



Co-occurrence and character convergence in two Neotropical bats

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When functionally similar species co-occur, they are expected to differ in at least 1 niche axis to avoid competition. In bats, small differences in body size can influence ecology, potentially reducing niche overlap. We used yellow-shouldered bats (genus *Sturnira*) in Mexico as a model to investigate whether interspecific differences in body size increase when 2 related and ecologically similar species occur in sympatry. We hypothesized that size divergence would take place in sympatry, following known patterns whereby larger bats eat larger fruits and smaller bats forage and roost in more cluttered habitats. We collected data on body mass, forearm length, and skull size from museum specimens to characterize the overall dimensions of these bats. Using linear mixed effect models and permutation tests, we tested for differences between areas where these species occur in sympatry or allopatry, while controlling for the confounding effect of environmental variables and sexual dimorphism. Contrary to our original hypothesis, we detected size convergence in sympatric areas, an uncommon pattern in bats. We found no evidence of character displacement for forearm length and body mass, but an effect of co-occurrence on overall skull size and head length. Convergence in overall skull dimensions may reflect shared environmental pressures and similar food resources, which may not represent a limiting factor. Interspecific differences in forearm length remain constant in sympatry or allopatry. These differences likely preceded the 2 species coming into contact and could have allowed initial and ongoing coexistence by influencing wing properties and flight. We highlight the need for multivariate approaches in the study of character displacement, as selective pressures can act differently on different traits allowing both local adaptation and coexistence.

Para que dos especies con hábitos ecológicos semejantes puedan coexistir, se espera que deben diferir en al menos un aspecto ecológico-funcional. En el caso de los murciélagos, incluso pequeñas disimilitudes en el tamaño corporal pueden promover diferencias ecológicas que potencialmente reducirían la competencia. Investigamos si las diferencias interespecíficas en el tamaño corporal aumentan cuando dos especies filogenéticamente cercanas y ecológicamente similares coexisten en simpatría. Para ello utilizamos ejemplares mexicanos del género *Sturnira*. Nuestra hipótesis es que existe divergencia de tamaño corporal en simpatría, lo que les permitiría repartirse los recursos y el espacio de acuerdo a su tamaño. Para caracterizar las dimensiones generales de las dos especies, tomamos medidas morfométricas (peso, antebrazo y cráneo) de ejemplares de museo. Utilizamos modelos lineales mixtos y permutaciones para determinar si existen diferencias significativas entre las regiones donde las especies habitan en simpatría o alopatría. En nuestro análisis consideramos el posible efecto de variables ambientales y del dimorfismo sexual. Contrario a lo planteado, en las regiones de simpatría detectamos señales de convergencia en el tamaño, un patrón poco común en murciélagos. No encontramos desplazamiento del tamaño en el largo del antebrazo y el peso, pero sí detectamos señales de convergencia en las medidas craneales. La convergencia de las dimensiones craneales podría deberse al consumo de alimentos similares o a presiones ambientales compartidas. Por otra parte, las diferencias interespecíficas en el largo de los antebrazos son constantes en regiones de simpatría

y alopatría. Es posible que estas diferencias existan desde antes del contacto entre las dos especies, y posiblemente favorecieron y preservaron su coexistencia. Destacamos la necesidad de utilizar análisis multivariados para analizar el desplazamiento de caracteres, ya que las presiones selectivas pueden actuar de manera diferencial en distintos rasgos, lo que permitiría desarrollar procesos de coexistencia así como de adaptaciones locales.

Key words: coexistence, ecogeographic, macroecology, Mesoamerica, Stenodermatinae

Related species often retain morphological and ecological characteristics from recent common ancestors, and thus play similar functional roles in ecosystems and rely on similar resources (Losos 2008). If 2 functionally similar species co-occur in the same area with limited resources, 1 is expected to be excluded through competition in the long term (MacArthur and Levins 1967). A shift in behavioral, ecological, or morphological traits, however, may reduce competition and allow species to coexist (Goldberg and Lande 2006). This process is known as ecological character displacement (Brown and Wilson 1956).

Body size is a fundamental ecological trait that has been relatively well-conserved in the evolution of mammals (Capellini et al. 2010). Body size influences a number of ecological traits such as metabolism and energy requirements, home range, diet, and foraging (Peters 1986). Therefore, it can promote niche differences that reduce resource competition through space and resource partitioning and changes in predator–prey relationships (Wilson 1975; Connell 1980). A popular approach for studying ecological character displacement is to test for increased trait divergence in sympatric lineages (Goldberg and Lande 2006). Trait divergence in sympatric lineages is widespread among animal taxa, such as differing beak sizes in coexisting ground finches and divergent body sizes for pairs of related *Anolis* lizards occurring on the same island (reviewed in Schluter 2000). Body size is one of the most widely used traits in studies of character displacement, and differences in body size are often greater when related species occur in sympatry (Dayan and Simberloff 2005).

Despite having a relatively narrow range of body sizes constrained by the physics of flight (Smith et al. 2013), bats are the second most taxonomically diverse mammalian order (Simmons 2005). This suggests that even slight differences in morphology or behavior can cause differing usage of niche space, allowing such impressive diversity (York and Papes 2007). The rich assemblages of plant-visiting leaf-nosed bats (Phyllostomidae) in the New World Tropics exemplify the fine partitioning of resources among coexisting species, both related and unrelated (Dumont 2003). For example, at least 26 species of plant-visiting phyllostomids were found to coexist on Barro Colorado Island, Panama (Giannini and Kalko 2005).

At a broad scale, Neotropical bats appear to co-occur most readily when they are morphologically similar. This is thought to result from environmental pressures selecting species with similar trait values (Shi et al. 2018). At a finer scale, known mechanisms for coexistence include differences in diet, habitat use, and morphology, which relate to properties of the foods consumed and to species' body size (Aguirre et al. 2002). Previous studies on frugivorous leaf-nosed bats found that larger bats tend to eat larger fruits (Fleming 1991), and that

smaller bats are more able to navigate, forage, and roost in cluttered forest habitats (Stockwell 2001).

Two species of yellow-shouldered bat (*Sturnira hondurensis* and *S. parvidens*) occur in Mexico, with overlapping distributions and body sizes. Phylogenetic and biogeographic analyses suggest that the species came into secondary contact in Mexico after the emergence of the Isthmus of Panama (Velazco and Patterson 2013). *Sturnira parvidens* and *S. hondurensis* are each other's closest co-occurring relative, and they are morphologically and functionally similar, so divergence along a niche axis could allow them to coexist in the same environment.

Phenotypic divergence has never been tested for this study system, and the ecogeographic distribution of the 2 species complicates how we can study it. At a finer scale, *S. parvidens* is a lowland species and *S. hondurensis* a montane species, so sympatry tends to occur at intermediate elevations. If these bats follow the common pattern in which body size covaries with elevation (Willig et al. 2009), character displacement might be obscured by the phenotypic variation associated with the conditions along an elevational gradient. Given the influence of environmental and abiotic factors on species' distributions and phenotypes, these variables should also be accounted for when testing for ecological character displacement.

Ecological character displacement has been suggested to take place in 2 species of *Carollia* (McLellan 1984), a genus of frugivorous phyllostomid very similar in ecology to *Sturnira*. Pine (1972) mentions that because of size divergence, specimens of the 2 species of *Carollia* from the same locality are more easily distinguished. The 2 species of *Sturnira* in Mexico are very problematic to tell apart. In this case, evidence for divergent character displacement would be useful from a practical stance, as it would help field biologists to distinguish the species in the field. Here, we examine the differences in body measurements between the 2 species of *Sturnira* in Mexico, testing for differences between sympatric and allopatric occurrence and accounting for phenotypic changes associated with sex and environmental variation. We predicted size differences to be more marked in areas where the species co-occur, irrespective of the effect of environmental conditions.

MATERIALS AND METHODS

Species data.—There are 2 species of yellow-shouldered bat (*S. hondurensis* and *S. parvidens*) in Mexico. *Sturnira hondurensis* is reported as the larger of the 2, but size alone is not diagnostic. Identification is possible, but it requires microscopic examination of dental characters (Velazco and Patterson 2014). We examined study skins (standard specimen preparation with the bones from 1 or both wings left in the skin) and

skulls housed at the Museo de Zoología “Alfonso L. Herrera,” UNAM, Mexico. This work was exclusively collection-based and no live animals were involved.

This sample only included specimens with legible locality data, undamaged forearms, and mandibular material for identification (using incisor and molar cusp morphology). We only examined adult individuals, aged based on dental wear and ossified growth plates near the epiphyseal regions (knuckles). Our final sample included 858 study skins (408 *S. parvidens*—232 female, 174 male; 450 *S. hondurensis*—267 female, 181 male and four specimens with no data for sex) and 243 skulls (117 *S. parvidens*—74 female, 43 male; 126 *S. hondurensis*—69 female, 57 male). After discarding records with incomplete data, the sample sizes were: 856 for the analyses of forearm length (FL), 802 for body mass, 243 for head length, and 233 for skull isosize. See [Supplementary Data SD8](#) for the list of specimens examined.

The final data set included 196 individuals with both skin and skull data. This represents roughly 80% of the total skull sample, and such overlap helps us rule out possible biases and data collection issues that could lead to spurious results. The samples are well-distributed throughout Mexico, covering a wide range of environmental conditions and representative of the geographic and elevational ranges of both species, especially in the areas of range overlap ([Fig. 1](#)). Although both species also occur in parts of Central America, these areas represent only a small portion of their overall range, and in the case of *S. parvidens*, populations in eastern Mexico share the same environmental preferences with those in Central America ([Hernández-Canchola and León-Paniagua 2017](#)).

Body size measurements.—Because overall body size in bats is unexpectedly difficult to represent with a single measurement, we considered 4 different proxies of body size: FL, body mass, skull isosize (a size metric derived from the geometric mean of multiple linear measurements), and head length.

Forearm length has been used extensively to reflect overall size in bats ([Presley et al. 2017](#)). FL is less affected by body

condition and its measurement is taken more consistently than total length, as some mammalogists include the tail in total length measurements. We collected FL values from specimen labels but consider that FL can be remeasured with minimal discrepancy. Absolute differences between label data and remeasurements for a random set of 10% of the sample were low (on average 0.6 mm). FL showed strong, significant correlations (Pearson product-moment, all cases $\rho > 0.74$; $P < 0.05$) with total length, hindfoot length, ear length, and body mass (also from specimen labels).

Skull size has also been shown to reflect overall body dimensions in bats ([Myers 1978](#); [Tomassini et al. 2014](#)). Skull size is less prone than FL to reflect changes caused by differences in wing loading, thermoregulation, and flight dynamics ([Findley and Wilson 1982](#)). To obtain an overall measure of skull size, we used multivariate ratio analysis (MRA) as describe by [Baur and Leuenberger \(2011\)](#). In MRA, the geometric mean of multiple linear measurements is used to define an isometric size axis (isosize) only reflecting differences in scaling ([Schweizer et al. 2014](#)). We performed MRA on these 9 skull measurements: braincase height (BRH), maximum zygomatic breadth (MZB), postorbital width (POW), mastoid width (Mast), width across the upper canines (CC), length of the maxillary tooth row (LMT), bullae length (BL), condylobasal length (CBL), and width of the mesopterygoid fossa (MSF). These cranial measurements were chosen from an original set of 16 for their low correlation with each other and for the likely functional implications of some skull structures in processing food. For example, the width across the upper canines and the length of the maxillary tooth row capture properties of the palate identified as biomechanically important for feeding ([Dumont et al. 2014](#)), while zygomatic breadth relates to gape and bite force ([Freeman 1988](#)). We measured these characters to the nearest 0.01 mm using digital callipers (Mitutoyo, Tokyo, Japan). These standard morphometric measurements are described in detail in ([McCarthy et al. 2005](#)). With this approach, we

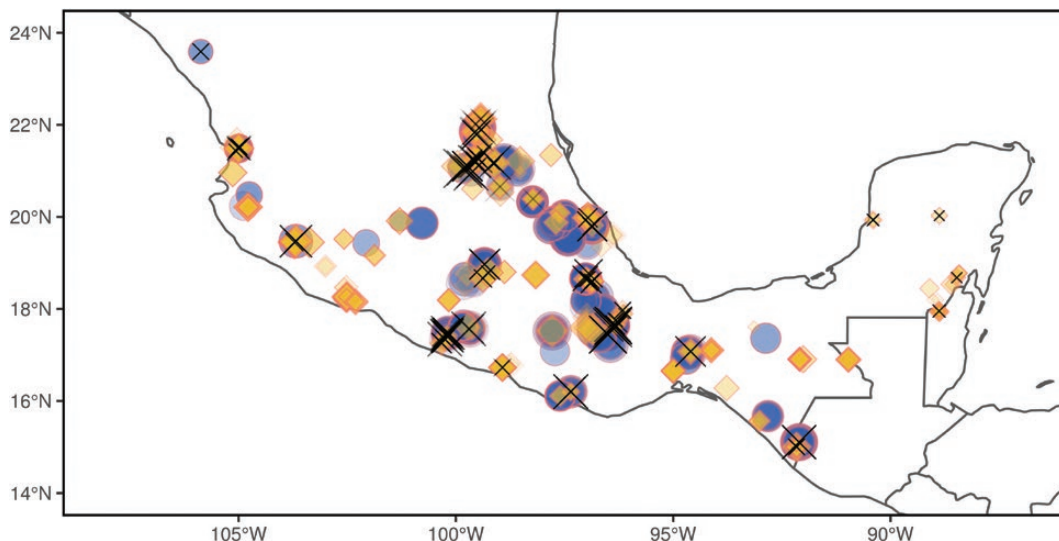


Fig. 1.—Specimen localities. Diamonds = *Sturnira parvidens*; circles = *Sturnira hondurensis*. Point size is scaled with forearm length. Crosses show localities with cranial measurements (scaled with head length). For visibility, the transparency of each point varies with the number of specimens at each point.

obtained a single isosize value for each skull, representing the centered geometric mean of the 9 measurements multiplied by the overall isometric size vector.

Because body mass is one of the most commonly used metrics for body size in comparative studies, including those investigating ecological character displacement (Stuart and Losos 2013), we also recorded body mass from specimen labels (i.e., recorded weight for live or freshly killed individuals). Head length is also indicative of body size. We reused 1 of our cranial measurements (condylobasal length) as an indicator of head length, which we consider comparable with condilocanine length or with the distance from the tip of the snout to the back of the skull when measuring live animals (Mutumi et al. 2017).

Defining sympatric and allopatric localities.— We considered species to co-occur only when their specimen records came from the same site. Because we were interested in fine-scale co-occurrence, we determined if 1 or both of the species were present for each locality using locality names (distinct combinations of state, municipality, and locality). At broad scales, range maps or species distribution models can identify areas of overlap. However, this approach would likely mask the local patterns of coexistence that occur within the extensive and topographically complex area of overlap. It would also limit the number of specimens in allopatric localities to a reduced and biased sample from the margins of the species' ranges, where other eco-evolutionary processes may be influencing body size (Gaston 2009).

Our approach risks overestimating the number of allopatric localities (e.g., by including potentially undersampled localities where only a single specimen from only 1 species was recorded but in reality, both species co-occur). By prioritizing the certainty of the sympatric locations, we expect that if our hypothesis is valid we will detect a signal in the data. The effect size of the signal might be underestimated as some allopatric locations might actually be sympatric. This idea is analogous to presence-only species distribution models in which real presences are contrasted with pseudo-absences, and the estimated probabilities of occurrence are interpreted as relative probabilities (Guillera-Arroita et al. 2015). To address this issue, we repeated the mixed effect model analyses to see if these potentially misleading data points would affect our results and their interpretation. In supplementary analyses, we first excluded localities with only 1 specimen. Then, we defined occurrence using density-based spatial clusters rather than localities (see [Supplementary Data SD3](#) and [SD4](#)). For these analyses, we considered how widely the species can move, because home range sizes influence the frequency and likelihood of inter- and intraspecific interactions. There are no published data on home range sizes for our study species. Instead, we considered published records of maximum nightly travel distances (3.2 km for *S. parvidens*—Fenton et al. 2000, and 1.5 km for *S. hondurensis*—Cortés-Delgado and Sosa 2014) when setting the epsilon parameter of the clustering algorithm to specify how close points should be to each other to be considered part of a cluster.

Environmental gradient.— We incorporated environmental variables in our analyses to detect character displacement while controlling for phenotypic variation along environmental gradients. We did not use elevation as a predictive variable because from a biological perspective, elevation acts as a proxy for climatic variables and because the same elevational values would not be comparable across a wide latitudinal range. Previous studies on bats found that body size varies along climatic gradients (Willig et al. 2009), so we included environmental variables that we considered a priori to relate to the heat conservation, seasonality, and productivity hypotheses of geographic body size variation (Blackburn et al. 1999). To select suitable climatic variables, we followed Correll et al. (2015), who aligned various environmental variables with the mechanisms and predicted patterns for the hypotheses that explain geographic body size variation.

We selected annual minimum temperature and potential evapotranspiration seasonality (the standard deviation of the monthly values for the potential evapotranspiration * 100). These 2 variables capture temperature, precipitation, and seasonality, which have been associated with variation in skull size in other frugivorous phyllostomids (Marchán-Rivadeneira et al. 2012) and with the overall physiological tolerances of bats (Peixoto et al. 2017). We derived these variables from a recent fine-scale (1 × 1 km), long-term climate raster data set (Karger et al. 2017), using the “envirem” R package (Title and Bemmels 2017) to generate the potential evapotranspiration seasonality layer.

Test for phenotypic differences.— To test for patterns indicative of character displacement, we used 2 methods designed to detect greater trait differences in sympatry than in allopatry (Kooyers et al. 2017). First, we used a linear mixed effect model approach to detect the effects of species co-occurrence on body size and repeated this for each body measurement. We used the body size measurements as response variables, and species identity, occurrence (allopatric or sympatric), and their interactions as covariates. To control for potential confounding factors, we also included climatic variables (PET seasonality and annual minimum temperature) and sex as additional covariates. We treated locality as a random effect. We determined the statistical significance of the model effects by ANOVA (Wald chi-square test, 1 *d.f.*). In this approach, a significant interaction between species identity and occurrence would suggest a morphological shift from allopatry to sympatry, a pattern consistent with ecological character displacement (Adams 2004).

To explore the more specific hypothesis that size divergence occurs in sympatry, we calculated the absolute difference between species trait means in sympatry (D_{sym}) and allopatry (D_{allo}), and also the difference between the differences ($D_{\text{sym-allo}}$). Greater difference in sympatry (positive $D_{\text{sym-allo}}$) implies divergent character displacement. To test if this observed differences are greater than expected by chance, we used the residual randomization procedure described in Adams and Collyer (2007). We fitted a reduced mixed effect

model without an interaction term between species and occurrence (allopatric or sympatric). Then, we added the estimated marginal means from this reduced model to its residuals to calculate observed $D_{\text{sym-allo}}$. To calculate expected $D_{\text{sym-allo}}$, we randomized the residuals from the reduced model and added them to the estimated marginal means. Repeating this procedure 9,999 times created a distribution of expected $D_{\text{sym-allo}}$. We assessed the statistical significance of the observed difference using a 1-tailed permutation test considering an alpha level of 0.05.

Lastly, we examined if the variability of the different traits changed in the presence of congeners. Typically, trait variation should be larger in the absence of competitors if variability relates to niche width (Meiri et al. 2005). We used modified signed-likelihood ratio tests (Krishnamoorthy and Lee 2014) to test for equality in the relative variability (coefficient of variation) of 3 of the 4 size variables. We excluded skull isosize because it is defined on an interval scale that can take positive and negative values and its mean is close to zero. In this case, the coefficient of variation no longer provides a useful indication of how big the standard deviation is when compared to the mean.

All analyses were run in R version 3.5.0 (R Core Team 2018) using the packages “nlme” (Pinheiro et al. 2017), “car” (Fox and Weisberg 2011), “cvequality” (Marwick and Krishnamoorthy 2018), and “emmeans” (Lenth 2017) for the main analyses, “cowplot” (Wilke 2017) for arranging plots, and “broom” (Robinson 2017) for handling model outputs. All supporting data and R code for this work are available as an archived GitHub repository (Verde Arregoitia et al. 2018).

RESULTS

Despite considerable overlap, our measurements and models showed that in general, *S. hondurensis* is larger than *S. parvidensis* (Fig. 2). The elevational distribution of the records also followed the reported preference of *S. parvidensis* for lowlands (most common between 0 and 1,400 m) and *S. hondurensis* for higher elevational montane habitat (most common between 900 and 2,200 m).

We found a significant interaction effect of occurrence (sympatry or allopatry) on skull isosize and condylobasal length (Tables 1 and 2). Sex and environmental conditions were also important predictors of variation in body size for the 2 species. Our results indicate some degree of sexual size dimorphism; males of both species tended to be significantly larger than females in all 4 measurements. Both FL and body mass showed a significant relationship with temperature (Table 2). These 2 “external” measurements decreased with increasing temperature (minimum annual temperature).

The interspecific difference between the mean values of all 4 measurements was greater in allopatry (D_{allo}) than in sympatry (D_{sym}), and the differences between these differences ($D_{\text{sym}} - D_{\text{allo}}$) were all negative (Table 3). This means that the species tended to converge rather than diverge in size when in sympatry (Fig. 3). However, these observed changes in trait values were not statistically significant (Table 3). While both species showed change in sympatry for most measurements, *S. hondurensis* changed more (Table 2; Fig. 3). The interaction effect was significant in the mixed model and evident in the plots, but without considerable morphological change in both species, the residual randomization approach is unlikely to show

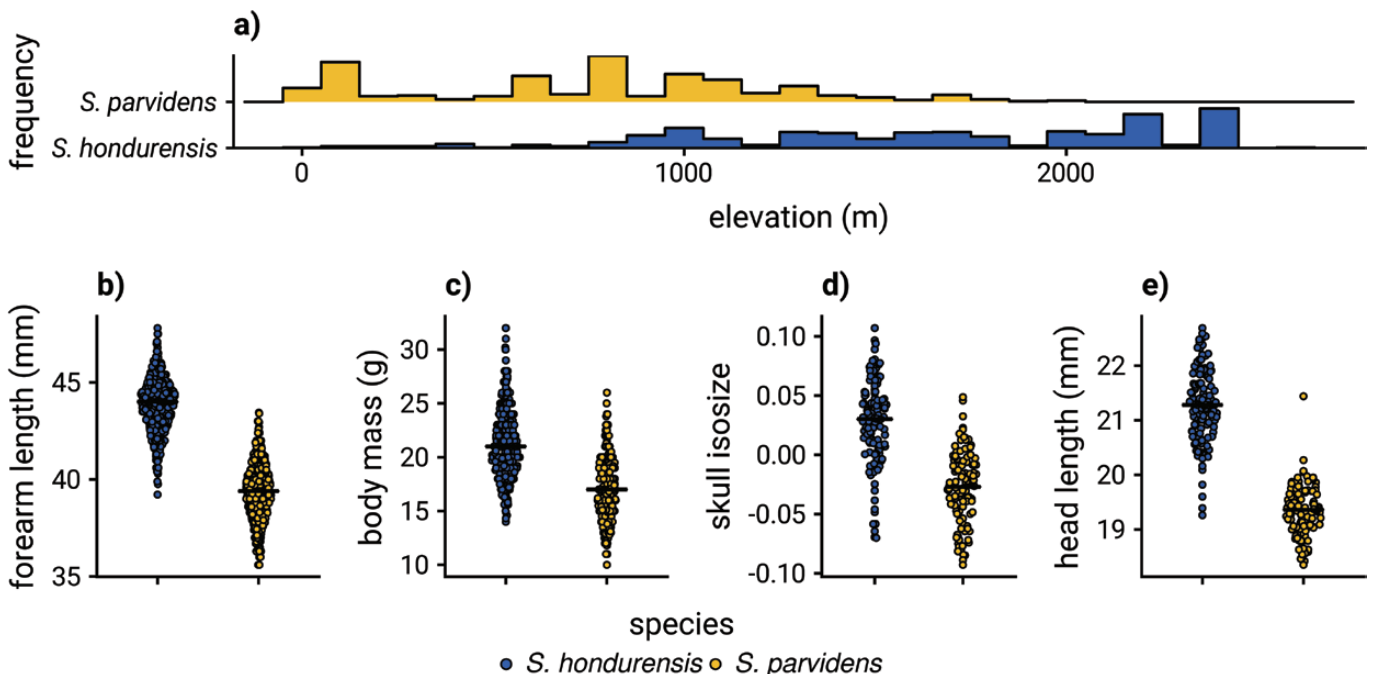


Fig. 2.—a) Elevational distribution of the specimen records for each species (100-m bins); b–e) body measurements by species, crossbars show median values. To show the distribution of the data, points are shifted horizontally according to their local density.

Table 1.—Parameter estimates with upper and lower 95% CIs for the linear mixed effect models fit separately for each body measurement.

Model	Variable	Estimate (95% CI)
Forearm length	Species (hondurensis)	44.524 (43.443 to 45.605)
	Species (parvidens)	40.191 (38.871 to 41.511)
	Sex (male)	0.532 (0.351 to 0.712)
	Minimum annual temperature	−0.058 (−0.103 to −0.013)
	Potential evapotranspiration seasonality	−0.005 (−0.051 to 0.040)
	Species (hondurensis):occurrence (sympatry)	−0.261 (−0.740 to 0.217)
Body mass	Species (parvidens):occurrence (sympatry)	0.293 (−0.172 to 0.759)
	Species (hondurensis)	21.492 (19.147 to 23.836)
	Species (parvidens)	17.041 (14.201 to 19.881)
	Sex (male)	1.334 (0.980 to 1.689)
	Minimum annual temperature	−0.130 (−0.225 to −0.035)
	Potential evapotranspiration seasonality	0.066 (−0.033 to 0.164)
Skull isosize	Species (hondurensis):occurrence (sympatry)	−0.869 (−1.894 to 0.156)
	Species (parvidens):occurrence (sympatry)	0.425 (−0.565 to 1.415)
	Species (hondurensis)	0.026 (−0.020 to 0.073)
	Species (parvidens)	−0.048 (−0.109 to 0.014)
	Sex (male)	0.029 (0.022 to 0.035)
	Minimum annual temperature	−0.001 (−0.003 to 0.002)
Head length	Potential evapotranspiration seasonality	0.001 (−0.001 to 0.002)
	Species (hondurensis):occurrence (sympatry)	−0.028 (−0.046 to −0.009)
	Species (parvidens):occurrence (sympatry)	0.005 (−0.015 to 0.024)
	Species (hondurensis)	21.248 (20.517 to 21.979)
	Species (parvidens)	19.028 (18.085 to 19.970)
	Sex (male)	0.609 (0.494 to 0.723)
	Minimum annual temperature	−0.002 (−0.039 to 0.036)
	Potential evapotranspiration seasonality	−0.002 (−0.032 to 0.029)
	Species (hondurensis):occurrence (sympatry)	−0.364 (−0.651 to −0.077)
	Species (parvidens):occurrence (sympatry)	0.168 (−0.147 to 0.483)

Table 2.—ANOVA results (Wald chi-square test, 1 *d.f.*) for the linear mixed models fit separately for each body measurement. Colons (:) represent variable interactions; *P*-values < 0.05 are presented in bold, and an alpha level of 0.05 was used for hypothesis testing.

Model	Term	χ^2	<i>P</i> -value
Forearm length	Species	9,805.96	<0.0001
	Sex	33.38	<0.0001
	Minimum annual temperature	6.49	0.01
	Potential evapotranspiration seasonality	0.05	0.82
	Species:occurrence	3.57	0.17
	Body mass	Species	680.71
Sex		54.65	<0.0001
Minimum annual temperature		7.21	0.01
Potential evapotranspiration seasonality		1.72	0.19
Species:occurrence		4.71	0.09
Skull isosize		Species	135.74
	Sex	80.74	<0.0001
	Minimum annual temperature	0.41	0.52
	Potential evapotranspiration seasonality	0.43	0.51
	Species:occurrence	9.06	0.01
	Head length	Species	5,136.60
Sex		110.37	<0.0001
Minimum annual temperature		0.01	0.94
Potential evapotranspiration seasonality		0.01	0.92
Species:occurrence		7.88	0.02

statistical support for character displacement (either divergent or convergent).

Varying our approach for classifying sympatric and allopatric occurrence for all the tests of phenotypic divergence did not influence our conclusions. There were 13 localities with only 1 specimen. The results after removing them from each of the analyses did not vary, giving similar model estimates

([Supplementary Data SD1–SD3](#)). Defining occurrence on the basis of spatial clusters also led to similar model estimates ([Supplementary Data SD4–SD6](#)).

When testing for equality in coefficients of variation rather than differences in trait means, we found that trait variability in FL, body size, and head length was not significantly different between allopatric and sympatric localities ([Supplementary Data SD7](#)).

DISCUSSION

Instead of evidence of divergent character displacement, we found convergence toward a similar body size in areas of co-occurrence. Co-occurrence was a significant predictor of size variation in 2 of the 4 measurements that we examined (skull isosize and head length), and the interspecific differences in trait means were smaller in sympatry for all 4 traits. This shift toward similar body measurements may not necessarily be a direct response to co-occurrence, but a reflection of convergent selective pressures, similar foods consumed, and shared environmental conditions apart from those controlled for in our models. When we examined morphological variability as an indicator of relative niche width, we found that the presence or absence of a potential competitor (sympatric or allopatric occurrence) did not influence trait variability. Overall, these patterns are in line with the results of Shi et al. (2018) of widespread sympatry for morphologically similar species of Neotropical bats, influenced strongly by abiotic factors.

Body size overlap between coexisting species is thought to be common in Neotropical bat communities (Bloch et al. 2011). However, this conclusion comes from studies that only consider body mass. The different measurements that we examined might reflect different niche axes, and subtle differentiation along these axes may be facilitating coexistence through resource

Table 3.—Differences in species trait means in sympatry and allopatry, calculated after adding the estimated marginal means from the reduced model to the observed model residuals. Observed significance levels (P -values) were empirically generated from 10,000 random permutations.

Model	D_{sym}	D_{allo}	$D_{\text{sym}} - D_{\text{allo}}$ (P)
Forearm length	3.840	4.050	-0.210 (0.11)
Body mass	3.293	3.714	-0.421 (0.10)
Skull isosize	0.043	0.048	-0.005 (0.16)
Head length	1.708	1.824	-0.116 (0.10)

partitioning. Species' phenotypes diverge in response to competitively mediated shifts in resource use (Stuart and Losos 2013), so tests for divergence should be aware of the functional links between traits and partitioned resources. By considering cranial characters and wing elements separately, we can address the roles of cranial characters in feeding and forearm bones in flight.

We found that Mexican *Sturnira* species shifted toward similar overall skull sizes and head lengths when in sympatry. Cranial features relate to the size and hardness of the fruits consumed (Dumont 2003), so this convergence may reflect similar environmental conditions and fruit resources available in the areas of co-occurrence. The dental characters that help us identify the 2 species do not necessarily correspond to the known craniodental correlates of diet in frugivorous bats, such as molar complexity or biting styles (Santana et al. 2011). Despite a known overlap in their diets, *S. parvidens* was found to have a higher digestive capacity and a broader diet breadth than *S. hondurensis* (Saldaña-Vázquez et al. 2015). *Sturnira parvidens* is able to consume low- and high-quality foods and maintain a constant intake of nutrients, including some fruits not consumed by *S. hondurensis*. The narrower diet breadth of *S. hondurensis* could relate to its greater phenotypic response and change in skull size in sympatry (Fig. 3).

On the other hand, differences in FL did not relate to co-occurrence, and *S. hondurensis* tended to have consistently longer forearms after accounting for variation related to sex and environmental conditions (Fig. 3). These differences may have existed before the species came into sympatry, facilitating their initial coexistence through ecological sorting after coming into secondary contact. Forearm bones are important structural components of bat wings and they influence wing-area parameters (Norberg and Rayner 1987). Consistent differences in FL can imply consistent differences in aerodynamic performance and foraging tactics. Coexistence through subtle differences in foraging has been reported for *Carollia castanea* and *C. perspicillata*. Both forage and compete for some of the same fruits,

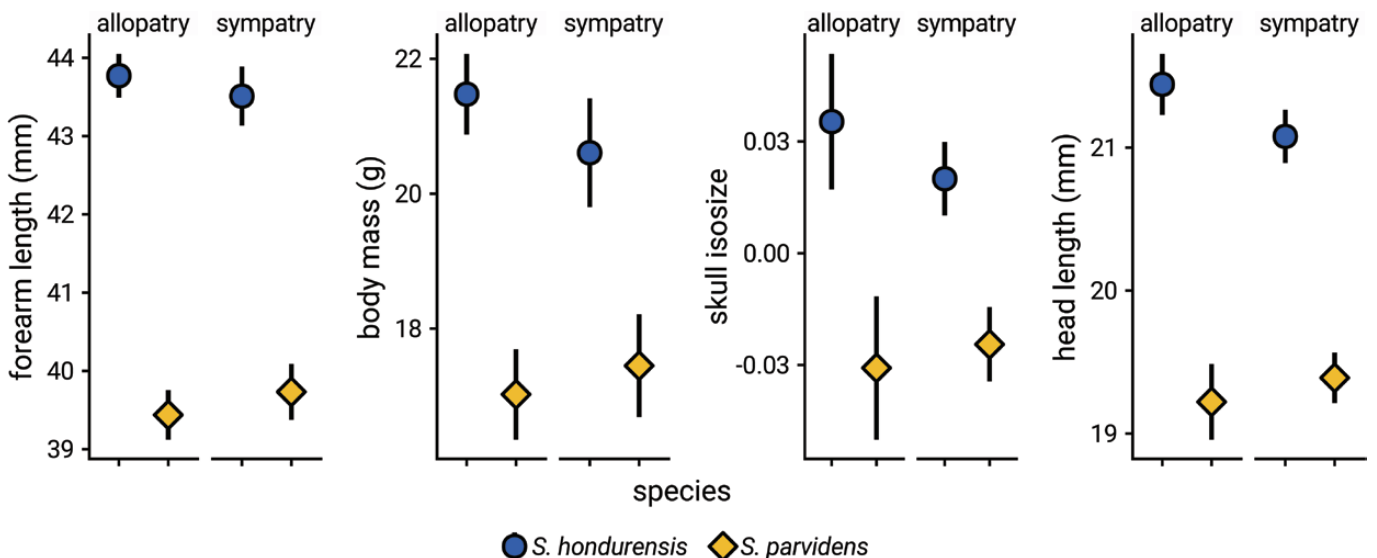


Fig. 3.—Estimated values of the 4 body measurements for each species when in sympatry or allopatry, holding the effects of sex and environmental variables constant. Vertical lines show upper and lower 95% CIs.

but the smaller body size and lower wing loading of *C. castanea* allow it to fly in forest clutter and exploit understory fruits not heavily consumed by larger congeners (Bonaccorso et al. 2007). Similar differences in wing aspect ratio and wing loading have been reported for *Sturnira* in southern Mexico (García-García et al. 2014).

The selective pressures of their roosting environment play a prominent role in the ecology and evolution of bats, and roosting preferences are known to influence the composition of bat communities (Voss et al. 2016). For example, roost preferences determined niche segregation between 2 ecomorphologically similar bat species in sub-Saharan Africa (Jacobs and Barclay 2009). The relationship between body size, FL, and roosting is unclear, but *S. hondurensis* and *S. parvidens* also differ slightly in roost preferences, which may facilitate coexistence. Both species roost primarily in standing tree cavities, but *S. parvidens* also uses roosts in more cluttered habitats such as arboreal termite nests, cracks in river banks, the bases of palm leaves, and vines (Cortés-Delgado and Sosa 2014).

Trait divergence is usually tested using species means in pairwise tests across large numbers of taxa. This approach can reveal broad patterns in large comparative data sets, but it often discards intraspecific variation, and fine-scale co-occurrence patterns. In these types of studies (Tobias et al. 2014), sympatry is defined focusing on broad-scale overlap independent of the joint occurrence of 2 species in the same habitat at the same time. In contrast with broad-scale studies, we focused on intraspecific variability, local co-occurrence, and environmental variation. In addition, character displacement and competition are typically expected to be stronger or more evident between sister species, so most studies focus on pairs of sister taxa (Schluter 2000).

Our study species are not sister taxa, but given their ecomorphological similarities and widespread sympatry, we still expected to find evidence of character displacement and use it as a way to help identify the species in the field. Neither *S. hondurensis* nor *S. parvidens* co-occur with their respective sister taxa, which are both recently described species (*S. burtonlimi* and *S. bakeri*, respectively) lacking detailed ecological and distributional data. The genus *Sturnira* is sister to all other stenodermines (Tavares et al. 2018). This deeper divergence is reflected in their functionally important cranial and dental characteristics that are neither totally similar to the other stenodermines nor like *Carollia* (Freeman 1988), a genus of frugivores from a separate subfamily but with very similar habits. Additionally, functionally similar species aside from close relatives could also compete with and influence the presence and phenotype of our study species. To varying degrees, *Sturnira* in our study area co-occur with other similar-sized frugivores such as species of *Carollia* or *Artibeus*. However, in addition to dental and cranial differences, these genera show dietary specialization to the fruits from different plant taxa relative to *Sturnira* (Saldaña-Vázquez 2014).

Given the problematic identification of these 2 species in the field and the general biogeographical and macroecological interest of testing for ecological character displacement, it is important to highlight how different proxies for body size can lead to different conclusions when analyzed separately. By

considering multiple characters relevant to competitive interactions, we reduced the risk of overlooking character displacement. However, we focused on character differences averaged across replicated sympatric populations. With only unidimensional data on phenotypes and occurrence, we cannot investigate resource partitioning caused by the idiosyncratic evolution of different character states across populations in response to similar ecological pressures (Germain et al. 2018). To do so would require an experimental approach and additional data not usually available for bats, such as resource availability and the abundance structure of communities.

We report a novel example of body size convergence in New World bats. Character convergence in sympatric conditions is well-documented in birds (Moynihan 1968) but it is often related to social and behavioral elements such as communal foraging or territoriality. Yellow-shouldered bats are nocturnal, less vocal than birds or insectivorous bats, at lower predation risk, and not gregarious, so convergence driven by diet and shared pressures of the physical environment could be a more likely explanation. Without clear differences in sympatry, measurements such as FL, head length, and body mass cannot help us identify the species in the field in places where the presence of both species is known or suspected. Our findings highlight the need for multi-trait studies of character displacement that consider fine-scale patterns of sympatry, the effect of abiotic factors, and the possibility of trait convergence.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Linear mixed model estimates, excludes localities with only 1 specimen.

Supplementary Data SD2.—ANOVA results for models that excluded localities with only 1 specimen.

Supplementary Data SD3.—Plot of estimated measurement values per species and occurrence pattern from models that excluded localities with only 1 specimen.

Supplementary Data SD4.—Linear mixed model estimates, defining sympatry using spatial clustering.

Supplementary Data SD5.—ANOVA results for models fitted using spatial clustering to define sympatry.

Supplementary Data SD6.—Plot of estimated measurement values per species and occurrence pattern from models fitted using spatial clustering to define sympatry.

Supplementary Data SD7.—Test statistics and *P*-values for tests for equality of coefficients of variation by species in relation to their co-occurrence.

Supplementary Data SD8.—Specimens examined.

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