Altitudinal Patterns in Two Syntopic Species of *Sturnira* (Mammalia: Chiroptera: Phyllostomidae) in the Montane Rain Forests of Argentina

Mariano S. Sánchez[1,2,3], and **Norberto P. Giannini**[1,2]

[1] CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas), Argentina

[2] Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Miguel Lillo 205, C. P. 4000, Tucumán, Argentina

ABSTRACT

We evaluated altitudinal segregation in two *Sturnira* species as a mechanism allowing their coexistence. Tests were devised to discern between interspecific interactions and regional responses to geographic and environmental variables, using extensive capture data from 18 montane rain forest sites. No significant correlation between captures was found. Additionally and according to the hypothesis of historical occupation of highland versus lowland forests, each species has shown specificity in their response to the geographical and environmental variables. Our results indicated that abundance patterns in these bats likely result from the regional distribution of each species rather than local interactions between them, a pattern that may have ancient roots within the group.

Abstract in Spanish is available in the online version of this article.

Key words: elevational segregation; environmental conditions; habitat choice; *Sturnira erythromos*; *Sturnira lilium*; temperature.

NEOTROPICAL COMMUNITIES often exhibit high species richness. Community diversity, and therefore structure, have been linked to factors such as species interactions, geographic gradients of diversity, and biogeographic processes (Connell 1980, Willig *et al.* 2003, Wiens & Donoghue 2004). However, the mechanisms that structure these communities, which affect the composition, abundance, and distribution of its constituent species, remain poorly understood (Ramos Pereira *et al.* 2009, McGill 2011). Neotropical frugivorous bats (Phyllostomidae) ordinarily co-occur in rich multi-species assemblages (Kalko *et al.* 1996). Postulated mechanisms allowing for their coexistence include dietary and morphological specialization (*e.g.*, Fleming 1986, Freeman 1988, Giannini & Kalko 2004), competitive exclusion (Henry *et al.* 2007); and spatial and temporal segregation in resource use (*e.g.*, use of plants from forest understory vs. large gaps, or use of the same plants during different activity periods; Thies & Kalko 2004, Bonaccorso *et al.* 2006).

One genus of frugivorous phyllostomids, *Sturnira*, comprises 14 currently recognized species (Simmons 2005), but at least 21 putative species level clades (Velazco & Patterson 2013). These bats are distributed in tropical and subtropical forests. Many species are montane, so the genus diversity peaks in the eastern slopes of the Andes, but some species are typical of lowland sites and occur in the Antilles (Rodríguez-Durán & Kunz 2001, Gardner 2007). The genus apparently has a Northern Andean and Chocó origin dating from the middle Miocene (Velazco & Patterson 2013). Diversity decreases with latitude; in NW Argentina, where the genus reaches its southernmost distributional boundary,

three species occur syntopically: *Sturnira lilium*, *Sturnira erythromos*, and *Sturnira oporaphilum* (Barquez & Díaz 2001). The latter is rare, but the first two species are extremely abundant and account for at least 70 percent, and up to 95 percent of mist net bat captures across localities (Giannini 1999, Sánchez *et al.* 2012a, b).

A number of studies have investigated the diet of these species and aspects of their spatial and temporal use of plant resources (Giannini 1999, Aguiar & Marinho-Filho 2007, Silveira *et al.* 2011, Sánchez *et al.* 2012a, b). *Sturnira* species consistently select fruits of *Solanum* (Solanaceae) and *Piper* (Piperaceae) and their species exhibit high trophic niche overlap, although preference for a given resource has been shown to depend on its regional, altitudinal, and seasonal availability (Giannini 1999, Sánchez 2011, Sánchez *et al.* 2012a, b). Giannini (1999) explored the trophic relationship between *S. lilium* and *S. erythromos* in one altitudinal gradient in NW Argentina, where he found a pattern of diffuse altitudinal segregation. Giannini (1999) postulated that the elevational pattern was an effect of the regional (highland vs. lowland) distribution of each species rather than the product of local ecological interactions. Local species interactions may be important in some birds (genus *Atlapetes*) that exhibit spatial segregation across the Andes (Remsen & Graves 1995), which would be consistent with a competitive segregation scenario (*e.g.,* Ricklefs 1987, Fischer 2000, Bonaccorso *et al.* 2006). For the case of *Sturnira*, if the regional hypothesis is correct, the geographic distribution of *S. lilium* in lowland rain forest versus the Andean distribution of *S. erythromos* is responsible of altitudinal differences in the abundance between the species with low- versus high-montane affinities.

Here, we report on a wide field sample of bats in the area of the Southern Yungas forests, NW Argentina, which may help

explain the patterns of abundance in these bats and reveal the importance of multi-scale spatial segregation as potential mechanism allowing the coexistence of frugivores. Our goal was to evaluate possible causes of spatial segregation between the two common, syntopic *S. lilium* and *S. erythromos*. To that end, we devised two tests: (1) interspecific correlation of captures; and (2) species-specific responses to geographic and environmental conditions. If the elevational segregation is the result of local ecological interactions, the species should avoid each other in the study range, so we expected a strong negative correlation between captures of these species across sites irrespective of altitude. Alternatively, if the altitudinal pattern of these bats reflects their regional distributional pattern (highland vs. lowland), captures of both species should be uncorrelated once potential confounding factors, such as the latitudinal effect, are removed. For the second test, we expected independent responses of species to environmental conditions, consistent with a scenario of autoecological differences. On this basis, we discuss the relevance of regional patterns, with their historical component, as a possible influence in the assembly of frugivorous bat guilds.

METHODS

Our focal species, *Sturnira lilium* and *S. erythromos*, are abundant, obligate frugivores, specialized on fruits of *Solanum* and *Piper* (Fleming 1986, Lobova *et al.* 2009), with small home ranges (<700 m daily commuting distance in *S. lilium*; Mello *et al.* 2008a). These species differ in coloration, dentition, and size. *Sturnira lilium* is larger than *S. erythromos* in body mass (21.7 g, SD = ±2.4, *N* = 241 vs. 15.8 g, SD = ±1.8, *N* = 169, respectively) and forearm length (44.4, SD = ±1.2, *N* = 160 vs. 40.8, SD = ±1.6, *N* = 198, respectively). *Sturnira oporaphilum* is a third, rare, and little known bat that co-occurs with the former two species in Andean rain forests and overlaps in size with *S. lilium* (Giannini & Barquez 2003).

The study was conducted in localities of the Southern Yungas biogeographic province, NW Argentina (Cabrera 1976), where these forests range from 400 to 3000 m asl. Climate is bi-seasonal, with a wet and hot austral summer (concentrating 80% of annual rainfall) and a dry and mild winter. Annual rainfall varies between 1000 and 2000 mm with altitude (Brown *et al.* 2001). Mean annual temperature is 19 °C (Minetti *et al.* 2005).

The dataset used in this study was developed from successive field research projects carried out between March 2004 and May 2008 (Sandoval *et al.* 2010, Barquez *et al.* 2011, Sánchez 2011, Sánchez *et al.* 2012a, b). We studied 15 sites located in the provinces of Jujuy, Salta, Tucumán, and Catamarca; these sites were scattered geographically along *ca* 700 km or *ca* 6 degrees in N–S direction and located somewhere in an elevational range from 380 to 1200 m asl (see Fig. S1; Appendix S1). We also included data from a previous study (Giannini 1999) in NW Argentina (see below). The geographic separation of sites guarantees that bat captures were independent across sites, especially considering the short commuting range of the species (see above).

In all sites, bats were captured using ten mist nets placed at ground and subcanopy level in suitable locations. We sampled each site during 3–5 consecutive nights and operated mist nets for 6 h from sunset. For each specimen, we recorded body mass to the nearest 0.5 g using a spring scale PESOLA™, forearm length to the nearest 0.1 mm using a digital caliper, sex, and age (juvenile or adult). Bats were marked by trimming the hair on the back to avoid multiple counting of recaptures, and were released near the capture site. Voucher specimens were deposited in Colección Mamíferos Lillo, Argentina. In Giannini's (1999) study, *Sturnira* bats were captured in a monthly sampling schedule over 2 yr in three sites along an altitudinal transect (800–1600 m asl).

For each site, we recorded the geographic variables latitude, longitude, and altitude with a Global Positioning System device GARMIN™ (Table S1; Appendix S1). Seven climatic variables obtained from WorldClim (http://www.worldclim.org/download) using the program Diva-GIS 5.2 (Hijmans *et al.* 2005) were compiled and used in subsequent analyses. The variables included: (1) annual mean temperature; (2) mean monthly temperature range; (3) maximum temperature of warmest month; (4) minimum temperature of coldest month; (5) temperature annual range; (6) annual precipitation; and (7) temperature seasonality.

We used bivariate linear regression analysis to quantify the relationship between the captures of each bat species (response variable) and each geographic and climatic variable across sites. Also, we applied multiple regression on the same dataset. The potential relationship between captures of bats of the two focal species was evaluated using the Pearson's product-moment correlation coefficient. We also calculated correlations among all climatic variables. All data were transformed to the $\log_{10}(x + 1)$ function before conducting the analyses. In the case of latitude, we only used data from sites located between 700 and 1200 m asl, given the differential effect of altitudinal range among sites north and south of the Yungas. All statistical analyses were performed in R (R Development Core Team 2013).

RESULTS

In our 15 sites (Fig. S1), we captured 1035 individuals of *S. lilium* (67.8%) and 492 of *S. erythromos* (32.2%), plus 912 individuals of both species (67 and 845 or 7.3% and 92.3%, respectively) added from Giannini (1999). *Sturnira erythromos* was absent from three sites (Table S1); at the remainder of sites, the two frugivorous bat species were captured in different ratios. In general, *S. lilium* was the common bat in sites of mid-to-low altitude (<1000 m asl), where it accounted for >60 percent of the sample, whereas *S. erythromos* was more common in highland sites (>1000 m asl; 70% of captures; Table S1). No correlation existed between log-transformed captures of both species across sites ($r = -0.08$, $P = 0.74$, df = 16).

Latitude was not associated with captures in either species (Table 1). Both bat species exhibited a significant but contrasting association with altitude and annual mean temperature: while captures of *S. lilium* responded negatively to increasing altitude, and positively to increasing mean annual temperature, the oppo-

TABLE 1. *Results of simple linear regression analysis for the two focal frugivorous bats and nine variables across 18 study sites. The models include: intercept with Y axis;* β, *slope;* P, *statistic significance;* R^2, *coefficient of determination.*

Variable	*Sturnira lilium*				*Sturnira erythromos*			
	Intercept	β	P	R^2	Intercept	β	P	R^2
Latitude	7.31	−4.59	0.348	0.53	−4.70	3.83	0.533	0.44
Altitude[*]	5.40	−1.55	0.031	0.71	−4.41	1.73	0.026	0.72
Annual mean temperature[†]	−9.78	8.19	0.010	0.77	9.88	−7.09	0.050	0.68
Maximum temperature of warmest month	−14.86	10.52	0.023	0.73	14.35	−9.17	0.077	0.65
Minimum temperature of coldest month	0.32	0.69	0.485	0.42	0.91	−0.32	0.769	0.27
Temperature annual range	−6.44	5.16	0.207	0.56	8.78	−5.74	0.195	0.57
Annual precipitation	−0.73	0.54	0.688	0.32	1.62	−0.33	0.824	0.24
Mean monthly temperature range	−4.84	4.99	0.077	0.65	7.41	−5.90	0.052	0.68
Temperature seasonality (SD × 100)	2.48	−0.62	0.865	0.21	−2.69	1.28	0.746	0.29

[*]Single variable retained by backward selection in the multiple regression model for *S. erythromos*.
[†]Single variable retained by backward selection in the multiple regression model for *S. lilium*.

site was true for *S. erythromos*. In addition, *S. lilium* was positively associated with the maximum temperature of warmest month, while *S. erythromos* responded negatively to mean monthly temperature range (Fig. 1; Table 1). The remainder of associations was non-significant (Table 1). Multiple regression modeling for each species selected only one variable each (altitude for *S. erythromos* and mean annual temperate for *S. lilium*; Table 1). In turn, several of these environmental variables were correlated among themselves (those with $r = > |0.7|$; see Table S2).

DISCUSSION

We evaluated possible causes of altitudinal segregation between two frugivorous bats in the genus *Sturnira* by means of tests that contrasted competitive interactions and autoecological responses to geographic and environmental conditions. Captures of these two highly similar bat species that are syntopic across the forested mountain ranges of NW Argentina showed no correlation, when a significant negative association was expected under a scenario of competitive ecological interactions. Latitude did not appear to be important for explaining bat captures, probably due to the relatively short geographic span of our study region (*ca* 6 degrees; Fig. S1). Each bat species showed its own suite of responses to change in geographic and environmental variables, including altitude (with significant but opposite trends between species) and temperature-related factors (Fig. 1; Table 1). The latter have been considered for explaining fluctuations in the abundance of *Sturnira* in other subtropical rain forests (Mello *et al.* 2008b).

This pattern of response is consistent with a simple autoecological model of species segregation. However, responses of species are indicative of deeper differences when the phylogenetic history of the group is taken into account. Captures of *S. lilium* decreased with altitude and responded positively to high-temperature conditions of lowlands; by contrast, captures of *S. erythromos*

increased with altitude and responded to low mean annual temperature and narrow mean monthly temperature range, which characterize montane environments (Fig. 1; Table 1) to which this species is physiologically adapted (Soriano *et al.* 2002). *Sturnira erythromos* may use distinct thermal strategies, including daily torpor, to maintain a favorable energetic equation in cool highlands (Soriano *et al.* 2002). These responses at the physiological level can be linked with the evolutionary history of the lineage, and if so, the patterns uncovered are deeply rooted in time and tied to the phylogeny of *Sturnira* and its Andean origin (see Velazco & Patterson 2013). Specifically, the species that belong to an Andean clade (*e.g., S. erythromos*) would exhibit a high-montane distribution along its geographic range and locally dominate captures on the upper side of the altitudinal range; the opposite would be true for the lowland species (*e.g., S. lilium*; see Giannini 1999). Our results support this hypothesis, thereby adding an ancient temporal dimension to the hypothesis of a regional influence on the local distributional patterns of each species. This does not completely exclude the possibility that other factors, such as competition in the past or difference in fruit availability across landscape, could have been important as a mechanism determining altitudinal distributions, although general support for such mechanism is lacking (see Connell 1980, Giannini 1999). The regional hypotheses can be tested with analyses involving species from different lineages with similar distributional patterns (*i.e.*, comprising lowland and highland species).

In conclusion, the abundance patterns exhibited by these frugivorous bats appear to be ultimately reflective of the regional distribution of the species. However, this pattern is clade-dependent and deeply rooted in time. Adding this time dimension means that our captures of each species responded differentially to geographic and environmental variability, in all likelihood due to their evolutionary history; chiefly, membership to highland versus lowland clades and the adaptation to each life style that these environments require. These results highlight the relevance of diffuse spatial segregation as influenced by the regional scale and
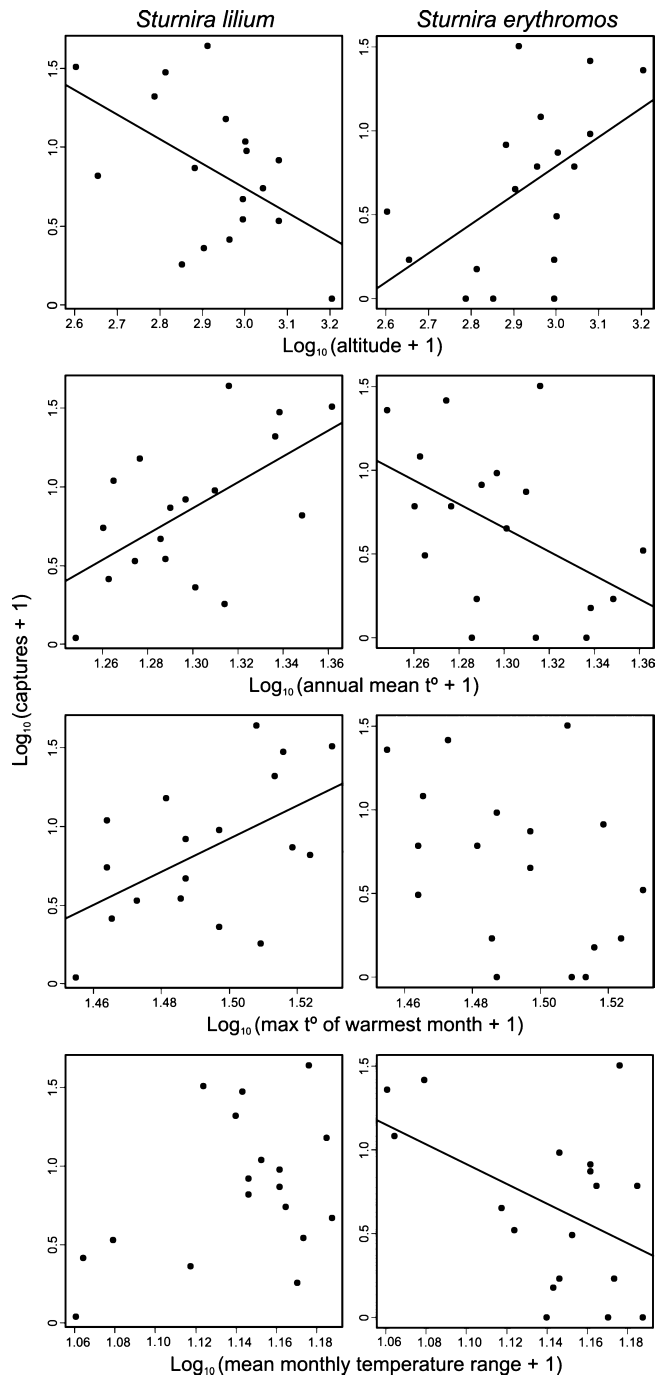
Sturnira lilium   *Sturnira erythromos*

FIGURE 1. Scatterplots of captures, altitude, and three environments variability that were significant in linear regression analysis for either *S. lilium* or *S. erythromos*. Regression lines indicate significant relationships at α = 0.05. Full regression model in Table 1.

the geological time scale, adding one mechanism to few others proposed (see Fleming 1986, Freeman 1988, Giannini & Kalko 2004, Bonaccorso *et al.* 2006, Henry *et al.* 2007) that may help explain the coexistence of species in diverse assemblages of frugivorous bats.

SUPPORTING INFORMATION

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

FIGURE S1. Map of NW Argentina showing the location of study sites listed in Appendix S1.

TABLE S1. *Dataset used in the statistic analysis from our 18 study sites.*

TABLE S2. *Results of correlation analysis among climatic and geographic variables.*

APPENDIX S1. Gazetteer of 18 localities studied in NW of Argentina.

LITERATURE CITED

Aguiar, L. M. S., and J. Marinho-Filho. 2007. Bat frugivory in a remnant of Southeastern Brazilian Atlantic forest. Acta Chiropterol. 9: 251–260.

Barquez, R. M., and M. M. Díaz. 2001. Bats of the argentine Yungas: a systematic and distributional analysis. Acta Zool. Mex. (n.s.) 82: 29–81.

Barquez, R. M., M. S. Sánchez, and M. L. Sandoval. 2011. Nuevos registros de murciélagos (Chiroptera) en el Norte de Argentina. Mastozool. Neotrop. 18: 11–24.

Bonaccorso, F. J., J. R. Winkelmann, D. Shin, C. I. Agrawal, N. Aslami, C. Bonney, A. Hsu, P. E. Jekielek, A. K. Knox, S. J. Kopach, T. D. Jennings, J. R. Lasky, S. A. Menesale, J. H. Richards, J. A. Rutland, A. K. Sessa, L. Zhaurova, and T. H. Kunz. 2006. Evidence for exploitative competition: comparative foraging behavior and roosting ecology of short-tailed fruit bats (Phyllostomidae). Biotropica 39: 249–256.

Brown, A. D., H. R. Grau, L. R. Malizia, and A. Grau. 2001. Argentina. In M. Keppelle, and A. D. Brown (Eds.). Bosques nublados del Neotrópico, pp. 623–659. Instituto Nacional de Biodiversidad, INBio, Santo Domingo de Heredia, Costa Rica.

Cabrera, A. L. 1976. Regiones fitogeográficas argentinas. Enciclopedia Argentina de Agricultura y Jardinería, Tomo 2, segunda edición, pp. 85. Editorial ACME, Buenos Aires, Argentina.

Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35: 131–138.

Fischer, P. 2000. Test of competitive interactions for space between two benthic fish species, Burbot *Lota lota*, and stone loach *Barbatula barbatula*. Environ. Biol. Fish. 58: 439–446.

Fleming, T. H. 1986. Opportunism versus specialization: the evolution of feeding strategies in frugivorous bats. In A. Estrada, and T. H. Fleming (Eds.). Frugivores and Seed Dispersal, pp. 105–118. Dr. W. Junk Publ, Dordrecht, the Netherlands.

Freeman, P. W. 1988. Frugivorous and animalivorous bats (Microchiroptera): dental and cranial adaptations. Biol. J. Linn. Soc. 33: 249–272.

Gardner, A. L. 2007. Family Phyllostomidae Gray, 1825. In A. L. Gardner (Ed.). Mammals of South America, Volume 1, Marsupials, Xenarth-

rans, Shrews, and Bats, pp. 207–376. The University of Chicago Press, Chicago and London.

GIANNINI, N. P. 1999. Selection of diet and elevation by sympatric species of *Sturnira* in an Andean rainforest. J. Mammal. 80: 1186–1195.

GIANNINI, N. P., AND R. B. BARQUEZ. 2003. *Sturnira erythromos*. Mamm. Species 729: 1–5.

GIANNINI, N. P., AND E. K. V. KALKO. 2004. Trophic structure in a large assemblage of phyllostomid bats in Panama. Oikos 105: 209–220.

HENRY, M., J.-F. COSSON, AND J.-M. PONS. 2007. Abundance may be a misleading indicator of fragmentation-sensitivity: the case of fig-eating bats. Biol. Conserv. 139: 462–467.

HIJMANS, R., L. GUARINO, P. MATHUR, AND A. JARVIS. 2005. DIVA-GIS Version 5.2. Available at: http://www.diva-gis.org/download.

KALKO, E. K. V., C. O. HANDLEY, Jr, AND D. HANDLEY. 1996. Organization, diversity, and long-term dynamics of a Neotropical bat community. In M. Cody, and J. Smallwood (Eds.). Long-term Studies in Vertebrate Communities, pp. 503–553. Academic Press, Los Angeles.

LOBOVA, T. A., C. K. GEISELMAN, AND S. A. MORI. 2009. Seed Dispersal by Bats in the Neotropics. p. 473. Memoirs of the New York Botanical Garden, 101. The New York Botanical Garden, Bronx, New York.

McGILL, B. J. 2011. Species abundance distributions. In A. M. Magurran, and B. J. McGill (Eds.). Biological Diversity, Frontiers in Measurement and Assessment, pp. 105–122. Oxford University Press, New York.

MELLO, M. A. R., E. K. V. KALKO, AND W. R. SILVA. 2008a. Movements of the bat *Sturnira lilium* and its role as a seed disperser of Solanaceae in the Brazilian Atlantic Forest. J. Tro. Ecol. 24: 225–228.

MELLO, M. A. R., E. K. V. KALKO, AND W. R. SILVA. 2008b. Diet and abundance of the bat *Sturnira lilium* (Chiroptera) in a Brazilian montane Atlantic Forest. J. Mammal. 89: 485–492.

MINETTI, J. L., M. E. BOBBA, AND C. HERNÁNDEZ. 2005. Régimen espacial de temperaturas en el Noroeste de Argentina. In J. L. Minetti (Ed.). El Clima del Noroeste Argentino, pp. 141–161. Laboratorio Climatológico Sudamericano (LCS), Editorial Magna, Argentina.

R Development Core Team. 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. Available at: http://cran.r-project.org/ (accessed 1 May 2013).

RAMOS PEREIRA, M. J., J. T. MARQUEZ, J. SANTANA, C. D. SANTOS, J. VALSECCHI, H. LIMA DE QUERIOZ, P. BEJA, AND J. M. PALMEIRIM. 2009. Structuring of Amazonian bat assemblages: the roles of flooding patterns and floodwater nutrient load. J. An. Ecol. 78: 1163–1171.

REMSEN, Jr, J. V., AND W. S. GRAVES IV. 1995. Distribution patterns and zoogeography of *Atlapetes* brush-finches (Emberizinae) of the Andes. Auk 112: 210–224.

RICKLEFS, R. E. 1987. Community diversity: relative roles of local and regional processes. Science 235: 167–171.

RODRÍGUEZ-DURÁN, A., AND T. H. KUNZ. 2001. Biogeography of West Indian bats: an ecological perspective. In C. A. Woods, and F. E. Serpile (Eds.). Biogeography of the West Indies: Patterns and Perspectives, (2nd Edition), pp. 355–368. CRC Press, Boca Raton, FL.

SÁNCHEZ, M. S. 2011. Interacción entre murciélagos frugívoros y plantas en las selvas subtropicales de Argentina. 'PhD Dissertation', Universidad Nacional de Tucumán, Argentina.

SÁNCHEZ, M. S., L. V. CARRIZO, N. P. GIANNINI, AND R. M. BARQUEZ. 2012a. Seasonal patterns in the diet of frugivorous bats in the subtropical rainforests of Argentina. Mammalia 76: 269–275.

SÁNCHEZ, M. S., N. P. GIANNINI, AND R. M. BARQUEZ. 2012b. Bat frugivory in two subtropical rain forests of Northern Argentina: testing hypotheses of fruit selection in the Neotropics. Mammal. Biol. 77: 22–31.

SANDOVAL, M. L., M. S. SÁNCHEZ, AND R. M. BARQUEZ. 2010. Mammalia, Chiroptera Blumenbach, 1779: new locality records, filling gaps, and geographic distribution maps from Northern Argentina. Check List 6: 64–70.

SILVEIRA, M., L. TREVELIN, M. PORT-CARVALHO, S. GODOI, E. N. MANDETTA, AND A. P. CRUZ-NETO. 2011. Frugivory by phyllostomid bats (Mammalia: Chiroptera) in a restored area in Southeast Brazil. Acta Oecol. 37: 31–36.

SIMMONS, N. B. 2005. Order Chiroptera. In D. E. Wilson, and D. M. Reeder (Eds.). Mammal Species of the World: A Taxonomic and Geographic Reference, Vol. 1 (3rd Edition), pp. 312–529. Johns Hopkins University Press, Baltimore.

SORIANO, P. J., A. RUIZ, AND A. ARENDS. 2002. Physiological responses to ambient temperature manipulation by three species of bats from Andean cloud forests. J. Mammal. 83: 445–457.

THIES, W., AND E. K. V. KALKO. 2004. Phenology of Neotropical pepper plants (Piperaceae) and their association with their main dispersers, two short-tailed fruit bats, *Carollia perspicillata* and *C. castanea* (Phyllostomidae). Oikos 104: 362–376.

VELAZCO, P. M., AND B. D. PATTERSON. 2013. Diversification of the yellow-shouldered bats, Genus *Sturnira* (Chiroptera, Phyllostominae), in the New World Tropics. Mol. Phylogenet. Evol. 68: 683–698.

WIENS, J. J., AND M. J. DONOGHUE. 2004. Historical biogeography, ecology and species richness. Trends Ecol. Evol. 19: 639–644.

WILLIG, M. R., D. M. KAUFMAN, AND R. D. STEVENS. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annu. Rev. Ecol. Evol. Syst. 34: 273–309.