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Artículo

Taxonomic identity of an insular population of sac-winged bat *Saccopteryx* (Chiroptera: Emballonuridae)

Identidad taxonómica de una población insular del murciélago de sacos *Saccopteryx* (Chiroptera: Emballonuridae)

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Abstract

Insular populations can differ from their continental counterparts since they are subject to particular pressures, biotic and abiotic, that can lead to variations in morphology and behavior; thus, the use of external characters may complicate taxonomic identification of insular populations. Even though the bat assemblage of Gorgona Island is a conservation target, there has been controversy about the taxonomic identity of bats from this Colombian National Natural Park. Specifically, our goal was to determine the taxonomic identity of the population of the sac-winged bat (genus *Saccopteryx*) resident in Gorgona, which have the peculiarity of having diurnal activity. Thus, we assessed differences among populations using morphometrics (traditional and geometric) and echolocation calls. Additionally, since the species of *Saccopteryx* involved have different mating systems, we assessed roosting association of Gorgona population as a surrogate for mating system. Despite the variation in skull morphometrics and echolocation calls among populations, Gorgona population was more similar to *S. leptura* than to *S. bilineata*. Besides, evolutionary allometry was significant, but size explained a small proportion of shape differences among populations. Finally, roosting association of Gorgona population suggests a monogamous mating system such as in *S. leptura*. We conclude that *Saccopteryx* from Gorgona corresponds to *S. leptura*. In addition, biogeographic history and geographic isolation of the island suggest that this population may have differentiated from their mainland counterparts through founder effect, genetic drift and/or adaptation to the local biotic and abiotic environmental conditions.

Key words: traditional morphometrics; geometric morphometrics; echolocation; insular populations; mainland populations.

Resumen

Las poblaciones insulares frecuentemente difieren de las continentales, en morfológica y comportamiento. Consecuentemente, utilizar características externas puede dificultar la identificación taxonómica de especies en las islas. En el Parque Nacional Natural Gorgona, particularmente, ha existido controversia sobre la identidad de varias especies de murciélagos residentes. Nuestro objetivo fue determinar la identidad taxonómica de la población de *Saccopteryx* de esta isla, que tiene la particularidad de tener actividad diurna. Evaluamos las diferencias entre las poblaciones mediante morfometría (tradicional y geométrica) y llamados de ecolocalización. Además, debido a que las especies difieren en su sistema de apareamiento, evaluamos la conformación de los grupos en los refugios. Pese a la variación en la morfometría craneal y los llamados de ecolocalización entre las poblaciones, la población de Gorgona fue más similar a *S. leptura* que a *S. bilineata*. Las conformaciones de los grupos en los refugios sugieren un sistema monógamo como en *S. leptura.* Por ende, concluimos que la especie de la isla es *S. leptura*. Adicionalmente, la historia biogeográfica y el aislamiento geográfico de la isla sugieren que esta población puede ser diferente de sus contrapartes continentales debido al efecto fundador, deriva genética y/o adaptaciones a las condiciones ambientales locales.

Palabras clave: morfometría tradicional; morfometría geométrica; ecolocalización; poblaciones insulares; poblaciones continentales.

Introduction

Geographic isolation may promote differences in shape, color, and behavior between insular and mainland populations (Meiri, Dayan, & Simberloff, 2005; McClain, Durst, Boyer, & Clinton, 2013) due to particular selective pressures of the islands (Libois, Fons, & Bordenave, 1993) and/or to genetic differences (Salgueiro, Ruedi, Coelho, & Palmeirim, 2007). Therefore, the use of external features to correctly identify species on islands may be inadequate. However, traditional and geometric morphometric analyses of mammalian cranium are useful for taxonomic studies since they allow differentiating between highly similar species, particularly in bats (Sztencel-Jabłonka, Jones & Bogdanowicz, 2009; Marchán-Rivadeneira, Phillips, Strauss, Guerrero, Mancina & Baker, 2010; Jansky, 2013). On the other hand, the structure of echolocation calls is a useful tool for classifying bats since is strongly related to bat feeding and flying (Neuwieler, 1983; Russo & Jones, 2002; Hintze, Barbier, & Bernard, 2016). In particular, the high-flying habits of insectivorous bats results in low capture rates with mist nets, which usually underestimate their abundance and diversity (Hintze et al., 2016; Cormier, 2014). Therefore, echolocation calls are fundamental for species identification and are commonly used for survey and monitoring insectivorous bats (Hintze et al., 2016; Cormier, 2014). Thus, insectivorous bats from different families differ in the structure of echolocation calls, whereas frequency parameters are useful to differentiate among related species (O'Farrel & Miller, 1999). Therefore, the use of echolocation calls, additionally to morphometric analyses, may help to correctly identify populations of insectivorous bats on islands.

In Gorgona National Natural Park (NNP), a continental island, the whole assemblage of bats is listed as a conservation target; but there has been controversy about the taxonomic identity of species (i.e. Murillo-García, 2014). Thus, the taxonomic identity of the population of sac-winged bats is uncertain; it was reported as *S. leptura* (Alberico, 1986; Murillo, Bedoya, Velandia-Perilla, & Yusti-Muñoz, 2014) and as *S. bilineata* (Cadena, Gómez-Laverde, Andrade, & Peñuela, 1990; Acevedo, Beltrán, & Caicedo, 2004). These two species in mainland can be sympatric and can share shelters occasionally (Bradbury & Emmons, 1974; Bradbury & Vehrencamp, 1976; Yancey, Goetze, & Jones, 1998a, 1998b). Additionally, they can feed at the same time and place without attitudinal segregation (Bradbury & Vehrencamp, 1976), which suggests potential differentiation in the preys they consume. As in other vertebrates, bats can reduce the effects of interspecific competition by decreasing niche overlapping through morphological variations; which may lead to populations with intermediate morphologies between species (Case & Sidell, 1983; Stevens & Willig, 1999). Individuals of Gorgona population share morphological traits with both species: presence of yellowish dormant lines as in *S. leptura*, however, those lines are strongly marked and have a dorsally darker fur with a lighter belly as in *S. bilineata*. Furthermore, external measures used to differentiate between them (i.e. forearm length) are intermediate between the two species. On the other hand, this population of *Saccopteryx* from Gorgona differs from their mainland congeners because they have diurnal activity (Cadena, 1990; Vivas-Toro & Murillo-García, in prep.), an extremely rare behavior in Yangochiroptera (Bradbury & Emmons, 1974; Moore, 1975; Russo, Cistrone, Garonna, & Jones, 2009; Russo, Maglio, Rainho, Meyer, & Palmeirim, 2010). Due to their conservation value, identifying correctly bat species is crucial to optimize monitoring and research efforts in this protected area.

The aim of this work was to determine the taxonomic identity of the population of *Saccopteryx* residing in Gorgona NNP. Consequently, we evaluated the degree of morphological and acoustic similarity between *Saccopteryx* population from Gorgona, and *S. bilineata* and *S. leptura* from mainland. In addition, since both species of *Saccopteryx* differ in their mating system, with *S. bilineata* being polygamous and *S. leptura* being monogamous (reference); we assessed roosting association of Gorgona population as a surrogate for mating system. Even though individuals from Gorgona looks externally similar but slightly bigger than expected for *S. leptura*, we predicted that population from Gorgona NNP would be *S. leptura* since populations of small mammals on islands tend to be larger than in mainland (Libois et al., 1993; Lomolino, 2005).

Material and methods

Morphometric analyses: We measured a total of 62 specimens deposited in the mammal's collection of the Universidad del Valle (UV) (Appendix I). We corroborated the identifications based on diagnostic traits proposed by Gardner (2007) and Diaz et al. (2016). For traditional morphometrics, we measured 23 skull traits (18 of cranium and 5 of the jaw, Appendix II) for *S. bilineata* (N = 9 individuals), *S. leptura* (N = 22) and Gorgona population (N = 21) using a digital caliper with 0.01 mm precision (Appendix III). For geometric morphometrics, ventral views of cranium and lateral views of jaw were digitalized for *S. bilineata* (7 craniums and 7 jaws), *S. leptura* (16 craniums and 16 jaws), and population from Gorgona (23 craniums and 19 jaws). Then, we digitized 13 landmarks for cranium and 15 for jaw (Appendix II) that were selected based on previous studies on insectivorous bats (Van Cakenberghe, Herrel & Aguirre, 2002; Sztencel-Jablonka et al., 2009; Jansky, 2013) with TpsDig v2.12 (Rohlf, 2008a) and TpsUtil v1.44 (Rohlf, 2009).

We performed Procrustes analyses to obtain shape (weighted matrix) and size variables (centroid size) of cranium and jaws with TpsRelw v1.1 (Rohlf, 2008b). Consensus configurations diagrams for craniums and jaws were plotted in CorelDRAW® X7. We also performed an analysis of repeatability to verify the consistency in locating landmarks. Then, we digitalized landmarks again for a random sample of 12 craniums and 19 jaws, and obtained repeatability values by using packages TETwin, VARwin, and MOGwin; included in CLIC program (Dujardin, 2015).

Acoustic analyses: We recorded echolocation calls of Gorgona population, and continental populations of *S. leptura* and *S. bilineata* (Appendix I) using an Echo meter touch acoustic detector (Wildlife Acoustics, 2016). For acoustic analysis, a total of 30 vocalizations, with at least 30 pulses each, were randomly selected for each population. Identify and differentiate among *S. leptura* and *S. bilineata* calls was relatively simple, since they strongly differ from each other (mainly in frequency) and from other insectivorous species and families of bats (Yancey et al, 1998a, 1998b; Jung, Kalko & Von Helversen, 2007; Jakobsen, Olsen & Surlykke et al. 2015; López-Baucells, Rocha, Bobrowiec, Bernard, Palmeirim & Meyer, 2016). For each vocalization we measured minimum signal frequency (Fpmin), power-weighted mean frequency (Fpmean), peak frequency (Fppeak), average duration of echolocation pulses (Dur), average maximum frequency, (Fmax), average minimum frequency (Fmin), time weighted average frequency (Fmean), lowest absolute slope of the end of the call body (Fc), average time offset from the beginning of the call to Fc (Tc), beginning of the call body (Fk), and the average time offset from the beginning of the call to Fk (Tk). Variables were measured with software Kaleidoscope v4.1.0 (Wildlife Acoustics, 2017, Appendix IV).

We compared morphology and echolocation calls among populations by using discriminant analyses (DA). To describe cranial shape, we used the weighted matrix from geometric morphometric analyses and cranial measurements from traditional morphometric. Additionally, to describe echolocation calls we used spectral and temporal call parameters. We performed separated DAs for traditional morphometric, geometric morphometric and echolocation calls using three groups: Gorgona population, *S. leptura* and *S. bilineata*. Then, we used values of the first two discriminant functions to calculate differences among groups, based on Mahalanobis distances; calculated from centroids of Gorgona population to all individuals. Afterwards, to compare the Mahalanobis distances between groups (from Gorgona centroid to *S. leptura* and *S. bilineata*) and within groups (from Gorgona centroid to all individuals of Gorgona population), we calculated the log-ratio (Hu, Greenwood & Beyene, 2009); which is an effect size measure of differences between groups and is independent of the sample size of the groups being compared. Finally, we compared 95 % confidence intervals to estimate morphological and acoustic differentiation between groups as described in Murillo-García (2014).

Allometry assessment: To assess differences in cranium and jaw size among populations, we conducted Kruskall-Wallis tests on values of the centroid size since they were not normally distributed ($KS = 1.00$, $P < 0.01$). Additionally, we evaluated the strength and significance of allometric effects on shape using linear regressions. We used centroid size to represent cranium size and the first dimension from DA on the weighted matrix to represent cranial shape. Finally, we used coefficient of determination R^2 (the square of the correlation coefficient between observed and predicted values) as a measure of the proportion of the observed shape variation that is explained by allometry. For analyses, we used the program R 3.5.0 (R Core Team, 2017), and the package MASS (Venables & Ripley, 2002) and rmeta (Lumley, 2018).

Roosting association: In order to identify the most likely mating system for Gorgona population, we identify the roosting association. Therefore, we identified and monitored roosting sites across Gorgona to establish the amount, gender and age of occupants.

Results

Traditional morphometrics: Cross-validation analyses for DA revealed a high agreement between the a priori and a posteriori classification (100 % for *S. bilineata*, 86 % for *S. leptura*, and 86 % for *Saccopteryx* from Gorgona). Confidence intervals for log-ratio indicated that all populations are morphologically different, but Gorgona population is more similar to *S. leptura* than to *S. bilineata* (Fig. 1A). The variable that most contributed to differentiation between *S. bilineata* and *S. leptura* was the height of the zygomatic arch (Factor load = 4.87) on the first dimension (Fig. 1B). On the other hand, maxillary canine-molar distance (Factor load = 4.47) was the variable that most contribute to differentiation between Gorgona population and both species along the second dimension (Fig. 1B).

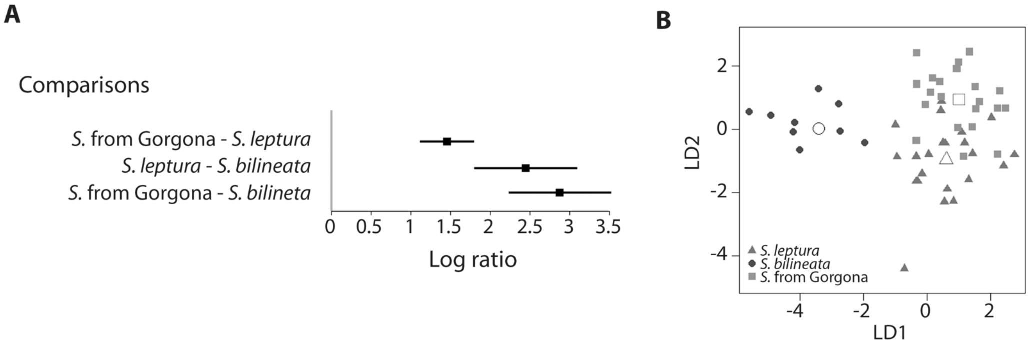

Fig. 1. Comparison of the population of *Saccopteryx* from Gorgona with *S. leptura* and *S. bilineata* by traditional morphometrics. **A**. 95 % confidence intervals for the Log ratio of between- and within-group Mahalanobis distances; and **B**. Scatter plot of cranial variation between *Saccopteryx* from Gorgona, *S. leptura* and *S. bilineata* (empty symbols represent centroids of the groups, LD1: first linear discriminant axis, LD2: second linear discriminant axis).

Geometric morphometrics: Repeatability analysis showed a 95 % of precision locating the landmarks on the cranium, and 89 % on the jaw. Cross-validation analyses for DA revealed a high agreement between the *a priori* and *a posteriori* classifications (100 % for cranium in all three populations, and, 100 % for jaw of *S. bilineata*, 95 % for *S. leptura*, and 95 % for Gorgona population). Log-ratio indicated differences in cranium and jaw morphology between populations (Fig. 2A, Fig. 2B), but *Saccopteryx* from Gorgona is more similar to *S. leptura* than to *S. bilineata* (Fig. 2C, Fig. 2D). This differentiation among populations for cranium and jaw was supported by consensus configurations resulting from Procrustes analysis (Fig. 2E, Fig. 2F). *S. leptura* has a narrower maxilla and a lower coronoid process compared with *S. bilineata* and Gorgona population (Fig. 2E). On the other hand, *S. bilineata* presents a larger maxilla, with a larger tooth row, and the back of the brain case wider than the other populations (Fig. 2F). Finally, the jaw from Gorgona population has a less pronounced curvature of the inferior border of mandibular corpus than their mainland congeners, with a different positioning of the teeth.

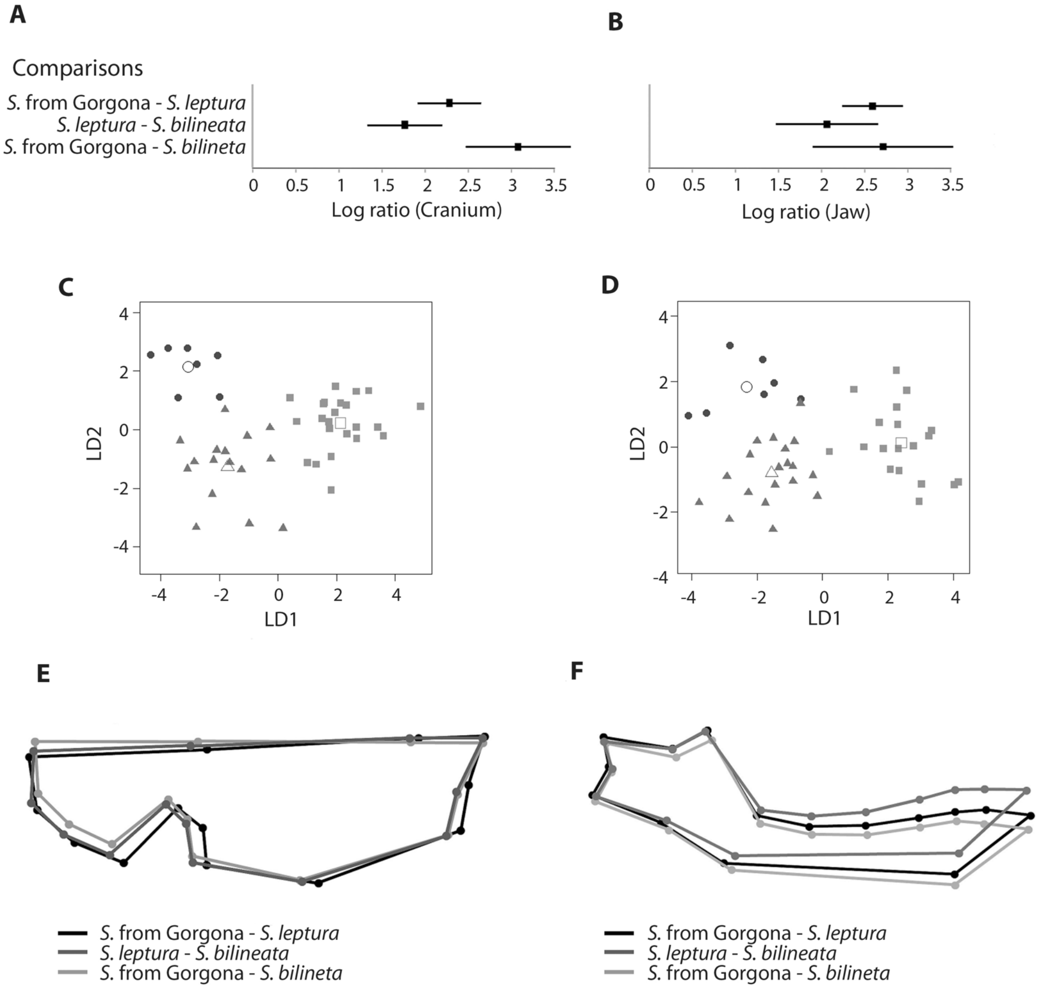

Fig. 2. Comparison of the population of *Saccopteryx* from Gorgona with *S. leptura* and *S. bilineata* for geometric morphometrics. 95 % confidence intervals for the Log ratio of between- and within –group Mahalanobis distances of cranium **A.** and jaw **B.**; scatter plot of cranial variation between *Saccopteryx* from Gorgona, *S. leptura* and *S. bilineata* for cranium **C.** and jaw **D.** (empty symbols represent centroids of the groups, LD1: first linear discriminant axis, LD2: second linear discriminant axis); and consensus configuration of landmarks for *S. leptura*, *S. bilineata*, and *Saccopteryx* from Gorgona NNP for cranium **E.** and jaw **F.**.

Acoustic analysis: Cross-validation analyses for DA revealed a high agreement between the *a priori* and *a posteriori* classifications (100 % for *S. bilineata*, 86 % for *S. leptura,* and 83 % for Gorgona population). Log-ratio confidence intervals indicated more affinities between Gorgona population and *S. leptura* than with *S. bilineata* (Fig. 3A); which is consistent with morphological evidence. Weighted average frequency (Fmean = -2.21) was the variable that most contributed to differences between *S. bilineata* and *S. leptura* on the first dimension, and the beginning of the call body (Fk = 3.21) to differentiate between *S. leptura* and Gorgona population on the second dimension (Fig. 3B). Finally, echolocation calls of *Saccopteryx* from Gorgona population have a slightly higher frequency compared with their mainland counterparts (Fig. 4).

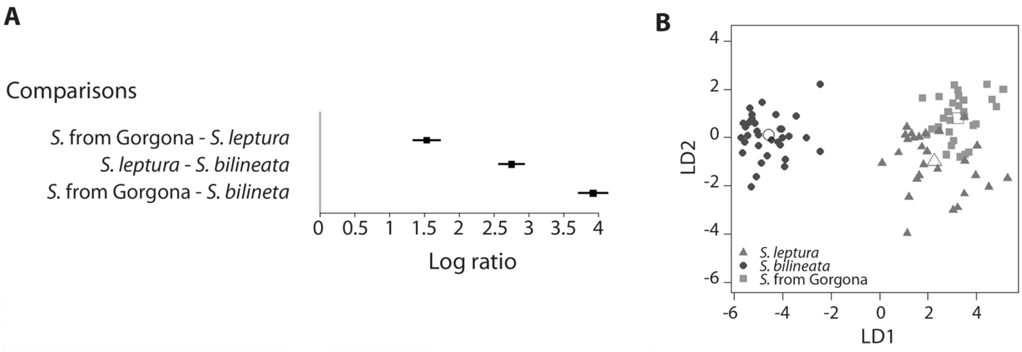

Fig. 3. A. Comparison of spectral and temporal parameters of echolocation calls of the population of *Saccopteryx* from Gorgona with *S. leptura* and *S. bilineata* for geometric morphometrics. **A**. 95 % confidence intervals for the Log ratio of between- and within-group Mahalanobis distances, and **B.** scatter plot of variation in echolocation calls between *Saccopteryx* from Gorgona, *S. leptura* and *S. bilineata* (empty symbols represent centroids of the groups, LD1: first linear discriminant axis, LD2: second linear discriminant axis).

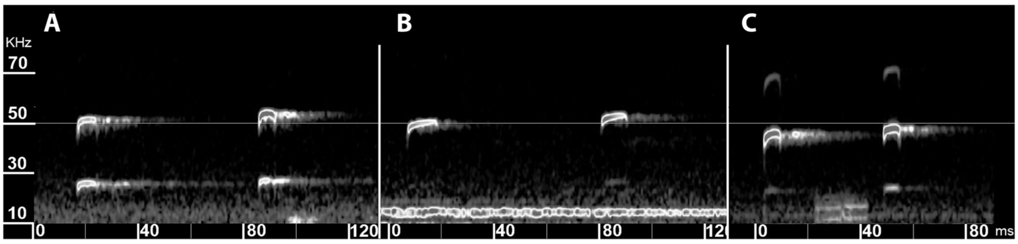

Fig. 4. Comparison of spectrograms for echolocation calls of **A.** *Saccopteryx* from Gorgona, **B.** *S. leptura*, and **C.** *S. bilineata.*

Allometry: Kruskal-Wallis test revealed significant differences in cranium (K-W = 16.29, d.f. = 2, $P < 0.05$) and jaw size (K-W = 12.59, d.f. = 2, $P < 0.05$) between the three populations. Additionally, a significant allometric relation was found for cranium ($F = 0.13$, $R^2 = 0.22$, d.f. = 44, $P < 0.05$) and jaw ($F = 0.56$, $R^2 = 0.01$, d.f. = 43, $P < 0.05$), indicating that 22 % of differences in conformation can be explained by variation in cranium size, and only 1 % for variations in jaw size.

Roosting association: Based in 23 shelters, we determined that the mean conformation of *Saccopteryx* groups was 2.47 ± 1.06 individuals where 41 % were couples, 23 % groups of two couples, 18 % a couple with a young, and 18 % solitary individuals. These results suggest that the most likely mating system for this population is monogamy.

Discusion

Gorgona population was more similar to *S. leptura* than to *S. bilineata* morphologically, vocally and reproductively. In addition, Gorgona population was bigger in size than continental populations, with a small proportion of shape differences in skull explained by size. Consequently, we conclude that *Saccopteryx* population from Gorgona corresponds to *S. leptura*. Since Gorgona Island has been isolated from mainland, at least from the last glaciation, differences with continental population of the species may be due to adaptations to environmental conditions of island, a founder effect and/or genetic drift.

Although all populations of sac-winged bats were morphologically different among themselves, population from Gorgona was more similar to *S. leptura* than to *S. bilineata*; which indicates that this population may correspond to *S. leptura*. Insular populations, for example, can often present considerable differences in size and/or shape with mainland populations (Libois et al., 1993, Welch, 2009; Murillo-García, 2014). *Saccopteryx* population of Gorgona was bigger than continental individuals, but allometric analyses showed that 22 % of variation in cranium can be explained by variations in size, whereas for the jaw just the 1 %. Gorgona is a continental island that has been connected to the continent in the past as a result of the sea level oscillation during Pleistocene glaciations, but isolated during interglacial periods (Alberico, 1986). Hence, it is considered that terrestrial populations of Gorgona have been separated from continental ones since the last glaciation, at least, 21 000 years ago (Seltzer et al., 2002). Consequently, the small founder population that colonized Gorgona has been isolated for many generations, and then genetic drift could have led to the random loss of additional alleles and fixation of others; reducing genetic diversity and increasing difference with mainland populations. Additional differentiation could have occurred through adaptations to the local environment of the island. Thus, adaptations to particular selective pressures of the island related with local environmental (i.e. temperature, humidity, luminosity) and biotic conditions (i.e. poor competitor and predator species richness) may explain differences between Gorgona and mainland populations.

Cranial variations observed might be due to differences in food resources derived from the diurnal activity of *Saccopteryx* on the island. Allometric changes in craniomandibular structures tend to occur as a dietary adjustment (Ravosa, Scott, McAbee, Veit, & Fling, 2015). Insectivorous bats that consume larger or hard-shelled preys tend to have big head, large gapes and tooth row, and a thicker jaw (Freeman, 1979; Fenton, 1988). Furthermore, prey texture may significantly influence craniomandibular structure (Ravosa et al., 2015; Böhmer & Böhmer, 2017). Individuals of Gorgona population have diurnal activity and they feed during the day (Vivas-Toro & Murillo-García, in prep.), which suggests a partially different diet from those in mainland since activity and density of potential insect preys changes between day and night. Compared to mainland, insular population has a higher coronoid process that can favor the closure of the jaw in lever (Van Cakenberghe et al., 2002), and a slightly larger maxilla that can be used to chew more sclerotized and/or larger preys. Besides, the increase in size of insectivorous bats can be advantageous on islands where resources are limited, because they can feed of insects of different sizes; but to take advantage of this feature, echolocation calls should modify the range of prey detection (Schnitzler & Kalko, 2001; Jung et al., 2007).

Echolocation calls also suggest that there is a greater similarity between *Saccopteryx* from Gorgona and *S. leptura* than with *S. bilineata.* However, calls from Gorgona population have a slightly higher frequency compared with their mainland counterparts, which suggest changes in prey consumption in this population. Echolocation frequencies usually have an inverse relation with the size of the bats, and higher frequencies are commonly used to detect small preys (Barclay & Brigham, 1994; Heller, 1995; Jung et al., 2007). This may indicate that *Saccopteryx* from Gorgona can potentially feed on smaller and harder insects with respect to mainland populations. Alternatively, echolocation structure can be very plastic among species, and can be modified according to habitat, flight height, and by many environmental and physiological factors (Schnitzler & Kalko, 2001; Russo & Jones, 2002). Hence, there may be significant changes in echolocation frequencies in populations of the same species that inhabits in different geographic areas (Heller & Helversen, 1989). However, echolocation calls of Emballonurids, specifically of genus *Saccopteryx*, tend to strongly preserve its structure and are clearly differentiated from the other species within the genus and family; making misidentifications unlikely despite where they live (Jung et al., 2007).

On the other hand, roosting association also supported the similarity between *S. leptura* and the population from Gorgona. The mean colony size for *S. bilineata* colonies is between 5.5 to 6.3 individuals /colony with majority of females, while for *S. leptura* the mean was between 2.6 to 4.6, usually grouped in couples; suggesting a polygynous mating system for *S. bilinetata* and a monogamous for *S. leptura* (Bradbury & Vehrencamp, 1976). Our mean value for roosts in Gorgona was 2.5, mainly conformed by couples, which suggests that individuals from Gorgona population are apparently monogamous such as *S. leptura*.

Identifying correctly bat species from Gorgona National Natural Park is crucial to optimize its monitoring and research since the whole assemblage is listed as a conservation target. In particular, the population of *Saccopteryx* is emblematic for the Park due to its singular diurnal activity. Even though population of sac-winged bats from Gorgona is different morphologically and vocally from both species, this population is more similar to *S. leptura* than to *S. bilineata*. Consequently, we conclude that *Saccopteryx* population from Gorgona corresponds to *S. leptura* based on morphology, echolocation calls and mating system. In addition, our results suggest that since Gorgona Island has been separated from continent for a long time (at least since the last glaciation), differences with continental population of the species may be due to genetic changes resulting from altered selection pressures and/or from stochastic effects of colonization on adaptive traits arising from founder effect and genetic drift.

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APPENDIX I

List of specimens of the mammal´s museum of the Universidad del Valle (UV) used for this research. We list each specimen with the respective museum code, locality and coordinates (when reported): CALDAS: **UV14902**, Guarinocito. CAQUETA: **UV11423**, San José Del Fragüa, Villa Garzón. CAUCA: **3787**, km 48, Panamericana way; **3788**, km48, Panamericana way; **3789**, km 48, Panamericana way; **UV11381**, Villa Garzón, Piamonte, Puerto Bello. Gorgona Island: **2061**; **3265**; **3266**; **3277**; **3278**; **3279**; **3280**; **3281**; **3282**; **3283**; **3285**; **3294**; **3295**; **UV13639**, 2°58’22” N - 78°10’11” W; **UV13640**, 2°58’22” N - 78°10’11” W; **UV13641**, 2°58’22” N - 78°10’11” W; **UV13642**, 2°58.153’ N - 78°10.608’ W; **UV13643**, 2°58.153’ N - 78°10.608’ W; **UV13644**, 2°58.153’ N - 78°10.608’ W; **UV13645**, 2°58.153’ N - 78°10.608’ W; **UV13740**, 2°58.153’ N - 78°10.608’ W; **UV13741**, 2°58.153’ N - 78°10.608’ W; **UV13742**, 2°56.622’ N - 78°11.974’ W; **UV13836**, 2°58.153’ N - 78°10.608’ W. META: **UV9859**, Carimagua, ICA. CHOCÓ: **3616**, Ensenada Utría, Bahía Solano; **3786**, Istmina way, Platinera brook. CUNDINAMARCA: **UV2440**, Villeta, Bagazal. PUTUMAYO: **UV14207**, Villa Garzón, Champagnat sidewalk, 0°57’32” N - 76°34’22” W; **UV14341**, Villa Garzón, Champagnat sidewalk, 0°57’36” N - 76°34’45” W SANTANDER: **12706**; **12707**.VALLE DEL CAUCA: Buenaventura: **3876**, Río Naya; **5953**, Bahía Málaga, Naval base; **5954**, Bahía málaga, Naval base; **5949**, Bahía Málaga; **UV7554**, Juanchaco**;** **UV7555,** Juanchaco; **UV7556,** Juanchaco; **UV7557,** Juanchaco**;** **UV7558,** Juanchaco; **UV7559,** Juanchaco; **UV7560**, Juanchaco; **UV7561,** Juanchaco; **UV7562,** Juanchaco; **UV11513**, Papayal sidewalk, Guaipare brook. Buga: **UV14580**, El vínculo, 3°50’8.1” N - 76°7’55.1” W. El cerrito: **UV13619**, Río amaime; **UV13620**, Río Amaime. Cali: **12528**, Meléndez, Universidad del Valle **UV13595**, Multicentro; **3690**, El Piñal, Caimancito brook; **3691**, El Piñal, Caimancito brook; **2062**, Meléndez, Universidad del Valle; **UV13992**, Meléndez, Universidad del Valle, 3°22’27” N - 76°31’51” W; **12708**, Meléndez, Universidad del Valle.

List of localities were echolocation calls were recorded. *Saccopteryx* from Gorgona island: CAUCA: Gorgona island (2° 57’ 54.9354” N - 78° 10’ 29.9994” W). *Saccopteryx leptura*: VALLE DEL CAUCA: Buenaventura (3° 50’ 39.45” N - 76° 47’ 24”; 3° 40’ 23.79” N - 76° 56’ 42.00” W). *Saccopteryx bilineata*: VALLE DEL CAUCA: Cali (3° 22’ 23.40” N -76° 31’ 51.60” W; 3° 20’ 47.46” N - 76° 35’ 24.00” W; 3° 19’ 41.2674” N - 76° 39’ 3.5994” W), Buenaventura (3° 50’ 39.45” N - 76° 47’ 24”; 3° 40’ 23.79” N - 76° 56’ 42.00” W; 3° 44’ 42.46” N - 76° 57’ 46.80” W).

APPENDIX II

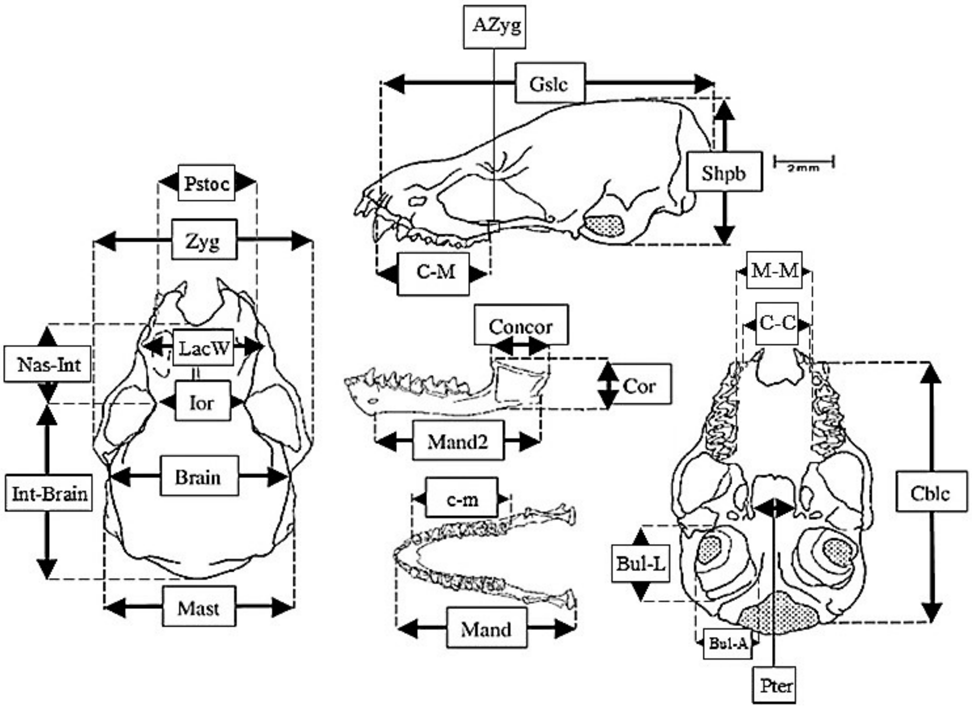

Figure 1. Measures used for traditional morphometrics for *Saccopteryx* from Gorgona, *S. leptura* and *S. bilineata*: **Cranium**: Gslc: greatest length of skull from posterior base of foramen magnum to maximum curvature of canine, Cblc: condyle-canine length, Ior: least inter-orbital width, LacW: lacrimal width, Pstoc: post-ocular width, Zyg: width across the zygomatic arches, Mast: width between mastoid processes, Brain: width of the braincase, C-M: toothrow, M-M: distance between molars, C-C: distance between canines, ShPb: height of the skull over the bullae, Int-Brain: length from inter-orbital zone to posterior base of the skull, Nas-Int: length from nasal base to inter-orbital zone, Pter: maximum width of pterygoid pit, Bul-A: maximum width of the bullae, Bul-L: maximum length of the bullae, AZyg: maximum height of the zygomatic arch at the anterior base. **Jaw**: Mand: length of the mandible, Mand2: length of the mandible from the ramus to the angular process, Cor: height of the coronoid process, Concor: distance between the condyle and coronoid processes, c-m: toothrow. Modified from Van Cakenberghe et al., 2002.

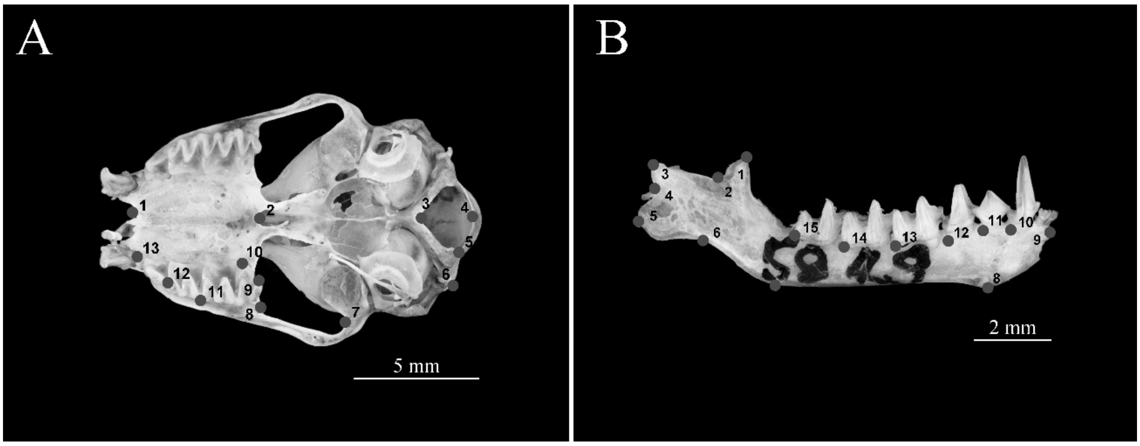

Figure 2. Landmarks used for geometric morphometrics for *Saccopteryx* from Gorgona, *S. leptura* and *S. bilineata*: **Cranium (ventral)** 1. Midpoint of the posterior curvature of the anterior part of the hard palate, 2. Posterior end of the hard palate, 3. Anterior limit of the foramen magnum, 4. Posterior limit of the foramen magnum, 5. Lateral limit of the foramen magnum, 6. Tip of the mastoid process: point of maximum curvature, 7. Posterior internal point of the zygomatic arch: point of maximum curvature, 8. Anterior internal point of the zygomatic arch: point of maximum curvature, 9. Tip of metastyle of M3, 10. Most distant point of protocone of M3, 11. Most distant point of parastyle of M2, 12. Most distant point of parastyle of M1, 13. Posterior base of C1. **Jaw (lateral)**: 1. Tip of coronoid process: point of maximum curvature, 2. Angle of mandibular condyle and coronoid process: point of maximum curvature, 3. Tip of mandibular condyle: point of maximum curvature, 4. Angle of mandibular condyle and angular process: point of maximum curvature, 5. Tip of angular process: point of maximum curvature, 6. Praemasseteric incision: point of maximum curvature, 7. Lower edge of the mandibular corpus: point of maximum curvature, 8. Most ventral point of mandibular symphysis: point of maximum curvature, 9. Most anterior point of the mandible corpus, 10. Posterior base of canine (at the alveolus), 11. Posterior base of p1 (at the alveolus), 12. Posterior base of p4 (at the alveolus), 13. Posterior base of m1 (at the alveolus), 14. Posterior base of m2 (at the alveolus), 15. Posterior base of m3 (at the alveolus).

APPENDIX III

Mean skull measurements ± standard deviation (mm.) for *Saccopteryx* from Gorgona, *S. leptura* and *S. bilineata* (see Appendix I for localities and catalog numbers)

	Saccopteryx from Gorgona	*S. leptura*	*S. bilineata*
Cranium			
Greatest length of skull	15.05 ± 0.94	14.90 ± 0.92	17.16 ± 0.58
Condyle-canine length	13.16 ± 0.68	13.14 ± 0.84	15.12 ± 0.82
Least interorbital width	2.54 ± 0.17	2.52 ± 0.17	2.66 ± 0.18
Lacrimal width	5.11 ± 0.37	5.05 ± 0.47	5.89 ± 0.10
Post ocular width	9.57 ± 0.32	9.38 ± 0.69	10.6 ± 0.51
Width across the zygomatic arches	7.75 ± 0.32	7.76 ± 0.39	8.49 ± 0.34
Width between mastoid processes	7.23 ± 0.26	7.19 ± 0.39	7.86 ± 0.19
Width of the braincase	5.91 ± 0.57	5.67 ± 0.51	6.95 ± 0.31
Toothrow	3.17 ± 0.15	3.18 ± 0.22	3.65 ± 0.20
Intern distance between molars	2.17 ± 0.18	2.13 ± 0.15	2.40 ± 0.22
Intern distance between canines	6.99 ± 0.36	6.95 ± 0.54	7.74 ± 0.35
Height of the skull over the bullae	9.62 ± 0.53	9.61 ± 0.47	10.76 ± 0.33
Interorbital - posterior base of cranium length	4.09 ± 0.23	4.25 ± 0.32	4.77 ± 0.25
Length from nasal base to interorbital zone	3.03 ± 0.20	3.00 ± 0.31	3.45 ± 0.18
Maximum width of pterygoid pit	2.84 ± 0.18	2.87 ± 0.32	2.97 ± 0.25
Maximum width of the bullae	2.67 ± 0.17	2.74 ± 0.30	2.81 ± 0.22
Maximum length of the bullae	3.82 ± 0.24	3.84 ± 0.44	4.61 ± 0.3
Maximum height of zygomatic arch (anterior base)	0.84 ± 0.08	0.88 ± 0.09	0.96 ± 0.08
Jaw			
Length of the jaw	2.45 ± 0.27	2.38 ± 0.34	2.76 ± 0.3
Length from the rami to the angular process	8.39 ± 0.79	7.87 ± 1.01	9.16 ± 0.53
Height of the coronoid process	6.32 ± 0.67	5.99 ± 0.63	7.03 ± 0.43
Condyle -coronoid processes distance	10.73 ± 0.91	10.53 ± 0.97	11.81 ± 0.64
Mandibular toothrow	2.70 ± 0.20	2.73 ± 0.18	2.99 ± 0.19

APPENDIX IV

Mean echolocation spectral and temporal variables ± standard deviation for *Saccopteryx* from Gorgona, *S. leptura* and *S. bilineata* (see Appendix I for localities)

	Saccopteryx from Gorgona	*S. leptura*	*S. bilineata*
Minimum signal frequency (KHz)	43.79 ± 1.37	43.91 ± 2.58	38.57 ± 2.12
Power-weighted mean frequency (KHz)	48.11 ± 3.41	51.12 ± 1.30	46.28 ± 0.91
Peak frequency (KHz)	52.74 ± 1.42	52.30 ± 1.57	46.77 ± 1.14
Average duration of echolocation pulses (ms)	4.45 ± 0.67	4.99 ± 0.67	5.85 ± 0.78
Average maximum frequency (KHz)	52.00 ± 1.82	51.19 ± 1.61	46.78 ± 1.39
Average minimum frequency (KHz)	48.88 ± 1.77	48.05 ± 1.67	43.51 ± 1.74
Time weighted average frequency (KHz)	51.00 ± 1.75	50.01 ± 1.69	45.68 ± 1.60
Lowest absolute slope of the end of the call body (Fc) (KHz)	51.42 ± 1.86	50.37 ± 1.79	45.97 ± 1.69
Average time offset from the beginning of the call to Fc (ms)	3.75 ± 0.56	4.18 ± 0.58	4.68 ± 0.59
Beginning of the call body (Fk) (KHz)	50.62 ± 1.62	49.54 ± 1.68	45.40 ± 1.55
Average time offset from the beginning of the call to Fk (ms)	1.02 ± 0.42	1.21 ± 0.53	1.78 ± 0.50