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Morphofunctional and geographic segregation among species of lasiurine bats (Chiroptera: Vespertilionidae) from the South American Southern Cone

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Abstract

Four morphologically similar species of insectivorous bats in the genus *Lasiurus* (Chiroptera: Vespertilionidae) regularly occur in the American Southern Cone. Three of them (*Lasiurus cinereus*, *L. blossevillii* and *L. ega*) are sympatric over many regions, whereas the remaining species (*L. varius*, closely related to *L. blossevillii*) is allopatric, occurring in the Patagonian Temperate Rainforest. A multivariate analysis of 14 craniodental variables for 99 specimens from the four species confirmed size separating two small species from two large ones, and revealed morphofunctional aspects of mastication segregating the two large species on the basis of differences in temporal muscle function (coronoid process height and length of rostrum). We predict ecological (trophic) differences among these lasiurines consistent with their segregation in the morphofunctional space and in combination with the sympatric vs. allopatric condition of species pairs or triads.

Keywords: Chiroptera; cranial morphology; *Lasiurus*; trophic partitioning.

Introduction

The tribe Lasiurini Tate, 1942 (Chiroptera: Vespertilionidae) comprises at least 15 (Gardner and Handley 2007) and possibly 17 or more species of bats distributed from Canada to Patagonia including the archipelagos of Hawaii, Bermuda, Galapagos and the Caribbean (Simmons 2005). Five of these species, namely *Lasiurus blossevillii* (Lesson and Garnot, 1826), *L. cinereus* (Palisot de Beauvois, 1796), *L. ega* (Gervais, 1856), *L. egregius* (Peters, 1870), and *L. varius* (Poeppig, 1835), occur in various Subtropical, Temperature and Subantarctic regions South of the Tropic of Capricorn, in the South American Southern Cone. A sixth named species from Central Argentina, *Lasiurus salinae* (Thomas, 1902), is recognized as valid by some including Mares et al. (1995), Tiranti and Torres (1998), Gardner and Handley (2007), and with reservations by Simmons (2005); however, we follow Barquez and Díaz (2001), Barquez (2006), and others in considering this form as conspecific with *L. blossevillii blossevillii*. In addition, *Lasiurus egregius* is known from only one specimen in the Southern Cone out of a total of just five specimens globally (Gardner and Handley 2007). *Lasiurus ega* has been at times segregated in the monotypic genus *Dasypterus* (Barquez 2006), differing from other species of typical *Lasiurus* chiefly in the lack of the minute first upper premolar (Kurta and Lehr 1995). However, phylogenetic analyses recover *ega* nested among other species of *Lasiurus* (Baker et al. 1988, Morales and Bickham 1995), thus justifying synonymy of *Dasypterus* (H. Allen, 1894) under *Lasiurus* (Gray, 1831) (see comments in Simmons 2005, Gardner and Handley 2007).

In this study, we focus on the morphometrics of the four species of lasiurine bats regularly occurring in the Southern Cone. Three of these species, *Lasiurus blossevillii*, *L. ega* and *L. cinereus*, share much of their geographic distributions, occurring in sympatry in numerous biomes including the Chaco, Paranaean gallery forests, Espinal thorn woods, the Monte desert, and the Yungas Andean rainforests (Barquez 2006). By contrast, *L. varius* is endemic to the Patagonian temperate forest and adjacent areas of the Patagonian steppe and is thus allopatric with regard to the other three species (possibly marginally sympatric with *L. cinereus* in Chile; see Gardner and Handley 2007). These aerial-hawking, insectivorous species are remarkably similar among themselves although they subtly differ in body size, pelage coloration, and details of the skull and tooth morphology (Kurta and Lehr 1995, Barquez et al. 1999, Barquez 2006). Thus, lasiurine bats inhabiting these vast South American regions represent an interesting case of similar, closely related species either coexisting in sympatry or segregated in allopatry, all of which could be very close ecologically.

Some studies have shown that a considerable niche separation exists among sympatric species of insectivorous bats,

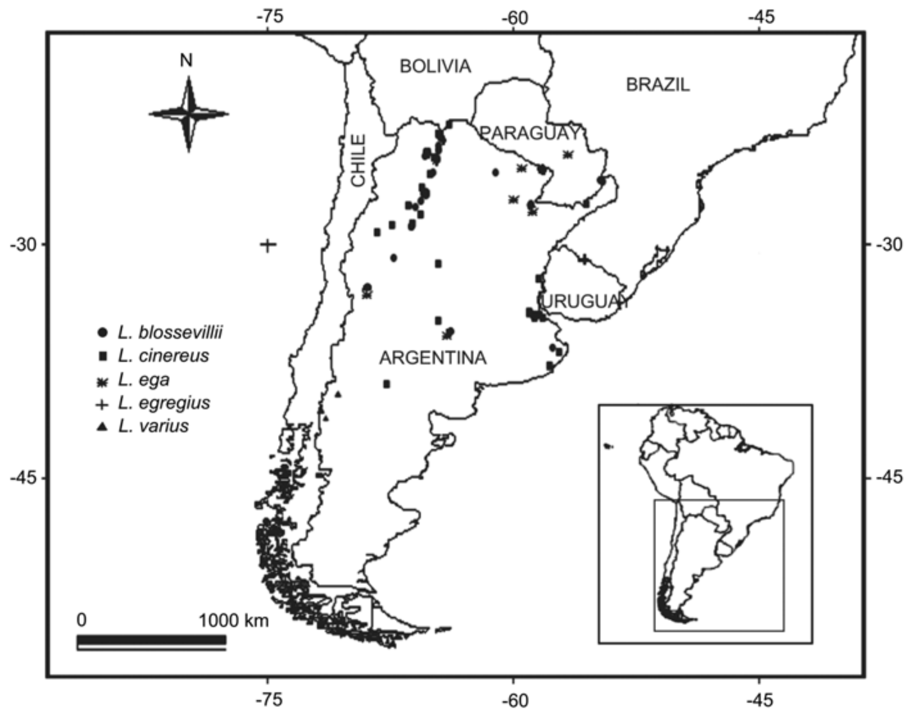

Figure 1 Localities of the studied specimens of the four species of *Lasiurus* and southern most locality for *L. egregius*.

including lasiurines (Saunders and Barclay 1992). In North America, dietary overlap between *Lasiurus cinereus* and *L. borealis* (the latter being very similar to *L. blossevillii* but clearly distinct at the species level; Morales and Bickham 1995), varies between years and reaches a peak when food abundance is minimal (Hickey et al. 1996). Therefore, there is potential for antagonistic interspecific interactions among lasiurines, whenever resource use overlap exists (Stevens and Willig 2000, Patterson et al. 2003, Ranivo and Goodman 2007). For this reason, segregation in niche space could be present among these species and it can occur along different dimensions, including morphofunctional variation (Freeman

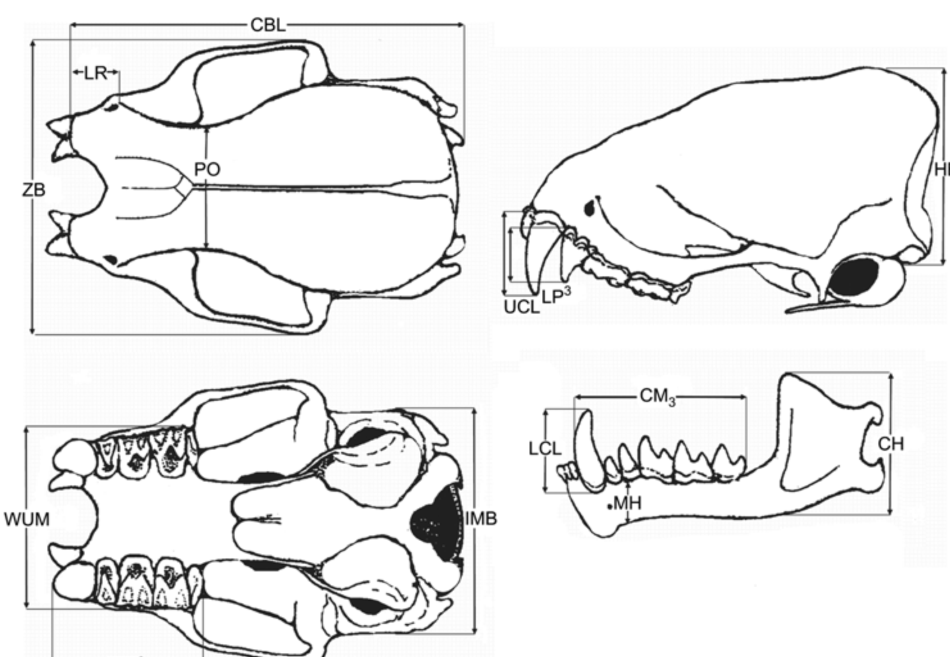

Figure 2 Skull measurements, modified from Kurta and Lehr (1995). See text for abbreviations.

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Table 1 Mean, ±1 standard deviation (SD), and range (minimum–maximum) of craniodental measurements from species of *Lasiurus* that regularly occur in the South American Southern Cone, and results from principal components analysis (PCA) based on a correlation matrix of these measurements.

Measurements	*Lasiurus ega* (n=16)		*Lasiurus cinereus* (n=38)		*Lasiurus blossevillii* (n=40)		*Lasiurus varius* (n=5)		PCA results	
	Mean±1 SD	Range	Mean±1 SD	Range	Mean±1 SD	Range	Mean±1 SD	Range	PC1 79.1%	PC2 6.7%
CBL	15.64±0.68	14.46–16.69	15.52±0.57	13.33–16.31	11.89±0.49	10.08–12.70	12.91±0.08	12.85–13.04	0.98	0.01
ZB	11.40±0.44	10.75–12.24	11.51±0.58	8.96–12.19	8.87±0.52	7.44–9.71	9.67±0.18	9.49–9.93	0.97	0.09
HB	6.66±0.29	6.17–7.35	6.89±0.27	6.06–7.28	5.70±0.20	5.25–6.15	5.85±0.16	5.62–6.06	0.93	0.18
IMB	9.09±0.36	8.51–9.89	9.68±0.21	9.19–10.23	7.52±0.28	6.97–8.13	7.92±0.11	7.77–8.04	0.96	0.21
WUM	7.28±0.26	6.73–7.67	7.64±0.45	5.73–8.23	5.54±0.50	4.74–7.96	6.26±0.23	5.93–6.55	0.94	0.17
CM^3	5.64±0.22	5.31–6.03	5.59±0.22	4.52–5.89	4.07±0.16	3.71–4.36	4.66±0.08	4.57–4.79	0.99	0.01
PO	4.77±0.18	4.47–5.03	5.48±0.16	5.14–5.83	4.47±0.16	4.07–4.77	4.66±0.09	4.52–4.74	0.80	0.55
LR	3.21±0.25	2.68–3.64	2.80±0.24	2.28–3.39	2.39±0.15	1.99–2.66	2.67±0.10	2.54–2.82	0.77	-0.47
UCL	2.74±0.34	1.92–3.22	2.69±0.37	1.21–3.23	1.95±0.27	1.04–2.49	2.18±0.32	1.62–2.41	0.85	0.03
LP^3	1.53±0.26	0.98 –1.84	1.44±0.20	0.74–1.71	1.06±0.17	0.73–1.46	1.37±0.16	1.16–1.51	0.71	-0.12
MH	1.99±0.22	1.64–2.38	1.84±0.21	1.38–2.28	1.40±0.18	1.06–1.86	1.42±0.12	1.26–1.59	0.79	-0.28
LCL	2.55±0.26	1.93–2.88	2.38±0.30	0.94–2.82	1.76±0.16	1.15–2.15	2.02±0.17	1.83–2.22	0.89	-0.09
CM_3	6.46±0.26	5.93–6.86	6.40±0.34	4.78–6.82	4.71±0.23	3.81–5.13	5.37±0.06	5.29–5.45	0.97	0.01
CH	3.70±0.22	3.35–4.19	3.40±0.20	2.66–3.67	2.65±0.18	2.25–3.09	2.92±0.26	2.74–3.39	0.84	-0.45

Sample size (n) is given for each species. See text for abbreviations of variables. Percentages indicate fraction of variation accounted for by principal components (PCs) 1 and 2 (85.8% total).

1981, 1998, Fenton and Bogdanowicz 2002), frequency of echolocation calls (Jones 1999, Kingston and Rossiter 2004), and diet (Hickey et al. 1996). In particular, skull robustness has been identified as an important trait that could determine the prey that a bat can consume: species with large, stout skulls tend to be durophagous (i.e., species that feed on hard-shelled insects, particularly coleopterans), whereas species with gracile skulls consume chiefly soft-bodied insects (Freeman 1981). Skull structure in lasiurines is relatively homogeneous across species, exhibiting an extremely short and wide rostrum, ample palatine emargination, weak zygomatic arches, and globose and posteriorly elevated braincase (Kurta and Lehr 1995). However, among closely related species, even subtle morphofunctional differences can reflect resource partitioning in nature or at least some decrease in resource use overlap (Aldridge and Rautenbach 1987), a mechanism that can allow coexistence of similar species (Kalko et al. 1996, Ranivo and Goodman 2007). Such morphological differences exist among lasiurines in our area and involve craniodental variables as well as body size (Kurta and Lehr 1995, Barquez et al. 1999).

Here, we explore interspecific patterns of variation of lasiurine species from the South American Southern Cone in a multivariate morphofunctional space defined by linear variables of the skull, dentition, and mandible. We relate those patterns with the distribution of species (sympatry vs. allopatry) in an attempt to identify functional conditions that could allow for the coexistence of species, and predict specific differences in trophic niche space.

Materials and methods

Study region

The South America Southern Cone is a complex mosaic of environments framed within the great macrohabitat of drylands that occupy almost the whole region, with the exception of mesophytic forests in Argentina, Brazil, and Uruguay (Mares 1992). This region comprises two major Neotropical units: the Brazilian and Patagonian domains (Hershkovitz 1958). The Brazilian subregion contributes the tropical elements of the Amazon basin through Paraguay, Northern Argentina, and Uruguay. By contrast, the larger Patagonian subregion incorporates temperate elements in Chile and Argentina, which are typical of the arid and semi-arid landscape that dominates the subregion (Redford and Eisenberg 1992, Ojeda et al. 2002). This wide variety of environments shelters a rich assemblage of bats species, including several sympatric species of *Lasiurus*.

Specimens and measurements

We excluded *Lasiurus egregius* from the analysis due to its rarity and marginal occurrence in the Southern Cone, and the consequent lack of a series of specimens from our area. We studied the craniodental morphology of specimens from the other four currently recognized species of *Lasiurus* of regular occurrence in the Southern Cone. These specimens, listed in Appendix 1, are stored in three collections in Argentina: Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires (MACN); Colección Mamíferos Lillo, Tucumán (CML); and Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza (IADIZA). Provenance of specimens generally covers the entire range of lasiurines in Argentina (Figure 1). Our sample comprised 99 specimens: 40 of *Lasiurus blossevillii*, 38 of *L. cinereus*, 16 of *L. ega*, and five of the relatively rare *L. varius*.

A total of 14 craniodental measurements, illustrated in Figure 2, were taken with a digital caliper to the nearest 0.01 mm. These are: condylobasal length (CBL), zygomatic breadth (ZB), height of braincase (HB), mastoid breadth (IMB), maximum external width between left and right upper molars (WUM), length of maxillary toothrow, from the anterior margin of the canine to the posterior margin of the last molar (CM^3), postorbital constriction (PO), length of rostrum (LR), upper canine length (UCL), length of upper third premolar (LP^3), mandibular body height at lower third premolar (MH), lower canine length (LCL), length of mandibular toothrow, from the anterior margin of the canine to the posterior margin of the last molar (CM_3), and coronoid process height (CH).

Multivariate data analysis

The morphometric data were transformed to the base-10 logarithm. We performed a principal components analysis (hereafter PCA) on a correlation matrix in order to determine patterns of specimen-based morphofunctional variation among the four species of lasiurines studied. For this analysis we used the program InfoStat v. 2010 (Di Rienzo et al. 2010).

Results

Intra-specific averages and dispersion statistics are given in Table 1 for all measurements and species. The first two principal components (PCs) accounted for 85.8% of total (standardized) variation. All variables correlated positively with the first component (PC1, 79.1% of variation). The variable best correlated with PC1 was CM^3, and the lowest correlation on the PC1 was that of LP^3 (Table 1). PC2 accounted for 6.7% of (standardized) variation and primarily expressed the positive correlation with postorbital constriction (PO) and the negative correlation with length of rostrum (LR) and coronoid process height (CH; Table 1).

PC1 chiefly separated two small species (*Lasiurus blossevillii* and *L. varius*) from two large species (*L. cinereus* and *L. ega*, Figure 3). In turn, PC2 segregated the two large species on functional grounds (Figure 3), probably reflecting differences in the performance of the temporal muscles. Specifically, *L. ega* exhibited a larger space for the origin of anterior fibers of the temporal (postorbital constriction smaller, PO) and a larger area of insertion in the mandible (coronoid process higher, CH). In addition, *L. ega* has a longer rostrum (LR); the canine was thus positioned further away from the temporomandibular joint, which increased the load arm for the action of the temporal muscle (posterior fibers). *Lasiurus cinereus* and *L. ega* probably differed in the function of anterior and posterior fibers of the temporal muscle

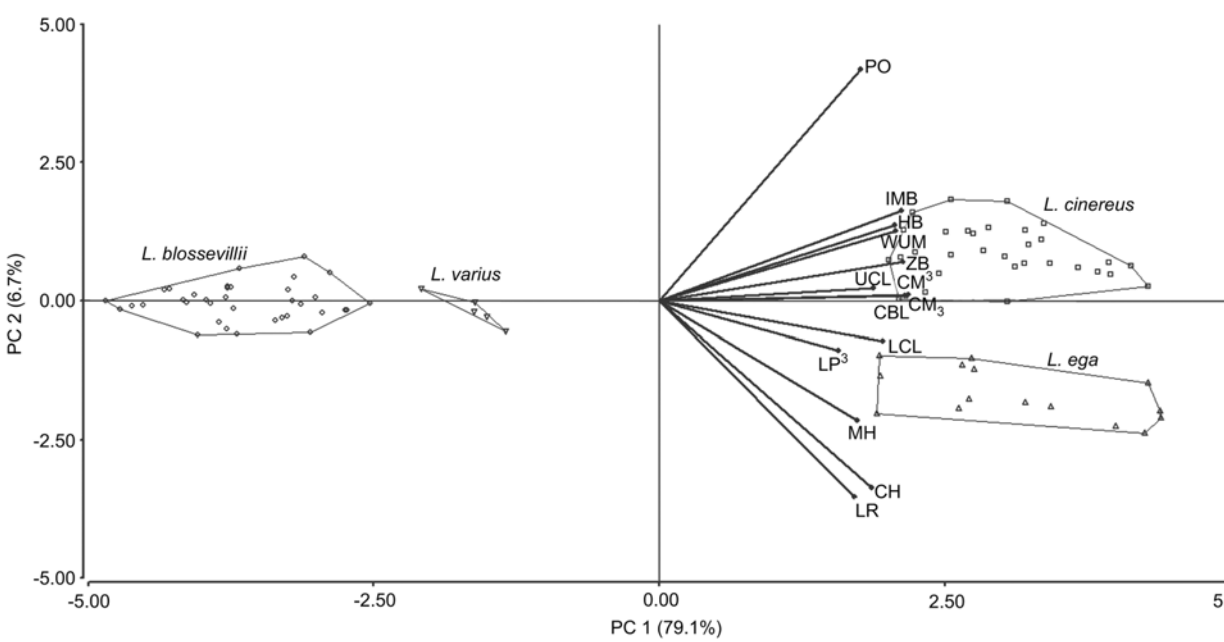

Figure 3 Segregation of the four species of *Lasiurus* in craniodental space (principal components analysis of 14 craniodental variables measured in 99 specimens). Polygons include specimens from each the four species. Vectors represent the strength of correlation of each variable to the plane of PC1 and PC2. See text for abbreviations.

and this could translate into the trophic ecology of these bats (see below).

The smallest species, *Lasiurus blossevillii* and *L. varius*, appeared very close in morphospace, with only minor segregation along the body size axis (PC1). Specimens of *L. varius* possess a skull very similar to that of *L. blossevillii* but larger on average, with the third lower premolar and lower canine comparatively longer.

Discussion

The distribution of specimens in the morphospace evinces a clear segregation of the lasiurine species of the South American Southern Cone, with the sympatric species widely separated from each other, and the two species more closely distributed in morphofunctional space (*Lasiurus blossevillii* and *L. varius*) being allopatric in geographic space. We associate these patterns with differences in size and function, and generate specific predictions about the trophic ecology of these insectivorous bat species, as follows. Among sympatric species, we expect a tendency in the two larger species, *L. cinereus* and *L. ega*, to capture prey (airborne insects) of a wider size range, given that larger bats can detect, track and capture both small and large airborne insects, whereas the small species would handle only small prey (Aldridge and Rautenbach 1987, Barclay and Brigham 1991, Hickey et al. 1996, Kalko et al. 1996). In addition, we expect the two larger species to differ in the frequency of prey they consume, particularly those with strong exoskeleton, consistent with the differential skull structure and use of the temporal muscle, which is the primary jaw-closing, prey-seizing muscle (Freeman 1979). Specifically, *L. ega* with its more gracile skull would be less durophagous than *L. cinereus*, with a more compact and robust skull. Finally, the allopatric *L. blossevillii* and *L. varius* would show little differences in terms of type of prey (e.g., proportion of small vs. large or soft- vs. hard-bodied insects), differing in diet only as a function of local prey availability in the different regions they inhabit.

Other factors could modify these predictions given that trophic ecology of bats is determined by several functional aspects, including morphological differences (Norberg 1994, Fenton and Bogdanowicz 2002) and echolocation parameters (Jones 1999, Kingston and Rossiter 2004). However, the chief differences among lasiurines reportedly involve body size and craniodental details (Kurta and Lehr 1995) such as those considered in this study. Therefore, with the caveat that some functional differences could prove to be compensatory, we predict that diet and trophic behavior of these lasiurine bats, as well as other groups of species that are also very similar among themselves due to common ancestry, will consistently reflect differences observed in the morphofunctional space.

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Appendix 1: specimens examined

Lasiurus blossevillii (n=40): Buenos Aires Province: Bella Vista (51.116 MACN, 52.2 MACN, 14076 MACN, 14304 MACN); Capital Federal (13805 MACN, 19207 MACN, 41507 MACN); Ituzaingó, Partido de Morón (21164 MACN); Partido de Maipú, Santo Domingo (21158 MACN). Catamarca Province: Departament of Capayán Chumbicha (4047 IADIZA); Departament of Capayán Chumbicha, 1 km NW of balneario (3232 CML, 3233 CML); Dique El Potrero, 13 km N of Andalagá (5415 CML). Corrientes Province: Departament of Capital, Barrio Las Lomas (22398 MACN). Jujuy Province: Departament of Belgrano, Río Las Capillas, Route 20, 15 km N of Finca Las Capillas (7060 CML); Departament of Belgrano, Tiraxi, Route 29, 1.5 km E on Tiraxi River (6220 CML, 6222 CML, 6223 CML); Departament of Yuto (483 CML), Laguna La Brea, 25 km W of Paloma Sola (5255 CML, 5256 CML); San Antonio Río Blanco, 9 km E of San Antonio over Blanco River (6221 CML). La Pampa Province: Departament of Mara-Co, General Pico (15570 MACN). Misiones Province: Río Uruguay, 30 km from Puerto Bemberg (49.464 MACN); Arroyo Uruguay, 10 km (51.145 MACN). Salta Province: Rosario de la Frontera, Banente Punco, 13 km S of Los Balos on Provincial Route 135 (1501 CML); Departament of Anta, Arroyo Las Salas Centro Administrativo (6053 CML); Departament of Metan, Río de las Conchas, 2 km N and 6 km W of Metan (5154 CML); Departament of Orán, 48.9 km NW of intersection of National Route 50 and Provincial Route 18, on the way to Isla de Cañas (5147 CML). San Juan Province: Departament of Valle Fértil, Astica (20426 MACN). Tucumán Province: Departament Capital (77 CML, 399 CML); Departament of Monteros, La Florida Provincial Reserve, Pueblo Viejo (5435 CML); Departament of Tafí Viejo, 5 km from El Siambón on coast of Grande River (7292 CML, 7088 CML); Departament of San Miguel de Tucumán, Barrio Victoria Larrea (7321 CML); Aguas Chiquitas Provincial Reserve, Arroyo Aguas Chiquitas (5257 CML); Santa Ana Provincial Reserve, El Salto (5454 CML); Tucumán (400 CML); Villa Amalia (999 CML).

Lasiurus cinereus (n=38): Buenos Aires Province: Buenos Aires (40.6 MACN, 4080 MACN, 15598 MACN, 17114 MACN); Capital Federal (28.6 MACN, 32.68 MACN, 49.2 MACN, 49.3 MACN, 13039 MACN, 13111 MACN, 36.174 MACN, 39753 MACN, 39771 MACN); Coronel Vidal (28.5 MACN); Gral Madariaga Villa Gesell (1535 CML); Laferrere (26.188 MACN); Partido de Pilar (14909 MACN); Plátanos (35.371 MACN); Zelaya (36.133 MACN). Catamarca Province: El Durazno, 8 km S of new and old Route 38 on old route (1419 CML); Dique el Potrero, 13 km N of Andalgalá (5410 CML); San Pablo River, 3 km NW of Concepción (2069 CML). Córdoba Province: Bialet Massé (39.182 MACN); Department of Punilla, Cruz Grande (14911 MACN). Entre Ríos Province: Primero de Mayo (143 CML). Jujuy Province: Departament of Belgrano, Las Capillas River, 15 km N of Finca Las Capillas on Route 20 (4314 CML); Departament of San Pedro, Lavayén River, 1 km N of Santa Rita (4162 CML). La Rioja Province: Departament of Famatina, Antinaco 1130 m (2712 CML); Villa Unión (34.380 MACN). Misiones Province: Bompland (18062 MACN). Río Negro Province: Departament of General Roca, Coronel J.F. Gómez (51.103 MACN). Salta Province: Departament of Anta, El Rey National Park, Arroyo Las Salas (6049 CML); Departament of Orán, Pescado River (1681 CML); Departament San Martín, 12.6 km W of Piquirenda Viejo (5095 CML); Metán (406 CML). Tucumán Province: Departament of Tafí (today Department of Yerba Buena), Villa Marcos Paz (1347 CML); Departament of Trancas, San Pedro de Colalao, Las Mesadas (1646 CML); Horco Molle, Río Las Piedras, Parque Biológico Sierra de San Javier (5258 CML).

Lasiurus ega (n=16): Buenos Aires Province: Delta (19385 MACN). Corrientes Province: Departament Capital, Caprim San Cayetano (2982 CML). Formosa Province: Departament of Patiño, Río Porteño, 64 km, 5 km S from Ea. Santa Catalina (2053 CML); Pilcomayo National Park, Abadie-Cue (20872 MACN); Pilcomayo National Park, Estero-Poi (20883 MACN); Pilcomayo National Park, Estero-Abadil (4665 CML). Jujuy Province: Departament of Capital, Las Capillas River, 15 km N of Finca Las Capillas (4163 CML). La Pampa Province: Departament of Mara-Co, General Pico (15568 MACN, 15569 MACN). Misiones Province: Departament of Cainguás, Aristóbulo del Valle (22425 MACN). Salta Province: Departament of Anta, El Rey National Park, Arroyo Las Salas (6051 CML); Department of Orán, San Martín de Tabacal (16772 CML). Tucumán Province: Departament Capital (34 CML, 1626 CML); Department Tafí Viejo, Tafí Viejo (1160 CML). Paraguay: Departament San Pedro (2238 CML).

Lasiurus varius (n=5): Neuquén Province: 19 km N of Villa La Angostura (3234 CML); Departament of Catán-Lil, Las Coloradas (13617 MACN, 13621 MACN, 13626 MACN). Río Negro Province: Bariloche, Isla Victoria, Centro Instrucción guardaparques (2005 CML).

References

Aldridge, H.D.J.N. and I.L. Rautenbach. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. J. Anim. Ecol. 56: 763–778.

Baker, R.J., J.C. Patton, H.H. Genoways and J.W. Bickham. 1988. Genic studies of *Lasiurus* (Chiroptera: Vespertilionidae). Occas. Papers Mus. Texas Tech Univ. 117: 1–15.

Barclay, R.M.R. and R.M. Brigham. 1991. Prey detection, dietary niche breadth, and body size in bats: why are aerial insectivorous bats so small? Am. Nat. 137: 693–703.

Barquez, R.M. 2006. Orden Chiroptera. In: (R.M. Barquez, M.M. Díaz and R.A. Ojeda, eds) Mamíferos de Argentina-sistemática y distribución. Sociedad Argentina para el Estudio de los Mamíferos (SAREM), Mendoza. pp. 56–86.

Barquez, R.M. and M.M. Díaz. 2001. Bats of the Argentine Yungas: a systematic and distributional analysis. Acta Zool. Mex. Nueva Ser. 82: 29–81.

Barquez, R.M., M.A. Mares and J.K. Braun. 1999. The bats of Argentina. Special Publications of the Museum of Texas Tech University, Lubbock.

Di Rienzo, J.A., F. Casanoves, M.G. Balzarini, L. Gonzalez, M. Tablada and C.W. Robledo. 2010. InfoStat. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina.

Fenton, M.B. and W. Bogdanowicz. 2002. Relationships between external morphology and foraging behavior: bats in the genus *Myotis*. Can. J. Zool. 80: 1004–1013.

Freeman, P.W. 1979. Specialized insectivory: beetle-eating and moth-eating molossid bats. J. Mammal. 60: 467–479.

Freeman, P.W. 1981. Correspondence of food habits and morphology in insectivorous bats. J. Mammal. 62: 166–173.

Freeman, P.W. 1998. Form, function, and evolution in skulls and teeth of bats. In: (T.H. Kunz and P.A. Racey, eds) Bat biology and conservation. Smithsonian Institution Press, Washington DC. pp. 140–156.

Gardner, A.L. and C.O. Handley Jr. 2007. Genus *Lasiurus*. In: (A.L. Gardner, ed) Mammals of South America. Marsupials, xenarthrans, shrews, and bats. The University of Chicago Press, Chicago. pp. 457–468.

Hershkovitz, P. 1958. A geographic classification of Neotropical mammals. Field. Zool. N.S. 36: 581–620.

Hickey, M.B.C., L. Acharya and S. Pennington. 1996. Resource partitioning by two species of vespertilionid bats (*Lasiurus cinereus* and *Lasiurus borealis*) feeding around street lights. J. Mammal. 77: 325–334.

Jones, G. 1999. Scaling of echolocation calls parameters in bats. J. Exp. Biol. 202: 3359–3367.

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. Academic Press, Los Angeles, CA. pp. 503–553.

Kingston, T. and S.J. Rossiter. 2004. Harmonic hopping in Wallacea's bats. Nature 429: 654–657.

Kurta, A. and G.C. Lehr. 1995. *Lasiurus ega*. Mammal. Species 515: 1–7.

Mares, M.A. 1992. Neotropical mammals and the myth of Amazonian biodiversity. Science 255: 976–979.

Mares, M.A., R.M. Barquez and J.K. Braun. 1995. Distribution and ecology of some Argentine bats (Mammalia). Ann. Carnegie Mus. 64: 219–237.

Morales, J.C. and J.W. Bickham. 1995. Molecular systematics of the genus *Lasiurus* (Chiroptera: Vespertilionidae) based on restriction-site maps of the mitochondrial ribosomal genes. J. Mammal. 76: 730–749.

Norberg, U.M. 1994. Wing design, flight performance, and habitat use in bats. In: (P.C. Wainwright and S.M. Reilly, eds) Ecological morphology: integrative organismal biology. The University of Chicago Press, Chicago, IL. pp. 205–239.

Ojeda, R.A., C.E. Borghi and V. Roig. 2002. Diversidad y conservación de Mamíferos de Argentina: un panorama sintético. In: (G. Ceballos and J. Simonetti, eds) Diversidad y conservación de mamíferos Neotropicales. Fondo de Cultura Económica, Mexico. pp. 23–63.

Patterson, B.D., M.R. Willig and R.D. Stevens. 2003. Trophic strategies, niche partitioning, and patterns of ecological organization. In: (T.H. Kunz and M.B. Fenton, eds) Bat ecology. The University of Chicago Press, Chicago, IL. pp. 536–579.

Ranivo, J. and S.M. Goodman. 2007. Patterns of ecomorphological variation in the bats of western Madagascar: comparisons among and between communities along a latitudinal gradient. Mammal. Biol. 72: 1–13.

Redford, K.H. and J.F. Eisenberg. 1992. Mammals of the Neotropics. The southern cone: Chile, Argentina, Uruguay, Paraguay. Vol. 2. University of Chicago Press, Chicago, IL.

Saunders, M.B. and R.M.R. Barclay. 1992. Ecomorphology of insectivorous bats: a test of predictions using two morphologically similar species. Ecology 73: 1335–1345.

Simmons, N.B. 2005. Order Chiroptera. In: (D.E. Wilson and D.M. Reeder, eds) Mammal species of the world: a taxonomic and geographic references. 3rd ed. Johns Hopkins University Press, Baltimore, MD. pp. 312–529.

Stevens, R.D. and M.R. Willig. 2000. Community structure, abundance, and morphology. Oikos 88: 48–56.

Tiranti, S.I. and M.P. Torres. 1998. Observations on bats of Córdoba and La Pampa Provinces, Argentina. Ocassional papers of the Museum of Texas Tech University. 173: 1–13.

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