

The effects of seasonality on host–bat fly ecological networks in a temperate mountain cave

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SUMMARY

Changes in the specialization of parasite–host interactions will be influenced by variations in host species composition. We evaluated this hypothesis by comparing the composition of bats and bat flies within a roost cave over one annual. Five bat and five bat fly species occupied the cave over the course of the study. Bat species composition was 40% different in the rainy season compared with the dry–cold and dry–warm seasons. Despite the incorporation of three new bat species into the cave during the rainy season, bat fly species composition was not affected by seasonality, since the bats that arrived in the rainy season only contributed one new bat fly species at a low prevalence. Bat–bat fly ecological networks were less specialized in the rainy season compared with the dry–cold and dry–warm seasons because of the increase of host overlap among bat fly species during this season. This study suggests that seasonality promote: (1) differences in host species composition, and (2) a reduction in the specialization of host–parasite ecological networks.

Key words: Mexico, Michoacan, Molossidae, Phyllostomidae, Streblidae, Verperilionidae.

INTRODUCTION

Climatic seasonality affects animal community structure, through variation in food resources that promotes migration and modifies abundance patterns (Pianka, 1973; Herbers, 1985; Bauer and Hoye, 2014). This phenomenon has been documented in temperate, subtropical and tropical forests (Stoner, 2005; Mello, 2009; Mysterud *et al.* 2016). Seasonality also affects the richness and abundance of ectoparasites (Lareschi and Krasnov, 2010; Lumbad *et al.* 2011; Fagir *et al.* 2015), since temporal variations in host availability produces changes in the prevalence of parasites (Mysterud *et al.* 2016). However, there is little information regarding the effects of seasonality on specialization in host–parasite ecological networks (Zarazúa-Carbajal *et al.* 2016). This information is necessary in order to understand the temporal dynamics of host–parasite ecological networks (Bauer and Hoye, 2014).

The specialization index (H_2') is one of the main informative ecological network indices since it is related to the degree of niche complementarity among species and integrates species-level specialization across the entire community (Blüthgen and

Klein, 2011). It has been documented that host–parasite ecological networks are highly specialized, where there are groups of species that interact more strongly with others, forming modules (Fontaine *et al.* 2011). The specialization and structure of these ecological networks are affected by changes in host composition and habitat use (Brito *et al.* 2014; Zarazúa-Carbajal *et al.* 2016).

An unresolved issue is whether the temporary occupation of a given habitat by the hosts could cause changes in the specialization of host–parasite ecological networks. Bats and their parasitic bat flies (Diptera: Streblidae) represent a suitable biological model with which to evaluate this idea. Streblids are obligate blood-sucking ectoparasites; the adults live and feed on bat skin and membranes (Wenzel *et al.* 1966) and the pupae develop in the roosting sites of their hosts (Dick and Patterson, 2006; Dittmar *et al.* 2009). On the other hand, the migratory behaviour of certain bat species implies a seasonal host availability that is reflected in the occupation patterns of caves used as daytime roosts (Kunz, 1982; Clark *et al.* 1997). This makes the bats and their ectoparasitic flies a particularly suitable biological model for evaluating the effects of temporary cave occupation by bats on the ecological networks they form with the bat flies.

The objective of this study was to compare: (1) the species composition of the bats and their ectoparasitic flies and (2) the specialization of host–bat fly ecological networks among the dry–cold, dry–warm

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and rainy seasons in a temperate mountain cave. We predict that (1) hosts and bat fly species composition will vary seasonal because the migratory behaviour of bats will modify species composition in the cave (Barclay, 1991; Stoner *et al.* 2003) and (2) the specialization of host–bat fly ecological interactions networks will differ significantly among seasons because of the changes in bat species composition and their associated ectoparasites (Zarazúa-Carbajal *et al.* 2016).

MATERIALS AND METHODS

Study area

The study was carried out at Tiristaran in the municipality of Morelia, in the state of Michoacan, Mexico (19°45'55'N; 101°20'31'W; 2170 m a.s.l.). The climate is temperate subhumid with summer rains (Cwa), and features hot summers and dry winters, with temperatures that range from 10 to 22 °C and rainfall of 600 to 1000 mm/year (INEGI, 2009; Table 1).

At the site, *Quercus* spp. trees dominate the forest, while secondary and cultivated fields are other common land uses (Rzedowski, 2006). The cave is located in the southeast of Tiristaran, at coordinates 19°45'378'N; 101°21'507'W. The cave is 89.5 m long and 13 m high, volcanic in origin and features only one entrance (Fig. 1).

Fieldwork

Bats and their associated bat flies were sampled one day per month, from October 2014 to September 2015. Bats were captured inside the cave using hand nets (60 and 80 cm in diameter) and one mist-net (12 × 3 m²). The mist-net was placed inside the cave, approximately 40 m from the entrance, before we began the capture of bats roosting in low cave walls. Capturing was conducted between 8:00 and 10:30 am. Bat flies were collected directly from the captured bats. Bat species in the cave not share the same roost sites. Therefore the possibility of Streblidae cross-contamination in our samplings was low. In addition, after each capture we revised and clean the hand nets in order to avoid Streblidae cross-contamination. While bats captured with the mist-net were individually placed in cloth bags to prevent contamination of ectoparasite samples. We try to minimize disruption of the bat colony having low time capturing sessions (<2 h of capture). In addition, we offer sugar solution and water to bats captured after they were examined for ectoparasites. Bats were identified to species with dichotomous keys (Medellín *et al.* 2008). The entire body of each bat was systematically examined with a fine-toothed comb and entomological forceps until no more bat flies were found. Bat flies were

placed in plastic vials containing 70% ethanol, using a separate vial for each individual bat. Bat flies were identified to species in the Laboratory of Arthropodology and Health of the Autonomous University of Puebla, using dichotomous keys (Wenzel *et al.* 1966; Wenzel, 1976; Guerrero, 1995; Dick and Miller, 2010).

Data analysis

To evaluate the dissimilarity of bat and bat fly species composition and specialization of host–bat fly interactions among seasons, we constructed two-dimensional matrix types: (1) season-species matrices, one for hosts and another for their ectoparasites (2 matrices) and (2) parasite–host interaction matrices, one for each sampling month (12 matrices). Host and ectoparasite species composition dissimilarity was evaluated among dry–cold, dry–warm and rainy seasons with a multivariate cluster analysis. We used the Bray–Curtis distance method to construct the dissimilarity distance matrix between the species observed in different seasons. This distance construction method utilizes abundance data in the dissimilarity distance matrix calculation (Legendre and Legendre, 2012). The ‘average’ distance method was used for the construction of the dendrogram. Furthermore, to test for statistically significant differences between the bat and fly species dissimilarities observed among seasons, we performed an analysis of similarities (ANOSIM) based on 999 permutations (Oksanen *et al.* 2013). The ANOSIM analysis calculates an *R*-value, which is a relative measure of the species composition similarity and ranges from zero to one. Values from 0 to 0.25 indicate no recognizable groups in the sample; values from 0.25 to 0.5 indicate recognizable groups in the sample but with a high percentage of overlap in the species composition, while values above 0.5 indicate recognizable groups in the sample, with a low percentage of overlap in the species composition (Sosa *et al.* 2008).

Specialization of host–bat fly interactions among seasons was evaluated with the specialization index (H_2') of ecological networks (Dormann *et al.* 2008). H_2' measures the degree of niche complementarity among species and integrates species-level specialization across the entire community (Blüthgen, 2010). Values of H_2' range from 0 to 1; values approaching 0 suggest a high complementarity of interactions (low specialization) or high redundancy of interactions in the network, while values approaching 1 suggest low complementarity (high specialization) of interactions of the network (Blüthgen 2010). For 3 months of the dry–cold season, the interaction matrices only present one host species with ectoparasites and it was therefore impossible to calculate the H_2' index for these months. These events reduce our sample size for

Table 1. Recognized seasons and temperature and precipitation at Tirstaran in the municipality of Morelia, Mexico, for the years of the study (2015–2016)

Season	Months	T_{\min} (°C)	T_{\max} (°C)	Precipitation (mm)
Dry–cold	October, November, December, January, February	7.22 ± 0.53	21.72 ± 6.87	0.95 ± 0.45
Dry–warm	March, April, May	8.83 ± 0.50	23.92 ± 0.42	1.88 ± 0.82
Rainy	June, July, August, September	10.85 ± 0.16	23.71 ± 0.29	4.35 ± 0.37

Values are mean \pm S.E., of month data. Data were obtained from the ‘3er. Mundo’ meteorological station of CONAGUA (19°45′54″N; 101°17′53″W) (<http://www.conagua.gob.mx>).

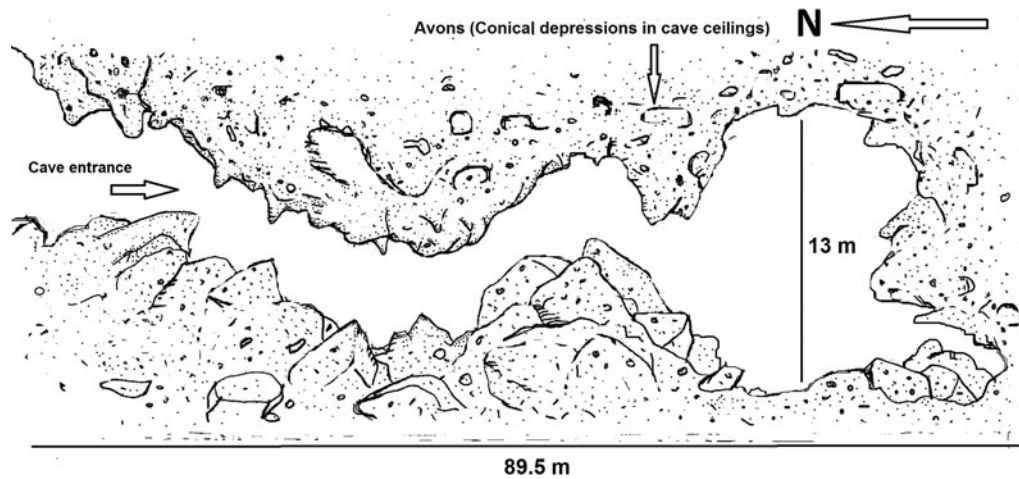


Fig. 1. Extended schematic of the cave, showing its complex morphology and entrance. Illustration by Daniel Ferreyra-García.

this season from five to two and prevented us from conducting statistical analysis. Comparison of the H_2' index per season was therefore conducted with the means and standard error (S.E.) of the month's sampling in each season. All analyses were performed with the vegan, bipartite and stats packages of the R 2.12.2 software (Dormann *et al.* 2008; R Core Team Development, 2012; Oksanen *et al.* 2013).

RESULTS

We collected a total of 836 bat flies, representing five species, from 318 host bats belonging to five species of the families Phyllostomidae, Molossidae and Vespertilionidae (Table 2). Host species composition was affected by season (Fig. 2A). The dissimilarity of bat species between seasons was moderate, since only the rainy season presented a difference of 40% in bat species compared with those of the dry–cold and dry–warm season (Fig. 2A). The *a posteriori* evaluation (ANOSIM) confirmed that there are recognizable groups per season, but with a great percentage of overlap ($R_{\text{season-bats}} = 0.45$, $P = 0.01$). Bat fly species composition was unaffected by season (Fig. 2B). The *a posteriori* evaluation (ANOSIM) confirmed that there are no recognizable groups per season ($R_{\text{season-flies}} = 0.17$, $P = 0.14$). We

found differences in specialization among the seasons: specialization was higher in the dry–cold season (mean $H_2' = 1$ S.E. ± 0) than in the dry–warm (mean $H_2' = 0.97 \pm 0.02$) and rainy (mean $H_2' = 0.70 \pm 0.07$, Fig. 3) seasons.

DISCUSSION

Our prediction that seasonality affects the specialization of interaction networks through changes in host composition was fulfilled. In the following sections, we discuss possible explanations for the lack of differences in bat fly composition among the seasons. Finally, we discuss the role of migratory host movements in the specialization of ecological networks observed among seasons.

Seasonal effects on host and bat fly composition

Bat species composition was strongly affected by season. In the study region, the richness and the relative abundance of insectivorous bats increase in the rainy season (Ferreyra-García, 2016), most likely because of the increase in environmental humidity that results in a higher availability of insect prey for them (Wolda, 1988; Pinheiro *et al.* 2002). One plausible explanation for changes in bat species composition among rainy and dry–cold and dry warm

Table 2. Bat species and their ectoparasite bat flies (Diptera: Streblidae) from the Tiristaran cave, Michoacán, Mexico

Bat species	No. of bats captured	No. of infected bats	Bat fly species	No. of flies collected
<i>Anoura geoffroyi</i> ⁿ	123	106	<i>Anastrebla modestini</i>	59
			<i>Exastinion clovisi</i>	329
<i>Leptonycteris nivalis</i> ⁿ	2	2	<i>Trichobius sphaeronotus</i>	54
<i>Leptonycteris yerbabuena</i> ⁿ	111	93	<i>Anastrebla modestini</i>	1
			<i>Exastinion clovisi</i>	1
			<i>Nycterophilia natali</i>	80
			<i>Trichobius sphaeronotus</i>	308
<i>Myotis velifer</i> ⁱ	3	2	<i>Trichobius major</i>	1
			<i>Trichobius sphaeronotus</i>	1
<i>Tadarida brasiliensis</i> ⁱ	79	2	<i>Nycterophilia natali</i>	2

The superscript letter ‘n’ means that the bat species is nectarivorous, while ‘i’ means insectivorous, based on Rojas *et al.* (2011) and Segura-Trujillo and Lidicker (2016).

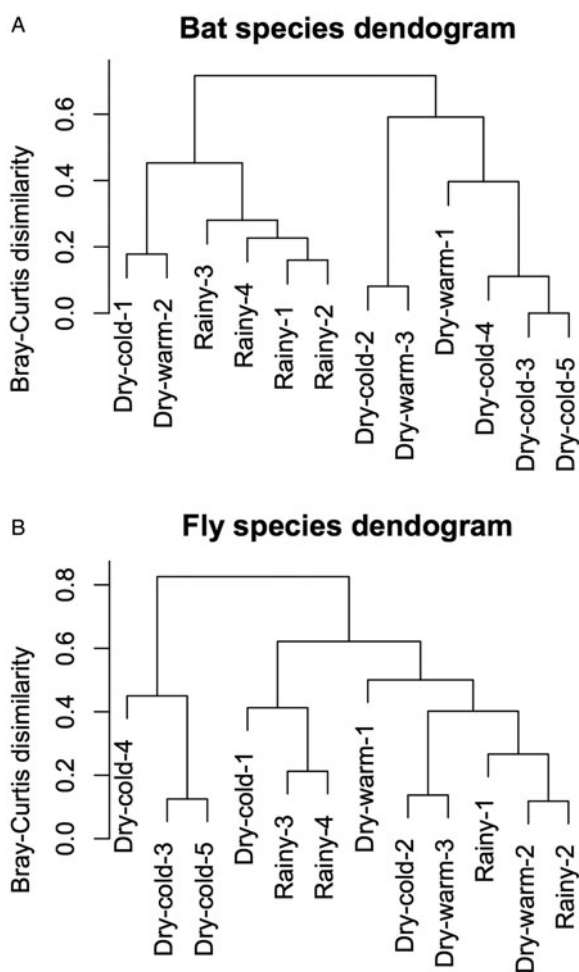


Fig. 2. Dissimilarity cluster graph of bat (A) and bat fly (B) species per sampling month and season.

seasons is therefore changes in prey availability for the insectivorous bats.

On the other hand, nectarivorous bats were present throughout the year, probably because there is a continuous availability of food resources in the region. For example, the chiropterophilic plant *Ipomoea murucoides* is available for

nectarivorous bats in the dry–warm and dry–cold season of the region (Carranza, 2007). This resource allows the presence of nectarivorous bats in the cave throughout the year. This hypothesis could be tested in the future, with a dietary analysis of the bats present in the cave.

Bat fly species composition was not affected by season. This result is a consequence of the low bat fly richness and prevalence of migrant bat species (*Myotis velifer* and *Tadarida brasiliensis*) that arrived to the cave during the rainy season (Table 2, Fig. 3). These bat species present altitudinal and latitudinal migrations and low richness and prevalence of Streblidae (Ritzi *et al.* 2001; Tlapaya-Romero *et al.* 2015), but higher rates of parasitism by other groups (fleas, nycteribiids and mites). Therefore their incorporation to the cave during the rainy seasons not affected significantly the bat fly species composition among seasons.

Seasonal effects in host–bat fly interaction networks

Specialization of the ecological networks differed throughout the year. The highest values of specialization were observed in the dry–cold and the dry–warm seasons. This is due to low interaction overlap between parasites and hosts in these seasons (Fig. 3). This pattern is contrary to that which could be expected from bats that share caves or roosts over long periods. For example, it has been observed that bat species that share caves or roosts are prone to becoming infested by ectoparasites of other species (Obame-Nkoghe *et al.* 2016). One possible explanation of the low ectoparasite overlap between bat species in cold and warm seasons is that the bats had low abundance and utilized separate roosts inside the cave. It has been reported that bat species form species-specific groups inside the caves (Torres-Flores *et al.* 2012); such roosting behaviour combined with low abundance could produce low rates of ectoparasite

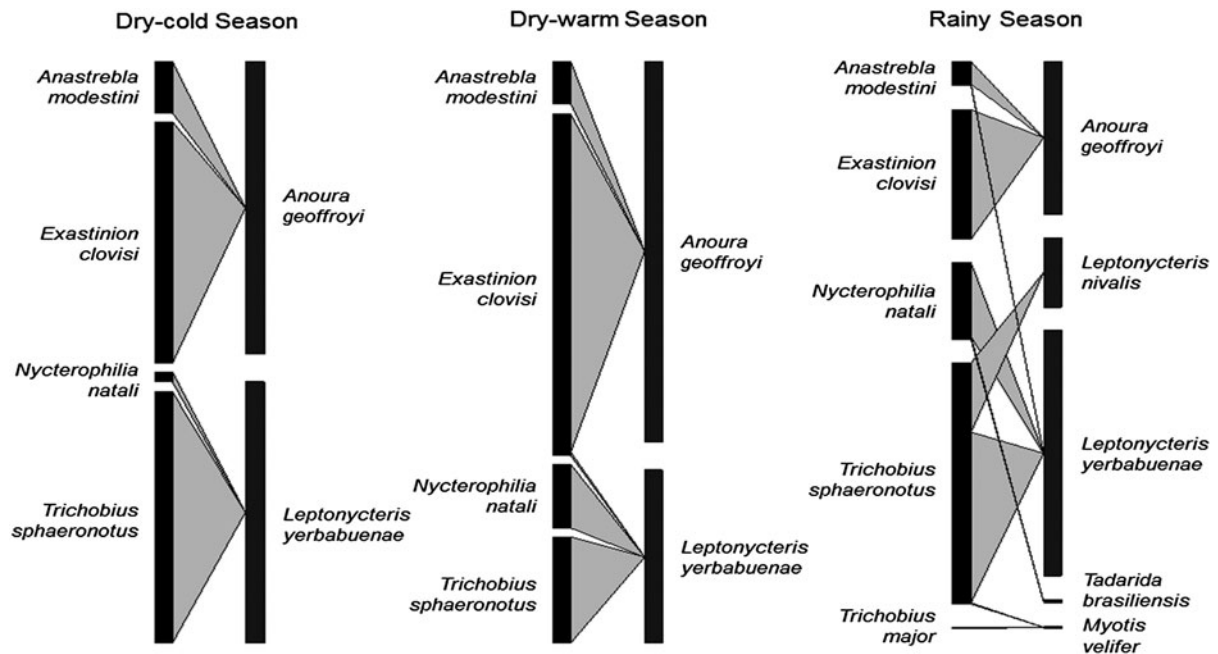


Fig. 3. Quantitative bipartite bat–fly interaction graph for the dry–cold, dry–warm and rainy seasons, in a temperate cave. In the bipartite graph, the left-hand bar size represents the number of bat flies species observed and right-hand bar size represents the number of bats for which bat fly samples was obtained. Linkage width indicates the frequency of each trophic interaction.

transfer among these nectarivorous bat species in the dry–cold and dry–warm seasons.

The lowest value of specialization was observed in the rainy season, when the migrant species, *Leptonycteris nivalis*, *M. velifer* and *T. brasiliensis*, arrive at the cave. Moreover, in this season, bats were found on most of the walls of the cave, presenting both an increase in the number of bats and in the air temperature of the cave during this season (Ferreira-García, 2016). It has been reported that the number of bats that occupy a cave influences the microclimate of the cave (Lundberg and McFarlane, 2015). The recorded increase in the bat colony size in the cave increased the air temperature and also the possibility of the horizontal transfer of bat flies among the individual bats. Despite the reduction of the specialization in the bat–fly interactions, in the rainy season, the low prevalence values in the migrant species suggest that the increase in the overlap interactions recorded are transitory (Dick *et al.* 2009).

Concluding remarks

Bat species composition was determined by seasonality, whereas bat fly species composition was not. The permanent presence of the nectarivorous bats *Anoura geoffroyi* and *Leptonycteris yerbabuena* in the dry–cold and dry–warm seasons enabled the permanent presence of their associated bat fly species and the higher specialization of the ecological networks during these particular seasons. The higher

overlap between bat flies and their hosts in the rainy season reflects a spillover effect, in that the migratory bat species introduced no additional bat flies to the network and were seasonally infested (at very low levels) by bat fly species whose primary hosts were permanent residents in the cave. Resulting in a lower specialization of ecological networks over that period. This observed pattern highlights the role played by animal migration in the temporal structure of parasite–host ecological networks.

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