Published by Associazione Teriologica Italiana
Hystrix, the Italian Journal of Mammalogy
Volume 31 (1): 58–63, 2020
OPEN ACCESS
Available online at:
http://www.italian-journal-of-mammalogy.it
doi:10.4404/hystrix-00244-2019

Research Article

Diversity and activity patterns of aerial insectivorous bats along an altitudinal gradient in a tropical forest in Costa Rica

Adriana Arias-Aguilar[1,*], Eduardo Chacón-Madrigal[2,*], Richard LaVal[3,*], Bernal Rodríguez-Herrera[2,*]

[1] *Universidade Federal do Rio Grande do Sul*
[2] *Escuela de Biología, Universidad de Costa Rica*
[3] *The Bat Jungle, Monteverde, Costa Rica*

Keywords:
species richness
weather conditions
elevation
acoustic monitoring
foraging activity
cloud forest

Article history:
Received: 01/10/2019
Accepted: 07/05/2020

Acknowledgements
We thank the Tropical Science Center for all the support provided, especially to the Investigation Program, and the Spanish Agency for International Development Cooperation (AECID) funding projects D/027406/09, D/033858/10 and A1/039089/11. We are very grateful to Julio Madriz for his field assistance.

Abstract

Bat diversity and activity have been documented to change with elevation and to be correlated with temperature variation, especially in temperate regions. Acoustic elevational studies of insectivorous bat fauna in tropical mountains are scarce. Here, we investigated diversity, general and species-specific activity patterns of aerial insectivorous bats along an elevational gradient in Costa Rica and tested the hypothesis that on tropical wet mountains species richness of insectivorous bats follows a decreasing pattern with elevation. We expected a peak of species diversity and activity at lower elevations and higher temperatures and no major differences between months. With simultaneous acoustic monitoring on five elevations, we recorded 11 984 bat passes during approximately 550 recording hours and identified 15 species, two genera and one sonotype at the family level. We found the highest diversity and activity of bats at mid-elevations, besides elevational, temporal and species-specific differences that were partially explained by temperature. The fact that in our transect humidity does not change with elevation may explain observed differences from the expected patterns. Climate change in Monteverde could be one of the factors resulting in elevational movements of bats to mid-elevations, probably affecting the availability of food resources, and thus the foraging activity of aerial insectivorous bats.

Introduction

Understanding patterns of biological diversity and activity along elevational gradients provides valuable insights for conservation at small geographical scales but yet for many mountain ecosystems these patterns are not well documented (Patterson et al., 1989; Lomolino, 2001; Sánchez-Cordero, 2001; Bender and Hartman, 2015). Small mammals like bats are particularly useful in the study of diversity along elevational gradients because they are key organisms in the structure, composition, and dynamics of tropical ecosystems; generally, they have high diversity and abundance, and participate in multiple biological processes such as pollination, seed dispersal, insect predation and food webs (Fleming et al., 1972; McNab, 1982; Fleming, 1986; Fenton, 1997; Mena et al., 2011). By understanding patterns and correlates of variation in activity of bats, the design of research and monitoring programs can be improved (Hayes, 1997). Studies of bats along elevational gradients in the Neotropics have been mainly focused on patterns of distribution and composition of species principally through the use of mist nets as the main capture technique (e.g., Patterson et al., 1996; Sánchez-Cordero, 2001; Echeverría-Tello, 2013; Refulio, 2015) and in a very few cases with acoustic methods (e.g., Ortiz-Badillo, 2015). As a result, aerial insectivorous bats have usually been underestimated (O'Farrell and Gannon, 1999; Ochoa et al., 2000). For this group, which may comprise about one-third of all bat species in the region (Jung and Kalko, 2010), it is feasible to monitor echolocation calls through the use of acoustic detectors because they allow species identification as well as the assessment of distributional patterns and habitat use (Fenton, 1997; Kalko and Schnitzler, 1998; Ochoa et al., 2000). Studies of the insectivorous bat fauna activity using acoustic detectors along elevational gradients are common in the Paleartic (e.g., Piksa et al., 2011; Müller et al., 2012) and Neartic realms (e.g., Grindal et al., 1999; Wolbert et al., 2014), but scarce in the Afrotropic (e.g., Linden et al., 2014) and, to our knowledge, almost none exist for the Neotropic. Bat diversity and richness have been documented to vary with elevation, been strongly correlated with temperature (McCain, 2007) and usually showing a decrease pattern with increasing altitude (Patterson et al., 1996; Heaney, 2001; Sánchez-Cordero, 2001; Curran et al., 2012; Linden et al., 2014). Commonly, in temperate regions, the pattern of species richness peaks at mid-elevations, while in the tropics, species richness declines with elevation (McCain, 2007). Meanwhile, bat activity shows a general decreasing pattern with elevation (Thomas, 1988; Barclay, 1991; Linden et al., 2014; Wolbert et al., 2014), probably as a result of higher temperatures favouring some reproductive and thermoregulatory strategies of bats as well as higher insect densities (Grindal et al., 1999; Cryane et al., 2000; Weier et al., 2016). Bat activity has been documented to be affected by weather factors, varying with habitat, region or season but this influence is poorly understood (Bender and Hartman, 2015). Here, we investigated the patterns of diversity and activity of aerial insectivorous bats along an elevational gradient within a continuous forest in the mountainous region of Monteverde, Costa Rica. Using acoustic surveys we aimed to determine the pattern of species diversity along the elevational gradient and to evaluate how the activity of aerial insectivorous bats responds to temperature variation between months at different elevations. As proposed by McCain, 2007, species richness of bats on tropical wet mountains follows a decreasing pattern with elevation, so we expected a peak of species diversity and activity at lower elevations where higher temperatures occur. As the sampling campaigns occurred during a short,

---

*Corresponding author
Email address: ariasaguilar.a@gmail.com (Adriana Arias-Aguilar)

doi:10.4404/hystrix-00244-2019
8th May 2020

almost non-seasonal period, we expected no major differences in bat activity between months.

Materials and methods

Study site

The study was conducted in the Monteverde Cloud Forest Reserve, and the Children´s Eternal Rainforest (10°18′33.3″ N, 84°47′45.8″ W) on the Caribbean slope of the Cordillera de Tilarán, Puntarenas and Alajuela provinces, Costa Rica (Fig. S1). The full description of climate and vegetation characteristics of the region could be found in Nadkarni and Wheelwright, 2014. Based on those authors we described our sampling area. The highest elevation, site one (1560 meters above sea level -m-) at the continental divide holds a dense cloud forest, with an annual rainfall of 2500 mm–3500 mm. In wind exposed hills, the canopy height varies between 5 m–10 m, characteristics of the dwarf forest. At site two (1360 m) the forest is composed of abundant and dense epiphytes and understory with a canopy height that varies between 20 m–30 m. At site three (1160 m) and lower elevations, the rainforest is essentially aseasonal; with annual precipitation of 3500 mm to 7000 mm and an almost imperceptible dry period in March and April. At site three, in exposed steep hills, the forest is reduced to 15 m–20 m height, with a more fragmented canopy, disordered structure, and little diversity. Sites four and five (960 and 760 m) include protected valleys and slight slopes, where the natural vegetation is dense, with abundant epiphytes and high biodiversity. The canopy is more uniform (30 m–40 m) and trees frequently exceed 50 m in height.

Sampling design

We conducted acoustic surveys at five sampling sites along a transect of continuous forest spanning 800 m altitude and a distance of approximately 14 km in a straight line. The minimum distance between sites was 2 km. The top of the gradient was at the continental divide -1560 m- down to 760 m in elevation where the forest was still well preserved. Ideally, lower elevations would have been surveyed, but no large fragments of intact forest exist below 600 m in this region of Costa Rica (McCain, 2004). We performed monthly sampling campaigns of seven consecutive nights, during the dry season from February to April and early rainy season during May of 2014.

Temperature data

We obtained hourly temperature data from four weather stations (Davis Vantage Pro2™ & Vantage Pro2 Plus™) located through the gradient at 1560 m, 1300 m, 950 m and 820 m. As weather stations and sampling points differed altitudinally, we used climatic data from the nearest weather station and estimated temperature according to the moist adiabatic cooling rate, average increases 0.6°C per 100 m in elevation (Barry, 1992).

Acoustic sampling of bats and identification

Acoustic sampling was simultaneously carried out at each of five sites with one bat detector (Song Meter SM2Bat or SM2Bat+ by Wildlife Acoustics) per site, programmed to record in real time for 6.5 hours from sunset, in lapses of 10 minutes each 10 minutes. When topographic conditions allowed it, we located the detectors along the trail and/or clearings within the forest, alternating places between sampling campaigns. Bat calls were analysed using Avisoft Saslab Pro, Version 5.0.24 (Raimund Specht, Avisoft Bioacoustics, Berlin, Germany). Call duration, pulse interval, start and end frequencies and peak frequency were registered. Bat echolocation calls were manually identified using previous literature as a reference (e.g. O'Farrell and Miller, 1999; Ochoa et al., 2000; Rydell.et al., 2002; Jung et al., 2007, 2014). All species identifications were corroborated by an expert (blind confirmations).

Data analyses

We display the acoustic data by elevation and species (Tab. 1). Variables were summarized by hour ± standard deviation; mean air temperature was estimated as the average of the temperatures by hour. Bat activity was quantified as the sum of the bat passes within each hour. Following Fenton et al., 1998, we consider a bat pass as a recorded sequence of ≥ 6 echolocation calls separated by at least four times the prevailing interpulse intervals from other echolocation calls produced by a bat. Using Hill numbers based on relative incidence in the assemblage (Chao et al., 2014), we constructed sampling-based (occurrence data) and coverage-based rarefaction and extrapolation sampling curves to investigate species diversity among sites. We estimated species richness (order q=0), Shannon ("typical" species) diversity (order q=1, the exponential of Shannon entropy), and Simpson ("dominant species) diversity (order q=2, the inverse of Simpson index) (*sensu* Jost, 2006) with the `iNext` package (Hsieh et al., 2016) for each elevation. Significant differences at a level of 5% among the expected diversities were considered if the 95% confidence intervals do not overlap (Chao et al., 2014).Nevertheless, partially overlapping intervals do not guarantee nonsignificance (Schenker and Gentleman, 2001). All analyses were run in R 3.3.1 (R Development Core Team, 2016). We evaluated which variables had an effect on the general activity of bats. We ran a generalised linear model assuming a negative binomial distribution of the response variable (bat passes / hour / species). The model includes elevation and month as factors and the mean temperature as a predictor. We tested multicollinearity of factors assessing the variance inflation factor with vif function of the R package `car` (Fox and Weisberg, 2019). We removed a factor if vif score was greater than 2 (Fox and Weisberg, 2019). We ran the model using a stepwise regression including one factor at a time and evaluate the performance of the model in respect of the previous model using the Akaike's Information Criterion. The statistical significance of regression terms was assessed by likelihood ratio tests. For each species with more than 500 records, we evaluated the effect of the site (elevation), period (month) and temperature in the activity (bat passes) by hour using generalised linear models assuming a negative binomial distribution and with the same procedure as we made with all the data. For all the models, the assumptions were evaluated by qq-plots of the residuals.

Results

Sampling summary

We recorded 11,984 bat passes during approximately 550 recording hours (for a total of 22–28 sampled nights per site) and identified 15 species, plus sonotypes of two genera of Molossidae and one sonotype of Vespertilionidae (Tab. 1). The number of species varied among sites, being highest at 960 m (14 species) and lowest at 1560 m (six species) (Tab. 1). The most common species recorded was *Myotis pilosatibialis* with 26.02 ± 4.81 bat passes/night/site. It was registered in all the elevations, but recurrently at 1160 m At that elevation and 960 m, *M. pilosatibialis* was the species with higher average bat passes recorded (Tab. 1). At elevations 760, 1360 and 1560 m, *Pteronotus mesoamericanus*, *Myotis riparius* and *Centronycteris centralis*, respectively, were the species with the highest activity. We recorded more than one bat pass/night for seven species (Tab. 1).

Species diversity among sites

In general, all sites show similar diversities (Tab. 2, Figs. S2-S3). The sample coverage for the five sites (760, 960, 1160, 1360 and 1560 m) was estimated as 99.47%, 100.00%, 99.91%, 99.84% and 95.67%, respectively, indicating that sampling is nearly complete for all sites. Sample-based diversity of the sites for species richness (q=0); exponential of Shannon entropy (q=1); and inverse Simpson index (q=2) decreased as follows: q=0: 1160>960>760>1360>1560 m; q=1: 1560>1360>1160>960>760 m and q=2: 1560>1160>1360>960>760 m (Fig. S2). Only the 95% confidence intervals for species richness of sites 3 and 1 (1160 and 1560 m, respectively) and Simpson diversity of site 5 (760 m) were nonoverlapping, implying significant differences. Coverage-based diversities for species richness (q=0); exponential of Shannon entropy (q=1); and inverse Simpson index (q=2) decreased as follows: q=0:

Table 1 – Mean ± standard error of bat passes/night for species recorded along an elevation gradient in a tropical forest in Costa Rica.

Species	Mean bat passes/night Elevation (m)					General mean bat passes / night / species
	760 m	960 m	1160 m	1360 m	1560 m	
Emballonuridae						
Centronycteris centralis	0.05 ±0.04	1.39 ±0.71	14.32 ±4.22	5.21 ±1.86	0.33 ±0.33	4.35 ±1.04
Peropteryx kappleri		0.36 ±0.35				0.08 ±0.08
Saccopteryx bilineata	8.32 ±3.03	0.50 ±0.18				1.55 ±0.58
Mormoopidae						
Pteronotus gymnonotus	1.32 ±0.79	0.14 ±0.08	0.48 ±0.21	0.11 ±0.11		0.38 ±0.15
Pteronotus mesoamericanus	12.00 ±1.32	16.14 ±2.86	26.08 ±4.69	3.29 ±1.34	0.17 ±0.09	11.53 ±1.42
Molossidae						
Eumops sp. sonotype 1	0.32 ±0.32	0.32 ±0.13			0.29 ±0.17	0.18 ±0.07
Molossus sp. sonotype 1	0.27 ±0.23	0.25 ±0.21	0.08 ±0.06	0.04 ±0.04	0.08 ±0.08	0.14 ±0.07
Tadarida brasiliensis		0.29 ±0.22	0.52 ±0.52			0.17 ±0.11
Vespertilionidae						
Eptesicus brasiliensis	0.05 ±0.05	2.79 ±1.35	0.12 ±0.08	1.11 ±0.49		0.89 ±0.33
Eptesicus furinalis				0.21 ±0.14		0.05 ±0.03
Eptesicus fuscus			0.04 ±0.04	1.61 ±1.20		0.36 ±0.26
Dasypterus ega		0.14 ±0.09				0.03 ±0.02
Myotis albescens	4.41 ±2.10	29.11 ±8.12	37.72 ±10.60	16.68 ±6.42		18.28 ±3.32
Myotis nigricans	1.18 ±0.77	8.04 ±3.13	82.76 ±18.07	0.86 ±0.79	0.04 ±0.04	18.46 ±4.57
Myotis pilosatibialis	0.05 ±0.05	33.00 ±7.77	87.84 ±17.39	6.36 ±2.64	0.25 ±0.17	26.02 ±4.81
Myotis riparius	4.32 ±2.32	3.57 ±1.76	21.40 ±5.72	27.79 ±14.01		11.87 ±3.43
Rhogeessa bickhami			0.04 ±0.04			0.010 ±0.008
Vesp.			0.04 ±0.04			0.010 ±0.008
Nights sampled	22	28	25	28	24	
General mean bat passes / night / site	32.27 ±6.13	96.04 ±9.76	271.44 ±31.12	63.25 ±20.77	1.17 ±0.47	94.36 ±11.46
Species number per site	11	14	13	11	6	

960>1160>1360>760>1560 m; q=1: 1360>1160>960>1560>760 m and q=2: 1160>1360>1560>960>760 m (Fig. S3). For coverage values higher than 40% the nonoverlapping of the 95% confidence intervals for site 4 (960 m) and site 5 (760 m) imply that the diversities of order q=0 (species richness) and q=2 respectively, are significantly different.

Activity patterns along the gradient

The summary of the adjusted model relating general bat activity with temperature, elevation and period are presented in Tab. 3. The GLM reveals significant variation in the number of bat passes / hour / species between the elevations and months (Tab. 3, Figs. 1,2). The site at 1160 m had the highest activity/hour/species during most of the four months, while site 1560 m had the lowest activity (Fig. 2). The pattern of activity per site was very similar during all months; however, in March, there was a general increment in the activity and particularly for the site at 1360 m regarding the other months (Fig. 1). Evaluating the overall range, we found temperature had a negative effect on the activity (Tab. 3, Fig. 2).

Table 2 – Diversity of all species based on incidence data ($^0\Delta$= species richness), of "typical" species ($^1\Delta$= Shannon diversity), and of dominant species ($^2\Delta$= Simpson diversity) at each elevation and its respective sample coverage (SC).

	Estimated diversity (SE)				
Elevation (m)	760	960	1160	1360	1560
$^0\Delta$ (Richness)	14.00 (4.50)	14.00 (0.39)	15.25 (3.40)	11.50 (1.32)	6.48 (1.27)
$^1\Delta$ (Shannon)	5.05 (0.19)	5.53 (0.12)	5.75 (0.06)	5.87 (0.18)	5.99 (0.93)
$^2\Delta$ (Simpson)	3.88 (0.17)	4.47 (0.08)	5.21 (0.07)	4.77 (0.18)	5.68 (0.96)
SC	0.99	1	1	1	0.96

Activity patterns by species

Only six species had more than 500 records: *Myotis albescens*, *Myotis nigricans*, *M. pilosatibialis*, *M. riparius*, *P. mesoamericanus* and *C. centralis*. The activity patterns were idiosyncratic among the species (Fig. 3). The summaries of the significant factors which adjusted to the models relating activity for the six bat species with temperature, elevation and period are presented in Tab. 4. The GLMs show that month was the factor affecting all the species (Tab. 4). However, when the elevation was included, it was the factor with more effect in the activity of the species except for *M. albescens* and *M. riparius*, for which the period (month) was the factor explained more variance in the activity (Tab. 4, Fig. 3). In general, all species had more activity at middle elevations, between 960 and 1360 m, and low activity in the lowest and the highest elevation analysed (Fig. 3). March was the month with the highest activity for the species *M. pilosatibialis*, *M. nigricans* and *M. riparius* and *P. mesoamericanus* (Fig. 3). When the temperature has an effect in the activity of bats, it was negative (Tab. 4, Tab. S1).

Discussion

To our knowledge, this is the first study to describe diversity and general and species-specific patterns of activity of aerial insectivorous bats

Table 3 – Likelihood Ratio Test for the generalized linear model to explain the bat passes/hour/ species in an elevation gradient in a tropical forest in Costa Rica using as predictor period (months), elevation and temperature. The significance of the effects are represented with ** for $pp < 0.01$ and *** for $p<0.001$.

Factor	Deviance	df	Residual deviance	df	p
Null			1342.05	888	
Elevation	444.56	4	897.49	884	<0.001***
Month	40.84	3	856.65	881	<0.001***
Temperature	7.26	1	849.4	880	0.007**

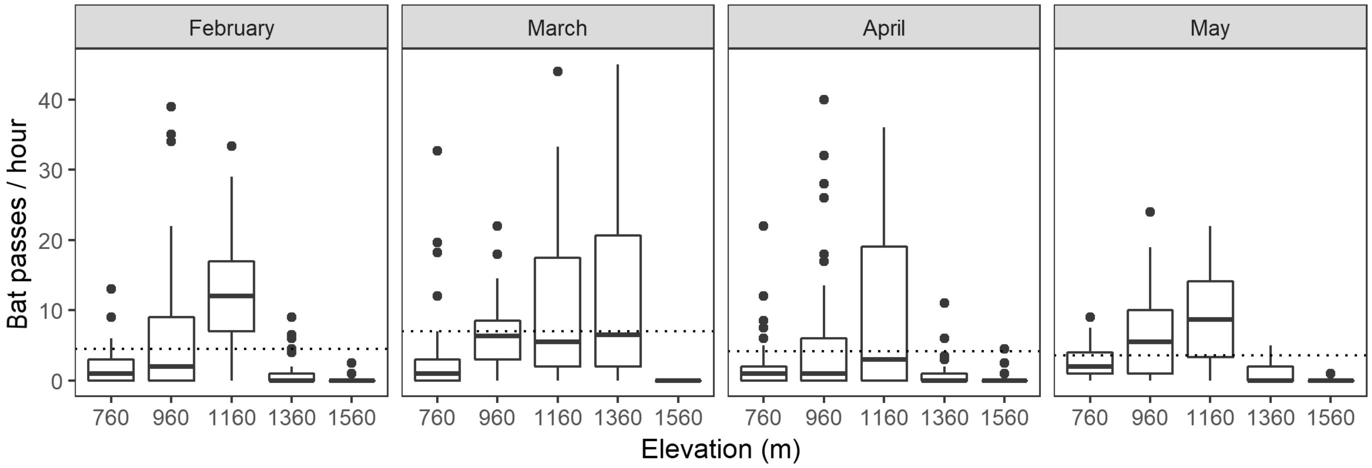

Figure 1 – Bat passes / hour for each site (elevation) and month analysed. The dotted line represents the mean of bat passes / hour for each month.

Table 4 – Likelihood ratio tests for the generalized linear models with negative binomial distribution to explain the bat passes/hour for each species with more than 500 records. The models were constructed using the effect of period (months), elevations and temperature. Models were tested using step AIC (Akaike Information Cirterion) and variables removed when the model was improved. Variables removed are marked with NI (not included). The significance of the effects are represented with * for $p<0.05$, ** for $p<0.01$ and *** for $p<0.001$.

Species	Factor	Deviance	df	Residual Deviance	df	p
Myotis pilosatibialis	Null			888.16		
	Elevation	403.29	4	484.86	884	<0.001***
	Month	42.7	3	442.17	881	<0.001***
	Temperature	4.06	1	438.11	880	0.04*
Myotis nigricans	Null			716.64		
	Elevation	353.61	4	363.03	884	<0.001***
	Month	39.77	3	323.26	881	<0.001***
	Temperature					NI
Myotis albescens	Null			463.42		
	Month	60.6	3	402.82	717	<0.001***
	Temperature	15.57	1	387.25	716	<0.001***
	Elevation					NI
Myotis riparius	Null			363.45		
	Month	122.7	3	243.75	717	<0.001***
	Elevation	33.03	3	210.72	714	<0.001***
	Temperature					NI
Pteronotus mesoamericanus	Null			702.34		
	Elevation	90.47	3	611.87	717	<0.001***
	Month	23.04	3	588.84	714	<0.001***
	Temperature					NI
Centronycteris centralis	Null			515.31	888	
	Elevation	174.38	4	340.93	884	<0.001***
	Temperature	51.13	1	289.8	883	<0.001***
	Month	9.02	3	280.78	880	0.03*

along an elevational gradient in a Neotropical rainforest, using exclusively acoustic methods.

General patterns along the gradient

Although the temperature decreased with elevation we found the highest richness, diversity and activity of the insectivorous bats in mid-elevations, and lower values at the lowest and highest site. These findings differ from previous results reported for other wet mountains in Mexico and South Africa (McCain, 2007; Weier et al., 2016) where the warmest–wettest conditions are towards the base of the mountain and support the highest bat species richness. In contrast with what was previously thought, we found that the increase in temperature by itself did not explain a higher species richness or activity, and the deviations from the expected pattern of species distribution may be partially attributed to lack of correlation between temperature and precipitation patterns. Despite we did not test that correlation, it is suggested by the fact that, in Monteverde precipitation does not decrease with elevation, it is highest at midlands (McCain, 2007) and by additional information from the weather stations (at 1560, 960 and 820 m) that revealed a higher average rainfall at site 960 m during our study period than at the other two elevations.

As an alternative explanation, despite the continuity of the forest along the gradient, the lowest species richness and lowest diversity at the site 760 m could be a consequence of habitat disturbance occurring at lower elevations (under 600 m). It has been argued, that montane communities adjoining areas of dense human settlement sustain lower species richness than within intact habitat (McCain and Grytnes, 2010). However, we do not know the magnitude of this effect on the community of insectivorous bats of Monteverde and as we did not sample in the lowlands this may be biasing the observed patterns. Overall foraging activity of bats along the gradient was slightly but negatively affected by temperature. Precisely why bat activity diminished with higher temperatures is uncertain. Previous studies from temperate regions revealed that the influence of temperature on bat activity could be positive (e.g. Vaughan et al., 1997; O'Donnell, 2000) or negative (e.g. Boonman et al., 1998; Ciechanowski et al., 2007). On the Neotropical region, increases in temperature due to climate change, besides other factors, has negatively impact insect density and species richness (Janzen and Hallwachs, 2019), so one has to wonder what has been the effect on diversity, abundance, activity, and elevational distribution of bats here due to drastic reduction of insect populations. Our results also showed a temporal variation on bat activity. Temporal changes on local levels of insectivorous bat activity may be related to local sampling conditions (Bender and Hartman, 2015) as unusually large hatches of insects or other factors area- and species-specific (Hayes, 1997). For example, horizontal, vertical or regional movements related (or not) with migration could be linked to temporal variations on the abundance of some species (Esbérard et al., 2011). Timm and LaVal (2014) reported that in Monteverde abundance variation of some mammals was due to elevational migration in search of food. Monthly variation in the activity of the insectivorous bats during our study period does not necessarily represent migration but it may reflect changes in food resources. In fact, some insects like butterflies, dragonflies, and wasps perform elevational migrations and in others, like some nocturnal beetles, species richness and diversity varied with elevation (Hanson, 2014).

Species-specific patterns

The activity of the most common insectivorous bats was differently affected by elevation, temperature and sampling month. Besides, as occurred with the overall bat activity, species responses to temperature varied along the gradient and within sites. Those differences could ex-

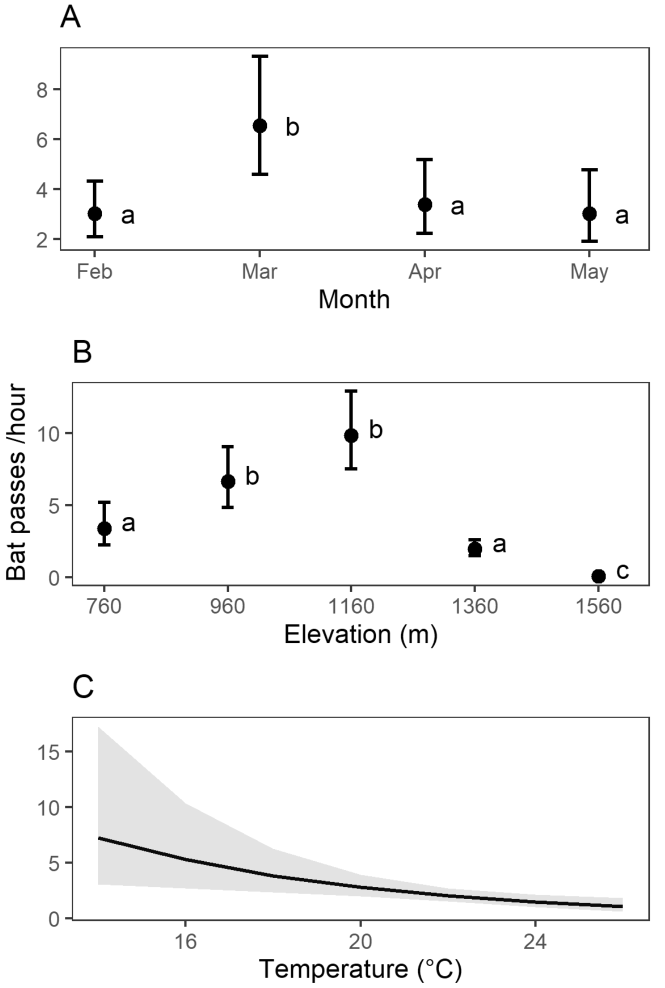

Figure 2 – Predicted values of bat passes / hour for each period (month) (A), elevation (B) and temperature (C) according to the generalized linear model. In A and B, dots represent the mean expected for each group and whiskers the standard error. Letters represent groups which are different between them ($p<0.05$). In C the line represents the fitted line and the gray shadow represents the standard error.

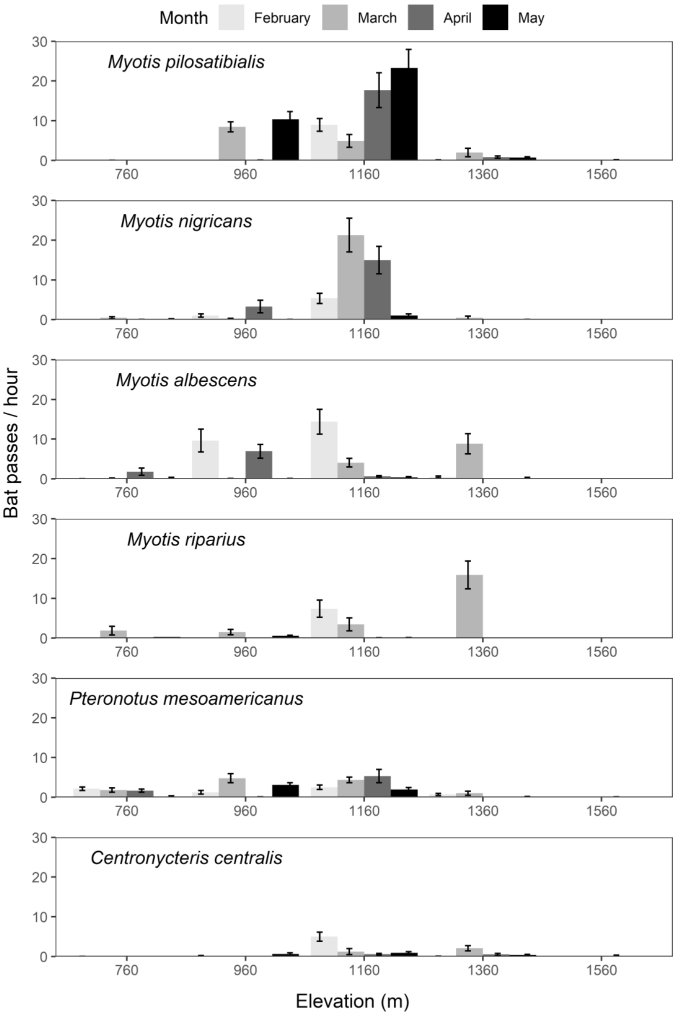

Figure 3 – Mean and standard error of the bat passes / hour for the six bat species in an elevation gradient of tropical forest in Costa Rica during four months.

plain the observed changes in the elevational distribution for some species (see LaVal and Rodriguez, 2002) in the Caribbean slope of Monteverde. *Myotis riparius*, *M. albescens* and *E. furinalis* occurred above their known distribution (above 700 m), while *E. fuscus* was found below their known distribution on the Caribbean slope (below 1650 m). Recently Frank et al., 2018 also reported the presence of *M. riparius* at high elevations (around 1400 m). For the first time, we reported the occurrence of *Centronycteris centralis* in Monteverde as well as its presence at middle and high elevations in Costa Rica. Our results support the hypothesis of LaVal, 2004 that lowland bat species in this region are moving upwards - colonizing mid-elevations and increasing species richness, as also occurred with birds (Pounds et al., 1999). Changes in Monteverde's climatic conditions could be one of the factors facilitating elevational movements of bats, as the species move up or down the mountain attempting to remain within the temperature and humidity limits to which they are adapted (Timm and LaVal, 2014). Nightly increases in minimum temperature within sites probably do not impose a physiological limit for bat activity, at least for our most commonly recorded species. However, tropical insects are relatively sensitive to temperature change and are currently living very close to their optimal temperature (Deutsch et al., 2008). Particularly, species found at middle elevations and on mountaintops are less tolerant to high temperatures than species restricted to lowland (Garcia Robledo et al., 2016). Besides temperature, insects may also be affected by vegetation density resulting in differences in activity between bat species with different foraging strategies (Müller et al., 2012). In this sense, further studies are therefore required to elucidate if the negative effects of temperature on insects may cause a decreased in the activity of insectivorous bats and how habitat structure affects its foraging behaviour in Monteverde.

Conclusions

We found that patterns of activity and diversity for aerial insectivorous bats in Monteverde differed from other tropical mountains where the wettest-warmest conditions are inversely correlated with elevation (McCain, 2007). Highest activity and diversity of bats occurred at mid-elevations and was partially explained by temperature with elevational, temporal and species-specific differences. However due to habitat disturbances under 600 m we did not sample lower elevations. Those differences, as previously suggested for temperate regions (Hayes, 1997; Bender and Hartman, 2015) may be a result of changes in the availability of food resources. However, it is unknown how local temperature changes impact the insects consumed by bats in Monteverde. Studies with other animal groups (like birds, lizards and frogs) showed that regional climate changes linked to changes on land use (e.g. deforestation of lowlands) affect cloud formation and precipitation regimes with negative ecological implications (Pounds et al., 1999; Nair, 2003). It will be necessary to explore how cloud and precipitation regimes, as well as the effect of wind together with air temperature, influence the activity and occurrence of aerial insectivorous bats in Monteverde.

References

Barclay R.M.R., 1991. Population structure of temperate zone insectivorous bats in relation to foraging behavior and energy demand. J. Anim. Ecol. 60: 165–178.
Barry R.G., 1992. Mountain weather and climate. Routledge, London.

Bender M.J., Hartman G.D., 2015. Bat activity increases with barometric pressure and temperature during autumn in Central Georgia. Southeast. Nat. 14: 231–242. 10.1656/058.014.0203

Boonman A., Boonman M., Bretschneider F., van de Grind W., 1998. Prey detection in trawling insectivorous bats: duckweed affects hunting behaviour in daubenton's bat, *Myotis daubentonii*. Behav. Ecol. Sociobiol. 44(2): 99-.107.

Chao A., Gotelli N., Hsieh T.C., Sander E.L., Ma K.H., Colwell R.K., Ellison A.M., 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol. Monograph. 84: 45–67.

Ciechanowski M., Zając T., Biłas A., Dunajski R., 2007. Spatiotemporal variation in activity of bat species differing in hunting tactics: effects of weather, moonlight, food abundance, and structural clutter. Can. J. Zool. 85: 1249-1263. doi:10.1139/Z07-090

Cryan P.M., Bogan M.A., Altenbach J.S., 2000. Effect of elevation on the distribution of female bats in the Black Hills, South Dakota. J. Mammal. 81: 719–725.

Curran M., Kopp M., Beck J., Fahr J., 2012. Species diversity of bats along an altitudinal gradient on Mount Mulanje, southern Malawi.J. Trop. Ecol. 28: 243–253.

Deutsch C.A., Tewksbury J.J., Huey R.B., Sheldon K.S., Ghalambor C.K., Haak D.C., Martin P.R., 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proc Natl Acad Sci USA 105: 6668–6672. doi:10.1073/pnas.0709472105

Echeverría-Tello J.L., 2013. Ensambles de murciélagos frugívoros y nectarívoros en un gradiente altitudinal de Costa Rica y su potencial distribución bajo escenarios de cambio climático. Tesis de maestría en ciencias, CATIE, Turrialba, Costa Rica.

Esbérard C.E.L., Lima I.P., Nobre P.H., Althoff S.L., Jordão-Nogueira T., Dias D., Carvalho F., Fabián M.E., Sekiama M.L., Sobrinho A.S., 2011. Evidence of vertical migration in the Ipanema bat Pygoderma bilabiatum (Chiroptera: Phyllostomidae: Stenodermatinae). Zool. 28: 717–724. 10.1590/S1984-46702011000600004

Fenton B.M., 1997. Science and the conservation of bats. J. Mammal. 78: 1–14.

Fenton B.M, Portfors C.V., Rautenbach I.L., Waterman J.M., 1998. Compromises: sound frequencies used in echolocation by aerial-feeding bats. Can. J. Zool. 76: 1174–1182.

Fleming T.H., 1986. Opportunism versus specialization: the evolution of feeding strategies in frugivorous bats. In: Estrada A., Fleming T.H. (Eds.) Frugivores and seed dispersal. Dr. W. Junk Publishers, Dordretch, The Netherlands. 1105–1118.

Fleming T.H., Hooper E.T., Wilson D.E., 1972. Three central american bat communities: structure, reproductive cycles and movement patterns. Ecology 4: 555–569.

Frank T.M., Gabbert W.C., Chaves-Campos J., LaVal R.K., 2018. Impact of artificial lights on foraging of insectivorous bats in a Costa Rican cloud forest. J. Trop. Ecol. 10.1017/S0266467418000408.

Fox, J., Weisberg, S., 2019. Companion to Applied Regression. Sage, Thousand Oaks, Canada.

García-Robledo C., Kuprewicz E.K., Staines C.L., Erwin T.L., Kress W.J., 2016. Limited tolerance by insects to high temperatures across tropical elevational gradients and the implications of global warming for extinction. Proc Natl Acad Sci USA 113: 680–685. doi:10.1073/pnas.1507681113

Grindal S.D., Morissette J.L., Brigham R.M., 1999. Concentration of bat activity in riparian habitats over an elevational gradient. Can. J. Zool. 77: 972–977.

Hanson P. 2014. Insects and spiders. In: Nadkarni N.M., Wheelwright N.T. (Eds.) Monteverde: Ecology and conservation of a tropical cloud forest. Oxford University Press, New York. 223–244.

Hayes J.P., 1997. Temporal variation in activity of bats and the design of echolocation-monitoring studies. J. Mammal. 78(2): 514–524.

Heaney L.R., 2001. Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. Glob. Ecol. Biogeogr. 10: 15–39.

Hsieh T.C., Ma K.H., Chao A., 2016. `iNEXT`: iNterpolation and EXTrapolation for species diversity. R package version 2.0.12. http://chao.stat.nthu.edu.tw/blog/software-download/

Janzen D., Hallwachs W., 2019. Perspective: Where might be many tropical insects? Biol. Conserv. 233: 102–108. 10.1016/j.biocon.2019.02.030

Jost L., 2006. Entropy and diversity.Oikos 113(2): 363–375.

Jung K., Kalko E.K.V., 2010. Where forest meets urbanization: foraging plasticity of aerial insectivorous bats in an anthropogenically altered environment. J. Mammal. 91: 144–153.

Jung K., Kalko E.K.V., Helversen O., 2007. Echolocation calls in Central American emballonurid bats: signal design and call frequency alternation. J. Zool. 272: 125–137

Jung K., Molinari J., Kalko E.K.V., 2014. Driving factors for the evolution of species-specific echolocation call design in new world free-tailed bats (Molossidae). PLoSONE 9(1): e85279.

Kalko E.K.V., Schnitzler H.U., 1998. How echolocating bats approach and acquire food. In: Kunz T.H., Racey P.A. (Eds.) Bat. Biology and Conservation. Washington, London: Smithsonian Institution Press. 197–204.

LaVal R.K., 2004. Impact of global warming and locally changing climate on tropical cloud forest bats. J. Mammal. 85: 237–244. 10.1644/BWG-016

LaVal R.K., Rodriguez-H B., 2002. Murciélagos de Costa Rica. 1st ed. Santo Domingo de Heredia, Costa Rica (Instituto Nacional de Biodiversidad,INBIO). 320 p.

Linden V.M.G., Weier S.M., Gaigher I., Kuipers H.J., Weterings M.J.A., Taylor P.J., 2014. Changes of bat activity, species richness, diversity and community composition over an altitudinal gradient in the Soutpansberg range, South Africa. ActaChiropterol. 16: 27–40. 10.3161/150811014X683246

Lomolino M.V., 2001. Elevation gradients of species-density: historical and prospective views. Glob. Ecol. Biogeogr. 10: 3–13.

McCain C.M., 2004. The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. J. Biogeogr. 31: 19–31.

McCain C.M., 2007. Could temperature and water availability drive elevational species richness patterns? A global case study for bats.Glob. Ecol. Biogeogr. 16: 1–13.

McCain C.M., Grytnes J.A., 2010. Elevational gradients in species richness. In: Encyclopedia of Life Sciences. John Wiley & Sons, Ltd, Chichester, UK. 1-10. 10.1002/9780470015902.a0022548

McNab B.K., 1982. Evolutionary alternatives in the physiological ecology of bats. In: Kunz T.H. (Eds.) Ecology of bats. Plenum Publishing Corporation, New York. 151–196.

Mena J.L., Solari S., Carrera J.P., Aguirre L.F., Gómez H., 2011. Small mammal diversity in the tropical Andes: an overview. In: Herzog S.K., Martínez R., Jørgensen P.M., Tiessen H. (Eds.) Climate change and biodiversity in the tropical Andes. Inter-American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE). 260–275.

Müller J., Mehr M., Bässler C., Fenton M.B., Hothorn T., Pretzsch H., Klemmt H.J., Brandl R., 2012. Aggregative response in bats: prey abundance versus habitat. Oecologia 169:673-84. 10.1007/s00442-011-2247-y\

Nadkarni N.M., Wheelwright N.T., 2014. Monteverde: ecology and conservation of a tropical cloud forest. Updated Chapters. Oxford University Press, New York.

Nair U.S., Lawton R.O., Welch R.M., Pielke R.A., 2003. Impact of land use on Costa Rican tropical montane cloud forests: Sensitivity of cumulus cloud field characteristics to lowland deforestation. J. Geophys. Res. 108: 4206. doi:10.1029/2001JD001135

O'Donnell C.F.J., 2000. Influence of season, habitat, temperature, and invertebrate availability on nocturnal activity of the New Zealand Long-tailed Bat (*Chalinolobus tuberculatus*). New Zeal. J. Zool. 27: 207–221.

Ochoa J., O'Farrell M.J., Miller B.W. 2000. Contribution of acoustic methods to the study of insectivorous bat diversity in protected areas from northern Venezuela. Acta Chiropterol. 2(2): 171–183.

O'Farrell M.J., Miller B.W., 1999. Use of vocal signatures for the inventory of free-flying Neotropical bats. Biotropica 31(3): 507–516.

O'Farrell M.J., Gannon W.L., 1999. A comparison of acoustic versus capture techniques for the inventory of bats. J. Mammal. 80: 24–30. 10.2307/1383204

Ortiz-Badillo R.M., 2015. Diversidad de murciélagos en un gradiente altitudinal en el estado de Nuevo León, México. Tesis de Maestría, Facultad de Ciencias Forestales.

Patterson B.D., Meserve P.L., Lang B.K., 1989. Distribution and abundance of small mammals along an elevational transect in temperate rainforests of Chile. J. Mammal. 70: 67–78.

Patterson B.D., Pacheco V., Solari S., 1996. Distribution of bats along an elevational gradient in the Andes of southeastern Peru. J. Zool. (London). 240: 637–658.

Piksa K., Bogdanowicz W., Tereba A., 2011. Swarming of bats at different elevations in the Carpathian Mountains. Acta Chiropterol. 13: 113–122.

Pounds J.A., Fogden M.P.L., Campbell J.H., 1999. Biological response to climate change on a tropical mountain. Nature 398: 611–615.

R Development Core Team., 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Refulio S.M., 2015. Diversidad de murciélagos a lo largo de una gradiente altitudinal en las Yungas de la cuenca del río Pampa Hermosa Junín, Perú. Tesis para optar al título profesional de Biólogo con mención en Zoología. Universidad Nacional Mayor de San Marcos Facultad de Ciencias Biológicas.

Rydell J., Arita H.T., Santos M., Granados J., 2002. Acoustic identification of insectivorous bats (Order Chiroptera) of Yucatan, Mexico. J. Zool. 257(1): 27–36.

Sánchez-Cordero V., 2001. Elevation gradients of diversity for rodents and bats in Oaxaca, Mexico.Glob. Ecol. Biogeogr. 10: 63–76.

Schenker N., Gentleman J. 2001. On Judging the Significance of Differences by Examining the Overlap Between Confidence Intervals. Am. Stat. 55: 182–186.

Timm R.M., LaVal R.K., 2014. Mammals. In: Nadkarni N.M., Wheelwright N.T. (Eds.) Monteverde: Ecology and conservation of a tropical cloud forest. Oxford University Press, New York. 223–244.

Thomas D.W., 1988. The distribution of bats in different ages of Douglas-fir forests. J. Wildl. Manage. 52: 619–626.

Vaughan N., Jones G., Harris S., 1997. Habitat use by bats (Chiroptera) assessed by means of a broad-band acoustic method. J. Appl. Ecol. 34: 716–730.

Weier S.M., Linden V.M.G., Gaigher I., White P.J.C., Taylor P.J., 2016. Changes of bat species composition over altitudinal gradients on northern and southern aspects of the Soutpansberg mountain range, South Africa. Mammalia 81: 49-60. 10.1515/mammalia-2015-0055

Wolbert S.J., Zellner A.S., Whidden H.P., 2014. Bat activity, insect biomass, and temperature along an elevational gradient. Northeast. Nat. 21: 72-85. 10.1656/045.021.0106

Associate Editor: L. Ancillotto

Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Figure S1 Map showing the geographic situation of Costa Rica and the relief map of the study area with locations of sampling sites and weather stations.

Figure S2 a) Comparison of sample-size-based rarefaction and extrapolation curves for each site b) Comparisons of five sites for each order of q.

Figure S3 Comparison of the coverage-based rarefaction and extrapolation, for insectivorous bat species diversity samples.