



Research Article

SEASONAL CHANGES IN THE HABITAT STRUCTURE AFFECT THE ABUNDANCE OF TWO SPECIES OF SMALL MAMMALS IN A TEMPERATE FOREST

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ABSTRACT S

One basic issue in ecology is to understand how seasonal shifts in habitat structure affect the abundance of species that coexist. To address this, we assessed the effect of the changes in the habitat structure (*viz.* biotic and physical components that structure the habitat), between two annual seasons (dry and rainy seasons) in a mid-latitude temperate forest on the abundance of two small mammals; *Peromyscus difficilis* and *Peromyscus melanotis*. The results of our analyses show different relationships between the habitat structure and the abundance of both species. As environmental conditions changed between dry and rainy season also changed the complexity of the habitat and this had an effect on the abundance of both species of *Peromyscus*. This study provides evidence of how two species of small mammals are affected by changes in the habitat structure. Our results provide information of habitat preferences for these two *Peromyscus* species that coexist and inhabits in an ecosystem at the edge of a megalopolis (Mexico City). Understand what elements of the habitat shape the abundance of the species is important to elaborate better strategies to preserve natural areas and the species that inhabit there. Urban growth produces fragmentation of natural microhabitats that are important to the small mammals, which play a fundamental role in the dispersal of seeds in the forest and as habitat architects.

Keywords: Coexistence, Habitat heterogeneity, *Peromyscus*, Small mammals' conservation, Habitat preferences.

INTRODUCTION

Changes in the habitat structure have a substantial impact on species coexistence (Valladares *et al.*, 2015). It has reported that changes in species population size can vary depending on the availability of the resources through the time (Valladares *et al.*, 2015). Model simulations have revealed the important role of the habitat complexity on species coexistence (Schreiber & Killingback, 2013; Valladares *et al.*, 2015). For instance, habitat heterogeneity should increase available niche spaces, allowing more species to coexist (Currie, 1991). Equally crucial for the maintenance of species coexistence is habitat heterogeneity over time, whose influence on natural communities also varies depending on the temporal scale (Valladares *et al.*, 2015). Temporal fluctuations in habitat structure can

stabilize coexistence via the “storage effect” (Chesson, 2000), when inter-annual variation in climate or resource availability favors one group of species over others (Zavaleta *et al.*, 2003).

In particular, small body size species such as small mice perceive spatial habitat heterogeneity at a fine scale (microhabitat) (Chesson, 2000). Therefore, in this study we focus on whether two species of small mammals (*Peromyscus difficilis* and *Peromyscus melanotis*) are capable of perceiving and responding to temporal changes in the habitat heterogeneity. Several studies have quantified variation in resource use in heterogeneous environments within a community among mice from the same family or genus (Kirkland & Layne, 1989). However, few of them have evaluated the effect of temporal changes in the habitat complexity to the abundance of species (but see Kalcounis

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Rüppell & Millar, 2002). Closely related species are especially valuable for studies of habitat use and resource partitioning, since they are most likely to be current or past competitors (Kalcounis Rüppell & Millar, 2002). Thus, the primary objective here was to analyze how changes in the habitat structure between the dry and rainy season affect the abundance of *Peromyscus difficilis* and *P. melanotis* which inhabits in a temperate forest of Central Mexico.

MATERIALS AND METHODS

Study area

The study area was located in a temperate mixed forest (coniferous and broad-leaved trees) at Desierto de Los Leones National Park in Mexico City (DLNP; CONANP, 2006). This forest is part of the Transmexican Neovolcanic Range (CONANP, 2006). The rainy season occurs from summer through early fall (June-October). The monthly average precipitation in this season is 252.92 ± 28.01 mm. The average monthly temperature in this same season is $11.72 \pm 0.53^{\circ}\text{C}$ (CONANP, 2006). In contrast, the dry season occurs from fall through winter (October-February). The monthly average precipitation in this season is 13.2 ± 3.11 mm and the average monthly temperature is 8.97 ± 0.68 (CONANP, 2006).

Habitat structure

To evaluate the habitat structure in our study zone, we set a $2,475\text{ m}^2$ ($55 \times 45\text{ m}$) surface plot at 2,289 m. The plot was gridded with 12 vertical lines (A-L) by 10 horizontal lines (1-10), with lines placed every 10 m. Intersections between vertical/horizontal lines were marked with buried wooden stakes to construct a coordinate system for 120 sampling stations. In each sampling station, we delimited a surrounding zone of 2.5 m^2 . Within these zones, we applied the Canfield's Line Intercept (LI) method (Canfield, 1941) to measure the percentage of vegetation coverage at two different heights (*viz.* 35 and 100 cm; VC35 and VC100, respectively). We also counted the number of all the herbaceous plants (H) and the number of all woody plants (W) within these zones. Plant species richness (SR) was registered as the number of different plant species found within these zones. The percentage of logs (Logs) covering the ground surface was also registered using the Canfield's method (Canfield, 1941). These habitat features were sampled once during the most representative month of the dry season (July 2017) and the rainy season (February 2018) (CONANP, 2006). All selected variables qualify as components of the vertical and horizontal structure of the habitat (Coppeto *et al.*, 2006; Jorgensen, 2004; Morris, 1984; Villanueva-Hernández *et al.*, 2017). These variables are indicators of possible refuges from predators, spaces for resting and mating and food resources (Jorgensen, 2004).

Mouse sampling

We captured *Peromyscus* mice alive over ten months to include data for the dry (October 2014 to February 2015) and rainy (March 2015 to July 2015) seasons. We set a

single live trap (H.B. Sherman, Inc., Tallahassee, FL 32303, USA), baited with oat flakes and vanilla extract at each sampling station of the plot ($n = 120$). Traps were set for one night each 15 days per month. We obtained a total of 20 capture events (10 months $\times$ 2 nights). At the end; we could have an estimate of the mice abundance for the dry and rainy season. To avoid recurrence behavior (*e. g.*, mice coming back to the traps for bait) or shyness (*e. g.*, mice avoiding traps due to other mice odors), all the traps were thoroughly cleaned and randomly oriented within each sampling station in each capture event. To prevent hypothermia during capture, we placed 3-5 cotton balls inside the trap and put the traps inside open plastic bags. Mice capture and handling followed the guidelines of the American Society of Mammalogists (Sikes *et al.*, 2019). Any mouse that died was prepared as voucher specimens and incorporated into the Mammal Collection of the Universidad Autónoma Metropolitana-Iztapalapa (Ramírez Pulido *et al.*, 1989). A scientific collecting permit, Semarnat-08-049-B, was issued to Alondra Castro-Campillo (ACC) by DGVS, SGPA-09712/13, Semarnat, Mexico.

Statistical analysis

All statistical analyses were performed using the JMP statistical package (v14.0; SAS Institute). Prior analyses, all variables were standardized to a mean of zero and a standard deviation of one ($\bar{x} = 0$, $SD = 1$) to meet normality. Student's *t*-test was used to evaluate mean differences in the six indicator variables of habitat structure between the rainy and dry seasons. The complexity of habitat structure depends on the interaction between different biotic and abiotic elements of the habitat. Thus, we carried out principal component analyses (PCA) using the six habitat indicators (variables) to produce new functions than could explain the complexity of the habitat structure in a detailed way. The PCA also helped to reduce data dimensionality. One PCA was performed for each season. We observed that in the dry season, the first three components explained 77.66 % of variance, while in the rainy season; the three first components explained 79.95 % of variance (Supplemental material 1). Therefore, we used these three principal components for subsequent analyses (*see below*). We constructed for each season (rainy and dry season), generalized lineal models (GLMs), using the abundance of each species (*P. difficilis* or *P. melanotis*) as response variable and the three main principal components as covariate effects. For all the GLMs, we assumed an identity link function and a normal distribution. The generalized linear coefficients (*viz.* β_i Lande & Arnold, 1983) obtained from the GLMs represent the strength and direction of the relationships acting directly on the abundance of the species in comparable units (standard deviations).

RESULTS AND DISCUSSION

During the dry season, the total number of individuals was 111: 64 individuals for *P. difficilis* and 47 individuals for *P. melanotis* (Figure 1). During the rainy season, the total

number of captures increased to 168:87 individuals for *P. difficilis* and 81 individuals for *P. melanotis* (Figure 1). The mean difference between seasons was significant for five of the habitat features (Table 1, Figure 2). The values of these five variables were higher in the rainy season (Figure 2). Only the coverage of logs of wood on the ground surface between seasons did not change (Table 1, Figure 2). Principal component analysis for the dry season showed that the first three compounds explained 77.66 % of the variance (Table 2). The highest loadings in the first component (PC1) were variables related with herbaceous

vegetation; VC35, species richness and number of herbaceous plants (Table 2). The PC2 was related with woody plants; W and VC100. The PC3 was related only with the coverage of logs of wood covering the ground surface (Table 2). In the rainy season, the first three compounds explained 79.95 % of variance (Table 2). The highest loadings in the first component (PC1) were variables related with plant richness, herbaceous and woody vegetation (Table 2). The PC2 was related with woody plants and logs of wood and the PC3 was related with logs of wood and herbaceous plants (Table 2).

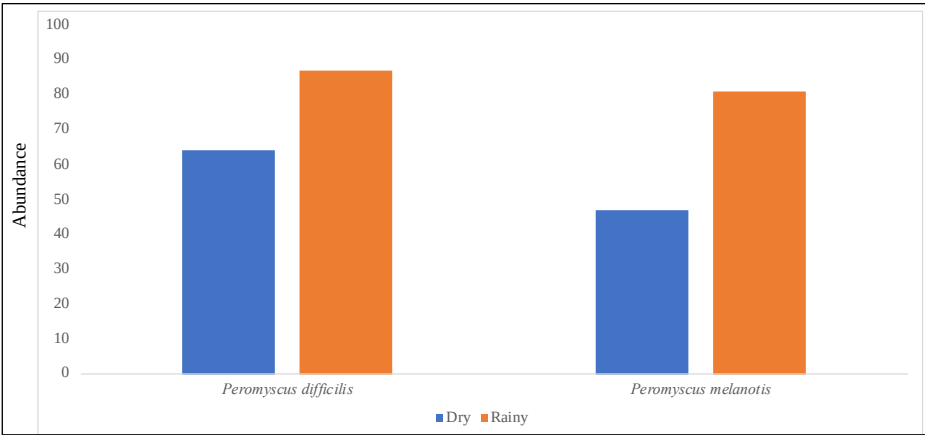


Figure 1. Abundance of *Peromyscus difficilis* and *Peromyscus melanotis* in the dry and rainy season.

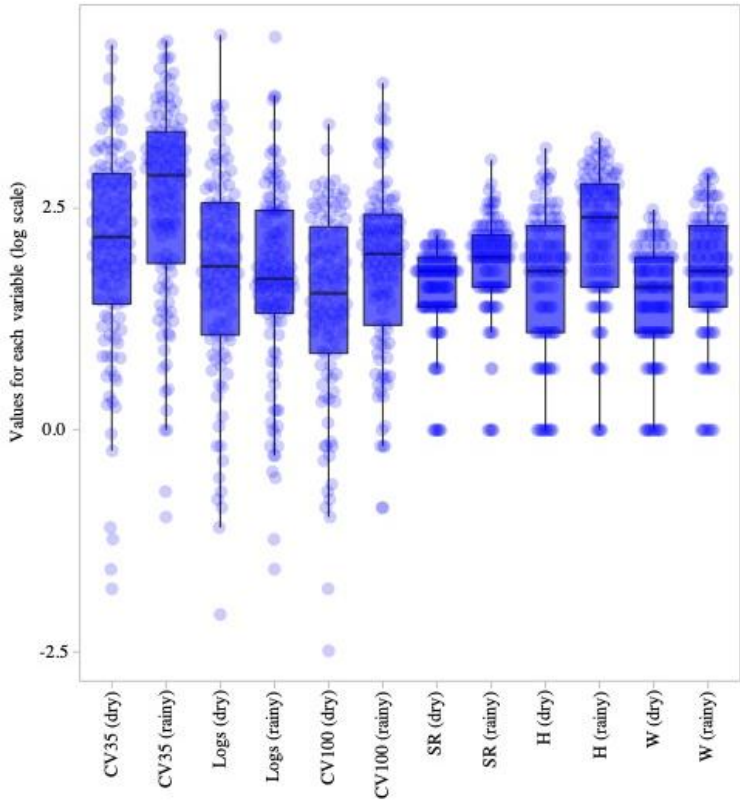


Figure 2. Boxplots that show the median differentiation of the habitat components between seasons. Seasons are specified in parentheses in each variable. Dots represent the sampling stations.

The GLM between the abundance of *P. difficilis* and the principal components in the dry season was significant (L-R chi-square = 37.38, AICc = 323.17; $p = 0.0001$) (Table 3, Figure 3). Significant predictors included the PC2 and PC3. Both principal components were positively related with the abundance of *P. difficilis* (Table 3, Figure 3). In the rainy season, the GLM between the abundance of *P. difficilis* and the principal components was also significant (L-R chi-square = 19.79, AICc = 353.09; $p = 0.0002$). The only significant predictor was the PC2. This component was positively related with the abundance of *P. difficilis* (Table 3, Figure 3). The GLM between the

abundance of *P. melanotis* and the principal components in the dry season was significant (L-R chi-square = 9.96, AICc = 341.47; $p = 0.0189$) (Table 3, Figure 3). In this model, the only significant predictor was the PC2 (Table 3, Figure 3). This component was positively related with the abundance of *P. melanotis* (Table 3, Figure 3). In contrast, in the rainy season, the GLM between the abundance of *P. melanotis* and the principal components was nearly significant (L-R chi-square = 7.53, AICc = 293.85; $p = 0.0566$). In this model, only the PC1 was significant and positively related with the abundance of *P. melanotis* (Table 3, Figure 3).

Table 1. Mean differences in habitat structure elements between seasons.

Habitat feature	N	Mean (SE)		<i>t</i>	<i>df</i>	<i>p</i>
		Dry season	Rainy season			
VC35	231	12.28 (1.17)	20.10 (1.59)	3.5	229	0.0005
VC100	211	5.42 (0.50)	8.28 (0.75)	2.84	209	0.0049
Logs	212	8.48 (1.03)	8.37 (0.98)	-0.36	210	0.7154
H	213	6.12 (0.47)	9.98 (0.65)	4.39	211	0.0001
W	224	4.80 (0.26)	6.55 (0.41)	3.19	222	0.0016
SR	231	5.19 (0.19)	7.02 (0.32)	4.2	229	0.0001

Table 2. Loadings of the principal components analyses for the dry and rainy season.

Dry season	PC1	PC2	PC3	PC4	PC5	PC6
VC35	0.47	-0.40	0.17	0.26	0.57	-0.43
Logs	-0.11	0.33	0.92	0.10	-0.03	-0.04
VC100	0.25	0.50	-0.23	0.78	-0.08	0.08
SR	0.53	0.17	-0.00	-0.29	-0.56	-0.51
H	0.51	-0.39	0.22	0.04	-0.27	0.67
W	0.37	0.53	-0.06	-0.46	0.51	0.28
Rainy season						
VC35	0.41	-0.33	0.56	-0.08	0.61	-0.11
Logs	-0.14	0.67	0.66	0.24	-0.09	0.08
VC100	0.38	0.03	-0.24	0.87	0.07	-0.13
SR	0.49	0.30	-0.04	-0.32	-0.29	-0.68
H	0.49	-0.27	0.23	-0.00	-0.61	0.49
W	0.40	0.50	-0.34	-0.25	0.38	0.49

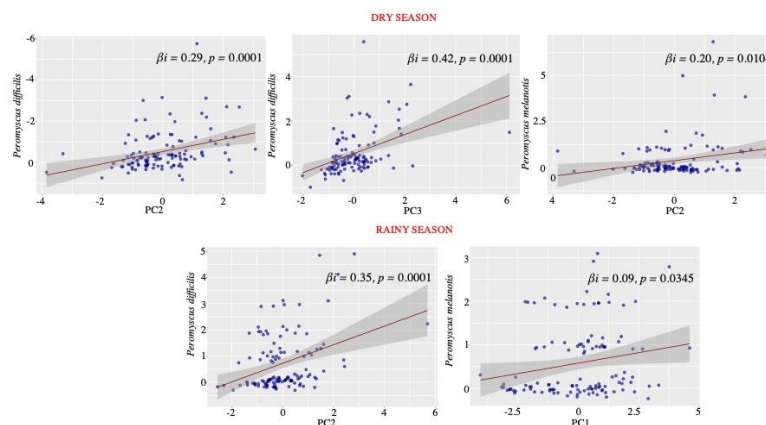


Figure 3. Relationships between the abundance of *Peromyscus difficilis* or *Peromyscus melanotis* with the principal components. Coefficients of the linear models and *p*-values are showed in the plots.

The results of our analyses showed different relationships between the habitat structure and the abundance of both species. As environmental conditions changed between dry and rainy season also changed the complexity of the habitat and this had an effect to abundance of both species of *Peromyscus*. We found that both *Peromyscus* were sensitive to slight changes in habitat structure and also our results shed lights about possible habitat preferences of both species. For instance, during the dry and rainy season, *P. difficilis* was mainly related with logs of wood, while *P. melanotis* was related with herbaceous and woody plants and plant coverage at 35 and 100 cm of height. Higher rodent frequency in higher-density understory habitats has been interpreted as a strategy to avoid predation by aerial hunters (Dalmagro & Vieira, 2005; Ramírez Pulido *et al.*, 1989). It seems that temporal differences in habitat structure, and the associated shifts in food and shelter availability, facilitate coexistence between these *Peromyscus* (Pianka, 1973). But why *P. difficilis* had a high affinity for places with the presence of logs of woods? Logs of woods on the ground surface represent small patches of microhabitat for small mammals with food sources, such as plant items and invertebrates (Bellows *et al.*, 2001), as well as sources for refuge and shelter (Bowman *et al.*, 2001). Individuals of *P. difficilis* could also use the large fallen logs as pathways for quick and straight locomotion within the forest (Bellows *et al.*, 2001). Indeed, fallen logs promote structural complexity of forests and may enhance positive interactions among species of small mammals (Bowman & Facelli, 2013).

We also observed that the abundance for both species increased in the rainy season. These changes in abundance could be related with the respective breeding seasons of both species (De-la-Cruz *et al.*, 2019). The main breeding activity in *P. difficilis* occurs during the dry season with another peak during the rainy season, while for *P. melanotis* the breeding occurs during the rainy season (Álvarez-Castañeda, 2005; De-la-Cruz *et al.*, 2019). The increase in number of captures or abundance for both species from the dry to the rainy season could be related with the fact that rains promote vegetation growing and hence an increase in food resources is observed during this season. These temporal changes in the relationships between species and habitat structure could also be related with the locomotive habits of each species. For instance, the long tail of *P. difficilis* enables it to rush and climb along shrubs, trees or logs of wood (Bowman & Facelli, 2013), thus increasing its preference for habitats with fixed elements (*e. g.*, fallen logs and twigs), where they can escape from predators or construct burrows. In contrast, smaller body size and a shorter tail (Álvarez-Castañeda, 2005), should enable the cursorial *P. melanotis* to escape very quickly from predators. This could explain why this species was related with a more complex habitat structure. Indeed, coverage by high shrubs provides both protections from predators and food sources, since seeds may be concentrated under shrub canopies (Mohammadi, 2010).

Table 3. Generalized linear models that show the relationship between the abundance of *Peromyscus difficilis* or *Peromyscus melanotis* with the three main principal components that explain the complexity of the habitat in the dry and rainy season.

Dry season	Effects	N	d.f.	Estimate	SE	t ratio	p
<i>P. difficilis</i>	PC1	120	1	0.05	0.05	1.11	0.2701
	PC2	120	1	0.29	0.07	3.98	0.0001
	PC3	120	1	0.42	0.08	5.03	0.0001
<i>P. melanotis</i>	PC1	120	1	0.08	0.05	1.41	0.1625
	PC2	120	1	0.20	0.08	2.61	0.0104
	PC3	120	1	-0.10	0.09	-1.13	0.2616
Rainy season							
<i>P. difficilis</i>	PC1	120	1	-0.07	0.05	-1.27	0.2053
	PC2	120	1	0.35	0.08	4.10	0.0001
	PC3	120	1	0.16	0.10	1.53	0.1277
<i>P. melanotis</i>	PC1	120	1	0.09	0.04	2.14	0.0345
	PC2	120	1	-0.01	0.06	-0.18	0.8611
	PC3	120	1	-0.14	0.08	-1.71	0.0904

Finally, this study provides evidence of how two species of small mammals are affected by changes in the habitat structure. Our results provide information of habitat preferences for these two *Peromyscus* species that coexist and inhabits in an ecosystem at the edge of a megalopolis (Mexico City). Understand what elements of the habitat shape the abundance of the species is important to elaborate better strategies to preserve natural areas and the species

that inhabits there. Urban growth produces fragmentation of natural microhabitats that is important to the small mammals, which play a fundamental role in the dispersal of seeds in the forest and as habitat architects.

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