability and its allocation for reproduction (Gittleman and Thompson 1988; Racey and Entwistle 2000). For example, the reproductive patterns observed in our study for *C.*

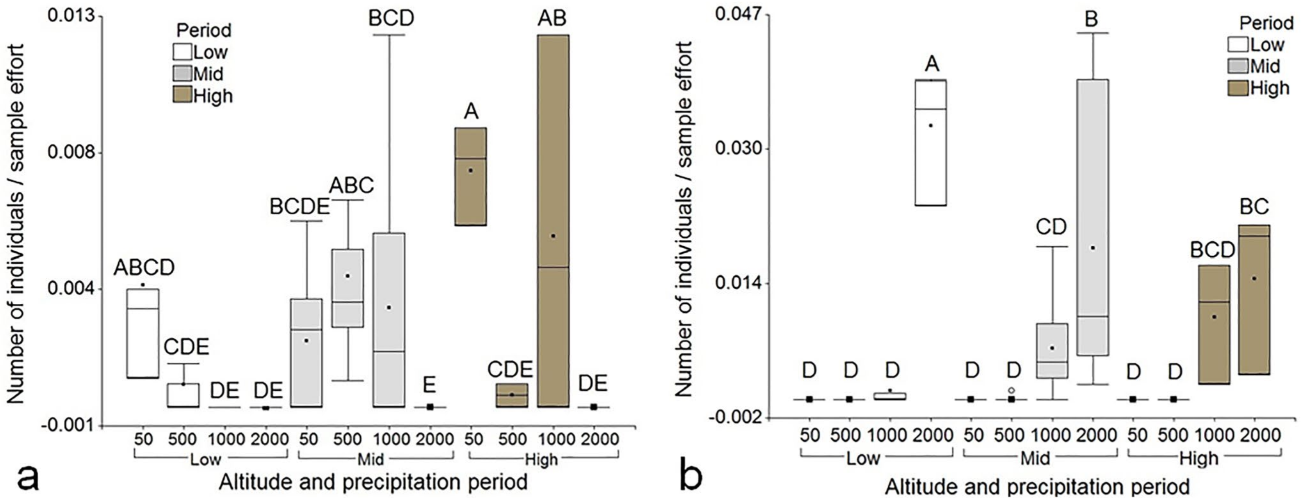


Fig. 3 Abundance per period (according to precipitation) and altitude of **a** *Carollia castanea* and **b** *Sturnira hondurensis* in the study site. Different letters denote significant differences among altitudinal ranges based on a posteriori Tukey-Kramer test

Table 4 Results of generalized linear models testing the effects of altitude and precipitation, and their interaction, on reproductive status (scrotal males, lactating females, pregnant females) of five species of Neotropical bats

Species	Reproductive status	Predictive variable	*d.f*	*F*	*p*
C. castanea	Lactating females	Altitude	3,55	3.45	**0.0227**
		Precipitation period	2,55	3.39	**0.0409**
		Interaction	6,55	2.47	**0.0345**
C. sowellii	Scrotal males	Altitude	3,55	3.54	**0.0204**
		Precipitation period	2,55	1.82	0.1709
		Interaction	6,55	1.15	0.3443
	Pregnant females	Altitude	3,55	9.49	**0.0001**
		Precipitation period	2,55	10.27	**0.0002**
		Interaction	6,55	5.81	**0.0001**
A. jamaicensis	Scrotal males	Altitude	3,55	2.15	0.1038
		Precipitation period	2,55	3.78	**0.0289**
		Interaction	6,55	1.42	0.2253
S. hondurensis	Pregnant females	Altitude	3,55	2.34	0.0838
		Precipitation period	2,55	4.70	**0.0130**
		Interaction	6,55	1.91	0.0961
S. mordax	Scrotal males	Altitude	3,55	4.26	**0.0089**
		Precipitation period	2,55	0.04	0.9607
		Interaction	6,55	0.15	0.9891
	Pregnant females	Altitude	3,55	1.14	0.3422
		Precipitation period	2,55	3.26	**0.0461**
		Interaction	6,55	1.24	0.3010

Significant effects after Bonferroni correction ($p < 0.05$) are printed in bold. The table only includes results for species in which a significant effect was observed (see Supplementary Material 3 for results on other species)

sowellii and *C. castanea* are similar to the ones found in an altitudinal gradient in Brazil by De Carvalho et al. (2019a, b), and in Costa Rica by Durant et al. (2013), where they found higher reproductive activity associated with higher precipitation and temperature, conditions that allow higher food availability (De Carvalho, et al. 2019a, b; Durant et al. 2013; Estrada and Coates-Estrada 2001; Lopez and Vaughan 2007; Mello and Fernandez 2000). We expected to find the majority of lactating females during periods of highest known food availability, which is often associated with more precipitation, yet we only found an effect of high precipitation on the number of lactating females in one of the six species studied (*C. castanea*). There was also an effect of high precipitation on the number of pregnant females for *C. sowellii*. Since pregnancy and lactation are highly energetically demanding stages (Kurta et al. 1989; Racey and Entwistle

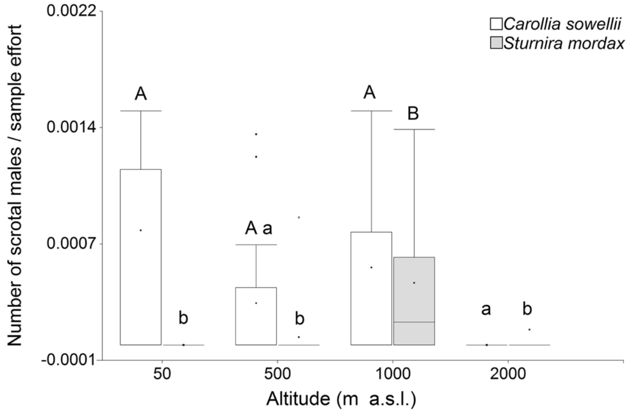


Fig. 4 Number of scrotal males/sample effort by altitude of *Carollia sowellii* and *Sturnira mordax* in the study site. Uppercases denote significant differences to lowercases of the same letter among altitudinal ranges within a species based on a posteriori Tukey-Kramer test

2000), timing these processes with high food availability might be crucial for successful reproduction and might help explain altitudinal and temporal distribution of Neotropical bat species. However, there is a clear gap on the information about productivity and food availability in the temporal or altitudinal dimensions for different taxa, which probably explains why we did not find support to our prediction for all species; therefore, long-term studies on plant phenology and arthropod abundance in tropical altitudinal gradients are necessary to understand the relationship between climatic factors, food availability and reproduction on Neotropical bat assemblages. The two mid- and high-elevation species of *Sturnira* studied are an example of this lack of information, given both showed an effect of precipitation (low) on the number or pregnant females, a result that requires further study. This information is needed to create local and regional conservation strategies aimed to protect as many species as possible and they are especially important for montane bats that have high extinction risk (McCain and Colwell 2011).

The temporal and altitudinal patterns that reproductive bats in our area showed (low vs. mid–high altitudes and low vs. high precipitation) reflect the diversity of ecological and evolutionary pathways of bat assemblages in tropical altitudinal gradients, and the importance of protecting continuous altitudinal forest tracks. Understanding how species abundance and reproductive patterns are influenced by altitude and precipitation is important as this would allow us to implement better conservation strategies that are species-orientated, including prioritization of habitat protection in the altitudinal ranges involved at the specific periods where bat abundance is higher or when critical reproductive activities are taking place. The temporal and altitudinal distribution of bat species detected and their interaction with reproductive status highlights the importance of studying and protecting altitudinal gradients that cover a wide range of habitats (De Carvalho et al. 2019a, b). Unfortunately, habitats found at different altitudes have suffered multiple threats; for example, habitat destruction and overexploitation threaten mostly lowland forests (Nogués-Bravo et al. 2008; White and Bennett 2015). Forest areas have also been almost completely eliminated from Tropical Moist and Tropical Premontane Moist Forests (Sánchez-Azofeifa et al. 2001), while montane forests have been affected by climate change, pollution by pesticides and forest conversion to agriculture and cattle ranching (Foster 2001; Shunthirasingham et al. 2011).

Given that bats have low reproductive rates, high longevity, high metabolic rates, and high energetic requirements, they are particularly susceptible to multiple threats (Voigt and Kingston 2016). Therefore, the recorded

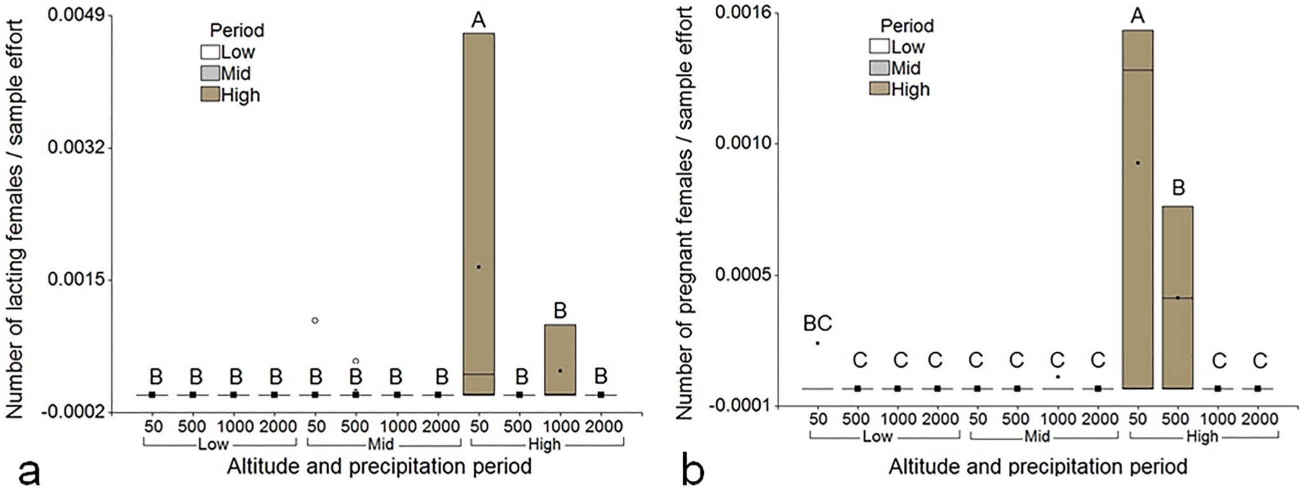


Fig. 5 Abundance per period (according to precipitation) and altitude of **a** lactating females of *Carollia castanea* and **b** pregnant females of *Carollia sowellii* in the study site. Different letters denote significant differences among altitudinal ranges based on a posteriori Tukey-Kramer test

altitudinal distribution of bat species, as well as their reproductive patterns, should be considered when planning conservation strategies especially because extinction risk increases when species show narrow altitudinal ranges (White and Bennett 2015), and particularly if species are forced to shift their altitudinal range due to changing environments (Bonebrake et al. 2018). Finally, it is important to study the impact of climate change in the altitudinal distribution and reproduction of bats, not only because the variation in precipitation probably affects food availability, but also because bats are unable to react quickly to short-term environmental changes given they may cue on seasonal changes to optimize their timing of reproduction (Racey and Entwistle 2000). Further studies on the temporal and spatial distribution of bats in tropical altitudinal gradients are crucial to detect changes in their reproductive patterns to create stronger tools that may guide effective conservation strategies and therefore tackle extinction risk, especially under different climate change scenarios (Manga Mongombe et al. 2019; Sundqvist et al. 2013).

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Author contributions All authors designed the research, performed field work, performed the statistical analysis, and drafted the manuscript.

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Availability of data and material Not applicable.

Code availability Not applicable.

Declarations

Conflict of interest None of the authors have conflict of interest to declare nor competing interest.

Ethics approval All research permits were issued by the Costa Rican Minister of Environment (MINAE): ACCVCR-R-INV-0013, 060-2012-ACCVCR-PI, and 021-2013- ACCVCR-PI. We also followed the guidelines of animal care and live capture for bats of Sikes y Gannon (2011).

Consent to participate All authors have consented to participate.

Consent for publication All authors have consented to publish this research.

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