Seasonal dietary niche contraction in coexisting Neotropical frugivorous bats (Stenodermatinae)

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Abstract
Tropical dry forests are characterized by punctuated seasonal precipitation patterns that drive primary production and the availability of fruits, seeds, flowers, and insects throughout the year. In environments in which the quantity and quality of food resources varies seasonally, consumers should adjust their foraging behavior to maximize energy intake while minimizing overlap with competitors during periods of low food availability. Here, we investigated how the diets of frugivorous bats in tropical dry forests of NW Mexico varied in response to seasonal availability and how this affected dietary overlap of morphologically similar species. We performed stable isotope analyses to understand temporal and interspecific patterns of overall isotopic niche breadth, trophic position, and niche overlap in the diet of six frugivorous species of closely related New World leaf-nosed bats (family Phyllostomidae, subfamily Stenodermatinae). We estimated seasonal changes in resource abundance in two complementary ways: (a) vegetative phenology based on long-term remote sensing data and (b) observational data on food availability from previously published insect and plant fruiting surveys. In all species, there was a consistent pattern of reduced isotopic niche breadth during periods of low food availability. However, patterns of niche overlap varied between morphologically similar species. Overall, results from our study and others suggest that seasonal food availability likely determines overall dietary niche breadth in Phyllostomidae and that despite morphological specialization, it is likely that other mechanisms, such as opportunistic foraging and spatiotemporal niche segregation, may play a role in maintaining coexistence rather than simply dietary displacement.

Abstract in Spanish is available with online material.

Keywords
bats, frugivory, fruiting phenology, Phyllostomidae, species coexistence, stable isotopes, trophic ecology, trophic niche, tropical dry forest
Seasonal resource limitation is driven by precipitation in tropical dry forests, where cyclical increases in rainfall during the wet season bring new vegetative growth, flowering, and fruiting (Stan & Sanchez-Azofeifa, 2019). Accordingly, flower, fruit, and arthropod abundance all peak during the wet season in coastal NW Mexico (Figure 1), and decrease in both diversity and abundance throughout the remainder of the year during the transition in tropical forests to the dry season (Borchert, Meyer, Felger, & Porter-Bolland, 2004; Valiente-Banuet, Maria, Coro, & Rojas-Martinez, and Laura Dominguez-Canseco., 1996). Thus, consumers should adjust their foraging behavior to maximize energy gains relative to costs as both resource quality and quantity fluctuate in seasonal environments (Abrams, 1991).

In Neotropical forests, leaf-nosed bats (Phyllostomidae) possess the greatest mammalian diversity with more than 70 species found sympatrically and serve as the predominant nocturnal predators, pollinators, and seed dispersers (Giannini & Kalko, 2004). Despite having insectivorous ancestors during the Miocene (Baker, Bininda-Emonds, Mantilla-Meluk, Porter, & Bussche, 2012), consumption of plant-based items is now widespread within the family: More than three-quarters of species primarily consume fruit or nectar (Baker et al., 2012). The most recent clade, the subfamily Stenodermatinae, contains > 43% of all described New World leaf-nosed bat species.

The explosive adaptive radiation within the Phyllostomidae has been largely attributed to morphological diversification associated with food acquisition, allowing the exploitation of specialized food types that promote local species richness (Freeman, 2000). For example, elaboration of morphological traits in the Stenodermatinae that create greater bite force allows for the consumption of hard canopy fruits (e.g., *Ficus* spp.) which are largely inaccessible to other frugivorous bats (Dumont, 1999; Dumont et al., 2011; Wendeln, Runkle, & Kalko, 2000). Despite morphological specialization related to dietary preference, previous studies have shown that many phyllostomid species appear to include plants, insects, and animals in their diets during different times of the year (Fleming, 1986; García-Estrada, Damon, Sánchez-Hernández, Soto-Pinto, & Ibarra-Núñez, 2012; Muñoz-Lazo, Franco-Trecu, Naya, Martinelli, & Cruz-Neto, 2019; York & Billings, 2009). In addition, within local assemblages there are often multiple, closely related species with similar morphology that suggests dietary niche overlap (Castaño, Carranza, & Pérez-Torres, 2018; Fleming, 1986; Fleming, Hooper, & Wilson, 1972; Rex, Czaczkes, Michener, Kunz, & Voigt, 2010). Nevertheless, it remains unclear to what extent seasonal patterns of availability within local communities drive dietary niche breadth, resource fidelity, and competitive interactions in these apparent specialist species.

Niche partitioning in bats and other species occurs in multiple dimensions, including diet, space use, and time (Kalko & Handley, 2001). The extent of direct competitive interactions can be estimated by measuring changes in resource use between potentially competing species during periods of high and low resource abundance. Interest in the dietary diversity of bats has a long history, and much of our knowledge comes either from direct observation, fecal, or molecular analysis (Castaño et al., 2018; Clare, Fraser, Braid, Brock Fenton, & Hebert, 2009; Fleming, 1991; García-Estrada et al., 2012; Kunz & Parsons, 1988; Painter et al., 2009). Although indispensable for taxonomic identification, fecal analysis is easily biased by digestibility and harder items such as seeds tend to be overrepresented compared to softer food items (Karasov & del Rio, 2007). In contrast, stable isotope analysis (SIA) typically provides little species-specific resolution, but instead provides an integrated view of fidelity to dietary items (Kelly, 2000). Thus, tissue isotope values contain information on an individual’s response to environmental

**Figure 1** Precipitation, vegetation phenology, and patterns of seasonal insect abundance in coastal dry forest along the western slope of Mexico. (a). Vegetation abundance (NDVI, solid circles) is positively correlated with precipitation (0.72). Maximum values in NDVI correspond with the period of greatest quantity of aboveground vegetation containing chlorophyll. (b) Insect abundance data (solid circles—Cantharidae, open squares—Cerambycidae, solid triangles—Coreidae, open diamonds—Staphylinidae) and plant flowering data are from previous studies in tropical dry forest in Mexico (see methods). NDVI values (solid circles) from subfigure A. are positively correlated with both peak insect abundance (solid line, 0.77) and peak flowering (gray bars, 0.55) shown in subfigure B.
conditions, such as habitat changes and food availability over time, and can provide insight into how individual responses influence general metrics of fitness at the individual and population level (Ben-David & Flaherty, 2012).

In this study, we asked whether coexistence of morphologically similar bat species pairs is facilitated by dietary niche differentiation based upon seasonal variation in the abundance and diversity of food resources. Optimal foraging theory predicts that individuals should specialize when resources are abundant but generalize when facing scarcity (Stephens & Krebs, 1986). In contrast, competition theory predicts that by minimizing niche overlap, mechanisms such as niche partitioning (MacArthur, 1958; Pianka, 1976) or character displacement (Hutchinson, 1959) facilitate coexistence among sympatric species with similar morphology, behavior, and habitat preferences. As a consequence of the dramatic seasonal changes in resource abundance in tropical dry forests, dietary consumer/bat diversity is likely to decrease during periods of low resource availability while also increasing competitive interactions between morphologically similar species relying on the same resources. To test these hypotheses, we used museum-archived bat tissue samples taken during both the wet and dry season and compared them to estimate the following: (a) isotopic niche breadth, (b) trophic niche, and (c) isotopic niche overlap between similar species pairs seasonally in a Bayesian framework. To complement our museum data, we collected remote sensing and survey data on fruit and insect abundance from the primary literature to document the degree of seasonality at our field site and provide a relative estimate of changing resource abundance.

More specifically, we tested seasonal changes in isotopic niche breadth, trophic position, and overlap against the following hypotheses: (a) optimal foraging theory, (b) competition theory, and (c) dietary inflexibility. The predictions of optimal foraging theory suggest that niche breadth and overlap should be indicative of specialization (smaller) during high food resource availability and generalist (larger) during periods of scarcity. In contrast, the predictions of competition theory suggest that during periods of low food resource availability, there should be decreased isotopic niche breadth and overlap between potentially competing species. If individuals are incapable of adjusting diet due to specialization or other constraints, then there should be no change in breadth or overlap in response to seasonal changes in food availability.

2 METHODS

2.1 Field site/Sample description

Our samples were collected in Cuauhtémcoc, Colima, Mexico (19° 19’ 45” N, 103° 35’ 57” W, 706 m a.s.l.). The site is in deciduous tropical dry forest and has a savanna climate, associated with high daily temperatures and seasonal rainfall and vegetation cover (Figure 1). The dry season occurs from December to May, and rainfall is concentrated between mid-June and October. Over 92% of the annual rainfall is concentrated within these five months (Nacional, 2013).

We used museum specimens collected from two expeditions: on 26 May–1 June 1972 (end of the dry, low primary productivity season at our site) and 8–13 January 1973 (end of the wet, high primary productivity season at our site), which were curated at the Sam Noble Museum of Natural History. We selected six species of leaf-nosed bats from the subfamily Stenodermatinae which we grouped into pairs based on mass: (a) Large: Artibeus lituratus (65 g) and Artibeus jamaicensis (52 g), (b) Medium: Sturnira parvidens (17.5 g) and Sturnira ludovici (21 g), and (c) Small: Dermanura phaeotis (11.8 g) and Dermanura toltecta (15.5 g). A list of species and sample sizes are provided in Table 1.

2.2 Phenology

We used long-term satellite records to estimate seasonal shifts in primary production at our site and tested the correlation between primary production data and other data from previously published studies on plant flowering and arthropod abundance in nearby forests (Borchert et al., 2004; Hernández & Caballero, 2016; Noguera, Ortega-Huerta, Zaragoza-Caballero, González-Soriano, & Ramirez-García, 2009). We estimated vegetation phenology and shifts in resource availability by sampling seven pixels within 5 km of the Cuauhtémcoc field site over 14 years.

| TABLE 1 Carbon and Nitrogen Isotopic Mean Values of Nail Keratin for Different Bat Species—The following values are from cross-sectioned nail keratin from museum specimens of various phyllostomid bat species capture at a field site in Cuauhtémcoc, Colima, Mexico. n is the number of individuals in the study for each season |
|---------------------------------|---------------------------------|---------------------------------|---------------------------------|---------------------------------|---------------------------------|---------------------------------|
| **Species**                     | **Dry season**                  | **Wet season**                  |
| **n**                           | **δC**                          | **σC**                          | **δN**                          | **σN**                          | **n**                           | **δC**                          | **σC**                          | **δN**                          | **σN**                          |
| Artibeus lituratus              | 4                              | -21.89                          | 0.12                            | 4.86                            | 0.99                            | 8                              | -22.33                          | 0.29                            | 6.13                            | 1.50                            |
| Artibeus jamaicensis            | 13                             | -22.19                          | 0.28                            | 6.03                            | 1.01                            | 4                              | -22.81                          | 0.62                            | 6.37                            | 1.25                            |
| Sturnira parvidens              | 6                              | -23.73                          | 0.57                            | 6.83                            | 1.52                            | 7                              | -24.27                          | 0.94                            | 5.30                            | 1.59                            |
| Sturnira ludovici               | 4                              | -23.93                          | 0.59                            | 5.39                            | 1.41                            | Species absent from sampling    |                                 |                                  |                                  |                                  |
| Dermanura phaeotis              | 4                              | -23.15                          | 0.37                            | 6.26                            | 0.60                            | 5                              | -24.12                          | 0.29                            | 9.53                            | 0.87                            |
| Dermanura toltecta              | 5                              | -22.73                          | 0.35                            | 6.31                            | 0.89                            | 4                              | -23.65                          | 0.51                            | 6.07                            | 1.53                            |
(2001–2014) using the Normalized Difference Vegetation Index (NDVI) dataset (MOD 13A2, 1km resolution) from the Moderate Resolution Imaging Spectroradiometer (MODIS). NDVI provides a multi-band measurement of the wavelength and light absorbed by different types of chlorophyll, and is indicative of the quantity of live vegetation within a pixel (Huete et al., 2002). We measured the correlation between each of these variables on arthropod abundance, flowering prevalence, vegetation phenology (NDVI), and precipitation (Nacional, 2013), using pairwise Pearson’s correlation coefficients.

### 2.3 Nail Keratin preparation

We selected single toenails from the fourth digit of the right foot from each of the museum specimens curated at SNMONH. Nails were cross-sectioned across the long axis, and samples from the proximal end were analyzed for nitrogen and carbon isotopic composition. We only used the most recent, proximal sample from each individual to minimize the effects of differences in nail length between different-sized species (sample length 0.4–0.7 mm). Growth rate estimates from other studies on nail keratin growth suggest our samples likely contain isotopic information for roughly the last 11–20 days, for example, *Passer domesticus* growth rate 0.035 mm/day ± 0.01 (Hahn, Dimitrov, Rehse, Yohannes, & Jenni, 2014). Samples were prepared and analyzed at the stable isotope facility at the University of Oklahoma. Nail keratin tissue was cleaned by immersing it in a 2:1 chloroform: methanol solution within an Eppendorf tube and shaking the tube for 30 s (Paritte & Kelly, 2009). We weighed nail keratin samples of 350 ± 10 μg and loaded them into 3.5-mm × 5-mm tin capsules. Samples were organized into runs of 49 that contained 40 samples and nine standards. Standards comprised seven replicates of an in-house standard (Kelly, Bridge, Fudickar, & Wassenaar, 2009) and one USGS-40 and one USGS-41 purchased from the National Institute of Standards and Technologies. Isotope ratio data were processed with a ThermoFinnigan Delta V isotope ratio mass spectrometer connected to a Costech elemental analyzer. Samples were automatically dropped from a 50-position zero-blank autosampler with standards spaced evenly through the run to allow correction for instrumental drift. Corrections follow methods described by (Sharp, 2007).

Ratios of $^{13}$C/$^{12}$C and $^{15}$N/$^{14}$N are expressed in δ notation as the relative difference (per mil ‰) between the samples and international standards (VPDB for C and air for N). For example, the δ$^{13}$C values are calculated as:

$$δ^{13}C = \frac{(^{13}C/^{12}C)_{\text{sample}} - 1 \times 1000}{(^{13}C/^{12}C)_{\text{standard}} - 1}$$

### 2.4 Estimates of niche breadth

We used the package “SIBER” in R v3.6.1 (Jackson, Inger, Parnell, & Bearhop, 2011) to calculate the bivariate normal distribution of carbon and nitrogen isotope values for each species in each season. For each species and season, the data were fitted to a 95% Confidence Interval ellipse to determine the ellipse area in isotopic niche space. We then used the “overlap” function in SIBER to measure the degree of overlap for the standard ellipse estimates between species. These results are summarized in Table 2 and in Figure 2.

### 2.5 Trophic level

We estimated trophic level for each individual using the following equation adapted from (Post, 2002):

$$\text{Trophic Level (T)} = \frac{δ^{15}N_{\text{bat}} - δ^{15}N_{\text{plant}}}{δ^{15}N_{\text{TEF}}}$$

where $δ^{15}N_{\text{bat}}$ is the $^{15}$N/$^{14}$N ratio of the bat nail keratin, and $δ^{15}N_{\text{PLANT}}$ = 2.54 ± 0.73‰ is the $^{15}$N/$^{14}$N ratio of plant material from our study area published in (Herrera, Gerardo, Hobson, Carlos Martinez, & Méndez, 2006) and Shipley (unpublished data). We used a trophic enrichment factor of $δ^{15}N_{\text{TEF}}$ = 3.453 ± 0.68‰ previously estimated from 67 Phyllostomid species using wing membrane samples in Rex

### Table 2

| Species          | Seasonal change | Estimated Niche breadth |
|------------------|----------------|------------------------|
|                  | $p$  | $F$  | $df$ | Wet season | Dry season | Between season | Change |
|                  | ellipse area | ellipse area | overlap area | ellipse area | |
| *Dermanura phaeotis* | <.05 | 25.38 | 2.6  | 0.94  | 0.78  | 0  | −17.1% |
| *Dermanura tolteca*  | <.05 | 4.92  | 2.6  | 2.82  | 1.31  | 0  | −53.6% |
| *Sturnira parvidens* | .13  | 2.51  | 2.10 | 5.47  | 3.15  | 1.01  | −42.5% |
| *Sturnira ludovici*  | –   | –    | –    | 2.45  | –    | –    | –     |
| *Artibeus jamaicensis* | <.05 | 3.94  | 2.14 | 1.39  | 0.56  | 0.48  | −59.8% |
| *Artibeus lituratus*  | <.05 | 7.84  | 2.9  | 2.73  | 0.89  | 0.05  | −67.4% |
et al., 2010, as values are unavailable for bat nail keratin. Thus, our measures of trophic positions are likely to be relative estimates.

2.6 | Statistical analyses

We used the package “Hotelling” (Curran, 2013) to calculate the two-sample Hotelling’s $t^2$ statistic for the carbon and nitrogen isotope ratio of each species. Hotelling’s $t^2$ allows us to simultaneously compare the isotopic ratios of multiple population means, a multivariate extension of a $t$ test. We first tested for homogeneity of variances between groups using Bartlett’s test. We made pairwise comparisons between the seasons within each species and between species of each of the three groups based on similarity in body mass—($D. \text{phaeotis}$ versus $D. \text{tolteca}$, $Sturnira \text{parvidens}$ versus $Sturnira \text{ludovici}$ (within a single season only), and $Artibeus \text{jamaicensis}$ versus $A. \text{lituratus}$). Finally, we used a non-parametric Mann–Whitney $U$ test to test for changes in trophic level between seasons.

3 | RESULTS

Seasonal shifts in vegetation abundance (quantified by NDVI), insect abundance (Hernández & Caballero, 2016; Jiménez-Sánchez, Zaragoza-Caballero, & Noguera, 2009; Noguera et al., 2009; Santacruz & Peredo, 2014), and flowering abundance (Borchert et al., 2004) were strongly correlated with monthly precipitation with pairwise Pearson’s correlation coefficients of 0.72, 0.77, and 0.52, for NDVI, insect abundance, and flowering abundance, respectively (Figure 1). Peak flowering diversity occurred during the beginning of the rainy season in May–June with > 50% of all plants flowering during these two months. Previous studies suggest peak insect

**FIGURE 2** Comparison of Isotopic Values for Phyllostomid Bats between Dry and Wet Season—Each row presents one of the morphologically similar species pairs sampled in tropical dry forest in the dry and wet season. The isotopic niche breadth for each species in each season is represented by the 95% confidence ellipses. The values from the dry season are typically more enriched in $\delta^{13}C$ than those from the wet season in all species sampled. However, the seasonal changes in $\delta^{15}N$ are far less predictable, with no evidence of a clear pattern within or between species.
abundance lags behind peak flowering in nearby tropical dry forests and August is the month of greatest insect abundance (Hernández & Caballero, 2016; Noguera et al., 2009).

Within a species, there was a significant decrease in isotopic niche breadth between the wet and dry season for four of the five taxa for which we had both wet and dry season samples ($p < .05$, see Table 2). Only in Sturnira parvidens was the difference in isotopic niche breadth between the two seasons not statistically significant (Hotelling $t^2$, $F_{2,10} = 2.51$, $p = .13$).

Between morphologically similar species pairs, the smallest species tended to be different in isotopic niche overlap during the wet season whereas the intermediate and large species were different during the dry season (Figure 2, Table 3). The smallest species pair, Dermanura phaeotis and D. tolteca, were significantly different from each other in isotopic niche overlap during the wet season (Hotelling $t^2$, $F_{2,6} = 12.37$, $p < .05$) but not during the dry season (hotelling $t^2$, $F_{2,6} = 1.31$, $p = .33$). The pattern was the opposite in the largest species pair Artibeus jamaicensis and A. lituratus, where there was a significant difference in isotopic niche overlap during the dry season (Hotelling $t^2$, $F_{2,14} = 5.39$, $p < .05$), but not during the wet season (Hotelling $t^2$, $F_{2,9} = 1.54$, $p = .27$). Similarly, in the intermediate-sized species Sturnira parvidens and S. ludovici, there was no significant difference during the wet season (hotelling $t^2$, $F_{2,10} = 0.20$, $p = .82$), and we lacked samples from S. ludovici for a dry season comparison.

There were no significant changes in trophic level for four of the five species that we had samples for in both the wet and dry season (Figure 3). However, one species (D. phaeotis), experienced a significant trophic shift and was estimated to be nearly a whole level higher during the wet season (Mann–Whitney $U$, $Z = 3.1096$, $U = 0$, $p = .002$).

### 4 | DISCUSSION

Changes in isotopic niche breadth, trophic level, and isotopic niche overlap appear to correspond with seasonal changes in estimated resource availability and/or diversity driven by precipitation. In general, the frugivorous bat species in this study responded to seasonal shifts in reduced food availability with contraction of overall isotopic niche breadth during the dry season (Figure 1).

For species with representation in both the wet and dry season, 4 out of 5 species had a significantly smaller isotopic niche breadth during the dry season, providing no clear support for the predictions of either competition or optimal foraging theory. In addition, the decreased niche breadth that we observed across species during the dry season suggests this is a consistent pattern independent of a body size, bite force, or morphology (Table 2). Previous studies have suggested that year-round abundance of certain dietary items, such as the fruits of Solanum and Vismia, or the asynchronous fruiting of Ficus species may provide a reliable and sufficient resource that minimizes limitation and thus interspecific competition during periods of reduced food diversity or abundance (Willig, Camilo, & Noble, 1993). As both fruit diversity and abundance tend to decrease during the dry season in tropical dry forests, we suggest the reduced isotopic niche breadth during this period is likely due to inclusion of non-preferred food items or relying on a subset of the total annual dietary breadth due to seasonally fluctuating availability (Mello, Schittini, Selig, & Bergallo, 2004; Tschapka, 2004; Willig et al., 1993).

The ability to retain dietary flexibility in response to local food resource availability is likely adaptive (Fleming, 1986; Rex et al., 2010),...
whether it is due to exploitation of high-quality resources to maximize energetic gain (Stephens & Krebs, 1986), increasing the likelihood of survival during periods of low resource abundance (Robinson & Wilson, 1998), or in response to changes in habitat structure or quality (Farneda et al., 2015; Muñoz-Lazo et al., 2019). Only one of our study species provided evidence of a seasonal trophic level shift, suggesting most consume a predominantly frugivorous diet throughout the year (Figure 3). However, Dermanura phaeotis appears to be including foods with enriched nitrogen in its diet during the wet season based on its estimated trophic level from $\delta^{15}N$. We found that D. phaeotis was nearly a trophic level higher in the wet season than during the dry season (change in $\delta^{15}N = 3.27$, wet season $T_L = 1.92$, dry season $T_L = 1.04$). Similarly, a study of 4 species of Carollia showed that most species tended to be intermediate in isotopic values between strict phytophagy or insectivory, suggesting seasonal insect consumption is more common than previously observed from fecal remains (York & Billings, 2009). These patterns of opportunistic consumption of insects may be driven by other aspects of the local habitat as well, as seasonality appears to affect the degree of frugivory in D. phaeotis (Bonaccorso, 1978; Rex, Michener, Kunz, & Voigt, 2011) as does extent of forest disturbance in A. lituratus (Farneda et al., 2015; Muñoz-Lazo et al., 2019). Our results suggest that the seasonality of food availability in tropical dry forests may elicit seasonal dietary shifts unobserved in less seasonal environments across a species’ range.

As resource abundance, quality, and diversity vary seasonally, we presented two alternative predictions for how potentially competing species would respond. However, we found no consistent pattern supporting either optimal foraging or competition theory among our species pairs in terms of isotopic niche overlap, either within or between seasons. In the smallest species pair (i.e., Dermanura phaeotis and D. tolteca), niche overlap was greatest during the dry season and reduced during the wet season (Figure 2, Table 3), suggesting that these species consumed different items during the wet season when resources are more abundant and diverse, but likely consume a more similar diet in the dry season. This difference in niche overlap is likely due to the inclusion of insects in the diet of D. phaeotis, as it had a larger overall isotopic niche breadth and was estimated at a higher trophic level during the wet season. In contrast, in the largest species pair (A. jamaicensis and A. lituratus), dietary overlap was greater during the wet season compared to the dry season despite reduced resource availability and diversity. Artibeus species specializing on mast-fruiting trees (e.g., Ficus spp.) may explain the large degree of overlap in niche breadth. Ficus tend to be in low density and produce figs asynchronously throughout the year with large, short-lived crops. In tropical dry forests, it appears this asynchrony is exaggerated (Smith & Bronstein, 1996) and some individual trees within a species are likely to be fruiting at different times throughout the year (Milton, Windsor, Morrison, & Estribi, 1982).

Field observations led Fleming (1986) to conclude that many Phyllostomids may behave as generalists despite morphological specialization, supplementing their preferred diet with alternative items opportunistically driven by temporal patterns of local abundance. Similarly, in a study of 67 phyllostomid species, there was no consistent pattern of dietary fidelity within feeding assemblages, suggesting that the combination of morphological and behavioral specialization combined with opportunistic omnivory may promote the high diversity within this group (Rex et al., 2010). In addition to opportunism, other has suggested that alternative mechanisms may work in concert alongside or without dietary differentiation to facilitate coexistence in phyllostomid bats. Other dimensions of niche differentiation including temporal segregation in timing of foraging activity (Mancina & Castro-Arellano, 2013; Mello, 2009; Presley, Willig, Castro-Arellano, & Weaver, 2009) spatial segregation between and within habitats (Kalko & Handley, 2001; Rex et al., 2011) or relationships between roost availability and maximal foraging distances all may modulate seasonal competition and help promote high local diversity in phyllostomid bats. For example, the asynchronous fruiting phenology leading to varying spatiotemporal availability of individual Ficus trees likely reduces the extent of direct competition between large Artibeus species, as individuals exploit their preferred resource at different times in different habitats. Future studies employing techniques that capture finer temporal and spatial scales, such as behavioral observations and radiotelemetry studies or more sophisticated fatty acid and compound-specific stable isotope analyses (Lam et al., 2013; Levin, Yom-Tov, Heftez, & Kronfeld-Schor, 2013), may elucidate even finer scale variation within this diverse clade across habitats and seasons.

Clearly, morphological specialization that leads to the ability to exploit novel resources provides a competitive advantage over similar species (Dumont, 2003; Dumont et al., 2011). However, seasonal changes in the availability and abundance of specialized resources likely limit the degree of reliance on them, leading to selection for opportunistic strategies when they increase survival during periods of low abundance. Based on our results and those from other recent studies, we conclude that the mechanisms promoting the high local diversity of phyllostomid bats are likely the result of dietary specialization during abundance despite adopting more generalist strategies during times of low food availability (Fleming, 1986; Rex et al., 2010). Thus, specialization allows for the exploitation of key resources that may be of particular value to a species and may lead to high rates of diversification, whereas opportunism allows species to persist during periods of low availability and/ or high competition.

**AUTHOR CONTRIBUTIONS**

JRS conceived and designed the experiment. JRS performed the experiments. JRS and CWT analyzed the data. JRS and CWT wrote and edited the manuscript.

**DATA AVAILABILITY STATEMENT**

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.905qfttgts (Shipley & Twining, 2020).

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