

Craniodental traits and interaction in the bite force of tropical frugivore bats (Phyllostomidae: Stenodermatinae)

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Abstract

1. Phyllostomid bats exhibit great diversity in skull size and morphology that reflects the degree of resource division and ecological overlap in the group. In particular, Stenodermatinae has high morphological diversification associated with cranial and mandibular traits that is associated with the ability to consume the full range of available fruits (soft and hard). In terms of morphology, performance (bite force) appears to play an important role in niche partitioning among bat species, however, very few studies have confirmed these relationships using functional cranial traits. 2. Here, we analyzed craniodental traits and their relationship to the bite force in 308 specimens distributed in seven species of stenodermatine bats with two foraging types: nomadic and sedentary frugivorous bats. We evaluated 19 functional traits of the skull and jaw related to feeding and bite force in live animals by correcting bite force with body size. We used a GLM model and post hoc tests to determine possible relationships and differences between cranial traits, species, and sex. 3. The results showed that there is significant interspecific variation between stenodermatines that are nomadic and sedentary. The greatest variation in bite force within species was explained by the mandibular tooththrow length (MANDL) between sexes, which was greater in females. The larger species of *Artibeus*, together with *Platyrrhinus helleri*, *Uroderma convexum* and *Sturnira giannae*, which have a greater length of the skull, condylo-incisor, condylo-canine, mandibular tooththrow and height of the coronoid, exhibit greater bite force. By contrast, the smaller species *A. anderseni* and *A. phaeotis* have short skulls and the lowest values of bite force, which suggests that the size of the skull confers a biomechanical advantage. 4. Our results highlight the usefulness of analyzing functional traits related to feeding to establish the performance of bats in terms of the bite force.

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1. Phyllostomid bats exhibit great diversity in skull size and morphology that reflects the degree of resource division and ecological overlap in the group. In particular, Stenodermatinae has high morphological diversification associated with cranial and mandibular traits that is associated with the ability to consume the full range of available fruits (soft and hard). In terms of morphology, performance (bite force) appears to play an important role in niche partitioning among bat species, however, very few studies have confirmed these relationships using functional cranial traits.
2. Here, we analyzed craniodental traits and their relationship to the bite force in 309 specimens distributed in seven species of stenodermatine bats with two foraging types: nomadic and sedentary frugivorous bats. We evaluated 19 functional traits of the skull and jaw related to feeding and bite force in live animals by correcting bite force with body size. We used a GLM model and *post hoc* tests to determine possible relationships and differences between cranial traits, species, and sex.
3. The results showed that there is significant interspecific variation between stenodermatines that are nomadic and sedentary. The greatest variation in bite force within species was explained by the mandibular tooththrow length (MANDL) between sexes, which was greater in females. The larger species of *Artibeus*, together with *Platyrrhinus helleri*, *Uroderma convexum* and *Sturnira giannae*, which have a greater length of the skull, condylo-incisor, condylo-canine, mandibular tooththrow and height of the coronoid, exhibit greater bite force. By contrast, the smaller species *A. anderseni* and *A. phaeotis* have short skulls and the lowest values of bite force, which suggests that the size of the skull confers a biomechanical advantage.
4. Our results highlight the usefulness of analyzing functional traits related to feeding to establish the performance of bats in terms of the bite force.

KEYWORDS

Ecomorphology, frugivores, morphometry, Stenodermatinae, skull, trophic performance.

1. INTRODUCTION

The skull of vertebrates is a complex assembly that is closely related to the resource collection, food processing, behavior, and ecology of the species (Bels & Herrel, 2019). Examining the patterns and mechanisms that lead to cranial variation, including shape and traits, enables an understanding of the morphology, ecology, and general fitness of animals (Santana, Dumont, & Davis, 2010). Bats have variation in cranial morphology attributed to evolutionary processes of ecological specialization, which result in a niche division between ecomorphologically similar species (Santana, Grosse, & Dumont, 2012). This variation responds mainly to functional requirements related to nutritional performance and the sensory system (Thiagavel et al., 2018).

Among chiropterans, New World leaf-nosed bats (Phyllostomidae) represents one of the largest and most morphologically diverse mammal families (Rossoni et al., 2017). Ecological diversification in Phyllostomidae is related to bite performance and mechanical demands of different diets, including frugivores, insectivores, nectarivores, carnivores, and sanguinivores (Dumont, 2007; Nogueira, Peracchi, & Monteiro, 2009; Manhães, Nogueira, & Monteiro, 2017). Dietary differences require specific mechanical modifications, including variation in the rostral length and height of the skull (Santana, Dumont, & Davis, 2010). However, there is a lack of understanding about the patterns in the variation of the shape and performance (López-Aguirre & Pérez-Torres, 2015). The remarkable specializations seen in these bats provide a unique opportunity for studying the relationship between cranial morphology, feeding performance, and dietary ecology (Aguirre, Herrel, Van Damme, & Matthysen, 2002; Rossoni et al., 2017).

The bite force is a biomechanical trait that determines various vital functions, such as feeding, mating, defense, and competition, and is closely related to body size and feeding performance (Santana, Dumont, & Davis, 2010). Therefore, an increase in bite force allows for a broader spectrum of food available (Santana & Dumont, 2009). Phyllostomid exhibit bite forces associated with the size and hardness of food (Aguirre, Herrel,

Van Damme, & Matthysen, 2003), resulting in strong morphological heterogeneity due to the particularities of the diet (Dumont & O’Neil, 2004).

Although various studies have addressed the relationships of craniodental morphology, bite force and diet (e.g., Aguirre, Herrel, Van Damme, & Matthysen, 2002; Dumont, Herrel, Medellín, Vargas-Contreras, & Santana, 2009; Santana, Grosse, & Dumont, 2012; Santana & Miller 2016), the evaluation of these variables has been carried out separately, evaluating each variable independently (Shi et al., 2020). Likewise, the information related to the craniodental traits responsible for generating bite forces in bats is limited without much attention to the functionally relevant components of the craniodental system and the musculature of the jaw (Herrel, Smet, Aguirre, & Aerts, 2008). The specific hardness of food and the bite force required to process food play an important role in the division of resources within frugivore bat communities (Dumont, 2007). According to Soriano (2000) and Giannini & Kalko (2004), fruit bats can be categorized as nomadic or sedentary, with preference for a specific type of plant, morphological diversity reflected in the physical properties of the fruits, and a tendency of specialization towards a specific fruit or group of fruits (Santana, Dumont, & Davis, 2010; Santana, Grosse, & Dumont, 2012).

Frugivorous bats provide an excellent model to study the relationship between craniodental morphology and bite force because they consume both hard and soft fruits, the result of adaptive pressures related to mandibular morphology (see Murillo-García, & De la Vega, 2018). We selected the members of the family Phyllostomidae due to the fact that they have the highest diversity of mammals with more than 70 species that are found sympatrically and serve as nocturnal predators, pollinators and predominant seed dispersers (Giannini & Kalko, 2004; Reid et al., 2015), and within this family, the Stenodermatinae subfamily, contains > 43% of all described New World leaf-nosed bat species (Shipley & Twining, 2020) and in central Colombia, department of Tolima, these chiropterans represent near the 13% in the sampled areas (see García-Herrera, Ramírez-Francel, & Flórez, 2019).

Our objective was to identify the functional traits associated with bite force in seven representative species of the Stenodermatinae subfamily occurring in Colombia. We hypothesize that large species and small-sized nomadic frugivorous species with narrow faces, wide palates and shorter length between molars will have a greater biomechanical advantage of stronger bite force in relation to sedentary frugivorous bats.

2. MATERIALS AND METHODS

2.1. *Samples and classification*

From February 2019 to January 2020, we registered bite force and skull morphology data of seven species of Stenodermatinae fruit bats (Appendix I). These bats were divided into two categories: (i) nomadic frugivores: *Artibeus anderseni*, *A. phaeotis*, *A. lituratus*, *A. planirostris*, *Platyrrhinus helleri*, *Uroderma convexum*; (ii) sedentary frugivores:

Sturnira giannae.

2.2. *Field collection and laboratory analysis*

We follow two procedures for collecting our data: i) fieldwork in selected areas of the Colombian tropical dry forest-TDF in the department of Tolima (Figure 1, red triangle marks) using conventional methodology, i.e., mist-nets placed along trails within forest areas, at the edge of forest remnants, and near waterbodies. Each sampling night consisted of four standard size mist nets (12 x 2.5m), eight nets (6 x 2.5m) in the sub-canopy and a Triple High net (30 X 7 m), with a sampling intensity of 36.288 m² nets/h, corresponding to 864 h in 144 nights. The captured bats were handled according to the American Society of Mammalogists guidelines for the use of wild animals for research purposes (Sikes & Animal Care and Use Committee of the American Society of Mammalogists, 2016). After capture, the age, sex, and reproductive status were evaluated, and only adult males and adult non-pregnant, non-lactating females were used for the measurements. Age and sex were identified based on the degree of ossification of the coat and tibia. Reproductive status in females was determined by examining the nipples and palpitation of the abdomen. Then, bats were put into cloth

bags and transferred to measure the bite force using a portable digital fruit hardness tester (Lutron, Indian) with a capacity of 196.10 Newton and precision ± 0.05 .

We follow the method of Freeman & Lemen (2008), and bite force was recorded at the molars, measurements were repeated five times for each bat with an inter-trial interval of at least 5 min. The maximum value of the five measurements was considered as the maximum bite force produced by that individual. The bite force of the species was calculated by averaging the maximum bite force of each individual. The captured specimens were used for direct measurements of the forearm length, body mass, then they were euthanized and handled for craniodental morphometry (Figure 2; see Table S1), and entry to biological collection of the University of Tolima CZUT-M (Ibague, Colombia). ii) The second procedure consisted of measurements of 16 craniodental traits and two body traits (Table 1, Figure 2) obtained of voucher specimens from the Zoological Collection of the University of Tolima (CZUT; Ibague, Colombia), Museo Javeriano de Historia Natural "Lorenzo Uribe, SJ" (MPUJ; Bogota, Colombia) and Royal Ontario Museum (ROM; Ontario, Canada). The revised specimens from these biological collections belong to 24 localities in Colombia (Figure 1; Appendix I). We verified that all adult specimens according to the ossification of the growth plates of the epiphysis of the phalanges of the fingers (Dietz et al., 2007).

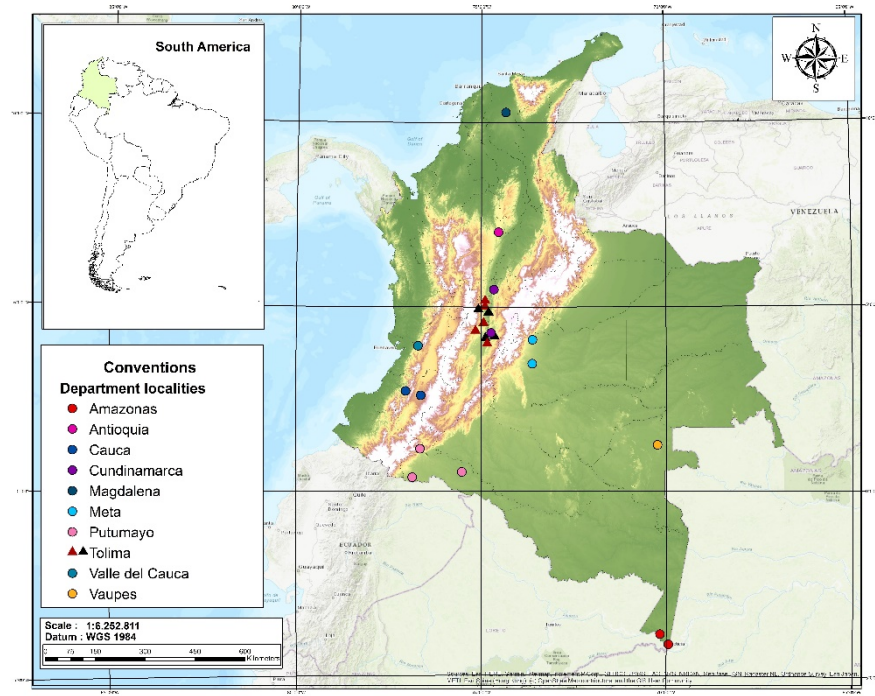


FIGURE 1 Geographic distribution of the locations of the Stenodermatinae bat samples used for the biometric analyzes. Triangle black marks represent sampling points where capture of Colombian Stenodermatinae bats was carried out in the department of Tolima; other circle marks represent records of other sampling sites obtained from voucher specimens (see text for more details).

TABLE 1 The craniodental, mandibular and external measurements used as functional traits in this study.

Variable	Main trait	Description
Bite force	Head	Maximum bite force produced by molars
Forearm length	Body	Distance from the olecranon process to anterior surface of carpals in the folded
Mass	Body	Physical quantity that allows to indicate the quantity of matter contained in

Variable	Main trait	Description
Greatest length of skull	Head	Distance from the posterior-most point of the occiput to the anterior-most point of the snout
Condylolincisive length	Head	Distance between a line connecting the posterior-most margins of the occipital condyles and the anterior-most point of the upper canine
Condyllocanine length	Head	Distance between a line connecting the posterior-most margins of the occipital condyles and the anterior-most point of the lower canine
Braincase breadth	Head	Breadth of the braincase, excluding mastoid and paraoccipital processes
Zygomatic breadth	Head	Breadth across the zygomatic arches
Postorbital breadth	Head	Breadth at the postorbital constriction
Mastoid breadth	Head	Greatest breadth across the mastoid region
Palatal length	Head	Distance between the posterior palatal notch and the anterior border of the hard palate
Maxillary tooththrow length	Head	Distance from the anterior-most surface of the upper canine to the posterior-most point of the upper molar
Width at M1	Head	Greatest width of palate across M1s
Width at M2	Head	Greatest width of palate across M2s
Palatal width at canines	Head	Least width across palate between alveoli of upper canines
Dentary length	Head	Length between midpoint of condyle to anterior-most point of dentary
Mandibular tooththrow length	Head	Distance from the anterior-most surface of the lower canine to the posterior-most point of the lower molar
Coronoid height	Head	Perpendicular height from ventral margin of mandible to tip of coronoid process
Width at mandibular condyles	Head	Greatest width between inner margins of mandibular condyles

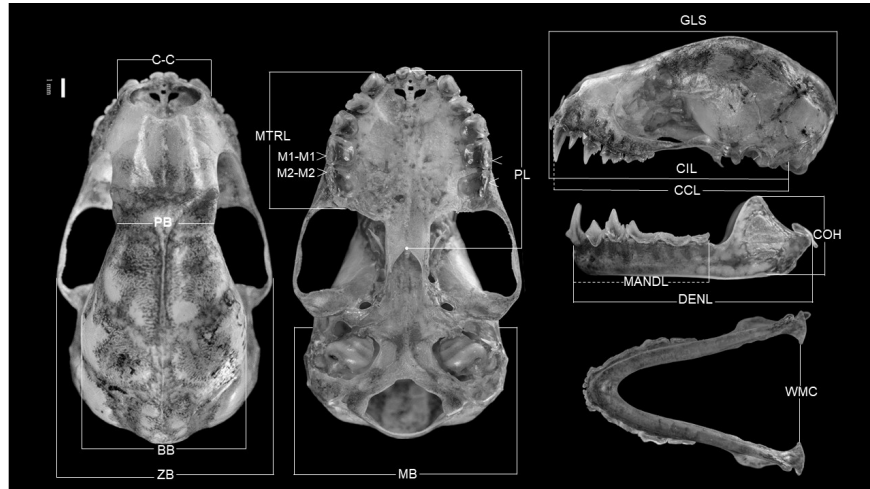


FIGURE 2 Lateral and dorsal views of the cranium and mandible (*Platyrrhinus helleri*, adult male), and ventral view of the cranium, measurements used in the craniodental morphometry. Abbreviations: GLS, greatest length of skull; CIL, condylolincisive length; CCL, condyllocanine length; BB braincase breadth; ZB, zygomatic breadth; PB, postorbital breadth; C–C, palatal width at canines; MB, mastoid breadth; PL, palatal length; MTRL, maxillary tooththrow length; M1–M1, width at M1; M2–M2, width at M2; DENL, dentary length; MANDL, mandibular tooththrow length; COH, coronoid height; WMC, width at mandibular condyles.

2.3. Statistical analyses

Data analyses were carried out by including both fieldwork and voucher specimen's data. A linear regression was performed to assess the effects of body parameters on the changes in bite force. In the models, the averages of the bite force and body size (forearm length, greatest length of skull) and mass of each species were used. $\ln(y) = \beta_0 + \beta_1x_1 + \beta_2x_2 + \epsilon$, where y corresponds to the bite force, x_1 and x_2 are the length of the forearm and greatest length of skull, respectively. β_0 is the intercept, β_1 , β_2 are the regression coefficients (for x_1 and x_2), and ϵ is the random error.

In order to analyze the intra and interspecific morphological variation, the mean \pm SD was calculated for all morphometric variables and to determine sexual dimorphism. The assumptions of normality and homoscedasticity were corroborated with the Shapiro-Wilk and Levene's test, respectively. The test results showed that our data fit a normal distribution, and accomplish the equality of variances, thus we used a two-way analysis of variance (ANOVA) to test differences between species and sexes. Post-hoc comparisons between sexes within species were performed to identify species with significant dimorphism.

To explore the differences in skull morphology and body traits among different species and sexes, we performed a Principal Component Analysis- PCA based on a correlation matrix. A threshold value of $\lambda > 1$ was used to determine the relevant traits that explain most of the observed variance. Based on the preliminary results of the PCA, the variables forearm length and mass were excluded because they presented a correlation close to one, while the other variables (17) were used for the Canonical Variate Analysis- CVA. A CVA was carried out, in order to establish the largest axes of discrimination between the groups identified *a priori*; find the linear combinations of the starting variables with maximum discriminating power between the groups; test whether the means of these groups along these axes are significantly different to find an ordering of the groups of individuals each represented by the vector of the means in all the variables; and to study the dimensionality of the data.

In order to determine the existence of significant variation between species and morphological traits, an analysis of variance was carried out using a generalized linear model (GLM). We used the bite force as the response variable and the cranial and body traits as covariates. The model used was: $Y_{ijk} = \mu + \tau_i + \delta_j + \Omega_k + \epsilon_{ijk}$, where Y_{ijk} represents the response of the bite force at the j th level of sex and i th species; μ general average, τ_i effect produced by the i -th species, δ_j effect produced by the j -th sex, Ω_k effect due to the R -th trait and ϵ_{ijk} the random error. For detecting the masked variability, an intuitive and qualitative procedure based on graphical representation was used, then we performed *post hoc* tests using the Fisher's Least Significant Difference (LSD) pairwise comparison procedure. We set the statistical significance for all tests of $P \leq 0.05$. All analyzes were performed in R 3.5.3 (R Core Team 2019).

3. RESULTS

Comparisons of morphological traits between males and females showed significant differences by species ($F = 72.04$, d.f. = 92, $p < 0.001$), sex ($F = 4.22$, d.f. = 17, $p < 0.001$) and their interaction ($F = 2.8$, d.f. = 94, $p < 0.001$, Table 2). Los rasgos craneales que presentaron mayor variabilidad fueron la longitud dentaria (DENL), la longitud de los dientes de la mandíbula (MANDL) con un coeficiente de variación de 47.2% y 18.50% respectivamente, mientras que los demás rasgos morfológicos presentaron una menor variación baja en 10%.

The PCA had the first two axes explaining 91.8% of all the variance. The first component (PC1) explained 87.4% of the total variance and is determined by the width across the upper first molars (M1-M1), zygomatic breadth (ZB), forearm length (AB), dentary length (DENL) and condylo-incisor length (CIL). The second component (PC2), explained 4.4% of the variance, and was associated with the traits of maxillary toothrow length (MTRL), width between the cingulate of the upper canines (C-C), greater length of the skull (GLS), postorbital amplitude (PB), braincase breadth; (BB), and the bite force (BF) (Figure 3).

The CVA had two main groups containing species of small-sized nomadic frugivorous and sedentary frugivorous bats; and large-sized nomadic frugivorous bats. Five subgroups were identified for *A. anderseni* and *A. phaeotis*; *S. giannae*; *U. conxum* and *Platyrrhinus helleri*; *A. planirostris*; and *Artibeus lituratus* (Figure 3). The traits that most contributed to the discrimination of the species in the CVA were MANDL, PL and WMC, which explained the greater morphological variation between species (Figure 4).

Table 2. Species, sample size (n) bats used to investigate bite force and jaw-skull shape relationships.

Species	Sex	n	GLS	CIL	CCL	ZB	BB	PB
<i>A. anderseni</i>		20	18.26 (0.46)	13.98 (1.50)	13.9 (1.40)	10.56 (0.57)	8.87 (0.39)	4.60

Species	Sex	n	GLS	CIL	CCL	ZB	BB	PB
<i>A. lituratus</i>		21	18.11 (1.83)	14.21 (0.58)	14.12 (0.39)	10.71 (0.58)	8.88 (0.40)	4.54
		33	30.69 (0.74)	24.35 (0.62)	23.76 (0.56)	18.34 (0.44)	14.12 (0.35)	6.58
		31	31.34 (0.55)	25.06 (0.67)	24.44 (4.16)	18.62 (0.51)	13.93 (0.56)	7.12
<i>A. planirostris</i>		26	27.87 (4.97)	22.58 (0.77)	22.07 (0.81)	16.78 (0.73)	13.32 (0.56)	6.63
		38	28.12 (0.85)	22.71 (0.83)	22.21 (0.77)	17.19 (0.40)	13.47 (0.70)	6.98
<i>A. phaeotis</i>		17	18.68 (0.64)	15.11 (0.78)	14.89 (1.00)	11.03 (0.48)	9.27 (0.47)	4.33
		11	18.33 (0.77)	14.21 (0.58)	14.24 (0.52)	10.71 (0.41)	8.95 (0.39)	4.45
<i>P. helleri</i>		9	21.25 (0.48)	17.58 (0.40)	17.21 (0.45)	10.44 (0.45)	8.58 (0.48)	4.89
		20	21.88 (0.68)	17.99 (0.60)	17.33 (0.52)	11.16 (0.47)	9.5 (0.62)	5.24
<i>U. convexum</i>		19	22.12 (0.65)	18.32 (0.67)	17.56 (0.49)	11.69 (0.52)	9.40 (0.36)	5.66
		21	22.34 (0.44)	17.58 (0.70)	17.25 (0.54)	11.67 (0.68)	10.24 (0.48)	5.32
<i>S. giannae</i>		13	22.25 (0.62)	17.81 (0.69)	17.22 (0.63)	12.09 (0.34)	10.45 (0.26)	6.08
		17	22.11 (0.49)	17.65 (0.47)	17.22 (0.41)	12.26 (0.41)	10.47 (0.36)	6.25
Manova (Wilks)			Value	Value	F	d.f.	P	
	Specie	Specie	5.20e-05	5.20e-05	72.04	92	<0.001	
	Sex	Sex	0.79	0.79	4.22	17	<0.001	
	Specie*Sex	Specie*Sex	0.39	0.39	2.8	94	<0.001	

* All measurements are presented in millimeters except for BS which are presented in Newtons.
Values are described as mean (\pm SD).

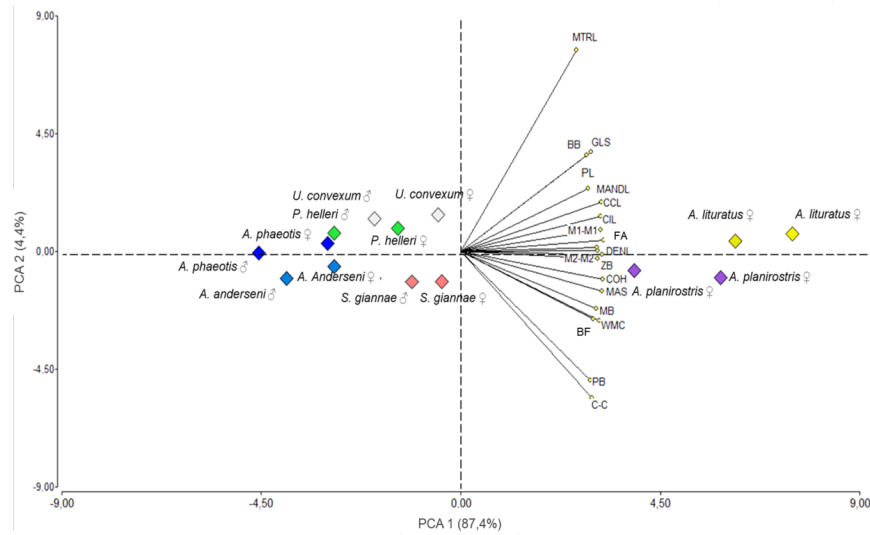


FIGURE 3 Distribution of body and craniodental traits for seven species of fruit bats based on a Principal Components Analysis (PCA).

The GLM determined significant differences both for species and for all traits ($F = 27.14$; $P < 0.001$) and variation between sexes ($F = 5.73$, $P = 0.017$; Figure 5). All pairwise comparisons were significant with $P [?] 0.01$.

3.1 Variation in the bite force associated with craniodental traits

Most of the variation in the bite force data according to test LSD was mainly explained for both males

and females by the MANDL trait ($t = 8.00$, $df = 12$, $P < 0.01$; Figure 5). It was identified that 15 traits are significantly associated with a high bite force, including greatest length of the skull, condylo-incisor length, condylo-canine length, postorbital breadth, mastoid breadth, zygomatic arch breadth, palatal length, mandibular tooththrow length, and height of the coronoids (Table 2).

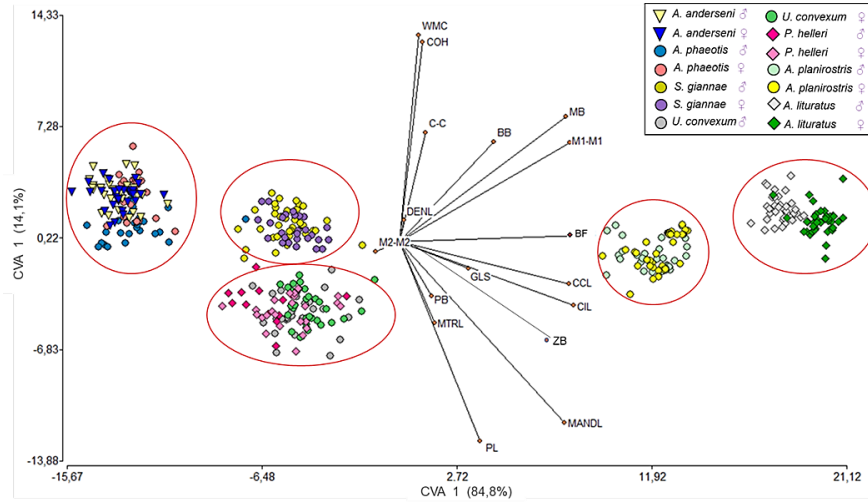


FIGURE 4 Canonical variate analysis with the description of body and craniodental traits and seven species of Stenodermatinae bats. The five ellipses (groups) are highlighted.

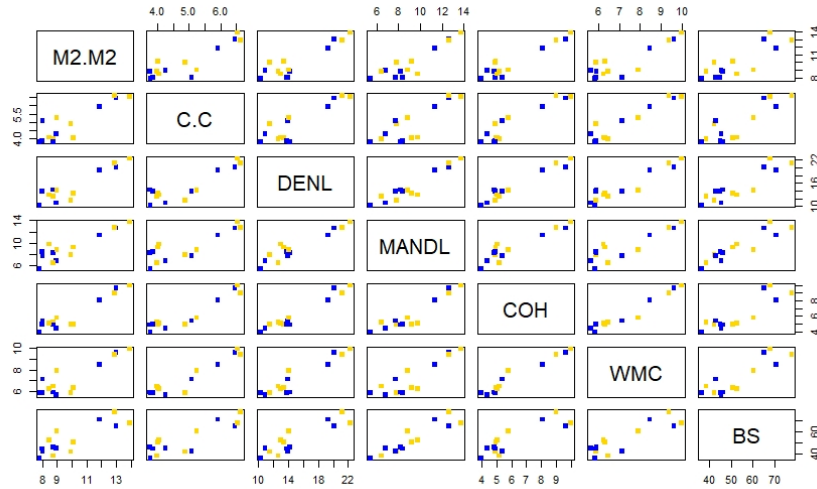


FIGURE 5 Pairwise relationships of craniodental traits with bite force for seven Colombian species of Stenodermatinae bats. Blue squares correspond to males and yellow to females. Abbreviations as in Table 1.

3.2 Interspecific bite force variation

The bite force varied between species; big-sized nomadic bats had the highest bite force, followed by small-sized nomadic bats (*P. helleri* and *U. convexum*), and then by the only sedentary bat (*S. giannae*).

The lowest force was recorded by small-sized nomadic bats of the species *A. anderseni* and *A. phaeotis* ($P < 0.001$). Significant intersexual differences between species were detected with the females registering a greater bite force compared to the males ($P < 0.04$; Figure 6).

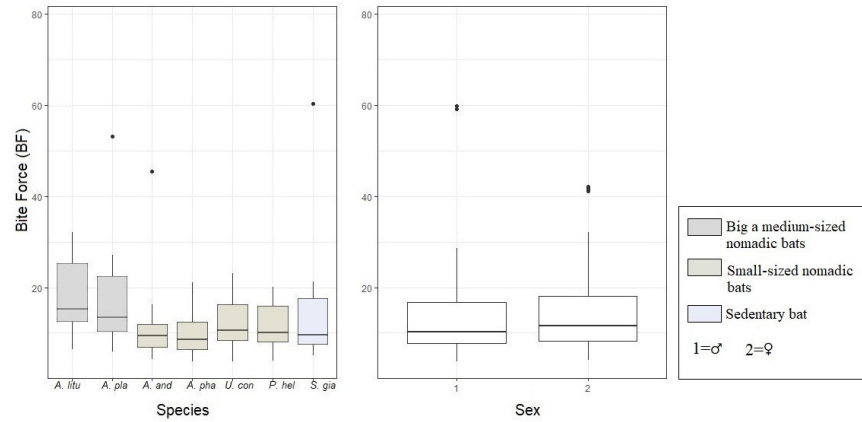


FIGURE 6 Box plot showing differences in relative bite force among bat species and sex. *A. lit* : *Artibeus lituratus*. *A. pla* : *A. planirostris*. *A. and* : *A. anderseni*. *A. pha* : *A. phaeotis*. *U. con*: *Uroderma convexum*. *P. hel* : *Platyrrhinus helleri* and *S. gia*: *Sturnira giannae*.

Our results revealed that big-sized nomadic bats, *A. lituratus*, and *A. planirostris* differed from the remaining species, as established by post-hoc tests ($P < 0.001$). Furthermore, it was established that *A. anderseni* and *A. phaeotis* are significantly different from *S. giannae* and *U. convexum*, while these last two species are similar to *P. helleri* and the small species of *Artibeus* (Table 3).

Differences between bite force between bat species .

In this study, significant differences in skull morphology and bite strength were observed between species. LSD post-hoc testing provided clustering indicators, the first group consisted of the large nomadic bats, *A. lituratus* and *A. planirostris*; the second by a nomadic species *U. convexum*; the third formed by the small species *P. helleri*, *S. giannae*, *A. phaeotis* and the fourth formed by *A. anderseni*, species that share cranial and corporal features in the third group (Table 4).

Table 3. Significance between pairs of species and relationship of bite force with other traits.

Species	P (value significant)	Traits	P (value significant)
<i>A. lituratus</i> - <i>A. phaeotis</i>	<0,001	Bf - C-C	<0,001
<i>A. lituratus</i> - <i>A. anderseni</i>	<0,001	Bf - CCL	<0,001
<i>A. lituratus</i> - <i>A. planirostris</i>	0,486	Bf - CIL	<0,001
<i>A. lituratus</i> - <i>P. helleri</i>	<0,001	Bf - COH	<0,001
<i>A. lituratus</i> - <i>S. giannae</i>	<0,001	Bf - DENL	<0,001
<i>A. lituratus</i> - <i>U. convexum</i>	<0,001	Bf - GLS	<0,001
<i>A. phaeotis</i> - <i>A. planirostris</i>	<0,001	Bf - M1-M1	<0,001
<i>A. phaeotis</i> - <i>A. anderseni</i>	0,84	Bf - M2-M2	<0,001
<i>A. phaeotis</i> - <i>P. helleri</i>	0,13	Bf - MANDL	<0,001
<i>A. phaeotis</i> - <i>S. giannae</i>	0,04	Bf - MASA	<0,001
<i>A. phaeotis</i> - <i>U. convexum</i>	0,05	Bf - MB	<0,001
<i>A. planirostris</i> - <i>A. anderseni</i>	<0,001	Bf - MTRL	<0,001
<i>A. planirostris</i> - <i>P. helleri</i>	<0,001	Bf - PB	<0,001
<i>A. planirostris</i> - <i>S. giannae</i>	<0,001	Bf - PL	<0,001

Species	P (value significant)	Traits	P (value significant)
<i>A. planirostris</i> - <i>U. convexum</i>	<0,001	Bf - WMC	<0,001
<i>A. anderseni</i> - <i>P. helleri</i>	0,08	Bf - ZB	<0,001
<i>A. anderseni</i> - <i>S. giannae</i>	0,08		
<i>A. anderseni</i> - <i>U. convexum</i>	0,04		
<i>P. helleri</i> - <i>S. giannae</i>	0,99		
<i>P. helleri</i> - <i>U. convexum</i>	0,73		
<i>S. giannae</i> - <i>U. convexum</i>	0,73		

Table 4. Post hoc test Least Significant Difference (LSD) pairwise comparison of bat species and body / cranial traits.

Species	Group
<i>A. lituratus</i>	a
<i>A. planirostris</i>	a
<i>U. convexum</i>	b
<i>P. helleri</i>	bc
<i>S. giannae</i>	bc
<i>A. pheotis</i>	bc
<i>A. anderseni</i>	c

4. DISCUSSION

We found that skull size and inter-sex morphology was significantly different, variation that can be associated with the diet of the selected bat species; possibly as a result of differences in energy requirements during the reproductive season (de Camargo & de Oliveira, 2012). Although sexual dimorphism has been relatively well documented in vespertilionid bats, being the females larger and heavier than males (Bornholdt, Oliveira, & Fabian, 2008), in phyllostomid bats this information is less documented despite it being the most diverse and distributed family in the Neotropics (Gardner 2008). However, López-Aguirre & Pérez-Torres (2015) identified that *Artibeus lituratus* females in Colombia had greater fluctuating asymmetry in the splanchnocranium presenting a differential on bite force.

4.1 Variation in the bite force associated with craniodental traits

Bite force has been established as an important performance trait for vertebrates that is associated with both cranial morphology and trophic ecology (Santana, Dumont, & Davis, 2010). However, studies in bats have based their conclusions on biomechanical models of the bite force without adequately testing the assumed correlation of it with the shape of the skull (Aguirre, Herrel, Van Damme, & Matthysen, 2002; Dumont, 2007; Herrel, De Smet, Aguirre & Aerts, 2008). Our study shows, for the first time, strong quantitative evidence of such a correlation by using a dataset of cranial traits involved in bite force within a morphologically diverse clade of New World fruit bats.

4.2 Interspecific bite force variation

Stenodermatinae represents a subfamily of Phyllostomidae bats with a diet that contains significantly more fruit than other family's bats (Santana, Grosse, & Dumont, 2012). They are morphologically diverse with cranial and mandibular traits that overlap with other feeding guilds (Santana, Grosse, & Dumont, 2012), which is reflected in the variety of foods as well as in the tendency of these species to specialize in a group of particular fruits (Rojas, Vale, Ferrero, & Navarro, 2012; Rossoni, Assis, Giannini, & Marroig, 2017). Several craniodental traits contribute to generate a greater bite force and the differences between these particular traits had showed a clear segregation between the species (Santana, Grosse, & Dumont, 2012).

The association in craniodental features and bite force by species can be explained by the type of fruit consumed. *A. phaeotis*, *P. helleri* and *S. giannae* (small-sized and sedentary nomadic fruit bats) formed an independent group. These species have a short skull and a shorter distance from the teeth to the jaw joint, which allows them to consume hard and soft fruits (Dumont et al., 2012). *P. helleri* and *S. giannae* are characterized by elongated and narrow snouts (Santana, Grosse, & Dumont, 2012), which is associated with the consumption of soft and smaller fruits such as those of Solanaceae (Arias & Pacheco, 2019; García-Herrera, Ramírez-Fráncel and Flórez, 2019). Species that share cranial and nutritional traits with *D. anderseni*. For its part, *Uroderma convexum* was distinguished from the other species studied here by having a parallel rostrum and a short face that abruptly expands from the apex to the edges of the lacrimal bone (Mantilla-Meluk, 2014). These characteristics allow them to exploit mainly hard fruits of plant species such as *Ficus* spp. (Sagot and Stevens, 2012).

All the big and small-sized nomadic frugivorous bat species studied here, except for *A. anderseni* and *A. phaeotis* had a stronger bite force, which was correlated to a greater length of the skull, shorter palate, narrower width between molars, dentary length, and higher coronoid process. These traits have been recognized as predictors of a biomechanical advantage for higher feeding performance (Dumont et al., 2012). Shortening and widening of the rostrum in *A. anderseni* and *A. phaeotis* was negatively correlated to bite force, although it should confer a greater biomechanical advantage; a pattern that has been repeatedly observed in placental and marsupial carnivores (Wroe & Milne, 2007). This is probably due to the fact that the variation in size could be the most dominant factor and it has been shown that the differential proportions of the skull determine the maximum value of the bite force (Herrel, Podos, Huber, & Hendry, 2005; Nogueira et al., 2009; Dollion et al., 2016). Recent studies have suggested that among closely related mammals, larger taxa exhibit relatively longer faces, whereas smaller taxa exhibit paedomorphic traits such as proportionally shorter faces and larger brains (Cardini & Polly, 2013; Cardini, Polly, Dawson, & Milne, 2015; Tamagnini, Meloro, & Cardini, 2017). This pattern called cranial evolutionary allometry, has been seen in antelopes, squirrels, fruit bats, cats and kangaroos (Tamagnini, Meloro, & Cardini, 2017).

Previous studies have demonstrated that skull size is important in determining interspecific differences in bite force, specifically, Nogueira, Peracchi & Monteiro (2009) found that, in phyllostomids, size-corrected bite forces were correlated with shorter rostra, alignment of the molars along the masseter insertion region, and expansion of the anterior zygomatic arch and angular process. On the contrary, our study determined that the variation in bite force in Stenodermatinal bats is better explained by the length of the skull, condylo-incisor, condylo-canine, mandibular toothrow and height of the coronoid, results similar to those reported by Herrel *et al.*, (2008) in a sample of bat species (including non-phylostomids).

Shortening and widening of the rostrum in *A. anderseni* and *A. phaeotis* was negatively correlated to bite force, although it should confer a greater biomechanical advantage; a pattern that has been repeatedly observed in placental and marsupial carnivores (Wroe & Milne, 2007). This is probably due to the fact that the variation in size could be the most dominant factor and it has been shown that the differential proportions of the skull determine the maximum value of the bite force (Herrel, Podos, Huber, & Hendry, 2005; Nogueira et al., 2009; Dollion et al., 2016). Recent studies have suggested that among closely related mammals, larger taxa exhibit relatively longer faces, whereas smaller taxa exhibit paedomorphic traits such as proportionally shorter faces and larger brains (Cardini & Polly, 2013; Cardini, Polly, Dawson, & Milne, 2015; Tamagnini, Meloro, & Cardini, 2017). This pattern called cranial evolutionary allometry, has been seen in antelopes, squirrels, fruit bats, cats and kangaroos (Tamagnini, Meloro, & Cardini, 2017).

Another factor that could explain our results is that bats modulate the force of the bite according to the exploited resources of soft and hard food (Santana & Dumont, 2009). Artibeus vary in the size and texture of the fruits they prefer (Wendeln, Runkle, & Kalko, 2000) and may exhibit differential maximum bite force, which can potentially increase by more than 10% when consuming hard fruits (Santana & Dumont, 2009). Another factor to consider is the possible variation in the intraspecific bite force in response to the temporal or geographical variation of food resources or the hormonal status of bats, as proposed by Irschick et al. (2006). Since the bats included in our study are composed of individuals from different localities and data

(fieldwork and voucher specimens; Appendix I), our data could be susceptible to this source of variation and therefore a more detailed study is needed to test this hypothesis and further improve our understanding of the relationships of bite force and craniodental traits.

Given that nomad bats consume similar fruits, they could require the same force to process, so we expected that all bats grouped in this category would present similar bite forces, however our results established that the species *Artibeus lituratus*, *A. planirostris*, followed *U. bilobatum* and *P. helleri* recorded the highest bite force, probably because these bats feed on food resources that clearly have different mechanical demands when consuming even other resources other than the fruits.

All Stenodermatinae are frugivores with short and wide rostrum, but our results show that can occur some divergent morphologies within the clade, which is seen in the large number of species within the subfamily and highly diverse genera (Murillo-Garcia & De la Vega, 2018). As has been documented in other vertebrates, closely related species exhibit strong positive relationships between large skulls and greater biomechanical advantage (Maestri et al., 2016; Santana & Miller, 2016). Our findings illustrate that skull size is a determining factor in the bite force and emphasizes that the use of functional traits is relevant to establishing the feeding performance of bat species. This highlights the importance of studying the relationships between morphology, bite force and the ecology of the species to get a better understanding of evolutionary adaptations of highly diverse Neotropical bat groups.

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Authors’ contributions

L.V.G-H., S.L.P. conceived the ideas and designed methodology; L.V.G-H., L.A.R-F established the activities in the field, developed the methodology and took the craniodental measurements in the different collections and museums evaluated; A.S-H., L.V.G-H., L.A.R-F and S.L.P. analyzed the data; B.L, G.G and G.R-F. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Accessibility

The data are available at <https://datadryad.org/stash/share/N6vW4UGTQZbdh132I0gaPR2GYsa4iDCy5YdsEeNaerM>

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APPENDIX I. SPECIMENS EXAMINED

The following list includes all specimens examined in this study, with their respective localities.

Artibeus anderseni (41)- AMAZONAS, Leticia (ROM 53614, 53615, 53616, 63061) ANTIOQUIA, Los Remedios (ROM 84982), CUNDINAMARCA, La Gran Curva, 114 km al oeste de Bogota (ROM 48959, 51790), Melgar (ROM 53613, 75300, 75302), Puerto Salgar (ROM 44956, 44957, 44965) TOLIMA, Alvarado, vereda Rincon de Chipalo, Parque Nacional del Arroz (CZUT-M 2089, 2090, 2091, 2099, 2100), Armero Guayabal, Centro Universitario Regional del Norte - Universidad del Tolima (ROM 1128, 1415, 1416, 1418, 1434, 1436, 1481, 1492, 1515, 1516, 1517, 1536, 1537, 1538, 1541, 1624, 1638, 1639, 1641, 1642), Espinal (ROM 88089), Ibague, vereda Aparco (CZUT-M 2098, 2103).

Artibeus lituratus (64)- CAUCA, Bellavista (ROM 63232, 63063, 64066, 64067, 64068, 64069, 64070, 64071, 67247, 67253, 67255, 67256, 67261), CUNDINAMARCA, Puerto Salgar (ROM 44811), META, Villavicencio, Puerto Lopez (ROM 88083), TOLIMA, Ambalema, vereda Chorrillo (CZUT-M 1410, 1546, 1567, 1569, 1668), Armero Guayabal, Centro Universitario Regional del Norte - Universidad del Tolima (CZUT-M 1124, 1413, 1545, 1546, 1564, 1565, 1566, 1596, 1628, 1629, 1631, 1704), Ibague, vereda Chucuni (CZUT-M 0763, 0764, 0766, 0835), Buenos Aires (ROM 44882, 44885), Melgar, Santo Tomas (MUJ 00826, 00827, 00828, 00829, 00830, 00832, 00833, 00834) Suarez, vereda Batatas (CZUT-M 0299, 0301, 0303, 0305, 0344, 0346), vereda Aguas Claras (CZUT-M 0363), vereda Los Arrayanes (CZUT-M 1230, 1231), PUTUMAYO, vereda Guascayaco (ROM 46356, 49206, 49209, 49211), VAUPES, Mitu (ROM 45258, 45259, 45260), VALLE DEL CAUCA (ROM 44889, 44890).

Artibeus planirostris (75)- META, Fuente de Oro, Km 9 Carretera Puerto Limon (ROM 90109, 91409), TOLIMA, Ambalema, vereda Chorrillo (CZUT-M 1468, 1469, 1470, 1471, 1472, 1473, 1474, 1475, 1476, 1477, 1494, 1544, 1568, 1583, 1584, 1585, 1586, 1587, 1588, 1589, 1590, 1591, 1592, 1599, 1600, 1605,

1632, 1643, 1644, 1645, 1646, 1669, 1670, 1671, 1672, 1673, 1695, 1696, 1697, 1699, 1700, 1701), Ibagué, vereda Aparco (CZUT-M 1994, 1995, 1996), Armero Guayabal, Centro Universitario Regional del Norte - Universidad del Tolima (CZUT-M 1412, 1414, 1493, 1513, 1514, 1542, 1543, 1593, 1594, 1595, 1598, 1698, 1705, 1712, 2008, 2049), Suárez, vereda Batatas (CZUT-M 0243, 0244, 0245, 0298, 0300, 0302, 0304, 0345, 0347, 2070), PUTUMAYO, vereda Guayaco (ROM 49211), Vereda San Miguel (67246).

Artibeus phaeotis (28)- AMAZONAS, Leticia (ROM 53610, 53611, 53612), CAUCA, Bellavista (ROM 64064, 64059, 64057), MAGDALENA, Santa Marta (ROM 79885), TOLIMA, Alvarado, vereda Rincon de Chipalo, Parque Nacional del Arroz (CZUT-M 2106), Ambalema, vereda Chorrillo (CZUT-M 1346, 1549, 1572, 1647) Armero Guayabal, Centro Universitario Regional del Norte - Universidad del Tolima (CZUT-M 1127, 1435, 1437, 1518, 1571, 1625, 1640, 1702, 1703, 1706, 1710, 1711), Mariquita (MUJ 0269, 0285, 0286), Melgar (MUJ 00835).

Platyrrhinus helleri (31) -MAGDALENA, Santa Marta (ROM 79882), TOLIMA, Alvarado, vereda Rincon de Chipalo, Parque Nacional del Arroz (CZUT-M 2009, 2062), Ambalema, vereda Chorrillo (CZUT-M 1709), Armero Guayabal, Centro Universitario Regional del Norte - Universidad del Tolima (CZUT-M 1539, 1547, 1570, 1602, 1626, 1630, 2010), Libano, Hacienda La Trinidad (ROM 88082), Ibagué, vereda Martínez (CZUT-M 0027, 0116), San Sebastián de Mariquita (CZUT-M 1063, 1065, 1072), Melgar (CZUT-M 1928), vereda Santo Tomás (MUJ 00837, 00838, 00839, 00841), Suárez, vereda Batatas (CZUT-M 0341, 0364, 1914), PUTUMAYO (ROM 403559, 46375, 46353, 63239), VAUPES, Mitu (ROM 45274, 45273),

Uroderma convexum (40)- MAGDALENA, Santa Marta (ROM 79886), TOLIMA, Alvarado, vereda Rincon de Chipalo, Parque Nacional del Arroz (CZUT-M 2093, 2101, 2104, 2105), Armero Guayabal, Centro Universitario Regional del Norte - Universidad del Tolima (CZUT-M 1126, 1438, 1511, 1512, 1540, 1597, 1601, 1622, 1623, 1633, 1634, 1635, 1636, 1637, 1694, 1707), Ibagué, vereda Aparco (CZUT-M 2095, 2096, 2097, 2102), San Sebastián de Mariquita (CZUT-M 1054, 1070), Melgar (CZUT-M 1927, MUJ 00842, 00843, 00844, ROM 62508), Suárez, vereda Batatas (CZUT-M 1915), PUTUMAYO, vereda Guascayaco (ROM 46360), vereda Horno (ROM 63240, 63240), VAUPES, Mitu (CZUT-M 45268, 45267, 45366, 45265).

Sturnira giannae (30)- TOLIMA, Ambalema, vereda Chorrillo (CZUT-M 1116, 1117, 1118, 1296, 1310, 1318, 1342, 1343), Armero Guayabal, Centro Universitario Regional del Norte - Universidad del Tolima (CZUT-M 1129, 1403), Ibagué, vereda Aparco (CZUT-M 2014, 2015, 2016, 2021, 2022, 2023, 2028), Mariquita (CZUT-M 1056, 1061), Suárez, vereda Batatas (CZUT-M 0234, 0246, 0307, 0362, 1236), PUTUMAYO (ROM 40374, 40313, 40349, 40375, 46373, 49184).