Exploring a Hidden Structure in New World Bats: The Pollex

DENNIS CASTILLO-FIGUEROA

¹Departamento de Biología, Unidad de Ecología y Sistemática (UNESIS), Pontificia Universidad Javeriana, Bogotá 11001000, COLOMBIA

²Departamento de Biología, Facultad de Ciencias Naturales, Universidad del Rosario, Bogotá, 111321, COLOMBIA

*Corresponding author. Dennis Castillo-Figueroa (dennis.castillof@gmail.com)

Received: 14 August 2021; Accepted: 9 December 2021

ABSTRACT. – Bats have an extraordinary morphological diversity and most of the studies have focused on exploring ecomorphology of wings, ears, nostrils, tooth, and skull. However, structures like the pollex have not been assessed yet. Here, I describe pollex measurements of 97 Neotropical bat species, analyze variation among guilds, and explore correlations with wing morphology. Besides sanguinivores, frugivores that use cluttered habitats and employ gleaning strategy showed larger pollex, whereas aerial insectivores that use open spaces presented smaller pollex. I found a negative relationship between pollex size and hand-wing length, but a positive relationship between pollex size and wing width. Results suggest a potential importance of the pollex on resource exploitation, especially in guilds associated to handling objects such as large fruits. Conversely, the pollex may be useless in aerial insectivores that employ other structures like uropatagium or dactylopatagium for prey capture and manipulation. The pollex is related to wing morphology and habitat use given that species with larger pollex and wide wings obtain their resources in cluttered habitats, while species with shorter pollex and longer wings acquire their preys over open spaces. It is important to keep documenting natural history of bats by studying unexplored structures that unveil the functional importance of morphology in resource exploitation.

KEYWORDS: Chiroptera, functional morphology, locomotion, new world bats, natural history

INTRODUCTION

There is no doubt about the extraordinary diversity of bats. With more than 1,400 recognized species (Mammal Diversity Database, 2021), Chiroptera represent a fifth of mammalian richness (Hutson et al., 2001; Frick et al., 2019), and is the second most diverse mammalian order (Wilson and Mittermeier, 2019). However, the bulk of the information, especially about natural history and ecology, has focused primarily on the trophic component (Giannini and Kalko, 2004; Ríos-Blanco and Pérez-Torres, 2015: Cely-Gómez and Castillo-Figueroa, 2019; Arango-Diago et al., 2020), locomotion (Norberg and Rayner, 1987; Marinello and Bernard, 2014; Castillo-Figueroa, 2020), habitat use (Fleming, 1981; Norberg, 1994; Olaya-Rodríguez et al., 2019), and community structure (Montaño-Centellas, 2015; Morales-Martínez et al., 2018; Cely-Gómez et al., 2021), but other aspects regarding bat morphology need more attention.

Neotropical bats constitute a very complex group not only for their high taxonomical diversity that represents roughly 400 species (Arita et al., 2014), but also for their outstanding morphological variety in all external structures (Freeman, 1981; Norberg and Rayner, 1987; Gardiner et al., 2011a; Santana et al., 2012; Brokaw and Smotherman, 2020). Hence, the study of ecomorphology is relevant to unveil the ability of species in resource exploitation (Rhodes, 2002), as well as to infer idiosyncratic characteristics of the ecology and behavior in New World bats (Marinello and Bernard, 2014; Castillo-Figueroa, 2020).

Overall, some ecomorphological studies have provided an in-depth understanding of the interplay between ecological attributes and morphological structures including wings (Norberg and Rayner, 1987; Marinello and Bernard, 2014; Castillo-Figueroa, 2020), nostrils (Brokaw and Smotherman, 2020), ears (Gardiner et al., 2011a), craniomandibular apparatus (Freeman 1981; 2000; Santana et al. 2012), and tooth structures (Freeman, 1998; Santana et al., 2011). In these studies, morphological variations have been analyzed by comparing several species and guilds. Nevertheless, there is a pervasive lack of data of other structures from which little have been examined to know their potential role in resource acquisition and exploitation.

One of these unexplored structures is the pollex (Castillo-Figueroa and Pérez-Torres, 2021), which is the only digit out of the wing membrane and is composed by two phalanges: the ungual and the proximal (Quinn and Baumel, 1993). Besides the remarkable exception of Desmodus rotundus (E. Geoffroy, 1810) that present a robust hindlimb skeleton in which the quadrupedal locomotion is frequently employed (Granatosky, 2018), there is no study that have evaluated the differences of the pollex structure among species and guilds. Therefore, the objectives of this paper were to: (1) describe pollex measurements of 97 Neotropical bat species (2) analyze the variation among guilds and (3) explore some correlations with wing morphology. Based on these results, I discuss the potential role of pollex in resource use and exploitation.

MATERIALS AND METHODS

Bat species

I obtained measurements from 1512 bat vouchers in the Mammalian Collection at the Museo Javeriano de Historia Natural of Pontificia Universidad Javeriana (MPUJ-MAMM. Bogotá, Colombia) (Appendix 1). All were dry specimens and corresponded only to adults. I excluded individuals bad preserved; that is, specimens with broken structures in the wings and the pollex. The average number of individuals measured for each species was 16 with a range between 1 to 243. The specimens belonged to 8 families, 43 genera, and 97 Neotropical bat species (Table 1). Taxonomic identification was corroborated by using the keys of Gardner (2007), and particularly for the genus Platyrrhinus, the classifications of Velazco (2005) and Velazco et al. (2010) were followed. Species names was based on the Integrated Taxonomic Information System (ITIS, 2021).

Pollex measurements

I measured length of the pollex (LP), length of the pollex's claw (Lc), and length of the pollex with claw (LPc) as is shown in Figure 1. I also measured forearm length (FL) and the length of the third (LD3), and fifth digits (LD5) according to Castillo-Figueroa (2020). To ensure high precision, wing and pollex measurements were taken with a digital caliper with an accuracy of 0.01 mm (Mitutoyo Calibrador Vernier Mod Cd6 -csx 150 Mm). All measurements were performed by the same researcher (DCF).

Data analysis

To characterize pollex traits for each of the 97 bat species, I calculated the statistical mean and standard deviation for LP, Lc and LPc when possible (some species were represented by just one individual). To explore variation in pollex morphology among bat ecological groups, I first classified bat species according to diet, foraging mode, and habitat use into 11 guilds following Kalko et al. (1996), Sampaio et al. (2003), Estrada-Villegas et al. (2010), and Aguirre et (2016) (Table 1). Thereafter, I compared pollex/forearm (LP/FL), claw/forearm (Lc/FL), and pollex with claw/forearm ratios (LPc/FL) among guilds. Since data followed a non-normal distribution, a Kruskal-Wallis rank sum test (H) with post-hoc comparisons (Dunn's method) were used to assess differences between guilds. For quantifying effect size, eta-squared (n2) estimate was obtained. Finally, I made Spearman correlations (rs) between pollex size (LP/ FL), hand-wing length (LD3/FL ratio) and wing width (LD5/FL ratio) (Dietz et al., 2006; Castillo-Figueroa, 2020), since assumptions of normally distributed residuals were not fulfilled. For each correlation, I

calculated 95% confidence intervals (CI). Probabilities at 0.05 were reported as significant statistically. All the analyses were performed in Rwizard 4.3 (Guisande et al., 2014) and JASP (JASP, 2020).

RESULTS

Pollex variation across species

Across the 97 bat species, *Thyroptera lavali* and *T. tricolor* presented the lowest pollex length (1.86 mm and 1.66 mm, respectively) whereas *D. rotundus* had the highest value (15.87 mm \pm 1.99) (Fig. 2, Table 1). On average, LP was 6.36 mm \pm 2.33, Lc presented 1.21 mm \pm 0.54, and LPc corresponded to 7.58 mm \pm 2.80 with the highest values in Phyllostomidae and the lowest ones in Thyropteridae, Emballonuridae, Natalidae and Mormoopidae (Fig. 2, Table 1).

Guild differences

The LP/FL ratio varied across the 11 bat guilds (H = 64.181, df = 10, P<0.001; $\eta 2 = 0.699$). After sanguinivores, bats that use cluttered habitats and use gleaning strategy like frugivores reached the highest values whereas aerial insectivores that use open spaces showed the lowest values according to Dunn test (Fig. 3a: Appendix 2). Consistently, the same pattern was found when analyzing Lc/FL ratio (H = 65.856, df = 10, P = 0.001; $\eta 2 = 0.674$, Fig. 3b) as well as LPc/FL ratio (H = 70.374, df = 10, P = 0.001; $\eta 2 = 0.754$, Fig. 3c), but it is important to highlight that frugivorous guilds presented species with the highest values in the claw lengths relative to size, surpassing even the hematophagous guild (Fig. 3b; Appendix 3).

Correlations between pollex and wing structures

I found a negative relationship between LP/FL ratio and LD3/FL ratio (rs = -0.609; P < 0.001; n = 97; CI = -0.721, -0.466; Fig. 4a) and a positive relationship between LP/FL ratio and LD5/FL ratio (rs = 0.731; P < 0.001; n = 97; CI = 0.622, 0.812; Fig. 4b).

DISCUSSION

Like other morphological structures in bats, the pollex showed a remarkable variation among the Neotropical species analyzed with one order of magnitude (Table 1, Fig. 2). Beyond the notorious function of the pollex in *D. rotundus* for moving secretively over its preys (Galetti et al., 2016; Granatosky, 2018), in the other species the role of this structure is not clear yet (Castillo-Figueroa and Pérez-Torres, 2021). Indeed, measurements and ratios of pollex are not traditionally included in morphological analyses and here I provide a first description of these variables in 97 New world bats (Table 1).

TABLE 1. Bat species analyzed including the number of individuals examined (n), corresponding acronym and guild. Mean and standard deviation are given for: length of the pollex with claw (LPc), length of the pollex without claw (LP), length of the pollex's claw (Lc). Measurements are in mm.

FAMILY/ Species	Acronym	Guild	n	LPc	LP	Lc
EMBALLONURIDAE Cormura brevirostris (Wagner, 1843)	Cobr	BAI	1	6.73	6.14	0.59
Peropteryx kappleri Peters, 1867	Peka	BAI	2	5.86 ± 0.08	5.33 ± 0.16	0.53 ± 0.25
Rhynchonycteris naso (Wied-Neuwied, 1820)	Rhna	BAI	1	4.90	3.70	1.20
Saccopteryx bilineata (Temminck, 1838)	Sabi	BAI	6	5.91 ± 0.74	5.48 ± 0.62	0.43 ± 0.17
Saccopteryx gymnura Thomas, 1901	Sagy	BAI	1	4.79	4.31	0.48
Saccopteryx leptura (Schreber, 1774)	Sale	BAI	12	3.87 ± 0.49	3.38 ± 0.43	0.49 ± 0.39
MOLOSSIDAE Cynomops planirostris (Peters, 1866)	Cypl	UAI	4	4.85 ± 0.82	4.35 ± 0.94	0.50 ± 0.13
Molossops temminckii (Burmeister, 1854)	Mote	UAI	5	3.89 ± 0.22	3.33 ± 0.17	0.56 ± 0.14
Molossus molossus (Pallas, 1766)	Momo	UAI	14	5.16 ± 0.62	4.41 ± 0.60	0.75 ± 0.26
Molossus pretiosus Miller, 1902	Mopr	UAI	1	6.78	5.61	1.17
Molossus rufus E. Geoffroy, 1805	Moru	UAI	5	7.86 ± 0.31	6.76 ± 0.20	1.10 ± 0.19
Tadarida brasiliensis (I. Geoffroy, 1824)	Tabr	UAI	1	5.62	5.10	0.52
MORMOOPIDAE Mormoops megalophylla (Peters, 1864)	Mome	CAI	12	4.19 ± 0.34	3.64 ± 0.43	0.55 ± 0.24
Pteronotus parnellii (Gray, 1843)	Ptpa	CAI	4	6.66 ± 0.63	5.31 ± 0.36	1.35 ± 0.29
NATALIDAE Natalus tumidirostris (Miller, 1900)	Natu	BAI	9	39.54± 0.41	76.52 ± 0.22	56.19 ± 0.22
NOCTILIONIDAE Noctilio albiventris Desmarest, 1818	Noal	ВТР	6	7.61 ± 0.37	6.28 ± 0.72	1.33 ± 0.48
Noctilio leporinus (Linnaeus, 1758)	Nole	BTP	2	9.68 ± 0.80	8.20 ± 0.64	1.48 ± 0.16
PHYLLOSTOMIDAE Carollinae						
Carollia brevicauda (Schinz, 1821)*	Cabr	CUF	72	7.36 ± 0.61	6.09 ± 0.51	1.27 ± 0.39
Carollia castanea H. Allen, 1890	Caca	CUF	56	6.65 ± 0.62	5.43 ± 0.53	1.22 ± 0.33
Carollia perspicillata (Linnaeus, 1758)	Cape	CUF	243	6.65 ± 0.67	5.43 ± 0.60	1.22 ± 0.38
Rhynophillinae						
Rhinophylla alethina Handley, 1966	Rhal	CUF	1	7.48	6.02	1.46
Rhinophylla fischerae Carter, 1966	Rhfi	CUF	3	7.13 ± 0.96	6.24 ± 0.53	0.89 ± 0.49
Rhinophylla pumilio Peters, 1865	Rhpu	CUF	2	7.23 ± 0.51	6.03 ± 1.55	1.20 ± 0.35
Desmodontinae						
Desmodus rotundus (E. Geoffroy, 1810)	Dero	CGS	43	18.21 ± 1.29	15.87 ± 1.99	2.37 ± 1.63
Glossophaginae						
Anoura cadenai Mantilla-Meluk and Baker, 2006	Anca	CGN	1	5.40	4.24	1.16
Anoura geoffroyi Gray, 1838	Ange	CGN	27	6.16 ± 0.44	5.07 ± 0.67	1.09 ± 0.22
Anoura latidens Handley, 1984	Anla	CGN	3	5.69 ± 0.44	4.79 ± 0.46	0.90 ± 0.22
Anoura luismanueli Molinari, 1994	Anlu	CGN	11	5.60 ± 0.49	4.73 ± 0.57	0.87 ± 0.19

TABLE 1. Continue

FAMILY/ Species Choeroniscus godmani (Thomas, 1903)	Acronym Chgo	Guild CGN	n	LPc 4.28 ± 0.27	LP 3.85 ± 0.30	Lc 0.43 ± 1.30
Glossophaga longirostris Miller, 1898	Gllo	CGN	1	6.13	4.91	1.22
Glossophaga soricina (Pallas, 1766)	Glso	CGN	85	6.22 ± 0.55	5.21± 0.51	1.01 ± 0.30
Lonchophyllinae	Giso	CGIV	05	0.22 = 0.55	3.212 0.31	1.01 = 0.50
Hsunycteris cadenai (Woodman and Timm, 2006)	Hsca	CGN	1	4.31	3.51	0.8
Hsunycteris thomasi (J. A. Allen, 1904)	Hsth	CGN	1	5.75	4.76	0.99
Micronycterinae	11001	001	•			0.22
Micronycteris hirsuta (Peters, 1869)	Mihi	CGI	1	8.88	7.41	1.47
Micronycteris megalotis (Gray, 1842)	Mime	CGI	4	6.24 ± 1.62	5.40 ± 1.13	0.84 ± 0.56
Micronycteris microtis Miller, 1898	Mimi	CGI	2	4.96 ± 0.05	4.21 ± 0.42	0.75 ± 0.37
Micronycteris schmidtorum Sanborn, 1935	Misc	CGI	2	4.57 ± 0.40	3.83 ± 0.25	0.74 ± 0.14
Phyllostominae	1/1100	001	-		0.00 = 0.20	017 1 = 017 1
Chrotopterus auratus (Peters, 1856)	Chau	CGC	1	17.40	14.87	2.53
Gardnerycteris crenulatum (E. Geoffroy, 1803)	Gacr	CGI	7	6.31 ± 0.55	5.46 ± 0.55	0.85 ± 0.22
Lophostoma brasiliense Peters, 1867	Lobr	CGI	1	6.91	6.33	0.58
Lophostoma silvicolum d'Orbigny, 1836	Losi	CGI	13	9.17 ± 0.82	7.90 ± 0.69	1.27 ± 0.44
Phylloderma stenops Peters, 1865	Phst	CUF	1	13.84	11.32	2.52
Phyllostomus discolor Wagner, 1843	Phdi	CGN	23	9.14 ± 0.82	7.52 ± 0.65	1.62 ± 0.40
Phyllostomus elongatus (E. Geoffroy, 1810)	Phel	CGO	1	9.10	7.64	1.45
Phyllostomus hastatus (Pallas, 1767)	Phha	CGO	13	12.70± 1.35	10.28 ± 1.35	2.42 ± 0.51
Tonatia saurophila Koopman and Williams, 1951	Tosa	CGO	1	10.33	8.71	1.62
Trachops cirrhosus (Spix, 1823)	Trci	CGC	6	10.51 ± 0.50	8.43 ± 0.46	2.08 ± 0.21
Stenodermatinae						
Artibeus anderseni Osgood, 1916	Aran	CCF	7	7.38 ± 0.44	6.21 ± 0.24	1.17 ± 0.48
Artibeus bogotensis K. Andersen, 1906	Arbo	CCF	5	7.27 ± 0.82	5.99 ± 0.59	1.27 ± 0.34
Artibeus cinereus (Gervais, 1856)	Arci	CCF	3	6.81 ± 0.81	5.47 ± 0.15	1.34 ± 0.69
Artibeus concolor Peters, 1865	Arco	CCF	1	7.87	6.06	1.81
Artibeus glaucus Thomas, 1893	Argl	CCF	56	7.65 ± 0.64	6.28 ± 0.54	1.37 ± 0.33
Artibeus gnomus Handley, 1987	Argn	CCF	1	7.61	6.71	0.9
Artibeus jamaicensis Leach, 1821	Arja	CCF	34	10.70± 1.11	8.87 ± 0.83	1.83 ± 058
Artibeus lituratus (Olfers, 1818)	Arli	CCF	197	12.43 ± 1.00	10.40 ± 0.76	2.03 ± 0.56
Artibeus phaeotis (Miller, 1902)	Arph	CCF	44	7.50 ± 0.54	6.41 ± 0.48	1.09 ± 0.31
Artibeus planirostris (Spix, 1823)	Arpl	CCF	58	11.30 ± 0.78	9.43 ± 0.62	1.87 ± 0.39
Artibeus rava (Miller, 1902)	Arra	CCF	12	7.66 ± 0.46	6.44 ± 0.50	1.22 ± 0.24
Chiroderma salvini Dobson, 1878	Chsa	CCF	4	9.27 ± 0.84	7.75 ± 0.77	1.52 ± 0.41
Enchisthenes hartii (Thomas, 1892)	Enha	CCF	6	8.34 ± 0.70	6.74 ± 0.42	1.60 ± 0.44
Mesophylla macconnelli Thomas, 1901	Mema	CUF	2	6.76 ± 0.82	5.86 ± 0.25	0.90± 0.57

TABLE 1. Continue

FAMILY/ Species	Acronym	Guild	n	LPc	LP	Lc
Platyrrhinus angustirostris Velazco, Gardner and Patterson, 2010	Plan	CCF	3	8.00 ± 0.94	6.85 ± 0.87	1.15 ± 0.07
Platyrrhinus dorsalis (Thomas, 1900)	Pldo	CCF	15	10.24 ± 0.98	8.60 ± 0.79	1.64 ± 0.42
Platyrrhinus helleri (Peters, 1866)	Plhe	CCF	42	9.10 ± 0.54	7.64 ± 0.56	1.45 ± 0.39
Platyrrhinus infuscus (Peters, 1880)	Plin	CCF	1	10.23	8.67	1.56
Platyrrhinus lineatus (E. Geoffroy, 1810)	Plli	CCF	5	9.54 ± 0.42	8.11 ± 0.38	1.43 ± 0.14
Platyrrhinus umbratus (Lyon, 1902)	Plum	CCF	4	10.20 ± 1.09	8.40 ± 0.55	1.80 ± 0.55
Platyrrhinus vittatus (Peters, 1860)	Plvi	CCF	6	13.41 ± 0.48	11.02 ± 0.38	2.39 ± 0.41
Sphaeronycteris toxophyllum Peters, 1882	Spto	CCF	1	8.74	7.42	1.32
Sturnira aratathomasi Peterson and Tamsitt, 1968	Star	CUF	3	12.73 ± 0.29	10.24 ± 0.25	2.49 ± 0.26
Sturnira bidens (Thomas, 1915)	Stbi	CUF	7	9.74 ± 0.47	7.99 ± 0.46	1.75 ± 0.28
Sturnira bogotensis Shamel, 1927	Stbo	CUF	27	9.95 ± 0.77	8.22 ± 0.70	1.73 ± 0.40
Sturnira erythromos (Tschudi, 1844)	Ster	CUF	25	8.95 ± 0.70	7.34 ± 0.66	1.61 ± 0.46
Sturnira lilium (E. Geoffroy, 1810)	Stli	CUF	65	8.76 ± 0.52	$7.25 {\pm}0.43$	1.51 ± 0.32
Sturnira ludovici Anthony, 1924	Stld	CUF	8	10.47 ± 0.64	8.51 ± 0.63	1.96 ± 0.28
Sturnira luisi Davis, 1980	Stlu	CUF	1	9.27	7.75	1.52
Sturnira oporaphilum (Tschudi, 1844)	Stop	CUF	9	10.18 ± 0.47	8.05 ± 0.36	2.13 ± 0.46
Uroderma bilobatum Peters, 1866	Urbi	CUF	56	8.58 ± 0.64	7.10 ± 0.58	1.48 ± 0.33
Uroderma magnirostrum Davis, 1968	Urma	CUF	16	8.64 ± 0.73	7.16 ± 0.65	$1.48{\pm}~0.26$
Vampyressa thyone Thomas, 1909	Vath	CCF	5	6.19 ± 0.41	5.24 ± 0.36	0.95 ± 0.09
Vampyriscus nymphaea (Thomas, 1909)	Vany	CCF	3	7.28 ± 0.50	5.97 ± 0.31	1.31 ± 0.22
THYROPTERIDAE Thyroptera tricolor Spix, 1823	Thtr	BAI	1	2.12	1.66	0.46
Thyroptera lavali Pine, 1993	Thla	BAI	1	3.24	1.86	1.38
VESPERTILIONIDAE Eptesicus andinus J. A. Allen, 1914	Epan	BAI	1	6.58	5.34	1.24
Eptesicus furinalis (d'Orbigny, 1847)	Epfu	BAI	1	5.36	4.90	0.46
Eptesicus brasiliensis (Desmarest, 1819)	Epbr	BAI	2	5.43 ± 0.37	4.79 ± 0.16	0.64 ± 0.21
Histiotus montanus (Philippi and Landbeck, 1861)	Himo	BAI	3	7.15 ± 1.06	6.20 ± 0.60	0.95 ± 0.45
Lasiurus blossevillii (Lesson and Garnot, 1826)	Labl	BAI	3	7.1 ± 0.13	5.96 ± 0.21	1.14 ± 0.27
Lasiurus ega (Gervais, 1856)	Laeg	BAI	2	6.62 ± 1.07	5.78 ± 1.52	0.84 ± 0.45
Lasiurus seminolus (Rhoads, 1895)	Lase	BAI	1	6.86	6.37	0.49
Myotis albescens (E. Geoffroy, 1806)	Myal	BAI	2	4.87 ± 0.08	4.19 ± 0.24	0.68 ± 0.32
Myotis keaysi J. A. Allen, 1914	Myke	BAI	9	5.57 ± 0.55	4.72 ± 0.44	0.85 ± 0.25
Myotis keenii (Merriam, 1895)	Mykn	BAI	1	6.21	5.35	0.86
Myotis nigricans (Schinz, 1821)	Myni	BAI	25	4.69 ± 0.56	4.03 ± 0.47	0.66 ± 0.27
Myotis oxyotus (Peters, 1867)	Myox	BAI	6	5.98 ± 0.39	5.21 ± 0.27	0.77 ± 0.25

TABLE 1. Continue

FAMILY/ Species	Acronym	Guild	n	LPc	LP	Lc
Myotis riparius (Rhoads, 1897)	Myri	BAI	1	4.36	3.82	0.54
Rhogeessa io Thomas, 1903	Rhio	BAI	5	3.99 ± 0.23	3.51 ± 0.23	0.48 ± 0.06

Note: Species were classified into the 11 ecological guilds proposed Aguirre et al. (2016); Sampaio et al (2003); Estrada et al. (2010) and Kalko et al. (1996): background cluttered space aerial insectivore (BAI); background cluttered space trawling insectivore/piscivore (BTP); highly cluttered space aerial insectivores (CAI); highly cluttered space gleaning canopy frugivore (CCF); highly cluttered space gleaning understory frugivore (CUF); highly cluttered space gleaning carnivore (CGC); highly cluttered space gleaning insectivores (CGI); highly cluttered space gleaning omnivore (CGO); highly cluttered space gleaning sanguinivores (CGS); uncluttered space aerial insectivore (UAI). *It has also been suggested *Carollia brevicaudum* (Schinz, 1821).

With my exploratory analysis I found differences among guilds; excluding the hematophagous bats whose large thumbs are well-recognized (Granatosky, 2018), frugivores (CUF, CCF) presented the largest pollex relative to size (Fig. 3a). These guilds use their forelimbs for food-handling (Vandoros and Dumont, 2004), so the pollex may contribute to better manipulate the resources consumed by them. This is especially true in frugivorous that require to process fruits of several shapes and sizes (Lobova et al., 2009). By contrast, insectivores that forage over open spaces (CAI, BTP, UAI, BAI) presented the lowest values in the pollex which probably may impose an energetic

cost by increasing air-resistance during flight. Also, it has been shown that these insectivores guilds forage mainly by using other structures such as the uropatagium (Saunders and Barclay, 1992; Kalko, 1995), hence pollex may be useless in prey capture. However, it is important to consider that pollex can be related to other functions such as scaling and locomotion, and probably insectivores that live in narrow holes can use the pollex to move and stabilize. For example, molossids are very agile on the ground (practically quadruped), so this structure may play an important role in its locomotion, but thus far we can only speculate about the real function of the pollex.

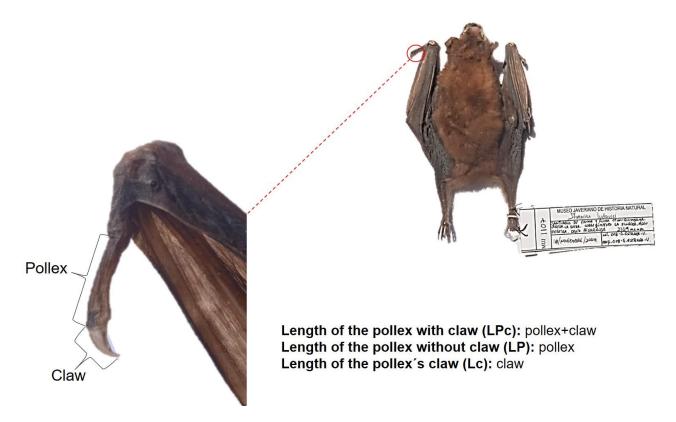


FIGURE 1. Pollex measurements taken from bat vouchers. The specimen shown in the figure corresponds to a male of *Sturnira ludovici* Anthony, 1924.

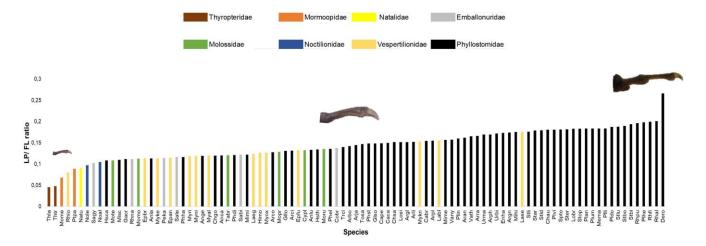


FIGURE 2. LP/FL ratio of 97 Neotropical bat species. Acronyms for bat species are defined in table 1. The colors indicate the family to which each bat species belongs.

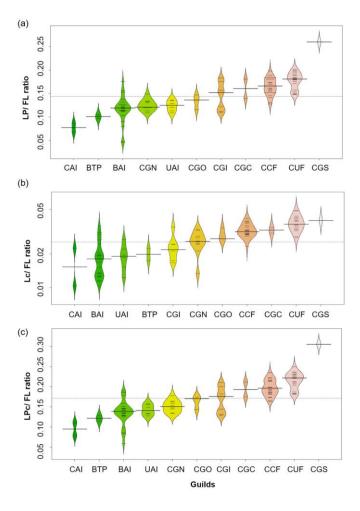


FIGURE 3. Beanplots of pollex measurements among 11 Neotropical bat guilds. Comparisons include (a) LP/FL ratio, (b) Lc/FL ratio, (c). LPc/FL ratio.

Experimental studies can be useful to unveil the relative importance of pollex in bat locomotion as has been conducted for other structures such as tail

membranes (Gardiner et al., 2011b; Adams et al., 2012).

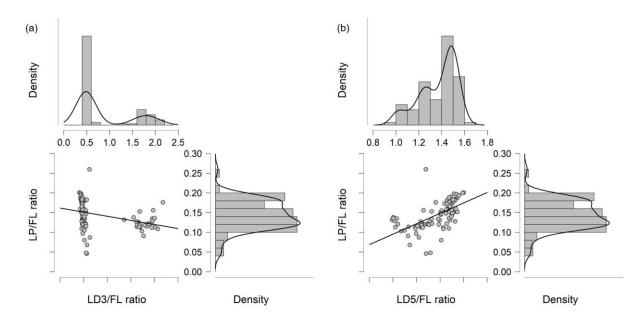


FIGURE 4. Correlations between pollex and wing morphology. Spearman correlations were performed between (a) LP/FL ratio and LD3/FL ratio as a measure of hand-wing length and between (b) LP/FL ratio and LD5/FL ratio as a proxy of wing width. Frequency histograms of each variable are also depicted.

When analyzing the claw length in relation to size, species that belonged to gleaning understory frugivores (CUF) such as Rhinophylla alethina Handley, 1966, Sturnira oporaphilum (Tschudi, 1844), and Sturnira aratathomasi Peterson and Tamsitt, 1968, presented the highest values, although guild mean was inferior than that of hematophagous bats (Fig. 3b, Table 1). Some studies have posed that for phytophagous species, and especially those that rely on landing on the flowers or fruits as foraging strategy, claws are useful in resource exploitation (Vieira and Carvalho-Okano, 1996; Tschapka, 2003; Sazima et al., 2003). In the case of frugivores, large claws are also employed in the manipulation of fruits (Uieda and Vasconcellos-Neto, 1984). For hematophagous bats, the pollex is not only adapted for propel themselves from the ground to fly by increasing the surface area in the pads, but also may serve to climb animals and cling to them for feeding purposes by employing its claws (Castillo-Figueroa and Pérez-Torres, 2021). Importantly though, in this study only one of the three blood-feeding bat species was analyzed, so caution should be exercised when considering guild comparison.

In line with previous results, I found strong relationships between pollex size (LP/FL) with wing width (LD5/FL), and wing length (LD3/FL) (Fig. 4ab). Although it is not a golden rule, bats with wider wings tend to forage in cluttered habitats (Norberg and Rayner, 1987; Marinello and Bernard, 2014; Castillo-Figueroa, 2020) and most of the gleaning species with larger pollex including frugivores, carnivores, and sanguinivores may obtain food items inside these

spaces (Fig. 4b). In stark contrast, species that presented higher wing length including all the aerial insectivores had lower pollex size, which may reflect a potential relationship between flight style and pollex size (Fig. 4a). Additional geometric morphometry studies should explore associations between the shape of pollex and wing as in this paper I only included linear measurements as a starting point to explore pollex ecomorphology.

As many other structures, adaptative radiation has driven an outstanding morphological variation in bats, yet some structures such as the pollex are unexplored in terms of its functional importance. Notably, because the pollex is not integrated to the wing membrane and is freely movable (Walldorf and Mehlhorn, 2013), other potential functions including climb, grab, hold and defend from enemies may be performed by this structure (Castillo-Figueroa and Pérez-Torres, 2021), however, further studies are needed to better understand the prime roles of this structure for each guild. Here, I provided measurements of the pollex structure in 97 Neotropical species. My analyses show that pollex size differ among guilds, suggesting a differential importance of the pollex for each ecological group which are bound to their natural history. The length and the width of the wing are linked to the foraging habitat and seem to have a potential relation to pollex size. This study is a groundwork for keep disentangling the role of unexplored structures in bats to improve our understanding in the ecology and natural history of New World bats.

ACKNOWLEDGEMENTS

All my gratitude goes to Jairo Pérez-Torres, the curator of the Mammalian Collection of Museo Javeriano de Historia Natural from Pontificia Universidad Javeriana (Bogotá, Colombia), for allowing me to access the specimens of the Collection. I also want to thank to the two anonymous reviewers and the editor for important suggestions and comments that improved the paper.

LITERATURE CITED

- Adams, R.A, Snode, E.R, and Shaw, J.B. 2012. Flapping tail membrane in bats produces potentially important thrust during horizontal takeoffs and very slow flight. PLoS ONE, 7(2): e32074. https://doi.org/10.1371/journal.pone.0032074.
- Aguirre, L., Montaño-Centellas, F., Gavilanez, M. and Stevens, R. 2016. Taxonomic and phylogenetic determinantes of functional composition of bolivian bat assamblages. PLoS ONE, 11(7): e0158170. 38. https://doi.org/10.1371/journal.pone.0158170.
- Arango-Diago, S., Castillo-Figueroa, D., Albarracín-Caro, J. and Pérez-Torres, J. 2020. Dietary variation and reproductive status of *Mormoops megalophylla* (Chiroptera: Mormoopidae) in a cave of northeastern Andes from Colombia. Mastozoologia Neotropical, 7(2): 258–265.
 - https://doi.org/10.31687/saremMN.20.27.2.0.13.
- Arita, H., Vargas-Barón, J. and Villalobos, F. 2014. Latitudinal gradients of genus richness and endemism and the diversification of New World bats. Ecography, 37(11): 1024–1033. https://doi.org/10.1111/ecog.00720.
- Brokaw, A.F. and Smotherman, M. 2020. Role of ecology in shaping external nasal morphology in bats and implications for olfactory tracking. Plos One, 15(1): e0226689. http://doi.org/10.1371/journal.pone.0226689.
- Castillo-Figueroa, D. 2020. Ecological Morphology of Neotropical Bat Wing Structures. Zoological Studies 59: 60. http://doi.org/10.6620/ZS.2020.59-60.
- Castillo-Figueroa, D. and Pérez-Torres, J. 2021. On the development of a trait-based approach for studying Neotropical bats. Papéis Avulsos De Zoologia, 61: e20216124. https://doi.org/10.11606/1807-0205/2021.61.24.
- Cely-Gómez, M.A. and Castillo-Figueroa, D. 2019. Diet of dominant frugivorous bat species in an oil palm landscape from Colombian Llanos: implications for forest conservation and recovery. Therya, 10(2): 149–153. https://doi.org/10.12933/therya-19-682.
- Cely-Gómez, M.A., Castillo-Figueroa, D. and Pérez-Torres, J. 2021. Bat Assemblage in an Oil Palm Plantation from the Colombian Llanos Foothills. Tropical life sciences research, 32(1): 47–61. https://doi.org/10.21315/tlsr2021.32.1.3.
- Dietz, C., Dietz, I., and Siemers, B.M. 2006. Wing measurement variations in the five European horseshoe bat species (Chiroptera: Rhinolophidae). Journal of Mammalogy, 87(6): 1241–1251. doi:10.1644/05-MAMM-A-299R2.1.
- Estrada-Villegas, S., Meyer, C., and Kalko, E. 2010. Effects of tropical forest fragmentation on aerial insectivorous bats in a land-bridge island system. Biological Conservation, 143(3): 597–608. https://doi.org/j.biocon.2009.11.009.
- Fleming, T.H. 1991. The relationship between body size, diet, and habitat use in frugivorous bats, genus *Carollia*

- (Phyllostomidae). Journal of Mammalogy, 72(3): 493–501. https://doi.org/10.2307/1382132.
- Freeman, P. W. 1981. Correspondence of food habits and morphology in insectivorous bats. Journal of Mammalogy, 62(1):166–173. https://doi.org/10.2307/1380489.
- Freeman, P. W. 1998. Form, function, and evolution in skulls and teeth of bats. In: Kunz, T.H and Racey, P.A. (Eds.). Bat biology and conservation. Smithsonian Institution Scholarly Press, Washington D.C., pp. 140–156.
- Freeman, P. W. 2000. Macroevolution in Microchiroptera: recoupling morphology and ecology with phylogeny. Evolutionary ecology research, 2: 317–335.
- Frick, W.F., Kingston, T. and Flanders, J. 2019. A review of the major threats and challenges to global bat conservation. Annals of the New York Academy of Sciences., 1469(1): 5–25 http://doi.org/10.1111/nyas.14045.
- Galetti, M., Pedrosa, F., Keuroghlian, A. and Sazima, I. 2016. Liquid lunch – vampire bats feed on invasive feral pigs and other ungulates. Frontiers in Ecology and the Environment, 14(9): 505–506.
- Gardiner, J.D., Codd, J.R. and Nudds, R.L. 2011a. An association between ear and tail morphologies of bats and their foraging style. Canadian Journal of Zoology, 89: 90-99.
- Gardiner, J.D., Dimitriadis, G., Codd, J.R. snf Nudds, R.L. 2011b. A potential role for bat tail membranes in flight control. Plos One, 6: e18214. https://doi.org/10.1371/journal.pone.0018214.
- Gardner AL (Ed.). 2007. Mammals of South America. Volume 1: Marsupials, Xenarthrans, Shrews, and Bats. The University of Chicago Press, Chicago, 669 pp.
- Giannini, N.P. and Kalko, E.K. 2004. Trophic structure in a large assemblage of Phyllostomid bats in Panama. Oikos, 105(2): 209–222. https://doi.org/10.1111/j.0030-1299.2004.12690.x.
- Granatosky, M.C. 2018. Forelimb and hindlimb loading patterns during quadrupedal locomotion in the large flying fox (*Pteropus vampyrus*) and common vampire bat (*Desmodus rotundus*). Journal of Zoology, 305: 63–72. https://doi.org/10.1111/jzo.12538.
- Guisande, C., Heine, J., González-DaCosta, J. and García-Roselló, E. 2014. RWizard Software. Available from: http://www.ipez.es/rwizard (Accessed on 23 Mar. 2021).
- Hutson, A.M., Mickleburgh, S.P. and Racey P.A. 2001. Microchiropteran Bats: Global Status Survey and Conservation Action Plan. IUCN/SSC, Switzerland, 256 pp.
- Integrated Taxonomic Information System on-line database (ITIS). 2021. Chiroptera. Available at: www.itis.gov. (Accessed 27 Dec. 2021.)
- JASP Team. 2020. JASP (Version 0.14.1). Available from: https://jasp-stats.org/. (Accessed 2021 May 12).
- Kalko, E.K.V. 1995. Insect pursuit, prey capture and echolocation in pipistrelle bats (Microchiroptera). Animal Behaviour, 50(4): 861–880. https://doi.org/10.1016/0003-3472(95)80090-5
- Kalko, E.K.V., Handley, C.O. and Handley, D. 1996. Organization, diversity and long-term dynamics of a Neotropical bat community. In: Cody, M.L. and Smallwood, J.A. (Eds). Long-term studies of vertebrate communities. Academic Press, San Diego, USA, pp. 503–553. https://doi.org/10.1016/b978-012178075-3/50017-9.
- Lobova, T.A., Geiselman, C.K. and Mori, S.A., 2009. Seed Dispersal by Bats in the Neotropics. The New York Botanical Garden, New York, 465 pp.
- Marinello, M.M. and Bernard, E. 2014. Wing morphology of Neotropical bats: a quantitative and qualitative analysis with implications for habitat use. Canadian Journal of Zoology, 92(2): 141–147. https://doi.org/10.1139/cjz-2013-0127.

- Mammal Diversity Database. 2021. American Society of Mammalogists. Available from: www.mammaldiversity.org. (Accessed 5 Jan 2021).
- Morales-Martínez, D., Rodríguez-Posada, M., Fernandez-Rodríguez, C., Calderón-Capote, M. and Gutiérrez-Sanabria, D. 2018. Spatial variation of bat diversity between three floodplain-savanna ecosystems of the Colombian Llanos. Therya, 9(1): 41–52. https://doi.org/10.12933/therya-18-537.
- Montaño-Centellas, F., Moya, M. I., Aguirre, L. F., Galeon, R., Palabrala, O., Hurtado, R., Galraza, I. and Tordoya J. 2015. Community and species-level responses of phyllostomid bats to a disturbance gradient in the tropical Andes. Acta Oecologica, 62: 10–17. https://doi.org/10.1016/j.actao.2014.11.002.
- Norberg, U.M. and Rayner, J.M. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society B: Biological Sciences, 316: 335–427. https://doi.org/10.1098/rstb.1987.0030.
- Norberg, U.M. 1994. Wing design, flight performance, and habitat use in bats. In: Wainwright, I.C. & Reilly, S.M. (Eds.). Ecological morphology: integrative organismal biology. Chicago, University of Chicago Press, pp. 205–239.
- Olaya-Rodríguez, H., Pérez-Torrez, J. and Londoño, M.C. 2019. Use of forest strata by bats according to wing morphology and habitat complexity in a fragment of tropical dry forest (Colombia). Journal of Bat Research and Conservation, 12(1): 83–91. https://doi.org/10.14709/BarbJ.12.1.2019.11.
- Quinn, T.H. and Baumel, J.J. 1993. Chiropteran Tendon Locking Mechanism. Journal of Morphology, 216: 197-208.
- Ríos-Blanco, M.C. and Pérez-Torres, J. 2015. Dieta de las especies dominantes del ensamblaje de murciélagos frugívoros en un bosque seco tropical (Colombia). Mastozoología Neotropical, 22(1): 103–111.
- Rhodes, M.P. 2002. Assessment of sources of variance and patterns of overlap in microchiropteran wing morphology in southeast Queensland, Australia. Canadian Journal of Zoology, 80(3):450–460. https://doi.org/10.1139/ z02-029.
- Sampaio, E.M., Kalko, E.K., Bernard, E., Rodríguez-Herrera, B. and Handley, C.O. 2003. A biodiversity assessment of bats (Chiroptera) in a tropical lowland rainforest of Central Amazonia, including methodological and conservation considerations. Studies of Neotropical Fauna and Environment, 38(1):17–31. https://doi.org/10.1076/snfe.38.1.17.14035.
- Santana, S.E., Strait, S. and Dumont, E.R. 2011. The better to eat you with: functional correlates of tooth structure in bats.

- Functional Ecology, 25(4): 839–847. https://doi.org/10.1111/j.1365-2435.2011.01832.x.
- Santana, S., Grosse, I. and Dummont, E. 2012. Dietary hardness, loading behavior, and the evolution of skull form in bats. Evolution, 66(8): 2587–2598. https://doi.org/10.1111/j.1558-5646.2012.01615.x.
- Sazima, M.; Buzato, S. & Sazima, I. 2003. *Dyssochroma viridiflorum*(Solanaceae): A reproductively bat-dependent epiphyte from the Atlantic rainforest in Brazil. Annals of Botany, 92: 725–730.
- Saunders, M. and Barclay, R. 1992. Ecomorphology of insectivorous bats: a test of predictions using two morphologically similar species. Ecology, 73(4): 1335–1345. https://doi.org/10.2307/1940680.
- Tschapka, M. 2003. Pollination of the understorey palm *Calyptrogyne ghiesbreghtiana* by hovering and perching bats. Biological Journal of the Linnean Society, 80(2): 281–288.
- Uieda, W. and Vasconcellos-Neto, J. 1984. Dispersão de Solanum spp. (Solanaceae) por morcegos, na região de Manaus, AM, Brasil. Revista Brasileira de Zoologia, 2(7): 449–458.
- Vandoros, J.D. and Dumont, E.R. 2004. Use of the wings in manipulative and suspensory behaviors during feeding by frugivorous bats. Journal of Experimental Zoology, 301A: 361– 366. https://doi.org/10.1002/jez.a.20040.
- Velazco, P.M. 2005. Morphological phylogeny of the bat genus *Platyrrhinus Saussure*, 1860 (Chiroptera: Phyllostomidae) with the description of four new species. Fieldiana Zoology, New Series 105:1–53. https://doi.org/10.3158/0015-0754(2005)105 [1:MPOTBG] 2.0.CO;2.
- Velazco, P.M., Gardner, A.L. and Patterson, B. 2010. Systematics of the *Platyrrhinus helleri* species complex (Chiroptera: Phyllostomidae), with descriptions of two new species. Zoological Journal of the Linnean Society, 159(3): 785–812. https://doi.org/10.1111/j.1096-3642.2009.00610.x.
- Vieira, M.F. and Carvalho-Okano, R.M. 1996. Pollination biology of *Mabea fistulifera* (Euphorbiaceae) in Southeastern Brazil. Biotropica, 28(1): 61–68.
- Walldorf, V. and Mehlhorn, H. 2013. Bats: A Glimpse on Their Astonishing Morphology and Lifestyle. In: Klimpel, S. and Mehlhorn, H. (Eds.). Bats (Chiroptera) as Vectors of Diseases and Parasites Volume 5 of the series Parasitology Research Monographs. Berlin, Springer, pp 7–24.
- Wilson D. E. and Mittermeier R. A. (Eds). 2019. Handbook of the Mammals of the World. Volume 9. Bats. Lynx Editions, Barcelona, 1008 pp.

Appendix 1. Bat vouchers used in this study. All the specimens were from Mammalian Collection of the Museo Javeriano de Historia Natural of Pontificia Universidad Javeriana (MPUJ-MAMM) (Bogotá, Colombia). Available at: https://osf.io/tm65e/

Appendix 2. Dunn test for pairwise comparisons between guilds for (a) LP/FL ratio, (b) Lc/ FL ratio and (c) LPc/FL ratio. Available at: https://osf.io/qdjky/

Appendix 3. Dataset employed for statistical analysis. Available at: https://osf.io/sfuy2/